THE MICRO AND MACRO IN BODY SIZE EVOLUTION

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Abstract.—The diversity of body sizes of organisms has traditionally been explained in terms of microevolutionary processes: natural selection owing to differential fitness of individual organisms, or to macroevolutionary processes: species selection owing to the differential proliferation of phylogenetic lineages. Data for terrestrial mammals and birds indicate that even on a logarithmic scale frequency distributions of body mass among species are significantly skewed towards larger sizes. We used simulation models to evaluate the extent to which macro- and microevolutionary processes are sufficient to explain these distributions. Simulations of a purely cladogenetic process with no bias in extinction or speciation rates for different body sizes did not produce skewed log body mass distributions. Simulations that included size-biased extinction rates, especially those that incorporated anagenetic size change within species between speciation and extinction events, regularly produced skewed distributions. We conclude that although cladogenetic processes probably play a significant role in body size evolution, there must also be a significant anagenetic component. The regular variation in the form of mammalian body size distributions among different-sized islands and continents suggests that environmental conditions, operating through both macro- and microevolutionary processes, determine to a large extent the diversification of body sizes within faunas. Macroevolution is not decoupled from microevolution.

Key words.—Body size, macroevolution, microevolution.

Received May 14, 1990. Accepted March 27, 1992.

Evolutionists have long sought to understand the diversification of phylogenetic lineages and the changes in particular traits that have accompanied such radiations. The evolution of body size has attracted particular attention, because size of both fossil and living forms is easy to quantify and is correlated with many attributes of morphology, physiology, and ecology (Peters, 1983; Schmidt-Nielsen, 1984; Calder, 1984). Speculation about the processes responsible for evolutionary trends in body size dates back to Cope and beyond. The apparent tendency for body size to increase over time in many diversifying taxonomic groups has been referred to as Cope’s Rule (Cope, 1887, 1896; see Stanley, 1973). Explanations for this trend have usually invoked specific advantages of large individuals, such as ability to tolerate short-term variation in the physical environment, capacity to extract energy and nutrients from a wider variety of poorer-quality food, and ability to avoid many kinds of predators (e.g., Stanley, 1973; Brown and Maurer, 1986, 1987). Many studies of natural and artificial selection show that microevolutionary processes operating through the differential survival and reproduction of individual organisms can indeed cause substantial directional evolution in body size (e.g., Wolda, 1963, 1967; Bantock and Bayley, 1973; Knights, 1979; Boag and Grant, 1981; Price, 1984; Price and Grant, 1984; Price et al., 1984). Patterns in geographic clines in body size and in distribution of large and small species on islands also point to adaptive processes being responsible for considerable body size evolution (see Discussion for details). Recently, Gould (1988) has questioned these standard microevolutionary interpretations and has suggested that purely macroevolutionary, cladogenetic processes (i.e., differential proliferation and extinction of species within lineages) may be sufficient to account for the diver-

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sification of sizes within lineages. Gould's argument is not that microevolutionary, anagenetic adjustments in body size do not occur, but that they are insignificant relative to the large changes caused by speciation and extinction events. Stanley (1973) had earlier called attention to the almost ubiquitous right-skewed (on a linear scale) distributions of body sizes within diverse taxa (see also Hutchinson and MacArthur, 1959), and suggested a macroevolutionary explanation. He argued that the apparent increase in size described as Cope's rule is a simple consequence of the fact that the common ancestor of a lineage was usually small and that there was a purely statistical tendency for the variance in size to increase as species diversity of the taxon increased. If the ancestral size were near the minimum ultimately attained by the lineage (because of some kind of constraint), cladogenesis would result in a right-skewed distribution. Although Stanley clearly pointed out that the direction of evolution would depend on the ecological success of different-sized individuals, Gould (1988) took the more extreme view that speciation and extinction are both necessary and sufficient to account for the evolution of body size and that "The appearance of Cope's rule is an automatic consequence of increasing variance in successful clades" (Gould, 1988; p. 323).

This argument is typical of claims that macroevolution is "decoupled" from microevolution and hence from the differential success of individuals in their environments that is the presumed mechanism of adaptation through natural selection (Eldredge and Gould, 1972; Stanley, 1975, 1982; Gould and Eldredge, 1977; Gould, 1980, 1982, 1988, 1989; Vrba and Gould, 1986). The extreme position has been taken by Gould (1988, 1989; Raup et al., 1973; Raup and Gould, 1974; Gould et al., 1977; Vrba and Gould, 1986), who has increasingly argued that random cladogenetic processes are sufficient to account for differences among species over time in the fossil record and within taxa of contemporary organisms. Other macroevolutionists have questioned the ability of random cladogenesis to produce patterns similar to those observed in real clades (e.g., Stanley et al., 1981) and have recognized the role of environmental conditions and ecological processes in the differential proliferation and extinction of species and in anagenesis (e.g., Stanley, 1973, 1979; Jablonski, 1986; Eldredge, 1989; McKinney, 1990). Evolutionary ecologists have tended to emphasize importance of ecological relationships and microevolutionary processes in the adaptive diversification of species assemblages (e.g., in the case of body size: Hutchinson and MacArthur, 1959; May, 1978, 1986; Brown and Maurer, 1986, 1989; Dial and Marzluff, 1988; Maurer and Brown, 1988; Morse et al., 1988), but some have recognized the role of macroevolutionary processes, especially of the differential extinction of species with certain traits (e.g., Brown and Maurer, 1986, 1987, 1989; Dial and Marzluff, 1988; Maurer and Brown, 1988).

The present paper considers two questions: 1) Are purely cladogenetic processes sufficient to account for the observed empirical distributions of body sizes? and 2) To what extent are microevolutionary and macroevolutionary processes of body size evolution uncoupled from each other and from the environment in which they occur? To address these issues we first document the empirical distributions of body sizes among species and genera of mammals inhabiting different-sized islands and continents. Any complete explanation of body size evolution must account for these patterns. Then we develop simulation models of cladogenetic and anagenetic body size change. We use these to ask whether purely cladogenetic models, with large changes occurring only as a result of speciation or extinction events, or models that incorporate both cladogenesis and anagenesis, with small changes also occurring between speciation events, better predict the empirical patterns. Finally, we discuss the role of the environmental setting and ecological interactions in the evolution of body size, and, more generally, in the coupling of macroevolutionary and microevolutionary processes.

**Empirical Patterns in Body Mass Distributions**

Hutchinson and MacArthur (1959) observed that there are more species of small body size than of large, and offered an adaptive explanation for this pattern. A histo-
gram of the number of species within a diverse taxon against body size is nearly always strongly skewed towards large body sizes. If body mass is plotted on a log scale the histogram is more symmetric. But how symmetric? Visually, the distributions often seem to have a substantial right-hand skew (Van Valen, 1973; May, 1978; Morse et al., 1988; Maurer and Brown, 1988; Bonner, 1988; Brown and Maurer, 1989), but few studies have attempted to quantify the extent to which the frequency distributions of species are skewed when body mass is scaled logarithmically. Here we present data on mammal and bird faunas of large continents that show a highly significant positive skew in the log body mass distributions. Further, we show that the distribution of sizes of mammals inhabiting continents and large islands varies in a systematic way with the size of the land mass.

**Methods**

We used data for North American terrestrial mammals collected by Brown (1981), for North American terrestrial birds assembled by Brown and Maurer (1987, see also Maurer and Brown, 1988), for Australian terrestrial birds obtained by Maurer et al. (1991), and for land mammals on different continents and large islands compiled by Rusler (1987). For each of 464 species of North American mammals, Brown (1981) obtained from the literature a value for average adult body mass in grams (for data see Brown and Nicoletto, 1991). Comparable data were assembled by Brown and Maurer (1987) for 380 species of North American terrestrial birds and by Maurer et al. (1991) for 426 species of Australian birds. Rusler (1987) compiled data on the body mass for the genera of mammals inhabiting Eurasia, Africa, South America, Australia, New Guinea, and Madagascar, and also for the species of Australia. We used her original data on body mass and body length. For those species or genera with no data available on body mass, we used Economos’ (1981) empirical regression equation to estimate mass from body length.

After plotting the distributions of body masses for each assemblage, we calculated a coefficient of skewness that is scaled to equal 0 for non-skewed distributions (Sokal and Rohlf, 1981). We tested for significant departures of this measure from 0 by calculating the standard error of the coefficient and doing an approximate Student’s *t* test (Sokal and Rohlf, 1981; p. 139).

**Results**

The log body mass distribution for 731 genera of terrestrial mammals from all continents combined was significantly skewed towards larger body masses (Fig. 1, Table 1). Although it is lacking a few genera (almost exclusively of small body size) that are endemic to small islands, this is a fairly accurate representation of distribution of the sizes of land mammal genera worldwide. Considering individual land masses, log body mass distributions of genera of mammals from large continents were also skewed (Fig. 2, Table 1), but those from small continents were not (Fig. 3, Table 1). The log body mass distributions for genera of North American and Australian terrestrial birds were also significantly skewed (Table 1). Hence, for collections of bird and mammal genera from large continents, and for terrestrial mammals worldwide, it is evident that the body mass distribution is not log-normal, but has a pronounced tail towards genera with larger average body mass.

The log body mass distributions among species were typically more skewed than
those for genera. This was true for both birds and mammals in North America and for mammals, but not birds, in Australia (Table 1). The reason for this is that small-bodied genera tend to have many more species than large-bodied genera (Fig. 4, Van Valen, 1973; Dial and Marzluff, 1988). The distributions of species for North American birds

Table 1. Skewness of log body mass distributions among species and genera of non-volant mammals and terrestrial birds on several continents.

<table>
<thead>
<tr>
<th>Group</th>
<th>Continent</th>
<th>N</th>
<th>Genera skewness (SE)</th>
<th>N</th>
<th>Species skewness (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birds</td>
<td>North America</td>
<td>176</td>
<td>0.71* (0.18)</td>
<td>380</td>
<td>0.94* (0.13)</td>
</tr>
<tr>
<td></td>
<td>Australia</td>
<td>179</td>
<td>1.03* (0.18)</td>
<td>426</td>
<td>1.00* (0.12)</td>
</tr>
<tr>
<td>Mammals</td>
<td>Eurasia</td>
<td>219</td>
<td>0.37* (0.17)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Africa</td>
<td>208</td>
<td>0.33* (0.17)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>South America</td>
<td>169</td>
<td>0.37* (0.19)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>North America</td>
<td>118</td>
<td>0.43* (0.23)</td>
<td>464</td>
<td>1.04* (0.11)</td>
</tr>
<tr>
<td></td>
<td>Australia</td>
<td>70</td>
<td>0.01 (0.29)</td>
<td>189</td>
<td>0.29 (0.18)</td>
</tr>
<tr>
<td></td>
<td>New Guinea</td>
<td>47</td>
<td>0.22 (0.35)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Madagascar</td>
<td>36</td>
<td>-0.27 (0.39)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>All continents</td>
<td>731</td>
<td>0.53* (0.09)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* P < 0.05, reject $H_0$: skewness not different from 0.
and mammals and Australian birds were significantly right-skewed on a logarithmic scale.

There were regular differences in the shapes of the log body mass distributions of mammalian genera as a function of the size of land mass (Fig. 2). These are described in detail in Rusler (1987) and will be summarized only briefly here. Only the four largest continents had significantly right-hand skewed distributions; the distributions for the three small land masses were relatively symmetrical and approached log-normal distributions. The change in the degree of skewness was due to the absence from the small land masses of large-bodied genera that comprised the right-hand tail of the frequency distributions for large continents. The smaller land masses supported fewer genera of mammals, but those that did occur there exhibited a narrower range of sizes. An important question regarding the patterns exhibited on small continents is whether they represent random samples of body mass distributions of mammals on larger continents, and thus, the absence of large species on small continents is simply a consequence of there being fewer species on the smaller continents. First, it should be noted that the genera represented on small continents are not a random sample of genera found on large continents. The mammalian faunas of Madagascar, Australia, and New Guinea are composed of many endemics found nowhere else (e.g., lemurs on Madagascar, many marsupials on Australia and
Fig. 4. Number of species per genus for terrestrial birds and mammals in North America, and for terrestrial mammals in Australia as a function of the average body size of species within each genus.

New Guinea). Second, if sample size were the only reason for large species being absent on small continents, then we would expect that at least on some small continents, species of relatively large size would be found. In fact, no small continent has a species larger than half the size of the largest mammal on the smallest large continent (South America). We conclude that the smaller maximum size of the largest species on small continents is not due to random sampling from larger continents.

The frequency distributions of other kinds of organisms within most speciose taxa on large land masses are amazingly similar to those that we have reported here for birds and mammals (e.g., May, 1978, 1986, 1988; Bonner, 1988). We conclude that, in general, frequency distributions of body mass are significantly right-skewed, even on a logarithmic scale; these distributions are not lognormal. Bonner (1988; Fig. 47) postulates that this is a general pattern exhibited by nearly every group of organisms.

Models of Body Size Diversification

The presence of a significant skew in the frequency distribution of the logarithms of body mass raises two questions:

1) Can such a skew arise from a completely random process of diversification as Gould (1988) implies? A normal distribution reflects additive combinations, whereas a lognormal distribution reflects multiplicative combinations of random variables (e.g., May, 1975). Therefore, a speciation process that resulted in production of daughter species that were larger or smaller than the ancestral species by some random additive amount would be expected to produce a normal distribution of body sizes, whereas one that produced daughter species larger or smaller than the ancestral species
by some random multiplicative factor should result in a lognormal distribution. A skewed distribution on a logarithmic scale would be expected only if there were significant size-specific biases in speciation and extinction rates as Stanley (1973) suggested. It is certainly not clear that the observed skewed distribution could be generated simply as a consequence of the inevitable increase in variance as the number of taxa in a lineage increased as Gould (1988) suggests.

(2) What are the relative contributions of anagenetic and cladogenetic processes to the skewed log body mass distributions? Is cladogenesis sufficient to produce the skew, or would significant anagenesis also be required? Macroevolutionists have argued that the fossil record suggests that virtually all significant evolutionary change occurs during and as a result of speciation and extinction events (Eldredge and Gould, 1972; Gould and Eldredge, 1977). This challenges the traditional Darwinian view that much evolution occurs between speciation events as a result of differential survival and reproduction of individuals within populations (e.g., Darwin, 1859; Simpson, 1944; Mayr, 1963; Grant, 1986).

The above questions cannot be answered directly from neontological data, although paleontological data would be relevant if there were virtually complete fossil records of the diversification of at least some lineages. Since such data are not generally available, we opted, instead, for the approach advocated by Raup and Gould (1974). We constructed simple simulation models that attempt to mimic both purely cladogenetic evolution and cladogenetic evolution coupled with directional anagenetic evolution. We did not try models based solely on anagenetic processes, because we agree with Stanley (1973) that differential speciation and extinction are probably always important in the diversification of body size during the history of a lineage.

Our purely cladogenetic model formalizes Gould’s (1988) assumption that all significant increases and decreases in body mass are associated with and caused by a speciation event. The ancestral species of a clade has a certain body size, and this founder species is assumed not to evolve at all. When speciation occurs, however, the descendent species can be proportionally larger or smaller than the ancestral species. Hence, over geological time, changes in the distribution of body masses among species in the clade occur essentially instantaneously in discrete “jumps” as species are added through speciation or are lost due to extinction. With respect to body size, these jumps are the punctuational events of the punctuated equilibrium paradigm.

In contrast, a model that included anagenetic processes would have the body mass distribution changing constantly over time. The addition of a new species or the extinction of an existing species would cause a rapid change in this distribution, but between speciation and extinction events the body mass distribution would change continuously as individual species underwent microevolutionary shifts in body size due to natural selection operating through the differential success of individuals within populations and other, nonadaptive processes of genetic change.

Using these assumptions, we developed simple simulation models of evolution with purely cladogenetic events and evolution with both anagenetic and cladogenetic changes. The basic premise of both models is that the size of the founding species of the clade becomes the modal size of the clade (Stanley, 1973; Gould, 1988). Our simple models examine the consequences of biasing the speciation and extinction rates of species with body sizes above and below the modal body size of the simulated clade, and thus address question (1) above. Dial and Marzluff (1988) argued that the skewness of body mass distributions on a linear scale must be due to differential speciation and extinction of large- and small-bodied forms. We extended their insight by assuming that such differential speciation and extinction rates do not necessarily balance one another, and thus may lead to skewed distributions on logarithmic scales. By comparing the effects of biased speciation and extinction rates on the skewness of log body mass distribution for both purely cladogenetic models and for models that include both processes, we address question (2).
ing the evolution of body size and contrast the model thus obtained with an equivalent model incorporating anagenesis, we performed a number of simulations. Each simulation was run as follows. The initial species in the clade was assigned an arbitrary body size of 100 (partly because our research has indicated that 100 g is close to the modal body size for both birds and mammals). First, speciation and extinction probabilities were chosen. Speciation and extinction probabilities were either equal for species above and below the modal body size (i.e., unbiased) or a small bias in these probabilities was added to favor species either larger or smaller than the modal size. The next step depended on whether the model was of anagenetic or cladogenetic evolution. For the cladogenetic model, at each time step each species either gave rise to a new species, went extinct, or did nothing depending on the speciation and extinction probabilities. For each new species, its body mass was either increased or decreased by a multiplicative factor relative to the species from which it originated. That is, if \( M \) is the mass of the ancestral species, species derived from that species had a body mass of either \( fM \) or \( M/J \) where \( f \) is a constant of proportionality. We developed two versions of the cladogenetic model. In the first, the instantaneous jump in body size was constant (i.e., \( f \) was assumed not to change). In the second, we assumed that the magnitude of the multiplicative factor of change was a random variable, so that for any speciation event, \( f \) could take on any number of values depending on the mean and variance of the sampling distribution of \( f \). We set \( f = 1.1 \) for the simulations in which the instantaneous jump in body size at species was constant, and used a normal distribution with mean 1.1 and standard deviation 0.01 for the sampling distribution of \( f \) when the instantaneous jump in body size was random, rather than fixed. The daughter species was larger than the parental species with probability 0.5.

The partially anagenetic model differed from the purely cladogenetic simulations in that each species was constantly changing in body size. The direction of change was determined randomly with probability 0.5 of moving in either direction, but each time a new species originated, it was assumed to begin evolving in the opposite direction of its parent. The size of each species was calculated as a function of time. Let \( M_0 \) be the initial body size of a species, then at time \( t \), \( M_t = M_0 \exp(rt) \), where \( r = \ln f \) if the species was increasing in size or \( r = -\ln (f) \) if the species was decreasing in size. Recall that \( f \) was the proportional increase or decrease used in the corresponding cladogenetic simulation. Using the same value of \( f \) in both the cladogenetic and anagenetic simulations assured that net evolutionary rates were comparable in both models. Speciation and extinction could occur at any instant in the anagenetic simulations. The instantaneous probabilities were calculated by assuming that the sum of instantaneous probabilities accumulated during a time interval were equal to the probabilities of speciation and extinction used for the cladogenetic simulations. This procedure assured that rates of cladogenesis were comparable in both anagenetic and cladogenetic models. That is, let the probability of a speciation (or extinction) event during a small time interval \( dt \) be \( p \, dt \), and \( P \) be the probability of speciation during the time interval from \( t_1 \) to \( t_2 \), then \( p = P/(t_2 - t_1) \).

Prior to running a simulation, speciation and extinction probabilities were chosen. Speciation probabilities were either unbiased, greater for species larger than the modal size (large-biased), or greater for species smaller than the modal size (small-biased). Likewise, extinction probabilities were either unbiased, large-biased, or small-biased. We ran each simulation until the evolving clade had accumulated 350 species. Then, descriptive statistics for the distribution of body sizes within the clade were calculated. Simulations for each of the nine combinations of speciation and extinction probabilities were run 500 times for both the fixed jump and random jump versions of the cladogenetic model, and for the anagenetic model. This provided a sample of 500 log body mass distributions for each combination of speciation and extinction probabilities for the three different models.

Results.—Of particular interest to the present discussion is the shape of the distributions obtained from the simulations. Gould's assumption is that the evolution of
body size occurs by both the random addition of species that differ somewhat from the parent species and by the random removal of species. What are the consequences of such random species sorting? Results from the simulated clades indicated that random sorting produced relatively symmetric log body mass distributions, on the average, for the fixed jump (Fig. 5) and random jump (Fig. 6) cladogenetic models, and for the anagenetic model (Fig. 7). Thus, any random multiplicative changes owing to speciation and extinction of large and small forms with equal probability will result in approximately lognormal frequency distributions (May, 1975), not in the highly skewed distributions observed empirically. Hence, the answer to question (1) is that a random increase in variance during diversification of a lineage cannot consistently produce a significant skew in a log body mass distribution.

When biases in speciation and extinction probabilities were introduced into the simulations, however, asymmetric distributions of log body sizes were obtained for some sets of conditions. For the partially anagenetic model, if speciation probability was greater for smaller species, or extinction probability was greater for larger species, this produced a positively skewed log body mass distribution. These effects of biases in speciation and extinction probabilities on the shape of the distribution were additive (Fig. 7). The results for both of the cladogenetic models were different. Although biasing speciation probabilities had the same effect in the fixed jump cladogenetic model as it did in the anagenetic model, biasing extinction rates had virtually no effect on the shape of the log body mass distribution (Fig. 5). In the random jump model, biasing extinction rates had effects similar to that

Fig. 5. Average skewness of 500 body mass distributions generated from a model of purely cladogenetic evolution of body size, where increases or decreases in body size at a speciation event are fixed. Note that the effect of biasing extinction rates for different sized species is relatively insignificant.

Fig. 6. Average skewness of 500 body mass distributions generated from a model of purely cladogenetic evolution of body size, where increases and decreases in body size at speciation events are randomly drawn from a normal distribution with a mean equal to the fixed increase or decrease in the cladogenetic model with nonrandom increases and decreases. Note that the effect of biasing speciation rates for different sized species is relatively insignificant.

Fig. 7. Average skewness of 500 body mass distributions generated from a model of body mass evolution that includes both anagenetic and cladogenetic evolution. Notice that the effects of biasing speciation and extinction for different sized species are not interactive, but additive.
in the anagenetic model, but the effects of biasing speciation rates were only partially evident (Fig. 6).

The difference between the results for the anagenetic and fixed-jump cladogenetic model was due to the discrete nature of body size variation in the cladogenetic model. Since species were increased or decreased at speciation by a constant ratio in the cladogenetic model, and then not allowed to change subsequently, there were only a relatively small number of body sizes that a species could have. Species tended to build up in these discrete body mass classes, so that when there were many species in the clade, deleting a proportion of species through extinction did not substantially alter the shape of the log body mass distribution since it did little to change the number of species in each of the discrete body mass classes. This could not happen in the anagenetic model because species were constantly changing in size. A bias in extinction rate tended to consistently remove species with distinct values from the distribution, and hence influenced the statistics that characterized the shape of the distribution. In the random-jump cladogenetic model, species did not attain only a limited number of discrete values, and therefore, extinction effects were similar to those in the anagenetic model. However, because the size of the increase or decrease in body size at speciation was random, the ability of biased speciation rates to effect changes in log body mass distributions was reduced. These results indicate to us that strictly cladogenetic evolution cannot act as an effect agent of directional sorting of species through biased speciation and extinction rates.

The results from these simulations have important implications for the evolution of body size within clades. In answer to question (2), a purely cladogenetic process cannot readily give rise to a highly right-skewed log body mass distribution through biases in the likelihood of extinction of species of a given size. In the purely cladogenetic models, the only conditions that gave substantially positive skewed distributions were small-biased speciation probabilities in the fixed-jumps case and large-biased extinction probabilities in the random-jumps case. Neither of these conditions produced as large a degree of positive skew as the anagenetic model. Likewise, neither cladogenetic model showed the additive effect of small-biased speciation and large-biased extinction that resulted in the strong positive skew in the anagenetic simulations.

Thus, Gould's (1988) verbal model of the simple increase in variance that occurs as a result of speciation and extinction processes during the proliferation of a clade from an ancestral species is not by itself sufficient to generate the highly positive skew in log body mass distributions observed empirically in continental faunas. Under certain conditions, small-biased speciation rates or large-biased extinction rates will result in moderate degrees of positive skew. However, only when significant anagenetic change occurs simultaneously with cladogenesis do appropriate biases in the probabilities of speciation and extinction act in an additive manner to produce highly positively skewed distribution similar to those observed in log body size distributions of continental bird and mammal faunas.

We should note that our simulations are relatively simple in the assumptions that they make about how anagenesis and cladogenesis work. Stanley's (1973) more sophisticated model of body size evolution incorporates many insights regarding the ecological and physiological significance of body size that would greatly complicate the simple models we examined in this section. However, our purpose was not to present complete models of body size evolution. Rather, we set about to examine Gould's (1988) claim that the increase in variance that accompanies random speciation and extinction is sufficient to explain patterns in the evolution of body size. Our simulations exclude Gould's (1988) simple model as a likely explanation for the patterns exhibited in body size distributions of organisms, and suggest that further progress in understanding body size evolution must incorporate the kinds of biologically detailed explanations that Stanley's (1973) insightful paper considered.

**Discussion**

The bird and mammal faunas of large continents exhibit body mass distributions among species that even on a log scale are
strongly skewed towards larger body sizes. Our simulations showed that such skewness is more likely to result from a diversification process that includes both biased speciation and extinction rates (cladogenesis) and directional change in body size within species (anagenesis) than from a process that incorporates only cladogenesis. Thus, cladogenesis is probably a necessary, but not a sufficient condition for the evolution of log body size distributions that are right-skewed. Anagenetic, microevolutionary change also appears to be necessary to explain the diversification of body mass among species in an evolving clade. Without size-biased speciation and extinction probabilities, and probably anagenetic changes as well, the increase in variance that inevitably accompanies diversification of a clade cannot account for the highly right-skewed distributions of the logarithms of body mass that are observed empirically. Contrary to Gould’s (1988) assertion, more than random cladogenetic events are required to account for evolutionary trends such as Cope’s rule.

The Ecology of Speciation and Extinction

The missing ingredient in many explanations of macroevolutionary patterns is the ecological mechanisms that are responsible for the macroevolutionary processes of speciation and extinction. Stanley’s (1973) original model for the diversification of body sizes had a distinct ecological emphasis. Stanley pointed out that each species may have an optimum body size for its niche, and that natural selection operating through the differential survival and reproduction may move the population towards that optimum. The diversification of body sizes then requires the additional ingredient of cladogenesis, allowing new species to occupy different niches, so that natural selection can again operate to adjust body size towards new optima. Stanley (1973) suggests specific mechanisms that can produce the differences in speciation and extinction rates between large- and small-bodied species as assumed by some of our simulations.

Both extinction and speciation are to a large extent ecological processes. Extinction is the consequence of sustained, negative population growth (Maurer, 1989). Although such negative population growth may occur relatively rapidly, in response to some catastrophic event, or more slowly due to a gradually deteriorating environment, extinction represents a consistent statistical trend of ecological failures of individual organisms sharing a similar genetic makeup.

Speciation must also have a significant ecological component. In many allopatric models of speciation, isolated populations of organisms diverge from parental populations through microevolutionary processes of selection and/or genetic drift. The environments that select for different genotypes and the barriers that isolate such populations are in nearly every conceivable case the result of ecological limiting factors. Furthermore, for a product of speciation to survive and be recognized as a distinct, new species, it must be capable of establishing a self-perpetuating population based on the ecological relationships inherent in its newly emerging gene pool. In other words, it must establish a new, viable ecological niche. Here again, a regular statistical trend of ecological success will determine whether the incipient species takes hold, or goes extinct without issue. In addition to the genetic processes that result in phenotypic divergence and reproductive isolation, speciation involves ecological processes that determine the abundance and distribution of populations.

Microevolution and the Diversification of Body Size

Because ecological processes are as important to body size diversification as are the consequences of gene pool isolation, microevolutionary processes must continually shape the evolution of body size. Clearly, both sexual dimorphism and intraspecific geographic variation in body size are the result of microevolutionary processes. Although we do not want to review the extensive literature on sexual dimorphism, we point out that differences in size between the sexes of the same species can often be as large as the differences between members of the same sex in closely related species (e.g., Dyan et al., 1989).

Two patterns in the geographic variation of body size are important to consider. First, clinal trends in body size along geographical
and ecological gradients, such as the positive correlation between latitude and body size known as Bergmann's rule, have been documented in a number of groups of organisms. Although a generally accepted explanation of this pattern remains elusive, the pattern is widespread in both ectotherms and endotherms (e.g., Ray, 1960; Lindsey, 1966; James, 1970; McNab, 1971). Furthermore, Johnston and Selander (1971) showed that such a cline developed in house sparrows (*Passer domesticus*) during the approximately 100 years since they colonized North America. Second, closely related, ecologically similar species often evolve body size differences when found together. Such body size differences can often be attributed to the selective advantage for divergence to reduce the intensity of interspecific competition (Brown and Wilson, 1956; Rosenzweig, 1966; Schoener, 1970; Roughgarden et al., 1983; Grant, 1986; Dyan et al., 1989).

Perhaps the strongest evidence for the importance of microevolutionary processes in shaping body size evolution comes from the extensive literature on body sizes of insular populations. One of the clearest patterns is seen in terrestrial mammals. There is a highly significant tendency for insular races of small species to be larger than their mainland relatives and for insular races of large species to be smaller than their nearest mainland relatives (e.g., Foster, 1964; Lawlor, 1982; Lomolino, 1985). The divergence of insular populations can occur rapidly (Lister, 1989) and can result in orders of magnitude differences in body mass (Roth, 1990). Lomolino (1985) quantified the relationship between island and mainland body sizes and explained the pattern in terms of ecological advantages of the different body masses on islands.

**Coupling of Micro- and Macroevolution**

Using the log-log regression of island body size on mainland body size given by Lomolino (1985), we calculated that 250 g is approximately the body mass at which island forms tend not to diverge from their mainland relative. Thus, at this size, there appears to be no ecological advantage to evolving towards either larger or smaller size. In the absence of coexisting species, 250 g appears to be roughly the optimal body mass for a terrestrial mammal. This optimum is determined by the interaction between the terrestrial environment and basic constraints on mammalian morphology, physiology, and behavior. We suggest that it is not coincidental that this body mass is similar to the median body mass for mammalian taxa (species or genera) on many continents (Table 2; see also Rusler, 1987).

Elsewhere, we have argued that macroevolutionary processes, especially the differential susceptibility of large species to extinction, have played a major role in shaping the body size distributions of mammals and birds on continents (Brown and Maurer, 1986, 1987, 1989). One consequence of these extinctions is the regular increase in the proportion of very large mammals in the fauna with increasing area of the land mass (Fig. 2; see also Rusler, 1987). The microevolutionary processes of differential success of individuals that have caused divergence of insular populations of mammals from their mainland relatives appear to reflect the same optimum as the macroevolutionary processes of differential speciation and extinction that have played a major role in the radiation of mammalian lineages on continents. At least in the evolution of body size on islands and continents, microevolution is not decoupled from macroevolution. Both seem to reflect the common influence of environmental conditions and ecological interactions.

No matter what combination of microevolutionary and macroevolutionary processes influences the evolution of body size, we contend that an understanding of them will be incomplete without supplementary ecological explanations for the form of the resulting frequency distributions (see also McKinney, 1990). Any complete explanation for the skewness of log body mass distributions must account for why speciation, migration, extinction, and microevolutionary processes should be biased to favor certain sizes over others. In addition, such explanations should also be able to illuminate why the range of sizes ultimately attained during the radiation of a lineage varies systematically with continent size or with the size of sample area within a continent (Rusler, 1987; Brown and Maurer, 1989; Brown
and Nicoletto, 1991). We suggest that an understanding of these evolutionary phenomena will ultimately require a knowledge of the relationship between directional micro- and macroevolutionary change, the constraints of phylogeny on the morphological, physiological, and behavioral traits that limit the direction and rate of evolutionary change, and the ecological limits and opportunities that cause differential survival of both individuals within populations and species within phylogenetic lineages.

CONCLUSIONS

Body size evolution is a consequence of the interplay between changes within species due to natural selection and differences in the rates of speciation and extinction of large and small species. Differences in the rates of speciation and extinction, in turn, depend on ecological relationships that determine barriers to gene flow, success of newly differentiated species, and the stability of populations. None of this is inconsistent with most of the views expressed by Eldredge and Gould (1972), Stanley (1973, 1975, 1979; Stanley and Yang, 1987), and other macroevolutionists. We suggest, however, that Gould's (1980, 1988, 1989; see also Raup et al., 1973; Raup and Gould, 1974; Gould et al., 1977) emphasis on randomness be replaced with an emphasis on deterministic outcomes that result largely from the role of ecological processes in speciation and extinction. Our results have specific application to the evolution of body size, but there is no reason to suppose that the evolution of other characteristics should be approached differently.

Macroevolution, in our view, is not a distinct set of processes that have nothing to do with microevolution and the ecological conditions that influence its course within populations. If there is any decoupling between macro- and microevolutionary processes, it is only partial (Maurer, 1989). Clearly, not every microevolutionary change results in a macroevolutionary change, so one cannot simply extrapolate from microevolutionary processes to macroevolutionary patterns (Hoffman, 1989). On the other hand, macroevolutionary changes (i.e., speciation or extinction) are driven by microevolutionary and ecological processes.

Hence, an understanding of the relevant microevolutionary processes is necessary, though not sufficient, to explain macroevolutionary change.

ACKNOWLEDGMENTS

We thank the numerous individuals who have discussed aspects of these ideas with us at various times and in diverse places. S. M. Stanley and two anonymous reviewers provided excellent reviews of previous versions of this paper. Our research has been supported by NSF BSR 88-07792 (J.H.B) and EPA R81-8358-010 (B.A.M.).

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Note: Statistics are for genera unless otherwise noted.
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Corresponding Editor: R. Holt