

CONCLUSION

The Way Forward

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A number of common themes run throughout this volume. First, one begins to appreciate just how much variation there is in body size among most groups of animals. For the most part, a clade is not a homogenous collection of similar bauplans. Even among volant taxa, such as birds and bats, substantial variation in body mass exists despite the considerable constraints imposed by flight (chaps. 3, 4, 8). Moreover, body size variation is clearly important in terms of community and ecosystem dynamics and structure (e.g., chaps. 6–9); how animals interact with their environment is strongly mediated by their body mass. Thus, the size of an organism is of great physiological and ecological significance (Peters 1983).

Second, there are remarkably consistent patterns in the body size distributions of some taxa across spatial and temporal gradients that may well reflect how organisms acquire and allocate energy. For example, right-skewed body size distributions seem to be quite common among diverse clades (chaps. 1–5). However, these regular patterns vary between groups in ways that we do not yet understand. As Maurer and Marquet (chap. 7) note, numerous processes have been invoked to explain the minimum, maximum, mode, and shape of body mass distributions. Which of these processes are universal? Which are unique to particular taxa or geological histories (e.g., response to glaciation; chap. 2)? Are size frequency distributions similarly skewed to the right because organisms contributing to these distributions share similar trophic or life history traits? To some extent, our inability to develop universal explanations may reflect a lack of fundamental information. For example, as Gaston and Chown (chap. 1) note, it is likely that only 9%–24% of

extant insect species have been described thus far. How robust are generalizations for insects based on such a restricted sampling of extant biodiversity?

Third, temperature is important. Many taxa demonstrate a clear response to underlying environmental gradients in temperature (chaps. 1, 2, 5). This ecogeographic pattern is known as Bergmann's rule: the principle that within a broadly distributed genus, species of larger size are found in colder environments, and species of smaller size are found in warmer areas (Rensch 1938, 1950; Mayr 1956). While Bergmann's rule holds for the majority (62%–83%) of vertebrates examined to date (Millien 2006), it is not clear how robustly other clades follow this pattern. Evidence within our volume is mixed; some insect groups do conform (fig. 1.4), but land snails apparently do not (fig. 2.1). Here, the role of evolutionary history may be particularly important, as much of the current diversity of snails may be related to the most recent glaciation events of the Pleistocene. Interestingly, dispersal may be implicated for the lack of a Bergmann-like cline, not only in snails (chap. 2), but in bats as well (chap. 4). Clearly, understanding the influence of temperature on organism body size is particularly important in this era of anthropogenic climate change. While considerable effort has gone into predicting how species will respond to the large anthropogenic climate shifts expected over the next few centuries, most studies focus on changes in the distribution and abundance of species (reviewed in Parmesan and Yohe 2003; Root et al. 2003; Ackerly et al. 2010). They tend to completely discount the possibility of in situ adaptation. Yet Bergmann clines over space and time demonstrate the ability of species to adapt to fluctuating abiotic conditions and highlight the strong selection imposed by the environment (Smith et al. 1995; Smith and Betancourt 2006). As the contributions in our volume demonstrate, changing environmental conditions may well result in shifts in the body size of organisms and communities, leading to wholesale alterations in energy use.

The observant reader will quickly notice several gaps in this compilation. First, our focus here has been exclusively on animals. A logical question is whether body size patterns across widely divergent groups display similar features. A qualified answer to this question is yes. At least for plants, where data compilations exist, strikingly regular patterns of "body size" exist. In the last decade, Brian Enquist, Karl Niklas, and others have made considerable progress in connecting individual attributes of plants with macroscopic patterns (Niklas 1994). For exam-

ple, plants show the same scaling of population density and body mass seen with animals (Niklas and Enquist 2001; Enquist and Niklas 2002). And vascular plants show at least as great a range of body mass variation as other taxa; approximately twelve orders of magnitude in mass (Enquist et al. 1999; Niklas and Enquist 2001). Much of this morphological variation is significantly related to structural complexity and life history diversity (Niklas 1994; Westoby 1998; Enquist et al. 1999; Enquist and Niklas 2002; Niklas and Enquist 2002a, 2002b; Westoby et al. 2002). Clearly, comparing patterns of body size, abundance, and/or distribution among diverse groups is likely to be extremely fruitful and an area where only a few workers have yet explored (e.g., Ernest et al. 2003; Hechinger et al. 2011).

But, even within animals, there are important groups lacking from our volume. With some exceptions, such as that of marine mollusks, not considered here because there is an entire volume on marine macroecology (Witman and Roy 2009), this largely reflects a lack of comprehensive data. For example, despite the considerable interest demonstrated by the public and others in dinosaurs, only a handful of studies have begun to try to use a macroscopic perspective to examine the distribution or abundance of species (Carrano 2006), although such efforts are ongoing (table C.1). Potential authors we contacted felt these data were too poor at the present time to try to synthesize patterns. In other instances, excellent data exist, but are focused on specific taxa limiting their utility for evaluating synoptic patterns. Research on fish, for example, has tended to focus on a few abundant species of commercial significance (Rice et al. 1991; Christensen 1995; Jennings et al. 2001). Indeed, the effects of overharvesting are well known to influence the body size distribution of remaining stocks (Law and Rowell 1993; Rowell 1993; Stokes and Blythe 1993; Law and Stokes 2005). However, we lack a comprehensive understanding of the overall body size distribution of animals in the world's oceans.

Second, despite the great strides made in molecular techniques over the last decade, for most groups a detailed species-level phylogeny is still lacking. This hampers our ability to examine the influence of evolutionary history on the body size patterns of animals. Just what are the relative contributions of phylogenetic autocorrelation, environmental factors, and architectural limitations? The authors of most chapters did attempt to incorporate phylogenies into analyses, but they often used taxonomy as a proxy for a true phylogenetic relationship. Clearly, as more

TABLE C.1 Synthetic Databases That Currently Exist That Contain Body Size Estimates of Various Taxa

Taxa	Database	Source and Reference	Spatial Extent	Temporal Extent	Description
All	PBDB	Paleobiology Database, http://paleodb.org ; organized and operated by an international group of paleobiological researchers led by J. Alroy	Global	Phanerozoic	Collection-based occurrence, taxonomic, and some measurement data for animals and plants; web-based software for statistical analysis
Coleoptera (beetles)		Buckland and Buckland 2006	Global	Pleistocene; 2 million years ago to present	Species-level habitat and distribution data; includes tools for climate and environmental reconstruction
Fish	Fishbase2004	http://www.fishbase.org/search.php ; supported by a consortium of nine research institutions	Global	Modern	Species-level biological and habitat data; includes mass and/or size, habitat, climate, description, biology and International Union for Conservation of Nature status
Lizards		Meiri 2008	Global	Modern	Species-level estimates of snout-vent length (mm) and mass (g)
Mammals	MOM v3.0	http://www.esapubs.org/archive/ecol/E084/094/ ; latest version: http://biology.unm.edu/fasmith/ ; Smith et al. 2003	Global	Late Quaternary	Species-level biological and habitat data; includes body mass, distribution, trophic characterization
Mammals	Pantheria	http://www.esajournals.org/doi/abs/10.1890/08-1494.1 ; Jones et al. 2009	Global	Historic	Species-level biological and habitat data; includes body mass, life history, distribution
Mammals	Mammal_lifehistories_v2.0	http://www.esapubs.org/archive/ecol/E084/093/ ; Ernest 2003	Global	Modern	Mammal life history characteristics

Mammals	Mammoth v1.0	latest version: http://biology.unm.edu/fasmith/	Global	Cenozoic	Maximum body mass of each mammalian order by subepoch, on each continent
Mammals	NOW	http://www.helsinki.fi/science/now/ ; M. Fortelius (coordinator), Neogene of the Old World Database of Fossil Mammals (NOW), University of Helsinki, http://www.helsinki.fi/science/now/			Neogene of the Old World; Eurasian Miocene to Pleistocene land mammal taxa and localities, with emphasis on the European Miocene and Pliocene
Mammals	FAUNMAP	http://www.museum.state.il.us/research/faunmap/query/	North America	Pliocene to present (5 million years ago to present)	Mammal fossils
Mammals	MIOMAP	http://www.ucmp.berkeley.edu/miomap/	North America	Oligocene to Pliocene (30 million to 5 million years ago)	Mammal fossils
Snakes		http://www.auburn.edu/academic/science_math/cosam/collections/reptiles_amphibians/projects/index.htm ; Boback and Guyer 2003	Regional	Modern	Body sizes (log10 [maximum total length]) of the largest and smallest species of snake in island assemblages and island area; body sizes (maximum snout-vent length) from island and main land populations for 30 species of snakes
Snakes		http://www.auburn.edu/academic/science_math/cosam/collections/reptiles_amphibians/projects/index.htm ; Boback and Guyer 2008	???	Modern	Body sizes (maximum total length, except for turtles, which are maximum carapace length) of vertebrates

detailed phylogenies become available, it will become possible to incorporate such information.

Third, a historical perspective is missing for most groups despite the best efforts of the chapters' authors to incorporate evolutionary history. Yet, a major question is whether the emergent statistical patterns observed over space also exist across time. And, if so, just how consistent have they been? Consistency across space and time would strongly suggest universal drivers. Moreover, the role of size in extinction and/or speciation is crucial to understanding current diversity and body size distributions. Several studies have examined the influence of body size in influencing species richness (e.g., Dial and Marzluff 1988; Gittleman and Purvis 1998; Orme et al. 2002), but more comprehensive tests across different lineages are required.

The lack of a comprehensive historical perspective for mammals was the reason we put together our Research Coordination Network (IMPPS; http://biology.unm.edu/impps_rcn/). Over the past five years, this group has focused on assembling body mass estimates for fossil lineages to allow comparison of body mass patterns over space with those over time. Recently, we published several papers examining the trajectory of mammalian body mass on the various continents over evolutionary time (Smith et al. 2010; Evans et al. 2012). Our results confirm much of what we know about mammalian body mass over geographic space (chap. 5). The evolutionary trajectory was quite similar on all continents across the last 100 million years, even within clades. It appears that the upper limit on mammalian body mass is related to both temperature and area of the continent (Smith et al. 2010). Patterns within orders are extremely similar on all continents, although there are interesting differences that relate to the evolutionary history of taxa. Our work in this area is ongoing.

Collecting these data was a major effort of our group. Consider that assembling our database Mammoth (v 1.0) took a core group of 10–12 individuals with different expertise on mammalian clades about three years; the equivalent of a single researcher working for nearly thirty years! Clearly, this is only feasible with a large collaborative group. But such large synthetic databases are essential if we are to detect patterns and processes not discernible at smaller spatial or temporal scales. Unfortunately, for projects such as ours that can take so long come to fruition, there is still little institutional funding. We were fortunate to secure funding through the National Science Foundation for our efforts,

but such grants are quite difficult to obtain. Thus, it is no wonder that comprehensive body size data for other terrestrial animal groups over deep time are still largely lacking.

As an aside, a major exception to the paucity of deep-time data is the marine invertebrate record. Here, extensive work has led to a reasonably complete picture of species occurrence (and in some instances, size) over the Phanerozoic (e.g., Sepkoski et al. 1981; Labandeira and Sepkoski 1993; Alroy et al. 2001, 2008). This compilation was jump-started by Jack Sepkoski, who began synthesizing diversity patterns over the Phanerozoic (e.g., Sepkoski et al. 1981; Sepkoski 1988, 1993). Since then, the Paleobiology Database (<http://paleodb.org/cgi-bin/bridge.pl>) has been the focus of intensive data collection by a multidisciplinary, multi-institutional, and international group of paleobiological researchers. Ultimately, the aim is to provide global data for marine and terrestrial animals and plants of any geological age. However, even this august group has had problems securing the appropriate funding.

As we move forward, it is clear that progress will depend on the continued development of large databases relating important attributes of organisms with body size and abundance. We have discussed the hurdles—often financial—in developing such databases. But, other issues remain. For example, different disciplines estimate “body size” in very different ways. While mammalogists routinely use mass (chaps. 5, 8), length (e.g., chaps. 1, 4), height (chap. 2), diameter (plants; Niklas 1994), and “biovolume” (aquatic groups; McClain et al. 2009) are also surrogates for an organism’s size. Paleontologists may use surface area (e.g., Jablonski 1997). Converting these metrics into a standard format is essential for synthetic studies (Payne et al. 2009).

Another issue that plagues the construction of large-scale databases is that of scientific attribution. Increasingly, journals relegate methods to online supplementary material, which are generally not indexed by electronic search engines (e.g., PubMed, Web of Science, Scopus, Google Scholar). This means that primary data, often from single investigators, are not credited in large databases, undervaluing their importance and lessening the impetus for workers to “share” data (Payne et al. 2012). Moreover, this also leads to a systematic undervaluation of the subdisciplines that disproportionately provide foundational data, such as taxonomy, systematics, and natural history. Yet large data compilations are dependent on the availability of large numbers of primary studies, which must be properly acknowledged.

Finally, we lack good methods for statistically analyzing large-scale patterns. The authors of the various chapters have used different tool kits, which provide slightly different perspectives but are not always comparable. The problem of appropriate statistical methods is one that pervades macroecological approaches, which are commonly used to examine the patterns and underlying causal mechanisms of body size (Smith et al. 2008). The use of nonexperimental or “natural” data and the broad geographic, taxonomic, and/or temporal scales mean that many modern statistical methods, which have been developed for traditional experimentally based science, are inappropriate. This is an area that requires further development.

While our volume does not provide answers to all the intriguing questions raised by the past few decades of research on body size, it does highlight many of these. Clearly, there are a number of profoundly important questions that remain unaddressed, including: (1) Why are distributions of mammals on the various continents so similar despite different taxonomies, geological conditions, and environments? (2) What limits the upper and lower size of organisms? (3) Does body size influence origination or extinction rates? Do large animals evolve “slower,” or are they more prone to extinction because of lowered productivity and densities, or less prone because of larger geographic ranges? and (4) Are there “rules” to body size evolution that are universal across organisms, modes of life, and/or life histories? One promising avenue may be the application of metabolic ecology to broad-scale patterns of body size. Metabolic ecology suggests that when corrections are made for body size, virtually all living things convert resources at a similar rate because of the geometry of transport systems (West et al. 1997, 1999). Clearly, the study of body size, the factors influencing it, and its attendant properties, are likely to be fruitful areas for further research for years to come.

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