Diversification of Body Sizes: Patterns and Processes in the Assembly of Terrestrial Mammal Faunas

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It is only a slight overstatement to say that the most important attribute of an animal, both physiologically and ecologically, is its size. Size constrains virtually every aspect of structure and function and strongly influences the nature of most interspecific interactions.

—G. A. Bartholomew 1981:46

The diversity of life is composed of two parts. In part it is made up of species diversity, which is the number of discrete evolutionary lineages. Over 4700 species of mammals are known to science, for example, and new forms, even new genera, are being described routinely (Wilson and Reeder 1993). Diversity is also reflected in the tremendous variety of characteristics that these organisms exhibit. This is particularly true with respect to features of structure and function. One particularly important characteristic, and the most visible feature of living organisms, is body size. The variation in body sizes is impressive: it ranges over 20 orders of magnitude, from the smallest microplasms weighing only $10^{-13}$ g to the largest known organisms, whales, some of which weigh more than $10^8$ g. Even within most large clades, size diversification spans many orders of magnitude. As an example, the class Mammalia spans $10^8$ g, from the tiniest shrews (e.g., Microsorex, 2.5 g) to the blue whale (*Balaenoptera musculus*, about $1.6 \times 10^8$ g). Within this class, sizes within the order Primates range from about 100 g (e.g., mouse lemur, *Microcebus murinus*, and pygmy marmoset, *Cebuella pygmaea*) to over 200 kg (*Gorilla gorilla*), the rodents from about 6 g (e.g., pygmy mouse, *Baiomys taylori*) to over 60 kg (capybara, *Hydrochaeris hydrochaeris*), and the Carnivora from 35 g (least weasel, *Mustela nivalis*) to nearly 800 kg (brown bear, *Ursus arctos*). Furthermore, within the Carnivora, the family Mustelidae exhibit body sizes from about 35 g (*M. nivalis*) up to 45 kg (otters, *Pteronura*).
and *Enhydra*), and the Felidae range from about 1.5 kg (e.g., flat-headed cat, *Felis planiceps*; margay, *Felis wiedii*) to over 300 kg (Siberian tigers, *Panthera tigris*). It is clear that this diversification in sizes is not simply a result of the domination of particular regions of the body size range by specific clades. Rather, we see that successively smaller subclades span a large portion of the total range in body sizes of the larger clade, and the overall pattern is gradually built up by the accumulation of nested groups.

In part because of the constraints of allometry, this diversity in body sizes is reflected in a similarly high diversity of other characteristics, ranging in spatial scale from characteristics of individual anatomy, to characteristics of home ranges, territories, and geographic distributions, and in temporal scale from physiological rates and patterns of daily activity to evolutionary probabilities of speciation and extinction.

If we are to understand the diversity of body sizes, we need to understand the structural and functional constraints that operate at the level of the individual. Additionally, we need to understand how these constraints influence other features that operate at greater spatial and temporal scales. To this end, we will borrow a metaphor from Hutchinson (1965), who referred to species as being actors in an evolutionary play being acted out in an ecological theater (figure 7.1). In our adaptation of Hutchinson’s metaphor, organisms of

**Figure 7.1. (Opposite)** A conceptualization of “the ecological theater and the evolutionary play” (Hutchinson 1965) as they interact to influence the evolution of body size. Local communities are represented by boxes with permeable borders; the solid arrows represent immigration (i) and local extinction (e) of species. The local ecological theater includes both the abiotic conditions (the stage scenery, e.g., soils, physiognomy, weather, etc.) and the biotic interactions present (other actors in the play). The local evolutionary play involves microevolutionary shifts in body size to adjust to the structure and dynamics of the local theater. Local communities are nested within regional assemblages, which also exchange individuals and species to some degree, but much less so than communities (indicated by less permeable boundaries and dashed immigration arrows). The ecological theater varies from place to place (i.e., riparian woodlands versus desert shrub land versus sand dunes within the Great Basin biome), but it still includes the biotic players and the abiotic stage scenery. As a result, the evolutionary play at the regional scale produces geographic variations in body size, which we perceive as races, varieties, or subspecies. Regional assemblages are nested within continental faunas, whose physical boundaries are even less permeable (although some intercontinental movements do occur). Inter-regional variations in the ecological theater (i.e., Boreal forest versus Chihuahuan desert) are similar in kind, but they are functionally coarser than the intraregional variations mentioned. Continental dynamics (e.g., area, shape, spatial heterogeneity) influence the macroevolutionary processes of speciation (both cladogenetic and anagenetic) and extinction of species possessing particular traits such as large versus small body sizes. Islands support small-scale communities that are relatively isolated and therefore receive limited immigration (hence the dashed immigration arrows).
different sizes are subject to the rules of allometry and the constraints of phylogeny. Different actors bring different sizes to the stage, and this in turn influences how they interact with other actors and with the abiotic environment. The stage scenery (the abiotic environment), as well as the number and kinds of other actors, varies over both space and time, and this in turn causes changes in other actors. These changes occur through the processes of microevolution and macroevolution: the modification of species by gradual adjustments to their environment, and the gain and loss of species by speciation or by extinction. In the present chapter, we consider how actors respond to changes in scenery and to changes in the other actors that are on stage, by modifying their body sizes and consequently their roles in the evolutionary play.

There are three approaches to the study of how actors in our theater change roles. One approach is to watch the play through time. However, we have only one good snapshot of the play (the present), and we must rely on paleontological records to deduce the condition of the actors and the stage in the past. Such records are very useful, but to varying degrees they are inevitably fraught with problems of incomplete preservation, and consequent difficulties in interpretation. A second approach is to reconstruct the play by means of phylogenetic reconstruction (e.g., Felsenstein 1985; Brooks and McLennan 1991). This approach has been useful in evaluating the evolution of community structure and body size in Caribbean Anolis (Losos 1995), tropical diversity of cockroaches (Grandcolas 1993), and parental care in fishes (Gittleman 1982). A third alternative is to observe the actors and their performances and how these vary over different parts of the stage. By understanding how players’ roles vary in ecological time and in different ecological settings, we can learn much about the evolutionary processes that have molded them.

We will focus our attention on terrestrial mammals. This diverse, conspicuous, and charismatic group of animals has received much attention by neontologists. As a result they are well understood ecologically. Additionally, their hard endoskeleton has resulted in a good fossil record with which evolutionary (and ecological) hypotheses may be tested. Hence they represent a good group for relating inferences from the paleontological record to insights from neontological studies.

Our approach will involve making comparisons of the roles of contemporary players over different spatial scales and in different environmental settings. We will employ a combination of inductive inference and mechanistic models to begin to evaluate hypotheses regarding the ecological and evolutionary processes that have produced the observed patterns of body size in terrestrial mammals. We will begin by outlining what we believe are the ma-
major patterns in body size. Then we will review three classes of processes that may produce these patterns. Third, we will compare several attempts to explain the evolution of body sizes. Finally, we will discuss the use of models in evaluating processes operating in body size evolution, and we will suggest several avenues of future work.

The Patterns

There are four principal patterns in body sizes that we attempt to explain. First, frequency distributions of body sizes at continental scales are highly modal and strongly right-skewed when plotted on a logarithmic scale (figure 7.2A; Maurer et al. 1992; Brown et al. 1993). This also is true at the generic level for all of the major continents (Rusler 1987; Maurer et al. 1992). Body size distributions on smaller continents (Australia, New Guinea, Madagascar) and islands are strongly modal but are relatively symmetrical (Rusler 1987; Maurer et al. 1992). This pattern has been known for many years (e.g., Hutchinson and MacArthur 1959; May 1978; Bonner 1988) and has been documented for a variety of taxa in addition to mammals. As such, this may be a very general characteristic of most or all large clades, in which case the arguments that we will present may be generally applicable to the cladogenetic evolution of body sizes.

Second, local ecological communities exhibit nearly uniform distributions of body sizes on a logarithmic scale (see figure 7.2C). Thus, species that coexist in local habitats are significantly nonrandom subsets of the continental faunas (Brown and Nicoletto 1991). The spacing between species, however, is not constant, and as a result there are clumps and gaps in local body size distributions (Holling 1993). Intermediate spatial scales, such as biomes or geographic regions within a continent, demonstrate correspondingly intermediate patterns. Hence, body size distributions for mammals in all of the principal biomes in North America are modal and right-skewed, but these distributions are much flatter than for the continent as a whole (see figure 7.2B; Brown and Nicoletto 1991).

Third, there is a macroevolutionary reduction in extreme body sizes as area of an isolated land mass decreases (figure 7.3A; Brown et al. 1993; Marquet and Taper ms). The largest species are generally smaller, and the smallest species are generally larger, as the size of the land mass decreases from the largest continents to the smallest islands. Note that the frequency distributions of body sizes among species is completely different for isolated land masses and for nonisolated sample areas within larger land masses. In the former case, the modal shape is retained but the range of body sizes becomes
Figure 7.2. Principal patterns in the frequency distributions of body size. (A) At the scale of continents or the entire globe, the distribution of body sizes of mammals is highly modal and strongly right-skewed on a logarithmic axis. The dashed line gives potential energetic fitness for mammals (after Brown et al. 1993). (B) Body size distributions within biomes also are skewed, but they are much flatter than those at continental scales. (C) At the scale of local communities, body size distributions are generally log-uniform and are significantly nonrandom subsets of larger spatial scales (all data from Brown and Nicoletto 1991).
Figure 7.3. Patterns of body size evolution on islands. (A) As the area of an isolated landmass decreases, there is a corresponding macroevolutionary loss of the smallest and the largest species. As a result, the smallest landmasses possess species of intermediate body size (about 100 g). (B) Island populations of small species exhibit microevolutionary trends toward gigantism, whereas those of large species exhibit dwarfism, with respect to the most closely related continental and ancestral populations (from Brown et al. 1993).
reduced; in the latter situation, the distribution becomes less modal but preserves the range in body sizes.

Fourth, there is a microevolutionary trend towards gigantism and dwarfism among insular populations of species when compared to conspecific populations on adjacent mainlands. This trend is a function of mainland body size, such that species of large size tend to develop dwarfs on islands, whereas species of small size develop insular races of giants (see figure 7.3B; Foster 1964; Lomolino 1985).

The Processes

There are three primary classes of processes that influence the evolution of body sizes. These are phylogenetic constraints, allometric constraints, and ecological relationships. We follow Maynard Smith et al. (1985) in defining constraint as “a bias on the production of variant phenotypes or a limitation on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system,” and we discuss both categories below.

Phylogenetic Constraints

Because of phylogenetic descent and inheritance of characters from common ancestors, related species tend to preserve a legacy of their phylogenetic history. As a result, species that are closely related tend to be more similar in size than more distantly related taxa. Additionally, because of the allometric constraints discussed later, and because phylogenetic proximity reflects recency of evolutionary divergence, closely related species tend to be similar in many ecological characteristics. Phylogenetic constraints are specific to a given taxon and therefore are a type of “historical” constraint (Gould 1994; the “local” constraint of Maynard Smith et al. 1985).

Allometric Constraints

Many physiological and energetic functions are known to scale to body size (Peters 1983; Schmidt-Nielson 1984; Calder 1984). Such allometric relationships reflect structural and functional constraints on the size and shape of the individual organism. As such, these are “universal” constraints (Maynard Smith et al. 1985; the “formal” constraint of Gould 1994).

If different organisms were merely isomorphic versions of a single body plan, then the physical laws of diffusion, and the known relations of surface area to volume, would result in three kinds of relatively straightforward allo-
metries. In such an idealized set of organisms, functions of volume would scale linearly with body mass, M, as $M^1$, while functions of surface area would scale as $M^{0.66}$, and linear relationships as $M^{0.33}$ (see, e.g., Schmidt-Nielsen 1984).

Real organisms are not isomorphic, however, and generally do not scale in this simple fashion. Whole-organism rate processes, including such processes as metabolic rate, growth rate, milk production, requirements for energy and limiting nutrients such as nitrogen, phosphorus, etc., generally scale as $M^{0.75}$. Conversely, mass-specific rate processes, including rates of cellular metabolism, clearance of toxins from the body, etc., scale as $M^{-0.25}$. Finally, biological times, including such features as gestation period, life span, the time required for blood to circulate through the body, etc., scale as $M^{0.25}$.

Because of these allometric constraints on structure and function, including energetic and nutritional requirements and timing and allocation in life histories, body size ultimately influences many features of ecology, biogeography, and evolution (Peters 1983; Calder 1984). While not all of these allometric relationships are well understood, size appears to place important constraints on such variables as dietary specialization, niche breadth, home range and territory size, population density, clutch size, area of geographic range, and the dynamics of extinction and speciation (Brown 1995 and included references).

The result of these allometric relations is that small organisms [but probably not the smallest (see later)] require fewer total resources but have large mass-specific requirements. They live fast and have large reproductive allocations, as reflected in short life spans, large and frequent litters, and high intrinsic rate of increase, $r_{max}$. They have high densities and small territories and home ranges, which they exploit over short time scales, and as a result they are able to avoid extinction and persist in small geographic ranges. Finally, small organisms likely have relatively high speciation rates. Larger organisms tend to have opposite patterns; importantly, they are ecologically constrained to low population densities and large geographic ranges, and they often appear to have high extinction rates during periods of catastrophic environmental change.

**Ecological Interactions**

The local environment in which an organism lives may act as an agent of selection, resulting in adaptive evolution of body size. Two processes appear to be involved. Organisms may be selected to alter their ecological functions in ways that can be accomplished by changing size, thereby reaping the benefits that are consequences of allometry. For example, because age at first re-
production scales as $M^{0.25}$, selection for reduction in the age of first reproduction, perhaps because of altered predation, may be achieved by evolving towards smaller size. In addition, however, interactions with the environment may cause organisms to be selected to break the constraints of allometry. Thus, selection on weasels to follow prey into burrows and refuges has apparently resulted in the evolution of a long and thin body shape. The result of this is that weasels differ from other mammals of similar mass by having greater body surface area, rates of heat loss, and food requirements at low ambient temperatures (Brown and Lasiewski 1972).

Because of the influence of phylogeny, related organisms will tend to be similar in size and other characteristics (Harvey and Pagel 1991). This tendency towards similarity will tend to be reinforced by the relative difficulties in breaking the constraints of allometry. Ecological pressures, however, will often tend to promote the divergence of closely related species. To the extent that speciation is allopatric, related organisms will tend to occur in somewhat different environments, to be subject to different selective pressures, and therefore to diverge in body size and other characteristics. Alternatively, to the extent that closely related allopatric species occur in similar environments, they may be selected to remain similar in body size and other characteristics. Allopatric species that occur in similar environments but are not closely related may be selected to converge. To the extent that speciation may be sympatric, or that closely related species have secondarily come to coexist, they may be subject to selection to diverge in body size and/or other characteristics. The most obvious selective pressure promoting such divergence is interspecific competition, and its evolutionary consequences have been referred to as character displacement (Brown and Wilson 1956; Taper and Case 1992). It is also possible that other ecological interactions, such as predation or even mutualism, could produce selection for divergence in body size or related characteristics.

**Explanations of Observed Patterns**

**Modal and Right-Skewed Distribution of Clades and of Faunas at Continental Scales**

**Hypotheses**

Three main explanations have been proposed to explain the continental pattern of body sizes.

Gould (1988) presented the null hypothesis, that the observed distribution reflects random divergence of species of a clade from a common ancestor. Because of Gould’s advocacy of punctuated equilibrium (e.g., Eldredge
and Gould 1972; Gould and Eldredge 1977), he considered natural selection operating differentially on individuals to be a less significant factor in the evolutionary diversification of body sizes than the large changes that occur during cladogenetic and extinction events.

Hutchinson and MacArthur (1959) argued that the high diversity of small body sizes can be attributed to the fact that these smaller species are more specialized than larger species, and that they operate at spatial and temporal scales at which the environment is inherently more heterogeneous. May (1978, 1986; see also Morse et al. 1988; Lawton 1990) recast Hutchinson and MacArthur’s (1959) hypothesis in terms of fractal geometry. If smaller species occupy narrower niches, and the environment exhibits a fractal structure so that niches are more abundant and more spatially fragmented, then it follows that smaller species should be more abundant.

Finally, Brown et al. (1993) hypothesized that the modal and right-skewed distribution of body sizes reflected an underlying energetic dynamic, and that the peak in diversity of body sizes occurred at an optimal mass, at which species could most readily obtain energetic resources from the environment and convert them into offspring. Brown et al. suggested that allometric constraints on energy and resource acquisition and allocation limit the reproductive power or potential energetic fitness (PEF) that can be realized by individuals of different size. They developed an allometric model of PEF that predicts the optimal size of a species within a clade, and that should correspond closely to the mode of the observed frequency distribution.

Evidence

Gould’s hypothesis has been subjected to a computer simulation (Maurer et al. 1992) in which faunas of 350 species evolved in response to either cladogenetic or anagenetic processes, or both. Additionally, speciation and/or extinction were incorporated and were modeled as unbiased or as biased towards either large or small species. Maurer et al. (1992) demonstrated that random cladogenetic events alone did not produce skewed frequency distributions, but when extinction probabilities were biased towards small or (especially) large body sizes, the resulting distributions were significantly skewed. These results were accentuated when anagenetic evolution was incorporated. Hence, the null hypothesis, that the evolution of body sizes is a product of random cladogenesis, was rejected, and some kind of deterministic process was implied to have produced the distributions of sizes observed empirically.

McShea (1994a) also used computer simulation to explore possible mechanisms affecting the distributions of quantitative traits in proliferating lineages. He compared different combinations of three kinds of models: (1) equiprobable random divergence, equivalent to the null model of Gould
(1988) and Maurer et al. (1992); (2) passive divergence with a boundary on one side that could be approached but not crossed, as might occur, for example, if some functional constraint placed an absolute limit on the smallest possible body size; and (3) divergence biased in one direction (i.e., driven) by differential speciation and/or extinction rates. McShea found that the null model of equiprobable divergence did not generally produce highly modal and skewed distributions, but that the passive and especially the driven models readily did so. He also compared the distributions generated by his simulation models with empirical distributions of body sizes and skeletal traits.

Hutchinson and MacArthur's (1959) argument provides a good fit to observed distributions, but it is not very testable. Fractal versions (May 1986, 1988a; Morse et al. 1988; Lawton 1990) predict that the largest number of niches should be available to the smallest species. Thus, they fail to account for the decline in frequency of species of extremely small size. All of these hypotheses based on size-related specialization are difficult to evaluate empirically, because they require an operational way of measuring specialization and the number of “unfilled niches” available to species of various sizes.

Finally, the distribution of PEF as a function of mass is unimodal and right skewed, and it is very similar in form to the empirical distribution of body sizes for the 464 species of North American mammals (see figure 7.2A). PEF predicts an optimal body size for mammals at about 100 g, which corresponds well with the peak of the observed distribution. The model of Brown et al. also makes predictions about the evolution of insular populations, as well as life history and demographic traits. This model does not explicitly explain the diversity of body sizes. Given that an optimum exists, why are not all species of this size? How do we account for the diversity of sizes found in ecological communities and continental faunas? To address this, we have been working with models of local community assembly that incorporate characteristics of PEF (see later). We hope that these may be extended to operate at greater spatial scales, and that they may provide testable hypotheses for the evolution of regional and continental faunas.

The Nearly Uniform Size Distribution Within Local Communities

Hypotheses
As described, we can envision three possible explanations for this local pattern. The most obvious null hypothesis is that local communities are a random selection from the pool of species that are present on the continent (Brown and Nicoletto 1991).

Alternatively, the distribution may reflect some form of local, ecological
displacement, most likely to avoid competition between species of similar size. Ecological displacement may arise from two mechanisms: ecological assortment or evolutionary adjustment, the dynamics of which are manifested at different spatial scales. Ecological assortment reflects the local compatibility of species and is a result of the daily interactions among species living in close proximity. It is mediated by local colonization/extinction dynamics, the capacities of species to immigrate into and persist in local communities depending on the extent to which they are similar to and compete with the other species that are present. In contrast, evolutionary adjustment influences the regional evolution of body sizes, producing races and subspecies, and reflects microevolutionary adjustments by species to different environmental conditions and to different faunal composition. The most common form of such adjustment is character displacement, the tendency for evolutionary divergence in body size and other characteristics, in response to selection to reduce competition with coexisting species (see Taper and Case 1992).

Finally, Holling (1993) has suggested that the environment presents a given array of niches, the dynamics and distribution of which are dictated by both biotic and abiotic environmental characteristics. As a result, species have sorted themselves into discrete body size categories that reflect the parameters of the available niches. Presumably, both ecological assortment and evolutionary adjustment can act as mechanisms to produce a match between the available niches and the body sizes of the species that fill them. Holling’s explanation places more emphasis on the presence of gaps and clumps in local body size distributions than on the overall, relatively uniform distribution.

An alternative to Holling (1993) invokes the overriding dominance of certain key taxa (Brown 1995). Certain widespread, abundant species occur in many local communities and habitats over large spatial scales, and they form the clumped nodes of body sizes over these scales. Such “continental keystone species” will also often be members of diverse and widespread lineages (e.g., Sorex cinereus, Peromyscus maniculatus, Canis latrans), and, therefore, where they are absent they will often be replaced by closely related taxa of similar sizes, reinforcing the observed clumping of body sizes at certain nodes. While Holling’s explanation suggests that niches are set in an a priori manner and hence should be relatively constant across biome types both within and among continents, our alternative suggests that they are dependent on the particular organisms present. Therefore, we would predict that the modal sizes depend on phylogenetic constraints and would often differ among communities in similar habitats, or biomes on different continents.
Evidence

The null hypothesis, that local communities are random subsets of the continental species pool, was tested and disproven by Brown and Nicoletto (1991), who found that random selection from the North American species pool produced simulated assemblages that had much more skewed body size distributions than real communities. It follows from this that some local process operates to inhibit local coexistence of similar-sized species. Competition is the most logical candidate, although we can imagine scenarios in which predation or mutualism might also produce such patterns (i.e., apparent competition; Holt 1977). Even if Holling's (1993) cross-scale explanation is right, some process operates to limit the number of species that occur within the nodal niches. We do not suggest that all similar-sized species interact competitively [e.g., least weasels, Mustela nivalis (45 g), do not compete with voles, Microtus (40 to 80 g)], but if competition operates within guilds, and the number of guilds is relatively small, then competition may spread species out within guilds.

While the observed local body-size distributions are not highly modal, and they are more dispersed than a random subsample of the North American pool, they do exhibit clumps and gaps at local and biome scale. Some mechanism appears to aggregate species into relatively discrete clumps. It will be very difficult to separate Holling's explanation from the alternative that we have presented above. Intercontinental comparisons will be difficult in many cases (e.g., are woodlands really comparable habitats in North America and Australia?) but may be feasible in others (Larrea shrublands are very similar in North America and South America).

Macroevolutionary Reduction in Extreme Sizes as Area of Isolated Land Mass Decreases

Hypotheses

The null hypothesis for this pattern is that the distribution of body sizes on smaller land masses is a random sample of the body sizes that are present in the global pool.

Alternatively, Damuth (1971) demonstrated that the probability of extinction scales positively with body size. Because local population density varies inversely, and area of geographic range varies directly, with body size, and because the probability of extinction is strongly influenced by total population size (e.g., MacArthur and Wilson 1967), it follows that extinction probability should be correlated directly with body size.
Finally, PEF (Brown et al. 1993) may explain the spatially dependent distribution of body sizes. According to this argument, as species richness decreases, species that are divergent from the optimum should be least likely to persist, so both maximal and minimal body sizes should converge towards the optimal body size for a taxon. For mammals, this body size is approximately 100 g (Brown et al. 1993). Hence, on the smallest islands, where only a single species is present, it should approximate this size.

**Evidence**

Marquet and Taper (ms) developed a simple randomization protocol to draw a given number of species (without replacement) from the global pool. They found that the smallest and largest body sizes on land masses with low richness were significantly larger and smaller, respectively, than those predicted by a random draw of the same number of species. We conclude that the reduction in extreme body sizes on smaller land masses is not a product of random selection.

Damuth’s argument accounts for the decrease in large species as land area decreases, but because his allometric relationships are linear, they do not account for the loss of the smallest species. In fact, a strict application of Damuth’s argument would suggest that as the number of species on a land mass is reduced to one, the final species present would be in the smallest size class (about 2 to 3 g for mammals), which is not observed (Brown et al. 1993).

The observed shift in the distribution of body sizes with decreasing richness agrees with the predictions of the PEF model of Brown et al. (1993). We note that their argument predicts the convergence on optimal size when only a single species is present, but it must invoke mechanisms of faunal buildup and species packing in order to develop larger faunas. Extensions of the PEF model (Kelt 1997; see later), which incorporate competitive interactions and character displacement, demonstrated remarkably good fit to empirical data.

**Microevolutionary Trends Towards Gigantism and Dwarfism in Insular Populations**

**Hypotheses**

The null hypothesis is that changes in body size in insular faunas reflect random changes (e.g., founder effects, genetic drift) with respect to the ancestral populations. In contrast, Brown et al. (1993) argued that insular species will converge towards the optimal size for a taxon. Because islands have fewer species, the number of competitors and predators likely is reduced, relative
to the mainland. With fewer competitors, species should experience micro-evolutionary shifts in body size towards the optimum. Species of large body size that encounter reduced predation pressure on islands also may become dwarfed on islands. We suggest that in both cases, selection for insular dwarfism involves allometric changes in life history traits, such as the production of offspring at earlier ages and a reduced interval between litters, which increase PEF. Selection for insular gigantism in populations of small original body size also involves allometric changes to increase PEF, but these would be attained by increasing the capacity for energy acquisition, rather than conversion.

Evidence
In contrast to the null model, Lomolino (1985) demonstrated that the direction of body size shifts among insular taxa are allometrically related, such that smaller species exhibit gigantism and larger species become dwarfed. A regression through these data is significant and crosses the zero-change isocline at approximately 200 g. Given the wide confidence intervals around the regression, this intersection is in reasonably close agreement with the 100 g predicted from PEF, and it further supports the underlying importance of an energetic definition of fitness in the evolution of body size. We emphasize that there is a substantial stochastic element in how insular colonization and extinction affect the species composition of insular faunas. The predicted direction and magnitude of body-size adjustment will depend on the time that the species has been on the island and on the number and sizes of other species that are present. As a result, we would predict a fair amount of variation around the predicted shift, and this is observed.

Implications for Spatial and Temporal Patterns of Species Abundance
Potential energetic fitness implicitly predicts that many ecological and physiological allometric relationships should change slope and perhaps even sign at approximately the optimal body size (Brown et al. 1993). In support of this, Brown et al. (1993; see also Brown 1995) noted that while both home range size and maximal population density varied with body size in mammals, these relationships are not well fit by standard allometric power functions. Instead, both parameters appear to have their maximal values at some intermediate size, which is very close to the modal size and the optimal size predicted by the model of PEF. These nonlinear relationships appear to have important consequences at geographic spatial scales and evolutionary time scales. Geographic range size and ecological specialization as reflected in hab-
that specificity are correlated with home range size and population density, so they also vary non-linearly with body size (Brown 1995). A consequence is that species near the modal body size tend to exhibit the greatest habitat specificity, have the smallest geographic ranges, and show the highest spatial turnover or beta diversity (Brown and Nicoletto 1991). At the same time, however, other species of near-modal size have very large geographic ranges and are habitat generalists. These species, together with ones of more extreme size, are widely distributed and form the core species of mammal communities across the North American continent.

We can speculate on the pattern of temporal turnover we might expect to see in the fossil record. On the one hand, since we expect extinction rates to be negatively correlated with geographic range size and habitat nonspecificity—and perhaps for speciation rates to show the same pattern—specialized species of modal size should turn over rapidly. On the other hand, the generalized species of near-modal size with dense populations and wide geographic ranges should exhibit the lowest rates of turnover. Species of extreme size, especially very large, should have high rates of extinction because their very low population densities do not compensate for their large geographic ranges.

Models of Size Diversification During Faunal Assembly

The simplest approach to modeling faunal diversification involves random cladogenesis. This was explored for the general case by computer simulations (Raup et al. 1973; Raup and Gould 1974; Gould et al. 1977). Gould (1988) suggested that such random diversification from a common ancestor could also account for the distribution of body sizes within clades, but he did not develop explicit models. Maurer et al. (1992) modeled the evolution of body sizes in continental faunas with a simulation approach and found that random cladogenetic processes alone were unlikely to account for the right-skewed distributions that are almost universally observed. They showed that incorporation of size-biased speciation or extinction into the model could generate right-skewed distributions, but their models did not incorporate any specific mechanisms through which body size could cause these biases. McShea (1994a) simulated lineage diversification in passive and directed and in bounded and unbounded conditions, with the goal of determining which gave resulting frequency distributions of quantitative morphological traits most similar to those observed empirically. He found that highly modal and skewed distributions rarely resulted from unbounded passive divergence, but that they could be produced either by passive divergence in the presence of a boundary or by directional forces. He found that the distributions of body
sizes in rodents and vertebral complexity in mammals resembled the simulations of random bounded divergence, while the distribution of body size in horses resembled his directional simulations. McShea's results supported Stanley's (1973b) earlier suggestion that the evolutionary trend towards larger body sizes seen in many lineages and taken to exemplify Cope's rule is more likely to reflect the greater diversity and higher speciation rates of lineages of small body size than directional evolution towards larger sizes.

None of these approaches have incorporated allometric relationships of body size. Recently, Kelt (1997) combined the model of PEF (Brown et al. 1993) with a general model of character displacement (Rummel and Roughgarden 1985; Taper and Case 1992) to simulate assembly of ecological communities. Kelt's model simulates the development of local communities as a consequence of immigration from a larger pool of species, followed by anagenetic shifts in body size to maximize fitness. Fitness is a function of both PEF and competitive displacement. Selection operates to shift body sizes towards the energetically optimal size. Opposing this, competitive interactions operate to shift species away from each other, thereby spreading them out along the mass axis. As species richness increases, the fitness landscape is gradually transformed from a unimodal humped distribution to one with multiple peaks and troughs. This model produces size-structured communities as a result of both evolutionary character adjustment and ecological sorting. Simulated local communities of up to 50 species were generated. These resembled real communities in having similar extreme sizes, and log uniform distributions of species between these limits. Simulated communities differed from real ones by lacking the clumps and gaps along the size axis noted by Holling (1993).

Kelt (unpublished) modified his original model to simulate cladogenetic faunal evolution, by incorporating both speciation and extinction. Assembly is initiated with a single species of random size, which shifts body mass to maximize fitness, as described. This species is allowed to speciate, and the resulting daughter species evolve anagenetically to maximize PEF and minimize competition (figure 7.4A). Cladogenetic diversification continues until the extinction rate, resulting from ecological carrying capacity, equals the speciation rate. As species richness increases, the fitness landscape is transformed from a unimodal to a polymodal distribution, and ultimately to a unimodal trough in which fitness is greatest at extreme sizes. Like the ecological model, the cladogenetic model produces faunas with species uniformly distributed along a logarithmic axis of body sizes.

An interesting outcome of the cladogenetic model is that it generates Cope's rule (Stanley 1973b). This occurs because, at any given point in time, species tend to be clustered under the peak in PEF, and competition for ener-
Figure 7.4. Results of a model of interactive faunal assembly involving both cladogenetic speciation and anagenetic body size shifts to maximize local fitness (see text). In the model presented in this figure, the probability of stochastic extinction upon reaching stability was set at 20 percent; in other words, there was a 20 percent probability that a randomly chosen species would go extinct once all species masses had stabilized. (A) Trajectories of body size change for 50 species; speciation events are marked with arrowheads (<), while stochastic extinctions (not including extinctions resulting from evolution to extreme body sizes) are noted with asterisks (*). (B) Proportional change in body size for 50 species, as a function of their initial body size. Even very small species may experience substantial increases in their mass. (C) Proportional change in body size for 50 species as a function of their duration. The majority of species clearly evolved towards greater body size, although one species in this simulation underwent dwarfism. Regression statistics: body size change = \((7.415 \times 10^{-6})\) (species duration) + 1.071, \(p < .0001\), \(r^2 = 0.303\).

Divergent resources is therefore greatest among species at modal body sizes. Because the slope of the fitness landscape is less steep at larger than at small body sizes, when speciation occurs there is a greater opportunity for anagenetic shifts to larger body sizes (see figure 7.4B,C).

Kelt's models further support the potential roles of energetics and interspecific interactions in the evolutionary diversification of faunas, as well as
the ecological organization of communities. At their present stage of development, however, these models do not generate the modal and right-skewed distributions of sizes characteristic of continental faunas. We believe this reflects the limited spatial scale that is considered in the current models. Brown and Nicoletto (1991) showed that the shift in the body size distribution from log-uniform at local scales to highly modal at continental scales is owing to the differential turnover of modal-sized species between habitats and over geographic regions. To address this, Kelt’s assembly models could be developed further to include the dispersion of species among habitats and across geographic space.

Prospectus

We have explored the utility of one approach to understanding Hutchinson and MacArthur’s (1959) evolutionary play. We have focused on an energetic fitness currency and on one of the most obvious features of its expression, body size, to describe how species respond to the stage scenery and to the other actors present, at any given moment during the ecological play. We do not suggest that life is so simple that a single parameter such as body size can be used to characterize the dialogue and choreography of the entire play. However, we suggest that the allometry of PEF offers testable hypotheses to explain some aspects of this dialogue and choreography that have remained elusive until now.

It is always reassuring when a single model or mechanism appears to be able to explain empirical observations made over broad spatial and temporal scales. Such was the general appeal of MacArthur and Wilson’s (1967) theory of island biogeography. PEF appears to hold much promise in explaining the distribution and evolution of body sizes, and energetics may provide a currency to synthesize and unify heretofore poorly integrated fields such as physiology, ecology, ethology, evolution, and paleontology. The PEF model predicts an optimal body size for a given taxon, and it provides a unified explanation for body size distributions at various spatial and temporal scales. Additionally, most features of local community assembly are predicted by simple models that incorporate PEF and ecological character displacement.

However, we stress that such models are only the first step of a research program, certainly not the final word on the evolution of body size. We do, however, believe that the generality of this modeling approach makes it a good starting point. We encourage the development and testing of alternative explanations for these patterns and of further extensions of our own models’ analyses. Some potentially fruitful avenues to pursue include:
• Alternative niche axes. Our analyses have emphasized body mass as a single axis of primary importance in ecological assembly and evolutionary diversification. Certainly, other factors, including trophic specialization, habitat structure and regional heterogeneity, interspecific interactions, microhabitat utilization, and climatic regimes, influence the assembly and diversification of ecological communities and continental faunas. Further work incorporating these factors, and considering their relationships to body size, should prove insightful.

• Incorporation of the fossil record. Our analyses provide predictions that may be tested by detailed investigation of the fossil record. There may not be a large number of fossil communities preserved with sufficient fidelity to test our ecological predictions, but the evolutionary patterns, such as Cope's rule, should be widely testable.

• Generalization to other taxa and clades. Our analyses have focused almost exclusively on the evolution and diversification of extant terrestrial mammals. Brown et al. (1993) presented data suggesting that their PEF model applies to other extant vertebrate groups. We urge the application and evaluation of these ideas with other taxa, both extinct and extant. Cases in which the model fails to provide a good fit to empirical data will provide useful insights into the limitations of the present model, and we can hope they will lead to greater understanding.

• Interactions between taxa or clades. Recognition that players share the ecological stage and interact with other kinds of organisms may have important influences on the patterns of body sizes at both ecological and evolutionary scales. For example, large insects may interact with the smallest mammals, influencing the lower size limit for the latter group. Similarly, the diminutive size and inconspicuous nature of mammals throughout the Mesozoic may have reflected competitive or other interactions with the several groups of giant reptiles (sensu lato) that were dominant members of ecosystems. And the diversification and dramatic increase in the body sizes of mammals may reflect altered interactions as a result of the extinction of the dinosaurs at the Cretaceous/Tertiary boundary about 65 million years ago.

Conclusion

The evolutionary diversification of body sizes within and among clades has produced a remarkable array of species, but understanding the dynamics of this diversification has been an elusive task for evolutionary biologists. We
suggest that this is partly because fundamentally different currencies are used by the various subdisciplines of biology. Physiological and ecosystem ecologists study the dynamics of energetic changes (e.g., $dE/dt$), whereas population and community ecologists investigate the dynamics of numerical changes (e.g., $dN/dt$, Brown 1994). We have attempted to bridge this gap with the use of PEF, which uses allometric functions to characterize the ability of an organism to acquire energetic resources from the environment, and to convert these resources to reproductive functions (Brown et al. 1993).

This approach has allowed for the prediction of an optimal body size for a clade; this was calculated to be approximately 100 g for mammals (Brown et al. 1993). Subsequent investigations have incorporated character displacement to model ecological assembly (Kelt 1997), and speciation and extinction dynamics to model evolutionary diversification of ecological communities (Kelt, unpublished). These studies support the suggestion that PEF is an important factor underlying the distribution of body sizes at both local and regional spatial scales, and over both ecological and evolutionary time scales.

PEF appears to provide testable hypotheses for important influences of ecology and allometry on the evolutionary diversification of species. We urge further explorations of this as well as alternative approaches. We tentatively suggest that at one level of abstraction, Hutchinson's play may be easier to understand than we may have thought.

Summary

Using terrestrial mammals as an example, we review four patterns in the frequency distributions of body sizes among species: (1) the modal and right-skewed distribution (on a logarithmic scale) characteristic of the faunas of large continents and the entire globe; (2) the log-uniform distribution at the scale of local ecological communities within continents; (3) the macroevolutionary tendency to lose species of extreme body sizes as the area of an isolated land mass decreases; (4) the microevolutionary trends towards gigantism in small species, and dwarfism in large species, when isolated on islands. We evaluate alternative hypotheses to explain these patterns.

A model of potential energetic fitness (PEF) appears to provide a single, unifying explanation for all of these patterns. As initially modeled by Brown et al. (1993), PEF predicts an optimal body size based on the allometry of energy acquisition and allocation to reproduction. Kelt (1997; unpublished) has extended this model, incorporating both ecological character displacement and cladogenetic evolution, to simulate the assembly of local communities. Kelt's models not only produce simulated communities similar in
many respects to real ones, but the cladogenetic models also generate the evolutionary trend toward increasing body size, known as Cope's rule.

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