DARWINIAN FITNESS AND REPRODUCTIVE POWER:
REPLY TO KOZŁOWSKI

We are glad that our article (Brown et al. 1993, hereafter referred to as BMT) has engendered enough interest to elicit so rapid a critique from Kozlowski (1996). We are grateful for this opportunity to make a few points that should clarify the energetic concept of fitness developed in our article and address the issues raised by Kozlowski.

Kozlowski’s first and most important criticism of BMT concerns the energetic definition of fitness that we use. Darwinian fitness is a very slippery concept, which has almost as many definitions as authors who have written about it. Kozlowski suggests that number of offspring produced in a lifetime (N_o) be used as a measure of fitness. This cannot be correct. Consider two genotypes that produce identical offspring. A female of genotype A produces two female offspring over a 2-yr lifetime, while a female of genotype B produces two female offspring over a 4-yr lifetime. Clearly, in a Darwinian sense, genotype A has greater fitness, because it produces otherwise identical offspring at a greater rate than genotype B.

Kozlowski further suggests that number of offspring produced per lifetime can be converted to an energetic measure of fitness by assuming that energy content per unit mass of offspring is constant, so that lifetime energy allocation to reproduction can be calculated as N_o M_o, where M_o is the average mass of an offspring. If such lifetime energy allocation to offspring could be equated to fitness, elephants would have much higher fitness than rats. Fitness clearly is a rate. Elephants do not have much higher fitness than rats largely because it takes elephants so much longer to produce their much larger babies. But if fitness is a rate, what is it the rate of? We suggest in BMT (see also Brown 1995) that it can be thought of as the rate at which organisms acquire energy and other scarce resources from the environment and convert them into offspring. We call this rate reproductive power, and our model gives the maximal reproductive power as a function of body size. J. Damuth (personal communication) has suggested that this maximal reproductive power be called “potential energetic fitness,” and we agree that this is a useful term. We recognize in BMT that energy is allocated to the survival of the parent as well as to the production of offspring, but we did not incorporate such features of life history explicitly into our model. We suggest, “Future elaborations of our model could incorporate these details of ecology, specifying how energy is allocated to survival and production of offspring over the lifetime. This would reconcile our treatment with theories of life history that are based on
traditional definitions of fitness in terms of age of first reproduction, survival, and fecundity" (p. 582).

Based on the allometry of individual energetics, the BMT model predicts the optimal size for a clade or taxonomic group of organisms in the absence of resource limitation. The intent of our model is to offer a general hypothesis for the characteristic shape of the frequency distributions of body sizes among species of mammals and other organisms. In his text and figure 1, Kozlowski advocates an alternative formulation based on variation in adult production and mortality with respect to body size. While we encourage the development and evaluation of alternative hypotheses, we note that Kozlowski's has three shortcomings. First, Kozlowski presents no theoretical or mechanistic justification for the equation that produces his hump-shaped function relating production to body mass (fig. 1 and legend). Specifically, why should the absolute rate of production decrease in species of very large body sizes? Second, Kozlowski similarly provides no explanation for the relationship between mortality rate and body mass, and his multiple curves in figure 1 suggest that an enormous range of variation is possible. This conflicts with the evidence that mortality is highly correlated with adult body mass, so that life span scales as $M^{0.25}$ (e.g., Peters 1983; Calder 1984; Charnov 1991). Third, Kozlowski's treatment does not succeed in expressing fitness as a common energetic currency. Although Kozlowski gives no units for the variables in his equations and figure, production and life span must be measured in different units, and only the first is explicitly energetic.

Kozlowski's second criticism is that our two-step acquisition/conversion model is unrealistic because it ignores animal behavior. Our treatment in BMT does indeed ignore the details of eating, resting, moving, watching for predators, and so on, but so does virtually every theory of life history, including Kozlowski's own model. We are, however, ready to make a prediction about behavior based on our model: in species above the optimum body size (which we suggest to be about 0.1 kg in mammals), individuals should spend a smaller proportion of their time feeding and a larger proportion resting than in species of smaller size. This is because our model explicitly assumes that as body sizes increase above the optimum, the fitnesses of individuals are limited more by energy allocation than by energy acquisition.

Kozlowski's third point is that our rate of energy allocation to offspring is "completely unrealistic," because our equations, and the units in which they are expressed, imply that reproductive production decreases as adult body size increases above the optimum. However, Kozlowski provides no explanation of how he calculated the obviously unrealistic gestation times that he claims are "predicted" by our model.

A reviewer has pointed out a problem with the units in the equations in BMT. In equations (1) and (2), there are quantities with units of energy (J), individuals (I), and time (t), so the units are $JI^{-1}t^{-1}$. The units of equations (3) and (4), however, are not consistent: the left-hand sides have units of $It^{-1}$, while the right-hand sides have units of $Jt^{-1}$. This should be corrected by dividing $K_0$ and $K_1$ by a constant $C_2$, which has units $JI^{-1}$, giving
This constant is canceled in deriving equation (6), however, and the remainder of the model is unchanged. Some readers may be unfamiliar with the treatment of the units in our model, because we follow the convention of writing allometric equations with the units incorporated in the constants (i.e., in the $C_0$, $C_1$, and $C_2$ of our equations). We explain this convention in the appendix.

Kozlowski is correct that the rate of conversion of energy into offspring, $K_1$, in our model is a per-individual rate. Of course, the actual rates of acquisition and conversion for any particular organism are functions of adult body mass, $M_a$, as described by equations (9) and (10). $K_0$ varies with the same allometric exponent as the adult per-individual metabolic rate, while $K_1$ varies with the same exponent as the adult mass-specific rate.

The BMT model does indeed imply that the per-individual rate of conversion of energy into offspring, $K_1$, decreases with increasing adult body size, $M_a$, as $M_a^{-0.25}$. Why should this be so? The rate of conversion of energy into offspring is limited by the time it takes an individual to grow to reproductive size, the duration of pregnancy and lactation, and the interval between litters. All of these rates scale as $M_a^{-0.25}$ (Peters 1983; Calder 1984); thus, the rate of turnover of resources into offspring scales as $M_a^{-0.25}$. For example, the size of the zygote in mammals (and in other organisms in which the egg does not contain large quantities of yolk) is independent of adult size (i.e., scales as $M_a^{0.0}$); and the rate at which the developing embryo uses energy, and hence the rate of exponential growth of the fetus, scales with the same exponent as the mass-specific metabolic rate of the parent, or as $M_a^{-0.25}$. Further, Peters (1983) and Calder (1984) point out that prenatal and postnatal growth rates and times scale similarly and that doubling times for mass increases of both embryos and neonates scale as approximately $M_a^{-0.25}$, so that growth rates scale as $M_a^{-0.25}$. We are aware that during the latter stages of pregnancy and especially during lactation, females of large body size allocate energy to their offspring at a much higher rate than females of near-optimal size. But this is not the rate that we hypothesize to limit fitness. We suggest that fitness is limited by the rate at which the female parent can turn over, transform, and transport energy and other resources that must be supplied to the offspring. This is the mass-specific metabolic rate. The result is that in species larger than the optimal size of approximately 0.1 kg in mammals, maximal rates of conversion of energy into offspring and maximal population production are predicted to scale inversely with adult body size, as approximately $M_a^{-0.25}$. This is in excellent agreement with the empirical relationships reported in Peters (1983).

To see the relationship among the rates of energy transformation, fitness, and body size more intuitively, it is perhaps easier to think in terms of the time that
it takes for an individual or population to double its numbers, energy content, or biomass. With unlimited food resources as assumed by our model, a population of rats, each weighing approximately 0.1 kg, can double in a few months. In contrast, a population of elephants, each weighing approximately 700 kg, will require several years to double. We are surprised that Kozlowski finds the "unrealistic" part of our model to be the decreasing rate of conversion of energetic resources into offspring and thus into fitness with increasing body size above the optimum. The intrinsic rate of natural increase, $r_{\text{max}}$, has long been accepted as a measure of fitness and has been found to scale inversely with body size, as approximately $M^{-0.25}$ (Peters 1983; Calder 1984; Charnov 1991). We expected that the most controversial part of our model would be that it predicts an optimal size, with a decrease in potential energetic fitness as body size decreases below this optimum.

We end with three general comments. First, we reiterate that our model should be regarded as only an initial step in an effort to develop a theory of fitness and life history based explicitly on energetics and thermodynamics. As BMT freely admitted and Kozlowski has reemphasized, there are several things that our model does not do. One is to predict the specific relationships among the important life-history variables—that is, the allometries and trade-offs that for particular kinds of organisms set the growth and production rates, juvenile and adult survivorships, magnitude and frequency of reproductive efforts, and size and number of offspring. Although Kozlowski and other readers apparently may want to predict such variables as gestation time from BMT equation (11), we view this as a misapplication of our model. A critical issue here is the period over which energy acquisition and allocation must be averaged to calculate the appropriate rate. We suggest that the appropriate time period is long, at least as long as the interval between litters and perhaps as long as the entire life span. The answer should come when we have a more complete theory of energetic demography.

Second, BMT do not model explicitly how reproductive power affects the ecological and evolutionary processes that influence the diversification of clades and the assembly of continental and insular faunas so as to produce the observed frequency distributions of body sizes around the optimum (figs. 1, 3, and 4 in BMT). We suggest in BMT that competition for limited resources and other environmental conditions have led to the evolutionary divergence of body sizes of species away from the optimum to produce the distributions that are observed empirically. Kozlowski legitimately questions whether competition and other factors can produce the orders-of-magnitude range of body sizes that are seen in mammals and many other groups of organisms. However, D. A. Kelt (personal communication; Kelt and Brown, in press) has used BMT's formalization of reproductive power and reasonable assumptions about interspecific competition to develop simulation models of mammal community assembly that produce distributions of body sizes similar to those observed in real communities.

The third and related general comment is that we, unlike Kozlowski, do not believe that the current data and theory of ecological energetics yet provide an adequate basis for a unified theory of life history or for an energetic characterization of fitness. Thus, we welcome models that are extensions of, or alternatives
to, our own. These models would be most useful if they were based on specific physiological mechanisms of individual organisms and if they made testable predictions. We try to do this in BMT (see also Brown 1995). We remain optimistic that it will ultimately be both possible and useful to develop a characterization of fitness based on physical principles of energetics and thermodynamics. After all, organisms are complex physical systems that transform energy to do the work of acquiring rare materials from the environment and of allocating these resources to their own growth, development, and survival and to the production of offspring.

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APPENDIX

Units in Allometric Equations

In BMT equation (12), the optimal mass is given as

\[ M^* = \left( \frac{-C_1 \cdot b_0}{C_0 \cdot b_1} \right)^{1/b_0 - b_1} \]  

(BMT 12)

The dimensional analysis of equation (BMT12) has puzzled a number of readers. We take this opportunity to clarify the units involved. The way we think of allometric equations is that they represent a functional relationship between mass on the right-hand side (rhs) and the quantity of interest on the left-hand side (lhs), not a direct conversion per se. In this framework, the constant on the right-hand side carries the units and the mass quantity is unitless (although its value will depend on the unit system in which it is measured):

(lhs quantity) \cdot (lhs units) = (constant) \cdot (lhs units) \cdot (mass value)^b.  

(A1)

If one chooses to include mass units in the equation, then the units of the constant must be adjusted:

(lhs quantity) \cdot (lhs units) = (constant) \cdot \left( \frac{\text{lhs units}}{\text{mass units}^b} \right) \cdot (mass value \cdot mass units)^b.  

(A2)

If one uses the convention of equation (A1), then \( C_0 \) and \( C_1 \) have units of energy per time (\( E \cdot T^{-1} \)). In BMT, \( C_0 \) and \( C_1 \) have units of watts (Joules per second); \( M^* \) is unitless. It is the coefficient of mass, not the mass itself. For example, if the optimal mass was 3 kg, \( M^* \) would be three, not the entire expression 3 kg. If one were to represent allometric relationships according to the convention of equation (A2), then \( C_0 \) would have units of energy per time per mass raised to the \( b_0 \) power (\( E \cdot T^{-1} \cdot M^{-b_0} \)) and \( C_1 \) would have units of energy per time per mass raised to the \( b_1 \) power (\( E \cdot T^{-1} \cdot M^{-b_1} \)). Plugging into equation (BMT 12), we see that \( M^* \) now carries the units, and if optimal mass is 3 kg, \( M^* \) is 3 kg.

As demonstrated here, our convention for representing allometric equations is certainly not the only approach. However, the convention of equation (A1) is quite standard (see, e.g., Peters 1983; Calder 1984; Schmidt-Nielson 1984). We do want to emphasize that the unitless nature of \( M^* \) is just a notational convenience and is very different from true
dimensionless quantities whose values are invariant to changes in units. $M^*$ depends on the mass unit because the values of $C_0$ and $C_1$ do.

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