

## THE MASS EXPONENT IN POPULATION ENERGY USE: THE FALLACY OF AVERAGES RECONSIDERED

The way energy is allocated among species continues to be a source of controversy among ecologists (see, e.g., Harvey and Godfray 1987; Sugihara 1989; Griffiths 1992). Estimates of population energy use ( $EU$ ) have been obtained from the product of population density ( $D$ ) and individual metabolic rate ( $MR$ ):

$$EU = D \times MR. \quad (1)$$

Because each component variable can be expressed as the mean value of an allometric relationship with body mass ( $M$ ), it follows that

$$EU \propto (M^x)(M^y) \quad (2)$$

and

$$EU \propto M^{x+y}, \quad (3)$$

where  $x$  is the slope of the allometric equation for population density, and  $y$  is the slope of the allometric equation for metabolism,  $0.67 \geq y \leq 0.75$ . In this way, the energy dominance of large- or small-sized species (if any) is inferred by examining the sign of the resulting mass exponent. For example, analyzing an extensive database, Damuth (1981, 1987) found that in general  $D \propto M^{-0.75}$ , and using Kleiber's (1961) equation for total energy requirements ( $MR \propto M^{0.75}$ ), he concluded that population energy consumption per unit of time is proportional to  $M^0$ ; that is, the population energy use is independent of body mass. On the other hand, and using a somewhat different reasoning, Peters (1983) hypothesized that small-sized species are the energy dominants because they tend to overcompensate their low energy requirements by attaining higher densities in local communities. Subsequently, Brown and Maurer (1986), using 0.67 as the exponent of the mass-energy requirements, concluded that contrary to Damuth's and Peters' hypotheses, population energy use tends to increase with increasing body mass (see also Maurer and Brown 1988; Du Toit and Owen-Smith 1989). More recently, Damuth (1993) provided evidence that within dietary groups containing small-sized mammal species, larger species tend to control more energy, but in groups containing large-sized species, small species do better.

### WHY DO MASS EXPONENTS DIFFER?

Explanations for differences observed in the slope of body mass–population energy use can in principle be treated as an extension of methodological problems

of estimating correctly the slope of the body mass–population density relationship (see discussions in Damuth 1987; Griffiths 1992; Currie 1993). However, irrespective of how well each component variable (density and metabolism) has been estimated, what has not been considered is the potential bias in slope produced by multiplying two allometric equations. Resulting slopes are calculated as the product of the mean component values rather than from the mean of their products, assuming that

$$T(x)T(y) = T(xy), \quad (4)$$

where  $T$  is a nonlinear transformation of variables  $x$  and  $y$ . Specifically, for population energy use,  $x$  is the slope of the allometric equation of population density against body mass, and  $y$  is the slope of the allometric equation of metabolic rate against body mass. However, there are two reasons why multiplying two allometric equations results in a bias. First, unless the variables are really independent, the two expressions in equation (3) are not equivalent, because the mean of the two component variables does not necessarily equal the function of the means of the two variables, a phenomenon named “the fallacy of averages,” after Wagner (1969). Welsh et al. (1988) analyzed several ecological studies that suffered from the fallacy of averages and documented the percentage of error of the mean of the product traits, especially in cases when there is no clear evidence that the two component variables are uncorrelated. Referring to the multiplication of allometric equations, Welsh et al. (1988) stated, “A comparable problem arises repeatedly in the study of allometric relationships whenever two or more allometric equations are multiplied together or divided by one another, because the estimates of the regression parameters are just weighted averages” (p. 278). They derived a number of formulas for dealing with that problem when the covariance among the two component variables is known, although they recommended taking the mean of products when possible. “For situations in which measurement of component variables on the same individuals is possible, individual product-trait values should be calculated and then averaged” (p. 286). Second, there is the additional and more fundamental problem that if  $T$  is nonlinear at all, then the equivalence in equation (3) does not hold because the formal definition of nonlinearity is violated. Consequently, both the nonindependence of the exponents of the two equations as the nonlinearity of the equations themselves may strongly affect the resulting mass exponent and population energy use estimates.

The aim of this note is to evaluate the extent to which the fallacy of averages affects the mass exponent in population energy use equations. Previous estimates of the mass exponent have assumed that slopes for regressions of density–body mass and metabolism–body mass are derived from perfect regressions having no scatter about the regression lines. This is not necessarily true, because deviations from linearity are frequently observed in regressions of population density on body mass specially at intermediate values of body size (see, e.g., Brown and Maurer 1987; Gaston 1988; Morse et al. 1988; Currie 1993). Although the idea that the maximum variance in density at intermediate values of body size relates to the maximum population density has been questioned on methodological grounds (see Lawton 1989, 1990 and Blackburn et al. 1990, 1992 for examples),

what has become increasingly clear is that simple linear analyses are not appropriate for assessing a functional relationship among the two variables (Pagel et al. 1991; Griffiths 1992). In addition, although previous studies assessing the relationship between population density and body mass have considered the effects of diet as a potential source of error (see, e.g., Peters and Raelson 1984; Robinson and Redford 1986; Damuth 1987), a similar treatment for allometric equations relating body size with metabolic rate in estimates of population energy use is lacking. This fact deserves special attention because food habits is the main factor that affects the level of mass-independent metabolism (McNab 1986, 1989; Elgar and Harvey 1987; Veloso and Bozinovic 1993). If residuals are nonrandomly distributed about the regression line, the mean value of metabolic rate may hide important variation when used as a component variable for estimates of population energy use.

#### THE FALLACY OF AVERAGES RECONSIDERED

We compiled original and published data of species-specific body mass, metabolic rate, food habits, and population density of 114 species of eutherian mammals. Data on total metabolic rate were obtained from McNab (1988, 1989) and Bozinovic and Rosenmann (1988). Data on population densities were obtained from O'Connell (1986), Robinson and Redford (1986, 1989), and Damuth (1987). Body mass data was obtained from Damuth (1987) and Bozinovic and Rosenmann (1988). Following McNab (1988), we distinguished six mammalian dietary categories: carnivores, frugivores, granivores, herbivores, insectivores, and omnivores.

Considering the recommendation of Welsh et al. (1987), we calculated directly the population energy use of each species as the product of the total metabolic rate and population density (see appendix, table A1), and then evaluated the percentage of error of the mass exponents obtained from the product of two allometric equations. We first evaluated the percentage of error considering that metabolic rate scales with body mass with an exponent of 0.75. In order to assess in more detail the effect of the product of two allometric equations, we made a second analysis, considering a more specific allometric equation for metabolic rate within trophic categories according to our compiled data of specific metabolic rates and body masses. In both cases the percentage of error was calculated with respect to the mass exponent calculated directly.

Our analyses revealed that considering 0.75 as the mass exponent for metabolic rate gave an overestimation of the slopes of the relationship between population energy use and body mass in five of six cases. The percentage of error ranged from 7.1%, in the case of herbivore species, to 80.0% for frugivores. Although the high error detected in frugivore species may be an effect of the low sample size, what is clear is that the use of a constant slope for inferring the relationship between population energy use and body mass introduces a global error in estimates of mass exponents of 21.0% (table 1). When the mass exponent was calculated with an observed allometric equation for metabolic rate within dietary groups, values were overestimated in three of six cases, with an error ranging from 3.6% in insectivores to 73.3% in frugivores. Pooling species, irrespective of

TABLE 1  
 MASS EXPONENTS OF POPULATION ENERGY USE IN EUTHERIAN MAMMALS

DIETARY CATEGORY	DIRECTLY CALCULATED*	<i>r</i>	MASS EXPONENT FOR METABOLIC RATE				
			.75	% Error	Observed Equation†	% Error	<i>N</i>
Carnivores	-.19	-.44	-.07	+63.2	-.18	+5.3	8
Frugivores	-.15	-.14	-.03	+80.0	-.04	+73.3	5
Granivores	.19	.27	.08	-57.9	.15	-21.0	14
Herbivores	-.14	-.22	-.13	+7.1	-.11	+21.4	38
Insectivores	-.28	-.41	-.15	+46.4	-.29	-3.6	17
Omnivores	-.15	-.25	-.12	+20.0	-.15	0	32
Total	-.19	-.24	-.15	+21.0	-.18	+5.3	114

NOTE.—The percentage of error associated with taking the product of two allometric equations is indicated. Signs + and - in the “% Error” column indicate overestimation and underestimation of the mass exponents, respectively, with respect to the directly calculated exponent.

\* Calculated from the mean of the product between specific metabolic rate and population density.

† Calculated from the observed metabolic rate and body mass.

diet, revealed that the percentage of error was 5.3%, a lower value than the 21.0% obtained when using a 0.75 constant value of mass exponent for metabolism (table 1).

Our results revealed that at least for the species of eutherian mammals examined here, an important error is introduced when the mass exponents are calculated from the product of two allometric equations. This effect is more evident when a single exponent is used for metabolism (e.g., 0.75). Similarly, estimates based on a small sample size may suffer to a larger extent the fallacy of averages than estimates based on more extensive data bases. This fact is well exemplified by the large percentage of error in the mass exponent of frugivore mammals.

In addition to the recognized methodological difficulties of estimating correctly the slope of the body mass–density relationship, we have presented evidence indicating that previous assessments of population energy use may have suffered from the fallacy of averages. Although the importance of different-sized species in determining how energy flows through local communities is not yet fully understood, a first logical step to gaining insight into that question is to make clear the shortcomings of methodologies in use at present. Future studies assessing the way energy is allocated among species should take into consideration the fallacy of averages as a potential source of error in estimates of the mass exponent in population energy use equations.

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## APPENDIX

TABLE A1

BODY MASS AND ENERGY USE FOR EUTHERIAN MAMMALS

Species	Dietary Category	Body Mass (kg)	Energy Use (W/km <sup>2</sup> )
<i>Alopex lagopus</i>	C	4.550	1.3
<i>Felis concolor</i>	C	39.075	5.8
<i>Felis pardalis</i>	C	10.438	14.5
<i>Martes americana</i>	C	.961	4.6
<i>Mustela erminea</i>	C	.144	18.3
<i>Mustela nivolis</i>	C	.079	35.5
<i>Panthera onca</i>	C	68.825	6.9
<i>Vulpes vulpes</i>	C	5.225	22.4
<i>Agouti paca</i>	F	8.678	384.5
<i>Cheirogaleus intermedius</i>	F	.239	273.0
<i>Perodicticus potto</i>	F	1.268	25.8
<i>Potos flavus</i>	F	2.445	61.9
<i>Proechimys semispinosus</i>	F	.649	1,024.3
<i>Dasyprocta leporina</i>	G	2.694	785.5
<i>Dipodomys agilis</i>	G	.061	180.8
<i>Dipodomys deserti</i>	G	.107	242.2
<i>Dipodomys merriami</i>	G	.038	290.7
<i>Glaucomys volans</i>	G	.066	109.6
<i>Heteromys anomatus</i>	G	.069	610.7
<i>Liomys salvini</i>	G	.042	163.5
<i>Muopsocta acouchy</i>	G	.733	24.2
<i>Perognathus intermedius</i>	G	.016	42.0
<i>Perognathus longimembris</i>	G	.008	11.4
<i>Tamias striatus</i>	G	.092	1,033.7
<i>Tamiasciurus hudsonicus</i>	G	.216	202.4
<i>Tayassu tacajú</i>	G	18.860	390.4
<i>Zapus hudsonicus</i>	G	.024	1,620.4
<i>Abrocoma benetti</i>	H	.262	138.4
<i>Arvicola terrestris</i>	H	.120	19,470.0
<i>Bradypus variegata</i>	H	3.758	7,535.0
<i>Capreolus capreolus</i>	H	20.350	366.0
<i>Cervus elaphus</i>	H	116.500	498.4
<i>Choloepus hoffmani</i>	H	3.875	850.1
<i>Connochaetes taurinus</i>	H	171.500	1,190.1
<i>Cryptomys hottentotus</i>	H	.070	279.9
<i>Ctenomys peruanus</i>	H	.445	5,186.2
<i>Cynomys ludovicianus</i>	H	1.121	5,844.8
<i>Dendrohyrax validus</i>	H	2.320	133.1
<i>Dipodomys microps</i>	H	.061	489.2
<i>Hydrochaerus hydrochaerus</i>	H	29.593	3,841.7
<i>Kobus ellipsiprymus</i>	H	147.000	255.5
<i>Lemur fulvus</i>	H	2.260	4,464.9
<i>Lepus americanus</i>	H	1.471	1,123.5
<i>Lepus californicus</i>	H	2.360	95.4
<i>Lepus timidus</i>	H	3.012	112.6
<i>Microtus californicus</i>	H	.058	7,600.2
<i>Microtus mexicanus</i>	H	.032	766.7
<i>Microtus montanus</i>	H	.037	3,105.3
<i>Microtus ochrogaster</i>	H	.043	4,044.1
<i>Microtus oeconomus</i>	H	.041	2,016.0
<i>Microtus pennsylvanicus</i>	H	.044	1,659.3
<i>Neotoma fuscipes</i>	H	.218	76.9
<i>Neotoma lepida</i>	H	.135	902.3
<i>Ochotona princeps</i>	H	.132	521.1
<i>Octodon degus</i>	H	.212	15,020.0
<i>Ovis canadensis</i>	H	70.450	207.9

TABLE A1 (Continued)

Species	Dietary Category	Body Mass (kg)	Energy Use (W/km <sup>2</sup> )
<i>Rangifer tarandus</i>	H	97.000	379.0
<i>Sigmodon hispidus</i>	H	.135	1,805.5
<i>Spermophilus armatus</i>	H	.335	4,228.8
<i>Spermophilus richardsoni</i>	H	.313	2,415.8
<i>Spermophilus spilosoma</i>	H	.141	54.2
<i>Spermophilus tridecemlin</i>	H	.191	184.7
<i>Sylvilagus auduboni</i>	H	.778	90.5
<i>Tachyoryctes splendens</i>	H	.196	3,229.5
<i>Thomomys talpoides</i>	H	.100	1,516.3
<i>Arctocebus colabarensis</i>	I	.208	6.2
<i>Blarina brevicauda</i>	I	.019	182.6
<i>Cyclopes didactylus</i>	I	.320	9.9
<i>Dasypus novemcinctatus</i>	I	3.410	59.3
<i>Erinaceus europaeus</i>	I	.778	1,134.0
<i>Euphractus sexcinctus</i>	I	6.270	20.8
<i>Manis tricuspis</i>	I	2.765	252.2
<i>Myrmeciphaga tridactyla</i>	I	25.300	2.6
<i>Nasua nasua</i>	I	3.940	84.6
<i>Notiomys macronyx</i>	I	.066	140.2
<i>Onychomys torridus</i>	I	.021	48.7
<i>Priodontes maximus</i>	I	42.295	6.8
<i>Proteles cristatus</i>	I	7.855	8.1
<i>Tamandua mexicana</i>	I	3.855	26.5
<i>Tamandua tetradactyla</i>	I	3.750	29.4
<i>Tolypeutes matacus</i>	I	1.113	15.6
<i>Tupaia glis</i>	I	.129	38.7
<i>Akodon azarae</i>	O	.025	1,980.9
<i>Akodon longipilis</i>	O	.047	1,229.0
<i>Akodon olivaceus</i>	O	.028	1,003.3
<i>Antilocapra americana</i>	O	39.250	46.7
<i>Aotus trivirgatus</i>	O	.990	257.0
<i>Auliscomys micropus</i>	O	.070	202.7
<i>Baiomys taylori</i>	O	.007	123.6
<i>Callithrix jacchus</i>	O	.216	766.1
<i>Calomys musculinus</i>	O	.028	44.7
<i>Canis latrans</i>	O	12.000	4.5
<i>Cebuella pygmaea</i>	O	.129	264.1
<i>Cercopithecus mitis</i>	O	6.650	827.9
<i>Clethrionomys gapperi</i>	O	.025	300.3
<i>Clethrionomys glareolus</i>	O	.024	616.5
<i>Clethrionomys rutilus</i>	O	.028	1,983.5
<i>Coendu prehensalis</i>	O	3.640	207.3
<i>Colobus guereza</i>	O	10.300	1,964.4
<i>Fossa fossana</i>	O	2.030	19.5
<i>Meles meles</i>	O	10.970	47.1
<i>Ochrotomys nuttalli</i>	O	.020	53.3
<i>Odocoileus virginianus</i>	O	75.210	1,336.6
<i>Oryzomys longicaudatus</i>	O	.037	219.5
<i>Peromyscus californicus</i>	O	.046	1,569.2
<i>Peromyscus eremicus</i>	O	.023	53.4
<i>Peromyscus maniculatus</i>	O	.020	231.3
<i>Peromyscus truei</i>	O	.029	1,546.0
<i>Phyllotis darwini</i>	O	.055	249.9
<i>Praomys natalensis</i>	O	.046	144.4
<i>Procyon cancrivorus</i>	O	4.110	18.4
<i>Rattus fuscipes</i>	O	.101	836.2
<i>Rattus rattus</i>	O	.127	3,426.6
<i>Thrichomys aperoides</i>	O	.312	625.1

NOTE.—C, Carnivores; F, frugivores; G, granivores; H, herbivores; I, insectivores; O, omnivores.

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