

Calculus for the Life Sciences

Lecture Notes – Allometric Modeling

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Spring 2017



Kleiber's Relationship

Metabolism and Size

- Kleiber asks, “Does a horse produce more heat per day than a rat...?”¹
- Obviously, **YES**
- “Does a horse produce more heat per day per kilogram of body weight than a rat?”
- Clearly, **NO**
- Animals benefit metabolically by increasing size

¹Max Kleiber (1947), “Body size and metabolic rate,” *Physiological Reviews*, **24**, 511-541



Outline

- 1 Kleiber's Law – Weight and Metabolism
- 2 Allometric Models
- 3 Review of Exponentials and Logarithms
 - Exponentials
 - Logarithms
 - Graphing Exponential and Logarithms
- 4 Allometric Modeling
 - Basic Power Law Model
 - Return to Kleiber's Law
 - Pulse and Weight
 - Island Biodiversity



Metabolism/Weight for Animals

Table of Metabolism (kcal) and Weight (kg) for Various Animals

Animal	Weight	Metabolism	Animal	Weight	Metabolism
Mouse	0.021	3.6	Dog	24.8	875
Rat	0.282	28.1	Dog	23.6	872
Guinea pig	0.41	35.1	Goat	36	800
Rabbit	2.98	167	Chimpanzee	38	1090
Rabbit	1.52	83	Sheep	46.4	1254
Rabbit	2.46	119	Sheep	46.8	1330
Rabbit	3.57	154	Woman	57.2	1368
Rabbit	4.33	191	Woman	54.8	1224
Rabbit	5.33	233	Woman	57.9	1320
Cat	3	152	Cow	300	4221
Macque	4.2	207	Cow	435	8166
Dog	6.6	288	Heifer	482	7754
Dog	14.1	534	Cow	600	7877



Modeling Data

Modeling the Data

- The data are clearly not linear
- There are general methods for finding the least squares best fit to nonlinear data
- These techniques are very complicated and often difficult to implement
- **Power Law** or **Allometric Models** are easier



Allometric Models or Power Law Model

Allometric Models

- Allometric models assume a relationship between two sets of data, x and y , that satisfy a power law of the form

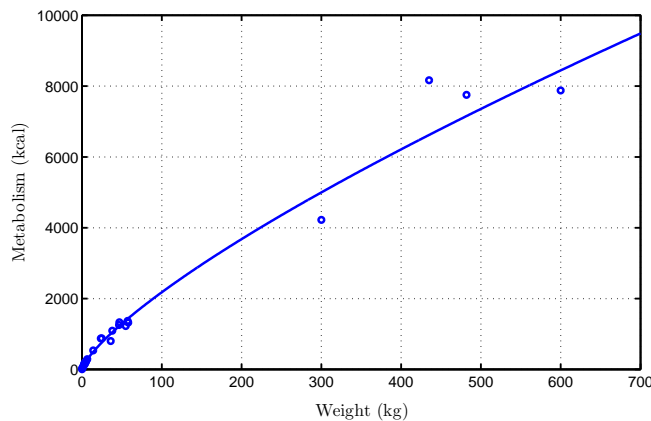
$$y = Ax^r$$

- A and r are parameters that are chosen to best fit the data in some sense
- This model assumes that when $x = 0$, then $y = 0$
- The method fits a straight line to the logarithms of the data



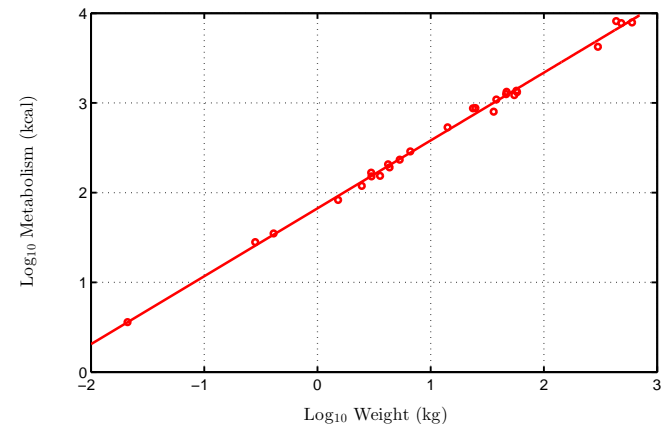
Allometric Model of Kleiber's Law

Graph of the Metabolic and Weight data



Allometric Model of Kleiber's Law

If w is the weight (kg) and M is the metabolic rate (kcal), then below is the graph of $\log_{10} M$ vs. $\log_{10} w$



Allometric Model of Kleiber's Law

Allometric Model of Kleiber's Law

- The best slope is $r = 0.7565$
- The best intercept is $\log_{10}(A) = 1.825$ with $A = 66.82$
- This gives the best fit power law for this model as

$$M = 66.82w^{0.7565}$$

- The minimum least squares for the log of the data gives $J(A, r) = 3.81 \times 10^6$
- **Nonlinear least squares best fit model (with a 4.5% better fit (SSE)) satisfies**

$$M = 63.86w^{0.7685}$$



Kleiber's Law

Allometric Model of Kleiber's Law

$$M = 66.82w^{0.7565}$$

- The graph of the power law provides a reasonable fit to the data
- The logarithm of the data closely lie on a straight line
- The coefficient $A = 66.82$ scales the variables
- The power $r = 0.7565$ often give physical insight to the behavior
 - If metabolism rate was proportional to mass, then $r = 1$
 - If metabolism relates to heat loss through skin, we expect $r = \frac{2}{3}$
 - **Why is $r = \frac{3}{4}$? This is Kleiber's Law.**



Allometric Model/Power Law

Allometric Model/Power Law

- When the logarithm of the data lie on a line, then a **Allometric Model** is appropriate
- Allometric Model can give insight into underlying biology of a problem
- Numerous examples satisfy allometric models
- Several Computer Lab problems based on allometric models
- Understanding Allometric models requires logarithms and exponentials



Review of Exponents

Properties of Exponents

1. $a^m a^n = a^{m+n}$,
2. $(a^m)^n = a^{mn}$,
3. $a^{-m} = \frac{1}{a^m}$,
4. $\frac{a^m}{a^n} = a^{m-n}$,
5. $(ab)^m = a^m b^m$,
6. $a^0 = 1$.

For solving equations with exponents, the inverse function of the exponent is needed, the **logarithm**



Definition of Logarithm

Definition: Consider the equation:

$$y = a^x$$

The inverse equation that solves for x is given by

$$x = \log_a y$$

The a in the expression is called the **base of the logarithm**



Review of Logarithms

Properties of Logarithms

1. $\log(ab) = \log(a) + \log(b)$,
2. $\log(a^m) = m \log(a)$,
3. $\log(1/a) = -\log(a)$,
4. $\log(a/b) = \log(a) - \log(b)$,
5. $\log_a(a) = 1$,
6. $\log(1) = 0$.

- The only property that requires the base of the logarithm for Property 5
- All other properties are independent of which base is used



Base 10 and e

Logarithms base 10 and e

- The two most common logarithms that are used are \log_{10} and \log_e
- The natural logarithm, often denoted \log or \ln
 - The natural logarithm is the default for most calculators and programming languages
 - However, Excel defaults to \log_{10}
- We will soon see the importance of the natural base e in Calculus



Graphing the Exponential Function

1

Graphing the Exponential Function

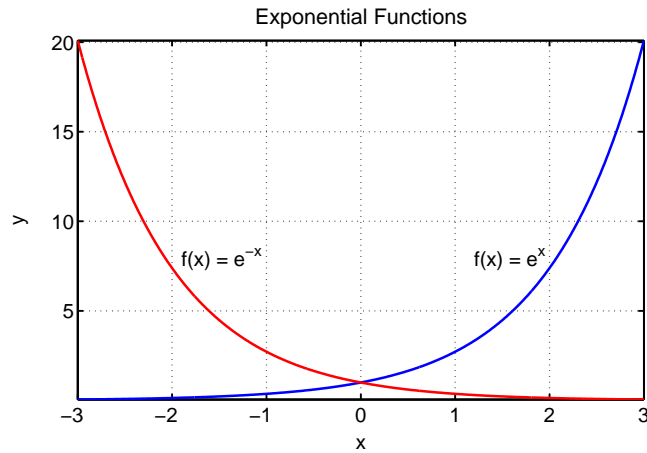
- For graphing purposes, e is an irrational number between 2 and 3, more precisely, $e = 2.71828\dots$
- The domain of e^x is all of x
 - e^x becomes extremely small very fast for $x < 0$ (a **horizontal asymptote of $y = 0$**)
 - It grows very fast for $x > 0$
- The graph of $y = e^{-x}$ has the same y -intercept of 1, but its the mirror reflection through the y -axis of $y = e^x$



Graphing the Exponential Function

2

The graphs of the $y = e^x$ and $y = e^{-x}$



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Graphing the Logarithm Function

1

Graphing the Logarithm Function

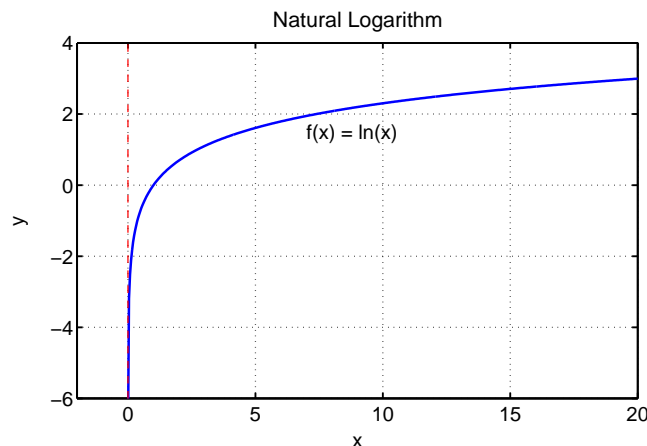
- Since $\ln(x)$ is the inverse function of e^x , the graph of this function mirrors the graph of e^x through the line $y = x$
- The **domain** of $\ln(x)$ is $x > 0$
- The **range** of $\ln(x)$ is all values of y
- As $y = \ln(x)$ becomes undefined at $x = 0$, there is a **vertical asymptote** at $x = 0$

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Graphing the Logarithm Function

2

The graph of the $y = \ln(x)$



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Example of Graphing the Exponential

1

Consider the exponential function given by

$$f(x) = 4 - e^{-2x}$$

Find the all intercepts and any horizontal asymptotes and graph this equation

Skip Example

Solution: Since

$$f(0) = 4 - e^0 = 4 - 1 = 3,$$

the y -intercept is $(0, 3)$

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Example of Graphing the Exponential

2

Solution (cont): Solving $4 - e^{-2x} = 0$ gives

$$e^{-2x} = 4 \quad \text{or} \quad e^{2x} = \frac{1}{4}$$

Thus, $2x = \ln(1/4) = -2 \ln(2)$ or $x = -\ln(2) \approx -0.6931$

The x -intercept is $(-0.6931, 0)$

For large values of x , e^{-2x} is very close to zero, so there is a **horizontal asymptote** for large positive x

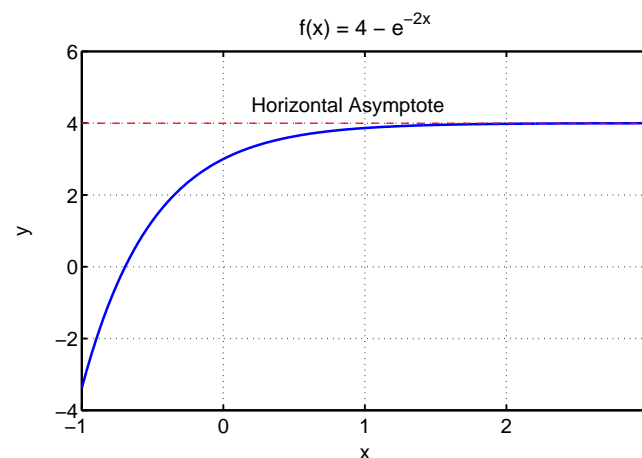
$f(x)$ tends toward 4

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Example of Graphing the Exponential

3

The graph of the $y = 4 - e^{-2x}$



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Example of Graphing the Logarithm

1

Consider the logarithmic function given by

$$f(x) = \ln(x + 2)$$

Find the all intercepts and any vertical asymptotes and graph this equation

Skip Example

Solution: The **domain** of $f(x)$ is $x > -2$

There is a **vertical asymptote** at the edge of the domain, where $x = -2$

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Example of Graphing the Logarithm

2

Solution (cont): When $x = 0$,

$$f(0) = \ln(2) \approx 0.6931$$

Thus, the y -intercept is $(0, 0.6931)$

Solving $\ln(x + 2) = 0$, gives

$$x + 2 = 1 \quad \text{or} \quad x = -1$$

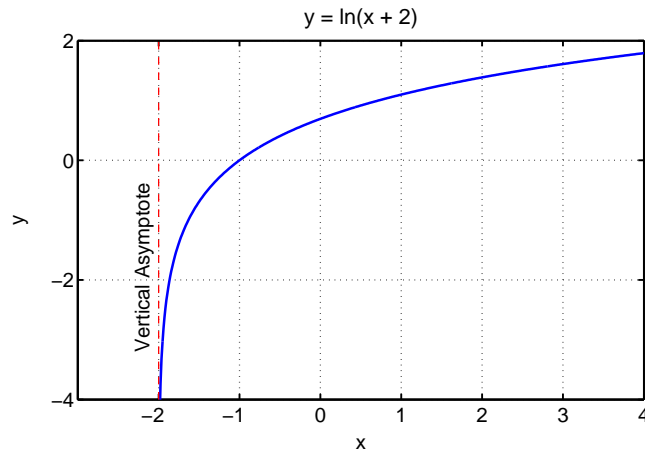
Thus, the x -intercept is $(-1, 0)$

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Example of Graphing the Logarithm

3

The graph of the $y = \ln(x + 2)$



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Allometric Models

The **Allometric Model** for two sets of data, x and y satisfies a power law

$$y = Ax^r$$

- The parameters A and r are chosen to best fit the data
- By properties of logarithms

$$\ln(y) = \ln(Ax^r) = \ln(A) + r \ln(x)$$

- Let $X = \ln(x)$, $Y = \ln(y)$, and $a = \ln(A)$, then

$$Y = a + rX$$

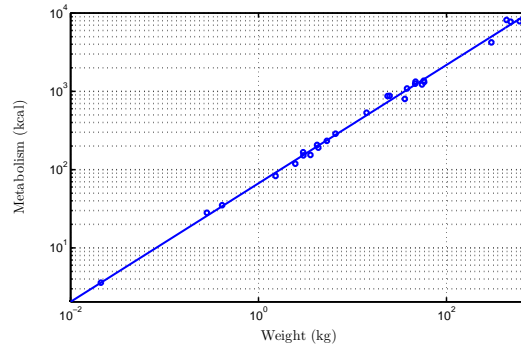
- This is a line with a slope of r and a Y -intercept of $\ln(A)$

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Example of Kleiber's Law

1

The data and model for Kleiber's Law is plotted with logarithmic scales



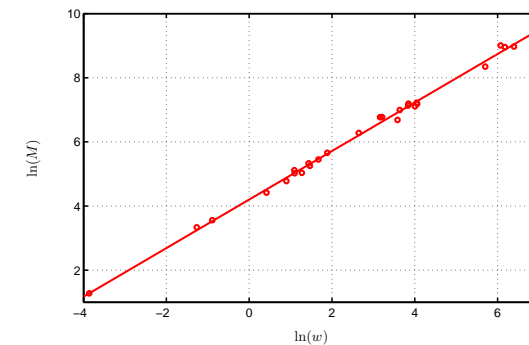
The log-log plot falling on a straight line suggests an **allometric model**

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Example of Kleiber's Law

2

The plot of the logarithms of the data for metabolism and weight of various animals



This graph is very similar to the previous graph

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Example of Kleiber's Law

3

Allometric Model of Kleiber's Law

- The least squares best fit of the straight line to the logarithms of the data
 - Best slope $r = 0.7565$
 - Best intercept $a = \ln(A) = 4.202$
 - It follows $A = 66.82$
- The best allometric model is

$$M = 66.82w^{0.7565}$$



Example of Weight and Pulse

2

Solution: An allometric model

$$P = Aw^k$$

Logarithms give

$$\ln(P) = \ln(A) + k \ln(w)$$

As noted above, this is a straight line in $\ln(w)$ and $\ln(P)$



Example of Weight and Pulse

1

Example of Weight and Pulse

- Smaller animals have a higher pulse than larger animals
- Suppose a 17 g mouse has a pulse of 500 beats/min and a 68 kg human has a pulse of 65
- Create an allometric model (other data support this form)
- Predict the pulse for a 1.34 kg rabbit

Skip Example



Example of Weight and Pulse

3

Solution (cont): Create a line through logarithm of data

Animal	Weight(kg)	$\ln(w)$	Pulse(beats/min)	$\ln(P)$
Mouse	0.017	-4.075	500	6.215
Human	68	4.220	65	4.174

The slope k is

$$k = \frac{4.174 - 6.215}{4.220 + 4.075} = -0.246$$

The intercept of $\ln(A)$ satisfies:

$$\ln(A) = -k \ln(w_0) + \ln(P_0) = 0.246(4.220) + 4.174 = 5.212$$



Example of Weight and Pulse

4

Solution (cont): The linear model in the logarithm of the data satisfies:

$$\ln(P) = -0.246 \ln(w) + 5.212$$

The **allometric model** is

$$P = 183.5w^{-0.246}$$

If we consider a **1.34 kg rabbit**, then the model gives:

$$P = 183.5(1.34)^{-0.246} = 171 \text{ beats/min}$$



Example of Island Biodiversity

2

From the model predict the number of bird species on **Island C**
 Also, determine how large an island would be required to support 20 species of birds near this chain of islands

Solution: The allometric model can be rewritten as the linear model of the logarithm of the data

$$\ln(N) = \ln(k) + x \ln(A)$$



Example of Island Biodiversity

1

Example of Island Biodiversity

There are three Pacific islands in a chain. **Island A** is **15 km²**, **Island B** is **110 km²**, and **Island C** is **74 km²**. An extensive biological survey finds **5 species** of birds on **Island A** and **9 species** of birds on **Island B**.

Skip Example

Assume an allometric model between the number of species, N , on each of these islands and their area, A , of the form

$$N = kA^x$$

Use the data from **Islands A** and **B** to determine constants k and x



Example of Island Biodiversity

3

Solution (cont): Create a line through logarithm of data

Island	Area	$\ln(A)$	Species	$\ln(N)$
A	15	2.708	5	1.609
B	110	4.700	9	2.197

The slope x satisfies

$$x = \frac{\ln(9) - \ln(5)}{\ln(110) - \ln(15)} \approx 0.295$$

The intercept of $\ln(k)$ satisfies:

$$\ln(k) = \ln(5) - x \ln(15) \approx 0.811 \quad \text{or} \quad k \approx 2.25$$



Example of Island Biodiversity

4

Solution (cont): The linear model in the logarithm of the data satisfies:

$$\ln(N) = 0.811 + 0.295 \ln(A)$$

The **allometric model** is

$$N = 2.25A^{0.295}$$

The model predicts that **Island C** has

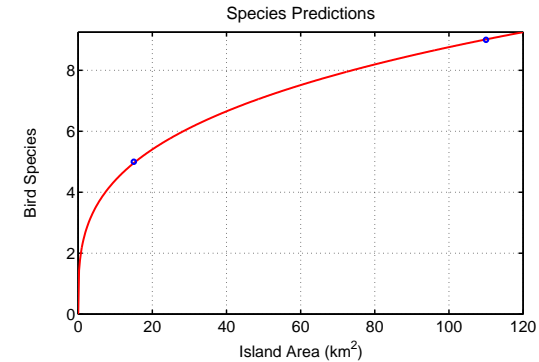
$$N = 2.25(74)^{0.295} \approx 8.01 \text{ species}$$



Example of Island Biodiversity

5

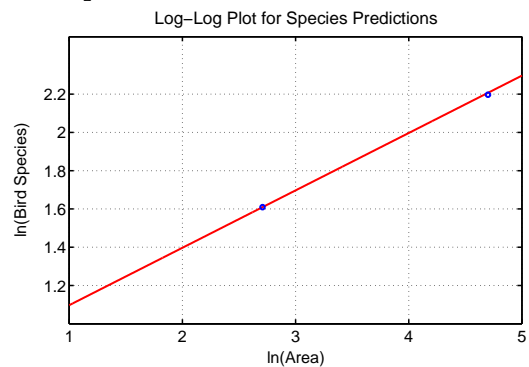
Below is a graph of the allometric model showing the area and the species predictions



Example of Island Biodiversity

6

Below is a graph of $\ln(A)$ and the $\ln(N)$, showing the linearity of the logarithmic plot



Example of Island Biodiversity

7

Finally, we want to predict the size of an island necessary to support 20 species

We solve the equation

$$20 = 2.25A^{0.295}$$

From properties of logarithms

$$\ln(20) = \ln(2.25) + 0.295 \ln(A)$$

$$\ln(A) = \frac{1}{0.295} (\ln(20) - \ln(2.25)) = 7.406$$

The model predicts that the area of the island needs to be $A = 1646 \text{ km}^2$

