Body Size and Allometry: The Scaling of Structure and Function

C. David Rollo

This document provides some lecture material but most of the slides are not available due to copyright issues and this remains a work in progress. Hope you find this useful anyway.

Despite incredible diversity in vertebrate form and function inter-specifically there is also remarkable unity amidst diversity [SLIDE: Allometry]. Some of this is reflected in highly conserved genes spanning vast phylogenetic distances and some is reflected in aspects such as the fundamental homology of skeletons spanning whales to elephants to bats. Considerable diversity can be explained by how elements of design relate to one another (INTEGRATION) and in particular, how these features change with 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, evolutionary adjustments of species to their niche commonly involve changes in size (i.e., this may be a path of least resistance).

Knowing the body mass of a species is sufficient to predict many of its important features. The estimate of how well a line fits a set of data is reflected by the coefficient of determination (r^2) (where 1.00 is a perfect fit with all data on the line). The r^2 value simply means the percentage of variation in a data set explained or accounted for by the fitted regression line (Zar 1974, p 207). For example, body size explains > 90% of variation in respiration in warm bodied vertebrates (i.e., $r^2 \sim 0.95$) and ~60% of variance in maximal longevities. In general, perhaps 60-80% of variation in numerous the design elements of mammalian species can be predicted or explained by body mass. The science of ALLOMETRY is concerned with how changes in size and shape are related to one another and how this impacts other features.

ALLOMETRY: The study of size and shape and how these relate to general features of organismal phenotypes.

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, Examples].

Over evolutionary time there is a trend for various phylogenies to increase in body mass. This trend is termed ORTHOGENESIS [SLIDES: Examples, Definition, rodents, Horse phylogenies] It is important to note that small species do not disappear. During extinction events larger species are more prone to demise. This may reflect their longer generation times and associated slower evolutionary potential.

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 than adults, and the human condition has been suggested to arise from retention of juvenile characteristics into the adult phenotype. This is termed NEOTENY [SLIDE: Neoteny]. In most cases, as in human evolution, changes may involve both size and form [SLIDE: skulls]. We must keep in mind that quality and organization may be just as important as size. Thus, the diminutive hominids found on the island of Flores and remarkably small (midget) humans retained advanced cognitive functions found in normally sized humans despite small brain size [SLIDES: Hobbits, Midget)

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. Such a proportional relationship of size to a particular feature is termed ISOMETRIC. More commonly, various design elements 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). Thus, across elephant lineages, the trunk becomes relatively larger in larger species [SLIDE Elephants].

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 than volume or mass as organisms get bigger. Note that this may not apply as strongly to plants and certain animals that express branching structures or numerous leaves. Otherwise the consequence is that larger animals have relatively less surface area (but there are indeed allometric analyses of plants as well). Many key processes of life involve diffusion or transport across surfaces. Examples include oxygen uptake in the lungs and transport into cells, uptake of nutrients by the digestive system and across cell membranes, ion and water movement associated with water balance and functions such as neurotransmission, excretion of gases like CO2 and metabolic waste products.

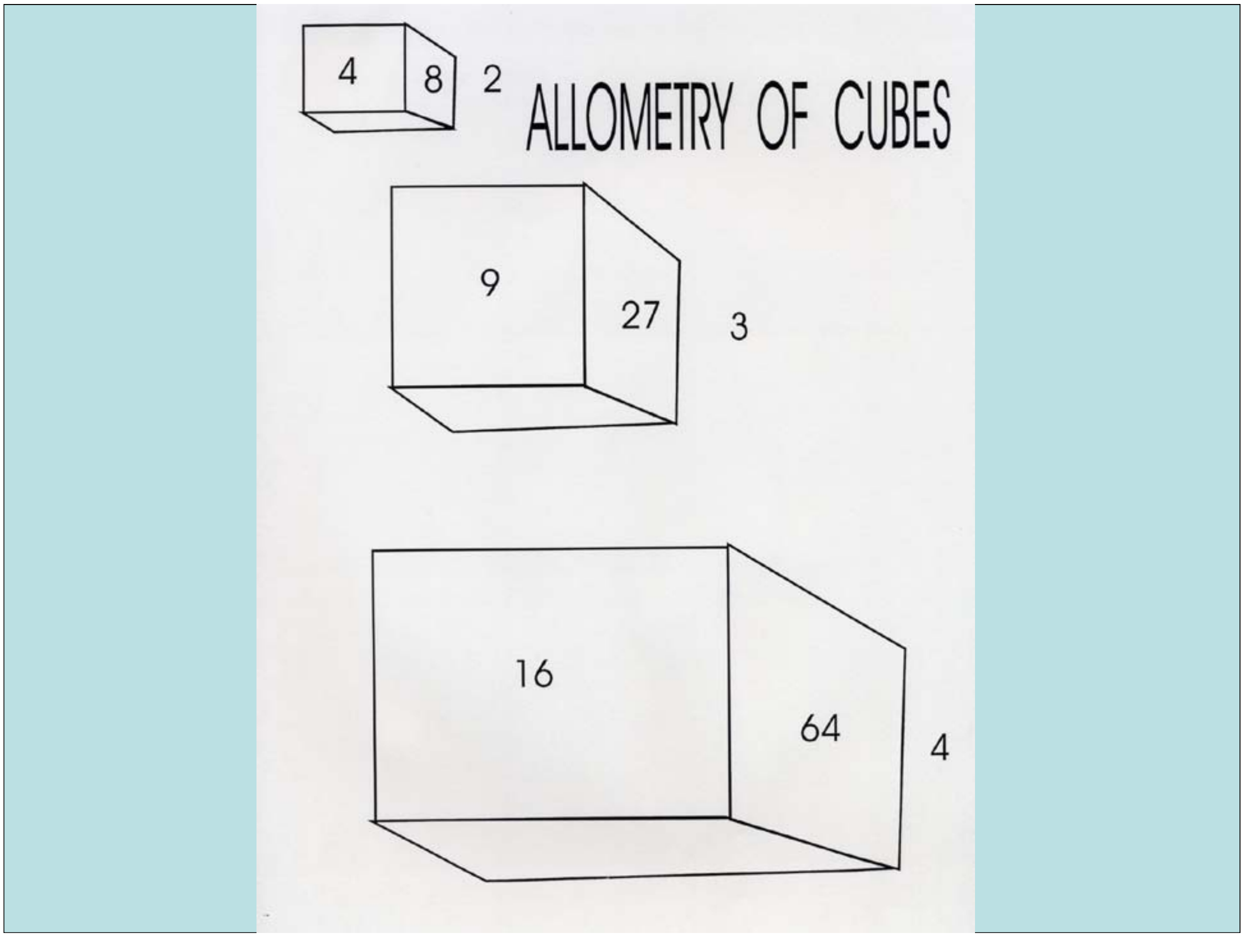
Cell membranes also express a plethora of receptors so regulatory and communication systems are sensitive to available surface areas. Heat and water balance are also strongly affected by the surface area to volume ratio, so small organisms may experience more rapid alterations in temperature and dehydration 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, there is a good reason why humans have such exceptionally large brains.

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 and whole organism levels. 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, number of mitochondria in cells, respiration rate, age of sexual maturity, energetic investment in offspring, protein content of milk, relative mass of skeletons, number of heartbeats and breaths per lifetime. Allometry can predict both the quantities of various elements, and rates of associated processes. For the latter, processes tend to have faster rates at smaller scales of size. Thus, body size allometry provides a fundamental unifying dimensionality relevant to most physiological processes [SLIDES **Processes and Rates**].

THE SURFACE AREA TO VOLUME RULE. Another 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 surface area represents length * length (or L^2) whereas volume represents 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**]. 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 is [***SLIDE: Graph***]:

$$\text{Surface area} = a\text{Mass}^{b} = a\text{Mass}^{(L2/L3)} \quad \text{or} \quad = a\text{Mass}^{0.67}$$

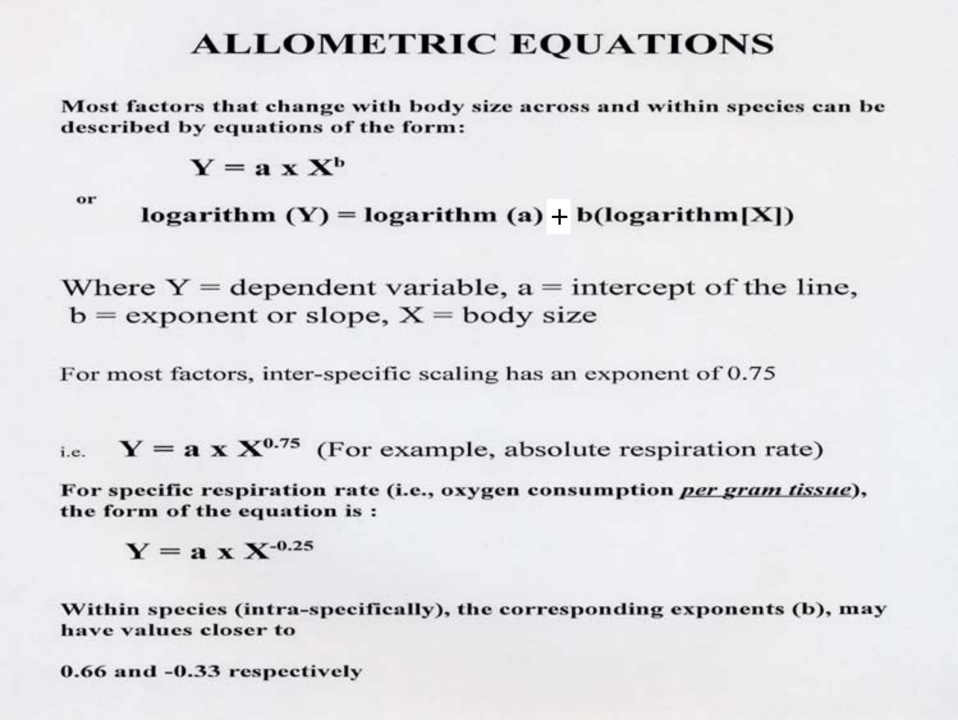
This says that the surface area of an animal increases more slowly than mass as the animal gets bigger. Since respiration – the literal fire of life – is largely limited by surface area (i.e., oxygen supply), the surface area rule predicts that respiration will scale with size as $\text{Mass}^{0.67}$. If this exponential equation is converted to logarithmic form it becomes a straight line:



Surface area of a side, whole cube and volume/mass for cubes of different linear dimensions.

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].

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 data. If metabolic rate scales according to the surface area rule, we would predict that the empirical estimate of the slope (b) will not statistically differ from 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 0.75 rather than 0.67 [***SLIDES*** Converting exponential to linear, Inter-specific Fitting, Mass versus Mass-specific fitting]. The possible reasons for the discrepancy between the theoretical prediction of the surface area rule and actual empirical measures has populated a vast number of journal pages.



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)

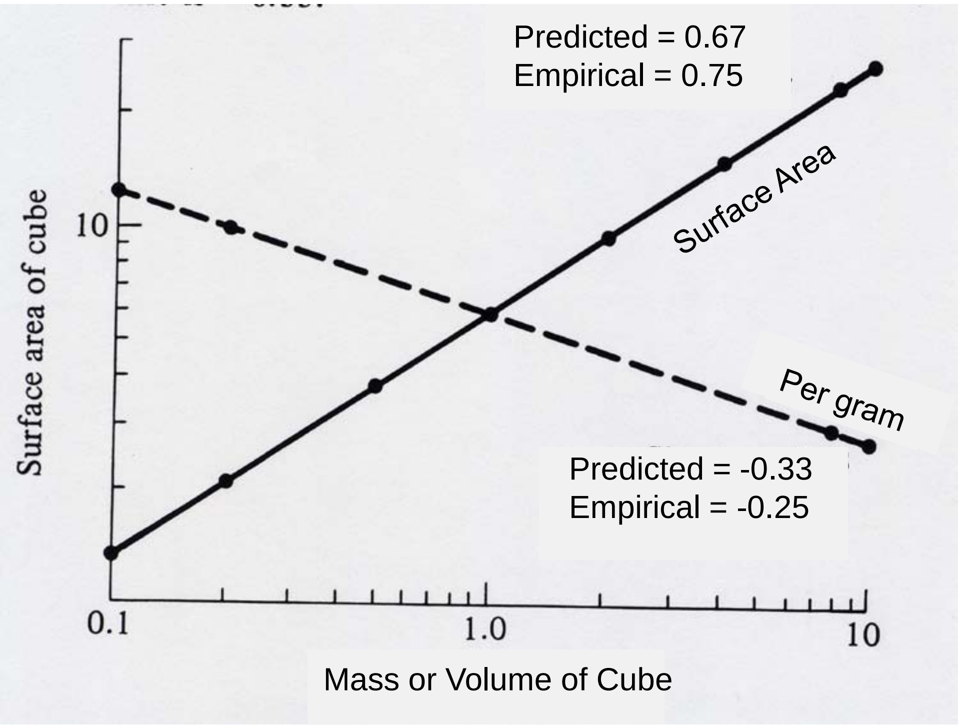
For specific respiration rate (i.e., oxygen consumption *per gram tissue*), the form of the equation is :

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

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

0.66 and -0.33 respectively

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 a negative impact of body size, but it is not as severe as predicted by the surface rule [***SLIDES; Allometry of Metabolic Rate***].



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 and a throughput digestive system with considerably enhanced surface area (e.g., great length, villi). Alterations in such features likely explain some of the discrepancy between empirical measures and the surface rule. One theory proposed that the value of 0.75 emerged from a fractal dimensionality associated with the branching and bifurcating structure associated with increasing surface area.

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 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***].

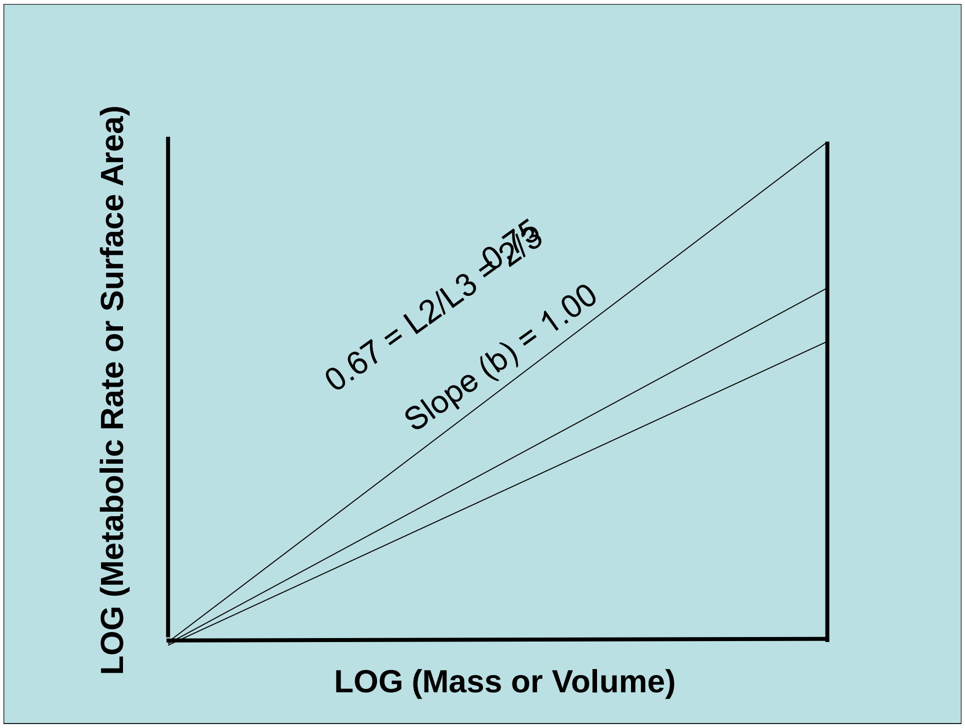
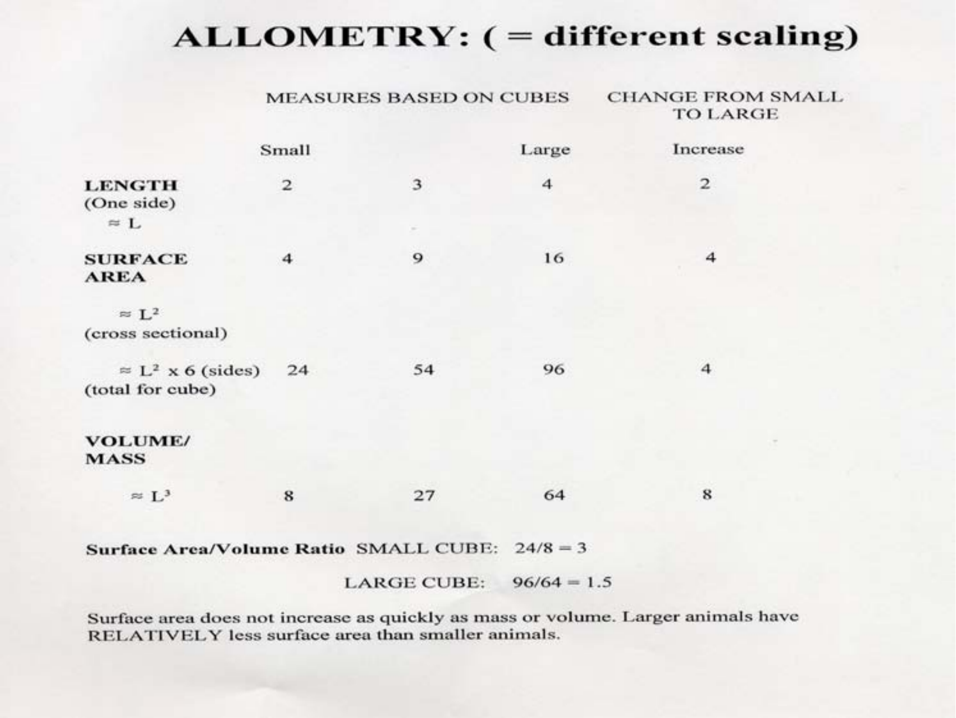


Figure. How the mass exponents relate to linear relationships. Note that a line with slope 0.75 comes closer to isometric (i.e., 1.00) than the theoretical surface rule of 0.67.

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 [210]. 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 and waste disposal. 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 and short term exertion. Adaptations to accomplish this likely involve alterations in circulation rates, ventilation rates, invagination/potential surface area and cooling mechanisms (e.g., evaporation, insulation, air flow).



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 ≈ L^2 (cross sectional)	4	9	16	4
≈ 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 aging rates [Rollo 2009]. The ability of small animals to maintain oxygenation levels closer to ambient is supportive that they might be ruled more by the surface area rule whereas larger species facing greater limitations may have been more strongly selected for offsetting adaptations, including avoidance of dissipation limits.

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. For eutherian mammals this is ~ 37^{o} C. Birds have 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.

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. Interestingly, large animals appear to be better at this than small animals. It seems possible that the metabolic rates of small species are closer to the maximum already and they have less scope for increases.

FEEDING. 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 CO2 produced should all scale as 0.75.

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, lungs, blood volume and haemoglobin content. Other anatomical features may show relative increases or decreases.

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

Skin Mass. 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 their they were unintelligent.

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

Skeletal Mass. 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 must increase relatively faster than body mass. In addition, depending on lifestyle, various bones may have a safety factor to avoid devastating injury. Presumably such adaptations may be greater in long-lived species.

Lungs. The lungs of whales are proportionally the same relative size as those of a shress (slope = 1.02).

AGING. Since the lungs, heart and amount of blood all scale isometrically to body mass (exponent of 1.00), the higher metabolic rates of small mammals must be met by changes in breathing and heart rates. Thus the rate of taking breaths and the beating of the heart should both scale as $b^{-0.25}$. This is 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 in disrepute.

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. 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 mammoth (especially since any remaining are frozen).

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. 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.

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 long lives.

ANTLERS. Some of the fastest growing tissues in animals are those associated with reproduction (especially in those with seasonal breeding seasons). 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:

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,” *Megalocervus giganteus* had such enormous antlers that they were suggested to be the cause of its extinction. Other than the fact that natural selection does not select for extinction, when compared allometrically with other relatives, the antlers of the Irish Elk were exactly the size predicted.

STARVATION RESISTANCE. The association of greater fat reserves and relatively lower metabolic rates and slower heat loss with larger size suggests that bigger animals will tend to have greater fasting and starvation resistance. This might also extend to increased ability to accumulate and carry energy reserves for periods of high energy demand such as competition for mates in the breeding season, migration, hibernation, pregnancy and lactation.

SLEEP. The fact that sleep shows allometric scaling highlights that it is somehow linked to metabolic rate. 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. Thus shrews obtain large amounts of sleep distributed in frequent short bouts across the day. Cats also tend to show a similar fractured distribution of sleep (possibly contributing to the term “cat nap?).

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 history is 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 much smaller 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 developed by Pearl in the 1920s. Because of this relative proportionality among features, ratios of some factors emerge as constants (i.e, they show size invariance). Exploring such relationships was described in a book by Charnov.

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