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Christopher McGowan
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1 A Matter of Scale

What happens when things get bigger? Suppose you had two apples in your hand, a small crab apple and a regular-sized apple whose diameter was twice as big. How much heavier would the larger apple be? Obviously, not twice as heavy. In fact, the larger one would be eight times heavier. You could verify this for yourself. There are many other objects to choose from besides apples – potatoes, onions, squash, and tomatoes come immediately to mind. If you went into your local supermarket armed with a ruler or measuring tape, you could find a suitable pair of fruit or vegetables where one was twice as large as the other. If you weighed them you would find that the larger one was not exactly eight times heavier – it might be less than eight or more than eight. Why? There are two reasons. First, the larger object is unlikely to be an exact replica of the smaller one. Thus, if photographs were taken of each one and prints were made to the same size, they could not be exactly superimposed. This is the nature of biological specimens. However, they are close enough to having the same shape (technically, having *geometric similitude*) that the larger one will not be far from eight times heavier than the smaller one.

A second, and probably lesser, reason for the discrepancy is measurement error. As the two objects were essentially spherical, you would have measured their diameters, or their circumferences, if using a tape. But it is unlikely that the diameter of, say, an onion, would be the same all around its circumference, because it is not a perfect sphere. To allow for this irregularity you would need to measure several diameters and take an average. However, even if the object had been a perfect sphere, it is unlikely that you would have been able to measure its diameter without error. As you will see later, measurement error always occurs when attempts are made to measure complex shapes, like animals and plants.

There are two sorts of measurement error, one attributable to a lack of accuracy and the other to a lack of precision. Although the terms accuracy and precision tend to be used interchangeably in our everyday language, they have different meanings when it comes to measurements. *Accuracy* is the closeness of a measurement to its true value. *Precision* is the closeness of repeated measurements of the same character. If you had a set of calipers with

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bent points, you would never be able to measure the length of a skull accurately, simply because your instrument would always give a false reading. However, if you were careful, you would be able to remeasure the skull length and get the same, or almost the same, measurement every time, showing that your measurements were precise. Measuring the length of a skull, or any other linear dimensions of an animal, is not as easy as measuring a regularly shaped object like a cube or cylinder. Consequently it is necessary to define how such measurements are made, as we shall see later. So much for length measurements, but how do we measure how heavy objects are?

The terms *weight* and *mass* are often used interchangeably, but they are not the same. The mass of a body – expressed in such units as grams, pounds, kilograms, tons – is a measure of the quantity of material, and it is invariant of gravity. If a person had a body mass of 70 kg, that person would have the same mass regardless of whether he or she were on Earth, the Moon, or in space. Weight, however, is dependent on gravity, and has the units of *force*. Force is the product of mass and acceleration, in this case the acceleration due to gravity. However, in everyday usage, weight has the same units as mass. A person might therefore be said to weigh 70 kg. But that weight would drop to about 11 kg on the Moon, simply because the Moon's gravity is only about 0.16 that of Earth's. In space a person's weight is zero because there is no gravity. Because of the confusion and ambiguity between the two terms, only mass will be used in this book.

Needless to say, metric units will be used throughout, with the occasional reference to imperial units, as these are universally used in science. However, the metric system is not without its problems, largely because of the many different units that are in use. To resolve these problems an international commission was established in 1960 to recommend which metric units should be used and how they should be abbreviated, and to define some new terms. This system of metric units, universally used in science and adopted by many countries, including Canada, is referred to as SI, from the French *Le Système International d'Unités*. The common SI units used in science to derive such variables as force, *work* (the product of force and distance), and *power* (the rate of doing work), are the meter (abbreviated m), the kilogram (kg), and the second (s). In my undergraduate days the units used to be the centimeter (cm), gram (g), and second.

Let's return for a moment to the relationship between length and mass. The reason why doubling the length increases the mass by eight is because volume, hence mass, increases with the cube of the length. This can be shown with a series of cubes built out of sugar cubes (Fig. 1.1). The cubes have edges of 1, 2, 3, and 4 sugar cubes. Their respective numbers of sugar cubes, hence their volumes and masses, are therefore 1, 8, 27, and 64. The fourth cube, for example, is four times longer than the first, and is therefore predicted to be $4 \times 4 \times 4 = 4^3 = 64$ times heavier, which you know to be true. Comparisons between any other pair of cubes would give similar confirmations of the predicted relationship.

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Figure 1.1. A series of cubes, built from sugar cubes.

The cubic relationship between length and mass holds only if the bodies being compared are the same shape, are solid, and have the same density. Comparing apples and pears does not work very well because of the shape differences, although the other two conditions are met (being solid and having the same density). Nor does it work for balloons of different sizes because most of their mass is accounted for by the rubber skin, that is, by area rather than by volume. Nor would it hold for a comparison between a brick and a gold ingot because of the differences in their densities.

The cubic relationship between length and mass can have some remarkable consequences. Consider two people of similar build, one of whom is six feet, six inches tall (1.98 m), the other five feet, two inches (1.57 m). This is not an enormous size difference, but the taller person would be twice as heavy as the other. This is because mass increases with the cube of the increase in size, and $[1.98/1.57]^3 = 2.0$. There are many similar examples lurking on supermarket shelves. I have two similarly shaped plastic containers of bathroom cleaner in front of me. The larger one is only a bottle cap and shoulder taller than the other (24.3 cm compared with 19.7 cm), but it contains twice as much cleaner (500 ml compared with 250 ml). What about different sized animals? Spector (1956) gives some body length and mass data for fishes, including a bonito (*Katsuwonus pelamis*) and a bluefin tuna (*Thunnus thynnus*). Both are members of the same family (Scombridae) and are of similar shape. The body lengths are given as 39 and 116 inches (approximately 1 m and 3 m), so the increase in mass should be by a factor of $[116/39]^3 = 26.3$. The mass of the bonito is given as 39 pounds (17.7 kg), producing a predicted value of 1,025.7 pounds (466.2 kg) for the tuna. The recorded mass is 977 pounds (444.1 kg), which is close. To take a more extreme example, a house mouse (*Mus musculus*) is about 8 cm long (ignoring the tail) and has a mass of about 36 g. An average African elephant (*Loxodonta africana*), which is only roughly similar in shape to a mouse, has a length of about 4 m. The magnification factor here is about 50, suggesting that the elephant would be about 125,000 (50^3) times heavier than the mouse. Multiplying 36 g by 125,000 gives a mass of 4.5 metric tonnes (abbreviated t), which is about the mass of an average elephant. Incidentally, a metric tonne is 1,000 kg, and an imperial ton (note different spelling) is 2,240 pounds, or 1,018 kg, which is virtually the same.

Whereas volumes, hence masses, increase with the cube of the length increase, areas increase only with the square. This can be shown by looking at the sugar cubes again. Consider the surface areas of the four cubes. Each cube

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has six faces, and the areas of each face are accordingly 1, 4, 9, and 16 for the four cubes (the units are "square sugar units"). The total surface area for the four cubes is therefore 6, 24, 54, and 96, respectively. Comparisons between any pair of cubes confirms the relationship between size increase and area increase. Take, for example, the first and third cubes. The size increase is 3, and the increase in surface areas is 54/6 = 9, which is (size increase)^2.

To summarize, as things get bigger, their volumes increase with the cube of the length increase, whereas their areas increase only with the square of the length difference. As a consequence, areas lag behind volumes, which can be expressed by the area-to-volume ratio. As we shall see, the area-to-volume ratio has universal importance. The values of this ratio for the four sugar cubes are 6/1 = 6, 24/8 = 3, 54/27 = 2, and 96/64 = 1.5. To see how area-to-volume ratio relates to size increase, all we need to do is make some pairwise comparisons between the cubes. For example, the size difference between the first and second cube is 2, whereas the difference in their area-to-volume ratios is 3/6 = 1/2. Similarly, the size difference between the first and third cube is 3, whereas the difference in their area-to-volume ratios is 2/6 = 1/3. For the first and fourth cubes the size difference is 4, and the difference in ratios is 1/4. The pattern is obvious: as things get bigger, the area-to-volume ratio changes according to the reciprocal of the size increase. The universal importance of this relationship, both in living and nonliving systems, cannot be overemphasized. It accounts for an infinite array of phenomena among living organisms, from why a mouse's heart beats about 700 times a minute compared with an elephant's 30, to why the heaviest animal that has ever lived, the blue whale (*Balaenoptera musculus*), is aquatic. Examples from the nonliving world range from why the peas on your plate cool far more rapidly than the baked potato, to why the development of 747-sized aircraft had to await the advent of the jet engine.

One aspect of area-to-volume ratios that I want to focus on concerns load bearing, with all its implications for skeletal support in vertebrates. Before returning to the four cubes to see how their load bearing changes with increasing size, we have to consider how to express load bearing. The simplest way is to assess the pressures acting on the bases of the four cubes. Pressure, or *stress,* the synonymous term that is used in preference here, is defined as force per unit area. The SI unit of force is the *newton* (N), 1 newton being defined as the force required to give a mass of 1 kg an acceleration of 1 m per second per second (1 ms^{-2}). Area is expressed in square meters, therefore stress is expressed in newtons per square meter (N/m^2). The SI unit for stress is the pascal (Pa), 1 Pa being the stress experienced when a force of 1 N acts upon an area of 1 square meter.

What stress do my shoes exert on the ground when I am standing still on both feet? My mass is 77 kg, the acceleration of gravity is 9.8 ms^{-2}, and my shoes have a total area of contact (both soles and both heels) of about 0.028 m^2. The force exerted by my body mass is therefore 77 × 9.8 N, so the

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stress is 77 × 9.8/0.028 = 26,950 Pa. As the stresses encountered in biology and in engineering often involve high numbers, it is usual to express results in multiples of pascals, such as the kilopascal, kPa, which is 1,000 Pa. The stress exerted by my body mass is therefore expressed as 26.95 kPa. Atmospheric pressure and blood pressure, still usually expressed in terms of millimeters of mercury, are beginning to be expressed in kPa. Atmospheric pressure is about 100 kPa, and normal blood pressure during systole (the beating of the ventricles) is about 16 kPa. The average pressure of the air inside a car tire is about 200 kPa.

How do the stresses acting on a body change with increasing body length? For the cubes, length is the same as height and width. For simplicity, I shall use their individual mass – the number of sugar cubes in each large cube – to represent force, thereby saving the trouble of multiplying each one by the acceleration of gravity. This shortcut is legitimate here because I am only comparing one cube with another.

The area of the bases of the four cubes of sugar are 1, 4, 9, and 16, respectively, so the stresses acting on their bases are 1/1 = 1, 8/4 = 2, 27/9 = 3, and 64/16 = 4. Thus stress increases according to the increase in size. The implication of this result is that the stresses exerted on the ground by an animal's feet are proportional to its size – double the length of an animal, and the loading on its feet is doubled. This relationship, of course, assumes geometric similitude. The relationship has important implications for vertebrate skeletons. The body mass of a terrestrial vertebrate is supported by its legs, and the stresses exerted by this mass are ultimately borne by the cross-sectional areas of the leg bones. Given that an elephant is about fifty times longer than a mouse, its bones theoretically have to withstand stresses that are fifty times higher. Bone, like any other material, has finite strength limits, so how should a large animal's skeleton be adapted to deal with the problem? One obvious strategy would be for the limb bones of large animals to be more robust than those of smaller ones. But how much should bones increase in girth in order to maintain the same stresses? That question can be answered by returning to the sugar cubes.

The cubes are geometrically similar, so the stresses exerted on their bases increase in step with the size increase. If you stood on a sugar cube it would probably crumble, so if you built a big enough cube out of them, the stresses acting on the bottom layer of sugar cubes would be high enough to crush them. Suppose that sugar cubes were very much weaker than they are, and that the maximum stress they could withstand before being crushed was equivalent to only a single cube. That would mean that if you stacked one cube on top of another, the one beneath would crumble. So how could you rearrange the four cubes to avoid crushing? Obviously they would have to be arranged into a single layer. The first cube would stay as it was. The second, which contains 8 sugar cubes, could almost be arranged into a perfect square whose edge was 3 cubes long, but there would be one cube short. The total

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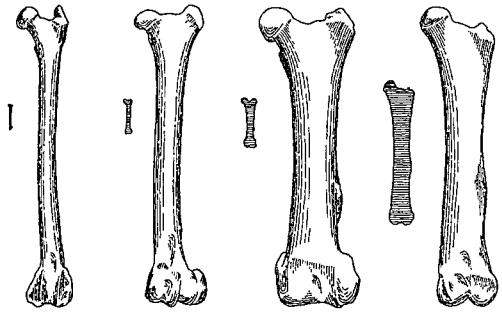

Figure 1.2. Selected femora from animals of increasing body mass. Left to right: dog, deer, hippopotamus, and African elephant. The relative lengths of each bone are shown in silhouette.

area of this irregular shape is 8. If we could crunch it into a perfect square, the edge would be slightly less than 3. In fact, the edge would need to be the square root of 8. This is because when the edge length is multiplied by itself to obtain the area of the square, this area is 8 ($\sqrt{8} \times \sqrt{8} = 8$). Similarly, if the third cube, which contains 27 sugar cubes, were made into a perfect square, its edge would be $\sqrt{27}$. The last cube, comprising 64 sugar cubes, would become a square of edge $\sqrt{64}$. The edge lengths of the four cubes are therefore $\sqrt{1}$, $\sqrt{8}$, $\sqrt{27}$, and $\sqrt{64}$, which can be rewritten as $\sqrt{\text{volume}}$. But volume is length^3, so the edge lengths can be written as $\sqrt{l^3} = l^{3/2} = l^{1.5}$. Therefore, to maintain the same stress, the newly configured sugar shapes have to increase in length, or width, according to $l^{1.5}$. Accordingly, if the stresses on the cross-sectional areas of a vertebrate's leg bones are to remain the same, the diameter of the bones have to scale according to (body length)$^{1.5}$. Do they?

The concept that the diameters of limb bones should scale with their lengths raised to the power of 1.5, to maintain similar bone stresses, is referred to as the theory of elastic similitude. Although some allometric studies supported elastic similitude (McMahon 1975), or showed that it was essentially true (Alexander 1977), they were confined to ungulates (hoofed mammals). When the studies were extended to include a wide range of vertebrates, they found limb bones to be more nearly isometric in their scaling (Alexander et al. 1979). The African elephant, for example, the largest living land animal, has a remarkably slender femur (Fig. 1.2). If large animals do not have relatively thick limb bones, how do they cope with the increased stresses on their bones? By analyzing films of a running elephant (*Loxodonta africana*) and buffalo (*Syncerus caffer*), Alexander and his colleagues (Alexander et al. 1979) concluded that larger animals keep their feet on the ground for relatively longer segments of each stride. They found that the fraction of the time that a given foot is on the ground, the *duty factor,* was 0.49 for the elephant and 0.35 for the buffalo, which was about one-fifth the elephant's mass. This makes good sense because having a longer duty factor reduces the peak stresses acting on the limbs. This observation seemed to resolve the problem of how large animals cope with their large body masses. However, measuring duty factors accurately is a difficult task, requiring a high-speed camera, and

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A. A. Biewener (1983b) pointed out that since Alexander and his colleagues did not use one, their measurement errors could be as high as 30 percent. Biewener used a high-speed camera to measure duty factors for animals ranging in size from mice to horses as they ran on a treadmill. He found that the duty factors were all about the same at similar equivalent speeds. This result suggested that large animals do not reduce bone stresses by having longer duty factors. So what is their solution?

In addition to measuring duty factors, Biewener (1983b) measured the angles of the limb bones. Significantly, the angles of the bones decreased with increasing body mass. Thus, larger animals held their limb bones more nearly vertical, thereby reducing the bending stresses acting upon them. Anatomists have long recognized that heavy-bodied animals, like elephants, hold their limb bones straight, with their legs functioning as vertical supporting columns. Such animals are described as being *graviportal*. Biewener's work therefore quantified that which was generally widely known.

You will be able to test for yourself how limb bone proportions change with increasing length in the last experiment of the practicals. However, before turning to these I want to discuss power functions, graphs, and allometry, which are simply ways of representing and analyzing the concepts we have been dealing with here.

If you had a series of cubes of different sizes and plotted a graph of their lengths (along the x axis) against the area of one of their surfaces (along the y axis), you would obtain a concave-shaped curve (Fig. 1.3). Given that x = length and y = area of one face, the equation of the relationship is $y = x^2$. You could plot a similar graph of length against total surface area. This time you would obtain a steeper curve, whose equation is $y = 6x^2$. Equations like these, where one variable changes according to another variable raised to a power, are called *power functions*. The power term, which is 2 in both of these equations, is called the *exponent*. The gradient of these two graphs is obtained by differentiating the equation. In the first equation, $y = x^2$; therefore, $dy/dx = 2x$. The gradient of the second equation, $y = 6x^2$, is $12x$. Since both gradients have an x term, it follows that the gradient is not constant but increases as x increases. This can be shown by drawing tangents to the graphs at various points.

If the logarithms of the data are plotted instead of the raw data, a straight line graph is obtained because the logarithmic transformation converts the power equation into a linear one. For example, when the second equation, $y = 6x^2$, is converted into logarithms it is transformed into the equation $\log y = \log 6 + 2 \log x$. This equation gives a straight line graph that cuts the y axis at log 6 (because when $\log x = 0$, $\log y = \log 6$). The gradient of the graph is 2; that is, the gradient has the same value as the exponent. This result can be shown by differentiating the logarithmic equation. Thus, if $\log y = \log 6 + 2 \log x$, then $dy/dx = 2$, the other terms disappearing on differentiation. A general form for these power equations is $y = bx^k$, the logarithmic transformation

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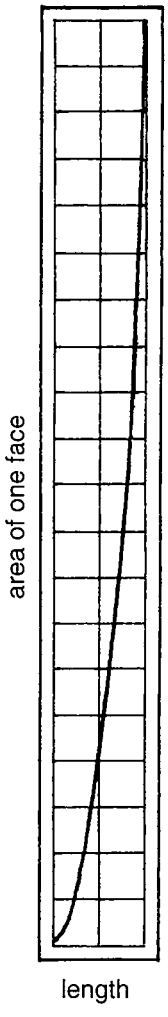

Figure 1.3. Power functions. The area of one face of a cube plotted against the length of one edge gives a curvilinear graph with an equation of $y = x^2$. The total surface area of a cube plotted against the length of one edge would give an even steeper curve, whose equation is $y = 6x^2$. The gradient of the equation $y = x^2$ is $2x$, and so becomes progressively steeper with increasing values of x.

being $\log y = \log b + k \log x$. If you have a mathematical background, all of this will be tediously obvious. However, if you find it hard going, do not despair. All you need remember are two things: (1) the general form of the power equation, and (2) if logarithmic data are plotted instead of raw data, you get a straight line instead of a curve, the gradient of which is the exponent. The constant, b, can be read from the graph as it intercepts the y axis.

As organisms grow their body proportions change. A familiar example is head growth. Babies, whether human or members of some other vertebrate group, are characterized by their large heads. A human baby's head is about one-third the length of the rest of its body, but as the head and body continue to grow, the head starts lagging behind. By adulthood, the head is only about one-fifth the length of the rest of the body. Such growth, where one part of the body grows at a different rate to the rest, is described as *allometric,* the phenomenon being *allometry* (Greek *alloios,* different; *metron,* measure).

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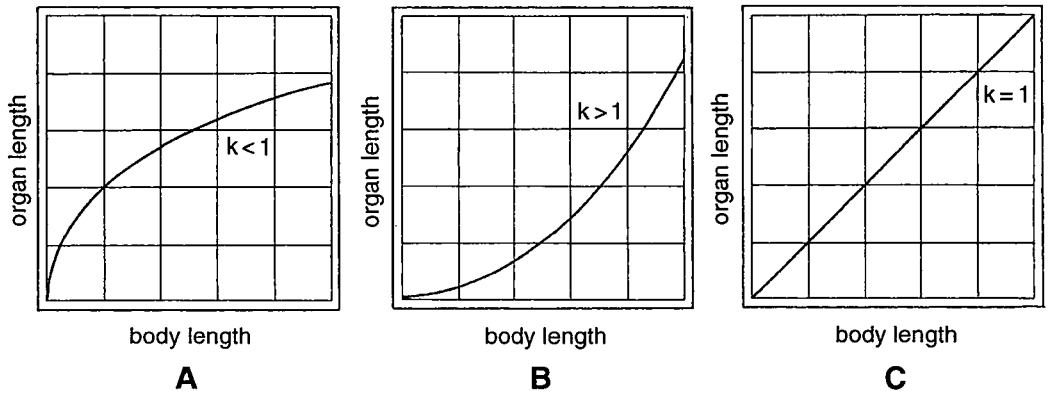

Figure 1.4. Allometric and isometric growth. When the exponent is less than 1, a convex curve is obtained and growth is said to be negatively allometric (A). Positive allometry, when the exponent is greater than 1, gives a concave curve (B). When the exponent equals 1, growth is said to be isometric (C).

Allometric growth is described by the general form of the power equation, $y = bx^k$, where y = organ size, x = body size, k = the exponent, often referred to as the allometric growth constant, and b is a second constant, usually of much less interest. Organ size here might be the diameter of the head, whereas body size is usually taken as body length. When the exponent is less than 1, as in head growth, a convex curve is obtained when organ length (y axis) is plotted against body length (Fig. 1.4A). Such growth is often referred to as negative allometry, because the organ becomes progressively smaller relative to the body length. The exponent for head growth has a value of about 0.7 for a wide variety of vertebrates. When the exponent is greater than 1, the organ becomes progressively larger, relative to the body length, as the animal grows. Growth is said to be positively allometric, and the curve obtained when raw data are plotted is concave (Fig. 1.4B). One of the most noteworthy examples of positive allometry is the claw of the male fiddler crab (*Uca pugnax*). During the early stages of development, both of the male's claws are small, but as growth proceeds, one of the claws becomes progressively larger until, in the adult, it is almost as big as the rest of the body. The strong positive allometry of the male's claw is a sexual character, the giant claw being used to attract females. The male's other claw, and both of the female's claws, grow in step with the rest of the body. Here the exponent is 1 (Fig. 1.4C), and growth is said to be *isometric* (Greek *isos*, equal).

The change in proportion as animals grow larger has been recognized for over a hundred years, but it was not until the first half of the present century that the subject of allometry was treated quantitatively. The central figure in these studies was the English zoologist Julian Huxley, grandson of Thomas Henry Huxley, staunch defender of Darwin. Huxley's book on allometry, published in 1932, had a considerable influence on the biologists of his day and

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stimulated a plethora of investigations into differential growth. Allometric studies are not confined to growth stages within a species; they include analyses among adults of the same species and adults of different species, too. Huxley (1932), for example, measured antler size against body size for adult red deer (*Cervus elephus*). Antlers are restricted to the male in true deer (cervids), except in the caribou (*Rangifer tarandus*). Like the male fiddler crabs' giant claw, antlers are used in the mating season, primarily in head-to-head ramming contests with rival males. The antlers are shed annually, and each year they grow back bigger than they were before. Huxley found that the antlers had a positive allometry, becoming relatively larger with increasing body length.

Before closing this discussion on allometric growth, I should point out that plotting a double logarithmic graph of growth data does not necessarily result in a straight line. This is because the growth of one part of an animal does not always maintain a constant relationship with the rest of the body. Such cases of nonconformity with Huxley's equation – where the allometric growth constant does not remain the same throughout the animal's growth – are described as *complex allometry*. Conformity with Huxley's equation is referred to as *simple allometry*. Complex allometry is frequently encountered where large size ranges are analyzed. For example, I carried out a study of the relative growth of the rostrum in the swordfish (*Xiphias gladius*). The specimens ranged in size from 6 mm long larvae to 3.7 m adults, and most of the double logarithmic graphs were markedly curvilinear (McGowan 1988). I simplified the problem of analyzing the growth changes by dividing the data into six subsets, based on body length. This division resulted in six linear graphs for each data set.

PRACTICAL

In this lab we will be investigating the relationship between the size of objects and their masses. We will start with nonliving systems, because they are the simplest to investigate, and then look at some biological examples. Whereas physical systems are usually predictable, biological systems are often not, but the departures from the expected results are generally the more interesting.

As you will be weighing and measuring, you are provided with a set of calipers and some scales.

Experiment 1 The relationship between length and mass in cubes.

You are provided with a series of plaster cubes of various sizes. Measure the lengths of their edges, in millimeters, and their masses, in grams. Plot a graph of the edge (x axis) against the mass (y axis). Plot a second graph, this time with logarithmic data. (Do not use double-logarithmic graph paper because the interpretations are less straightforward.)

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