portance of small species. In addition to these statistical inadequacies, counting bias in bird censuses is likely to underestimate slopes. Although a great range of abundances of small species will be recorded, large species will, in general, be represented by few individuals or recorded as present densities < 1 individual per census area. Species in the latter category are usually omitted from regression analyses, thereby artificially raising slopes.

A similar analysis to that of Brown and Maurer for pelagic ecosystems[4] found slopes ranging between -0.77 and -1.18, with medians close to -1.0. However, this analysis used total densities, summed over all the species within a size class. To test if data treatment affected the conclusions I carried out both species density/species mass (Sp) and total density/size class mass (C1) regressions for the first 24 censuses reported in Griffiths[5]. For perfect correlations the estimated slopes of Sp and C1 regressions were -0.95 (95% limits -0.60 and -1.29) and -1.14 (-0.84 to -1.44) respectively. These estimates are not significantly different from each other or the estimate from the data of Brown and Maurer. Furthermore the slopes of Sp and C1 regressions for each census are strongly correlated with each other ($r = 0.83$, $P < 0.001$). Hence species/mass and total individuals/mass regressions both indicate that small organisms are energetically more important than large ones.

Harvey and Lawton[6], in a News and Views comment, pointed out that (even if Brown and Maurer were correct) the total importance of small organisms was probably greater than that of large because there are usually relatively more small species than large in communities. The similarity of the Sp and C1 slopes casts doubt on this: there are approximately equal numbers of large and small species per logarithmic size class.

Analysis of insect samples from a variety of tropical habitats[7,8] gives a median abundance/length slope of -3.4 (range -1.53 to -4.24, $n = 18$). Hence small insects are as or more important than large ones, depending on the mass–length relation used[9], consistent with an earlier analysis of some of these data[10,11].

Although most data suggest that small species and organisms are energetically at least as important as large ones this might not always be true. The biomasses of large mammals in tropical habitats[12] are more than an order of magnitude greater than those of small mammals[13] (small mammals 28–1,500, median 84 kg km^{-2}, $n = 9$; large mammals 405–19,928, median 4,387 kg km^{-2}, $n = 24$). Because large and small mammals cover approximately the same relative size range these figures are directly comparable.

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BROWN AND MAURER REPLY — Virtually all of Griffiths' comments on our recent paper[1] are either incorrect or misleading. We make four points.

First, the slope of the regression between log population density and log body mass that we reported for mammals is not significantly different from zero, but it is significantly different from the values (-0.67 to -1.0) claimed in other studies[2,3].

Second, our data on birds do indeed show a significant correlation between the values for the slopes and the correlation coefficients. This is to be expected, because the correlation coefficient can be expressed mathematically (ref. 4, equation 15.7) as the slope multiplied by the ratio of the standard deviations of the two variables. This hardly invalidates our analyses. There is no justification for assuming, as Griffiths does, that the best estimate of the slope can be obtained by extrapolating this relationship to a perfect negative correlation ($r = -1.0$). To extrapolate slopes and correlations beyond the range of the data is a serious abuse of regression analysis[5]. In making this extrapolation Griffiths apparently assumes that all variation in population density or energy use among species of a given body mass can be attributed to measurement error. If there is significant error in the estimation of the two variables, a correct procedure would be to use some form of Model II regression. We showed that reduced major axis regression gave results similar to the Model I regressions that Griffiths criticizes. The wide variation in population density among organisms of similar size is undoubtedly real. Because this variation is heteroscedastic, we cautioned against fitting any linear relationship to these data and performed a more robust nonparametric analysis on the large data set for birds. This gave the same qualitative result: energy use per species is greater for large than for small birds.

Third, like comparable previous analyses[2,3,6] that had reached opposite conclusions, we considered only how energy use per species varied with body size. Harvey and Lawton[7] and Griffiths raise the very different, but equally interesting question of how the collective energy use of all species within a logarithmic body size category varies with body mass. Our as yet unpublished analyses for birds are remarkably similar to those of Strayer[8] for freshwater zooplankton, showing that total energy use for all species in a size class first increases and then remains approximately constant as body mass increases.

Finally, Griffiths' letter and the analysis of Peters[6] suggest that log population density per species scales with log body mass, with a slope of -1.0. This implies that energy use per species varies inversely (slope -0.25 to -0.33), and biomass per species is constant (slope $= 0.0$) with respect to body mass. Although our analyses suggest the contrary, we concede that this might be true within some taxonomically defined communities. It cannot be true for all organisms or entire ecological communities because that would require that the biomasses of all species-specific parasites and symbionts equal those of their hosts. Obviously not only biomass but also energy use per species of many kinds of small organisms must be much less than that of the rarest large ones.

We stand by our claim that energy use per species increases with body mass within local communities of many different kinds of organisms. Furthermore, even though there are often more species and higher population densities of small organisms than of large ones, total energy use of all species within logarithmic size classes probably does not decrease with increasing size.

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Scientific Correspondence

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