TUTORIAL 1 Scaling

Background and motivation: Scaling is one of the fundamental principles in biology and has vast implications for physiology and biomechanics. Scaling 'laws' dictate how certain physical properties change with respect to other properties. For example, how does limb length grow with body size. Usually, these laws are either derived from 1st principles (e.g. geometry) or from well-established empirical data.

Why do we care?

a). Knowledge of these 'laws' helps us make predictions about how size limits either anatomy or performance. For example, as terrestrial vertebrates grow larger their posture changes and their top speed slows such that the bones don't break [1].

b). Knowledge of scaling relationships is useful when data from a given species is not available. For example, an experimentally supported scaling relationship between limb length and energy cost of running could be used to predict the energy consumption of extinct animals [2].

c). Scaling 'laws' (based either on empirical or 1st principles) may lead to novel insights. For example given body size vs. cost of transport, some species might fall below this line, indicating that they are perhaps more efficient for their size. Further investigation of these below-the-line outliers may lead to a novel mechanism of increasing efficiency [ref. needed].

Aims of this tutorial:
*** Review basic geometric scaling laws**
*** Derive scaling predictions based on geometric and empirical arguments**
*** Test the above predictions**

Skills required prior to this tutorial: Arithmetic of exponents and logarithms, basic introduction to Mathematica

Skills gained from this tutorial:
*** How to make scaling predictions based on fundamental units**
*** Understand the scaling of certain muscle properties**
*** Mathematica software (see the bottom of this document for links to video tutorials):**
-Make data tables by manual entry
-Open, manipulate and plot experimental data in *MM*
-Log-transform data
-Linear regression with r^2

■ 1. **Using the allometric equation to understand geometric scaling**

The 'allometric equation' predicts how Y changes as a function of X.

$$Y = aX^b$$

Where *a* is the scaling multiplier and *b* is the scaling exponent. This is written as an exponential equation because the relationships that are relevant to biology are often non-linear. In practice, it's easier to log-transform this equation to make it linear:

$$\text{Log } Y = \text{Log } a + b{*}\text{Log } X,$$

where *Log a* is the *Y*-intercept and *b* is the slope.
Example: How does the area of a circle grow as its radius grows? Or, what biomechanists usually say "how does circle area scale with radius?" In other words, what is the scaling exponent (*b*) given a known relationship between area (*Y*) and radius (*X*). Based on what we know about geometry:

$$\text{circle area} = \pi * \text{radus}^2$$

So, circle area scales in proportion to radius2 (i.e. *b*, a.k.a. the slope a.k.a the scaling exponent = 2).

►**In mathematica '*MM*':** Make a data table (i.e. x and y values) for circle area, log transform both x and y. What is the slope? What is the Y-intercept?

1: Define a variable to contain x values, e.g. "xValues":
xValues = {0.1, … whatever values you choose};

2. Define the corresponding y values by plugging the x values into the area equation. Note that *MM* will perform an arithmetic operation on an entire list by performing the operation on each element.
yValues = Pi*xValues^2;
MM will automatically square each element of xValues then multiply each element by Pi. Each element of yValues is now a corresponding area calculation.

Hint: you can press ctrl+6 (on a PC) to get a superscript in Mathematica

3. Define another variable 'logXvalues' to log transform the data. Note that the Log[b, x] takes the log of num using a base b ($Log_b x$). Importantly, *MM* assumes b = *e*. We'd rather use base 10 so our scales increment in orders of magnitude:

logXvalues = Log[10, xValues];
Then do the same for yValues.

4. Organize your data values into one big table with x-y pairs. It should generally look like this:
{{x1, y1},{x2, y2},{x3, y3},{x4, y4},…} where {{…}} denotes a list-of-lists, i.e. a list of x,y pairs. Whenever you plot x vs. y data in *MM*, always use this data format.

Use the "Thread[]" function to automatically weave together your x-y data:
logXY = Thread[{logXvalues, logYvalues}]; (*note the curly brackets!*)

5. Finally, plot your data points. Whenever you're plotting x vs y data points, use ListPlot[]. Confusingly, Plot[] is only for mathematical functions whereas ListPlot[] is for discrete data points.

ListPlot[logXY] to plot just points OR ListLinePlot[logXY] to connect the points with lines

Hint: R-click the graph and select "Get Coordinates" and the plot will interactively show you the x-y values where your mouse is. Click on two different points on the curve, then ctrl+c to copy those data points. Paste into the notebook and you'll see every point you clicked as an x-y pair: {{x #1, y#2}, {x #2, y #2}… etc}. Calculate the slope by indexing this list-of-lists:

points[[2,2]] – points[[1,2]] etc.

■ 2. Testing scaling predictions with data measurements

You can make an **isometric** prediction either based on 1st principles (e.g. geometry) or empirical data. Isometry is simply what 1st principles predicts. For example, we want to test whether the cross-sectional area of bones obey our scaling prediction above. So, the isometric prediction would be as bone radius grows, the cross-sectional area grows in proportion to *b* which happens to be 2 according the circle equation above.

If the measured slope of the log-transformed measurements is greater than 2, then the data are said to be **positively allometric** . If less than 2, the data are **negatively allometric.** A biomechanist or physiologist would say "The data scale with positive allometry" OR "The data scale isometrically", etc.

In another example, strong experimental evidence showed that metabolic rate scales in proportion to body mass$^{0.75}$ (Kleiber's law). The reason for this observation is not immediately apparent, but it's taken as 'law' because it seems to be obeyed almost universally. Thus, if one were to make a prediction about species that haven't yet been measured, you would expect that species to scale according to Kleiber's law.

In other words, isometry and allometry describe how scaling data compares to 1st principles predictions OR known empirical scaling relationships.

By the way, if we only care about the change in Y, we can ignore the intercept and replace the "=" with "α" meaning "scales in proportion to". Mathematically, "α" can be treated like "="as you'll see below.

Here is a table of common scaling laws based on geometry. M=mass; L=length; A=area

X	Y	Example	Derivation	Scaling 'law'	How we say it
Mass (M)	volume (Vol)	muscle volume	$L^3 \alpha M$	Vol α M^1 (eq 1)	Vol scales in proportion to M^1
Mass (M)	Length (L)	limb length	$L^3 \alpha M \rightarrow \sqrt[3]{L^3} = \sqrt[3]{M} = M^{1/3}$ Take the cube root of both sides	L α $M^{1/3}$ (eq 2)	L scales in proportion to $M^{1/3}$
Mass (M)	Area (A)	tendon cross sectional area	$A \alpha L^2 \rightarrow$ substitute into eq 2 $\rightarrow$ $A \alpha (M^{1/3})^2$ $= A \alpha M^{2/3}$	A α $M^{2/3}$ (eq 3)	A scales in proportion to $M^{2/3}$
Mass (M)	Gravitational force (F_g)	compressive force on a bone	$F_g = M \times g$ g is constant (i.e. $g \alpha M^0$) $\rightarrow$ $F \alpha M^1 \times M^0$	F α M^1 (eq 4)	F scales in proportion to M^1

Special case: Muscle force αmuscle cross sectional area: $F_{muscle} \alpha A_{muscle}^{1}$

Examples:
[Ex. a] How would you expect muscle stress (=force/muscle cross-sectional area) to scale with muscle mass? I.e. what is the scaling exponent?

Step 1. Write the allometric equation: how would you expect **stress (Y)** to scale with **muscle mass (X).**

$$\textbf{muscle stress } \alpha\ M_{muscle}^{\ b}$$

Step 2. Write down the scaling relationships for X and Y. Specifically, how do X and Y scale in proportion to a *known* parameter (e.g. body mass)?

We know (or would predict):

muscle force α A_{muscle}^{1} (as stated above)

Since we want scaling with respect to mass, let's re-write the previous expression in terms of mass:

$$A_{muscle} \ \alpha \ M_{muscle}^{2/3}$$

This comes from (eq 3, above – remember: we expect $A_{parameter\ X}\ \alpha_{parameter\ X}^{2/3}$, regardless of what parameter x is)

Step 3. Substitute into our original allometric equation:

knowing that stress = force/muscle area, we can substitute the scaling relationships into the ratio given that the α is treated like an "=":

muscle stress α (mass scaling of muscle force/mass scaling of muscle area) = $M_{muscle}^{2/3} / M_{muscle}^{2/3}$

muscle stress α ($M_{muscle}^{2/3}$ / $M_{muscle}^{2/3}$)

Step 4. Treat the "α" like an "=" and solve for b:
Where's *b*? Remember, we want the scaling exponent of M_{muscle}. Since the right-hand-side is all in terms of M_{muscle}, b is simply 2/3 minus 2/3 …

$$M_{muscle}^{2/3} \ / \ M_{muscle}^{2/3} = M_{muscle}^{0}$$

b = 0. In other words, geometry would predict muscle stress to be independent of muscle mass. For example, a frog muscle should produce ~20N/cm^2 of stress, regardless of the size of the frog.

[Ex. b]: According to Kleiber's law and geometry how would you expect metabolic rate to scale with bone cross-sectional area? I.e. what is the scaling exponent? This is a silly hypothetical scaling relationship, but let's indulge it so we can see the method:

Step 1. Write the allometric equation: how would you expect **metabolic rate (Y)** to scale with **bone cross-sectional area (X).**

metabolic rate α bone cross-sectional area^{b}

Step 2. Write down the scaling relationships for X and Y. Specifically, how do X and Y scale in proportion to a *known* parameter (e.g. body mass)?

We know (or would predict):

metabolic rate α $M^{3/4}$ (Kleiber's law)

bone cross-sectional area α $M^{2/3}$ (basic geometry, eq 3 in table)

Step 3. Substitute into our original allometric equation:

metabolic rate α bone cross-sectional area^{b}

$$M^{3/4} \alpha (M^{2/3})^b$$

Step 4. Treat the "α" like an "=" and solve for b:

Knowing that exponents raised to a power get multiplied…

$(2/3)*b = (3/4) \Rightarrow$ **b = 9/8**

Exercises:

1. Based on geometry, how would you predict muscle force to scale with muscle mass? I.e. what is *b*?

2. Based on geometry, how would you expect lung volume to scale with hip height?

3. Based on geometry, how would you predict bone circumference to scale with limb length? What is the scaling exponent and the scaling multiplier (i.e. intercept on log-log plot)?

4. In *MM*: Using the Bird Scaling Data (sample data provided) write the allometric equation representing wing area vs. body mass (e.g. wing area= A*body mass^b). Is this isometric scaling?

5. Imagine a circulatory system which has a single ventricle. In order to provide sufficient blood flow to the body, the ventricle must pump at least a certain critical volume in each stroke (V_{crit}) for the animal to survive. However, as the heart grows larger, the total muscle volume increases at the expense of volume of the internal space (V_{stroke}). The following scaling relationships apply:

$V_{heart} \alpha 2.5M_{body}^{1}$, and the allometric equation scale factor *a* is 1

$$V_{crit} = 0.5M_{body}^{5/4}$$

$$V_{muscle} = 1.2M_{body}^{1}$$

$$V_{stroke} = V_{heart} - V_{muscle}$$

Given that survival requires $V_{stroke} \geq V_{crit}$, what would be the predicted theoretical maximum body mass, given the above limitation of the circulatory system?

6. Let's say, hypothetically, someone measured a scaling exponent of 0.55 for fish fin area vs. body mass (i.e. $A_{fin} \alpha M_{body}^{0.55}$).

a. Is this isometry or positive/negative allometry?

b. Given some assumptions, let's say the thrust force produced by the fin is proportional to some function of the fin's distance from the fin base(*r*, units=m), the fin's area (A_{fin}, units=m^2) as well as its angular velocity (ω, units=1/s):

$$\text{fin thrust } \alpha\, r^2 A_{fin}\omega^2$$

Given the expression above, how would you predict fin thrust force to scale in proportion to muscle force (i.e. thrust αF_{muscle}^{b}) if ω is independent of size (i.e. $\omega \alpha M_{body}^{0}$)?

c. Assuming you were correct, what is the biological problem with your answer in part b? Predict the scaling exponent of ω (with respect to body mass) in order to avoid this problem.

Further reading:

Biewener, Andrew A. Animal locomotion. Oxford University Press, 2003.Chapter 1.

References:

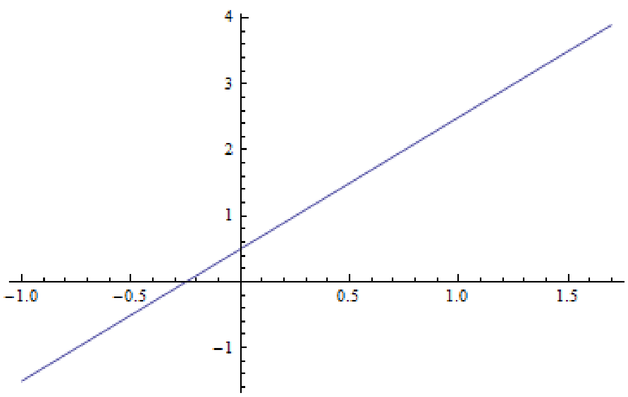
[1] Biewener, Andrew A. "Scaling body support in mammals: limb posture and muscle mechanics." Science 245.4913 (1989): 45-48.

[2] Pontzer H, Allen V, Hutchinson JR (2009) Biomechanics of Running Indicates Endothermy in Bipedal Dinosaurs. PLoS ONE 4(11): e7783. doi:10.1371/journal.pone.0007783

MM code:

```
xValues = {0.1, 0.2, 0.3, 0.4, 0.5, 1.0, 15., 20., 50.};
yValues = Pi * (xValues)^2;
logXvalues = Log[10, xValues];
logYvalues = Log[10, yValues];
logXY = Thread[{logXvalues, logYvalues}];
ListPlot[logXY, PlotRange → All, Joined → True]
```

Out[40]=




```
points = {{1.148, 2.744}, {0.6583, 1.776}};
slope = (points[[1, 2]] - points[[2, 2]]) / (points[[1, 1]] - points[[2, 1]])
```

Mathematica Video Tutorials:

Welcome to Mathematica (6:38):
http://youtu.be/UTM_FDBPEjc

How to Load Spreadsheet (text) Data to Mathematica (3:30)
http://youtu.be/CEolAaIE8vw

How to do a linear regression (best fit line) of XY data in Mathematica (5:09)
Video url: http://youtu.be/BypTzePw2lc