Body Size Allometry: The Geometric Scaling of Form and Function

C. David Rollo

Understanding complex phenomena is facilitated by identifying unifying frameworks. Despite incredible diversity in vertebrate form and function across species there is also a remarkable “unity amidst diversity” that emerges from the geometry and physics of body size [SLIDE: Allometry, Mouse and Elephant]. Other frameworks facilitating general understanding include strong conservation of genes and their regulatory pathways across vast phylogenetic distances (e.g., Yeast to Humans) and in aspects such as the underlying homology of skeletal design spanning humans to elephants to bats (UNITY AMIDST DIVERSITY).

Considerable diversity can be explained by how elements of design relate to one another (INTEGRATION) and in particular, how features change with respect to the critical dimension of body size. Size is strongly linked to growth and development within species, and with adult functional sizes across species. Perhaps because developmental programs are already organized to properly adjust integration as size changes during development, evolutionary adjustments of species to changing or new niches commonly involves changes in adult body size (i.e., this may be a path of least resistance).

Allometry is an entire subject unto itself and it spans multiple areas of biological science. Of those, physiology is of prime importance. Knowing the body mass of a species is sufficient to predict many of its most important features. This is because most features of animals change very predictably with their size. The further advantage of analyzing organismal features (such as respiration rate) with respect to body size is that the math is as simple as it gets – straight lines. The estimate of how well a straight line fits a set of data (such as respiration rates of a thousand species spanning sizes of mice to elephants) is reflected by the coefficient of determination (r^2)

(where 1.00 is a perfect fit with all data for each species falling on the line). The r^2 value is obtained by statistical regression analysis and simply reflects the percentage of variation in a data set explained by or accounted for by the best-fitting regression line (Zar 1974, p 207). The power of body size analysis can be immediately appreciated by the fact that body size explains >90% of variation in respiration among warm-bodied vertebrates (i.e., r^2 ~ 0.95) as well as ~50% of the variance in maximal longevities. In general, perhaps 60-80% of variation in numerous design elements of mammalian species can be predicted or explained just by knowing their size. The science that explores how body size relates to organismal features spanning the molecular to population ecology is known as ALLOMETRY. Basically allometry is concerned with how changes in size and shape are related to one another and how this impacts other aspects of organismal design.

ALLOMETRY: The study of size and shape and how these relate to the general features of phenotypes. [SLIDE Samaras]

Among mammals, body size ranges from ~1.5g for Kitti's Hognose bat to 136,000,000 g for the blue whale - the largest animal that ever lived [SLIDES: Bat, Whale,, Etruscan Shrew]. Over evolutionary time there is a trend for various phylogenies to increase in body mass. This trend is termed ORTHOGENESIS, although the classical definition proposed some endogenous force that mysteriously drove progressive changes. Here we use the term to refer to evolutionary trends that are driven by measurable selection criteria.

ORTHOGENESIS: A trend for progressive change in one direction due to some internal or external factors. [SLIDES: Evolutionary Trends, Definition]

There are many selective forces that can favour selection for larger sizes, just as other circumstances may select for smaller individuals [SLIDES: rodents, dinosaurs, horse phylogenies]. A recent paper suggests that in the billion years preceding the emergence of complex organisms, this transition was limited by levels of oxygen only 0.1% of current values (Planavsky et al. 2014). Temperature is another key factor. It is important to note that as larger species evolve, smaller species do not simply disappear. During extinction events larger species are generally more prone to demise. This may reflect their longer generation times and associated slower evolutionary potential. In this regard, a trend could also emerge because smaller species may be more likely to acquire new adaptive features. Subsequently, new species generated with the new features may also be bigger.

Allometry is also concerned with changes in shape or form that take place during development [SLIDE: Human development]. In some cases, evolutionary changes appear to have involved developmental shifts. For example, juvenile primates have features that are more human-like than adults, and so the human condition has been suggested to involve extension of juvenile features into the adult phenotype. This is termed NEOTENY [SLIDE: Young and old Chimps]. In most cases, as in human evolution, changes may involve both size and form [SLIDE: skulls].

NEOTENY: The retention of juvenile features in adults (e.g., expression of gills in some adult salamanders).

We must keep in mind that quality and organization may be just as important as size. Thus, dwarf hominids found on the island of Flores had a brain size similar to that of a chimpanzee, and some argued that this meant that they could not have been using the advanced tools found with them. However, remarkably small (midget) humans retain advanced (normal) cognitive functions found in normally-sized humans. In some human dwarfs the head is disproportionately large but in others, brain size is significantly smaller [SLIDES: Hobbits, Midget].

Selection on the standard poodle breed (considered one of the most intelligent dogs) to produce “teacup” miniature poodles also have proportionately tiny heads, but the miniature dogs seem just as smart as their larger relatives. Island animals generally show an orthogenic trend for smaller sizes (termed insular dwarfism) although some species actually become larger. Hobbits shared the Island of Flores with the Komodo Dragon and a dwarf (*Stegodon*) elephant. Dwarf elephants evolved on many islands from the Central Pacific to the coast of California, the Mediterranean (including Sicily, Crete and Cyprus), the Bering Sea (diminutive mammoths) and the Arctic Ocean. This nicely illustrates the power of reduced food supplies on islands to adjust body mass of large animals. It seems likely that evolutionary advances in a feature like intelligence would be strongly selected for retention as body size decreased. https://en.wikipedia.org/wiki/Brain-to-body_mass_ratio

If all design elements scaled proportionally to body size (i.e., one to one) then a deer would simply be a scaled up version of a mouse. For example if a deer is 1000 times bigger than a mouse and the length of the ear on a deer is also 1000 times longer, such a proportional relationship of size to ears would be termed ISOMETRIC. Consider, however, that the length of the trunk of proboscoids (elephants) becomes proportionally longer as the body size of species increases.[SLIDES Elephant evolution] In fact it is more common for various design elements to scale non-linearly or to different degrees as size varies. Thus, scaling of features as size changes is termed allometry (from the Greek “alloios” meaning **different**). Or “ALLOMETRIC”

A crucial and fundamental cause underlying the allometric relationships of numerous features with size is that the relative amount of surface area increases proportionally more slowly (and predictably) than volume or mass as organisms get bigger. In fact relative surface area declines exponentially with increasing volume or mass in higher animals. Allometric analyses are also broadly applied to plants, although plants and certain animals that have a branching morphology or numerous leaves can avoid the limitation of surface area as size increases to some extent.

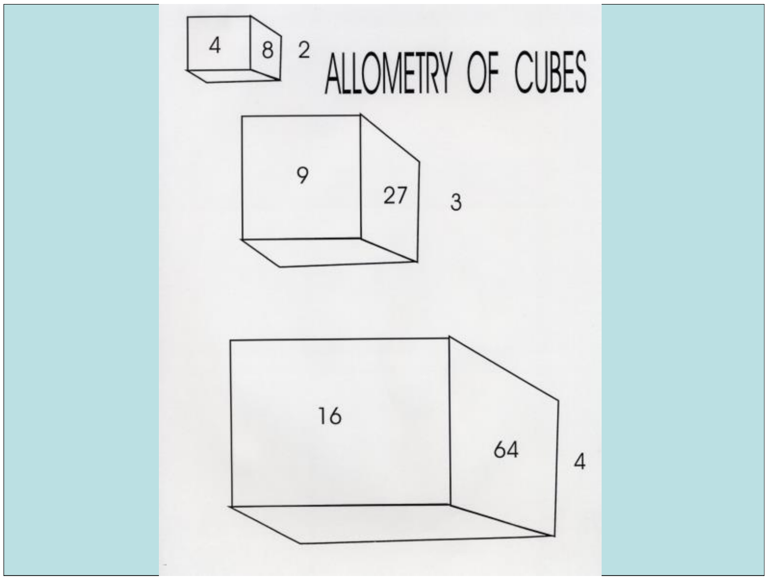
Many key processes of life involve diffusion or transport across surfaces. Examples include oxygen and carbon dioxide exchange in the lungs and all cells of the body, uptake of nutrients by the digestive system and across cell membranes, ion and water movement associated with water balance and functions such as neurotransmission, and excretion of metabolic waste products.

Cell membranes also express a plethora of receptors so regulatory and communication systems are sensitive to available surface areas. Heat and water balance are also strongly affected by the surface area to volume ratio, so small organisms may experience more rapid changes in temperature and dehydration than larger ones. For some features such as the brain and cognition, larger size allows more cells, interconnections and structural complexity. Although organization may be crucial, as discussed above, it remains that there is a good reason why modern humans have such exceptionally large brains (but significantly smaller than elephants or Neanderthals).

Given the range of processes that involve surface area dynamics, it is not surprising that allometry applies to features ranging from the molecular to the physiological to whole organisms. Even ecological and community levels of biological organization express allometric patterns of key attributes. Aspects impacted include the amount of cytochrome c in a cell, age at sexual maturity, energetic investment in offspring, protein content of milk, relative mass of skeletons, number of heartbeats and breaths per lifetime, sleep duration, speed of muscular action (House flies and cats are faster than us), life span and population growth rates. Allometry can predict both the quantities of various elements (e.g., mitochondria per cell) and rates of associated processes like respiration. In general, rates of various processes allometrically decrease as size increases. Thus, body size allometry provides a fundamental unifying dimensionality relevant to nearly all physiological and behavioural processes [SLIDES **Processes and Rates**].

A good example of how size and surface area affect critical processes can be demonstrated with coal [SLIDE: Coal and coal dust]. It is actually fairly difficult to get a fist-sized lump of coal to burn as its outer surface area is relatively small. Holding a match against it does little. However, if you pound the lump into a fine powder the available surface area enormously increases. Throw this into the air and light a match, and you can get a fairly impressive explosion. This is why explosive fires can occur in coal mines. Similarly, in warm air a giant ice cube will melt more slowly than an equivalent mass of separated snowflakes.

THE SURFACE AREA TO VOLUME RULE. A powerful aspect of allometry is its mathematical simplicity. This largely traces to the geometric and physical basis of the "surface area to volume rule" that provides the core theoretical foundation for allometry. If we consider that dimensionality is described by length (**L**), surface area by length * length (or $\mathbf{L}^2$) and volume reflects $\mathbf{L}^3$, then we see that volume increases by an order of magnitude faster than surface area (i.e., L^2 versus L^3) [***SLIDE:*** **Cube**].



From left to right: surface area of a side, volume (=mass), and length for cubes of different size.

This means that as animals get larger their surface area *relative to* their volume diminishes exponentially. Since the density of animal tissue is relatively similar across species, volume and mass can be used interchangeably. Thus the simple exponential equation for the surface area rule relative to body mass (or volume) is [***SLIDE: Graph***]:

Surface area = $a\mathrm{Mass}^{b}$ = $a\mathrm{Mass}^{(L2/L3)}$ or = $a\mathrm{Mass}^{2/3}$ or = $a\mathrm{Mass}^{0.6667}$

Where "a" = a constant specific to the feature being examined, "b" = the exponent describing how surface area is related to volume, and L = length. The exponent 2/3 is equal to 0.666 which is usually just rounded off to 0.67. Thus, 0.67 represents the exponent predicted by the fundamental surface area rule and thus is also the theoretical expectation derived from actual i.e., empirical) studies measuring how animal surface area processes change with size. The fact that the exponent is less than 1.00 says that surface area processes are expected to show relative decreases as size increases because mass increases faster than surface area. Thus, since respiration – the literal fire of life – is largely limited by surface area (i.e., oxygen supply), the surface area rule predicts that respiration will scale with body size as $\mathrm{MASS}^{0.67}$.

If this exponential equation is converted to logarithmic form it becomes a straight line:

Log(Surface Area) = Log(a) + b(Log[Mass]),

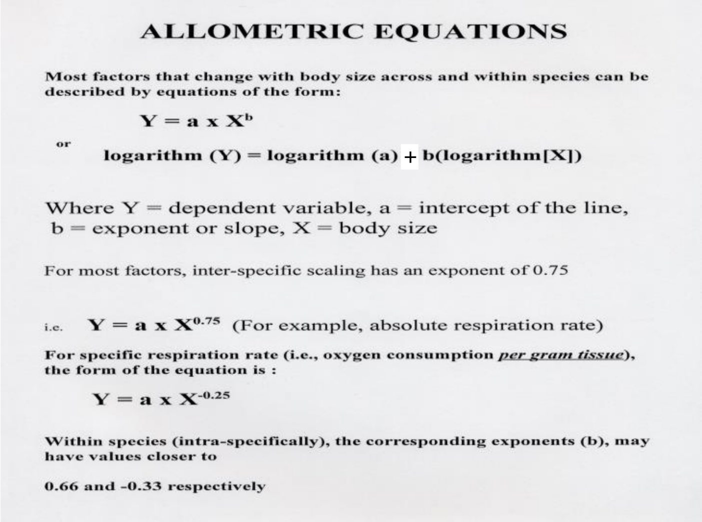
where "a" is the intercept of the line and "b" is the slope [***SLIDE: Equations***].

Thus, the value of b (0.67) describes the slope of the straight line relating surface area to mass or volume. [*SLIDE:* Mass and Mass-specific Relationships]. Also remember that a value of b=1.00 means that a feature scales on a one-to-one basis with mass or "isometrically." A value less than 1.00 means the feature is exponentially decreasing with mass, and a value greater than one is exponentially increasing with mass.

Humans tend to think linearly and generally have difficulty appreciating the power of exponential processes. Changing exponential processes to straight lines makes them easier to compare but also hides the real power of exponential change. What exponential means is that things don't just change at constant increments, they change in a multiplicative or compounding way. Thus, in an example from an ecological book about the limits to growth, you are asked to consider that some lily pads growing on a pond are doubling the amount of the pond they cover each day. The question is, if the lily pads will cover the entire pond on the 30th day, how much is covered on day 29? If you figured that right you will also realize that on day 27 it is only an eighth and on day 28 only a quarter. Growth is exponential. Thus many physiological processes like metabolism and growth vary exponentially with body size. A small increase in size has large (exponential) consequences. Appreciating exponentials in biology is crucially important but people tend to think linearly [SLIDE: Straight versus exponential].

Now consider that we perform a regression analysis relating metabolic rate as the dependent variable against mass across many species varying in size from that of mice to that of elephants. Regression analysis calculates an estimate of the value of b from the real (empirical) data. If metabolic rate scales according to the (theoretical) surface area rule, we would predict that the **empirical** estimate of the slope (b) will be 0.67. Although this is sometimes the case, more often it is not. In fact, most allometric studies obtain *empirical* estimates of b centered around an exponent of ~0.75 rather than 0.67 [***SLIDES*** Converting exponential to linear, Inter-specific

Fitting, Mass versus Mass-specific fitting].



ALLOMETRIC EQUATIONS

Most factors that change with body size across and within species can be described by equations of the form:

$$Y = a \times X^{b}$$

or

$$\text{logarithm}(Y) = \text{logarithm}(a) + b(\text{logarithm}[X])$$

Where Y = dependent variable, a = intercept of the line, b = exponent or slope, X = body size

For most factors, inter-specific scaling has an exponent of 0.75

i.e. $Y = a \times X^{0.75}$ (For example, absolute respiration rate)

For specific respiration rate (i.e., oxygen consumption *per gram tissue*), the form of the equation is :

$$Y = a \times X^{-0.25}$$

Within species (intra-specifically), the corresponding exponents (b), may have values closer to

0.66 and -0.33 respectively

The possible reasons for the discrepancy between the theoretical prediction of the surface area rule and actual empirical measures has generated a vast number of journal pages over more than fifty years of debate. It is worth putting this in context. If a particular feature scaled isometrically with size, the mass exponent (b) would have a slope of 1.00. Thus, as mass increased by 10 fold so would the feature of interest. A value > 1.00 would mean the feature was more accentuated at larger sizes. This is actually true of skeletons and antlers as you will see. Alternatively, a value of 0.67 means that the feature of interest is falling short relative to increasing mass (i.e., bigger animals have relatively lower metabolic rates). So a value of 0.75 means that there is indeed a negative impact of body size, but it is not as severe as predicted by the surface rule [***SLIDES; Allometry of Metabolic Rate*****].** Animals are doing *better* than predicted.

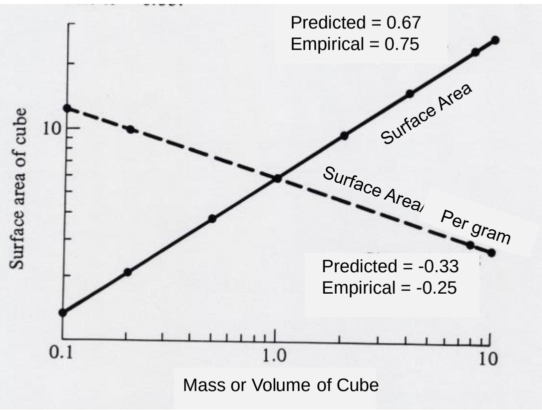


Figure: Note the opposite positive and negative slopes for the MASS versus MASS-SPECIFIC analyses.

If we consider the graph in the context of respiration rate, the amount of oxygen consumed is indeed increasing for larger animals (e.g. a mouse compared to an elephant), but not isometrically. If it were isometric the per gram rate would be the same in the mouse and the elephant. Instead the respiration rate of cells is actually declining exponential with body size.

One proposed theory suggested that the value of b within species (intra-specific) was in fact close to 0.67, but across species (inter-specific) it was 0.75 [***SLIDE; Inter- versus intra-specific Allometry***]. Animals are not solid but present an involuted fluid circulatory system pumped by the heart, a gas exchange system supported by active ventilation like a bellows and a throughput digestive system with considerably enhanced surface area (e.g., great convoluted length, villi). The length of the digestive system even adapts to the quality of the diet. Mammalian lungs are also highly branched thus increasing internal surface areas considerably and blood pigments allow binding and carrying oxygen at concentrations higher than might be obtained by water. Insects have a highly branching tracheal system such that oxygen is directly injected into muscles with each contraction of the bellows-like abdomen or the high-speed contractions of flight muscles. In fact if the surface area rule dictated maximal respiration rates, larger insects would likely be unable to fly.

A predominant theory proposes that the value of 0.75 emerges from a fractal dimensionality associated with the branching and bifurcating structure associated with increasing surface area. Fractals are the physical dimensionality associated with processes reflecting “Chaos Theory.” The key mechanism is most likely that surface area is greater than expected due to internal bifurcation, forced ventilation and peristalsis. Since many biological structures like the lung may well have a genuine fractal structure, it is certainly possible for this signature to also emerge in empirical measurements {SLIDE: Fractal puddles]..

More recently the value of b itself has been shown to scale with body mass. Thus, small endotherms tend to have values close to the theoretical prediction of 0.67, whereas larger species have values of 0.75 or higher. This might arise because the tissues of smaller species have access to oxygen at close to atmospheric values. Large animals on the other hand, may have considerably reduced internal supply that can be boosted by adaptations like increased surface area and ventilator functions. Thus, the cells inside a shrew access oxygen at levels close to atmospheric ambient. Although elephant cells will respire similarly to a mouse or shrew in vitro (i.e., in a dish rather than in the body) at atmospheric oxygen (~22%), their respiration is highly constrained inside the elephant (in vivo) [***SLIDE: In Vitro versus In Vivo respiration rates of animal tissues***].

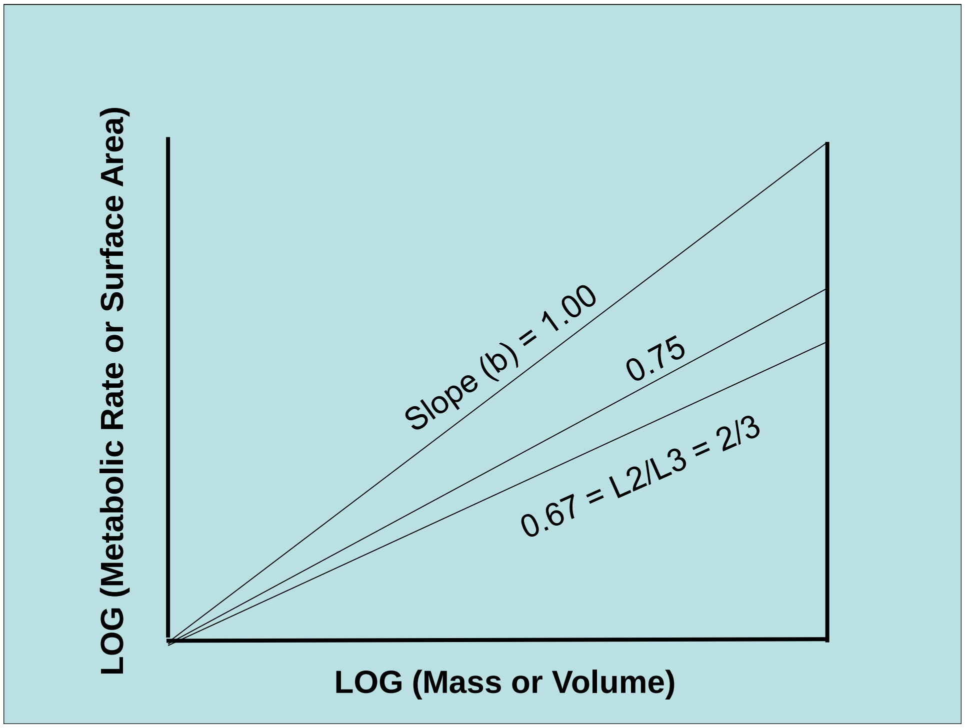
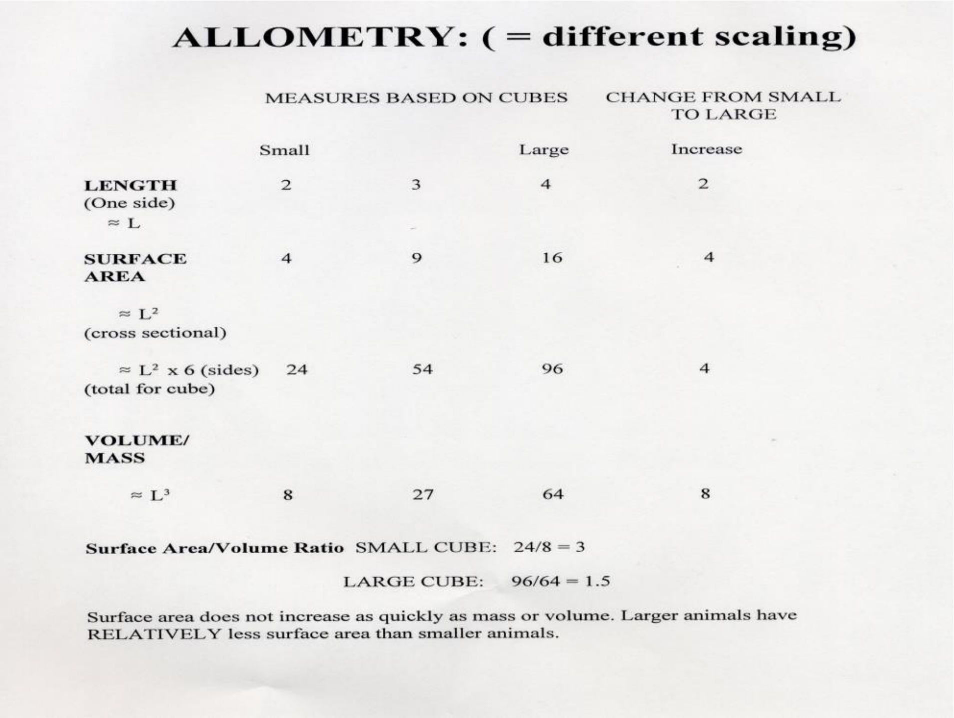


Figure. How the mass exponents relate to linear relationships. Note that a line with slope 0.75 comes closer to isometric (i.e., 1.00) than the theoretical surface rule of 0.67.

A recent breakthrough was the finding that metabolic mass exponents vary with body size such that small species approach values of ~0.67 but values increase with body mass to an asymptote ~0.75. This was also supported by a comparison of small and large species by White et al. (2009) that obtained exponents of 0.69 for small species and 0.76 for large species. This and other sources of variation go a very long way to explaining why empirical estimates vary so greatly. A mass exponent of 0.76 for larger species suggests that they do much better than the surface rule predicts. The value of 0.69 for small species may reflect that their tissues are less remote from atmospheric oxygen so they are more directly ruled by surface area. Small animals may scale as 0.67 because their tissues have relatively more direct access to oxygen. Large animals may show larger scaling exponents because they must improve over the basic surface area rule to maintain relatively high metabolic rates and temperatures, and still maintain sufficient scope to meet contingencies of reproduction, short term exertion and dissipation rates. Adaptations to accomplish this likely involve alterations in circulation and ventilation rates, available surface area and cooling mechanisms.



ALLOMETRY: (= different scaling)

	MEASURES BASED ON CUBES			CHANGE FROM SMALL TO LARGE
	Small		Large	Increase
LENGTH (One side) ≈ L	2	3	4	2
SURFACE AREA	4	9	16	4
≈ L^2 (cross sectional)				
≈ L^2 x 6 (sides) (total for cube)	24	54	96	4
VOLUME/ MASS				
≈ L^3	8	27	64	8

Surface Area/Volume Ratio SMALL CUBE: 24/8 = 3

LARGE CUBE: 96/64 = 1.5

Surface area does not increase as quickly as mass or volume. Larger animals have RELATIVELY less surface area than smaller animals.

Notice how the degree of increase does not matter whether you look at a single side of the cube or all 6 sides.

An interesting discovery was that cell cultures from variously sized animals all converged on similar metabolic rates [Brown et al. 2007]. Comparing the difference between in vitro versus in vivo metabolic rates suggests that the in vivo metabolic rate of tissues in smaller animals more closely approached levels of in vitro cell cultures (i.e., they can better deliver oxygen to tissues throughout their small bodies). Large animals however, have progressively lower mass-specific metabolism compared to in vivo cell cultures, suggesting that their cells are adapted to relative hypoxia that could influence metabolic and aging rates [Rollo 2009]. Such studies also highlight that allometry at the level of species likely works so well as cells do not differ that much in size among species, and that the fundamental biochemistry (e.g. the Krebs cycle) is very highly conserved. Considerable evidence suggests that oxygen concentrations can strongly impact the evolution of body size, particularly maximum sizes of insects that rely on direct tracheal supply rather than a closed circulatory system with haemoglobin. [SLIDES: Oxygen and size]

Discussion of cell cultures also raises some issues that you should know when you read studies done in cell culture dishes (*in vitro*) versus in animals (*in vivo*). Most cell culture work is done with atmospheric levels of oxygen (about 22%) compared to physiological levels in large animals that may be less than 5%. There are incubators that can yield physiological levels of O_2 for cell cultures, but such studies are far less common. Secondly, cells in the body show strong circadian rhythmicity regulated by a central clock. As you will see later, the entire genome is regulated as a circadian program. Cell cultures are generally arrhythmic – meaning the important timing signals crucial to normal regulation are absent (although embryonic zebra fish cells can be entrained to have rhythmicity). Finally, the growth medium for cell cultures is rich in growth factors whereas such factors show cycles in the body and growth normally occurs at a specific time and only for a few hours each day. There are other issues as well. You should always keep these aspects in mind when interpreting *in vitro* research because the cell culture environment has little relationship to cells in the body.

If the whole-organism metabolic rate scales as 0.75, then the gram-specific metabolic rate scales as –0.25 (instead of -0.33 as predicted by the surface rule). Thus, whereas an elephant breaths much more oxygen than a mouse, 1 gram of mouse tissue has a much higher metabolic rate than 1 gram of elephant tissue [***SLIDE: Whole animal versus mass-specific metabolism***].

ACTIVE METABOLIC RATES. Most discussion of respiratory allometry is based on basal metabolic rates (fasted, resting metabolism at thermal neutrality). If we examine scaling factors for animals that are exercising, the exponents are often much higher and can even approach 1.00. Of course these cannot be sustained but such bursts of activity are crucial for fitness and must be highly selected. Elevated exponents suggests that animals are well adapted to support high metabolic rates during high physical activity. Consider that Tuna can maintain warm body temperatures in cold water since their high speed drives water over the gills – the same principle as a jet engine. Interestingly, large animals appear to be better at this than small animals. Perhaps small species are closer to their maximum possible metabolic rate so they have less scope for increases?

Multicellular life was only possible when levels of oxygen accumulated to critical levels (Noah et al. 2014 – nothing to do with the Ark). Thus the fossil record shows a burst of evolution in multicellular animals that founded all of the major existing taxons and other designs that failed along the way (Gould 1989: Wonderful Life). Body size would have been of great significance as this determined the oxygen supply available for various physiological functions including locomotion and reproduction. High levels of atmospheric oxygen were associated with evolution of giant insects and other terrestrial arthropods. High oxygen was also correlated to the evolution of flight. Besides allowing greater respiration, a denser atmosphere may have rendered flight more effective (SLIDE 34, 35,36,37). Birds were particularly favoured for flight as they evolved from dinosaurs that employed air sacs in breathing. Air sacs allow oxygen to be extracted by the lungs both on the inhale and on the exhale. The only other remaining dinosaur lineage besides birds are the crocodilians – and they also have a respiratory system that utilizes air sacs (SLIDE 38). Snakes and modern lizards are not in the same lineage as dinosaurs.

FEEDING AND STARVATION RESISTANCE. If metabolic rate scales as 0.75, then other features related to metabolism must express similar scaling. Thus the amount of food ingested, oxygen consumed and CO_2 produced should all scale as 0.75. Large animals individually need more food, but they also can carry more fat storage, they have lower metabolic rates and they lose heat more slowly (cheaper heating bills). Consequently larger animals are more resistant to starvation. The phenomenon of insular dwarfism (small animals on islands) attests to selection on individual food requirements. Survival time under starvation scales positively as $MASS^{0.25}$. Greater ability to accumulate and carry energy reserves is also an important advantage for periods of high energy demand such as competition for mates in the breeding season, migration, seasonal cold and food shortages, hibernation, pregnancy and lactation.

ANATOMICAL ALLOMETRY. Although functions dependent on surface area display strong body size allometry that scales between 0.67 and 0.75, this is not true for many other features. In particular, many anatomical features tend to scale almost isometrically across species (i.e., they express exponents close to 1.00). Examples include heart, lung, and blood volume as well as haemoglobin content. Other anatomical features may show relative increases or decreases.

LIVER. Declining relative liver size with increasing body size may reflect reduced need to process metabolic poisons or manufacture sugar and other materials related to metabolic support (such as antioxidants?).

SKIN. Reduced skin mass relative to body size makes sense as it largely covers surfaces which decline in area relative to body size. Some surfaces in tissues like the intestine or lungs may be more invaginated in larger species to offset the limitations of declining surface area.

BRAIN SIZE. The size of the brain declines relative to body mass, probably because the control system does not need to increase in size much to perform its regulatory function. Thus, the microprocessor that runs a calculator, car or jumbo jet may not differ that much in size. Consequently, the fact that dinosaurs had relatively smaller brains does not necessarily reflect that they were unintelligent.

FAT STORAGE. White adipose tissue increases relative to body mass, possibly reflecting the generally increased efficiency of transport associated with larger bodies.

SKELETONS. Skeletons scale with an exponent greater than 1.00 (i.e. increase proportional to body size). Because supporting the weight of the body is mainly related to the cross-sectional area of the columnar limbs, the diameter of bones (L^2) must increase relatively faster than body mass (L^3). In addition, depending on lifestyle, various bones may have a safety factor to avoid life-threatening injuries. Presumably such adaptations may be greater in long-lived species.

ANTLERS. Some of the fastest growing tissues in animals are those associated with reproduction (especially in those with seasonal breeding). Antlers and testicles can show enormous growth rates in seasonal breeders. In the family Cervidae, the mass exponent for antler growth ranges from 1.4 to 1.7:

$\text{Mass (Antlers)} = 0.0016(\text{Mass})^{1.6}$

The number of points on the antlers also is related to antler size, so larger cervids have more points. Interestingly, Scottish red deer are smaller and have less points than their European counterparts which suggested they are separate species. However when introduced to New Zealand, the Scottish deer grew larger and sported more points. Evidently they were simply stunted in Scotland. The famed “Irish Elk,” *Megaloceros giganteus* had such enormous antlers (spanning 12 feet or 3.65 m) that they were suggested to be the cause of its extinction. Other than the fact that natural selection does never selects for extinction, when compared allometrically with other relatives, the antlers of the Irish Elk were exactly the size predicted. This most gigantic of all deer managed to survive the ice age – could its large size have been a factor?

LUNGS. The lungs of whales are proportionally the same relative size as those of a shrews (slope = 1.02). This seems surprising given the strong changes in respiration/metabolic rates with body size, but perhaps the relatively shorter distances needed for the blood to circulate are offsetting. Someone should look at the relative surface area of lungs across animal body sizes.

AGING. Since the lungs, heart and amount of blood all scale isometrically with body mass (exponent of 1.00), the higher metabolic rates of small mammals must be met by changes in breathing and heart rates. The heart of the Etruscan shrew beats 25 times **per second**. That equals about 1,500 beats per minute. In comparison the human heart beats about 72 times per minute. The rate of taking breaths and the beating of the heart should both scale as $b^{-0.25}$. This proves true for both. The heartbeat of a mouse is so fast that one cannot discern its beating, but rather it "hums." The same is then also true for the time required for blood to complete a circuit around the circulatory system. Because longevity scales with body mass and metabolic rate inter-specifically, the number of heart beats and breaths in the lifetime of a mouse is roughly the same as in an elephant. This is so even though the "Rate of Living Theory" for aging is now generally rejected. The main reason for this is that when one examines the lifetime consumption of calories across animal species, exceptionally long lived animals like humans, birds and bats (with low predation) process much more energy in a lifetime compared to short lived (highly predated) animals like most rodents and rabbits. In fact, humans are about the longest lived mammal relative to our body size. My own perspective is that the rate of living may be one major determinant, but other factors also strongly contribute.

DIVING DURATION. Can allometric patterns be applied to physiological and ecological understanding? Consider that the potential duration of diving increases with body mass according to the exponent 0.25 (i.e. $M^{0.25}$ due to metabolic limits). This suggests that a direct route for obtaining diver of longer duration would be simply to increase in size – as in whales. For diving mammals, temperature (i.e., cooling rates) are also an important factor determining giving durations. This is particularly true for small animals such as water shrews. At water temperatures of 10-12^{o}C, the body temperature of a shrew may drop 1.4^{o}C in only 30 seconds.

Porpoises can only dwell in water by maintaining basal metabolic rates above the mouse-elephant curve, in addition to maintaining a disproportionate allocation of fat to outer blubber. Increased fat in fact is a general trend with increasing body size in mammals. Incidentally, the sustained singing of canaries as part of their mating strategy (27 second durations), approaches the diving durations found in small mammals.

THERMOREGULATION. A critical factor contributing to the generality of allometric analyses is the relative phylogenetic conservation of temperature. Thus, not only is the basic biochemistry of eukaryotes largely conserved, mammalian species tend to maintain similar body temperatures. If body temperature varied widely and randomly among species, allometric comparisons would be more difficult.

For eutherian (placemtal) mammals the body temperature varies but averages ~ 37^{o} C. Birds have generally higher temperatures (~44^{o}C) and marsupials and monotremes are cooler (~32^{o}C). Differences in basal temperatures do not alter the mass exponent (i.e., slope of the lines remains similar at ~0.75) of allometric relationships (such as that for organismal size versus metabolic rate), but do alter the intercept (higher for birds, lower for marsupials and monotremes) *[SLIDE: Metabolic rate of homeotherm lineages]*. This further extends to poikilothermic lineages that have lower intercepts than homeotherms *[SLIDE: Homeotherms versus Poikilotherms]*.

POIKILOTHERMS: Organisms whose temperature varies and is similar to that of its surrounding environment.

Many animals that are classified as poikilotherms (because they generate little internal heat and have no set body temperature) actually engage in considerable thermoregulation. Thus, a moth under a light on a cold night may not be able to fly if disturbed. They begin to “shiver” their wings, which indicates that they are using the contractions of their flight muscles to generate heat. Very shortly they *will* fly away and escape your attention. Most insects must have a body temperature of more than 30°C to fly and many regularly have body temperatures close to ours (sitting on heated substrates, basking in the sun, insulating their nests, etc).

Heat loss is a critical problem for endothermic mammals, and allometry predicts that the costs of endothermy decrease as animals get bigger. This makes small size an extreme disadvantage in the cold, which likely explains why most true hibernating mammals are relatively small. Alternatively, some suggest that heat dissipation may be a serious problem for large endotherms (Speakman). If an elephant allocated the same proportion of energy to thermogenesis as a mouse, it would be unable to dissipate the heat load (e.g., by flapping their large surface area ears) and they would die. Note that the same problem would be unlikely for a living mammoth (and especially those remaining that are all frozen).

COST OF TRANSPORT. In general the cost of transporting a gram of tissue a given distance declines with increasing body mass. This means that larger species can more cheaply carry larger fat reserves or other features such as antlers or developing infants.

GROWTH. Growth scales similarly to metabolic rate, reflecting their close linkage. Gestation time (reflecting embryonic growth) also scales closely to expectations for metabolic rate:

Gestation Time = $0.19\text{AdultMass}^{0.23}$

Embryonic Growth Rate = $0.0088\text{AdultMass}^{0.66}$ g/time (Calder 1984, p 274)

As does time to puberty

Maturation = $0.92\text{AdultMass}^{0.30}$

A critical advantage for homeotherms is that they can grow faster than poikilotherms for a given temperature. This means that the advantages of endothermy may be reduced in warm environments where poikilothems can take advantage of the thermal subsidy provided by a warm environment (e.g., crocodilians). Despite differences in rates, the slopes of their metabolic and growth rates relative to body mass are relatively similar among endotherms versus poikilotherms (despite differing elevations). Similarly, marsupials have slower growth than placental mammals.

A disadvantage of thermoregulation is that a relatively significant proportion of ingested food is dissipated as heat rather than being converted into tissue. Thus the “production efficiency” related to food intake is less for homeotherms. Poikilotherms may even do better than homeotherms if they are supported by a warm environment. In some tropical countries large herbivorous iguanid lizards are considered excellent meat sources as there they are much more efficient than warm-bodied animals of similar size (rabbits). That is, for a given amount of feed, they produce more meat.

Growth rate also appears to be closely related to aging rates and maximal longevities. As the pace of growth speeds up in smaller species, so does the rate of aging (Calder 1984, p 273). Anthropoidea (and especially humans) have very slow growth, extended infancy and exceptionally long lives for their body size.

SLEEP. The fact that sleep shows allometric scaling highlights that it is somehow linked to metabolic rate and general physiological functions. Despite the perception that small, highly active animals like shrews sleep less, so large animals must sleep more, the opposite is actually true. Over a 24 h day, smaller animals sleep more and larger animals less. When the duration of sleep bouts is considered, however, smaller animals indeed have shorter durations of sleep, but more bouts. Thus shrews obtain large amounts of sleep distributed in frequent short bouts across the day. Cats also show a fractured distribution of sleep (possibly contributing to the term “cat nap?). So smaller animals generally have more sleep but shorter duration of each sleep period.

LACTATION. Not only does the milk of smaller species contain a higher concentration of protein, a 20g mouse produces thirty five times as much milk for their size as does an elephant at 2600 Kg.

LIFE HISTORIES. Life histories are the life schedule of a species (i.e., gestation time, growth, maturation, reproduction, longevity). All life history features show body size allometry among eutherian, marsupial and monotreme mammals. At higher ecological levels, the rates of population growth and population densities also scale with body mass.

In general, the life schedules of animals tend to telescope outwards in time as species become larger. Thus, elephants do everything over much longer time scales (slower) and at slower rates than a mouse, but as a proportion of the lifetime, the *relative* timing of animals tends to be very similar. This is very reminiscent of an early theory of aging, the “Rate of Living” theory (Pearl 1926). Because of this relative proportionality among features, ratios of some factors emerge as constants (i.e, they show size invariance). Thus as a proportion of lifespan, the time to reach maturity tends to be similar. It is likely that the exceptionally long childhood of humans compared to other species is also related to our exceptional longevity for our body size. Exploring such “life history invariants” was explored by Charnov (1993).