HANK STEVENS

PRIMER OF ECOLOGY WITH R

Contents

Preface

Goals and audience   In spite of the presumptuous title, my goals for this book are modest. I wrote it as

- the manual I wish I had in graduate school, and
- a primer for our graduate course in Population and Community Ecology at Miami University[1]

It is my hope that readers can enjoy the *ecological content* and ignore the R code, if they care to. Toward this end, I tried to make the code easy to ignore, by either putting boxes around it, or simply concentrating code in some sections and keeping it out of other sections.

It is also my hope that ecologists interested in learning R will have a rich yet gentle introduction to this amazing programming language. Toward that end, I have included some useful functions in an R package called `primer`. Like nearly all R packages, it is available through the R projects repositories, the CRAN mirrors. See the Appendix for an introduction to the R language.

I have a hard time learning something on my own, unless I can *do* something with the material. Learning ecology is no different, and I find that my students and I learn theory best when we write down formulae, manipulate them, and explore consequences of rearrangement. This typically starts with copying down, verbatim, an expression in a book or paper. Therefore, I encourage readers to take pencil to paper, and fingers to keyboard, and copy expressions they see in this book. After that, make sure that what I have done is correct by trying some of the same rearrangements and manipulations I have done. In addition, try things that aren't in the book — have fun.

A pedagogical suggestion   For centuries, musicians and composers have learned their craft in part by *copying by hand* to works of others. Physical embodiment of the musical notes and their sequences helped them learn composition. I have it on great authority that most theoreticians (and other mathematicians) do the same thing — they start by copying down mathematical expressions. This physical process helps get the content under their skin and through their skull. I

[1] Miami University is located in the Miami River valley in Oxford, Ohio, USA; the region is home to the Myaamia tribe that dwelled here prior to European occupation.

encourage you to do the same. Whether otherwise indicated or not, let the first assigned problem at the end of each chapter be to copy down, with a pencil and paper, the mathematical expression presented in that chapter. In my own self-guided learning, I have often taken this simple activity for granted and have discounted its value — to my own detriment. I am not surprised how often students also take this activity for granted, and similarly suffer the consequences. *Seeing* the logic of something is not always enough — sometimes we have to actually *recreate* the logic for ourselves.

Using a text editor (such as the simple one in the R GUI) is one of the huge benefits of using R. Using a text editor to write code and to make extensive comments to yourself (and others!) makes R *truly* interactive. You interact with yourself by putting your thoughts on (virtual) paper, highlighting concepts and details you learn along the way, and documenting clearly what it is you have done. The code and the comments are two halves of the whole. Your comments also allow you to interact with others in a very complete way. You cannot realistically and reliably interact with others unless you put something in writing. If you use an application that is a pure GUI, you would have to describe the buttons you click and be absolutely certain that you leave nothing out and that you can actually communicate what you did. By writing and commenting code, you can send your scripts to anyone (your advisor, your instructor, your students, employees, boss, regulatory agency, collaborators...).

Martin Henry Hoffman Stevens
Oxford, OH, USA, Earth
February, 2009

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Theory in Ecology

In this chapter, we introduce a perspective on scientific theories in general and ecological theory in particular. We focus on an example of an efficient theory, metabolic scaling.

Scientific theory is a body of knowledge that provides an organized and mechanistic view of how the world works (Scheiner 2010). Theories concerning gravity, general relativity, and evolution by natural selection provide structured ways of connecting observations, patterns, and processes that provide insight into why the world is the way it is. This stands in stark contrast to the colloquial use of *theory* that implies a lack of knowledge, as when someone says "oh, that's just a theory", referring to a guess without much evidence. Scientific theory is a set of explanations whose validity has been tested repeatedly by experiments and new data.

1.1   Examples of theories

Ecology has lots of theories, of all different types. Below I discuss some which may be prevalent, important, useful, or some combination.

1.1.1   Hierarchy theory

An early and persistent organizing theory in ecology is based on *hierarchy theory* (O'Neill et al. 1986; Rose et al. 2017, and references therein). It posits that ecological systems are structured *hierachically*, such that each entity comprises subunits. For instance, an entity such as a population of big bluestem grass (*Andropogon gerardii*) is part of a larger ecology community of many species. The population of big bluestem comprises subpopulations separated in space, a subpopulation comprises separate individuals, that each individual comprises multiple ramets and a set of organ systems and tissues, which comprise different cell types. This theory posits that each entity gives rise to emergent properties to the hierarchical level above it, and influences

processes within each smaller sub-entity in the hierachical level be-
low it. As a disciplinary organizing principle, this approach structures
nearly all of the ecology curriculum.

Hierarchy theory gets more complicated when the levels of a hierar-
chy start to include fundamentally different types of entities. The big
bluestem hierarchy above included only biotic components–a individ-
ual is part of a population which is part of a community of individu-
als of multiple species, and is made up of organ systems and tissues.
Ecology, however, includes both the biotic and the abiotic parts of en-
vironments. An ecosystem includes a community of species, but also
the nutrients, water, light, and other abiotic components, along with
the spatial arrangement of all of these things.

Different hierarchies are useful for different questions. An individual
can play very different roles in different hierarchies. To understand
how grasses evolve, we need to know about the *genetic traits* of each
individual–traits associated with reproductive fitness, the heritability
of those traits, the genetic bases of those traits. the relative frequency
of important genes in the population, and the size of the population.
On the other hand, to understand how prairie plants compete, we
need to know about the *functional traits* of individuals, such as how
plants take up, store, and use nutrients, and how they dispersal and
establish.

1.1.2   A general theory of ecology

Good scientific theories exist within a hierarchy of disciplinary knowl-
edge (Scheiner and Willig 2011). They explain phenomena within a
domain of knowledge which is organized around *principles* and *as-
sumptions*. Scheiner and Willig posit a theory of biology that explains
phenomena relating to the "diversity and complexity of living systems".
One of the ten principles on which this theory depends is that "the
cell is the fundamental unit of life". Subsumed within their theory of
biology is the theory of cells whose domain is "cells and the causes of
their structure, function, and variation." This theory in turn is based
on principles and has theories to organize our understanding of cells
and what cells do.

Models are specific and explicit manifestations of more general
theories. In this book, we focus on popular mathematical models
that are specific manifestions of theories of ecology. In this chapter,
we highlight the metabolic theory of ecology, and models that relate
metabolic rate to body mass and temperature.

Scheiner and Willig (2011) propose a theory of ecology, some of
which we cover in this book. Here is part of this theory:

The General Theory of Ecology

Domain: The spatial and temporal pattern of the distribution and abundance of organisms, including causes and consequences.

Principles:

1. Organisms are distributed in space and time in a heterogeneous manner.
2. Organisms interact with their abiotic and biotic environments.
3. Variation in the characteristics of organisms results in heterogeneity of ecological patterns and processes.
4. The distributions of organisms and their interactions depend on contingencies.
5. Environmental conditions as perceived by organisms are heterogeneous in space and time.
6. Resources as perceived by organisms are finite and heterogeneous in space and time.
7. Birth and death rates are a consequence of interactions with the abiotic and biotic environment.
8. The ecological properties of species are the result of evolution.

These principles constitute what we know is true about ecological systems. Some of these principles provide the focus for a single chapter while other principles apply broadly to many chapters in this book.

Here is my own perspective on a general theory of ecology:

Domain: The house of life[1]: its constituent entities, causes, and consequences.

[1] "ecology" derives from the Greek "oikos" which means the rules of the house

Principles: In addition to the laws of conservation, thermodynamics, and life,*

1. Entities[2] are open systems with inputs and outputs.
2. Entities have internal complexity.
3. Entities include self-replicating components (living elements).
4. Entities interact via inputs, outputs, and behavior.
5. Rates of change, including inputs and outputs, are influenced directly by physical factors: space, temperature, and concentration.

[2] An entity may be an ecosystem, a community, a population, an individual, or some other system with operationally defined boundaries.

You will see elements of these principles throughout this book as well.

1.1.3 Efficient theory

Marquet et al. (2014) argue that the best theories are those which are *efficient*. Such theories tend to be based on *first principles*, which are observations and laws that are fundamental assumptions in a scientific domain. In biology, such principles can include the laws of thermodynamics, and mathematical properties such as the central limit

theorem. Theories built upon first principles are thus well-grounded in reality as we understand it and lead logically to refinements. Thus good theory has good architecture. Marquest and his colleagues also claim that efficient theory is expressed in mathematics. Mathematics is a universal language that is unamibiguous. It forces us to be as clear as possible about what we mean when we state a theory.[3] Last, efficient theories are those that make a large number of predictions using only a small number of free parameters.[4] Examples of efficient theories we cover in this book include metabolic scaling, exponential growth, density dependence, and ecological neutral theory.

Marquet et al. and Scheiner and Willig emphasize slightly different features of the definition of "theory". Scheiner and Willig emphasize relatively broad ideas that are well-supported by experiments and repeated observation. Marquet and colleagues tend to mean something fairly specific and narrow, typically something that can be expressed mathematically. Scheiner and Willig might refer to such theory as "constitutive theory" or even simply a "model".

Let's take a look at what theory can do for us with a simple toy example. Consider a birch leaf in the cool spring air sitting in the sun. A qualitative prediction would be that "the leaf should be warmer than the air," because we know from experience that things get warm when they are in the sun. Can we do better that? Probably....

One first principle that relates to the temperature of a leaf in the sun: Newton's law of cooling (Roughgarden 1998). This law tells us that the rate of change of temperature of an object due to convection depends on the *difference* in temperature between the the body, b, and the surrounding medium (e.g. air, a). Heat flux depends on the convection heat-transfer coefficient, h, where

$$\frac{dQ}{dt} = hA(b - a)$$

Q is Joules, A is m^2, and a and b are Kelvin (but note that the difference of two Kelvin temperature is the same as that for Celsius). Units for h are $J/(s\,m^2\,°K)$ or $W/(m^2\,°K)$.

Now we add heat coming into the leaf from the sun. Let the solar radiation absorbed by a small green leaf is about $q = 1$,J/s. Let the temperature of the air a and birch leaf b on a cool spring day both be at $10\,°C$. Now we are prepared to ask, "what will the temperature of the leaf be, given inputs of solar radiation and convective cooling? We answer this question using this relation,

$$db/dt = q - hA(b - a)$$

where q is heat gain in the leaf, and the rest is heat loss. We check units to make sure that our variables and parameters make sense in

[3] $E = mc^2$ - need I say more?

[4] Variables are quantities we measure and which change through time (e.g., population size). *Parameters* are (usually) fixed constants that govern the rates of change of variables (e.g., per capita birth rate).

this relation. We do that by plugging them in and seeing what cancels out.

$$\frac{J}{s} = \frac{J}{s} - \frac{J}{sm^2K}m^2(K - K)$$

Simplifying, we have

$$\frac{J}{s} = \frac{J}{s} - \frac{J}{s}$$

Which shows what we did is consistent because the units on the left hand side (LHS) are the same as those on the right hand side (RHS). Well done!

So...to what temperature will our leaf warm up? A good way to interpret that question is to ask "when will the rate of change fall to zero, or $db/dt = 0$?" Let's rearrange to find out.

$$0 = q - hA(b - a)$$
$$hA(b - a) = q$$
$$b = \frac{q}{hA} + a$$

Now we do simple math in R. We assign values to named objects using the assignment operator in R, `<-`.

```
a <- 10 # deg C
q <- 1 # J/s flux on the small leaf
h <- 10 # J/(s deg C of the small leaf)
A <- 0.002 # Area of the leaf
q  / (h*A) + a # the prediction
```

```
## [1] 60
```

This gives us a quantitative prediction about what the temperature of the birch leaf would be under this amount of warming with just convective cooling. The answer we get is in the right direction (it is warmer than the air), and that may be a good sign. It is also way too big. The first thing we should do is double check that the numbers we used for each parameter are sound and based on good research. If we find that they are, what next? Perhaps we left out other mechanisms of cooling. *This is one reason why we like efficient theory.* It allows us to test quantitative predictions that guide us to better questions. In this case, we considered only convective cooling, but not transpiration and conductive cooling. Those processes might also be important in cooling leaves.

Next, I describe the Metabolic Theory of Ecology. This theory is based on first principles, and its central tenets are expressed mathematically. Further, it has a very small number of free parameters

(fitted constants) and makes a very large number of testable predictions. Parts of this theory are supported by a very large number of observations. It fits everyone's definition of theory.

1.2   An example: Metabolic Theory of Ecology

Body size and temperature are very important determinants of metabolic rate, and metabolic rate is central to how rapidly individuals forage for, consume and use resources, reproduce and die. The *metabolic theory of ecology* (Brown et al. 2004) is our body of knowledge about the underlying mechanisms, and the resulting profound and wide-ranging consequences for populations and ecosystems.

Body size and temperature are fundamental properties of organisms and the environment. The study of how body shape and body processes scale with body size is *allometry*. Because body size affects metabolic rate, body size indirectly helps determine population growth rates and how species interact with each other. Temperature affects how molecules vigorously molecules vibrate and move, and so increasing temperature tends to speed up chemical reactions. As metabolism is really just a complex network of biochemical reactions, temperature influences metabolic rate.

This theory is encapsulated in a simple quantitative equation which we present toward the end of this section. Next we walk through the body size- and temperature-dependence separately.

1.2.1   Body-size dependence

There is a profoundly simple and general rule describing the effect of interspecific variation in body size on metabolism. Metabolic rate may be measured by variables tied directly to metabolism, such as the rate of oxygen or energy consumption, or CO_2 production. This biological law is referred to as the Kleiber law (Kleiber 1932), or *quarter power scaling* (Brown et al. 2004). When we compare the basal (i.e. resting) metabolic rates of different species, across a wide range of body sizes spanning many orders of magnitude, we find that

whole-organism resting metabolic rate increases with organism mass raised to the three-quarter power, or,

$$B = aM^z   ;   z = 3/4$$

In this equation, B is basal, or resting, metabolic rate, M is body mass, a is a proportionality constant, and z is the *power law scaling coefficient*. The proportionality constant a varies depending on the type of organism such as arthropods, fish, or mammals. Plants scale in the same manner (Niklas and Enquist 2001), although size or mass can

a little trickier to measure. The scaling coefficient, z, is the seemingly magical constant that many have argued does not vary substantially among organisms.

Here we plot this relation in R in two different ways, using `curve()` in the `graphics` package of R that is included in the base installation as one of the core packages. We also plot it using `ggplot()` in the `ggplot2` package. The function `curve()` can plot any curve that be expressed as a function of `x`. Below, we draw a curve of a dotted 1:1 line for comparison, and then *add* the power function $x^{3/4}$.

```r
## using curve, let your variable be 'x'.
## set
a <- 1
{par(mar=c(5,4,1,0), mgp=c(1.5,.4,0) ) # set figure margins in "lines"
curve(a*x, from = .01, 100, ylab = "Metabolic rate (B)",
      xlab="Body mass (M)", lty=3)
text(80, 90, "1:1") # add text
curve(a*x^(3/4), from = .01, to = 100, add=TRUE)
text(80, 80^.8, expression(M^0.75))}
```
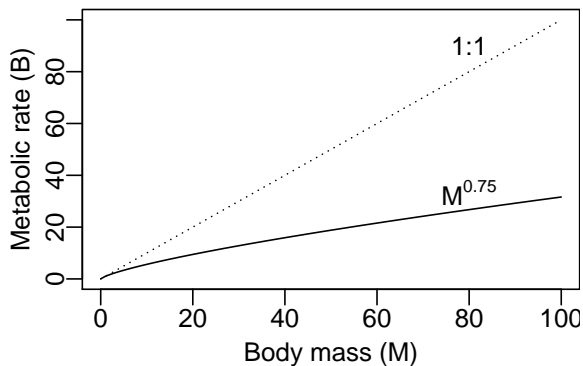

Figure 1.1: Metabolic rate increases predictably with species body sizes.

Now we do it using `ggplot2`. We will use `ggplot2` extensively in this book. First let's create the function we want.

```r
# library(ggplot2) # load the package if you haven't already
eq = function(M, a,z){a * M^z} # create the function you want
```

The `ggplot` graphs require that the data be in a *data frames*, so we create that, where `M` sets the `from-to` limits we used in `curve` above.

```r
myData <- data.frame( M=c(0.01, 100) ) # ggplot requires a data frame
myData
```

```
##        M
## 1 1e-02
## 2 1e+02
```

Now we graph everything. Using `ggplot`, we build figures piecewise, starting with the data, and then adding the type of plot we want (`geom_xx()`), and scaling and annotation, and other ways of looking at the data. We add these elements with the plus sign `+`.

```r
## the graph:
p <- ggplot(data=myData, aes(x=M)) + # set the basic properties of the plot
  # in the stat_function, we indicate the parameters in our equation.
  stat_function(fun=eq, geom="line", args=list(a=1, z=3/4)) + # set the function to plot
  annotate("line", x=c(0.01, 100), y=c(0.01, 100), lty=3) + # add annotation
  xlab("Body mass (M)") + ylab("Metabolic rate (B)") + # add labels
  annotate("text", x=80, y=90, label = "1:1")  +
  annotate("text", x=80, y=30, label="M^0.75", parse=TRUE)
# parse = TRUE tells annotate to treat the label as a math expression

# now show the plot
p
```
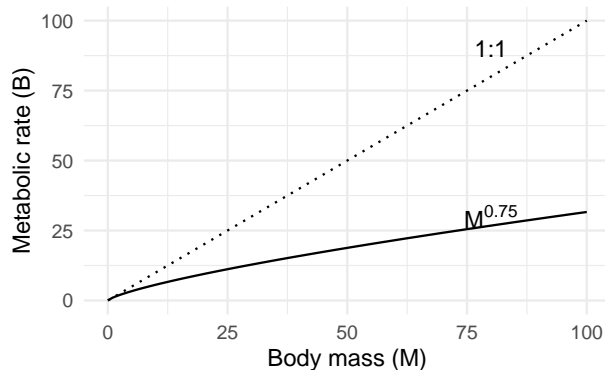

The above relation applies to interspecifc variation in body mass. We may also be interested in *mass-specific* metabolic rates. "Mass-specific" means on a per-gram basis. With plants, we often measure something called "specific leaf area", SLA, which is the two dimensional area of a leaf divided by its mass. Mass-specific metabolic rate is basal metabolic rate of an individual divided by its mass, or B/M. We can estimate this from the above metabolic scaling principle and the using rules exponents

$$\frac{B}{M} = a\frac{M^z}{M^1} = aM^{z-1} = aM^{-1/4}$$

From this, we now have the rule that

   mass-specific metabolic rate declines with organisms mass raised to the negative one quater power

```
eq2 = function(M, a){a*M^-0.25}
ggplot(data.frame(x=c(0.1, 100)), aes(x=x)) +
  stat_function(fun=eq2, geom="line", args=list(a=1)) +
  xlab("Mass (M)") + ylab("Mass-specific metabolic rate (B/M)")
```
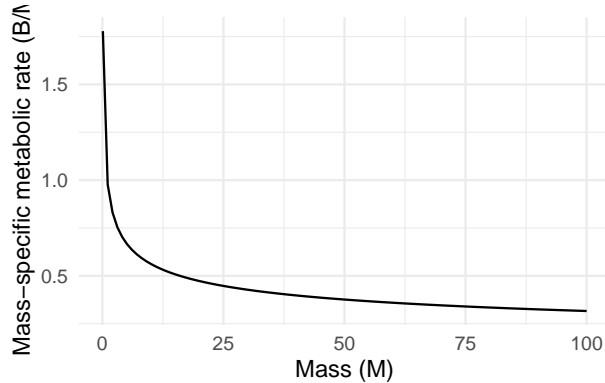

Figure 1.2: Mass-specific metabolic rate declines predictably with species body sizes.

Over the years, there has been heated debate about (i) the precise value of the scaling coefficient z, and (ii) the underlying mechanism. Early arguments suggested that $z \approx 2/3$ because metabolic processes such as heat dissipation scale with surface area of a given volume. Let us envision the volume of an organism having three linear dimensions, so the volume scales to the cube of linear dimensions $V \propto L^3$ ("V is proportional to L cubed"). The surface area, A, scales to the square of these linear dimensions, $A \propto L^2$. The metabolism, B, scales linearly with area, $B \propto A$. This allows us to relate metabolic rate to body volume and mass as:

$$B \propto L^2 \propto L^{3(2/3)} = V^{2/3} \propto M^{2/3}$$

This theory is good because it starts with first principles (heat dissipation and geometry), results in the prediction of a single parameter, and makes predictions about how metabolic rate scales with body mass. Metabolic rate governs a huge amount of biology and ecology, including resource consumption rates, lifespan, and maximum population growth rates. Therefore, this theory and this model can be powerful tools for understanding the world and making testable predictions.

The above model is good because it can be tested. That is what has been done, and it led to mismatch between observations and the theory. Investigators showed that the value of the exponent appeared closer to 3/4 raher than 2/3. In the 1990s, a group including Jim Brown and Geoffrey West proposed an underlying mechanism that explained *why* it should be 3/4. They assumed that orgarnisms must distribute resources through a linear network to all parts of the body.

Their specific model first assumed that the linear network must fill the entire volume of the organism, so it must be fractal-like. Second, it assumed that the last branch of the network must be a fixed size regardless of the size of the organism - essentially the size of a single blood cell, i.e. a capillary. Last, it assumed that the energy required to distribute the resources must be minimized, that less energy-efficient designs would be lost through natural selection. The prediction that results from these assumptions was that the exponent would be 3/4. This theory and model begin with different first principles and makes a different prediction.

Soon Jayanth Banavar and his colleagues challenged this work (Banavar et al. 2002), arguing that the assumption of the fractal-like network was not correct, and in any event, did not apply to all organisms. They proposed different theory with less restrictive assumptions and found nonetheless that the exponent was predicted to be 3/4. At the base of all these arguments is the geometry of the resource distribution system. All organisms take in limiting resources and have to distribute those resources to each part of each cell in the body. The key point is that *the larger the organism, the greater the portion of the resources are in transit at any instant in time*. This leads to an increasingly inefficient system, in which the metabolism of larger organisms has to run more slowly per unit resource:

Larger organisms can process more resources per unit time ($B = aM^{3/4}$), but do so less and less efficiently ($\frac{B}{M} = aM^{-1/4}$) due to resources in transport.

Banavar, Brown and others eventually collaborated to address quarter power scaling in animals in particular which led to additional novel predictions (Banavar et al. 2010).

This theory remains a fertile and active area of research (Glazier 2018). The interested reader should be careful to distinguish between patterns observed across many species of very different sizes, versus patterns observed in a single species with individuals of different sizes versus other types of patterns. Subtly different patterns may be driven be very different mechanisms.

1.2.2   Temperature dependence

We finish metabolic scaling by describing the effect of temperature. Here, a commonly used expression is related to the Arrhenius equation which is used to describe the effects of temperature, T, on enzymatically mediated chemical reaction rate, R,

$$R = ae^{\frac{-E_a}{kT}}$$

where a is a fitted constant, e is the exponential, E_a is the average activation energy of rate-limiting enzymes (units, eV), k is Boltzmann's

constant (units $eV\,K^{-1}$), and T (units deg K). Bolztmann's constant
($\sim 8.6 \times 10^{-5}\,eV\,K^{-1}$) converts the macroscopic property of temperature to kinetic energy of molecules. This rate is the temperature multiplier of whatever reaction we are interested in.

Organisms are governed by many, many such reactions, so Gillooly and others have used this relation to help build a foundation for the metabolic theory of ecology (Brown et al. 2004). They have estimated that the average activation energy is approximately $E_a = 0.23\,eV$ (Gillooly 2000). Subsequent work has described this as "temperature sensitivity", where larger numbers imply that organisms respond more strongly to temperature variation. This relation is a little more complicated that a simple power law.

```r
# with base R
par(mar=c(5,4,1,0), mgp=c(1.5,.4,0) ) # set figure margins in "lines"
curve(10^4*exp(-0.23/(8.5 * 10^-5 *x)), 276, 316,
      ylab="Effect of temperature on B",
      xlab='Temperature (deg K)')
```
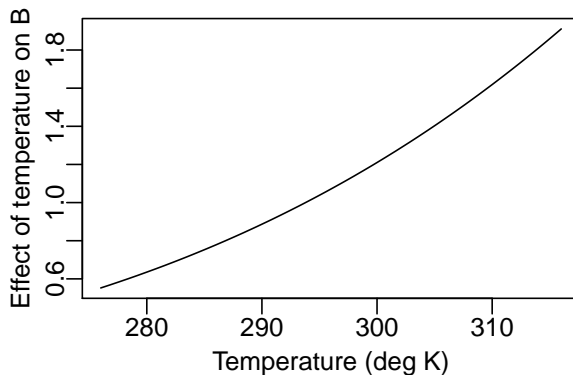

Figure 1.3: The effect of body temperature on ectothermic metabolic rates can be approximated with the Arrhenius function, $R = ae^{-E_a/(kT)}$. Here $a = 10^4$, and $E_a = 0.23$. It is similar in shape to a power law with $z > 1$, over the range of biologically relevant temperatures.

Or same as above with `ggplot2`.

```r
eq.t <- function(t,a=10^4,E=0.23,k=8.6 * 10^-5){a*exp(-E/(k*t))}
temps <- data.frame(t=276:316)
ggplot(data=temps, aes(x=t)) + # set the basic properties of the plot
  # in the stat_function, we indicate the parameters in our equation.
  stat_function(fun=eq.t, geom="line") + # set the function to plot
  xlab("Temperature (K)") + ylab("Metabolic rate (B)")  # add labels
```
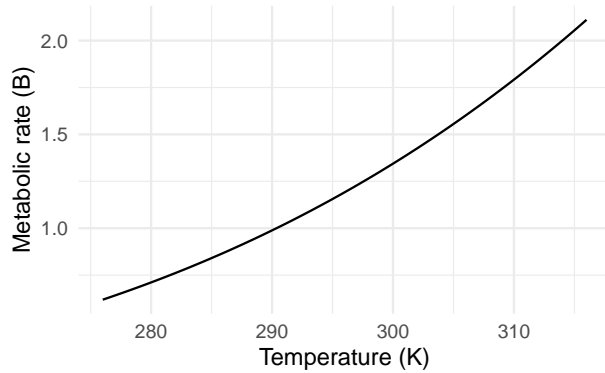
So, there you have it. The metabolic theory ecology is the algebraic product of body size- and temperature-dependence:

$$B = aM^{3/4}e^{\frac{-E_a}{kT}}$$

This theory makes quantitative predictions regarding all kinds of ecology phenomena (Brown et al. 2004), including

- home range size
- population growth
- population size
- resource uptake
- predation and other species interactions, and
- ecosystem cycling.

Note that these relations are based on first principles of geometry and thermodynamics, and that they depend on only a small number of parameters (a, $-E_a$, and perhaps $z = 3/4$), and makes a tremendous number of predictions. Therefore, Marquet et al. (2014) propose that this is "good" theory, and very *efficient*.

1.3   Power law scaling implies constant relative differences

In power law scaling, relative change is constant. That is, a proportional change in one variable results in a constant proportional change in the other. For instance, when we compare a smaller species to a larger species with $100\times$ the body mass, we can expect to see metabolic rate increase by $31.6\times$, *regardless of the mass of the smaller species.* For now, we will verify this numerically for some limited cases.

```
# define body mass and metabolic rate
m <- c(.01, 1, 100, 10000)
b <- m^.75
```

Now we will divide each mass i by the next smallest mass $i-1$. We do that using a vector by dividing each mass except the first one, by each mass except the last one.

	Small	Med.	Big	Huge
Mass	0.01	1.00	100.00	10000.00
Basal.metabolic.rate	0.03	1.00	31.62	1000.00
Relative.change.m	NA	100.00	100.00	100.00
relative.change.b	NA	31.62	31.62	31.62

Table 1.1: As we increase mass by a constant multiplier (10x), power law scaling results in a constant proportional change in basal metabolc rate.

```
# round(x, digits=0) rounds number to zero decimal places
round( m[-1]/m[-length(m)], digits = 0)
round( b[-1]/b[-length(b)], digits = 1)
```

When we do these divisions, we see the constant relative change (1.1).

We can verify this generally using algebra, not just in the particular case above. We will show that if mass increases by a constant multiplier, metabolic rate will also, regardless of the particular masses involved.

Let $m_2 = cm_1$ and $b = am^{3/4}$ where m is mass, b is metabolic rate, and a and c are constants. Thus,

$$\frac{m_2}{m_1} = c$$

.

We would like to show that b_2/b_1 is also a constant, regardless of the masses:

$$b_2 = a(cm_1)^{3/4} = ac^{3/4}m_1^{3/4}$$
$$\frac{b_2}{b_1} = \frac{ac^{3/4}m_1^{3/4}}{am_1^{3/4}}$$

When we reduce this fraction, we a left with

$$\frac{b_2}{b_1} = c^{3/4}$$

This shows that with power law scaling, increasing x by a constant *multipier* (or proportion), y increases by the same proportion raised to that power.

Ecologists typically describe metabolism-mass relations (and other power law behavior) using logarithmic scales. When we do that, power law relations become linear. Using our rules for exponents and logarithms, metabolic scaling becomes

$$\log B = \log a + z \log M$$

so that $\log B$ increases linearly with $\log M$ with a slope of 3/4.

Our brains can process and compare linear relations much more easily than curvilinear ones. Let's represent this graphically in a couple of ways, reusing data we made up previously in this chapter. First,

we just change the axes themselves, so that the units of the scales are multiples of 10 (often in scientific notation).

```
# using base R
par(mar=c(5,4,0,0), mgp=c(1.5,.4,0) )# set figure margins in "lines"
curve(x^(3/4), from = .01, to = 100, log="xy", ylab="Basal metabolic rate", xlab="Mass")
text(10, 80^.7, expression(M^0.75))

# using ggplot to build on a previous figure from above.
# 'p' is the graphic object we made earlier
# now we add different scaling for the axes
p + scale_x_log10() + scale_y_log10()
```
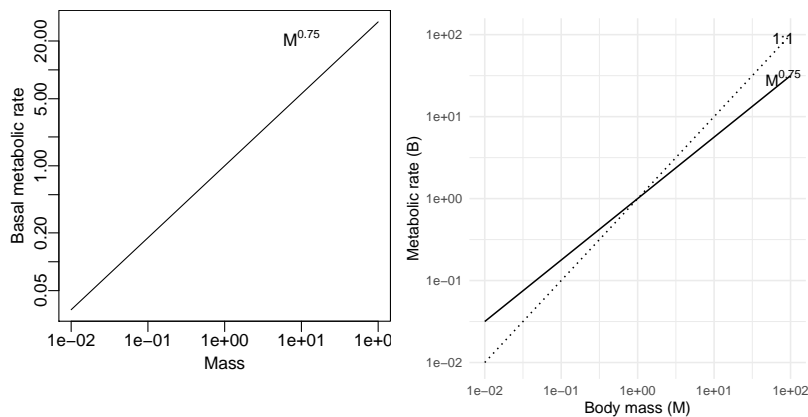

Figure 1.4: changing the scales of the axes to linearize power law relations. Note scales are logarithmic, using the original linear values.

Of course, we can also transform the same data we created above, and plot the log values.

```
df.log <- data.frame(lm = log10(m), lb = log10(b))

par(mar=c(5,4,1,0), mgp=c(1.5,.4,0) )
plot(lb ~ lm, data=df.log, type='l', xlab = "log(M)", ylab="log(B)")
text(0, 2, "Slope = 3/4")

ggplot(data=df.log, aes(x=lm, y=lb)) + geom_line() +
  labs(x="log(M)", y="log(B)")
```
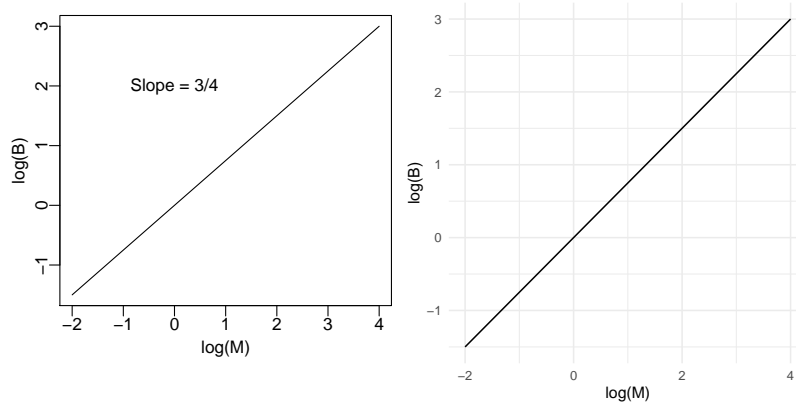
Figure 1.5: Power laws, such as metabolic scaling, are linearized when we use logarithms of the variables. Note the axes are linear, using the transformed log-values.

2
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