

29. Differential equations. The conceptual basis of allometry

Did it occur to you in Lecture 3 why Fibonacci would even care how rapidly a rabbit population grows? Maybe he wanted to eat the rabbits. If so, then he would be less concerned about total number of rabbit pairs than total weight of rabbit meat, which varies continuously (as opposed to discretely). Let $W(t)$ be weight at time t . Then W is an ordinary function. But what kind of function is W ? In this lecture we investigate. Over a very short time interval $[t, t+h]$, weight increases by $\text{Diff}(W, [t, t+h]) = W(t+h) - W(t)$, with average rate of increase $\text{DQ}(W, [t, t+h]) = \text{Diff}(W, [t, t+h])/h$. Although weight changes on $[t, t+h]$, it changes only a little, so it is always $W(t) + O[h]$. Therefore average increase *per rabbit* on $[t, t+h]$ is $\text{DQ}(W, [t, t+h])/W(t) + O[h]$. As h approaches zero, this expression approaches

$$(29.1) \quad \lim_{h \rightarrow 0} \frac{\text{DQ}(W, [t, t+h])}{W(t) + O[h]} = \frac{W'(t)}{W(t)} = r(t),$$

say, where r has the same domain as W and W' . We call r the **relative growth rate**. The preceding argument applies virtually without change to the growth of any mass of tissue. In particular, it applies to the growth of a single organ or organism. That is, if $W(t)$ denotes size at time t of an organ or organism, then

$$(29.2) \quad W'(t) = r(t)W(t)$$

where r is relative growth rate. Equation (2) embodies Julian Huxley's first "essential fact" about growth, namely, "that it is a process of self-multiplication of living substance—i.e. that the rate of growth of an organism growing equally in all its parts is at any moment proportional to the size of the organism" (Huxley, 1932, p. 6).

What kind of function is r ? Taking our cue from Lecture 5, where Fibonacci rabbit pairs reproduce at a constant rate (of 12 times per annum), we conjecture that r may be constant, say $r = \lambda (> 0)$. Then (2) implies $W'(t) = \lambda W(t)$ or, if $y = W(t)$,

$$(29.3) \quad \frac{dy}{dt} = \lambda y.$$

This is a very simple example of an **ordinary differential equation, or ODE**. How do we "solve" this ODE? In other words, how do we find y if we know dy/dt ? Hitherto we have used the fundamental theorem. But we cannot apply it to (3), because the right-hand side is an unknown function of time. On the other hand, if W is invertible with inverse U , so that $y = W(t)$ is exactly the same thing as $t = U(y)$, then from (20.39) we have

$$(29.4) \quad \frac{dy}{dt} \left\{ \frac{dy}{dt} \right\}^{-1} = \lambda y.$$

So we can rewrite (3) as

$$(29.5) \quad \frac{dy}{dt} = \frac{1}{\lambda y},$$

and now it follows from the fundamental theorem that

$$(29.6) \quad t = U(y) = C + \int_y^a \frac{\lambda u}{1} du = C + \frac{1}{\lambda} \int_y^a \frac{\lambda}{u} du,$$

where C is a constant. To obtain the value of C , we set

$$(29.7) \quad a = W(t_0),$$

where t_0 is initial time, and so a is initial weight. Then (6), with $y = a$, implies

$$(29.8) \quad U(a) = C + \int_a^a \frac{1}{\lambda u} du = C + 0.$$

But $a = W(t_0)$ implies $U(a) = t_0$, because U and W are inverse functions. So (8) implies $C = t_0$, from which (6) implies

$$(29.9) \quad \begin{aligned} t &= t_0 + \int_y^a \frac{1}{\lambda u} du \\ &= t_0 + \frac{1}{\lambda} \ln(u)|_y^a \\ &= t_0 + \frac{1}{\lambda} \{\ln(a) - \ln(y)\} \\ &= t_0 + \frac{1}{\lambda} \ln(y/a) \end{aligned}$$

on using Table 22.6 and Exercise 22.1. So $\lambda\{t-t_0\} = \ln(y/a)$, or $\exp(\lambda\{t-t_0\}) = y/a$. That is,

$$(29.10) \quad y = a \exp(\lambda\{t-t_0\}) = ae^{\lambda t - \lambda t_0}.$$

In other words,

$$(29.11) \quad y = W(t) = Ae^{\lambda t}$$

with

$$(29.12) \quad A = ae^{-\lambda t_0}.$$

When $W(t) = Ae^{\lambda t}$, it is traditional to say that W exhibits **exponential growth** at

rate λ (although what is actually meant is that W has relative growth rate λ). There is

evidence that organisms do grow exponentially during early development, although

relative growth rate appears to decrease later on. The crux of the evidence is that (11)

implies

$$(29.13) \quad \begin{aligned} \ln(y) &= \ln(W(t)) = \ln(Ae^{\lambda t}) = \ln(A) + \ln(e^{\lambda t}) \\ &= \ln(A) + \lambda t. \end{aligned}$$

That is, if growth is exponential, then $\ln(y)$ is a linear function of t . So we can test an

exponential growth hypothesis by plotting $(t, \ln(y))$ data pairs and drawing the straight

line that fits them best. The closer the fit, the more confident we are in the hypothesis.

TIME t (days)	WEIGHT y (grams)	$\ln(y)$	TIME t (days)	WEIGHT y (grams)	$\ln(y)$
6	18	4	53	0	0
18	30	9	60	1.386	62
30	42	17	74	2.197	71
39	74	2.833	93	2.833	74
46	26	3.258			

Table 29.1 Backman's data on growth in weight of maize. Source: Exercise 5.10

For example, from Thompson (1942, p. 115) we have Backman's data on weight y (grams) of maize at time t (days); see Table 1. From Figure 1(a), where $\ln(y)$ is plotted against t , the data points fall very close to a straight line for times between 18 and 60

days. This six-week period is an exponential growth phase. The dotted line in Figure 1(a), determined by the method of Appendix 2A, has equation

$$(29.14) \quad \ln(y) = 0.2279 + 0.06574t.$$

Comparing with (13), $\lambda = 0.06574$, $\ln(A) = 0.2279$ and so $A = \exp(0.2279) = 1.256$. Thus

$$(29.15) \quad W(t) = 1.256e^{0.06574t}$$

provides an excellent description of growth in weight of maize on [18, 60]; see Figure 1(b). On the other hand, (15) provides a very poor description at later times.

It isn't difficult to see why. By (2), a constant relative growth rate implies that W' keeps increasing. But the data in Figure 1 and Table 1 imply that W' eventually approaches zero, in which case, r approaches zero, too. Intuitively, growth per unit weight declines with weight because more cells compete for the same resources. The simplest possibility is that r decreases linearly with W , say

$$(29.16) \quad r(t) = \lambda \left(1 - \frac{W(t)}{K} \right)$$

where K is another parameter. We assume that

$$(29.17) \quad W(t_0) > K,$$

where t_0 is the initial time; i.e., W has domain $[t_0, \infty)$. Then r is positive and decreases toward zero as $W(t)$ increases toward K .

Substituting (16) into (2) and setting $y = W(t)$, we obtain a new ODE

$$(29.18) \quad \frac{dy}{dt} = \lambda y \left(1 - \frac{y}{K} \right)$$

in place of (3). Assuming as before that W is invertible with inverse U , we have

$$(29.19) \quad \frac{dy}{dt} = \frac{\lambda y(K-y)}{K}$$

in place of (5), and it follows from the fundamental theorem that

$$(29.20) \quad t = U(y) = C + \int_y^a \frac{\lambda u(K-u)}{K} du,$$

where C is a constant. Exactly as above, $a = W(t_0)$ implies $C = t_0$. Thus

$$(29.21) \quad t = U(y) = t_0 + \frac{1}{\lambda} \int_y^a \frac{\lambda u(K-u)}{K} du.$$

Table 22.6 and Exercise 22.1 now imply that

$$t = t_0 + \frac{1}{\lambda} \ln \left(\frac{K-u}{K-y} \right)$$

$$(29.22) \quad = t_0 + \frac{1}{\lambda} \left[\ln \left(\frac{K-y}{y} \right) - \ln \left(\frac{K-a}{a} \right) \right]$$

$$= t_0 + \frac{1}{\lambda} \ln \left(\frac{K-a}{K-y} \right).$$

So $\lambda(t-t_0) = \ln((K-a)y/(K-y))$, implying

$$(29.23) \quad e^{\lambda(t-t_0)} = \frac{K-y}{a(K-y)}$$

or, after straightforward algebraic manipulations (Exercise 1),

$$(29.24) \quad y = \frac{aKe^{\lambda(t-t_0)}}{ae^{\lambda(t-t_0)} + K - a}$$

In other words,

$$(29.25) \quad W(t) = \frac{K}{1 + Ae^{-\lambda t}}$$

where

$$(29.26) \quad A = \{K/a - 1\}e^{\lambda t_0}$$

Note that

$$(29.27) \quad W(t_0) = a,$$

Correspondingly,

$$(29.28) \quad W'(t) = \lambda W(t) \left(1 - \frac{K}{W(t)} \right) = \frac{\lambda K A e^{-\lambda t}}{(1 + A e^{-\lambda t})^2}$$

from (18) and (25).

Growth according to (24) is traditionally called **logistic growth**. From (17) and (28), $K/a > 1$, implying $A > 0$. So $W(t)$ is less than K but approaches K asymptotically as $t \rightarrow \infty$ because $e^{-\lambda t} \rightarrow 0$ as $t \rightarrow \infty$. We interpret K as maximum possible weight. In Figure 2, the functions W and W' are plotted against Backman's data with $A = 389$, $K = 75.5$ and $\lambda = 0.119$ (values were obtained by a method similar to that of Appendix 2A). We find that the logistic model provides a much better overall fit, with maximum

growth during day 51; see Exercise 2.

We conclude this lecture by observing that Huxley used a pair of ODEs to secure a conceptual foundation for allometry. He reasoned that "the growth-rate of any particular organ is proportional simultaneously (a) to a specific constant characteristic of the organ in question, (b) to the size of the organ at any instant, and (c) to a general factor dependent on age and environment which is the same for all parts of the body" (Huxley, 1932, p. 6). If y is the size of an allometric organ and x the size of its body, and if k_2, k_1 are the specific constants for part and body, respectively, then because both organ and body are exposed to the same environment, (a)–(c) imply

$$(29.29) \quad \frac{dx}{dt} = k_1 x G(t)$$

and

$$(29.30) \quad \frac{dy}{dt} = k_2 y G(t)$$

where t denotes time and G is some unknown function. Dividing (30) by (29), we have

$$(29.31) \quad \frac{dy}{dx} \left\{ \frac{dx}{dt} \right\}^{-1} = \beta \frac{y}{x}$$

where

$$(29.32) \quad \beta = \frac{k_1}{k_2}$$

Note that the organ is positively or negatively allometric according to whether $k_2 > k_1$ or $k_1 > k_2$, and hence according to whether $\beta > 1$ or $\beta < 1$, as in Lecture 22. Assuming that x is an invertible function of time, and hence t an invertible function of x ,

$$(29.33) \quad \frac{dx}{dt} = \left\{ \frac{dx}{dt} \right\}^{-1}$$

by analogy with (4). So (31) can be rewritten as

$$(29.34) \quad \frac{dy}{dt} = \beta \frac{dx}{x}.$$

If y is a function of t , however, and t is a function of x , then y is also a function of x . So the chain rule reduces (34) to

$$(29.35) \quad \beta \frac{dy}{Y} = \frac{dx}{x},$$

another ODE. Comparing with (3) and (18), we find that the right-hand sides of (3) and (18) involve only the dependent variable, whereas the right-hand side of (35) involves the independent variable as well; nevertheless, (35) is no more difficult to solve. We proceed as follows.

According to the chain rule, if y is a positive function of x then

$$(29.36) \quad z = \ln(y)$$

defines a composition with derivative

$$(29.37) \quad \frac{dz}{dx} = \frac{dz}{dy} \frac{dy}{dx} = \frac{d}{dx} \{\ln(y)\} \frac{dy}{dx} = \frac{1}{y} \frac{dy}{dx},$$

on using Table 22.6. So (36) reduces (35) to

$$(29.38) \quad \frac{dz}{z} = \frac{dx}{x}.$$

It now follows from the fundamental theorem that

$$(29.39) \quad z = C + \beta \int_x^a \frac{1}{u} du = C + \beta \ln(u)|_x^a$$

so that (36) and properties of the logarithm imply

$$(29.40) \quad \ln(y) = C + \beta \ln\left(\frac{a}{x}\right) = C + \ln\left(\frac{a}{x}\right)^\beta.$$

Properties of the exponential now imply that

$$(29.41) \quad y = \exp\left(C + \ln(x/a)^\beta\right) = \exp(C) \exp(\ln(x/a)^\beta) = \exp(C) x^\beta \frac{a^\beta}{x^\beta}.$$

On setting $a^{-\beta} \exp(C) = \alpha$ we have $y = \alpha x^\beta$, agreeing with (22.32).

References

Huxley, Julian S. (1932). *Problems of Relative Growth*. The Dial Press, New York
 Thompson, D'Arcy W (1942). *On Growth and Form*. Cambridge University Press.

Exercises 29

29.1 Verify (24)-(27).

29.2 Show that the logistic growth curve $y = W(t)$ defined by (25) has an inflection point at $t = t^*$, defined by $t^* = \ln(A)/\lambda$. Verify that $W(t^*) = K/2$.

29.3 Show that (28) implies

$$W'''(t) = \lambda^3 W(t) \left\{ 1 - \frac{K}{W(t)} \right\} \left\{ 1 - \frac{K}{6W(t)} \left(1 - \frac{K}{W(t)} \right) \right\}.$$

Hence show that the curve $y = W'(t)$ has inflection points where

$$t = \frac{1}{\lambda} \ln \left(\left\{ 2 \pm \sqrt{3} \right\} A \right),$$

i.e., where $t = 39$ and $t = 61$ in Figure 2(b).

Answers and Hints for Selected Exercises

29.2 From (28), we have

$$W'(t) = \lambda W(t) \left(1 - \frac{K}{W(t)}\right).$$

So

$$\begin{aligned} W''(t) &= \frac{d}{dt} \left\{ W'(t) \right\} = \lambda \frac{d}{dt} \left\{ W(t) \left(1 - \frac{K}{W(t)}\right) \right\} \\ &= \lambda \left\{ W'(t) \cdot \left(1 - \frac{K}{W(t)}\right) + W(t) \cdot \frac{d}{dt} \left(1 - \frac{K}{W(t)}\right) \right\} \\ &= \lambda \left\{ W'(t) \cdot \left(1 - \frac{K}{W(t)}\right) + W(t) \cdot \left(0 - \frac{K}{W(t)^2} W'(t)\right) \right\} \\ &= \lambda \left\{ W'(t) \cdot \left(1 - \frac{K}{W(t)}\right) - \frac{K}{W(t)} W'(t) \right\} \\ &= \lambda W'(t) \left\{ 1 - \frac{K}{2W(t)} \right\} \\ &= \lambda^2 W(t) \left(1 - \frac{K}{W(t)}\right) \left\{ 1 - \frac{K}{2W(t)} \right\}. \end{aligned}$$

implying $W''(t^*) = 0$ where $W(t^*) = 0$ or $1 - W(t^*)/K = 0$ or $1 - 2W(t^*)/K = 0$. From (25), however, we have $W(t^*) = K/(1 + Ae^{-\lambda t^*})$, so that $W(t^*) = 0$ is

impossible, and

$$1 - \frac{K}{W(t^*)} = 1 - \frac{K}{1 - \frac{K}{1 + Ae^{-\lambda t^*}}} = \frac{K}{1 + Ae^{-\lambda t^*}}.$$

so that $1 - W(t^*)/K = 0$ is impossible (except in the limit as $t^* \rightarrow \infty$). So the inflection point must be determined by $1 - 2W(t^*)/K = 0$. But

$$1 - \frac{K}{2W(t^*)} = 1 - \frac{K}{2} \frac{1 + Ae^{-\lambda t^*}}{K} = \frac{1 + Ae^{-\lambda t^*}}{2} - 1 = \frac{1 + Ae^{-\lambda t^*} - 2}{2}.$$

Thus $1 - 2W(t^*)/K = 0$ implies $Ae^{-\lambda t^*} = 1$ or $e^{-\lambda t^*} = 1/A$. Hence $-\lambda t^* = \ln(1/A) = -\ln(A)$, and $\lambda t^* = \ln(A)$ or $t^* = \ln(A)/\lambda$.

Note that, because $0 < W(t) < K$, the sign of $W''(t)$ is completely determined by $1 - 2W(t)/K$, which is positive if $t < t^*$ but negative if $t > t^*$. Thus W' has maximum $W'(t^*)$. You can verify that $W''(t^*) = 0$ corresponds to a minimum (as opposed to a maximum) of W' by checking the sign of $W'''(t^*)$:

from Exercise 3,

$$W'''(t^*) = \lambda^3 W(t^*) \left\{ 1 - \frac{K}{W(t^*)} \right\} \left\{ 1 - \frac{K}{6W(t^*)} \right\} \left\{ 1 - \frac{K}{W(t^*)} \right\} = -\frac{8}{\lambda^3 K},$$

which is negative.