

INTRODUCTION

On Being the Right Size: The Importance of Size in Life History, Ecology, and Evolution

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“For every type of animal there is an optimum size.” —J. B. S. Haldane, *“On Being the Right Size”*

Living things vary enormously in body size. Across the spectrum of life, the size of animals spans more than twenty-one orders of magnitude, from the smallest (mycoplasma) at $\sim 10^{-13}$ g to the largest (blue whale) at 10^8 g (fig. I.1, table I.1). We now know that much of this range was achieved in two “jumps” corresponding to the evolution of eukaryotes and metazoans, at 2.1 Ga and 640 Ma, respectively (Payne et al. 2009). Yet the drivers behind these jumps, the factors underlying similarities and differences in body size distributions, and the factors selecting for the “characteristic” or “optimum” size of organisms remain unresolved (Smith et al. 2004; Storch and Gaston 2004).

The study of body size has a long history in scientific discourse. Some of our earliest scientific treatises speculate on the factors underlying the body mass of organisms (e.g., Aristotle 347–334 B.C.). Many other eminent scientists and philosophers, including Galileo Galilei, Charles Darwin, J. B. S. Haldane, George Gaylord Simpson, and D’Arcy Thompson, have also considered why organisms are the size they are and the consequences of larger or smaller size. As Galileo stated, “Nature cannot produce a horse as large as twenty ordinary horses or a giant ten times taller than an ordinary man unless by miracle or by greatly altering the proportions of his limbs and especially of his bones” (Galileo 1638). The

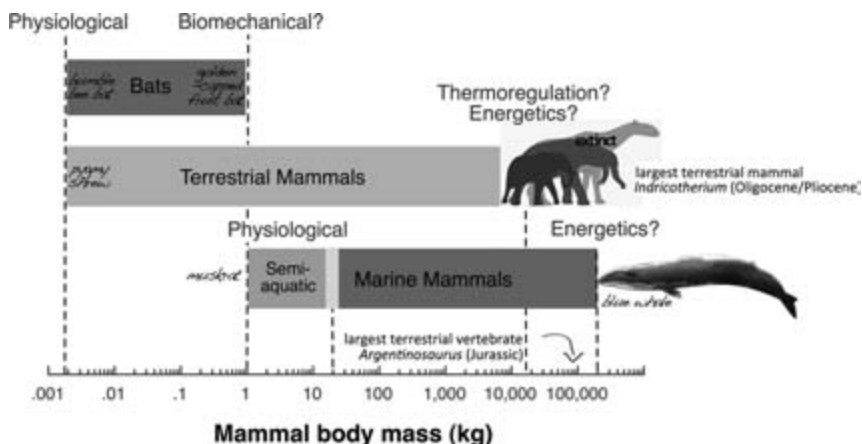


FIGURE 1.1. Factors influencing the minimum and maximum size of mammals. Note that the minimum size of ~ 1.8 g is represented by both volant and nonvolant mammals; aquatic mammals have a much larger minimum body size, which appears to be set by the thermoregulatory demands of living in an aquatic environment (see text). The largest terrestrial mammal, *Indricotherium*, reached masses reportedly in excess of 12–15 tons. Interestingly, this is about an order of magnitude smaller than the largest terrestrial dinosaurs and could reflect a difference between endothermic and exothermic animals if resources limit size in terrestrial environments.

fascination with body size stems not only from the ability to clearly characterize it, but also from the fact that it so clearly matters.

Over the past few decades, considerable research has gone into understanding the physiological consequences of being a certain size. This was inspired in part by the almost concurrent publication of three seminal books on body size in the mid-1980s: Peters (1983), Calder (1984), and Schmidt-Nielsen (1984). Thanks to these and other works (e.g., Kleiber 1932), we now know just how many fundamental physiological, ecological, and evolutionary factors scale allometrically (i.e., $y = x^b$, where y = represents some organismal trait, x represents body mass and b , an exponent that is generally less than 1) with mass. These include fecundity, energetic requirements, diet, territory and home range size, longevity, and even extinction rates (Bourliere 1975; Niklas 1994).

There has also been a recent and exciting development of mechanistic mathematical models, rooted in specific aspects of individual anatomy and physiology. These models attempt to bridge the gap between body size patterns that are present across differing temporal and spatial

TABLE 1.1 **The Range of Body Size of Various Taxa**

Taxon	Smallest		Largest		Range of Size (Orders of Magnitude)
	Organism	Size	Organism	Size	
Class Mammalia (aquatic)	<i>Enhydra lutris</i> (sea otter)	~27 kg	<i>Balaenoptera musculus</i> (blue whale)	~180 tons	8 (mass)
Class Mammalia (terrestrial)	<i>Suncus etruscus</i> (pygmy shrew)	~1.8 g	<i>Indricotherium transouralicum</i> (extinct)	12–15 tons	7 (mass)
Class Reptilia (marine)	<i>Keichousaurus</i>	0.454 kg	<i>Hainosaurus</i>	~15 m, ~15 tons	4 (mass)
Class Reptilia (terrestrial; nondinosaurs)	<i>Spaerodactylus ariasae</i> (gecko)	16 mm	<i>Sarcosuchus imperator</i> (extinct)	~12 m, ~13.6 tons	3 (length)
Class Reptilia (turtles)	<i>Homopus signatus</i> (speckled padloper tortoise)	8 cm	<i>Archelon ischyros</i> (extinct)	4.84 m, 2200 kg	2 (length)
Class Reptilia (dinosaurs)	<i>Archioernis</i>	34 cm, 110 g	<i>Argentiosaurus</i> (extinct)	~80–90 tons	6 (mass)
Class Aves	<i>Mellisuga helenae</i> (bee hummingbird)	6.2 cm, ~1.8 g	<i>Struthio camelus</i> (North African ostrich)	~2.75 m, ~156 kg	2 (length)
Class Amphibia (frogs)	<i>Eleutherodactylus Iberia</i> (Monte Iberia eleuth)	~9.8 mm	<i>Conraua goliath</i> (goliath frog)	~32 cm, 3.3 kg	~2 (length)
Superclass Osteichthyes	<i>Paedocypris progenetica</i>	~7.9 mm long	<i>Rhincodon typus</i> (whale shark)	12.6 m long	4 (length)
Class Amphibia (all)	<i>Brachycephalus didactylus</i> (Brazilian golden frog)	9.8 mm	<i>Prionosuchus</i> (extinct)	9 m	3 (length)
Class Bivalvia	<i>Sphaeriidae</i>	0.2 mm	<i>Platyceramus platinus</i> (extinct)	3 m	4 (length)
Class Gastropoda	<i>Ammonicera rota</i>	0.05 cm	<i>Syrinx aruanus</i>	91 cm, 18 kg	3 (length)
Class Cephalopoda	<i>Idiosepius notoides</i> (pygmy squid)	7 mm	<i>Mesonychoteuthis hamiltoni</i> (colossal squid)	13 m, 494 kg	4 (length)
Class Trilobita	<i>Ctenophyge ceciliae</i> (extinct)	3 mm	<i>Isotelus rex</i> (extinct)	720 mm	3 (length)
Division Angiospermae	<i>Salix herbacea</i> (dwarf willow)	1–6 cm tall	<i>Sequoiadendron giganteum</i> (giant sequoia)	83.8 m tall	3 (length)
Class Arachnida	<i>Patu marplei</i> (Samoan moss spider)	0.3 mm	<i>Theraphosa blondi</i> (goliath bird-eating spider)	28 cm, 170 g	4 (length)
Class Insecta	<i>Nanosella fungi</i> (feather-winged beetle)	0.25 mm	<i>Goliathus goliatus</i> (goliath beetle)	>110 mm	3 (length)
Domain Bacteria	<i>Mycoplasma genitalium</i>	~200 nm	<i>Epulopiscium fishelsoni</i>	0.7 mm	5 (length)

Note: Mass scales as the cube of length for roughly cylindrical organisms. Thus, a difference of one order of magnitude in length is approximately equal to a three-order difference in mass.

scales and have shown that animals and plants share many similar allometric scaling relationships (e.g., Brown et al. 1993; West et al. 1997; Enquist et al. 1998; Maurer 1998; West et al. 1999). This is an important insight, as it suggests that across diverse groups of organisms (i.e., plants and animals) body size distributions may in fact not only be similar but also predictable. Yet how the complex and dynamic interactions among intrinsic structure and function, environment, and historical and/or phylogenetic evolution result in particular body sizes remains unclear.

Paleontologists, ecologists, and comparative evolutionary biologists have also extensively studied body size. The detailed analysis of size patterns has led to the formation of several well-supported large-scale biogeographic and temporal “rules,” such as Bergmann’s, Cope’s, and Foster’s rules, and the plant self-thinning law (Bergmann 1847; Cope 1887; Yoda et al. 1963; Foster 1964). Just how pervasive these spatial and temporal phenomena are, however, is still the subject of considerable debate (Weller 1987; Lonsdale 1990; Jablonski 1997; Alroy 1998). With few exceptions (e.g., Brown and Maurer 1986; Jablonski 1993; Brown 1995; Jablonski and Raup 1995; Smith et al. 1995; Smith and Betancourt 1998) biogeographic and temporal patterns have been studied separately, with ecologists focusing on the former, and paleoecologists on the latter (e.g., Cope 1887; Mayr 1956; Stanley 1973; MacFadden 1987; Damuth and MacFadden 1990, and references therein; Morgan et al. 1995; Hadly 1997; Jablonski 1997; Alroy 1998; Enquist et al. 1998). Likewise, although comparative biologists have made admirable progress examining trait evolution in contemporary taxa (e.g., Harvey and Purvis 1991; Purvis and Harvey 1997; Bininda-Emonds et al. 2001), they have had difficulty linking ecological processes with evolutionary ones and often ignore the fossil record. There is little integration across the divergent scales studied by ecologists, comparative evolutionary biologists, and paleoecologists, and limited attempts have been made to span taxonomic or other boundaries.

To some extent, these issues have stemmed at least partially from difficulties in assembling appropriate data. Several earlier studies investigated the influence of environmental conditions and evolutionary constraints on size, for example, but were limited in geographic or taxonomic scope (Hutchinson and MacArthur 1959; May 1978, 1986; Brown and Nicoletto 1991; Pagel 1999; but see Alroy 1998; Harvey 2000; Blackburn and Gaston 2001). Other authors compared body size and/or life history traits across continents but focused on particular orders where data were

available, utilized a subset of taxa, or conducted analyses at the generic or familial level (e.g., Read and Harvey 1989; Maurer et al. 1992; Kappele and Heymann 1996). In particular, the impact of phylogeny on the pattern and similarity of body size remains underexplored, especially across different taxa and scales. Methods for exploring the phylogenetic signal in traits, however, are becoming more robust (e.g., Freckleton et al. 2002; Blomberg et al. 2003) and a number of synthetic datasets have become available (e.g., Smith et al. 2003, among others; Jones et al. 2009).

Thus, there are a number of profoundly important questions that remain unaddressed by any subdiscipline of biology. First, how do the complex interactions between organic structure and function, environment, and historical and/or phylogenetic evolution engender particular body sizes, and, second, how do these interactions evoke the apparently remarkably consistent body size patterns seen across taxa, space, and time? A potentially powerful hypothesis is that size frequency distributions are similarly skewed to the right or to the left because the organisms contributing to these distributions share similar trophic or life history traits despite their other phyletic differences. Do organisms of similar size demonstrate similarities in life history traits? If so, what are the relative contributions of phylogenetic autocorrelation, environmental factors, and architectural limitations? Do spatially averaged distributions have a different form from those of temporally averaged distributions? Do emergent statistical patterns also exist across time, and if so, how consistent have they been over time? How similar are body size patterns across plant and animals species? How do these important factors interact for different taxa? Do certain sizes make clades more likely to speciate by either decreasing the chances of extinction or increasing the likelihood of speciation? 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. Last, what are the mode and tempo of body size change through evolutionary and ecological time, and across different taxa?

All of the papers here take a macroecological approach to examine the patterns and underlying causal mechanisms of body size. That is, they emphasize description and explanation of the emergent statistical properties of large numbers of ecological “particles,” be they individuals, populations, or species (Brown 1995). This is not surprising:

body size has been a key variable for many macroecological studies. Indeed, the use of a macroecological approach is increasingly common when addressing fundamental questions in ecology and paleoecology at large spatial and temporal scales (Smith et al. 2008). The book is divided into two parts: “Body Size Patterns across Space and Time” and “Mechanisms and Consequences Underlying Body Size Distributional Patterns.” Within each section, we have included papers reflecting different taxonomic, hierarchical, and/or scientific perspectives.

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 address many of these issues. For example, several papers (e.g., those by Gaston and Chown; Nekola et al.; Maurer; Lyons and Smith; Ernest; and Maurer and Marquet) deal with the fundamental interactions between body size and population, community, and/or ecosystem structure and function. Others explore the role of life history (Safi et al.; Brown et al.) or modes of life (Smith et al.) in patterns of body size. Divergent scientific perspectives are presented, including explicit phylogenetic or taxonomic (Gaston and Chown; Maurer; Safi et al.; Smith et al.), theoretical (Brown et al.) and paleoecological approaches (Lyons and Smith). By compiling these contributions in one volume, we have attempted to highlight some of the patterns common across spatial, temporal, and/or taxonomic scales. However, despite the recent resurgence of interest in understanding and explaining emergent patterns of body size at varying scales, there is still no consensus on the drivers or triggers underlying these processes. We hope this volume will help inspire new research on some of these big, important, and still unanswered questions.

References

- Alroy, J. 1998. “Cope’s rule and the dynamics of body mass evolution in North American fossil mammals.” *Science* 280 (5364): 731–734.
- Aristotle. 347–334 B.C. *De partibus animalium*. In *The complete works of Aristotle*, edited by J. Barnes, translated by L. Dittmeyer (1907; rev. ed., Princeton: Princeton University Press, 1984).
- Bergmann, C. 1847. “Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse.” *Göttinger Studien* 3:595–708.
- Bininda-Emonds, O. R. P., J. L. Gittleman, and C. K. Kelly. 2001. “Flippers versus feet: Comparative trends in aquatic and non-aquatic carnivores.” *Journal of Animal Ecology* 70:386–400.

- Blackburn, T. M., and K. J. Gaston. 2001. "Local avian assemblages as random draws from regional pools." *Ecography* 24 (1): 50–58.
- Blomberg, S. P., T. Garland, and A. R. Ives. 2003. "Testing for phylogenetic signal in comparative data: Behavioral traits are more labile." *Evolution* 57: 717–745.
- Bourliere, F. 1975. "Mammals, small and large: The ecological implications of size." In *Small mammals: Their productivity and population dynamics*, edited by F. B. Golley, K. Petrusewicz, and L. Ryszkowski. Cambridge: Cambridge University Press.
- Brown, J. H. 1995. *Macroecology*. Chicago: University of Chicago Press.
- Brown, J. H., P. A. Marquet, and M. L. Taper. 1993. "Evolution of body size: Consequences of an energetic definition of fitness." *American Naturalist* 142 (4): 573–584.
- Brown, J. H., and B. A. Maurer. 1986. "Body size, ecological dominance and Cope's rule." *Nature* 324 (6094): 248–250.
- Brown, J. H., and P. F. Nicoletto. 1991. "Spatial scaling of species composition: Body masses of North American land mammals." *American Naturalist* 138 (6): 1478–1512.
- Calder, W. A. 1984. *Size, function, and life history*. Cambridge, MA: Harvard University Press.
- Cope, E. D. 1887. *The origin of the fittest*. New York: Appleton.
- Damuth, J., and B. J. MacFadden. 1990. *Body size in mammalian paleobiology: Estimation and biological implications*. New York: Cambridge University Press.
- Dial, K. P., and J. M. Marzluff. 1988. "Are the smallest organisms the most diverse?" *Ecology* 69:1620–1624.
- Enquist, B. J., J. H. Brown, and G. B. West. 1998. "Allometric scaling of plant energetics and population density." *Nature* 395 (6698): 163–165.
- Foster, J. B. 1964. "Evolution of mammals on islands." *Nature* 202:234–235.
- Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. "Phylogenetic analysis and comparative data: A test and review of evidence." *American Naturalist* 160 (6): 712–726.
- Galileo, G. 1638. "Discorsi e dimostrazioni matematiche, intorno à due nuove scienze." In *Mathematical discourses and demonstrations, relating to two new sciences*, translated by Henry Crew and Alfonso de Salvio (Leiden: Elsevier, 1914).
- Gittleman, J. L., and A. Purvis. 1998. "Body size and species-richness in carnivores and primates." *Proceedings of the Royal Society B: Biological Sciences* 265:113–119.
- Hadly, E. A. 1997. "Evolutionary and ecological response of pocket gophers (*Thomomys talpoides*) to late-Holocene climatic change." *Biological Journal of the Linnean Society* 60:277–296.

- Harvey, P. H. 2000. "Why and how phylogenetic relationships should be incorporated into studies of scaling." In *Scaling in biology*, edited by J. H. Brown and G. B. West. Oxford: Oxford University Press.
- Harvey, P. H., and A. Purvis. 1991. "Comparative methods for explaining adaptations." *Nature* 351:619–624.
- Hutchinson, G. E., and R. H. MacArthur. 1959. "A theoretical ecological model of size distributions among species of animals." *American Naturalist* 93:117–125.
- Jablonski, D. 1993. "The tropics as a source of evolutionary novelty through geological time." *Nature* 364 (6433): 142–144.
- . 1997. "Body-size evolution in Cretaceous molluscs and the status of Cope's rule." *Nature* 385 (6613): 250–252.
- Jablonski, D., and D. M. Raup. 1995. "Selectivity of end-Cretaceous marine bivalve extinctions." *Science* 268 (5209): 389–391.
- Jones, K. E., J. Bielby, M. Cardillo, S. A. Fritz, J. O'Dell, C. D. L. Orme, K. Safi, W. Sechrest, E. H. Boakes, C. Carbone, C. Connolly, M. J. Cutts, J. K. Foster, R. Grenyer, M. Habib, C. A. Plaster, S. A. Price, E. A. Rigby, J. Rist, A. Teacher, O. R. P. Bininda-Emonds, J. L. Gittleman, G. M. Mace, and A. Purvis. 2009. "PanTHERIA: A species-level database of life-history, ecology and geography of extant and recently extinct mammals." *Ecology* 90:2648.
- Kappeler, P. M., and E. W. Heymann. 1996. "Nonconvergence in the evolution of primate life history and socio-ecology." *Biological Journal of the Linnean Society* 59:297–326.
- Kleiber, M. 1932. "Body size and metabolism." *Hilgardia* 6:315–351.
- Lonsdale, W. M. 1990. "The self-thinning rule—dead or alive?" *Ecology* 71:1373–1388.
- MacFadden, B. J. 1987. "Fossil horses from "Eohippus" (*Hyracotherium*) to *Equus*: Scaling, Cope's law and the evolution of body size." *Paleobiology* 12:355–369.
- Maurer, B. A. 1998. "The evolution of body size in birds. I. Evidence for non-random diversification." *Evolutionary Ecology* 12 (8): 925–934.
- Maurer, B. A., J. H. Brown, and R. D. Rusler. 1992. "The micro and macro in body size evolution." *Evolution* 46 (4): 939–953.
- May, R. M. 1978. "The dynamics and diversity of insect faunas." In *Diversity of insect faunas*, edited by L. A. Mound and N. Waloff. New York: Blackwell Scientific Publications.
- . 1986. "The search for patterns in the balance of nature: Advances and retreats." *Ecology* 67:1115–1126.
- Mayr, E. 1956. "Geographical character gradients and climatic adaptation." *Evolution* 10:105–108.
- Morgan, M. E., C. Badgley, G. F. Gunnell, P. D. Gingerich, and J. W. Kappel-

- man. 1995. "Comparative paleoecology of paleogene and neogene mammalian faunas: Body-size structure." *Palaeogeography, Palaeoclimatology, Palaeoecology* 115:287–317.
- Niklas, K. J. 1994. *Plant allometry: The scaling of form and process*. Chicago: University of Chicago Press.
- Orme, C. D. L., N. J. B. Isaac, and A. Purvis. 2002. "Are most species small? Not within species-level phylogenies." *Proceedings of the Royal Society B: Biological Sciences* 269 (1497): 1279–1287. doi: 10.1098/rspb.2002.2003.
- Pagel, M. D. 1999. "Inferring the historical pattern of biological evolution." *Nature* 401:877–884.
- Payne, J. L., A. G. Boyer, J. H. Brown, S. Finnegan, M. Kowalewski, R. A. Krause, S. K. Lyons, C. R. McClain, D. W. McShea, P. M. Novack-Gottshall, F. A. Smith, J. A. Stempien, and S. C. Wang. 2009. "Two-phase increase in the maximum size of life over 3.5 billion years reflects biological innovation and environmental opportunity." *Proceedings of the National Academy of Sciences of the United States of America* 106 (1): 24–27.
- Peters, R. H. 1983. *The ecological implications of body size*. Cambridge: Cambridge University Press.
- Purvis, A., and P. H. Harvey. 1997. "The right size for a mammal." *Nature* 386:332–333.
- Read, A. F., and P. H. Harvey. 1989. "Life-history differences among the Eutherian radiations." *Journal of Zoology* 219:329–353.
- Schmidt-Nielsen, K. 1984. *Scaling, why is animal size so important?* Cambridge: Cambridge University Press.
- Smith, F. A., and J. L. Betancourt. 1998. "Response of bushy-tailed woodrats (*Neotoma cinerea*) to late Quaternary climatic change in the Colorado Plateau." *Quaternary Research* 47:1–11.
- Smith, F. A., J. L. Betancourt, and J. H. Brown. 1995. "Evolution of body-size in the woodrat over the past 25,000 years of climate-change." *Science* 270 (5244): 2012–2014.
- Smith, F. A., J. H. Brown, J. P. Haskell, S. K. Lyons, J. Alroy, E. L. Charnov, T. Dayan, B. J. Enquist, S. K. M. Ernest, E. A. Hadly, K. E. Jones, D. M. Kaufman, P. A. Marquet, B. A. Maurer, K. J. Niklas, W. P. Porter, B. Tiffney, and M. R. Willig. 2004. "Similarity of mammalian body size across the taxonomic hierarchy and across space and time." *American Naturalist* 163 (5): 672–691.
- Smith, F. A., S. K. Lyons, S. K. M. Ernest, and J. H. Brown. 2008. "Macroecology: More than the division of food and space among species on continents." *Progress in Physical Geography* 32 (2): 115–138.
- Smith, F. A., S. K. Lyons, S. K. M. Ernest, K. E. Jones, D. M. Kaufman, T. Dayan, P. A. Marquet, J. H. Brown, and J. P. Haskell. 2003. "Body mass of late Quaternary mammals." *Ecology* 84 (12): 3403–3403.

- Stanley, S. M. 1973. "An explanation for Cope's rule." *Evolution* 27:1–26.
- Storch, D., and K. J. Gaston. 2004. "Untangling ecological complexity on different scales of space and time." *Basic and Applied Ecology* 5 (5): 389–400.
- Weller, D. E. 1987. "A reevaluation of the $-3/2$ power rule of plant self-thinning." *Ecological Monographs* 57:23–43.
- West, G. B., J. H. Brown, and B. J. Enquist. 1997. "A general model for the origin of allometric scaling laws in biology." *Science* 276 (5309): 122–126.
- . 1999. "A general model for the structure and allometry of plant vascular systems." *Nature* 400 (6745): 664–667.
- Yoda, K., T. Kira, H. Ogawa, and K. Hozumi. 1963. "Self-thinning in overcrowded pure stands under cultivated and natural conditions." *Journal of Biology of the University Osaka City* 14:107–129.