EVOLUTION OF BODY SIZE: CONSEQUENCES OF AN ENERGETIC DEFINITION OF FITNESS

JAMES H. BROWN, PABLO A. MARQUET, AND MARK L. TAPER*

Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131

Submitted July 24, 1992; Revised October 26, 1992; Accepted October 30, 1992

Abstract.—We develop a general model for the effect of body size on fitness. We define fitness as reproductive power, the rate of conversion of energy into offspring. Reproductive power is assumed to be limited by a two-step process: first, the rate of acquisition of energy from the environment, which scales allometrically as body mass raised to approximately the 0.75 power, and then the rate of conversion of energy into offspring, which scales as mass to approximately the −0.25 power. The model predicts (1) the distinctive right-skewed shape of the frequency distribution of logarithms of body sizes among species that is observed in a wide variety of organisms from bacteria to mammals; (2) a taxon-specific optimal body size, which for mammals is approximately 100 g and is supported by data on the body sizes of mammals on islands; and (3) that in each taxon the relationships between such life-history and ecological characteristics as longevity, clutch size, home range size, and population density will change both slope and sign on either side of the optimal size. An energetic definition of fitness has the potential to unify areas of ecology and evolutionary biology that have previously used models based on different currencies.

Thermodynamics and energetics provide a unifying conceptual basis for much of the theoretical and empirical research in physiological, behavioral, and ecosystems ecology but not in evolutionary biology or population and community ecology. In these latter disciplines the unifying concept is fitness, which has traditionally been defined in terms of the relative rate of increase of a genotype or population. Some noted physicists have suggested that fitness could be characterized in thermodynamic and energetic terms. Thus, Boltzmann (1905, cited in Odum 1971, p. 6) says, “[The] struggle for existence is a struggle for free energy available for work,” and Lotka (1922, p. 147) writes, “In the struggle for existence, the advantage must go to those organisms whose energy-capturing devices are most efficient in directing available energy into channels favorable to the preservation of the species” (see also Schrödinger 1947). In the present article we revive this physical perspective, develop an energetic definition of fitness, and use it to model the evolution of body size.

From bacteria to insects to mammals, a seemingly universal feature of large taxonomic groups is a frequency distribution of body sizes among species that is highly right skewed, even on a logarithmic scale (see, e.g., Stanley 1973; May 1978, 1986; Bonner 1988; Dial and Marzluff 1988; Brown and Maurer 1989) (fig.

* Present address: Department of Biology, Montana State University, Bozeman, Montana 59717.
Fig. 1.—Frequency distributions of number of species with respect to logarithms of body mass for North American terrestrial mammals, land birds, and freshwater fishes. Note that these distributions are all very similar: right skewed, with a clear decline in the number of species on both sides of the modal value. These data were compiled from a variety of sources; allometric equations relating body length to body mass were used to estimate mass for those species for which direct data were not available.
1. Hutchinson and MacArthur (1959), who first called attention to this pattern, hypothesized that it occurs because smaller species tend to be more specialized and thus subdivide environments and resources more narrowly than their larger relatives. Recent investigators have applied concepts of fractal geometry to account for the specialization and proliferation of species of small size (Morse et al. 1985; Lawton 1986; May 1986). Contrary to the prediction of the specialization hypothesis, however, the smallest size class does not contain the greatest number of species (fig. 1).

Here we present an alternative to the specialization hypothesis. We derive a model for an optimal body mass, based on energetic correlates and consequences of size that appear to be characteristic of all organisms. We begin with the well-established empirical relationships between size and such attributes as metabolic rate and turnover time, ontogenetic development time, and life span (Peters 1983; Calder 1984; Schmidt-Nielsen 1984). These allometric relationships set fundamental limits on organic structure and function and determine the trade-off between the relative advantages of small and large size.

**FITNESS REDEFINED**

We begin by defining fitness in energetic terms. Organisms must acquire and transform energy, nutrients, and sometimes other limited resources, such as water, that must be obtained from the environment in order to maintain homeostasis and produce offspring. We assume that evolution under frequency-independent natural selection tends to maximize the fitness of individuals. Fitness is defined here as the rate that resources, in excess of those required for growth and maintenance of the individual, can be harvested from the environment and used for reproduction.

Thus, we equate fitness with reproductive power, the rate of conversion of energy into useful work for reproduction. This is an application of the maximum power principle of Lotka (1922, 1925; Odum 1971; see also Van Valen 1976). Traditionally, evolutionary biologists have defined fitness in terms of the rate of production of offspring, but such definitions are complicated by variation in the quality as well as the number of offspring (see, e.g., Gadgil and Bossert 1970; Stearns 1976; Endler 1986). Because quality depends on characteristics of the environment as well as of the offspring themselves, there is no single optimal number of offspring for a given amount of reproductive work (Schaffer 1974; Slatkin 1974; Stearns 1976; Gillespie 1977). By defining fitness in terms of power, we shift the emphasis from the traditional trade-off between number and quality of offspring to the more general capacity to transform energy to reproductive work.

**THE MODEL**

Reproductive power is modeled as the consequence of two limiting rates: the rate at which an individual can acquire resources from its environment and the rate at which it can convert those resources into reproductive work. We assume
that the process is analogous to a two-step chemical reaction in which the individual, \( I \), catalyzes the conversion of resources, \( R \), to work, \( W \):

\[
R + I_0^{K_0} \rightarrow I_1
\]

(1)

and

\[
I_1^{K_1} \rightarrow I_0 + W,
\]

(2)

where \( I_0 \) and \( I_1 \) represent individuals before and after the acquisition of resources from the environment; \( I_0 \) and \( I_1 \) can be thought of either as the proportion of time a single individual spends in these two states or as the proportion of the two kinds of individuals in the population. We assume in this initial report that reaction 1 is saturated with respect to resources. Consequently, the rates of disappearance of \( I_0 \) and production of \( I_1 \) are

\[
\frac{dI_0}{dt} = -K_0I_0 + K_1I_1
\]

(3)

and

\[
\frac{dI_1}{dt} = K_0I_0 - K_1I_1.
\]

(4)

We discuss below some of the likely results of relaxing this assumption. Reproductive power of an individual is given by

\[
\frac{dW}{dt} = K_1I_1.
\]

(5)

At steady state, \( dI_0/dt = dI_1/dt = 0 \). Remembering that \( I_0 \) and \( I_1 \) sum to unity, we have

\[
\frac{dW}{dt} = \frac{K_0K_1}{K_0 + K_1}.
\]

(6)

If \( K_0 \) is large, then reproductive power is limited by the rate of conversion of resources, and

\[
\frac{dW}{dt} \rightarrow K_1.
\]

(7)

On the other hand, if \( K_1 \) is large, then resource acquisition becomes limiting, and

\[
\frac{dW}{dt} \rightarrow K_0.
\]

(8)

We further assume that the maximum values of both \( K_0 \) and \( K_1 \) that can be expressed by an individual are allometric functions of body mass, \( M \):

\[
K_0 = C_0M^{b_0}
\]

(9)
and

$$K_1 = C_1 M^{b_1}. \quad (10)$$

Thus, reproductive power is given by

$$\frac{dW}{dt} = \frac{C_0 M^{b_0} C_1 M^{b_1}}{C_0 M^{b_0} + C_1 M^{b_1}}. \quad (11)$$

Finally, maximizing power, $dW/dt$, with respect to body mass and rearranging terms give the following simplified expression for the optimal body mass, $M^*$:

$$M^* = \left( \frac{-C_1 b_0}{C_0 b_1} \right)^{\frac{1}{(b_0 - b_1)}}. \quad (12)$$

The biological interpretation of this model is straightforward. The smallest individuals have a great capacity to convert resources into reproductive work, but they are limited by the rate of acquisition of resources for reproduction. They must spend most of their time foraging just to meet their high mass-specific maintenance metabolism. In contrast, large individuals have a great capacity to acquire resources, but they are constrained by the rate at which these can be converted into viable offspring. The trade-off between these two limiting processes results in an optimal size. Previous authors (Case 1979; Ziolk and Kozlowski 1983; Reiss 1989) also use energetic considerations to derive an optimal body size, but they do not incorporate the constraint on conversion of energy into offspring expressed in our equation (10).

**IMPLICATIONS**

The most direct application of the model is that it predicts the value of the optimal body size if the values of the allometric constants $b_0$, $b_1$, $C_0$, and $C_1$ are known. We suggest that the values of $b_0$ and $b_1$ remain virtually constant among different kinds of organisms. We assumed that $b_0$, which scales the rate of energy acquisition in excess of maintenance needs, is 0.75, the same as the allometric exponent for individual metabolic rate, productivity, and growth rate (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Yodzis and Innes 1992). We assumed that $b_1$, which scales the rate of transformation of energy to reproductive work, is $-0.25$, the same as the allometric exponent for rates of mass-specific metabolism and nearly all biological conversion processes (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Yodzis and Innes 1992). Some authors have suggested on theoretical or empirical grounds that $b_0$ and $b_1$ might be 0.67 and $-0.33$, respectively. We follow Yodzis and Innes (1992) and others in using 0.75 and $-0.25$ and also in noting that the model is not sensitive to small differences in the exact values of these general scaling exponents.

In contrast, $C_0$ and $C_1$ are taxon-specific parameters. We used data from Peters (1983; data for peak milk production in app. VIIIId and for population production in app. VIIIic) to estimate $C_0$ and $C_1$ for mammals as 6.0 and 0.2 W, respectively, when $M$ is measured in kilograms. Substituting these values into equation (12)
Fig. 2.—The hump-shaped curve of reproductive power as a function of the logarithm of body mass (dashed line) predicted by our model when reasonable values for mammals were substituted for the exponents and constants in eq. (11). Note that the model predicts an optimal body size and a distribution of reproductive power that closely matches the observed frequency distribution of body masses among species of North American mammals (histograms: as in fig. 1). This correspondence is not expected to be precise, however, because the “Platonic” fitness function predicted by the model does not include the effects of resource limitation and interspecific interactions.

gives an optimal body size for mammals of 100 g and a distribution of reproductive power that is very similar to the observed frequency distribution of species (fig. 2). While there may be some uncertainty about the exact values of \( C_0 \) and \( C_1 \), substituting a reasonable range of empirical estimates of these parameters for mammals gave remarkably similar distributions and an optimal size that was usually between 80 and 250 g. That the optimum lies within this range is supported by two characteristics of insular and continental mammal faunas (fig. 3): populations of species that on continents are larger than this size tend to evolve dwarf insular races, whereas populations of smaller species tend to evolve giant insular races (Lomolino 1985); and as the area of a land mass and the number of species present decrease, the range of sizes represented in the fauna also decreases, so that when there is only a single species present, it tends to be close to the optimal size (P. A. Marquet and M. L. Taper, unpublished manuscript; see also Maurer et al. 1992).

One may ask, If there is such an optimum, then why are not all species at the optimum? Why is there such a wide range of sizes within each taxon? Our model develops a Platonic fitness function that is based on general physiological processes that operate independently of particular ecological settings. In the real world, this fundamental fitness function can be modified by the influence of abi-
**Fig. 3.**—Two empirical patterns in the body sizes of mammals on islands and continents that suggest the existence of an optimal body size between 80 and 250 g. 

A. Microevolutionary trends in insular populations of mammals, which show that populations above and below the optimum tend to evolve dwarf or giant insular forms, respectively (data reanalyzed and replotted from Lomolino 1985). 

B. Maximum (squares) and minimum (stars) body sizes of terrestrial mammals inhabiting a large sample of islands and continents. Note that, as the size of the land mass and the number of species present decreases, the range of body sizes tends to converge toward the optimal body mass (from P. A. Marquet and M. L. Taper, unpublished manuscript).
otic environmental conditions and the presence of other organisms. Thus, contrary to the assumption of equation (3), the supply of resources often does limit the rate of acquisition. The capacity of individuals to use the spectrum of available resources varies with body size. For example, in mammalian herbivores the capacity to extract usable energy and nutrients from different kinds of food depends on allometric anatomical and physiological constraints on digestion (Demment and Van Soest 1985; Justice and Smith 1992). The result is that, when a species of the optimal size is present and using one part of the resource spectrum, other species are more likely to invade and persist if they are of different sizes and use different resources (Rummel and Roughgarden 1985; Taper and Case 1992).

The differentiation in size observed within a taxon of related organisms is the result of frequency-dependent processes: both microevolutionary changes within species and macroevolutionary processes of origination and extinction. Our model predicts that, when only a single species is present, it should be close to the optimal size. As the number of species increases as a result of speciation or colonization, other sizes will tend to become established, using more completely the distribution of reproductive power diagramed in figure 2. Thus, the intraspecific evolutionary size trends in mammals on islands (fig. 3A) are largely the result of microevolutionary processes, whereas the diversity of sizes of species on continents and islands (fig. 3B) is largely a consequence of macroevolutionary processes. Both, however, appear to reflect the influence of the same taxon-specific fitness function (Stanley 1973; Maurer et al. 1992; P. A. Marquet and M. L. Taper, unpublished manuscript).

The evolutionary diversification of lineages involves the making and breaking of constraints. Constraints are expressed in the way that evolutionary history and phylogenetic relationships limit variation in the structure and function of contemporary organisms (see, e.g., Brooks and McLennan 1991; Harvey and Pagel 1991). In terms of the model, constraints are expressed as taxon-specific (or more rigorously as clade-specific) values of the constants $C_0$ and $C_1$. These limit both the range of body sizes and the distribution of body sizes of the species within a lineage. Thus, the distributions of sizes for mammals, birds, and fishes (fig. 1) are quantitatively different because of taxon-specific values of the $C$'s, but they are qualitatively of nearly identical shape because of identical values of the $b$'s. The same pattern holds for different levels of phylogenetic differentiation within these taxa. For example, within birds, constraints owing to diet, digestive physiology, and other factors cause owls (order Strigiformes) to be larger on the average than flycatchers (family Tyrannidae), but each of these taxonomic groups exhibits its own unique right-skewed distribution (fig. 4).

A unique feature of our model is that it predicts that many ecological and some physiological allometric relationships should change slope and sign at approximately the optimal size, as the rate-limiting process shifts from resource acquisition to resource conversion. This is a hard, a priori prediction that is readily subject to empirical test. In fact, there is already some evidence to support this prediction. For example, home range sizes of mammals are inversely related to body mass in species smaller than approximately 100 g and positively correlated with body size in species larger than this threshold value (Brown and Maurer
Fig. 4.—Frequency distributions for the number of species as a function of body size (on a logarithmic axis) for two lineages of North American land birds: top, the owls, order Strigiformes; and bottom, the flycatchers, family Tyrannidae, order Passeriformes.

1989; Brown and Zeng 1989); maximum population densities of mammals and birds exhibit the opposite pattern (Brown and Maurer 1987, 1989; see also Damuth 1981; Lawton 1990; Marquet et al. 1990). Some life-history attributes and foraging characteristics show similar patterns. For example, hummingbirds and insectivorous bats, among the smallest birds and mammals, respectively, have life spans longer than their somewhat larger relatives and much longer than predicted for their sizes from the allometric equations derived from data for birds and mammals of a wide range of sizes (Calder 1989; Findley 1993).

So far as we are aware, ours is the only model that predicts nonlinear allometric relationships for many life-history and ecological characteristics of species within large taxonomic groups. In evaluating this prediction, it must be borne in mind that the allometric equations reported in the literature are almost always derived from linear regressions fitted to log-transformed data for all species in a taxon for which measurements are available. Nonlinearities in allometric relationships have often not been detected, because the majority of species are larger than the
optimal size (fig. 1), and they bias the data to which linear allometric equations are fitted. If the slopes and signs of allometric relationships do indeed change on either side of the optimal size, this will often be apparent only in the substantial deviations of values for the smallest organisms from those predicted from the published allometric equations.

With this caveat, our model offers a single parsimonious explanation for many allometric patterns in ecology and evolution. The fact that the maximum rate of population growth, $r_{\text{max}}$, scales as mass raised to the $-0.25$ power (Peters 1983), follows directly from equations (7) and (10) but only for the large majority of species that are above the optimal body size. The model complements treatments of life-history evolution (see, e.g., Harvey et al. 1989; Reiss 1989; Charnov 1991), which explicitly consider the relationship between body size and allocation of energy to reproduction. These other treatments assume that when individual growth, whose rate scales as $M^{0.75}$, ceases, resources can then be devoted entirely to reproduction. They then consider the effect of size on the trade-off between the rate of resource acquisition and the timing of reproductive maturation. This trade-off is important, especially in adjusting specific suites of life-history traits to particular environmental conditions. These models assume, however, that fitness is limited by resource acquisition, whereas ours assumes that there are also physiological constraints on energy conversion. These two constraints of energy acquisition and conversion, by themselves, are sufficient to produce a hump-shaped distribution of reproductive power (fig. 2), which in turn predicts both the optimal body size and the allometry of many correlated life-history traits.

We define reproductive power, $dW/dt$, as the instantaneous rate of conversion of energy into offspring in a mature organism. Actually, $dW/dt$ reflects the energetic limits on the capacity to produce offspring. We have deliberately not specified how this energy is reflected in the quantity and quality of these offspring. The optimal allocation of this energy will depend on the particular environment experienced by each population and the effect of these conditions on growth, survival, and reproduction. 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 (see, e.g., Roff 1981; Harvey et al. 1989; Charnov 1991).

SYNTHESIS

The concept of reproductive power integrates certain aspects of the physiological and behavioral ecology of individuals with the evolutionary ecology of populations and communities. It provides an energetic and thermodynamic basis for fitness. Our model develops an explicit relationship between the fundamental energetic characteristics of individuals embodied in equations (1) and (2) and the allocation of energy to produce new individuals. Heretofore, ecologists who have studied interactions with the abiotic environment, foraging, and reproduction of individuals have used energy as an explicit currency in both theoretical models
and empirical studies. In contrast, ecologists and evolutionary biologists who have studied structure and dynamics of populations and communities and the genetics of evolutionary change have used the rate of change in population size or allele frequency as the currency of interest. Recently, however, Yodzis and Innes (1992; see also Peters 1983; Calder 1984) have demonstrated the utility of modeling population dynamics from the perspective of energetics and allometry. By extending this approach to include a much wider range of ecological and evolutionary processes, our model offers a unified thermodynamic basis for understanding population dynamics, community organization, evolutionary genetic change, and organism-mediated ecosystem processes. It represents the kind of physical biology envisaged by Boltzmann (1905) and Lotka (1922) in the quotes above (see also Schrödinger 1947).

ACKNOWLEDGMENTS

We thank W. A. Calder III, T. J. Case, E. L. Charnov, P. H. Harvey, A. Kodric-Brown, J. H. Lawton, B. A. Maurer, F. A. Smith, and E. Toolson for comments and the National Science Foundation for support (grant BSR-8807792).

LITERATURE CITED


Editor: Mark D. Rausher