BODY SIZE RELATIONSHIPS: SCALING AND ALLOMETRY

Animals undergo interrelated changes in size and shape on both **developmental** and **evolutionary time scales**. For example, the dramatic size changes from fetal development through adolescence occurs on a developmental time scale. Many evolutionary lineages also show a pronounced size increase through time, with early species being considerably smaller than later species (Cope's Rule). Accompanying these size changes are significant modifications of shape. These shape changes occur because specific body plans are not infinitely expandable; the physical constraints on body form are known to vary with size.

The fundamental problem faced by all organisms is called **surface area - volume paradox**, where the ratio between surface area and volume does not increase linearly (1:1). For example, consider two cubes, A = 1 cm on each side and B = 3 cm on each side. If L = length of a side, then the surface area L^2 (= **squared, or $\mathbf{L^2}$, function**) and volume L^3 (= **cubic, or $\mathbf{L^3}$ function)**. Consequently, cube B has 9 times the surface area and 27 times the volume of cube A. This creates severe problems at larger sizes, since nutrients and oxygen are consumed and waste and CO_2 are produced at rates proportional to volume (i.e., they are cubic functions), while exchange rates at body surfaces are proportional to surface area and are squared functions. In all systems there occurs a **critical size** above which squared functions can not keep up with cubic functions.

The mathematical basis for analyzing the scaling relationships within organisms is described mathematically as:

$$y = ax^b$$

or, alternatively

$$\log y = \log a + b(\log x)$$

where: a is the y-intercept and b is the slope

If the slope (b) is equal to 1, then the variables x and y exhibit equal proportional changes, and demonstrate **isometry**. In isometric relationships shape does not change as size increases. Instead, organisms exhibit geometric similarity for the variables being studied.

However, most variables in organisms do not scale isometrically. Instead, they have unequal proportional changes, that can take a variety of forms:

- **independence** ($b = 0$);
- **positive allometry** ($b > 1$);
- **negative allometry** ($0 < b < 1$);
- **inverse allometry** ($b < 0$).

All allometric relationships are manifested as size-related changes in shape, which are necessary to maintain functional efficiency. Consequently, shape differences between animals of unequal sizes must be evaluated very carefully when making paleobiological reconstructions.

Because allometric relationships are a power function (i.e., they have an exponent) they form a curved line when graphed on arithmetic axes (Figure 1 & 2). Since curved lines are relatively difficult to evaluate, allometric relationships are typically either graphed on logarithmic scales (Figure 3 & 4) or log-transformed values are plotted on arithmetic scales (Figure 5 & 6). Note that logarithmic scaling and log-transformed data give identical plots. We will work with base 10 log-transformed data in this course, because it simplifies calculations for data sets that cover huge size ranges. Unfortunately, humans do not have an easy familiarity with logarithms. Stating that the logarithm of the estimated body mass of the tyrannosaurid theropods *Tyrannosaurus rex* (in kg) is 3.756, while that of *Tarbosaurus bataar* is 3.322 means very little. But by converting back to actual masses ($T.\ rex = 10^{3.756}$ and $T.\ bataar = 10^{3.322}$) we obtain 5700 and 2100 kg, respectively.

There are several important points to remember when working with log-transformed data. First, as illustrated by the tyrannosaurid data, even a small difference in logarithm values can reflect a very large difference in arithmetic values. Second, arithmetic plots which look superficially similar, may have very different equations. For example, the arithmetic plots in Figure 1 (a & d) look superficially similar, but have different causes. Figure 1 has the value of $\boldsymbol{b}$ held constant, while the value of $\boldsymbol{a}$ varies ($y = 2x^2$ and $y = x^2$). Figure 2 has the converse, the value of $\boldsymbol{a}$ is held constant, while the value of $\boldsymbol{b}$ varies ($y = x^{2.0}$ and $y = x^{1.9}$). Finally, $\boldsymbol{a}$ and $\boldsymbol{b}$ have different effects on log-scaled and log-transformed data. Changing the value of $\boldsymbol{a}$ (Figures 3 & 5) produces parallel lines with identical slopes, but different origins. This is not unexpected, since $\boldsymbol{a}$ is the y-intercept value. Changing the values of $\boldsymbol{b}$ (Figure 4 & 6) produces nonparallel lines with the same origin. Again, this is expected, since $\boldsymbol{b}$ represents the slope.

The purpose of this laboratory is to familiarize you with the analysis of allometric relationships. You will be performing two analyses in this exercise. The first analysis is simply to familiarize you with the techniques for analyzing shape data and uses data from common carpentry nails. The second analysis concerns the relationship between body length and body mass in theropod dinosaurs.

Scaling in Carpentry Nails

Common sense would suggest that carpentry nails should exhibit simple isometry; a nail that is twice as long as second one, should also have twice the diameter. But is this actually the case?

Carpentry nails ranging in size from three penny common (abbreviated 3D) to thirty penny common (30D) are available in the laboratory for analysis. **Using**

calipers, measure the length and mid-shaft diameter in millimeters for one nail of each size and record your data in a spreadsheet for analysis. As with most allometric analyses, the data will need to be log-transformed before it is graphed. Once the data has been entered and analyzed, plot a graph of log LENGTH vs. log DIAMETER.

Scaling of Theropod Body Length and Body Mass

In the second portion of this exercise, you will be evaluating the relationship between body length and body mass for theropod dinosaurs. Data has been provided from published information for all theropod species for which reasonable accurate length and mass estimates are available (data from G. S. Paul. 1988. *Predatory dinosaurs of the world. A complete illustrated guide.* Simon and Schuster, New York, NY, 464 pp.). NOTE: Paul used an idiosyncratic system of taxonomic nomenclature for his book. Standard taxon names, as of 2007, are provided below along with Paul's 1988 names.

- Plot a graph for log LENGTH vs. log MASS.
- Obtain a regression equation for the log transformed data.

Table. Estimated body length and body mass for theropod dinosaurs known from relatively complete skeletons.

Dinosaur Species	Body Length (m)	Body Mass (kg)
Staurikosaurus pricei	2.08	19.0
Coelophysis bauri	2.68	15.3
Coelophysis rhodesiensis	2.15	13.0
Elaphrosaurus bambergi	6.2	210
Liliensternus liliensterni	5.15	127
Dilophosaurus wetherilli	6.03	283
Ceratosaurus nasicoris	5.69	524
Eustreptospondylus oxoniensis	4.63	218
Metriacanthosaurus? sp.	3.8	130
Allosaurus fragilis	7.4	1010
Allosaurus atrox	7.9	1320
Gorgosaurus libratus	5.8	700
Gorgosaurus libratus	8.6	2500
Daspletosaurus torosus	9.0	2300
Tarbosaurus bataar	5.8	760
Tarbosaurus bataar	7.7	2100
Tyrannosaurus rex	10.6	5700
Deinonychus antirrhopus	3.06	45
Deinonychus antirrhopus	3.43	73
Velociraptor mongoliensis	2.07	15

Ornithomimus edmontonicus	3.3	110
Ornithomimus brevitertius (=edmontonicus)	3.66	144
Gallimimus bullatus	2.15	27
Gallimimus bullatus	6.0	440

Questions

1) Do nails exhibit isometry?

2) Why might nails change shape with increasing size?

3) The relationship between body length and body mass in theropods correlates a linear measurement (= length) with a cubic measurement (= mass). Theoretically, what would you predict as the value for b?

4) Does your value of b deviate from this prediction, and if so, why?

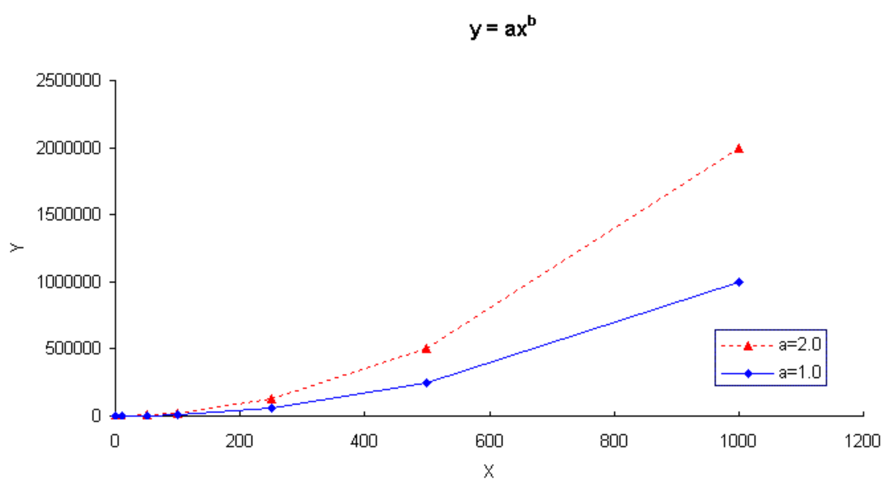

Figure 1: Effect of a on an allometric plot (arithmetic scale).

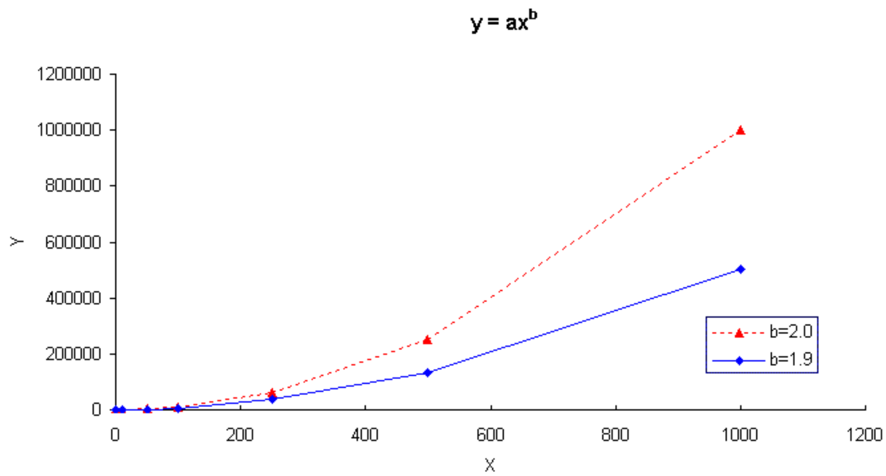

Figure 2: Effect of $\boldsymbol{b}$ on an allometric plot (arithmetic scale).

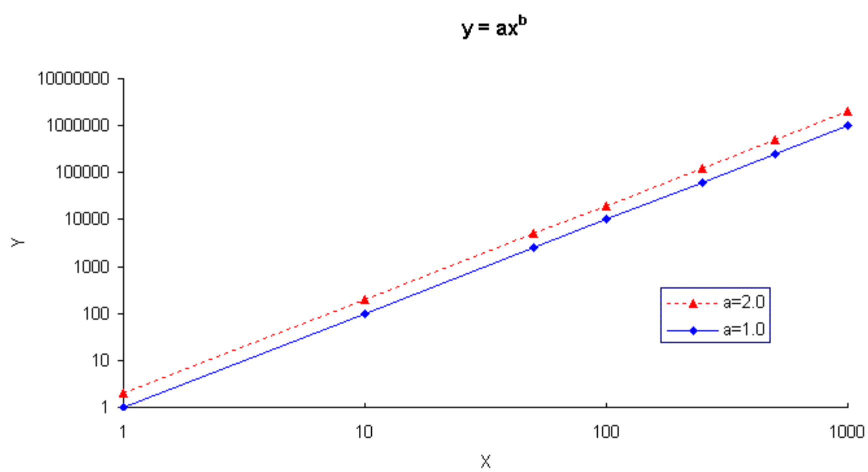

Figure 3: Effect of $\boldsymbol{a}$ on an allometric plot (logarithmic scale).

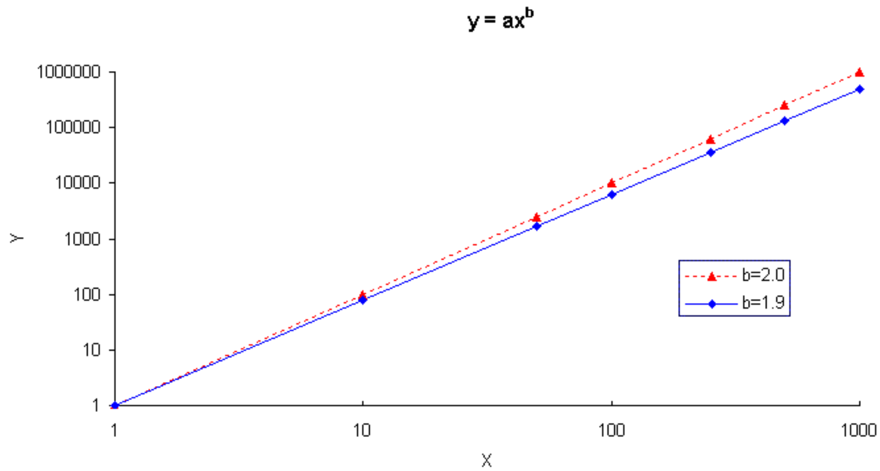

Figure 4: Effect of $\boldsymbol{b}$ on an allometric plot (logarithmic scale).

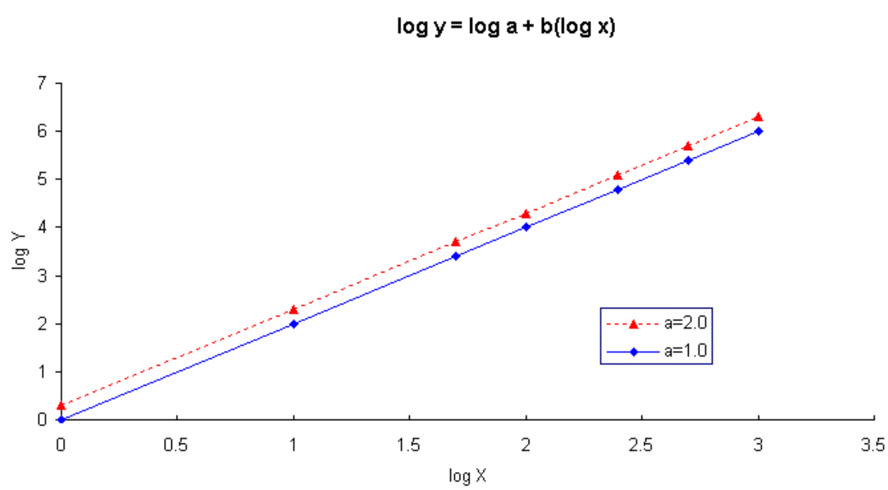

Figure 5: Effect of log-transformed $\boldsymbol{a}$ on an allometric plot (arithmetic scale).

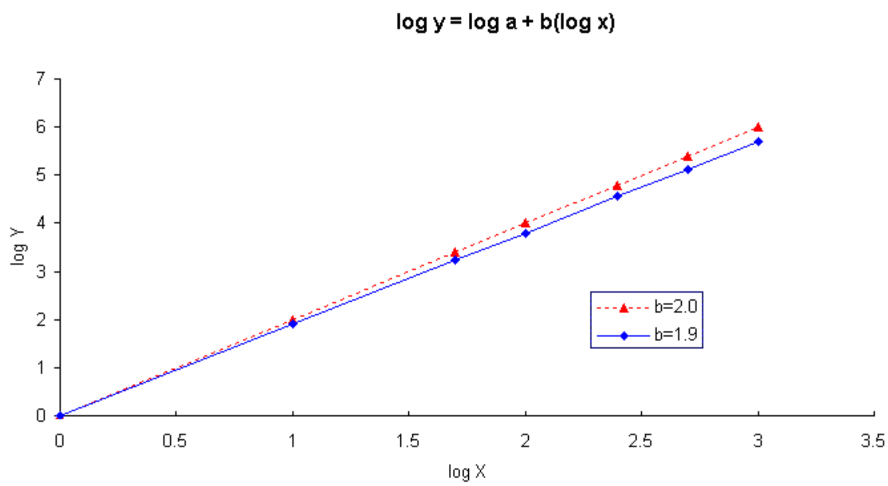

Figure 6: Effect of log-transformed ***b*** on an allometric plot (arithmetic scale).