

Scaling in Biology: The Consequences of Size¹

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ABSTRACT A review of major ideas pertaining to the importance of the body size of animals. It discusses the size range of living organisms and the possibilities and constraints that result from the design of animals and the materials used in their supporting structures. The change in size of similarly organized animals is considered in the light of the principles of scaling, with examples chosen both from morphology and physiology. The mechanical consequences of body size in relation to locomotion is also discussed.

The term Comparative Physiology implies that organisms are more or less alike and therefore can be compared. As a consequence, Comparative Physiology is concerned both with similarities and differences.

The study of biological similarities has been enormously fruitful; it has dominated biology for several centuries and it forms the foundation of modern biology. Let me mention some examples in the order they were formulated by some of the greatest biologists who have ever lived: (1) The natural system of classification (Linnaeus, 1707–1778) which classified animals according to similarities, (2) The principle of natural selection in evolution (Charles Darwin, 1809–1882) which established that small deviations from a given form constitute the major basis of evolutionary change, and (3) The formulation of the laws of inheritance (Gregor Mendel, 1822–1884) which again was concerned with the similarities between offspring and the parent generation. As we all know, these general principles have, with justification, completely dominated the development of biology as a science.

During the last several decades entirely new fields of biological study have opened up, extending to the molecular level our knowledge of universal similarities in biological systems. Let me mention some such similarities between organisms that are at the foundation of modern biology. (1) It was realized early in the last century that all animals and plants are made up of cells. The credit for the cell theory is commonly given to the botanist Schleiden

(1804–1881) and the zoologist Schwann (1810–1882), although the concept of the cell actually evolved earlier. (2) In this century it has become clear that the energy metabolism of animals, the use of fuel, the metabolic enzymes and pathways, etc. universally are based on the same general principles. (3) More recently, revolutionary progress has been made with the revelation of striking similarities in the transmission of genetic information at the molecular level. (4) Another area in which general biological similarity has been established is concerned with cell membranes, membrane potentials, action potentials, and the very active field of membrane transport processes. These areas, the cell concept, the biochemistry of energy metabolism, the nature of genetic information, and the functional importance of membrane potentials are all examples of striking, unifying principles of biological similarity of the greatest importance.

However, one field that deserves more attention than usually given to it is concerned, not with similarities, but with differences. I have in mind the enormous differences that, in spite of similarities in function, exist in the size of living organisms. In view of its fundamental importance, the size of organisms has received surprisingly meager attention. Perhaps this is because the study of similarities has been so important to the needs of biologists. As a consequence, morphology, although often concerned with point-by-

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point differences, takes its origin in the greater similarities which remain the underlying principle of classification. However, in addition to its general design, the size of an organism affects it critically, both in structure and in function. Size has profound consequences for structure and imposes severe constraints on function. In this field we find great regularity of observed fact, but we often lack adequate interpretations or explanations. However, it is my hope that future generations of biologists will find adequate solutions to unsolved problems and clearly outline underlying unifying principles.

THE SIZE OF ORGANISMS — SIZE LIMITS

The immense differences in the size of organisms raise two fundamental questions, (1) What are the size limits for a certain type of organism? and (2) For a given size, how must an organism be designed?

It is difficult to give answers to these questions, but we can examine available information, discuss some well known conclusions, and raise many additional questions.

The enormous size range of living organisms is indicated in table 1. It ranges from the largest animal that has ever lived, the blue whale, which may exceed 100 tons, or 10^8 grams, to the smallest, the pleuropneumonia-like organism, or PPLO (*Mycoplasma*). PPLO is the smallest micro-organism known that can live and reproduce in an artificial medium, and thus is an independent living organism rather than a virus. Its non-aqueous cell mass is less than 10^{-14} gram, and its linear dimension less than $0.3 \mu\text{m}$. It is reasonable to assume

TABLE 1

The size range of living organisms, arranged with examples chosen to show a thousand-fold difference between each step

Blue whale	>100 tons	> 10^8 gram
Human	70 kg	10^5
Hamster	100 g	10^2
Bee	100 mg	10^{-1}
Large amoeba	0.1 mg	10^{-4}
<i>Tetrahymena</i>	0.1 μg	10^{-7}
Malaria parasite	0.1 ng	10^{-10}
PPLO (<i>Mycoplasma</i>)	<0.1 pg	< 10^{-13}

that this organism is close to the lowest size limit for a living organism, for a cell must have sufficient size to house the metabolic equipment (notably enzymes) needed to carry on its metabolic processes, and it must also contain the necessary genetic information for the replication of the entire system. To illustrate the small size of the single PPLO organism, Morowitz ('66) calculated that, if the cell content is at pH 7, its volume is just sufficient to contain on the average a total of 2 hydrogen ions.

Table 1 shows that the size range from the smallest to the largest living organism is in the ratio of 10^{21} . We know that this is a very large number, but most of us have difficulties in conceptualizing what exponential numbers really mean. Let us estimate the size of a hypothetical super-organism, larger than the blue whale by the same ratio, 10^{21} . This hypothetical giant organism would have a size of 100 times the volume of the earth. Perhaps an even more convincing way of illustrating the magnitude of the number 10^{21} is to mention that the estimated total mass of the universe is 10^{80} grams.

It has been suggested, and more or less accepted as fact, that the blue whale can reach its enormous size only because it is an aquatic animal whose weight is supported by water, and that land mammals of a similar mass would collapse under their own weight. The largest living land mammal is the five-ton elephant, and the smallest is the shrew, which is 10^6 times smaller, or about 5 grams. The enormous size of the large whales and the fact that they are aquatic have been used to support the contention that an animal much bigger than the elephant could not live on land, and that the extinct giant dinosaurs must have been semi-aquatic. The paleontological evidence for this statement, however, is poor.

The size of the largest dinosaur, *Brachiosaurus*, was estimated by Colbert ('62) to be 78 tons, his calculations being based on estimates from scale models.² The longest dinosaur, *Diplodocus*, reached a length of 28.6 meters, but was not as heavy. Compared to these, the *Brontosaurus* was a midget, a mere 32 tons. Paleontologists have considered that "the long neck was an

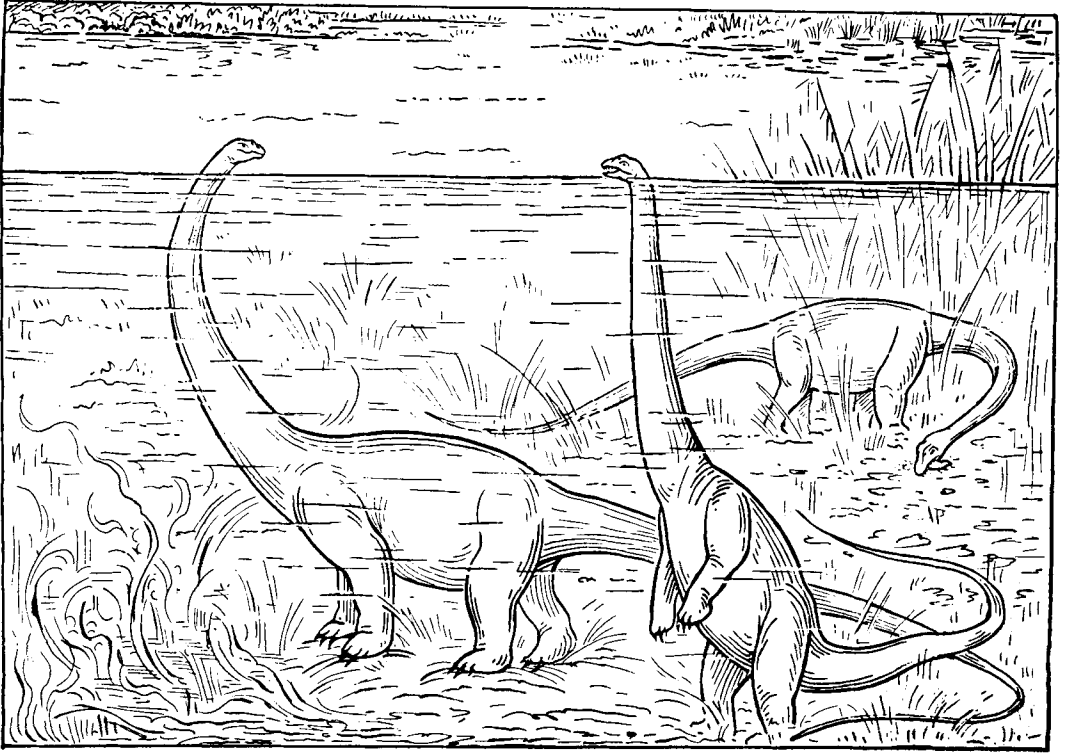


Fig. 1 The largest extinct dinosaurs supposedly were so heavy that they were unable to move freely on land and therefore led a semi-aquatic life. When submerged as shown here, the animals would have difficulties in moving about, and in addition they would encounter serious difficulties in breathing (Gregory, '51).

adaptation for life in deep waters," and that "this greatly simplified the problems of support and locomotion" (Romer, '66). This way of life is illustrated in figure 1, which shows the pleasant semi-aquatic life of dinosaurs grazing on underwater vegetation and using their long necks as a snorkel.

We have good reasons to doubt this picture. One is that numerous fossil footprints of large dinosaurs exist which show a clarity of detail that indicates that they must have been made on land and not under water (Gregory, '51). Anybody who has walked up to his neck in water knows that this does not exactly simplify the problem of support and locomotion, and that he is unlikely to leave clear footprints in the mud. A physiologist also recognizes that breathing through a snorkel at a depth of 5 meters requires the chest to support the enormous pressure of the surrounding

water, which at that depth is 5000 kg per m². A man can barely breathe through a snorkel at about one-half meter's depth, and at 5 meters his chest would be crushed by the water pressure. We must conclude that the giant dinosaurs could not be semi-aquatic as shown, and that the claim that they were too heavy to move on land is unsupported by the evidence. Would it be possible for vertebrates the size of the dinosaurs to be terrestrial? Or is a terrestrial life a mechanical impossibility for these giant vertebrates?

The largest land mammal that has ever lived is a herbivorous relative of the rhinoceros, the *Baluchitherium*, from the Oligocene period (fig. 2). It stood over 5 meters at the shoulder and weighed an

²Colbert used for his estimate an assumed density of 0.9. However, it is more probable that the density of dinosaurs, as that of other vertebrates, was close to 1.0, and that the estimate therefore was too low by about 10%.

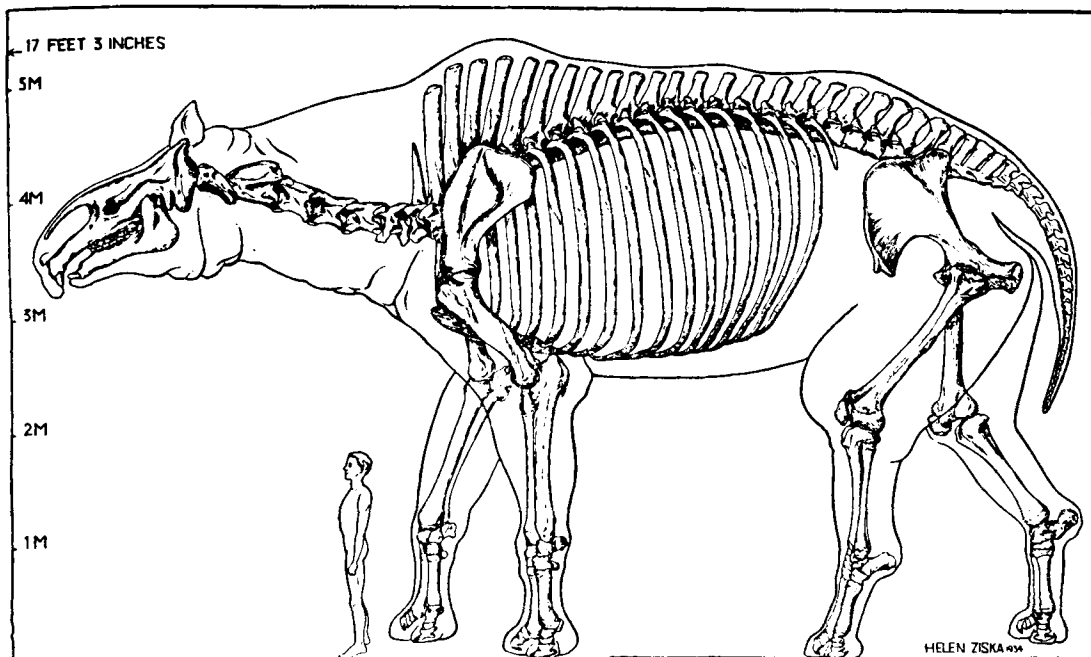


Fig. 2 The largest land mammal that has ever lived, the *Baluchitherium*, was a relative of the modern rhinoceros. Its estimated body weight was about 30 tons (Gregory, '51).

estimated 30 tons, or about 10 times as much as a medium-sized elephant (Granger and Gregory, '35). Was this enormous animal too large to be safely supported by its skeleton? Figure 3 shows specimens of the metacarpal bone of *Baluchitherium*, compared to the same bone from a modern rhinoceros at the far left. The diameter of the largest metacarpal was about 140 mm. Since the compressive strength of bone is known (1800 kg cm^{-2} [Wainwright et al., '75])³, it is easy to calculate that this metacarpal could withstand a load of about 280 tons. This gives a safety factor of nearly 10 times the body weight, a figure which is amazingly close to the safety factor for the leg bones of humans, which also is about 10-fold. This may seem like a substantial safety margin, but we should realize that the greatest stresses on the bones do not occur when the animal stands still, but rather during activity when the forces of acceleration and deceleration far exceed the static loads. This is evident from the many pulled muscles, tendons, and sprained bones which occur in humans when they participate in competitive

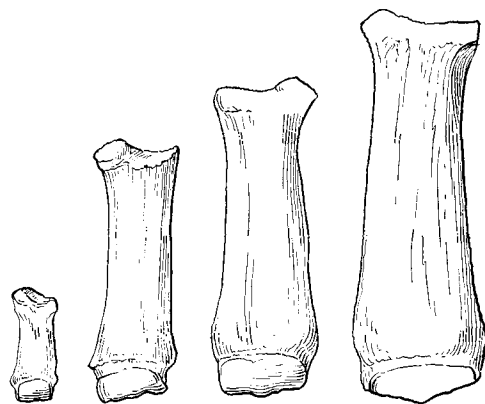


Fig. 3 The metacarpal bones from three specimens of *Baluchitherium*, compared to the same bone from a modern rhinoceros (far left). The compressive strength of the largest metacarpal shown can be calculated from its dimensions. It would be about 280 tons, or nearly 10 times the body weight of the animal (Gregory, '51).

³ The maximum compressive strength of bone must be considered a biological invariant. Vertebrate bone is a composite material consisting of hydroxyapatite crystals imbedded in a matrix of collagen, and neither the inherent mechanical characteristics of the component materials nor the composite structure can be sufficiently modified to give any drastic change in the compressive strength.

sports, an activity which brings the organism close to or at times beyond the safe limits of its mechanical design.

No paleontologist has seriously doubted that *Baluchitherium* was a plant-eating, land-living mammal. It was one-third the size of the largest dinosaur, and its existence shows beyond doubt that land animals much larger than the elephant are indeed quite feasible.

Since the safety factor for *Baluchitherium* is more than adequate we can indeed imagine that even bigger animals would be structurally sound. What is the ultimate limit to the size of land animals? Unfortunately, we are unable to give an adequate answer, and we cannot study the question experimentally by building a bigger elephant.

It could be suggested that food is a limitation to size, for all the very large land mammals are plant eaters, and plant material is bulky and cellulose digestion is a relatively slow process. In this regard the whales are better off, for their food is found in a three-dimensional mass of water, the largest whales are plankton eaters which utilize a short food chain, their food has a high energy value, and the nature of the food permits a high rate of digestion. Again, we are not in a position to say how important these factors are in the evolution of the giant whales, for as in most evolutionary questions, we can examine available evidence but *ex post facto* experimentation is not feasible.

ENGINEERING AND PROBLEMS OF DESIGN

Although we cannot experiment by constructing elephants of super-size, we have a great deal to learn from the engineer who constantly encounters the problem of building bigger structures, taller skyscrapers, longer bridges, bigger ships, and so on.

The size of a brick house can be increased if the foundation and the walls are made heavier. There is, however, a limit to this avenue inherent in the limit to the compressive strength of brick. If the engineer wants to design a skyscraper, he changes to the use of steel, rather than brick, as the main supporting material. Another avenue is to change to a new design, for example, by changing from the

use of compression elements to tension elements in the main supporting structures. Brick and stone are very strong in compression, but they are weak in tension and break easily. Steel, on the other hand, has a high tensile strength, and by using relatively light tensile elements for support, the engineer can span rivers more than a hundred times wider than is possible with the use of compression elements (fig. 4).

We thus find three avenues open for the design of larger structures, (1) changed dimensions such as thicker walls, (2) changed materials such as brick to steel, and (3) changed designs such as from compression to tension elements.

Also in biology we find that novel design is fundamentally linked to and essential for an increase in size. For example, ciliary or amoebic locomotion is used only by very small organisms, and larger organisms must use other propulsive mechanisms. Likewise, when the organism is too large to be adequately supplied with oxygen by diffusion alone, the novel principle of convection is added to speed up the supply process. Convection in the external medium, whether water or air, is what we call ventilation. Convection of the body fluids to augment the transport of oxygen over distances where diffusion is inadequate is what we call circulation. Added to this new principle of mass transport by convection we frequently find another novel design, an increase in the oxygen capacity of the circulated fluid by respiratory pigments such as hemoglobin or hemocyanin. Each such new invention in design alters the limiting constraints and extends the possible size range of the organism.

In regard to the internal transport of gases, insects have gone their own separate route. Rather than using convection in a fluid (blood) for improved gas transport, their respiratory system is based on diffusion in gas rather than in water. The tracheal system of insects extends throughout the body, and the fact that the diffusion coefficient in air is some 10,000 times higher than in water insures the adequate distribution of oxygen without the aid of circulation. Even so, highly active insects use mass movement, or convection, for

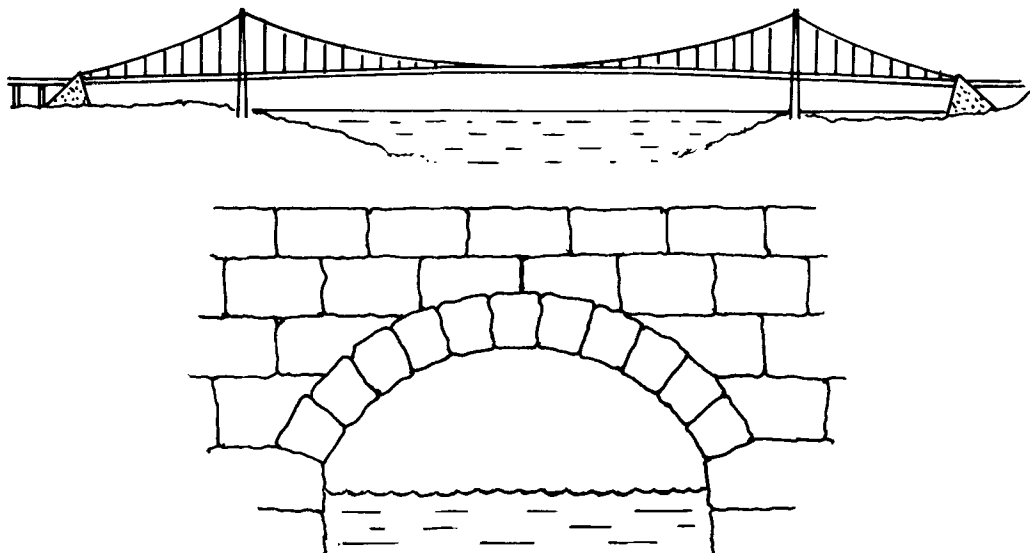


Fig. 4 Two different design principles used in bridge building. In the bridge supported by stone arch (bottom) the supporting elements are in compression. In the suspension bridge (top) the main supporting elements, the steel cables, are in tension. Stone has a high compressive but low tensile strength; steel, in contrast, has high tensile strength.

renewal of air in their respiratory system. Active ventilation of the tracheal system is used to speed up the gas exchange when diffusion alone is insufficient. Even in an insect as small as the fruitfly, active ventilation of the thorax appears necessary to supply the flight muscles with oxygen at the required high rate (Weis-Fogh, '64).

It has been suggested that the design of the respiratory system imposes a limit on the size that insects can attain but it appears that, when the larger tracheae are actively ventilated, the dimensions of the tracheal system are amply sufficient for the supply of oxygen even to the most active tissues. The body size of insects, therefore, is probably not limited by problems of oxygen supply. A more likely limitation on size is the fact that an exoskeleton has some severe mechanical limitations. Although we do not fully understand the principles of skeletal design, we can consider some consequences and limitations.

The exoskeleton of insects is both armor and support, and it must withstand both static loads, bending moments, and forces of impact. For a given amount of material, a hollow tube is stronger than a cylindrical rod made of the same material, but as the diameter of the tube is increased

(keeping the amount of material constant), the wall thickness decreases until it is so thin that the whole structure buckles and collapses under its own weight. Similarly, the protective value of surface armor decreases as the mass of the animal increases with the third power of linear dimensions, and the risk of puncture of even a good armor is vastly increased. For a large animal it seems that, if dynamic forces are considered, the advantages of an exoskeleton are reduced and may even disappear (Currey, '67).

Another difficulty associated with an exoskeleton is that of growth; to increase in a similarly distorted shape. This limits a larger volume before the new cuticle hardens. While the new cuticle is still soft, the forces of gravity would distort a very bulky insect, with the consequence that the new cuticle would harden in a similarly distorted shape. This limitation on size applies specifically to terrestrial animals. Aquatic arthropods, notably crustaceans, have their weight supported by water and thus are not subject to these gravitational limitations; witness the Japanese Spider Crab whose legs may span 4 meters (Schmitt, '65).

The two main groups of terrestrial ani-

mals, arthropods and vertebrates, have gone each their own way, one depending on exo- and the other on endoskeletons. Since evolution apparently does not permit major design changes in mid-stream, we are now unable to say whether this dichotomy is an historical accident, or is maintained by the requirements and constraints imposed by the size of the animals, in turn also limiting the possible size they can attain.

Although we can point to some factors that may limit the size of insects, we cannot formulate a simple conclusive statement. Principles, to have general validity, should have predictive value, and we are again faced with the difficulty that we can establish observed fact, but we can no more build a beetle with an endoskeleton than a bigger elephant to verify our hypothesis. Nevertheless, we wish to understand the hows and whys in biology, and we must explore other avenues in the search for general principles. Let me therefore turn to the subject that in engineering is known as scaling.

SCALING — WHAT IS SCALING?

Scaling is concerned with the effects or consequences of a change in size. When an engineer changes the size of a structure, he must consider the consequences, he must operate within constraints or limitations dictated by dimensions, materials, and design, and he can calculate the ultimate limits beyond which the size cannot be increased.

The engineer faces problems of scaling when he builds taller buildings, bigger ships, or longer bridges. He starts with the desired size, he can select a suitable design, and for the chosen material he calculates the required dimensions. For the biologist the problem is reversed, he sees the final result, the size of the organism and its design, and he wants to understand the hows and whys of what makes this living animal viable and functional.

What scale should the biologist apply when he measures the size of an organism? Two fundamental quantities that can be measured with relative ease are mass and linear dimension. Of these, the measurement of mass usually is much to be preferred. If a linear measurement were

chosen, which particular measurement is the most characteristic expression of the size of an organism? The problem is obvious, and if organisms of widely different shapes and designs are to be compared, how can we find a suitable linear dimension which provides the necessary basis for comparisons? In contrast, weighing can be carried out with great accuracy and can be used for organisms of widely different structure. Furthermore, mass is of fundamental importance because of consequences in regard to the strength of supporting materials (skeletons) the muscular system (locomotion), and metabolic requirements in general. Furthermore, since the density of nearly all animals is close to 1.0, mass is an adequate measure of their volume as well. However, within limits, characteristic linear dimensions may provide a suitable or useful measure, and I shall later give an example of the use of linear dimensions as a more meaningful measure of scale than would be obtained by the use of mass.

I shall now mention a few scaling effects, using an example from elementary geometry, a few from mammalian morphology, and then devote the remainder of this article to examples from physiology.

Figure 5 shows a group of cubes, the eight small cubes at the right having a combined volume equal to the single cube at the left. This simple diagram illustrates the well known principle that the relative surface area of a body increases in the same proportion as a characteristic linear dimension decreases. This applies not only to cubes, but to all geometrically similar bodies, whatever their shape. Bodies that are *geometrically similar*, or *isometric*, are characterized by equality of linear proportions, i.e. a change in any one characteristic linear dimension is accompanied by a change in all other linear dimensions in exactly the same proportion. The essentials of isometric geometry, as they will be used in the following, can be summarized as follows:

$$\begin{aligned}\text{Surface} &\propto (\text{Length})^2 \\ \text{Volume} &\propto (\text{Length})^3 \\ \text{Surface} &\propto (\text{Volume})^{2/3}\end{aligned}$$

The last line above simply states that as the volume of a body is increased, its surface does not increase in the same pro-

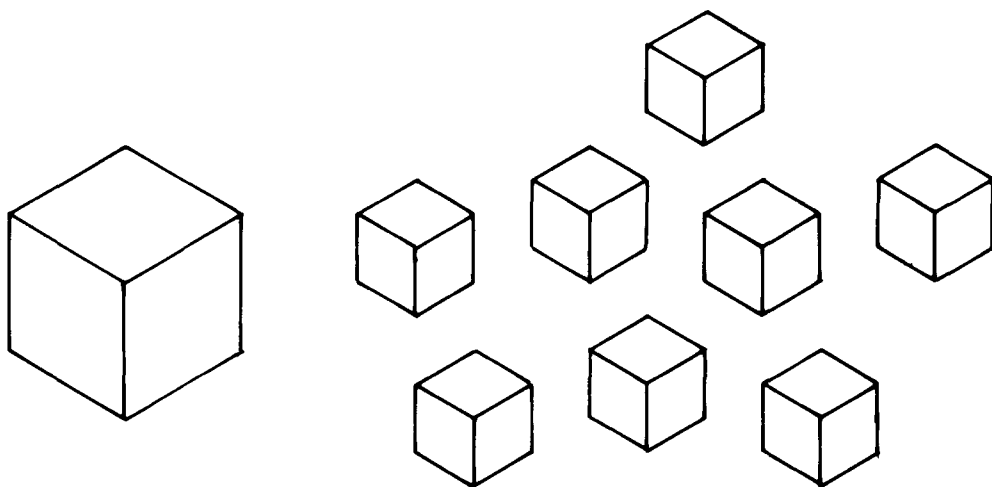


Fig. 5 The eight small cubes at the right have a combined volume equal to the single cube at the left. The side of the small cubes is one-half of that in the large one; the combined surface area of the small cubes is twice that of the large one.

portion, but only in proportion to the two-thirds power of the volume, a fact so well known that I wish to apologize for restating it here.

Real organisms of different size, even when organized on a similar pattern, usually are *not* isometric. Instead, certain proportions change in a regular fashion, and I shall soon mention some examples. Such *non-isometric* scaling is referred to as *allometric* (from the Greek *allos* which means different). An amazing number of morphological and physiological variables are scaled, relative to body mass, according to allometric equations which are of the general form

$$y = b x^a$$

or $\log y = a \cdot \log x + \log b$

This equation expresses the simple statement, thoroughly familiar to biologists, that when the two variables are plotted on logarithmic coordinates, the result is a straight line. A great variety of observations that relate biological variables to body size conform to this general equation, in which the exponent a represents the slope of the straight line obtained in the logarithmic plot.

EXAMPLES OF SCALING — MORPHOLOGY

Animals within similarly organized groups, mammals for example, are similar

but they are not alike. In this context we are not concerned with those characteristic point-by-point differences that are used to establish taxonomic groups, but rather with certain deviations from isometric scaling whose magnitude and direction can be highly informative.

The first scientist to publish on the subject of allometric scaling was probably Galileo Galilei (1637). In his *Dialogues* he discussed the necessary size and strength of the bones of large animals. He realized that the skeleton of a large mammal, such as the elephant, must have dimensions out of proportion to the increase in linear scale, for the mass of the animal increases with the third power of its linear dimensions, and the supporting skeleton must be sufficiently strong to support this increase in mass. Galileo's discussion was accompanied by a drawing (fig. 6), which incidentally reveals a mistake. The large bone, which shows a three-fold increase in length, is given a nine-fold increase in diameter. This gives a greater distortion than required by the increase in mass, which would call for an increase of, not 3^2 , but $3^{1.5}$ (or $5.2 \times$).

We can also trace to Galileo the thought that giant-sized animals must be aquatic so that their enormous weight is supported by water. This he does by having *Simplicio* raise the question of "the enormous size

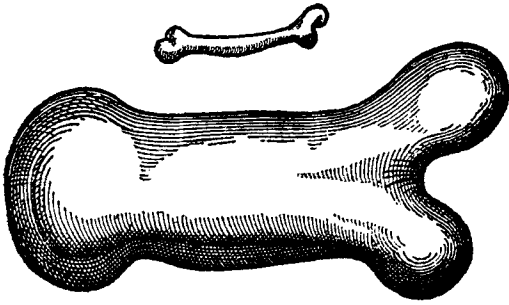


Fig. 6 Galileo was probably the first to point out that larger animals, for reasons of mechanical support, must have bones with dimensions out of proportion to their linear scale in order to support their greater mass (Galilei, 1637).

reached by certain fish, such as the whale which, I understand is 10 times as large as an elephant." In his answer, *Salviati* points out that in spite of the enormous weight of their bones, these animals do not sink, and "The fact then that fish are able to remain motionless under water is a conclusive reason for thinking that the material of their bodies has the same specific gravity as that of water; accordingly, if in their make-up there are certain parts which are heavier than water there must be others which are lighter for otherwise they would not produce equilibrium" (Galilei, 1637).

The fact that the bones of large mammals are proportionately heavier than those of small mammals is familiar to all of us. Suppose that all mammals instead had the same proportion of their body weight as skeleton, say 10% of the total body weight. The skeleton weights would then fall on the dashed line in figure 7. This would be a case of simple proportionality, and the slope of the regression line would be 1.0 (the dashed line). In reality, the skeleton of the elephant is 2.5 times heavier and makes up 25% of the elephant's body weight, and the slope of the regression line that best fits the observed skeleton weights is 1.13.

If the dimensions of the skeleton were scaled on the basis of its ability to support static loads, and if the safety factor should remain the same, the weight of the skeleton should increase with body weight to the power 1.33. Obviously, the skeleton of the elephant, by this consideration, is not

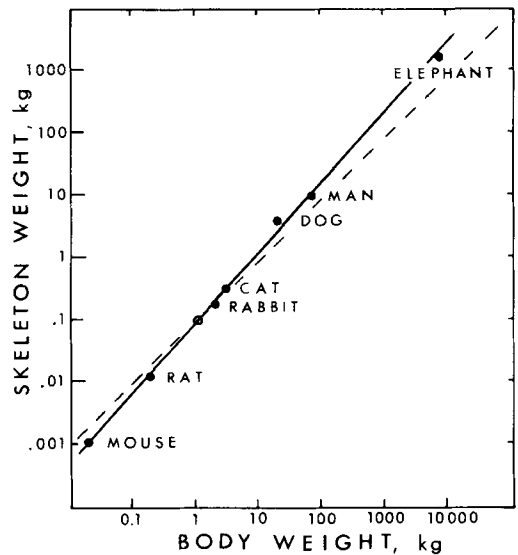


Fig. 7 The relative weight of the mammalian skeleton increases with increasing body size. The skeleton of the elephant makes up 25% of its body weight. If the mammalian skeleton were simply proportional to body weight, the values would fall along the dashed line, which is drawn to represent 10% of the body weight (data from Kayser and Heusner, '64).

scaled as an engineer might design it. The explanation is not that elephant bone is inherently stronger, for the maximum compressive strength of bone is an invariable, or non-scaleable, constant, based on the maximum strength of a composite material consisting of hydroxyapatite in a collagen matrix. Rather, the safety factor for static loads is probably unimportant. We must assume that the safety factor must be scaled according to the needs of the maximum forces that the skeleton must withstand. This occurs during rapid acceleration and deceleration, such as running and jumping. We would therefore predict that, in this sense, the skeleton of the elephant is under-dimensioned, for if an elephant could jump, its bones would probably break on take-off and the animal collapse on impact.

As I mentioned above, allometric scaling is a powerful tool that can lead to important generalizations. As an example, consider the poorly documented but frequently repeated statement that the giant dinosaurs relative to their body size had very small brains, and that this was a major reason

that they ultimately succumbed in competition with larger-brained mammals. The range of brain size, relative to body size, for various vertebrate groups is shown in figure 8. It is obvious that the mean brain size of any vertebrate group is characteristic for that group and follows a regression line which shows that brain mass is approximately proportional to the body mass to the two-thirds power. Jerison ('70) plotted the brain size of dinosaurs in a similar diagram (fig. 8, bottom). A brief inspection of his graph tells us that there is little support for the contention that the dinosaurs had disproportionately small brains. On the contrary, they fall within the expected range of brain size for reptiles as a group, including the most highly developed of living reptiles which have survived successfully in spite of having only reptilian-sized brains.

Instead of graphs, we can use the equations which arithmetically represent the best fitting regression lines for our data. Let us examine the brain size of mammals in this way (table 2). The first line in this table shows that a typical mammal of 1 kg body size has an expected brain size of 10 grams, and that the brain size is expected to increase in proportion to the body mass to the power 0.7. We note that the brain sizes of the various primate groups all vary with nearly the same power of the body mass, 0.67. When the numerical value of the exponent in these equations is the same, the factor preceding the exponential term directly expresses the relative magnitude of the variable in question. By looking only at these factors we find that monkeys in general have brains two or three times as large as typical mammals, that great apes have brains twice as large monkeys, and humans twice as large again. This information, in a nutshell, describes the essential differences in brain size between monkey and man, and we can make this

comparison directly, although the two groups do not overlap in body size. Thus, we have arithmetically compared brain sizes in the same way that we used a graphical method to compare reptiles and mammals in figure 8.

THE SCALING OF FUNCTION —
PHYSIOLOGY

The most universal feature of living organisms is their turnover of energy. Animals, with few exceptions, obtain energy by the oxidation of organic compounds, and the rate of energy turnover, or the metabolic rate, is often measured by the rate of oxygen consumption. The fact that there is a regular relationship between the metabolic rate, or rate of oxygen consumption, and the body size of animals is thoroughly familiar to biologists.

What is the basis for this regular relationship? First of all, small and large animals have cells that are roughly of the same size, within an order of magnitude of 10 μ m (Teissier, '39). A large organism, therefore, is not made up of larger cells, but of a larger number of cells of roughly the same size. One might therefore predict, incorrectly, that a large animal should have a metabolic rate in direct proportion to the number of metabolizing cells, i.e. the same rate per unit mass.

It has long been understood that this cannot be so. In the early part of the last century French scientists realized that the heat dissipation from warm-blooded animals must be roughly proportional to their free surface, and since small animals have a larger relative surface, they must also have a higher relative rate of heat production than large animals (Sarrus and Rameaux, 1838-1839). This argument was taken up by Bergmann (1847), leading to the formulation of Bergmann's rule, which states that animals in colder climates are of larger body size (i.e. have smaller relative external surface area) than their relatives from warmer climates. The validity of this rule has been questioned and has led to much controversy.

About 100 years ago Rubner (1883) studied the metabolic rate of dogs of various size, and confirmed that their heat production was more closely related to body surface than to body mass. This resulted

TABLE 2
*Equations expressing brain size in relation to
body mass (M, in kg), for mammals and
various groups of primates*

Mammals	$0.01 \times M^{0.70}$
Monkeys	$0.02 \text{ to } 0.03 \times M^{0.66}$
Great apes	$0.03 \text{ to } 0.04 \times M^{0.66}$
Humans	$0.08 \text{ to } 0.09 \times M^{0.66}$

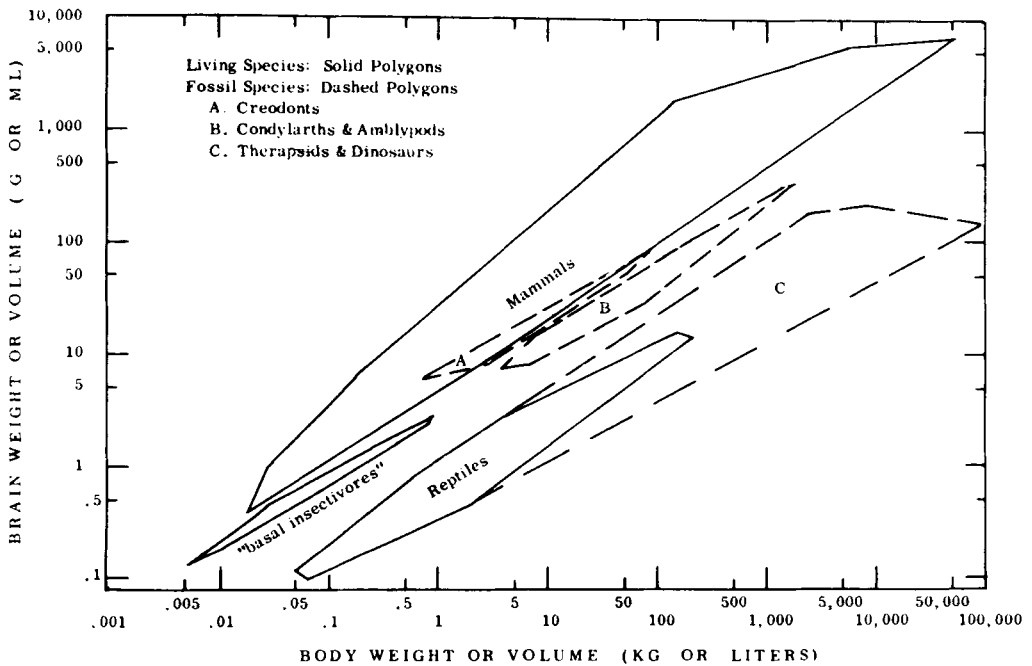
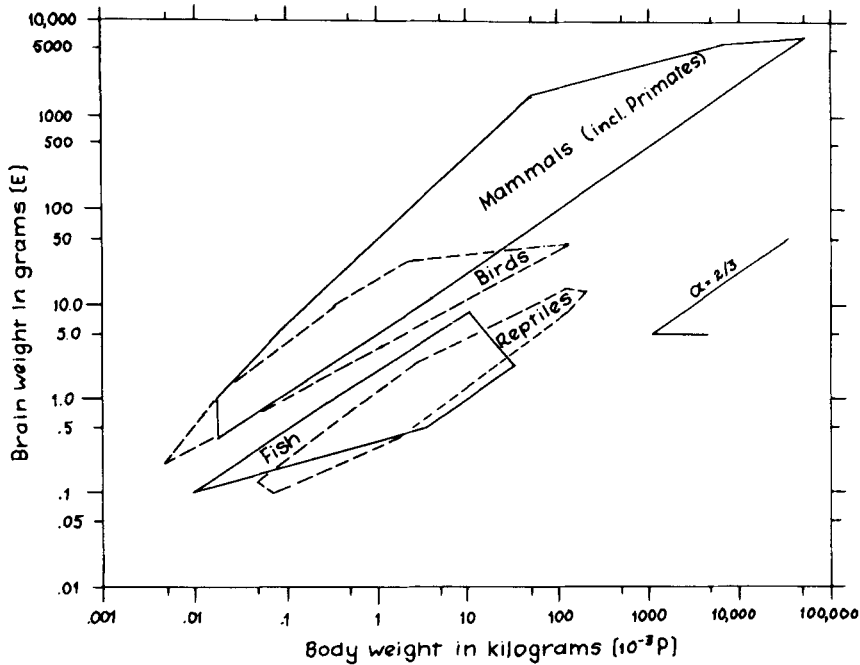


Fig. 8 The brain weights of vertebrates fall within ranges characteristic for each vertebrate group (top). Within each group the brain weight tends to increase with body weight to the two-thirds power. The brain weights of the large dinosaurs fall within the dashed polygon marked C (bottom), and thus within the relative brain size characteristic of living reptiles (Jerison, '70).

in the acceptance of a "surface rule," which, although it misrepresents a mass of available data, for many years has dominated in the analysis of metabolic rates. It is to the credit of Max Kleiber that he instead expressed the relationship between metabolic rates and body mass of mammals as an allometric equation which accurately describes the available information (Kleiber '32). Further support for the use of allometric equations in metabolic studies was accumulated by distinguished investigators such as Brody and Procter ('32), Brody ('45), Benedict ('38), Krebs ('50), Zeuthen ('53), Hemmingsen ('60), and many others.

A tremendous amount of information has been accumulated and compiled, and we can now say with certainty that the metabolic rate of warm-blooded vertebrates is not scaled relative to body surface (body

mass to the power 0.67), but rather to the body mass to the power 0.75, a highly significant difference when we consider that the size range of the mammals studied is about one million-fold, from the shrew to the elephant.

The best known such compilations usually present some version of a plot known as the mouse-to-elephant curve. It shows that the rates of heat production or oxygen consumption of birds and mammals generally are similar, and, when plotted against body weight on logarithmic coordinates, fall on a straight line (fig. 9). A more detailed comparison of mammals and birds, based on extensive compilations of data, was presented by Lasiewski and Dawson ('67). These investigators found that, if passerine and non-passerine birds are treated separately, their metabolic rates fall on lines with the same slope as

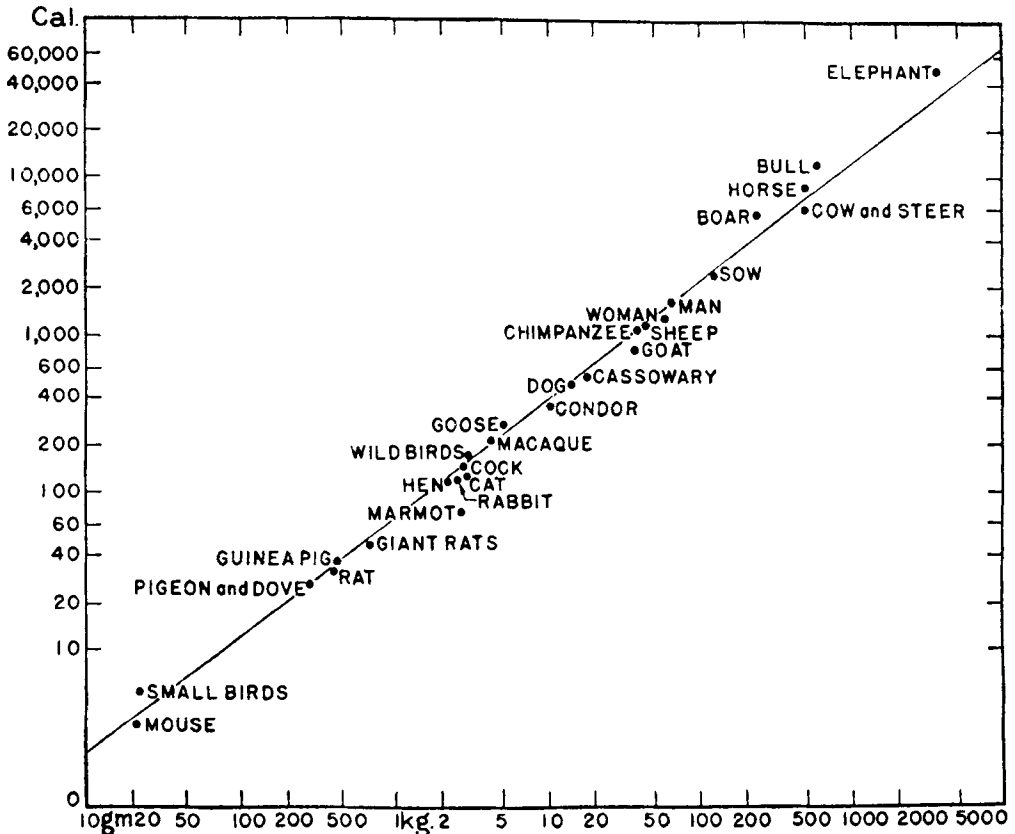


Fig. 9 The total heat production of birds and mammals, when plotted against body size on logarithmic coordinates, tends to fall along a straight line. This regression line has become known as the "mouse-to-elephant curve" (Benedict, '38).

mammals, i.e. statistically indistinguishable from the slope 0.75.

The analysis of bird metabolism was further refined by Aschoff and Pohl ('70) who showed that if observations obtained during the night, or natural rest period (called rho-values), are treated separately from daytime observations (alpha-values, obtained at rest but during the normal period of activity), the scatter in the data is reduced and the statistical significance of the slope can be established with even higher accuracy. Since alpha-values are about 25% higher than rho-values, the inevitable but unanswerable question is, which observations represent the "true" resting metabolic rate?

The metabolic rate of marsupials shows a relationship to body size similar to that of the eutherian mammals, although the regression line for marsupials is somewhat lower (MacMillen and Nelson, '69; Dawson and Hulbert, '70).

The metabolic rates characteristic of each of the major groups of warm-blooded vertebrates can now be compared, each represented by the equation for the regression line in the logarithmic plot of metabolic rate against body mass (table 3). Since the value of the exponent in these equations is the same, the ratio of the numerical factors preceding the exponential term directly expresses the relative magnitude of the metabolic rate at any body weight. We see that marsupial mammals in general have lower metabolic rates than eutherian placentals, that non-passerine birds are similar to eutherian mammals, and that passerine birds tend to have metabolic rates nearly twice as high as other birds. This, in brief, is the essence of all accumulated information about the metabolic rates of warm-blooded vertebrates at rest.

The common occurrence of the expo-

nent 0.75 in these equations has led to much speculation, but until recently no adequate explanation had been proposed.

Constraints. It has long been obvious that the metabolic rates of mammals could not be proportional to their body mass, if for no other reason because of the requirement of maintaining their normal body temperature. This was convincingly expressed by Kleiber ('61) in the following way: If a steer were designed with the same weight-specific metabolic rate as a mouse, it would be able to dissipate heat at the rate it is produced only if its surface temperature were well above the boiling point. Conversely if a mouse had the same low weight-specific metabolic rate as a steer, to keep warm it would need to be insulated with fur at least 20 cm thick. Obviously, a consideration of thermal problems confirms that heat production cannot be directly related to body mass.

A consideration of other physiological variables leads to similar conclusions. The supply of oxygen is a case in point; oxygen uptake takes place across the alveolar membrane and the rate of uptake is directly related to the available surface area. This area in turn cannot increase as the third power of linear dimensions. Similar considerations can be applied to the extensive data that have been accumulated on the scaling of lungs, circulatory system, size of the heart and its frequency, dimensions of the aorta and other blood vessels, linear velocity of the blood, oxygen capacity of the blood, unloading pressures for oxygen, capillary density and diffusion distance in the tissues, and so on. Each of these variables can be analyzed to show that the scaling of metabolic rates in direct proportion to body mass would meet with insurmountable obstacles or constraints (e.g. Schmidt-Nielsen and Larimer, '58; Tenney and Remmers, '63; Stahl, '67; Schmidt-Nielsen, '70, '72a).

All these considerations lead to the suggestion that metabolic rate cannot be scaled in proportion to the third power of a linear dimension and must closely follow a second power relationship. However, the empirical data show that there are regular deviations from simple surface relationships, the slope of metabolic regression lines being, not 0.67 but rather 0.75, and

TABLE 3

The metabolic rates (P, in watts) relative to body mass (M, in kg), of major groups of higher vertebrates, expressed as allometric equations

Marsupial mammals	$P = 2.36 \times M^{0.737}$
Eutherian mammals	$P = 3.34 \times M^{0.75}$
Non-passerine birds	$P = 3.79 \times M^{0.723}$
Passerine birds	$P = 6.25 \times M^{0.724}$

the many related variables being scaled accordingly. These statistically highly significant deviations are repeated from animal group to animal group, and are found also among many invertebrates where problems of heat dissipation are irrelevant.

For many years the attempts at "explaining" the observed deviations from the surface-related exponent have suffered from a certain metaphysical quality. It was speculated that, although the scaling of metabolic rate to body size for a variety of reasons cannot deviate too much from a surface relationship, yet a "desire" of the larger animals to achieve a mass-related metabolic rate leads them to arrive at a "compromise" exponent of about 0.75.

Quite recently this problem was subjected to a more rational analysis by McMahon ('73). McMahon started with the well-known fact that vertebrates are not geometrically similar or isometric. I have already mentioned the size of the skeleton and the brain as examples. McMahon suggested a model based on the analysis of functional requirements of elastic similarity between animals. This model, which is based on sound engineering principles, requires a distortion from geometric similarity whereby length dimensions of bones are multiplied by one factor and diameters by another as body size changes. McMahon presents cogent arguments that metabolically related variables should be scaled according to elastic similarity with body weight raised to the power 0.75, and that biological frequencies should be scaled inversely as body weight to the power 0.25. As McMahon's model is extended and applied to the analyses of an increasing number of functional variables, notably in animal locomotion, the approach becomes increasingly convincing.

ANIMAL ACTIVITY — THE DEMANDS OF LOCOMOTION

For many years we have studied metabolic rates of animals sitting confined in various boxes or containers which we call metabolic chambers. At times darkness is used to ensure that the animal will be inclined to remain inactive within the confined space. This interest in the animal at rest is reasonable, for it establishes a base with which other measurements can be

compared. The concept that there is a "basal" level below which the metabolic rate will not fall has been thoroughly discredited, but the resting animal does maintain a rather constant metabolic level which can be called the resting or maintenance level. In the preceding I have alluded to the great body of metabolic information that has been accumulated and to its analysis in the light of scaling principles.

Animals, however, do not spend their lives sitting still, at rest, only maintaining themselves. Characteristically, they move about, feed, mate, pursue prey, and escape from predators. Indeed, locomotion is a most characteristic animal activity, and there is a premium on high speed, for the animal that is too slow won't eat and will be eaten.

The last few years have witnessed an upsurge in the interest in animal locomotion. Animals have been studied as they move in water (swimming), in air (soaring and flapping flight), and on land (walking and running). It appears that the amount of energy used to move one unit body mass over one unit distance declines regularly with increasing body size, whether the animal moves in water, in air, or on land. Each kind of locomotion seems to have its characteristic scaling function, resulting in straight lines when the cost of locomotion is plotted against body size on logarithmic coordinates (Schmidt-Nielsen, '72b). However, there are characteristic differences between the three kinds of locomotion, so that for a given body size, flying a certain distance requires less energy than walking or running, and swimming the same distance is cheaper than flying. The reasons for these differences are not fully understood, and are subject of intensive study. In the following I shall concern myself mostly with locomotion on land.

The amount of energy that various mammals use when running was examined by Taylor and his collaborators ('70). Some of their observations on mammals running at various speeds are shown in figure 10. As expected, the oxygen consumption or energy expenditure, increases with the speed of running. This, of course, is something that we already know from personal

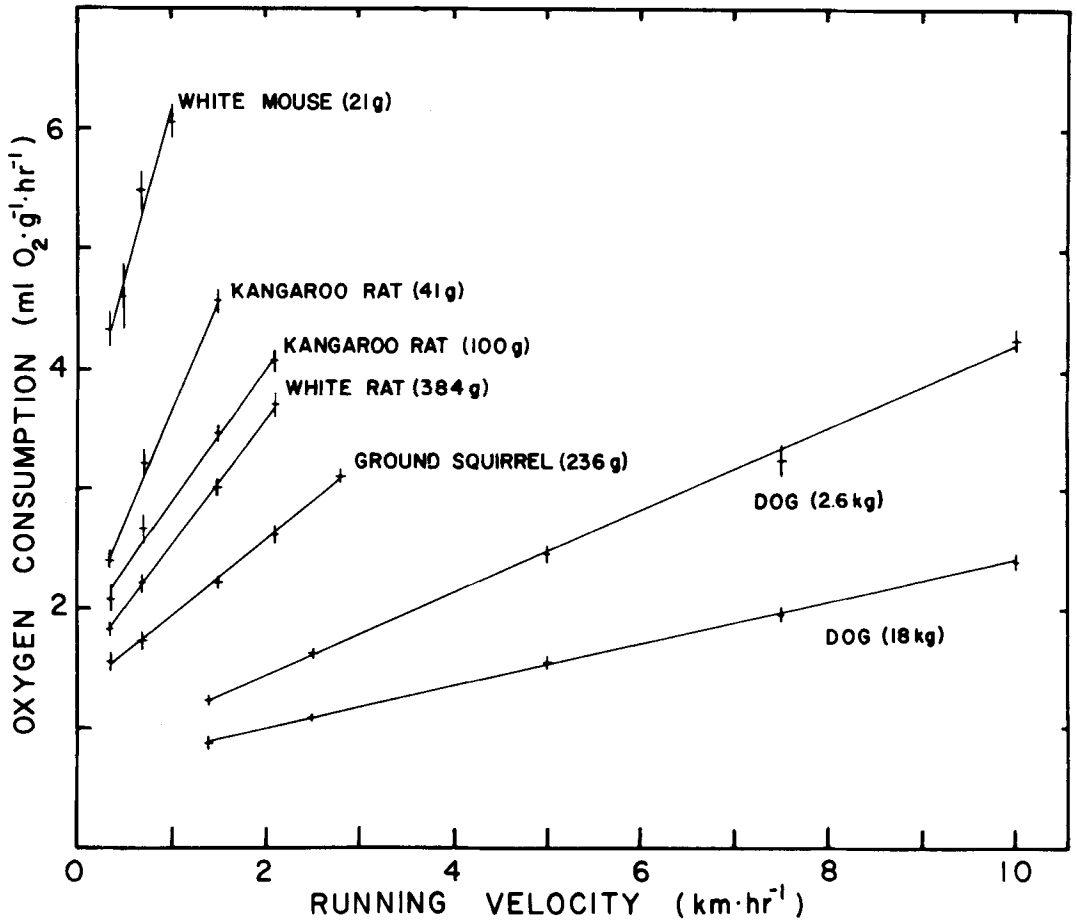


Fig. 10 The oxygen consumption of running mammals increases with the speed of running. For each species the increase is linear, but the oxygen consumption increases more steeply for a small than for a large animal (Taylor et al., '70).

experience. It may be surprising, however, that the cost increases linearly with the running speed. The graph also shows that the cost increases much faster in a small animal (steeper slope) than in a large animal. The slopes of the regression lines, in fact, indicate the cost of running, or more precisely, the energy used to move one unit of body weight over one unit distance. If we plot these slopes against the body size, we obtain the graph shown in figure 11. The units on the ordinate indicate how many ml of oxygen are consumed when the animal moves one gram of its body weight over one km, in other words, a sort of weight-related mileage cost of running.

The graph shows that the cost of run-

ning decreases regularly with increasing body size; i.e. the large animal moves about at less expense than the small animal. Data from man are represented by the open circles, which indicate that his cost of moving is roughly twice that of a four-footed mammal of his size. Is bipedal locomotion always more expensive?

Bipedal mammals are not very common, but birds run on two legs. Data for birds that have been collected by Fedak et al. ('74) show a pattern similar to that for mammals. Thus, the cost of running for both birds and mammals is regularly scaled relative to body size, and the cost is of the same magnitude for the two groups. However, the regression lines, relative to body

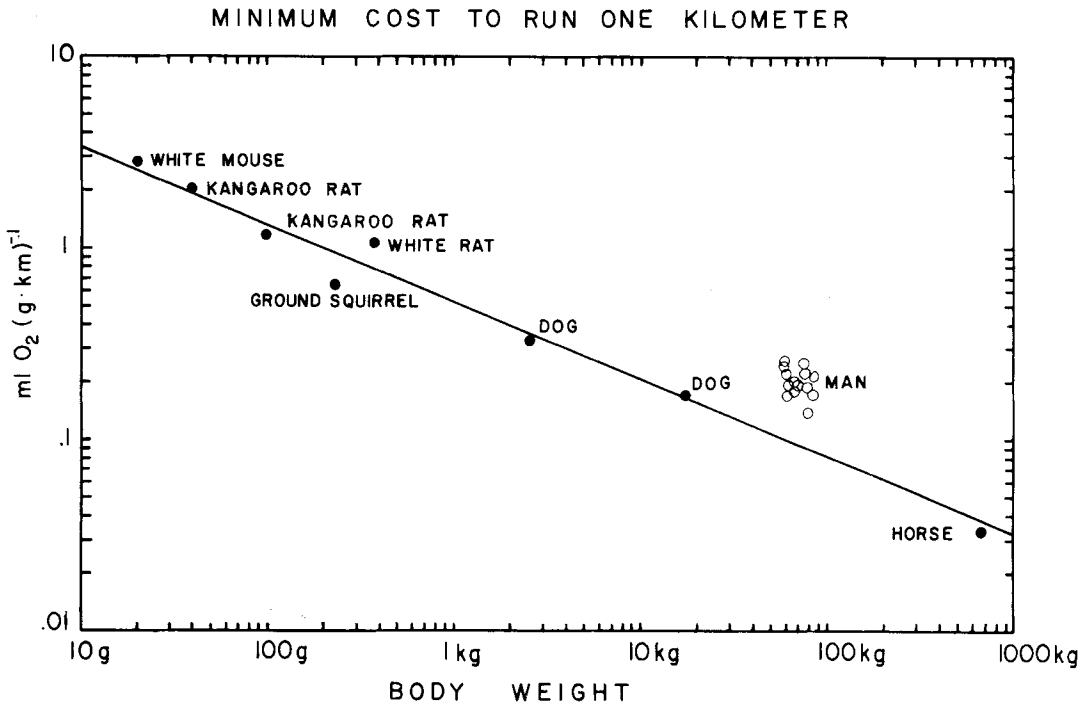


Fig. 11 The cost of running, expressed as the oxygen needed to transport one gram of body weight over one km, decreases regularly with increasing body size. Data for man (bipedal running) fall above the line representing data from mammals running on all four legs (Taylor et al., '70).

size have significantly different slopes, that for mammals being -0.4 and for birds -0.2 . The two lines intercept at a body size of somewhat less than 1 kg, and birds and mammals of this size can be expected to run at the same energy cost. A larger bird could be expected to run at a higher cost than a similarly sized mammal; the reverse would be true for small birds which could be expected to run at less expense than mammals of the same body size. At the present time there is no satisfactory mechanical analysis of this consistent difference between birds and mammals. We therefore cannot say whether it is due to fundamental differences between birds and mammals and the way they solve the problems of terrestrial locomotion, or to inherent mechanical differences in bipedal and quadrupedal locomotion.

The problem of whether bipedal and quadrupedal locomotion results in different costs of moving was recently examined by Taylor and Rowntree ('73), who chose

two primates that can move about, either on two or on four legs, the capuchin monkey and the chimpanzee. They found no significant difference in the energy cost, whether these animals moved on two or on four legs. However, both species are of intermediate size (3.3 and 17.5 kg, respectively), and in this size range the regression lines for birds and mammals (bipedal and quadrupedal running) run fairly close to each other. The question of whether bipedal and quadrupedal locomotion fundamentally should differ in energy cost therefore remains open.

The difficulty in analyzing the cost of locomotion rests on the deficiencies in our knowledge of how energy is used when an animal runs. An animal that runs horizontally performs a trivial amount of external work, restricted to air resistance and to friction against the ground, which at most account for a few per cent of the total energy expended. The remainder of the energy is dissipated internally as heat.

Energy must be used to overcome friction in the joints and viscous resistances in muscles and other tissues. The movement of the limbs requires that kinetic energy is imparted to them on acceleration, and again removed as they are decelerated and the motion is reversed. Also the up-and-down movement of the center of mass in the field of gravity implies a constant shift between potential and kinetic energy. We do not have, except for man, even an approximate idea of how much of the kinetic energy can be stored in elastic elements during one phase of the stride and can be recovered during other phases.

An easily understood example of elastic storage of energy is provided by the jumping of the kangaroo. If a fast moving kangaroo were to make each stride as a separate standing jump, it would soon be exhausted. Instead, as the animal hits the ground at considerable speed, much of the kinetic energy is stored in elastic elements of muscles and tendons, to be recovered on the next jump, much as when a tennis ball bounces over the ground. This model is consistent with the studies of Dawson and Taylor ('73), who showed that the energy cost of the jumping kangaroo does not increase with increasing speed, once the speed of jumping has been attained.

An early attempt at developing a model which would scale the energy cost of locomotion to body size of mammals was made by the eminent British physiologist, A. V. Hill ('50). Hill made the correct assumptions that maximum force per cross-sectional area of a muscle is a constant, and that the maximum work of a single contraction per unit mass of muscle is also constant. His assumption that mammals are of isometric build, however is only an approximation. Hill's model predicted that stride length should be directly and stride frequency inversely related to the linear dimension of the animal (or body mass to the power 0.33). The conclusion was that all mammals should be able to run at the same top speed.

Hill's model applied to top speed (i.e. maximum power output), and an experimental test is therefore difficult to carry out. Not only is it difficult to determine top speed for a variety of animals, but meta-

bolic studies at this speed meet with formidable technical obstacles.

A rational approach to this difficulty was presented in a recent issue of *Science* by Taylor's group (Heglund et al., '74), who studied the stride frequencies of mammals of sizes from 9 to 500,000 grams. During walk or trot, the stride frequency increased linearly with speed, but once the animal started to gallop the frequency remained nearly constant as the animal further increased its speed. In this sense galloping is reminiscent of the jumping kangaroo, which also alters its speed within a several-fold range without appreciably changing the jumping frequency (Dawson and Taylor, '73).

The transition from trot to gallop was constant for each animal and showed the maximum sustained stride frequency for that animal. From species to species this maximum stride frequency decreased regularly with body size (fig. 12). The speed of transition can be considered as a functionally similar speed for animals of different size, and once this transition point is defined, it can be used to refine the analysis of locomotion and how it is scaled relative to body size. It appears that each transition to a faster gait recruits additional elements of the body for storage of elastic energy, so that in gallop the entire trunk is involved in elastic storage. This speculation needs confirmation, but it is in accord with McMahon's approach, using elastic similarity in the analysis of animal function as related to body size. It can be expected that the further analysis will lead to generalized models of how animal locomotion is scaled, thus providing a unifying principle which at the present time is lacking.

So far, all the examples I have mentioned have used body mass as the variable to which the scaling of function has been related. I do not wish to leave the impression that body mass is the only fundamental quantity that is useful in problems of scaling, and I shall mention an example where a function is more clearly understood if scaled against a linear dimension, rather than mass. This applies to the swimming speed of fish of different sizes. Figure 13 shows the swimming speed of the small fresh water fish, the dace, as meas-

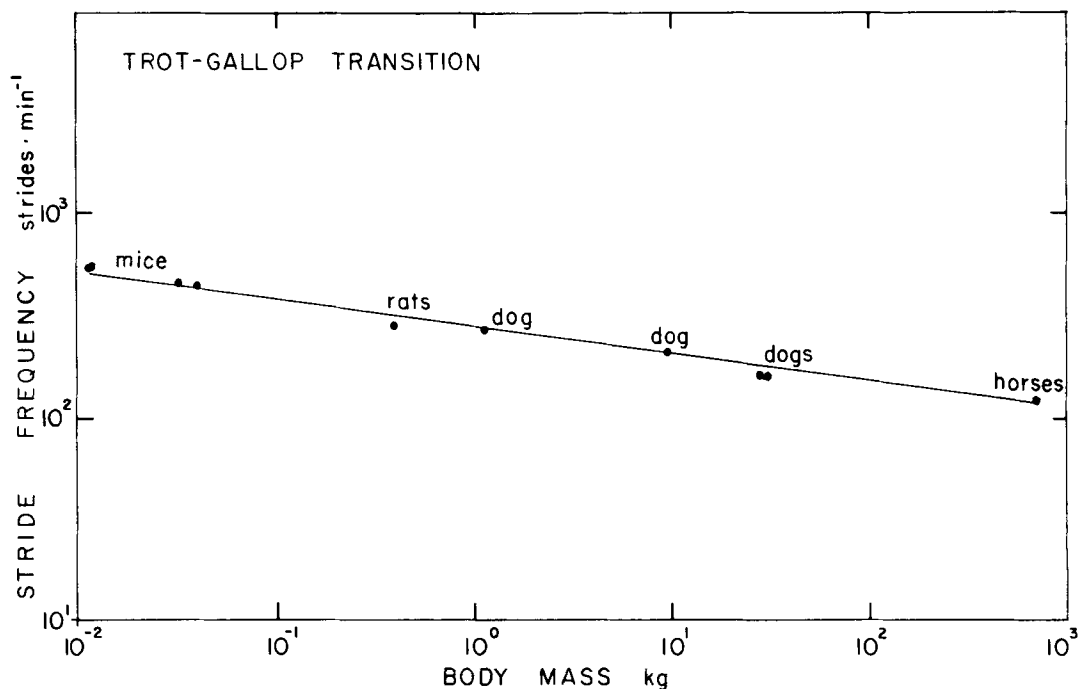


Fig. 12 The transition between trot and gallop for a running mammal takes place at a certain stride frequency, characteristic for each species. When the stride frequency at the transition point is plotted against body size on logarithmic coordinates, the points fall on a straight regression line (Heglund et al., '74).

ured by Bainbridge ('58). As expected, the swimming speed increases with increasing frequency of tail beat. The fact that the increase is linear is an interesting but less predictable observation. The linearity extends over a wide size range of the fish, but for any given tail beat frequency the swimming speed is higher for the larger fish.

If instead we express the speed in relation to body length, i.e. the fraction of the body length that a fish moves in one second, the resulting graph (fig. 13, bottom) reveals a fundamental similarity between the different sized fish. The coordinates of this graph have the same dimensions, second to the power minus one. Thus the slope of the regression line is a non-dimensional number. In simple words, it expresses that, irrespective of the size of the fish, the distance traveled for one beat of the tail is always the same fraction of its body length.

Since the linear dimension of the fish is related to its mass (the small and large

fish are virtually isometric), we could equally well use the body mass as the basis for our scaling as we so often do. However, this would give a more complex expression that in this case obscures the simplicity of the relationship. The use of the linear dimension, body length, is more revealing and makes the results intuitively understandable.

There is presently a growing interest in studies of animals during activity, and the examination of a variety of species gives us an increasing appreciation of the importance of comparative physiology. In

Fig. 13 The swimming speed of the dace (*Leuciscus leuciscus*) increases with the frequency of tail beat. At any given frequency, the swimming speed is greater for large fish than for small fish (top). However, if the data are combined by expressing the distance traveled in one second relative to body length of the fish, the resulting graph (bottom) reveals that the distance traveled for each beat of the tail is the same fraction of the body length for all fish, irrespective of size (redrawn from Bainbridge, '58).

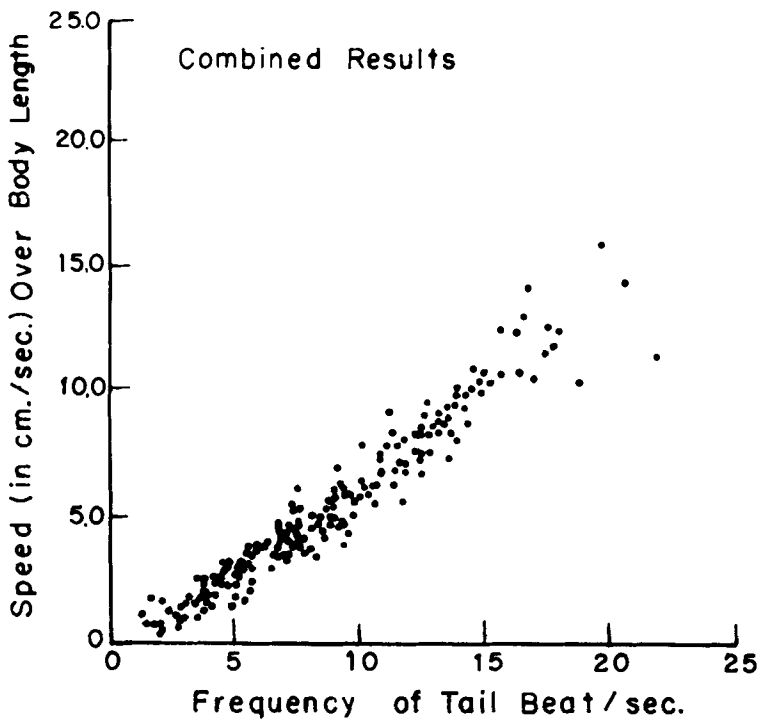
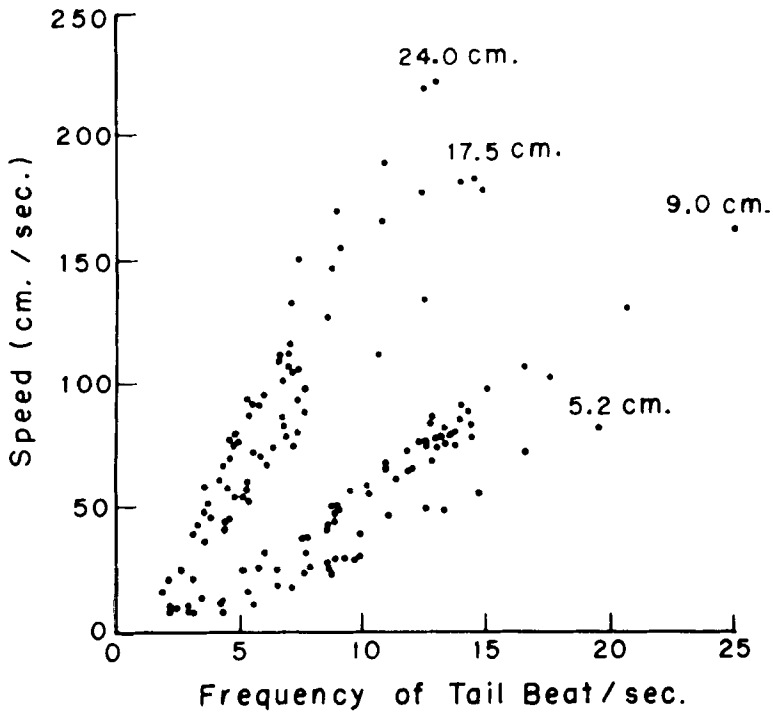


Figure 13

particular, it is becoming more and more evident that the size of an animal is one of the most significant aspects of its endowment and involves both possibilities and limitations in regard to function. We have for so long focused our interests on similarities that we have tended to overlook one of the most fundamental differences between animals, the size of their bodies.

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