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RESPONSE TO FORUM COMMENTARY ON “TOWARD A METABOLIC THEORY OF ECOLOGY”

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We welcome the opportunity to respond to the commentaries in this Special Feature. We are well aware that this is not the last word. A full evaluation of the metabolic theory of ecology (MTE) will be rendered over time by the wider ecological community and will probably take years. Here we address some general and specific issues raised by the commentaries. The MTE is very much a work in progress—hence the “toward” in the title of Brown et al. (2004). To facilitate progress, we try to clarify some of the controversial or at least still unresolved issues, rather than simply defend our paper.

We begin with some general points that emerged from several commentaries.

Is the exponent $\frac{2}{3}$ or $\frac{3}{4}$?—The values of the allometric exponents for whole-organism metabolic rate and other biological rates and times are ultimately empirical questions. These questions have intrigued biologists for about 70 years, ever since Kleiber (1932) measured the basal metabolic rates of mammals and birds spanning a wide range of body masses, and found that the slope of his log–log plot was almost exactly $\frac{3}{4}$. Extensive studies, culminating in several synthetic books on allometry in the 1980s, appeared to have resolved the issue. These books unanimously concluded that most allometric exponents were quarter powers rather than the third powers expected on the basis of Euclidean geometric scaling (McMahon and Bonner 1983, Peters 1983, Calder 1984, Schmidt-Nielsen 1984).

The issue was reopened recently, in particular when Dodds et al. (2001) and White and Seymour (2003) analyzed data on basal metabolic rates of mammals and

birds and obtained exponents closer to $\frac{2}{3}$ than $\frac{3}{4}$. Savage et al. (2004) have commented on these studies. We summarize only the two key points:

1) It is problematic to claim a definitive value based on analyses of existing data on mammalian and avian basal metabolic rates. The estimated exponent varies from ~ 0.65 to 0.85 , depending on which measurements and taxa are included, and which statistical procedures are used.

2) Dodds et al. (2001) and White and Seymour (2003) compiled and analyzed data only on basal metabolic rates of mammals and birds. Savage et al. (2004) performed analyses of many additional data sets, including basal, field, and maximal whole-organism metabolic rates, and many other biological rates and times. The data included not just mammals and birds, but many other taxa from both terrestrial and aquatic environments. The variables ranged from cellular and molecular to whole-organism and population levels. The exponents varied, but showed distinct peaks and mean values at almost exactly $\frac{3}{4}$ for whole-organism basal and field metabolic rates, $\frac{1}{4}$ for mass-specific metabolic rates and many other biological rates (e.g., heart rates and population growth rates), and $\frac{1}{4}$ for biological times (e.g., blood circulation times and gestation periods).

Based on this evidence, Savage et al. (2004) concluded that there is little justification for reopening the argument that biological allometries in general have third-power exponents. Important additional evidence for the pervasiveness of quarter-power exponents comes from our recent research, which is based on new compilations and analyses of published data. For example, refer to Figs. 2, 5, and 8 in Brown et al. (2004), which plot data for rates of whole-organism biomass production, maximal population growth (r_{\max}), and ecosystem carbon turnover across a wide range of body

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sizes, taxa, and environments. The exponents, 0.76, -0.23 , and -0.22 , respectively, are very close to the predicted values of $\frac{3}{4}$, $-\frac{1}{4}$, and $-\frac{1}{4}$, and the 95% confidence intervals do not include the Euclidean alternatives of $\frac{2}{3}$, $-\frac{1}{3}$, and $-\frac{1}{3}$.

What is the mechanistic basis for quarter-power exponents?—The data on biological allometries are well described by power laws, implying that they are the result of self-similar or fractal-like processes. West et al. (1997, 1999a, b) developed general mechanistic models based on geometric and biophysical principles that explain the quarter-power exponents. These models address the general problem of distributing metabolic resources within an organism and, more specifically, describe the structure and function of mammal and plant vascular systems. The models of West et al. hypothesize that the quarter-power scaling exponents reflect the optimization of these transport networks due to natural selection. Although the organisms themselves are three-dimensional, an additional length variable is required to describe the branching networks, resulting in scaling exponents with 4, rather than the Euclidean 3, in the denominator. The structures and dynamics of resource distribution networks are hypothesized to be dominated by self-similar fractal-like branching, although it is likely that some networks may be “virtual” (e.g., within cells of prokaryotes) rather than “hard wired” (e.g., vascular systems of vertebrates and higher plants).

These models of West et al. have been criticized by several authors. Cyr and Walter (2004) cite most of the published critiques. West and collaborators are trying to respond to the most serious criticisms, but this takes considerable effort and introduces inevitable time lags (see Brown et al. 1997, Enquist et al. 1999, West et al. 2002; 2003a, b, *in press*, Allen et al. 2003, Brown et al. 2003, Gillooly et al. 2003). Several other responses are still in press or unpublished. We will not address the criticisms here, except to state that we have yet to see compelling theoretical or empirical evidence that would cause us to retract or substantially change the models of West et al. Like the content and implications of the broader MTE, the rigor and realism of the models for quarter-power scaling will be decided not by the participants in the immediate debates, but by the broader scientific community in the fullness of time.

What is a mechanism, and a mechanistic theory?—Several commentaries question the extent to which MTE, as we have presented it, is truly mechanistic. We have three responses.

The first is that there is considerable variation in what scientists consider to constitute a mechanism; one person’s mechanism is another’s empirical phenomenology. This is a long-standing problem. For example, physicists still don’t completely understand the mechanistic basis of gravity, even though the force of gravity can be characterized by analytical equations and used as a first principle to make useful, accurate predictions

about everything from satellite orbits to biomechanical properties of bones. We freely admit that there is abundant room for additional research on mechanisms: from (1) how the kinetics of the multiple biochemical reactions of metabolism determine the observed activation energies at whole-organism and ecological levels of organization; to (2) how the kinetics of species interaction, evolution, coevolution, speciation, and extinction cause the observed temperature dependence in biogeographic gradients of species diversity. We hope other research groups will investigate some of the mechanisms and we welcome all contributions to producing a more complete and mechanistic conceptual framework for MTE.

The second response is that mechanisms are described in much more detail in our other publications. Most equations in Brown et al. (2004) are the result of mathematical models described in separate publications. These models make explicit mechanistic connections between the metabolic processes of individual organisms and their ecological and evolutionary consequences.

The third response is that empirical support for these models and, in particular, for the predicted scalings with size and temperature, suggests that metabolic rate is indeed the most fundamental biological rate, and that its manifestations ramify to affect all levels of biological organization, from molecules to ecosystems. Data sources and statistical procedures are not described in Brown et al. (2004), but are documented in the original papers. It is important to recognize that the figures in Brown et al. (2004) are not just descriptive statistical regression equations. Two points should be emphasized: (1) theoretically predicted values for allometric exponents and activation energies, based on metabolic processes within individual organisms, are incorporated directly into the analyses and into the plots of the data; and (2) support for model predictions comes not only from the high proportions of variation explained by the regression equations (high values of r^2), but more importantly from the fact that 95% confidence intervals for the slopes almost always include the predicted allometric exponents and activation energies.

What about all the variation?—The authors of the commentaries represent a wide spectrum of biologists and ecologists, from those who seek unifying principles, to those who emphasize diversity and complexity. Both approaches are valid—indeed both are required to keep the science focused, balanced, realistic, and progressing. We are at one end of the spectrum, unabashedly seeking unifying theory. For those who are more concerned about the variation, we have three comments.

First, the influence of metabolism on ecology is most apparent when comparisons can be made across wide ranges of body size and temperature, where the pervasive influences of allometry and kinetics are strong. When body mass differs by only two- or threefold, or

temperature varies by only a degree or two, other factors can assume equal or greater importance. Many of these factors are outside the domain of metabolic theory. For example, allometry and kinetics are of little value in explaining coexistence and species diversity of herbs in an old field or warblers in a forest, because there is little variation in both body size and temperature. In effect, these variables are “controlled” by the design of the study, thereby allowing other factors to be evaluated. Nevertheless, many systems studied by population and community ecologists have sufficient variation in body size and temperature for metabolic theory to be directly applicable. For example, our model can explain ~90% of the variation in growth rates of zooplankton (Gillooly et al. [2002]; see also egg-hatching rates in Brown et al. 2004: Fig. 3). The magnitudes of intra- and inter-specific variation in body mass and seasonal variation in environmental temperature make these results directly relevant to population and community dynamics of zooplankton in temperate lakes.

The second comment is that effects of allometry and kinetics on individual organisms and ecological systems are powerful and pervasive. The very fact that body size and temperature account for most of the variation in log-scaled “microbe to monster” and “oceans to forests” plots is evidence that the allometry and kinetics of metabolic rate are fundamental to biology and ecology. These processes are still operating even when their influences may be obscured by variation due to other processes. Suppose that we want to understand the processes involved in secondary succession from an old field to a forest. Then, the influence of plant size on species interactions and ecosystem processes assumes major importance. Or suppose that we want to predict the ecological consequences of a rise in average environmental temperature by 2°C. The actual responses will undoubtedly be complicated by time lags, transient dynamics, initial species composition, effects of limiting material resources, and other variables. Despite these sources of variation, however, metabolic theory provides a good starting point: it predicts that rates of individual-, population-, community-, and ecosystem-level processes will increase as described by the Boltzmann factor with an activation energy of 0.6–0.7 eV (1 eV = 96.49 kJ/mol).

The third point, also made in several commentaries, is that a theory soundly based on first principles, provides a baseline—a point of departure—from which to understand the residual variation. Deviations from predictions can be grouped loosely into four categories: (1) measurement errors or other biases in the data; (2) effects of factors not included in the model or theory; (3) exceptions that “prove the rule” by showing how violating specific model assumptions leads to predictable deviations; and (4) discrepancies that expose serious flaws in the assumptions or operations of the model. Having a theoretically predicted baseline helps one to evaluate these possibilities.

Specifics.—Most commentaries raise specific issues that warrant attention, but we address only two here.

First, Cyr and Walker (2004) extol the virtues of the dynamic energy budget (DEB) approach of Kooijman, Nisbet, and collaborators (e.g., Kooijman 2000, Nisbet et al. 2000). DEB models do indeed describe growth and reproduction of individuals in terms of metabolic processes and first principles of energy and material balance. And they do indeed incorporate more detail—many more variables and functions—than our deliberately simple MTE. How much complexity in a model is desirable or necessary is in part a matter of taste, and in part a matter of the purpose for which the model is used. We view the DEB and MTE approaches as complementary. They make different trade-offs between specificity and generality, and consequently have different strengths, weaknesses, and applications.

Second, Sterner (2004) asks whether “one cardinal equation of macroecology, $X = M^{3/4}e^{-E/KT}R + \text{error} \dots$ ” with a “. . . single linear term in R is enough to do the job” (where R is the “amount” of some limiting material resource). This is a straw man. We never claimed that this is the “one cardinal equation of macroecology.” We explicitly stated that many ecological phenomena, including macroecological species–area and species–abundance relationships, are outside the purview of MTE. We did not suggest that the unexplained variation should be regarded as “error.” We explicitly noted that residual variation may be due to deterministic influences of stoichiometry, phylogenetic or functional group affinity, environment, and other factors that are not included in our models. We did not say that resource limitation is due to a single reagent and is linear with respect to R and “organism nutrient content.” We do agree with Sterner that “there is quite a bit more work to do” on ecological stoichiometry and its relationship to energetics, and for this reason we deliberately omitted a term for resource abundance from our models (our Eqs. 4–8) for rates and times at the individual organism level. We did include a linear term, R , in our Eqs. 9–11 for abundance, biomass, and productivity at the population to ecosystem levels. These models can be taken as testable hypotheses for the effects of limiting material resources, together with body size and temperature, on these ecological variables. The chemical compositions of the fluxes and pools of material resources are central to organismal metabolism and must be an essential ingredient of any complete MTE. Our earlier work has concentrated on allometry and kinetics. As indicated in Brown et al. (2004), we have begun to address many of the interrelationships between energy and materials in both organisms and ecosystems. A major research program of Sterner, Elser, and others has concentrated on ecological stoichiometry, and represents a major contribution (e.g., Elser et al. 2000, Sterner and Elser 2002). However, we strongly disagree with Sterner that “we are beyond that . . . previous era in ecology, where bio-

energetics was *the* hoped for organizing concept.” Just change *the* (our italics) to *a*. Energetics, updated, based more firmly on first principles, and interrelated to stoichiometry, is *a* powerful organizing concept for ecology.

We end by emphasizing that MTE is not intended to be the theory of everything that is interesting and important in ecology. Nor is it intended to account for all of the variation among living things and ecological systems. Within its domain, however, MTE offers mechanistic explanations for linking many ecological patterns and processes to biological, physical, and chemical constraints on individual organisms. MTE suggests that underlying the diversity of living things and the complexity of ecological systems are fundamental unities, some of which reflect how first principles of biology, physics, and chemistry govern the fluxes and pools of energy and materials within organisms and between organisms and their environments.

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