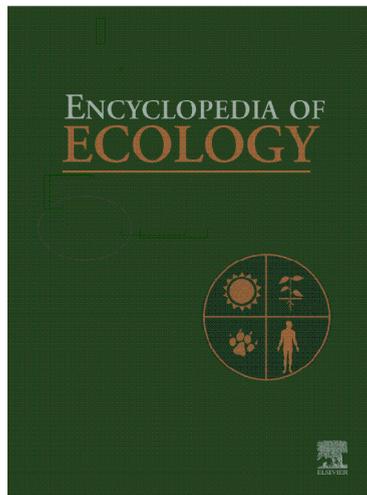


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Body Size, Energetics, and Evolution

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Introduction

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Introduction

Living things vary tremendously in their characteristic body size. The range of mass spans more than 21 orders of magnitude, from the smallest known organisms (mycoplasma) at $\sim 10^{-13}$ g to the largest (blue whale) at 10^8 g (180–200 t). Even insects, a group typically thought of as relatively diminutive, have body sizes ranging over more than three orders of magnitude (Table 1). This includes feather-winged beetles, which readily could move through the eye of a needle, and the Goliath beetle from Africa, which is bigger than a typical dinner plate. The

body mass span is extended considerably if one considers extinct insect species such as *Meganeura* with wingspans of ~ 70 cm. For centuries, biologists have been interested in what underlies this incredible diversity; why organisms evolve a certain size; and what the ecological and evolutionary consequences and tradeoffs are of each.

Body Size Matters

How animals interact with their environment is strongly influenced by their body size: the relative importance of

Table 1 Examples of the range of body size seen in various taxa

Taxa	Smallest		Largest		Orders of magnitude
Mammal	<i>Suncus etruscus</i> (pygmy shrew)	~ 1.8 g	<i>Balaenoptera musculus</i> (blue whale)	~ 180 t	8 (mass)
Bird	<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)
Tree	<i>Salix herbacea</i> (dwarf willow)	1–6 cm tall	<i>Sequoiadendron giganteum</i> (giant sequoia)	83.8 m tall	3 (length)
Fish	<i>Paedocypris progenetica</i>	~ 7.9 mm long	<i>Rhincodon typus</i> (whale shark)	12.6 m long	4 (length)
Frog	<i>Eleutherodactylus iberia</i>	~ 9.8 mm	<i>Conraua goliath</i> (Goliath frog)	~ 32 cm, 3.3 kg	~ 1 –2 (length)
Spider	<i>Patu marplei</i> (Samoan moss spider)	0.3 mm	<i>Theraphosa blondi</i> (Goliath bird-eating spider)	28 cm, 170 g	4 (length)
Insect	<i>Nanosella fungi</i> (Feather-winged beetle)	0.25 mm	<i>Goliathus goliatus</i> (Goliath beetle)	> 110 mm	3 (length)

For roughly cylindrical organisms, mass scales as the cube of length, so a difference of one order of magnitude in length equates to a three-order difference in mass.

forces like the surface tension of water, and the influence of gravity and temperature differ greatly depending on the absolute size of organisms. A cat cannot walk on water or up a wall, but some insects or lizards can. Likewise, both tree trunks and the limbs of terrestrial animals must be strong enough to provide support against the force of gravity but not so large that they are crushed under their own weight, or interfere with efficient functioning (transport of water and nutrients in the case of a tree, locomotion in the case of the animal). For a quadrupedal animal, ~ 140 t is the estimated maximum mass before the width of the limbs would have to be so large as to support the weight of the animal without interfering the movement; this value is close to that estimated for the sauropod *Argentinosaurus*, the largest known terrestrial animal (~ 100 t). Aquatic organisms face different constraints. Although the influence of gravity is ameliorated, allowing the evolution of much larger size (~ 200 t in the case of the blue whale), water has ~ 24 times the heat conductance of air (0.58 vs. $0.024 \text{ W m}^{-1} \text{ K}^{-1}$). In practical terms, this means that endotherms (animals maintaining a constant body temperature) must expend considerably more energy maintaining homeostasis. This likely limits the minimum body size; the smallest truly aquatic endotherms are ~ 100 kg, a mass that reflects selection on the ability of neonates to successfully thermoregulate. Because neonate mass is tightly correlated with maternal mass, an adult mass less than 100 kg results in offspring too small to successfully thermoregulate in water.

Biological Scaling

Not only do the structure of organisms and their dimensions change in a regular way with size, but many fundamental physiological, ecological, and evolutionary factors also scale in predictable ways. If the relationship is linear or geometric with body mass with a slope of ~ 1 , the scaling is termed isometric (iso = same, metric = measure); the gut capacity of animals is an example of a trait that scales isometrically with body mass. Many relationships scale nonlinearly with body mass, with slopes less than or greater than 1; these are known as allometric relationships (allos = different, metron = measure; **Figure 1**), a term coined by Julian Huxley and Georges Teissier in 1936. Allometric relationships were first noted in the late 1890s by Eugene Dubois and Louis Lapicque working independently on the relationship between brain and body mass, and have been extensively explored in paleontology, physiological ecology, and other disciplines.

Among traits that scale allometrically are many fundamental physiological processes such as metabolic rate, fecundity, home range, and cost of locomotion. Allometric or isometric relationships with body size are often formulated as power functions:

$$Y = aM^b$$

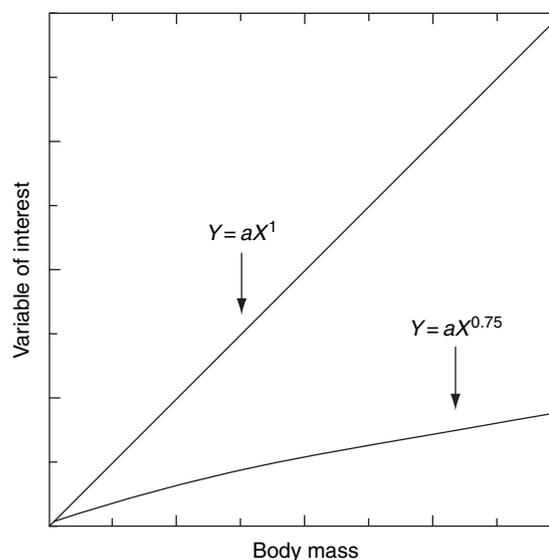


Figure 1 Difference between isometric and allometric scaling in arithmetic space. Such relationships are typically logarithmically transformed to obtain a linear slope for ease in computation and take the form $\log Y = \log a + b \log X$.

where Y is the variable of interest, M is body size, b is the slope of the relationship (representing how the variable of interest changes with differences in body size), and represents a taxon-specific constant, sometimes referred to as the normalization or proportionality constant (the intercept at unity body mass when $M = 1$). Power laws are often logarithmically transformed such that

$$\log Y = \log a + b \log M$$

because the exponent becomes the slope of a straight line, facilitating computations and comparisons. The intercept often varies in a regular way among groups; marsupials, for example, have a metabolic rate 30% lower than other mammals, which is reflected in the value of their normalization constant. These body size relationships allow comparisons within and among species at different taxonomic levels and also allow reasonably accurate predictions of many biological rates and times. Often what appear to be significant differences among organisms are a simple consequence of scaling effects. True deviations from predicted values can provide important insights into evolutionary history and adaptation. Considerable research has gone into formulating and comparing allometric relationships for a whole variety of traits and taxa.

Body Size, Energetics, and Food Acquisition

All organisms require energy for the essential activities of survival, reproduction, and growth. Consequently, knowledge of energetics is central to an understanding of the

selective forces that shape an organism's physiology, natural history, and evolution. The environment imposes intense selective pressures on organisms over both short and long time intervals. The occupation of novel environments, or abrupt environmental alterations, for example, can radically alter the pattern of energetic allocation between the essential activities of survival, reproduction, and growth.

The rate at which energy (E) is acquired, transformed, and used is known as the metabolic rate (MR); it drives the rate of all biological activities of and within the organism. Biologists often measure metabolic rate in calories (cal; defined as the energy required to heat 1 g water by 1°C) or joules ($1 \text{ cal} = 4.1840\text{J}$). More fundamentally, the metabolic rates of organisms reflect their energetic demands or footprint on the environment. Strikingly, the metabolic rate of mammals scales consistently with body size with an exponent of $3/4$ (Figure 2); this is often referred to as the 'mouse to elephant curve'. The $3/4$ scaling relationship between metabolic rate and body size was first proposed by Max Kleiber in 1932 and has been the object of intense debate and study. Much of the controversy centered on whether the relationship was related to surface area, which would result in an exponent of $2/3$, or whether it reflected other constraints. Several comprehensive studies have firmly demonstrated a $3/4$ scaling exponent and extend the relationship to organisms as diverse as microbes, invertebrates, to the largest mammals and trees. Over 90% of the

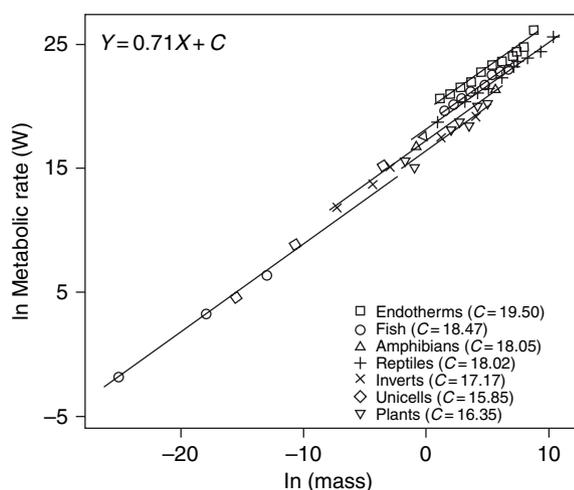


Figure 2 The logarithmic relationship between temperature-corrected metabolic rate (in watts) and body mass (in grams) for various taxa, ranging from unicellular organisms, invertebrates, and different groups of vertebrates, to plants. The overall slope provides an estimate of the allometric exponent; the intercepts are the normalization or proportionality constants for each group (see text). Differences in the intercepts reflect taxon-specific biology. The observed slope of 0.71 ± 2 is close to the predicted value of $3/4$. Drawn with permission from Brown JH, Gillooly JF, Allen AP, Savage VM, and West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85: 1771–1789.

variation in metabolic rate across species can be explained by body mass, with the residual variation reflecting unique evolutionary or biological adaptations specific to particular groups. Although still somewhat controversial, recent studies convincingly demonstrate that the underlying constraints are a result of the design properties of the vascular system. Specifically, the mechanism involves limitations on rates of uptake of resources across surfaces and rates of distribution across fractal-like branching networks within organisms.

The ecological and evolutionary consequences of allometric scaling of metabolism are profound. In practical terms it means that each gram of an animal the size of a mouse or shrew uses 20 times more energy than a gram of elephant or giraffe. Thus, food acquisition, processing, and passage rates are typically much more rapid for small animals (Figure 3), and the type of digestive strategy that can be utilized is heavily influenced by body size. True herbivory – that is, the ability to obtain energy from plant structural materials as opposed to relying largely on the easily digestible cell contents – is largely controlled by residence time in the gut or fermentation chamber. If passage rates are rapid as they are for small animals, insufficient time may elapse for the microbes to ferment plant materials and consequently limited energy can be obtained from this digestive strategy. Some small herbivores have evolved specialized adaptations to get around these constraints. These include a highly convoluted cecum and microvilli (increasing surface area), or shunts for selectively retaining materials to effectively increase residence time. While such adaptations may allow more efficient use of plant structural materials, the consequence is that small

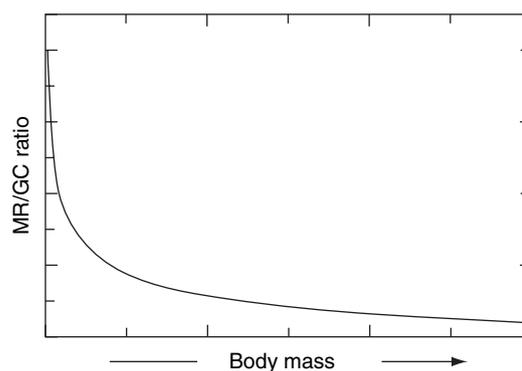


Figure 3 While metabolic rate scales allometrically with mass to the $3/4$ power, gut capacity is isometric with body mass. Thus, the ratio of metabolic rate to gut capacity scales negatively with mass to the $1/4$ (e.g., $M^{0.75}/M^1 = M^{-0.25}$). This fundamental constraint mandates higher-quality food and/or high passage rates for small animals to meet their higher per gram metabolic requirements. Food that takes longer to process (i.e., plant structural materials such as leaves) becomes progressively more difficult to handle and digest. Consequently, the smallest vertebrates are insectivores, subsisting on a ubiquitous and high-energy food source that is relatively easy to process.

herbivores are often energetically limited, which in turn influences other essential activities such as reproduction. Most small animals are much more selective and forage on higher quality resources.

The Influence of Temperature

Temperature plays a crucial role in energetics. The total energy required by an animal is not only a function of size, but is also dependent on whether it maintains a constant body temperature, that is, whether it is endo- (endo = inside) or ectothermic (ecto = outside, thermic = to heat). Endotherms maintain their body temperature within a narrow range by means of heat generated by their metabolism. Maintaining homeothermy (a constant body temperature) consumes ~90% of the energy intake of the animal, but allows activity largely independent of environmental temperatures. Only birds and mammals have adopted this evolutionary pathway – mammals typically maintain core temperatures of ~37–40 °C, while birds maintain slightly higher core temperatures of ~39–43 °C. Ectotherms, such as reptiles, fish, and other taxa, do not utilize metabolic energy to maintain a constant body temperature. Consequently, their absolute energy requirements are considerably less. However, ectotherms are generally incapable of intense activity over sustained periods of unfavorable environmental temperatures. Moreover, the metabolic rate of ectotherms is influenced by ambient environmental temperatures. Some ectotherms behaviorally thermoregulate by shifting among different microclimates to maintain a more consistent core temperature. The thermal inertia resulting from huge body masses achieved by sauropods in the Mesozoic probably meant that they were, for all practical purposes, homeothermic. The implications of endo- versus ectothermy go beyond differing metabolic requirements. In general, ectotherms grow slower and mature at a larger body size in colder environments. Fecundity is related to adult body size, with larger individuals having larger clutches.

It is well known that rate of biological activity rises exponentially with temperature. Mechanistically, this is because the increase in the kinetic energy of molecules results in substrates colliding with active sites more frequently. Physiologists express the relationship between metabolic rate and temperature as the Q_{10} , the rate increase for each 10^0 rise in temperature. A Q_{10} of 2, for example, means that the metabolic rate doubles for each 10^0 rise.

Recently, investigators have incorporated the important influence of temperature on metabolic rate (MR) by adding the Boltzmann factor to the allometric equation relating it to body size. In this formulation, the relationship is stated:

$$MR = M^{3/4} e^{-E/kT}$$

where E represents the activation energy, k is the Boltzmann's constant, and T is the absolute temperature in degrees kelvin. Similarly, the rates of many other fundamental life-history traits demonstrate temperature dependence. Thus, the addition of the Boltzmann factor into allometric relationships allows comparisons across the entire range of living organisms, regardless of thermal regulation regime, life history, or size (Figure 2). The robust relationships found suggest that the combined effects of body size, temperature, and resource supply constrain metabolic and other fundamental biological rates for all taxa.

Factors Influencing Body Size over Space and Evolutionary Time

Regular patterns of morphological variation with abiotic factors (especially temperature) have been observed repeatedly over time and space. These 'ecogeographic' gradients often involve body size, although coloration or dimensions can be influenced as well. The existence of ecogeographic patterns across space demonstrates the ability of species to adapt to fluctuating abiotic conditions, as well as underscoring the strong selection imposed on organisms by their environment.

Bergmann's Rule

Bergmann's rule is 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. Although originally formulated in terms of species within a genus, it is often recast in terms of populations within a species. The rule (named after the German physiologist, Carl Bergmann) appears to be valid for the majority (62–83%) of vertebrates (Figure 4). This includes endotherms (e.g., birds and mammals) as well as numerous species of ectotherms (bacteria, protists, plants, insects, marine organisms, and

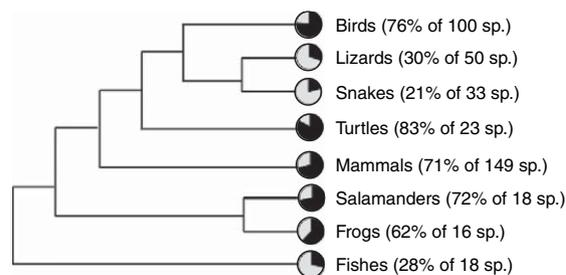


Figure 4 Percent of various vertebrate groups that conform to Bergmann's rule. Although endothermic vertebrates demonstrate a strong body size-cline with temperature, ectotherms are much more variable in their adherence to the rule. Drawn with permission from Millien V, Lyons SK, Olson L, Smith FA, Wilson AB, and Yom-Tov Y (2006) Ecotypic variation in the context of global climate change: Revisiting the rules. *Ecology Letters* 9: 853–869.

turtles). The most notable exceptions include lizards and snakes. There may be a tendency for larger-bodied animals to conform to the rule more closely than smaller bodied animals, perhaps reflecting a reduced ability to avoid stressful environments by burrowing or other means. In addition to being a general pattern across space, Bergmann's rule has been observed in populations over historical and evolutionary time when exposed to varying thermal regimes (Figure 5).

Environmental temperature directly influences the energetic relationships and physiology of animals.

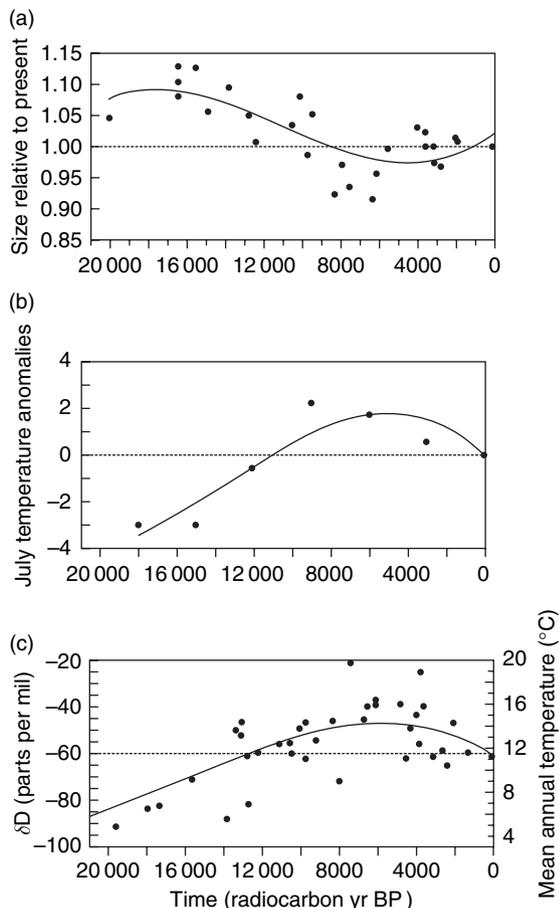


Figure 5 Third-order regression equations fitted to data for woodrat body size and environmental temperature over the Late Quaternary illustrating adherence to Bergmann's rule over evolutionary time. (a) Mean body size of woodrats from various locations across the southwestern United States plotted as a function of radiocarbon date and expressed relative to the size of the animals at the same sites today. (b) Simulated July temperature anomalies from the National Center for Atmospheric Research Climate Circulation Model (NCAR-CCMO) expressed as deviations from modern temperature. (c) Mean annual temperature as estimated from deuterium isotope ratios measured in fossil leaves. All regression equations were constrained to yield contemporary values (as indicated by the dotted line in each panel) at 0 years BP. Drawn with permission from Smith FA, Betancourt JL, and Brown JH (1995) Evolution of body size in the woodrat over the past 25 000 years of climate change. *Science* 270: 2012–2014.

Consequently, Bergmann's rule is often interpreted as a direct response to temperature. As organisms increase in body size, surface area increases more slowly than does volume (surface area \propto length², vs. volume \propto length³), such that SA scales as $\sim V^{2/3}$. Because heat loss is proportional to surface area, this means that larger animals lose less heat per unit mass than smaller animals and are at an advantage under cold environmental conditions. Conversely, smaller animals have a greater surface to volume ratio and are more capable of dissipating heat under thermally stressful conditions. Numerous other mechanisms have also been postulated to explain the size-cline, including productivity gradients, selection on life-history characteristics, development rates, and other factors related to thermal characteristics of the environment. Although the validity of the rule is generally accepted, no general consensus has yet been reached about the underlying mechanism(s) generating the gradient in size.

Island Rule

The island rule, or Foster's rule, is the general principle that larger vertebrates isolated on islands tend to become smaller, and small ones tend to become larger. It was originally proposed by J. Bristol Foster in 1964 in an analysis of islands of the coast of western North America and Europe. Over the past few decades, considerable research has gone into establishing the fundamental patterns and proposing a variety of underlying casual mechanisms. The island rule has been amply demonstrated for many groups of mammals and reptiles, although whether mammalian carnivores conform to this pattern is still unclear. The fossil record is replete with examples of both gigantism and dwarfism on islands: during the Pleistocene the Mediterranean islands contained numerous pygmy species of elephants, rhinos, deer, as well as giant rabbits, shrews, and mice. Pygmy mammoths occupied the Channel Islands off the California coast and giant hutias ranged on islands in West Indies, with one species reaching masses of 50–200 kg. Giant birds related to the pigeon were found on Fiji and the Mascarenes, and giant tortoises ranged on numerous islands in the Indian Ocean. Many of these large animals have subsequently gone extinct, in large part due to human exploitation.

Classical explanations for the island rule focus on energetics. Island communities are typically relatively depauperate compared to mainlands. The reduced species diversity often results in few or fewer competitors or predators. With the removal of constraints imposed by the diverse mainland suite of predators and competitors, organisms evolve to a size that increases the net energy that they can obtain in the insular habitat. For large animals, where large size no longer ameliorates predation pressure, this may result in dwarfing of body size. For small animals gigantism may be favored because of increased ecological or physiological access to food resources (Figure 6). The degree of

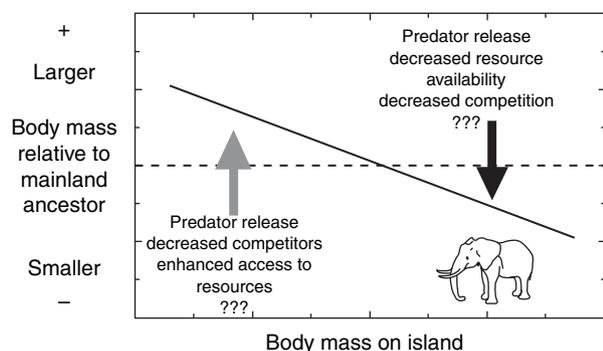


Figure 6 Schematic of body size changes in insular habitats leading to dwarfing or gigantism. Some of the selective forces postulated to be important factors in insular habitats are indicated; these may or not apply (and depending on the taxa may select for or against larger body size). These are not meant to be inclusive list. The magnitude of evolutionary shifts is known to be dependent on the size of the island and on the degree of isolation.

dwarfing or gigantism may be related to the reduction in overall species diversity as well as resource availability. Note that the distinctive selective pressures on islands have also resulted in other major evolutionary transformations, such as the tendency for a loss of flight in birds, and reductions in the dispersal ability of plants.

Cope's Rule

Cope's rule is an avowed tendency for lineages of organisms to become larger over evolutionary or geologic time. Named for Edward Drinker Cope, a prominent paleontologist who first proposed it in 1896, it remains unclear whether it is a valid phenomenon or an artifact of sampling or investigator biases. Studies of several vertebrate groups such as mammals and dinosaurs appear to have generally upheld the tendency for descendent lineages to be larger than ancestral ones. Other studies, including those of marine organisms have not. Moreover, no clear underlying causal mechanism has yet been accepted to explain why an evolutionary trend toward larger body size should be favored over geologic time. Larger body size can increase the fitness of an organism if it results in a net increase in the ability to acquire resources and energy from the environment. Several traits such as foraging ability, predator avoidance, reproductive success, and thermal efficiency may be positively related to larger size. Although the fitness of the individual may increase with size, there are considerable disadvantages to large body size at the population, species, or clade level. Significant among these is that longer generation times and lowered population densities concomitant with large size might render organisms more susceptible to environmental perturbations and/or extinction events.

Patterns at Higher Taxonomic Levels

Because body size so strongly constrains the energetic demands of organisms and their interaction with the environment, it is not surprising that it also influences space and home range requirements, population densities, and other important population and community level characteristics. The statistical study of broad, consistent patterns between organisms and their environment is called macroecology, a term coined by James Brown and Brian Maurer in 1989. For example, the population density of mammals scales negatively with body mass, with about the same exponent, as does the positive scaling of metabolic rate. The coupling of these relationships results in a well-known macroecological pattern dubbed the 'energetic equivalence rule', which suggests that the energy used by a local population of a species in a community is largely independent of its body size. Similar allometric relationships have been observed between abundance and body size for other groups including algae, terrestrial plants, and marine phytoplankton. Evidence from recent research suggests that there may well be general mechanisms that link the metabolism of individuals to higher-order emergent properties of communities and ecosystems. Thus, the study of body size is likely to continue to be a fruitful area of research in years to come.

See also: Ecological Efficiency; Ecophysiology.

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