

DISCONTINUITIES IN BODY-SIZE DISTRIBUTIONS

A View from the Top

Pablo A. Marquet, Sebastian Abades, Juan E. Keymer,
and Horacio Zeballos

BODY-SIZE DISTRIBUTIONS have become a major focus of research in ecology because they seemingly reflect the operation of fundamental principles underlying the otherwise idiosyncratic nature of ecological systems (e.g., Hutchinson and MacArthur 1959; May 1986). They have been analyzed at different scales of space and time, from local communities (e.g., Brown and Nicoletto 1991) to continents and the biosphere (Blackburn and Gaston 1994a, 1994b), and from millions of years in the past (Jablonski 1996). At the landscape scale, it has been hypothesized that they reflect the existence of fundamental discontinuities in the temporal and spatial distribution of resources within ecosystems (i.e., the Textural Discontinuity Hypothesis, Holling 1992) that provide windows for persistence and invasiveness of species along the size spectra (Holling 1992; Lambert and Holling 1998; Allen, Forsys, and Holling 1999; Allen and Saunders 2006).

It is not clear how the Textural Discontinuity Hypothesis, notwithstanding its theoretical appeal and empirical support, can be connected and reconciled with large-scale patterns and their explanations. As we outline in this chapter, there are several complications to performing such as synthesis across scales. Our aim is not to propose a solution to this problem, for that goal is still beyond our reach, but to present a framework to put the problem in perspective. To do this, we focus on some of the explanations put forward to understand discontinuities and aggregations in body-size distributions at continental scales.

It is customary to start a paper on body size by citing the work of Peters (1983), Calder (1996), and Schmidt-Nielsen (1984) while making the point that an organism's size and statistical distribution are of paramount importance to understanding ecological as well as evolutionary patterns and dynamics across scales in time, space, and levels of organization. However, as we aim to underscore in this

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chapter, body size is in a fundamental way a double-edged sword, a blessing and at the same time a curse, a sunny day and a storm.

It is safe to say that a biological system's size affects most processes that take place within it and in interactions among its biotic and abiotic elements, which is accomplished by regulating fluxes of energy and materials (e.g., Brown et al. 2004; West and Brown 2005; Marquet et al. 2005). However, this relationship does not go only one way, for the size of a system is also affected by the internal and external process it regulates, in a dance of mutual codetermination or circular causality (Hutchinson 1948; Maturana and Varela 1987; Marquet et al. 2004, 2005). The logic behind this statement is rooted in the emergent character of size. By *emergent*, we signify that the size of any biological system cannot be explained or predicted by observation of its component units (Salt 1979), but rather emerges in full complexity, novelty, and surprise as the result of the operation of many entangled processes, including how components interact among themselves and with the external environment. For the sake of generality, we can group these processes in three major categories: (1) external processes and states, related to the biotic and abiotic environment wherein the target biological entity unfolds (we use the word *biological entity* to designate any biological self-replicating system that possesses well-defined boundaries, from a subcellular organelle up to the biosphere); (2) internal processes and states, or those processes built into the entity and necessary in order to maintain its structure, function, and fitness; and (3) historical processes that describe the trajectory of the two-way interaction between the biological entity and its environment through time (the history of the interaction between internal and external processes and states). These three kinds of processes define the phase space wherein the system drifts (see fig. 4.1) or, more precisely, where we as observers make it understandable (i.e., so that the processes define an explanatory domain). In principle, any attribute of a biological entity (such as the number of components it possesses or the number species in the context of an ecosystem) can be understood, at least in principle, using any of these three major axes as a departure point (Marquet et al. 2004) and will occupy a position in this explanatory domain, which reflects the relative contribution of each of these axes to the pattern or attribute under investigation.

To see how these three axes interact in explaining patterns in body-size distributions at continental scales, we focus on the distribution of body size of mammalian species in the Americas. In figure 4.2, we show the shape of this distribution for 1,314 species of North American and South American terrestrial mammals based on data updated from Marquet and Cofré (1999) and from Smith and colleagues (2003). Interestingly, both distributions show coincident aggregations or modes for small and large sizes, but differ in a third intermediate mode apparent only in South American mammals. In the following paragraphs, we try to explain these aggregations using the three axes shown in figure 4.1.

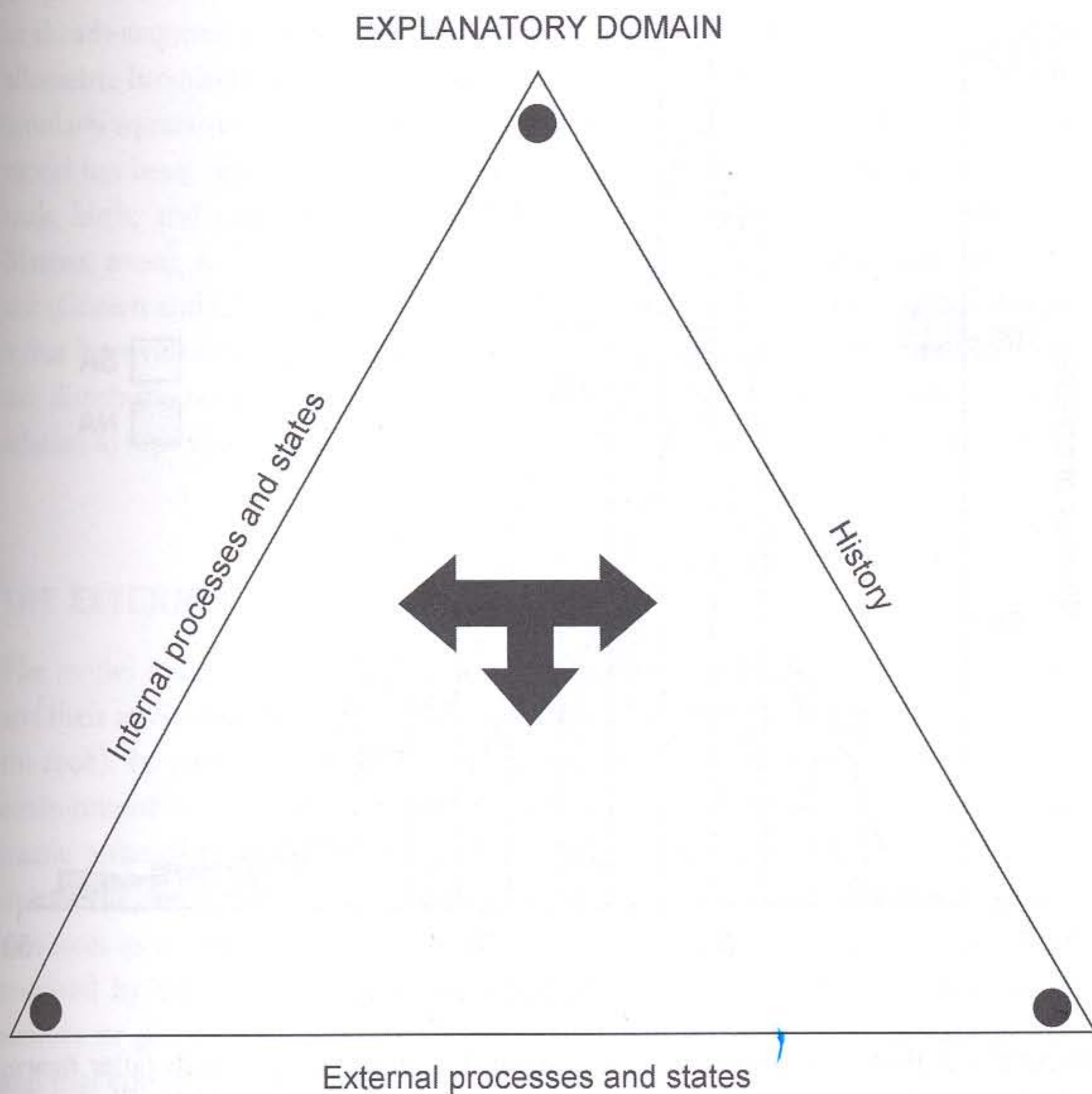


FIGURE 4.1 Explanatory domain for ecological patterns in nature. Details are provided in the text.

THE INTERNAL APPROACH

As shown in figure 4.1, the internal axes of the explanatory domain emphasizes explanations rooted in processes inherent to the organisms, which are essential to maintain their structure, function, and fitness. In this context, the explanation proposed by Brown, Marquet, and Taper (1993) provides a paradigmatic example.

Brown, Marquet, and Taper (1993) propose a model to account for the ubiquitous mode in body-size distributions of species within high-order taxa, such as mammals, birds, and reptiles. They reason that this mode reflects the evolutionary advantage of organisms of certain size given by the conflicting demands that size imposes on the rate of resource acquisition and allocation, both of which vary with size. This model has been criticized in terms of internal dimensional consistency and in terms of biological realism (e.g., Kozłowski 1996; Perrin 1998).

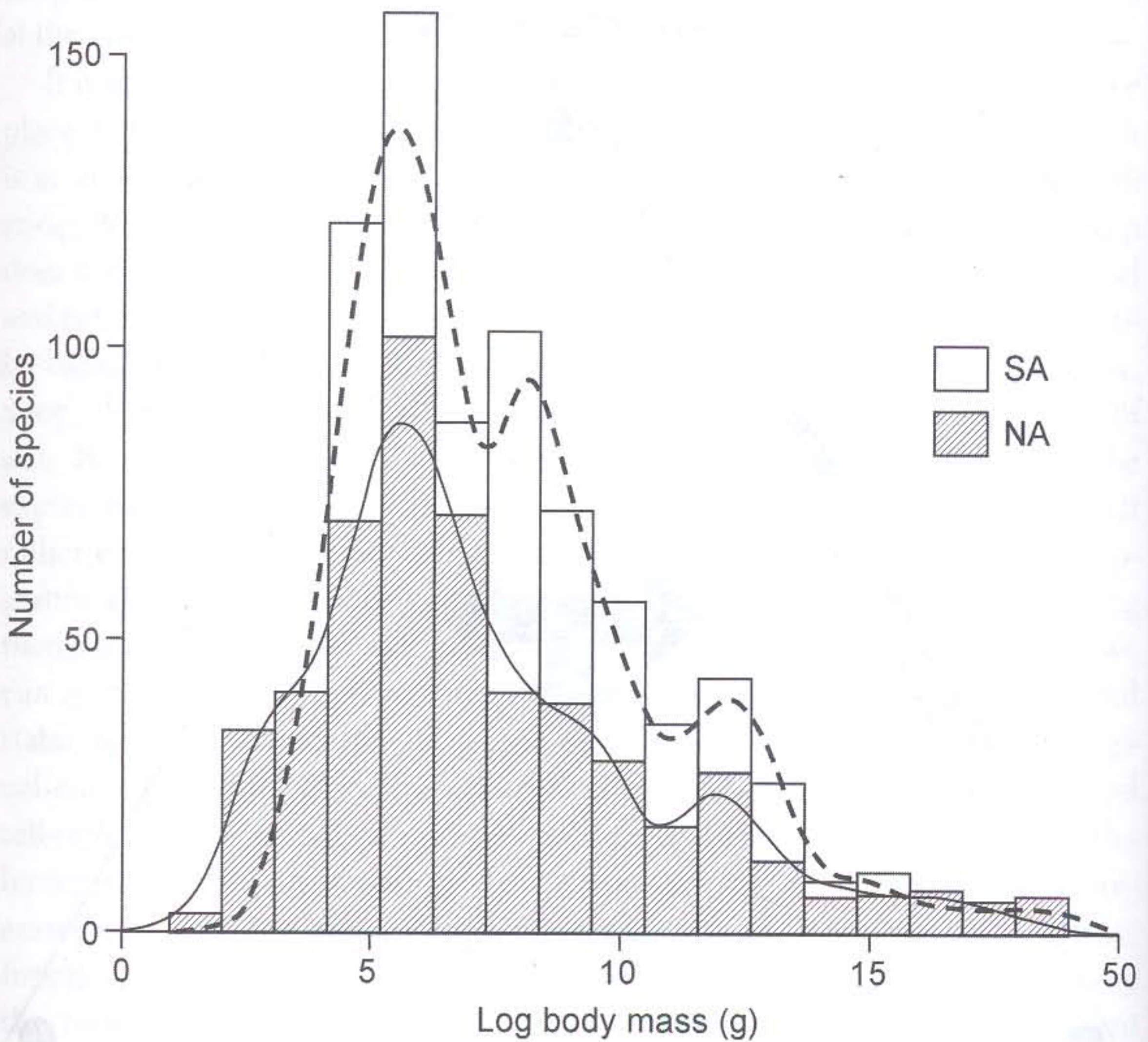


FIGURE 4.2 Body-size distributions for North American (a) mammals (after Brown, Marquet, and Taper 1993); (b) birds (after Maurer 1998a, 1998b); and (c) mollusks (after Roy, Jablonski, and Martien 2000). The functions correspond to the predicted distribution according to the model proposed by Brown, Marquet, and Taper (1993).

To solve these issues, we use the definitions given by Brown, Taper, and Marquet (1996) and follow the suggestions made by Perrin (1998). We sidestep the issue of biological realism and do not attempt to fit the model to real data, but rely on its qualitative behavior. The model is:

$$R + I_0 \xrightarrow{K_0} I_1 \xrightarrow{K_1} I_0 + w \quad (1)$$

$$\frac{dw}{dt} = \frac{c_0 M^{b_0} c_1 M^{b_1}}{c_0 M^{b_0} + c_1 M^{b_1}}, \quad (2)$$

where I_0 and I_1 are dimensionless quantities that refer to the proportion of time an individual spends in states 0 and 1 respectively. K_0 and K_1 refer to the rates of energy (resource) acquisition and transformation in units of $J s^{-1}/J$ or s^{-1} . Thus, they

are pure rates of transformation of energy either available in the environment (K_0) or already acquired and available within the organism (K_1), and are assumed to be allometric functions of body size (M) expressed as $c_0 M^{b_0}$ and $c_1 M^{b_1}$, respectively. Similarly equation 2 is also a rate and has the same units ($J s^{-1}/J$) as K_1 and K_0 . The model has been applied to understand body-size distributions observed in mammals, birds, and mollusks (fig. 4.3) (Maurer 1998a, 1998b; Roy, Jablonski, and Martien 2000). Although the model's parameterization is complex and problematic (Chown and Gaston 1997; Perrin 1998; Bokma 2001), its fundamental insight is that it provides an explanation for the existence of a mode in mammalian body-size distributions based on first principles of energy acquisition and allocation in relation to reproduction (Brown, Marquet, and Taper 1993; Maurer 2003).

THE EXTERNAL APPROACH

The model makes several assumptions regarding the life history of organisms and their environment (Brown, Marquet, and Taper 1993; Kozłowski 1996; Perrin 1998). In particular, it assumes that energy or resource availability in the environment is not limited. However, ecological realism and basic thermodynamic principles inform us otherwise (e.g., Lindeman 1942). If resources are indeed limiting, then they become explicit in the equations. We can model resources as a dimensionless quantity (i.e., as a proportion of the total amount required by organisms); thus, R should vary between 0 and 1 (either no resources or plenty of resources, respectively). Under these considerations, we find that equation 2 becomes

$$\frac{dw}{dt} = \frac{Rc_0M^{b_0}c_1M^{b_1}}{Rc_0M^{b_0} + c_1M^{b_1}} \quad (3)$$

In equation 3, it is apparent that acquisition of resources becomes a limiting process if R is less than 1; otherwise, equation 2 applies. This equation gives rise to a family of distributions, depending on the availability of resources in different environments and is shown graphically in figure 4.4. Interestingly, as resources become more limiting, the mode in body size moves toward larger sizes, thus suggesting that aggregations might emerge as a result of resource limitation (we call this the Resource Limitation Hypothesis). The reason for this result is associated with the fact that energy requirements increase with body size at a decreasing rate, and although large animals require more energy in absolute terms, they require less per unit gram, thus becoming more efficient in energy utilization (Geoffrey West, personal communication, July 2005). Thus, under resource limitation, it pays to be more efficient. In this context, if resource limitation has driven evolution toward large body size, then aggregations in body-size distributions

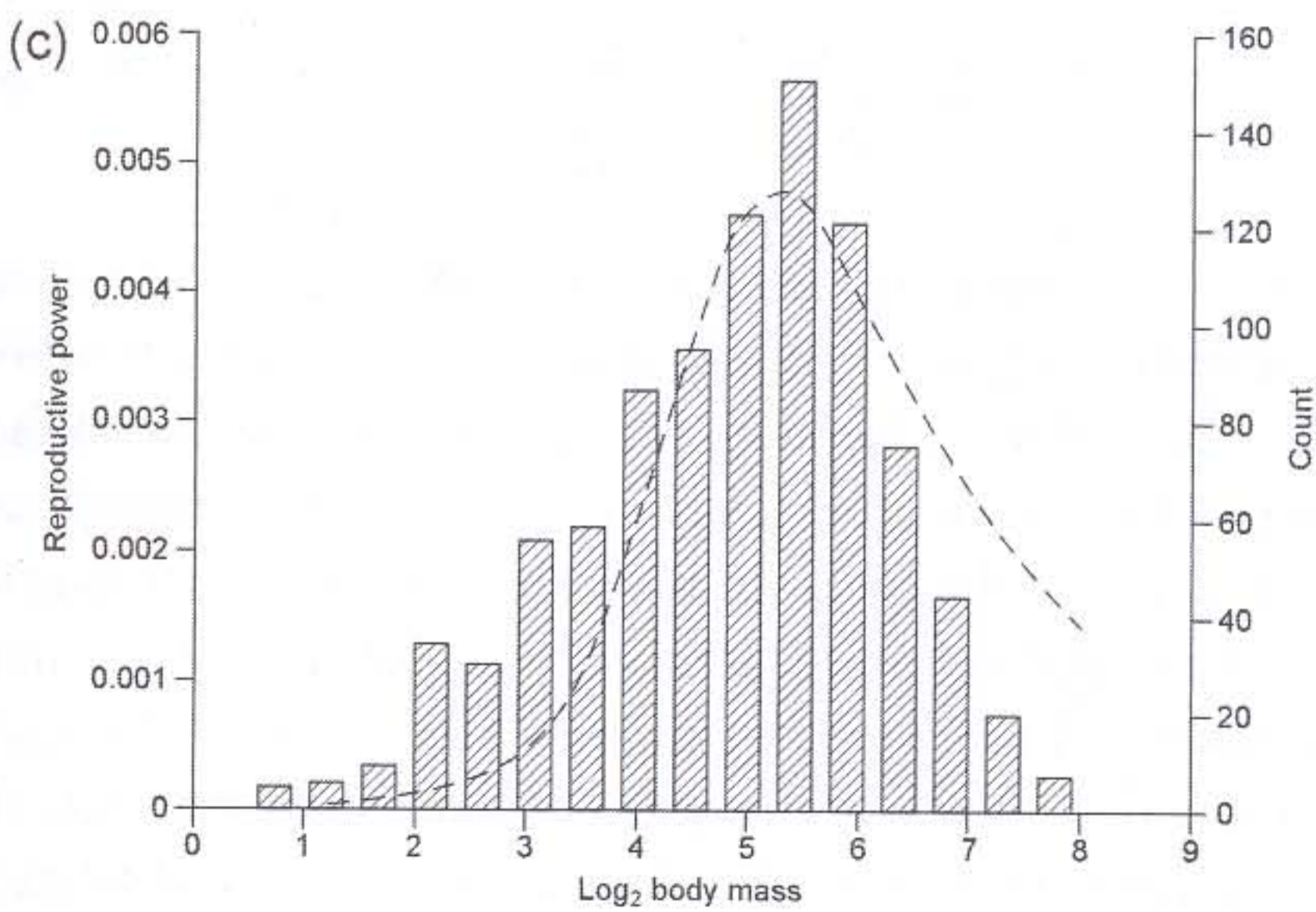
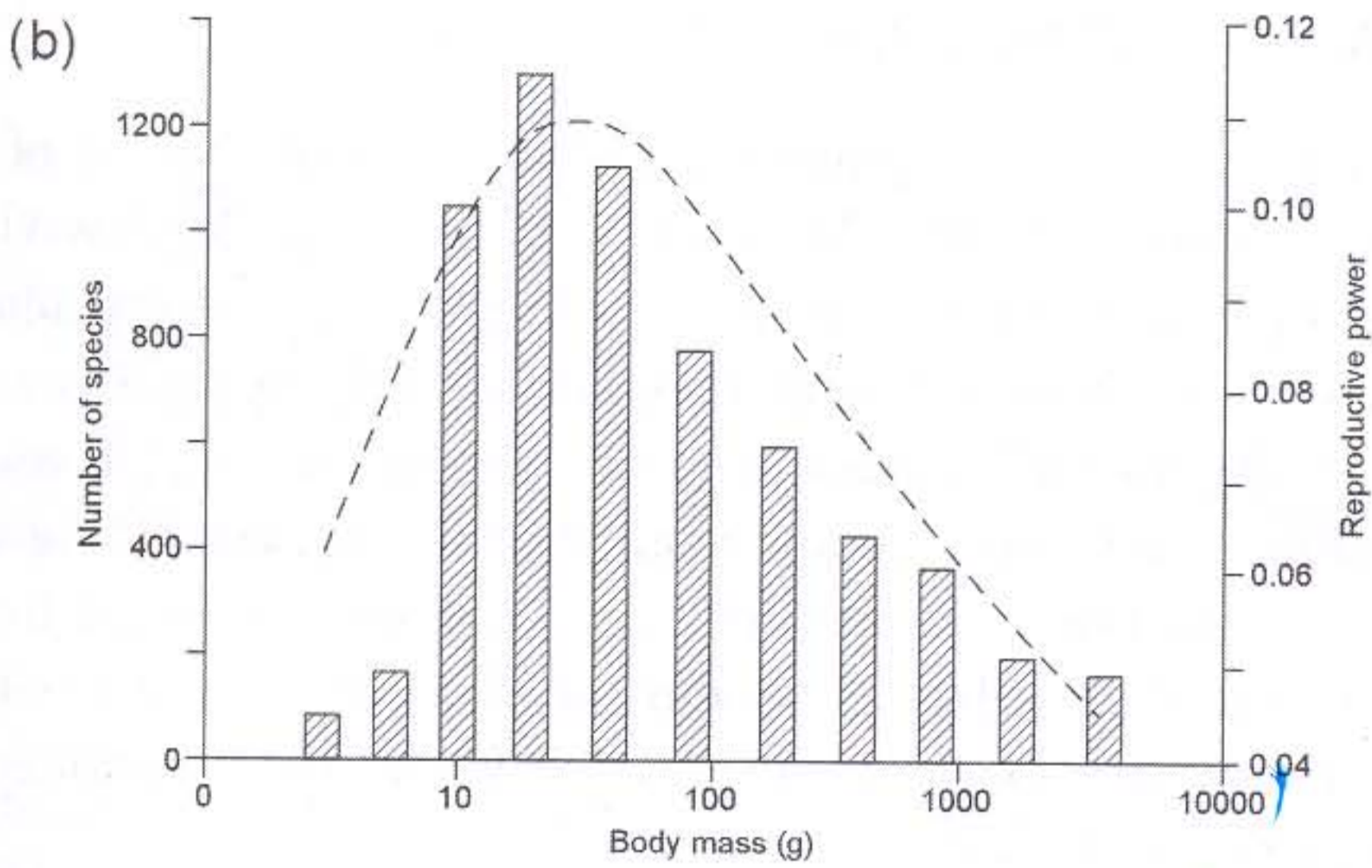
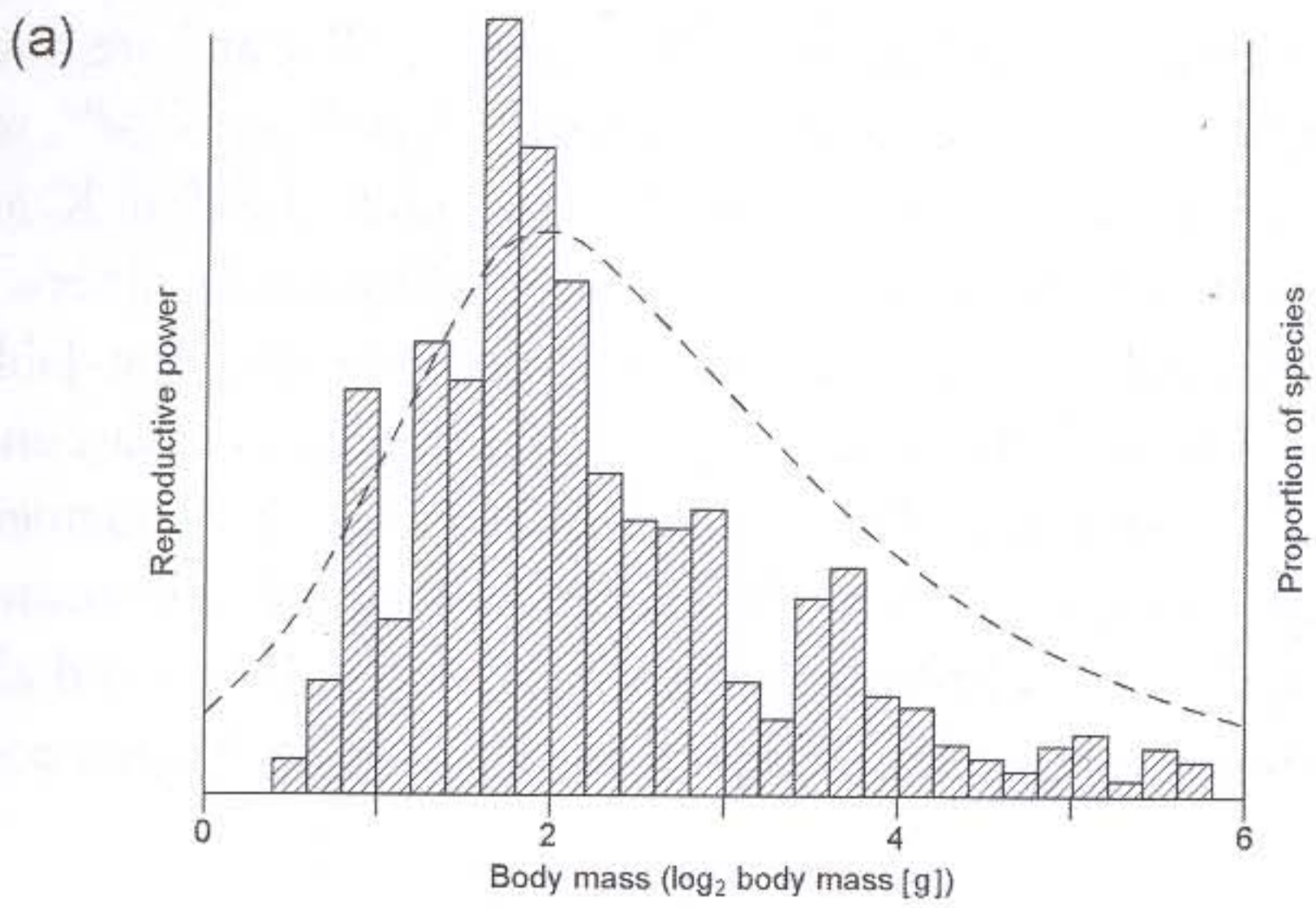


FIGURE 4.3 Body-size distributions for North American (a) mammals (after Brown, Marquet, and Taper 1993); (b) birds (after Maurer 1998a, 1998b); and (c) mollusks (after Roy, Jablonski, and Martien 2000). The functions correspond to the predicted distribution according to the model proposed by Brown, Marquet, and Taper (1993).

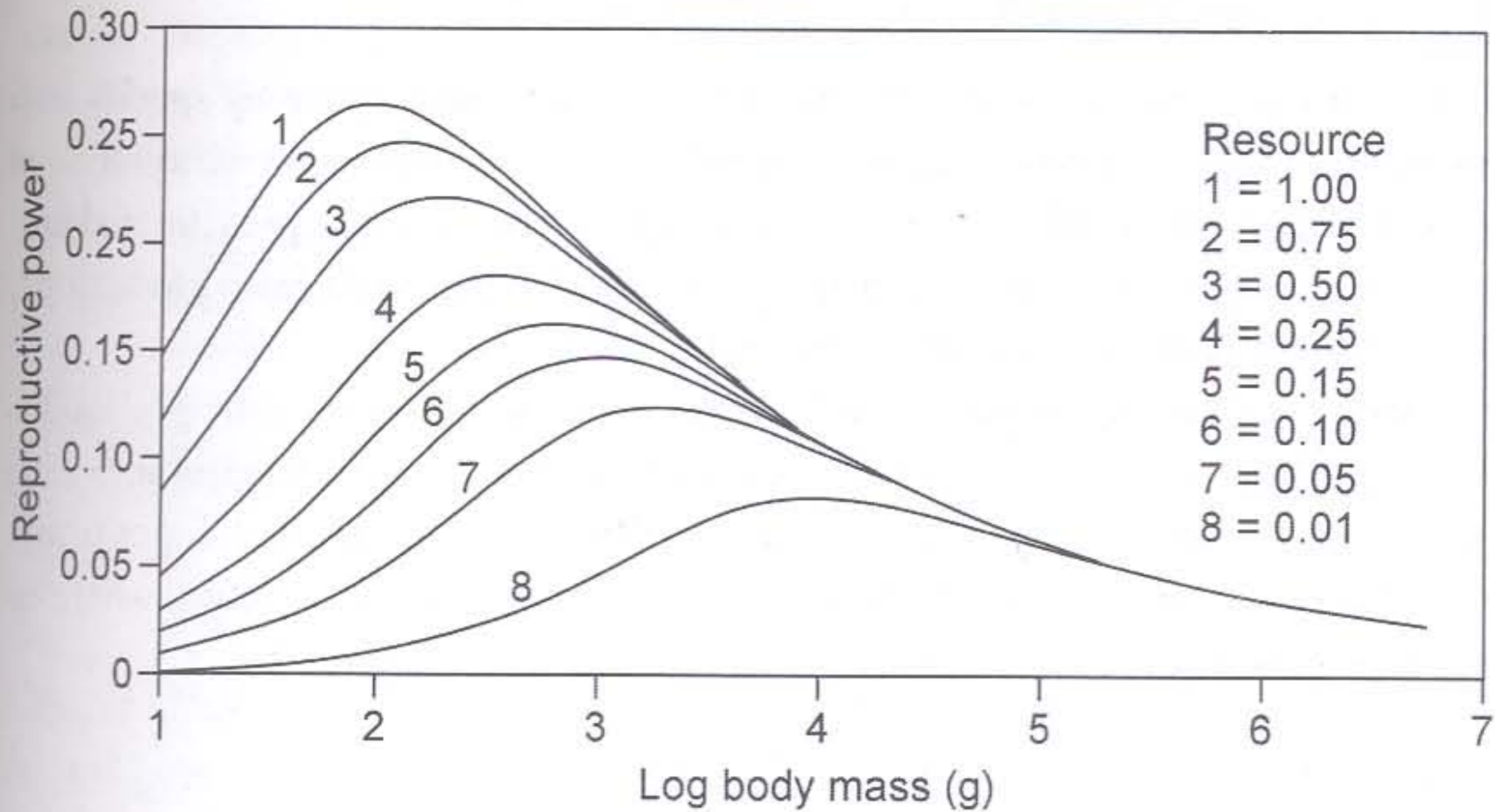


FIGURE 4.4 Predictions of the Brown, Marquet, and Taper (1993) model under different scenarios of resource limitation.

likely reflect different strategies to deal with resource shortages. Because high-quality resources tend to be rare in the environment relative to low-quality ones (Demment and Van Soest 1985), resources tend to be of lower quality as they become limiting, which for an herbivore means a higher concentration of fiber. Further, as discussed by Demment and Van Soest (1985), when body size increases, animals expand their diets to include low-quality food. In evolutionary time, this process has been accomplished by the emergence of some key innovations to deal with low-quality food, such as the emergence of gut structures that tend to delay the passage of fibrous food (e.g., rumen). Thus, the third mode observed in figure 4.2 might result as a consequence of this process. An alternative hypothesis for this aggregation in body size is based on what we call the Mode Hitchhiking Hypothesis. According to this hypothesis, it is expected that one mode can affect the emergence of other modes (i.e., through a mode-mode interaction). The most obvious case is probably represented by predator-prey interactions. In particular, the existence of empirical regularities in the relationship between prey and predator body size in ecological communities (e.g., Vézina 1985; Carbone et al. 1999; Carbone and Gittleman 2002; Cohen, Jonsson, and Carpenter 2003; Sinclair, Mduma, and Brashares 2003) may potentially emerge as aggregations in body-size distributions at large spatial scales. Thus, under this hypothesis, the existence of a large number of organisms in the 0.1 kg mode might drive the evolution of hypercarnivores of a size that will match this mode. To test for the plausibility of this hypothesis, we developed a simple model for predator- and prey-size evolution and its potential impact in body-size distributions.

THE HITCHHIKING HYPOTHESIS: A MODEL

We simulated the evolution of body mass for predator and prey species in a model that emphasized predators' dependency on the frequency distribution of available prey items. We started simulations with one hundred predator and prey species having body masses uniformly distributed in the range from 1 to 10,000 g. Body mass was always in logarithmic scale.

We let body-mass frequency distribution of prey evolve according to the following rules: extinction probability is minimal at 100 g and increases for values lower and higher than that, as suggested by Brown, Marquet, and Taper (1993). We chose to model this dependency by means of two linear regimes, where extinction probability for species weighing less than 100 g is given by

$$P_{<100\text{g}} = 1 - 0.5 * [\text{prey mass}],$$

whereas the extinction probability for species weighing more than 100 g is

$$P_{>100\text{g}} = -0.5 + 0.25 * [\text{prey mass}].$$

Parameter values were chosen in order to assign a probability of extinction of 1 to species tending to zero and $1 * 10^7$ grams, respectively. For every time iteration, we evaluated the extinction probability of each prey species according to the functions given here and compared the resulting value against a randomly chosen number taken from a uniform distribution $u = U(0,1)$. Whenever P was greater than or equal to u , the species in question went extinct.

We let body masses evolve by anagenesis for a random fraction of extant species, adding a random normally distributed number with mean 0 and standard deviation 0.1, as suggested by Bokma (2002). Similarly, in each time step, we allowed a random fraction of extant prey species to produce new species by cladogenesis. The rule was simply to assign a random uniform number $c = U(0,1)$ to every species and to compare it with a threshold value t (set to 0.8 in the present report). If the condition " c is greater than or equal to t " was satisfied, a new prey species was added to the extant pool. The body mass of the new species was taken from a normal distribution with mean equal to the parent species and standard deviation 0.1.

For predator species, extinction was determined by the frequency distribution of prey species. The range of prey available for a given predator was defined by the upper limit

$$ul = -1.379 + 1.819 * [\text{predator mass}],$$

whereas the lower limit was set by

$$ll = -2.618 + 2.359 * [\text{predator mass}].$$

Parameter values for these linear functions were estimated from published data on the range of prey consumed by predators (Vézina 1985; Sinclair, Mduma, and Brashares 2003). Note that ul and ll account for the fact that large species tend to prefer a broader spectrum of prey than smaller species do. Once the range of prey required by a given predator species was estimated, we scanned the frequency distribution of prey to check for the number of prey species available, A . If A equaled zero (no prey was available), the predator went extinct; otherwise, we asked for the maximum number of prey species required to sustain a predator. We modeled this latter condition as

$$M = 9.85 - 3.038 * [\text{predator mass}].$$

This function accounts for the fact that smaller predator species will require a more diverse diet than will larger ones. If M was greater than A , the predator went extinct. Anagenetic and cladogenetic changes were allowed for predators following the same rules stated for prey species.

To avoid the unbounded exponential accumulation of species, we set a limit to the maximum number of species in the system. When this limit was surpassed, we randomly removed species until the number of species fell below this level. However, to avoid distortions of the patterns generated by the evolutionary dynamics, we eliminated prey and predator species, preserving the existing ratio between them before the limit was exceeded. Similarly, we did not allow the maximum number of predators to surpass half the number of prey.

We let the system evolve for five hundred time iterations and recorded changes in the frequency distribution for both prey and predator species separately. To improve graphical display, we smoothed the frequency distributions by fitting them with a Gaussian kernel. As seen in figure 4.5, this mechanism can give rise to discontinuous, aggregated body-size distributions. Interestingly, the number of predators is the highest in the third mode (located at approximately 4 kg; see fig. 4.6). However, further research is needed to assess this hypothesis and to develop more realistic models that better include the complexity associated with predator-prey interactions.

THE HISTORICAL APPROACH

So far we have been able to provide explanations based on internal and external approaches. The internal approach has emphasized the inherent constraints on organisms due to the costs of acquisition and allocation of energy for reproduction. The external approach underscores the external environment's effects in

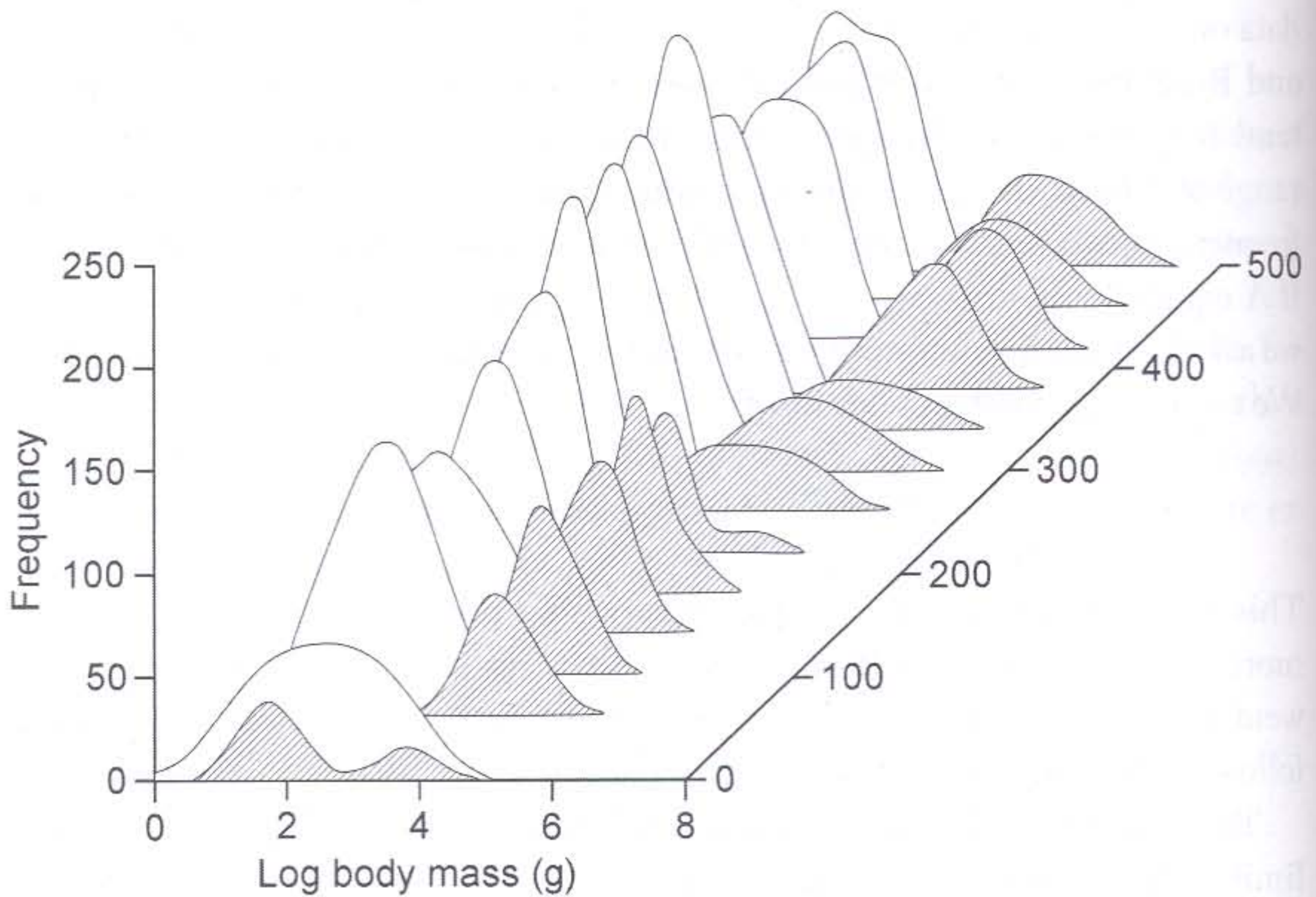


FIGURE 4.5 Simulation results illustrating the evolution of predator (hatched lines) and prey (white) body-size distributions under the Hitchhiking Hypothesis.

terms of controlling acquisition processes through resource availability. In this section, we introduce the historical approach and show that historical processes, too, may leave a mark on the body-size distribution of mammalian species in the Americas.

For South American mammals, one of the most important events that drastically changed the composition of the biota and the course of species evolution and subsequent interactions at local scales was the Great American Biotic Interchange. This event, which occurred around 2.5 million years ago, after the formation of the Isthmus of Panama, allowed the invasion of the South American continent by seventeen families of land mammals, most of which diversified and became well represented in local communities across the continent (e.g., Simpson 1980; Webb 1985, 1991; Vermeij 1991). Thus, this historical event not only altered the composition of the South American biota as a whole, but also had an enormous ecological impact in changing the pool of potential species available to assemble into local communities (Marquet and Cofré 1999). Marquet and Cofré (1999) show that for the body-size distribution of South American mammals (fig. 4.7), the first, or left-most, mode is composed primarily of species derived from North American ancestors, whereas the second mode is composed primarily of mammalian species derived from South American ancestors (mostly marsupials and Hystricognath rodents). This distinction

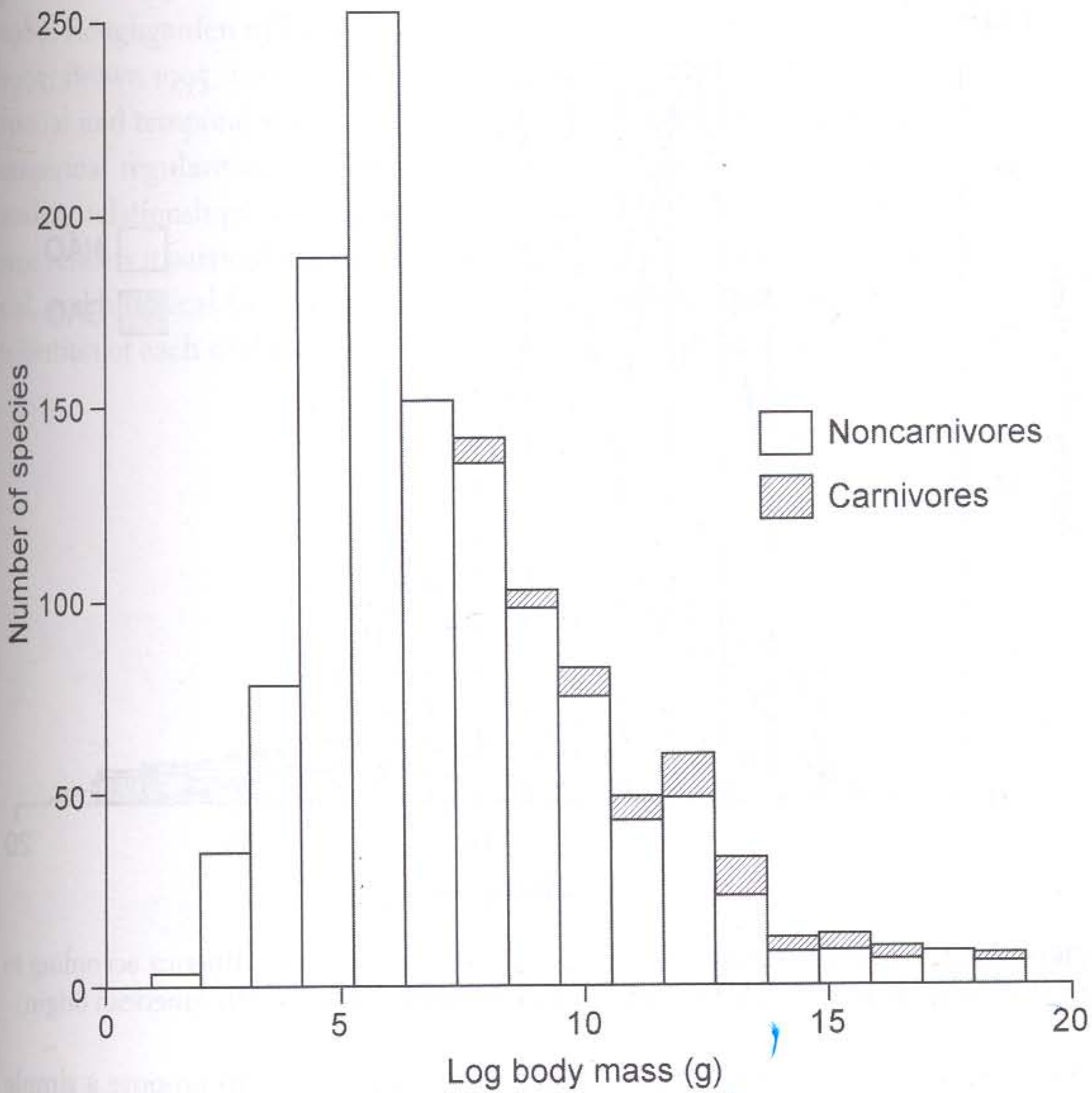


FIGURE 4.6 Body-size distribution of carnivore and noncarnivore mammal species in the Americas.

led Marquet and Cofré to propose that this bimodal distribution reflects a key event in the history of the development of the South American mammalian biota: the Great American Biotic Interchange. Marquet and Cofré hypothesize that the mode contributed by species of South American origin was also characteristic of the preinterchange continental distribution of body masses in South America and that mammals of North American origin succeeded in invading South America because of higher speciation rates (see also Lessa and Fariña 1996), which is particularly apparent in the extraordinary diversity that medium-size species (mostly rodents) of North American origin achieved in South America. This diversity might be linked to the evolutionary advantage associated with medium size (around 100g) in mammals (e.g., Brown, Marquet, and Taper 1993).

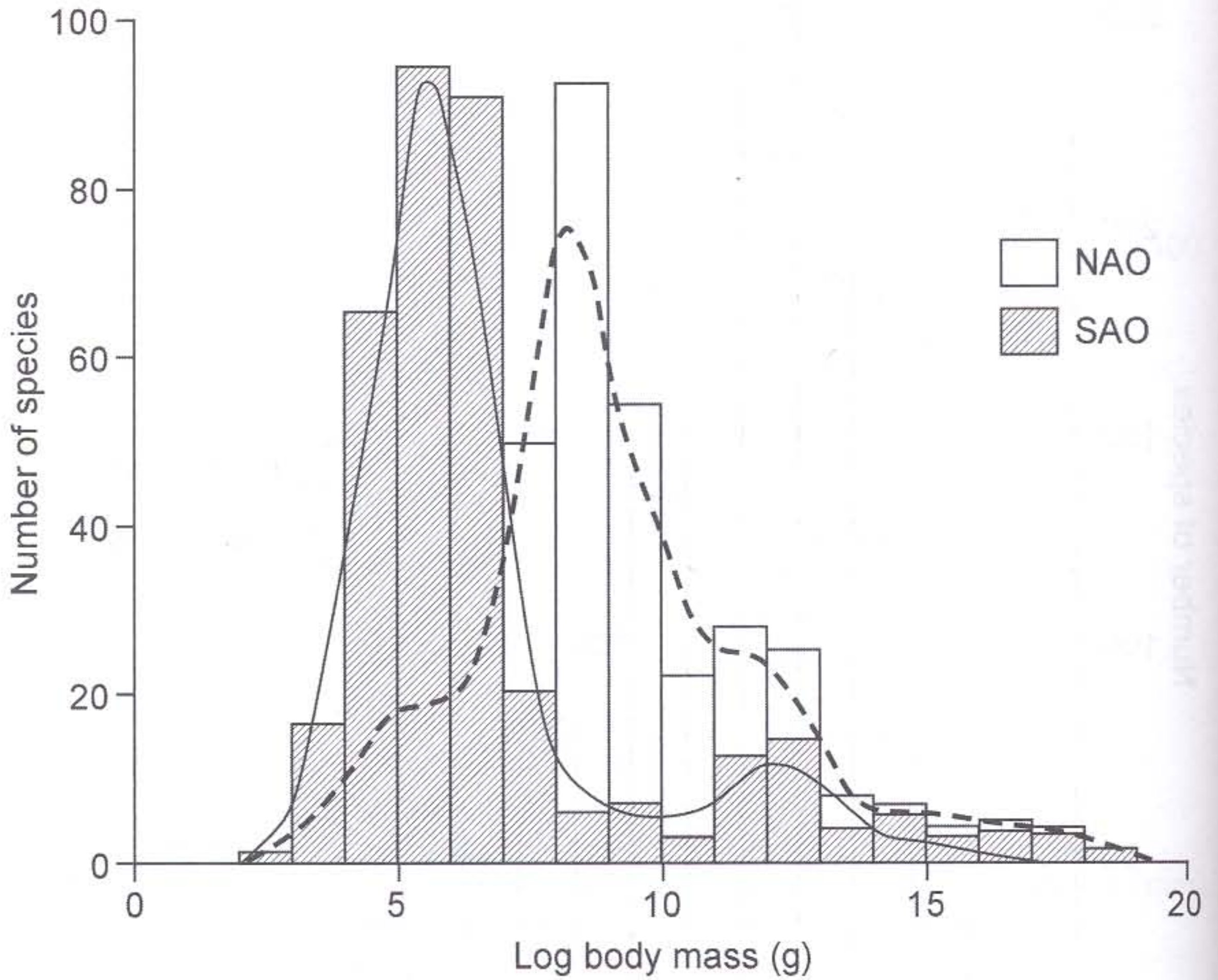


FIGURE 4.7 Body-size distribution of mammal species in South America according to their geographic origin (NAO = North American origin, SAO = South American origin).

As stated at the beginning of this chapter, our goal has been to propose a simple framework in order to put in perspective the problem of understanding discontinuous body-size distributions. As we outlined and demonstrated by analyzing the body-size distribution of mammalian species in the Americas, the main obstacle to achieving an explanation of discontinuities in body-mass distributions, at least at continental scales and for mammals, is that of multiple causality, a characteristic of ecological systems and a hallmark of their complexity (e.g., Huston 1994; Hilborn and Mangel 1997; Marquet, Keymer, and Cofré 2003; Belovski et al. 2004; Marquet et al. 2004, 2005). Ecological systems and the patterns we can discern within them reflect the history of interactions between internal and external processes and states (fig. 4.1). Consequently, they carry the signal of all these factors with different intensity and can be explained only by focusing on the explanatory domain delimited by these factors. This connection is likely more apparent when systems are analyzed at large spatial scales, such as those usually used by macroecologists (e.g., Brown 1995; Gaston and Blackburn 2000), where large-scale biogeographic patterns are thought to emerge as the result of the interactions among individual-level physiological characteristics, species' tolerances to biotic and abiotic conditions, and the large temporal- and spatial-scale

process of dispersal, extinction, and speciation (e.g., Brown and Maurer 1987, 1989; Roughgarden 1989; Brown and Nicoletto 1991; Brown, Marquet, and Taper 1993; Brown 1995, 1999). It is not serendipity that most of this integration across spatial and temporal scales and across levels of organization is usually based on empirical regularities that involve the size of organisms in the form of simple scaling relationships (e.g., Marquet et al. 2005). The emergent character of body size renders it particularly suited for the task of integrating physiological, ecological, and historical factors, but at the same time makes assessing the relative contribution of each of these factors to observed patterns extremely difficult.