17. Sex allocation and the product rule

Whenever two quantities depend on a third, that dependence implies a relationship between the first two quantities. For example, how many daughters and how many sons can an animal raise to maturity? Both numbers depend on parental investment. So each depends on the other, with more sons meaning fewer daughters, and vice versa. Then how should an animal allocate resources between the sexes? In this lecture, we investigate. To that end, we introduce a labor-saving formula for the derivative of a product, analogous to the formula in Lecture 16 for the derivative of a sum of multiples.

Accordingly, let u be the proportion of an individual's resources that it invests in female progeny, and let v be the corresponding proportion for male progeny, so that

$$u + v = 1. \qquad (17.1)$$

Let $X = F(u)$ denote the number of females expected to survive to reproductive age as a consequence of investment u, and let $Y = G(v)$ denote the number of males expected to survive to reproductive age as a consequence of investment v; F stands for females, G for guys. Both F and G are nondecreasing (and typically increasing) on [0, 1]; that is,

$$F'(u) \geq 0, \qquad G'(v) \geq 0 \qquad (17.2)$$

for $0 \leq u, v \leq 1$, where we assume F and G to be piecewise-smooth. Moreover, no investment means no progeny, so

$$F(0) = 0, \qquad G(0) = 0. \qquad (17.3)$$

To simplify calculations, we scale X and Y with respect to their maxima. Denote Max(F, [0, 1]) by X_{max} and Max(G, [0, 1]) by Y_{max}, so that (2) implies

$$X_{max} = F(1), \qquad Y_{max} = G(1). \qquad (17.4)$$

To scale X, we define f on [0, 1] by

$$x = f(u) = \frac{F(u)}{X_{max}} = \frac{X}{X_{max}}, \qquad (17.5)$$

so that (2)-(4) imply

$$f(0) = 0, \qquad f'(u) \geq 0, \qquad f(1) = 1. \qquad (17.6)$$

We scale Y similarly, by writing $y = Y/Y_{max}$, which depends on v. But v is determined by u, through (1). So it is more convenient to work in terms of u alone. Accordingly, we define g on [0, 1] by

$$y = g(u) = \frac{G(1 - u)}{Y_{max}} = \frac{Y}{Y_{max}}, \qquad (17.7)$$

so that (2)-(4) and (7) imply

$$g(0) = 1, \qquad g'(u) \leq 0, \qquad g(1) = 0. \qquad (17.8)$$

Now, in terms of u alone, average numbers of female and male progeny are given by $X = f(u)X_{max}$ and $Y = g(u)Y_{max}$.

As u increases from 0 to 1, the point with coordinates (f(u), g(u)) traces a curve from (f(0), g(0)) = (0, 1) to (g(1), g(1)) = (1, 0). Because this curve embodies a tradeoff in expected future reproductive success — or "fitness" — between male and female investment, we will call it the **fitness curve**, and we will refer to

$$x = f(u), \qquad y = g(u), \qquad 0 \leq u \leq 1 \qquad (17.9)$$

as the curve's equations.[1] The fitness curve expresses a relationship between x and y that their mutual dependence on u implies. Suppose, e.g., that average number of females surviving to reproductive age is directly proportional to investment or, as economists

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[1] More generally, for any functions x, y defined on [a, b], $x = x(u)$, $y = y(u)$, $a \leq u \leq b$ are the equations of the curve traced out between (x(a), y(a)) and (x(b), y(b)). These equations are often called "parametric" equations; however, this terminology would be inconsistent with our usage of parameter in Lecture 2.

often say, the "rate of return" $F'(u)$ on investment u is constant; whereas the average number of surviving males may exhibit "diminishing returns on investment." That is, we allow for rate of return $G'(v)$ on investment v in males, although positive ($G'(v) > 0$), to decrease with further investment ($G''(v) < 0$). Then a possible model of returns on investments u in females and v in males is given by

$$F(u) = X_{max} u, \tag{17.10a}$$

$$G(v) = Y_{max} v^{\gamma} \tag{17.10b}$$

with $\gamma > 0$; or, on using (5) and (7),

$$x = f(u) = u \tag{17.11a}$$

$$y = g(u) = (1-u)^{\gamma}. \tag{17.11b}$$

By Exercise 2.2, investment in males exhibits constant or decreasing returns according to whether $0 < \gamma < 1$ or $\gamma = 1$.

On eliminating u, (11) reduces to a single equation

$$y = (1-x)^{\gamma} \tag{17.12}$$

so that y is a function of x; see Figure 1, where the upper panels illustrate $\gamma = 1/2$. But y is not invariably a function of x. Consider, e.g., the alternative model of returns on investment defined by

$$F(u) = \begin{cases} uX_{max}/\delta & \text{if } 0 \le u \le \delta \\ X_{max} & \text{if } \delta \le u \le 1 \end{cases} \qquad G(v) = Y_{max} v \tag{17.13}$$

with $0 < \delta < 1$ or, on using (5) and (7),

$$f(u) = \begin{cases} u/\delta & \text{if } 0 \le u \le \delta \\ 1 & \text{if } \delta \le u \le 1 \end{cases} \qquad g(u) = 1-u. \tag{17.14}$$

In this case, eliminating u yields

$$x = \begin{cases} (1-y)/\delta & \text{if } 0 \le y \le 1-\delta \\ 1 & \text{if } 1-\delta \le y \le 1 \end{cases} \tag{17.15}$$

(Exercise 11), which makes x an uninvertible function of y, so that y is not a function of x; see Figure 1, where $\delta = 2/5$ in the lower panels. Charnov (1982, p. 226) suggests that the second model could describe brood space limitation, with returns to investment in females saturating at proportion δ; and a whole variety of factors could lead to a law of diminishing returns on male investment, as described by our first model. Note, by the way, that each model is in turn a special case of the two-parameter model defined by

$$F(u) = \begin{cases} uX_{max}/\delta & \text{if } 0 \le u \le \delta \\ X_{max} & \text{if } \delta \le u \le 1 \end{cases} \qquad G(v) = Y_{max} v^{\gamma} \tag{17.16}$$

with $0 < \delta \le 1$, $0 < \gamma < \infty$. The first model assumes $\delta = 1$, the second assumes $\delta < 1$ and $\gamma = 1$. In every case, F and G are piecewise-smooth, as assumed.

Having modelled the returns on investment, we are better equipped to ask how resources are allocated between the sexes. Specifically, what proportion of an animal's resources should we expect to see invested in female progeny? In terms of the model devised by Shaw and Mohler (1953), which MacArthur (1965) later refined, the answer is remarkably simple: we should expect to see animals invest u*, where u* is the proportion that maximizes the product $p = f \bullet g$. We will refer to u* as the optimal allocation, because it maximizes p. But why should animals behave in this way? The answer is that any other behavior would be selected against, and so would not persist. Indeed we prove in Appendix 17 that the proportion u* is **evolutionarily stable**, by which we mean that if genes coding for u* are fixed in a population, then mutant genes coding for any other proportion would be selected against. Here, we take for granted that u* is the proportion we expect to observe and focus instead on how to calculuate it, which has more to do with calculus.

Now, you already know that the maximum of any function p is determined by where p is increasing or decreasing, which in turn is determined by its derivative p' (if we assume, as we do, that p is piecewise-smooth). But what is the derivative of a product? We need a new formula. So let us obtain one. Because p is defined by

$$p(u) = f(u)g(u) \tag{17.17}$$

we have $p(u + h) = f(u + h)g(u + h)$, which implies the difference quotient

$$DQ(p, [u, u+h]) = \frac{p(u+h) - p(u)}{h} = \frac{f(u+h)g(u+h) - f(u)g(u)}{h} \tag{17.18}$$

To find p' we must extract the leading term. It is shown in Appendix A, however, that

$$\frac{f(u+h)g(u+h) - f(u)g(u)}{h} = f'(u)g(u) + f(u)g'(u) + O[h]. \tag{17.19}$$

Thus

$$p'(u) = f'(u)g(u) + f(u)g'(u) \tag{17.20}$$

or, in mixed notation,

$$\frac{d}{du}\{f(u)g(u)\} = f'(u)g(u) + f(u)g'(u). \tag{17.21a}$$

As usual, the truth of this general result does not in any way depend upon the symbols we choose for functions and variables, as long as we use them consistently on both sides of the equation. So another way to state the very same result would be, e.g.,

$$\frac{d}{dx}\{F(x)G(x)\} = F'(x)G(x) + F(x)G'(x). \tag{17.21b}$$

We call this formula the **product rule**.

The product rule enables us to compute u*. Suppose, for example, that $\theta = 1/2$ in the first model. Then we have $f(u) = u$, $g(u) = (1 - u)^{1/2}$ and so (21a) implies

$$\begin{aligned} p'(u) &= \frac{d}{du}\{f(u)g(u)\} = f'(u)g(u) + f(u)g'(u) \\ &= 1 \cdot g(u) + u\,g'(u) \\ &= (1-u)^{1/2} + u\,g'(u), \end{aligned} \tag{17.22}$$

on using Table 16.2. What about $g'(u)$? Setting $f = g$ in (21a) with $g(u) = (1 - u)^{1/2}$ yields

$$\frac{d}{du}\{g(u)^2\} = g'(u)g(u) + g(u)g'(u) = 2g(u)g'(u), \tag{17.23}$$

or

$$\frac{d}{du}\{1-u\} = 2(1-u)^{1/2}g'(u). \tag{17.24}$$

But $d\{1 - u\}/du = d\{1\}/du - d\{u\}/du = 0 - 1 = -1$, on using Table 16.2. So (24) yields

$$\frac{d}{du}\{(1-u)^{1/2}\} = g'(u) = -\frac{1}{2}(1-u)^{-1/2}, \tag{17.25}$$

from which (22) in turn yields

$$p'(u) = (1-u)^{1/2} + u\{-\tfrac{1}{2}(1-u)^{-1/2}\} = \tfrac{1}{2}(1-u)^{-1/2}\{2-3u\} \tag{17.26}$$

after simplification. Thus $p'(u)$ is positive if $0 < u < 2/3$ but negative if $u > 2/3$, so that p has a maximum where $u = 2/3$. That is, $u^* = 2/3$ (if $\theta = 1/2$). An individual allocates two thirds of its resources to females and only a third to males, or twice as much to females as to males. Expected returns on female investment are $X = f(u^*)X_{max} = u^*X_{max} = 2X_{max}/3$, or 67% of maximum, and returns on male investment are

$$Y \quad = \quad g(u)Y_{max} \quad = \quad \sqrt{1 - u^*}\; Y_{max} \quad = \quad \frac{Y_{max}}{\sqrt{3}}, \tag{17.27}$$

or 58% of maximum.

If, on the other hand, investment is governed by our second model then, by (14), finding u* requires us to find the derivative of the join p defined on [0, 1] by

$$p(u) \quad = \quad f(u)g(u) \quad = \quad \begin{cases} \frac{1}{\theta}u(1-u) & \text{if } 0 \le u \le \theta \\ 1-u & \text{if } \theta \le u \le 1 \end{cases}. \tag{17.28}$$

In this case, because $d\{u(1-u)\}/du = d\{u-u^2\}/du = d\{u\}/du - d\{u^2\}/du = 1-2u$ (from Table 16.2) and $d\{1-u\}/du = -1$ (from above), we have

$$p'(u) \quad = \quad \begin{cases} \frac{1}{\theta}(1-2u) & \text{if } 0 \le u < \theta \\ -1 & \text{if } \theta \le u < 1 \end{cases}. \tag{17.29}$$

Although $p' < 0$ throughout $[\theta, 1)$, whether p' is positive or negative on $[0, \theta)$ depends on θ. If $\theta < 1/2$ then $1 - 2\theta$ is positive, which makes $1 - 2u$ positive throughout $[0, \theta)$; then, because p is increasing on $[0, \theta)$ but decreasing on $[\theta, 1)$, its maximum occurs where $u = \theta$. If, on the other hand, $\theta > 1/2$ so that $1 - 2\theta$ is negative, (29) implies $p'(u) > 0$ on $[0, 1/2)$ but $p'(u) < 0$ on $[1/2, \theta)$, so that p is maximized where $u = 1/2$. So the optimal allocation is

$$u^* \quad = \quad \begin{cases} \theta & \text{if } 0 \le \theta < \frac{1}{2} \\ \frac{1}{2} & \text{if } \frac{1}{2} \le \theta \le 1 \end{cases} \tag{17.30}$$

For further practice with the product rule, which facilitates considerable expansion of the list of functions whose derivatives we consider known, see Exercises 1-10.

Finally, the evolutionarily stable **sex ratio**, say σ, is defined as the evolutionarily stable proportion of males in the population. Suppose that a parent's total resources are R, and that (in the same units) it costs c_1 to raise a female and c_2 to raise a male, so that the (male to female) **cost ratio** is

$$c \quad = \quad \frac{c_2}{c_1}. \tag{17.31}$$

Then, because investment u*R in female progeny produces u^*R/c_1 females while investment (1–u*)R in male progeny produces $(1-u^*)R/c_2$ males, the evolutionary stable sex ratio is

$$\sigma \quad = \quad \frac{(1-u^*)R/c_2}{u^*R/c_1 \; + \; (1-u^*)R/c_2} \quad = \quad \frac{(1-u^*)}{1 \; - \; (1-c)u^*}. \tag{17.32}$$

It is sometimes more convenient to quote this result as a ratio of males to females:

$$\frac{\sigma}{1-\sigma} \quad = \quad \frac{1-u^*}{cu^*}. \tag{17.33}$$

For example, if $\theta = 1$ in our first model, then $u^* = 1/2$ (Exercise 13) and (33) predicts $\sigma/(1-\sigma) = 1/c$. That is, the sex ratio is inversely proportional to the cost ratio; or, if you prefer, the sex ratio is always biased towards the cheaper sex. In particular, if sons and daughters are equally costly to raise, then we expect to observe them in equal numbers. This result was first articulated by Fisher (1930).

References

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Exercises 17

17.1 From Lecture 16, net rate of photosynthesis at temperature x in maize is F(x), where F is defined on [12, 51] by

$$F(x) \quad = \quad m_0 x(x - 12)(51 - x)(1884 \; - \; 71x \; + \; x^2)$$

with $m_0 = 1.23353 \times 10^{-7}$. Use the product rule to deduce that

$$F'(x) \quad = \quad -m_0(5x^4 - 536x^3 + 20907x^2 - 324288x + 1153008),$$

in agreement with (16.20).

17.2 (i) Net rate of photosynthesis at temperature x in wheat is F(x), where F is defined on [0, 51] by

$$F(x) \quad = \quad w_0 x(17 + x)(51 - x)(5025 \; - \; 127x \; + \; x^2)$$

with $w_0 = 6.8441 \times 10^{-9}$. Use the product rule to deduce the gradient $F'(x)$.

(ii) From Lecture 8, an alternative definition of F is

$$F(x) \quad = \quad w_0(4356675x \; + \; 60741x^2 \; - \; 8476x^3 \; + \; 161x^4 \; - \; x^5).$$

Use Lecture 16's rule for the derivative of a sum of multiples to deduce $F'(x)$, verifying that your result agrees with (i).

17.3 Calculate $d\left\{x^5\right\}/dx$ by applying the product rule to $x^5 = x \cdot x^4$.

17.4 (i) Use the product rule with $F(x) = x^{1/2} = G(x)$ to show that

$$\frac{d}{dx}\left\{\sqrt{x}\right\} \quad = \quad \frac{1}{2\sqrt{x}}.$$

(ii) Use the product rule with $F(x) = x^{3/2} = G(x)$ to show that

$$3x^2 \quad = \quad 2x^{3/2} \cdot \frac{d}{dx}\left\{x^{3/2}\right\},$$

and hence that

$$\frac{d}{dx}\left\{x\sqrt{x}\right\} \quad = \quad \frac{3}{2}\sqrt{x}.$$

17.5 Calculate $d\left\{x^2\sqrt{x}\right\}/dx$ by applying the product rule to $x^2\sqrt{x} = x \cdot x\sqrt{x}$ and using Exercise 4.

17.6 Calculate $d\left\{x^{-1/2}\right\}/dx$ by applying the product rule to $x^{-1} = x^{-1/2} \cdot x^{-1/2}$ and using Table 16.2.

17.7 Calculate $d\left\{x^{-3/2}\right\}/dx$ by applying the product rule to $x^{-3/2} = x^{-1/2} \cdot x^{-1}$ and using Exercise 6.

17.8 Calculate $d\left\{x^{-5/2}\right\}/dx$ by applying the product rule to $x^{-5/2} = x^{-3/2} \cdot x^{-1}$ and using Exercise 7.

17.9 Calculate both $d\left\{x^{1/3}\right\}/dx$ and $d\left\{x^{2/3}\right\}/dx$ by applying the product rule twice, first with $F(x) = x^{1/3}$ and $G(x) = x^{2/3}$, second with $F(x) = x^{1/3} = G(x)$.

17.10 What is $d\left\{x^{5/3}\right\}/dx$?

17.11 (i) Verify that (14) implies (15).
(ii) Verify (D8)-(D9) imply (D10).
(iii) Verify that (D.12) implies □ = 0 in (D.11).
(iv) Verify that □ < 0 above the line in Figures 2-4 and that □ > 0 above the line, where □ is defined by (D.11).

17.12 Show that u < □ along the upper segment of the fitness curve in Figure 4 for □ > 1/2, implying x = u/□, y = 1 – u, u* = 1/2. Thus verify (D14). <u>Hint</u>: Use (14) and (30).

17.13 What is the evolutionarily stable allocation of resources to female progeny when □ = 1 in the first investment model?

17.14 Use (25) and (23) with $g(u) = (1 - u)^{1/4}$ to find $d\{(1 - u)^{1/2}\}/du$. Hence, what evolutionarily stable sex ratio is predicted by the first investment model if □ = 1/4 and daughters are twice as costly to raise as sons?

17.15 A function f is defined on [0, 3] by

$$f(t) = \frac{1}{3}t(9t - 2t^2 - 12).$$

Use the product rule to find an expression for $f'(t)$, verifying that your result agrees with the one you obtained in Exercise 14.3.

17.16 The function f is defined on [0, 7] by

$$f(t) = \frac{1}{6}(2t^2 - 19t + 41)(t - 1).$$

Use the product rule to find an expression for $f'(t)$, verifying that your result agrees with the one you obtained in Exercise 14.4.

17.17 Functions P, F are defined on [0, 3/2] by

$$P(x) = 8 - 2x - x^2, \qquad F(x) = \sqrt{8 - 2x - x^2}.$$

(i) Find $P'(x)$
(ii) Observing that P(x) = F(x)F(x), use the product rule to find $F'(x)$.
(iii) A third function G is defined on [0, 2] by G(x) = xF(x). Find $G'(0)$.

17.18 (i) Functions P, F are defined on [1, 2] by

$$P(x) = 9x - x^3, \qquad F(x) = \sqrt{9x - x^3}.$$

(i) Find $P'(x)$
(ii) Observing that P(x) = F(x)F(x), use the product rule to find $F'(x)$.
(iii) A third function G is defined on [1, 2] by G(x) = xF(x). Find $G'(1)$.

Appendix 17A: On the product rule

The purpose of this appendix is to establish that

$$P(x) = F(x)G(x) \tag{17.A1}$$

implies

$$DQ\big(P, [x, x+h]\big) = F'(x)G(x) + F(x)G'(x) + O[h] \tag{17.A2}$$

Because DQ(F, [x, x + h]) = $F'(x) + O[h]$ and DQ(G, [x, x + h]) = $G'(x) + O[h]$, we have

$$F(x+h) = F(x) + h\{F'(x) + O[h]\} \tag{17.A3a}$$

and

$$G(x+h) = G(x) + h\{G'(x) + O[h]\}, \tag{17.A3b}$$

respectively. So the numerator on the left-hand side of (A2) is

$$\begin{aligned} \mathrm{Diff}(P,[x,x+h]) &= (F(x) + h\{F'(x) + O[h]\})(G(x) + h\{G'(x) + O[h]\}) - F(x)G(x) \\ &= h\{F'(x)G(x) + F(x)G'(x)\} \\ &\quad + hO[h]\{F(x) + G(x)\} + h^2O[h]\{F'(x) + G'(x)\} \\ &\quad + h^2F'(x)G'(x) + h^2\{O[h]\}^2 \end{aligned} \tag{17.A4}$$

after straightforward algebraic manipulations. Dividing by h, we obtain

$$\begin{aligned} DQ(P,[x,x+h]) &= F'(x)G(x) + F(x)G'(x) \\ &\quad + O[h]\{F(x) + G(x)\} + hO[h]\{F'(x) + G'(x)\} \\ &\quad + hF'(x)G'(x) + h\{O[h]\}^2. \end{aligned} \tag{17.A5}$$

But $\{O[h]\}^2 = O[h]$ from (13.28) and $hO[h] = O[h]$ from Exercise 13.14, so that $h\{O[h]\}^2 = hO[h] = O[h]$. Also $h = O[h]$. Thus

$$\begin{aligned} &O[h]\{F(x) + G(x)\} + hO[h]\{F'(x) + G'(x)\} + hF'(x)G'(x) + h\{O[h]\}^2 \\ &\quad = \big(F(x) + G(x) + F'(x) + G'(x) + F'(x)G'(x) + 1\big)O[h], \end{aligned} \tag{17.A6}$$

which in turn is O[h], by (13.29). So (A5) reduces, as required, to (A2).

Appendix 17B: Derivatives of integer power functions

The purpose of this appendix is to establish that

$$\frac{d}{dx}\left\{x^{n}\right\} = nx^{n-1} \tag{17.B1}$$

and

$$\frac{d}{dx}\left\{x^{-n}\right\} = -nx^{-n-1} \tag{17.B2}$$

for any integer $n \geq 1$. We use a "mathematical induction" principle. This principle says that a sequence of statements is true if the first statement is true *and* the truth of any subsequent statement in the sequence implies the truth of the next.

To establish (B1), let the sequence {Statement(k)} on $[1 \ldots \infty)$ be defined by

$$\text{Statement(k)} \quad \text{means} \quad \frac{d}{dx}\left\{x^{k}\right\} = kx^{k-1}. \tag{17.B3}$$

Then Statement (1) is true, because $x^1 = x$, $d\{x\}/dx = 1$ by Table 16.2, and $1 = 1x^0 = 1x^{1-1}$. Because the first statement in the sequence is true, every statement must be true if it can be shown that Statement (n) implies Statement(n+1) for any positive integer n. For then Statement(1) implies Statement(1+1) = Statement(2), which in turn implies Statement(2+1) = Statement(3), and so on, ad infinitum. Showing that Statement (n) implies Statement(n+1) means assuming Statement (n) and deducing Statement(n+1). So assume the truth of Statement(n). Then (B3) implies (B1) and, from the product rule, we have

$$\begin{aligned}\frac{d}{dx}\left\{x^{n+1}\right\} = \frac{d}{dx}\left\{x \cdot x^{n}\right\} &= \frac{d}{dx}\left\{x\right\}x^{n} + x\frac{d}{dx}\left\{x^{n}\right\} \\ &= 1 \cdot x^{n} + x \cdot nx^{n-1} \\ &= x^{n} + nx^{n}.\end{aligned} \tag{17.B4}$$

But this is simply the statement that

$$\frac{d}{dx}\left\{x^{n+1}\right\} = (n+1)x^{n} = (n+1)x^{(n+1)-1} \tag{17.B5}$$

or Statement(n+1), as required.

To establish (B2), let {Statement(k)} on $[1 \ldots \infty)$ be redefined as

$$\text{Statement(k)} \quad \text{means} \quad \frac{d}{dx}\left\{x^{-k}\right\} = -kx^{-k-1} \tag{17.B6}$$

on $[a, \infty)$, where $a > 0$. Then Statement (1) is true, by Table 16.2. So the truth of (B6) is established for any $k \geq 1$ if we can show that Statement (n) implies Statement(n+1).

Accordingly, assume the truth of Statement(n). Then (B6) implies (B2) and, from the product rule, we have

$$\begin{aligned}\frac{d}{dx}\left\{x^{-(n+1)}\right\} = \frac{d}{dx}\left\{x^{-n} \cdot x^{-1}\right\} &= \frac{d}{dx}\left\{x^{-n}\right\}x^{-1} + x^{-n}\frac{d}{dx}\left\{x^{-1}\right\} \\ &= \{-nx^{-n-1}\}x^{-1} + x^{-n}\{-x^{-2}\} \\ &= -nx^{-n-2} - x^{-n-2}.\end{aligned} \tag{17.B7}$$

But this is simply the statement that

$$\frac{d}{dx}\left\{x^{-(n+1)}\right\} = -(n+1)x^{-n-2} = -(n+1)x^{-(n+1)-1} \tag{17.B8}$$

or Statement(n+1), again as required.

Appendix 17C: The derivative of a polynomial

The purpose of this appendix is to show that the derivative of a polynomial of order m is a polynomial of order m–1. To establish this result, let F be a polynomial defined on [a, b] by

$$F(x) \quad = \quad \sum_{n=0}^{m} c_n x^n. \tag{17.C1}$$

Then m + 1 applications of Lecture 16's result for the derivative of a sum of multiples yield

$$\begin{aligned} F'(x) \quad &= \quad \frac{d}{dx}\left\{\sum_{n=0}^{m} c_n x^n\right\} \quad = \quad \frac{d}{dx}\left\{c_0 x^0 + \sum_{n=1}^{m} c_n x^n\right\} \\ &= \quad \frac{d}{dx}\left\{c_0 x^0\right\} \quad + \quad \sum_{n=1}^{m} \frac{d}{dx}\left\{c_n x^n\right\} \\ &= \quad \frac{d}{dx}\left\{c_0\right\} \quad + \quad \sum_{n=1}^{m} c_n \frac{d}{dx}\left\{x^n\right\}. \end{aligned} \tag{17.C2}$$

But $d\{c_0\}/dx = 0$ from Table 16.2, and it is shown in Appendix B that

$$\frac{d}{dx}\left\{x^n\right\} \quad = \quad n x^{n-1} \tag{17.C3}$$

on [0, ∞) for any positive integer n. So (C2) implies

$$F'(x) \quad = \quad \sum_{n=0}^{m} n c_n x^{n-1} \quad = \quad \sum_{n=1}^{m} n c_n x^{n-1}, \tag{17.C4}$$

i.e., F' is a polynomial of degree m – 1.

Appendix 17D: On evolutionarily stable sex allocation

Why is u* evolutionarily stable? Suppose that the current generation consists of N + 1 brood-raising individuals, of which N invest proportion u* of total resources in females, while the remaining individual — a lone mutant — instead invests proportion u. The mutant's expected returns from investment in females and males (as proportions of maximum possible returns) are x = f(u) and y = g(u), respectively; whereas expected returns to the rest of the population are f(u*) and g(u*), respectively. Let us denote these quantities by x* and y*, i.e.,

$$x^* = f(u^*), \qquad y^* = g(u^*). \tag{17.D1}$$

Thus the mutant's returns could correspond to any point (x, y) on the fitness curve in Figure 2, whereas the rest of the population sits firmly at the point with coordinates

$$(x^*, y^*) = \left(\tfrac{2}{3}, \tfrac{1}{\sqrt{3}}\right). \tag{17.D2}$$

How many genes will this mutant transmit to the second generation (i.e., the next generation but one)? If the organism is diploid, any gene present in the second generation is equally likely to have been transmitted by a father or a mother in the first generation. Hence, on average, half of all genes in the second generation will have come through sons of the current generation, and half of all second-generation genes will have come through the current generation's daughters. Now, what would our mutant like to have happen (if it were able to do anything about it)? It craves the greatest possible genetic representation in the second generation. In other words, it would like to maximize the probability that a gene selected at random from the second generation belongs to our mutant. This probability, which we denote by W, is a measure of the mutant's expected future reproductive success, or fitness. Let us write

$$\text{Prob}(\text{MUT}\mid\text{M}) = \text{Prob}(\text{GENE TRANSMITTED TO MOTHER FROM MUTANT IF IT CAME THROUGH MOTHER})$$

$$\text{Prob}(\text{MUT}\mid\text{D}) = \text{Prob}(\text{GENE TRANSMITTED TO FATHER FROM MUTANT IF IT CAME THROUGH FATHER})$$

$$\text{Prob}(\text{M}) = \text{Prob}(\text{GENE CAME THROUGH MOTHER})$$

$$\text{Prob}(\text{D}) = \text{Prob}(\text{GENE CAME THROUGH FATHER}).$$

Then, by the law of total probability,

$$\begin{aligned} W &= \text{Prob}(\text{GENE CAME FROM MUTANT}) \\ &\quad \text{Prob}(\text{MUT}\mid\text{M})\cdot\text{Prob}(\text{M}) + \text{Prob}(\text{MUT}\mid\text{D})\cdot\text{Prob}(\text{D}). \end{aligned} \tag{17.D3}$$

We have already established, however, that

$$\text{Prob}(\text{M}) = \text{Prob}(\text{D}) = \frac{1}{2} \tag{17.D4}$$

(because the organism is diploid). Thus, substituting into (D3), we find that

$$\begin{aligned} W &= \text{Prob}(\text{MUT}\mid\text{M})\cdot\frac{1}{2} + \text{Prob}(\text{MUT}\mid\text{D})\cdot\frac{1}{2} \\ &= \frac{1}{2}\{\text{Prob}(\text{MUT}\mid\text{M}) + \text{Prob}(\text{MUT}\mid\text{D})\} \end{aligned} \tag{17.D5}$$

But what is Prob(MUT | M)? From above, the expected number of female progeny is $f(u)X_{max}$ for the mutant, who allocates proportion u of its resources to females, but $f(u^*)X_{max}$ for every other individual, because all N of them allocate proportion u*. So expected number of females in the first generation is $f(u)X_{max} + Nf(u^*)X_{max}$, implying

$$\text{Prob}(\text{MUT}\mid\text{M}) = \frac{\text{NUMBER OF FEMALES IN FIRST GENERATION WHO ARE DAUGHTERS OF THE MUTANT}}{\text{NUMBER OF FEMALES IN FIRST GENERATION}}$$

$$= \frac{f(u)X_{max}}{f(u)X_{max} + Nf(u^*)X_{max}} = \frac{f(u)}{f(u) + Nf(u^*)} = \frac{x}{x + Nx^*}. \qquad (17.D6)$$

Similarly, because expected number of male progeny is $g(u)Y_{max}$ for the mutant but $g(u^*)X_{max}$ for every other individual, we have

$$\Pr ob(MUT|D) = \frac{\text{NUMBER OF MALES IN FIRST GENERATION WHO ARE SONS OF THE MUTANT}}{\text{NUMBER OF MALES IN FIRST GENERATION}}$$

$$= \frac{g(u)Y_{max}}{g(u)Y_{max} + Ng(u^*)Y_{max}} = \frac{g(u)}{g(u) + Ng(u^*)} = \frac{y}{y + Ny^*}. \qquad (17.D7)$$

From (D5)-(D7), we have

$$\begin{aligned} W &= \frac{1}{2}\left\{\frac{f(u)}{f(u) + Nf(u^*)} + \frac{g(u)}{g(u) + Ng(u^*)}\right\} \\ &= \frac{1}{2}\left\{\frac{x}{x + Nx^*} + \frac{y}{y + Ny^*}\right\} \end{aligned} \qquad (17.D8)$$

for the fitness of the mutant.

Now, if the mutant were instead to allocate proportion u*, just like everyone else, then its fitness would be

$$W^* = \frac{1}{2}\left\{\frac{f(u^*)}{f(u^*) + Nf(u^*)} + \frac{g(u^*)}{g(u^*) + Ng(u^*)}\right\} = \frac{1}{N+1} \qquad (17.D9)$$

The mutant allocation will be selected for if W > W* (when u ≠ u*), but it will be selected against if W < W* (when u ≠ u*). So we expect to see u* if there is no other u such that W > W*. Is this really true?

We need to show that W* – W is positive (when u ≠ u*). Straightforward algebraic manipulation of (D8)-(D9) establishes (Exercise 11) that

$$\begin{aligned} W^* - W &= \frac{N\{x^*y^* - xy + (N-1)\Delta\}}{(N+1)(x+Nx^*)(y+Ny^*)} \\ &= \frac{N\{p(u^*) - p(u) + (N-1)\Delta\}}{(N+1)(f(u)+Nf(u^*))(g(u)+Ng(u^*))} \end{aligned} \qquad (17.D10)$$

where $p = f \bullet g$ is defined by (17) and

$$\Delta = x^*y^* - \frac{1}{2}\{y^*x + x^*y\}. \qquad (17.D11)$$

Because u* maximizes p, p(u*) ≥ p(u) for every possible u. So, from (D10), W* > W when u ≠ u* if Δ > 0 when u ≠ u*. Now, in Figure 2 the dashes denote the straight line with equation

$$y = y^*\left(2 - \frac{x}{x^*}\right). \qquad (17.D12)$$

It is straightforward to show that every point (x, y) on this line satisfies Δ = 0 (Exercise 11). It is also straightforward to show that Δ < 0 above the line (where y > y*(2 – x/x*)) and that Δ > 0 below the line (where y < y*(2 – x/x*)). But it is clear from the diagram that the fitness curve lies below the line, except at (x*, y*) itself. Therefore Δ > 0 unless u = u*, as required. Note that, because (x*, y*) always lie on both (D2) and the fitness curve, our result will more generally hold whenever the fitness curve is **convex**, i.e., whenever any straight line joining two points on the curve lies on the same side of the curve as the origin of coordinates.

Figure 3 is the corresponding diagram for our second model when [illegible] < 1/2, and so

$$(x^*, y^*) \quad = \quad \left(1, 1 \square \square\right) \tag{17.D13}$$

by (30); again, □ > 0 everywhere on the fitness curve except (x^*, y^*), and so $W^* > W$ unless $u = u^*$, as required. In Figure 4, however, which is the corresponding diagram when □ > 1/2, □ = 0 along the entire upper segment of the fitness curve. So there are many points (x, y), other than (x^*, y^*), at which □ is not positive. Does this mean that our theory has broken down? Not at all. Although □ > 0 is a sufficient condition for $W^* > W$, it is by no means a necessary one. Inspection of (D10) reveals that $p(u^*) > p(u)$ will guarantee $W^* > W$ whenever □ = 0; and you can easily show (Exercise 12) that, for any (x, y) along the upper segment of the fitness curve in Figure 4,

$$p(u^*) \; \square \; p(u) \quad = \quad \frac{1}{4\square} \; \square \; \frac{u(1 \square u)}{\square} \quad = \quad \frac{1}{\square}\left(u \square \tfrac{1}{2}\right)^2 \quad = \quad \frac{1}{\square}(u \square u^*)^2, \tag{17.D14}$$

which is positive if $u \neq u^*$, as required.

Answers and Hints for Selected Exercises

17.1 From the product rule, we have

$$\frac{d}{dx}\{(x-12)(51-x)\} = \frac{d}{dx}\{x-12\}(51-x) + (x-12)\frac{d}{dx}\{51-x\}$$
$$= (1-0)(51-x) + (x-12)(0-1) = 63 - 2x,$$

implying

$$\frac{d}{dx}\{x(x-12)(51-x)\} = \frac{d}{dx}\{x\}(x-12)(51-x) + x\frac{d}{dx}\{(x-12)(51-x)\}$$
$$= 1\cdot(x-12)(51-x) + x(63-2x)$$
$$= -3(x^2-42x+204).$$

So

$$F'(x) = m_0\frac{d}{dx}\{x(x-12)(51-x)(1884 - 71x + x^2)\}$$
$$= m_0\frac{d}{dx}\{x(x-12)(51-x)\}(1884 - 71x + x^2) +$$
$$m_0 x(x-12)(51-x)\frac{d}{dx}\{1884 - 71x + x^2\}$$
$$= -3m_0(x^2-42x+204)(1884 - 71x + x^2) +$$
$$m_0 x(x-12)(51-x)(0 - 71 + 2x),$$

which readily reduces to (16.20).

17.4 (i) With $F(x) = \sqrt{x} = x^{1/2}$, setting F = G in (21b) yields

$$\frac{d}{dx}\{F(x)^2\} = F'(x)F(x) + F(x)F'(x) = 2F(x)F'(x)$$

or

$$\frac{d}{dx}\{x\} = 2\sqrt{x}\,\frac{d}{dx}\{\sqrt{x}\}$$

But $d\{x\}/dx = 1$ (from Table 16.2). So

$$\frac{d}{dx}\{\sqrt{x}\} = \frac{1}{2\sqrt{x}}.$$

17.5 Set $F(x) = x$ and $G(x) = x\sqrt{x} = x^{3/2}$ in (21b), so that $F(x)G(x) = x^2\sqrt{x} = x^{5/2}$. Then

$$\frac{d}{dx}\{x^2\sqrt{x}\} = F'(x)G(x) + F(x)G'(x)$$
$$= \frac{d}{dx}\{x\}\cdot x\sqrt{x} + x\cdot\frac{d}{dx}\{x\sqrt{x}\}$$
$$= 1\cdot x\sqrt{x} + x\cdot\frac{3}{2}\sqrt{x} = \frac{5}{2}x\sqrt{x}$$

17.6 From the product rule, we have

$$\begin{aligned}\frac{d}{dx}\left\{x^{-1}\right\} &= \frac{d}{dx}\left\{x^{-1/2}\cdot x^{-1/2}\right\}\\ &= \frac{d}{dx}\left\{x^{-1/2}\right\}x^{-1/2} + x^{-1/2}\cdot\frac{d}{dx}\left\{x^{-1/2}\right\}\\ &= 2x^{-1/2}\cdot\frac{d}{dx}\left\{x^{-1/2}\right\}.\end{aligned}$$

So, from Table 16.2,

$$\frac{d}{dx}\left\{x^{-1/2}\right\} = \frac{1}{2}x^{1/2}\frac{d}{dx}\left\{x^{-1}\right\} = \frac{1}{2}x^{1/2}\left\{-x^{-2}\right\} = -\frac{1}{2}x^{-3/2}.$$

17.7 From the product rule, we have

$$\begin{aligned}\frac{d}{dx}\left\{x^{-3/2}\right\} &= \frac{d}{dx}\left\{x^{-1/2}\cdot x^{-1}\right\} = \frac{d}{dx}\left\{x^{-1/2}\right\}x^{-1} + x^{-1/2}\cdot\frac{d}{dx}\left\{x^{-1}\right\}\\ &= -\frac{1}{2}x^{-3/2}\cdot x^{-1} + x^{-1/2}\cdot\left\{-x^{-2}\right\} = -\frac{3}{2}x^{-5/2}\end{aligned}$$

17.8 From Exercise 7 and the product rule, we have

$$\begin{aligned}\frac{d}{dx}\left\{x^{-5/2}\right\} &= \frac{d}{dx}\left\{x^{-3/2}\cdot x^{-1}\right\}\\ &= \frac{d}{dx}\left\{x^{-3/2}\right\}\cdot x^{-1} + x^{-3/2}\cdot\frac{d}{dx}\left\{x^{-1}\right\}\\ &= -\frac{3}{2}x^{-5/2}\cdot x^{-1} + x^{-3/2}\cdot\left\{-x^{-2}\right\}\\ &= -\frac{3}{2}x^{-7/2} - x^{-7/2} = -\frac{5}{2}x^{-7/2}.\end{aligned}$$

17.9 From the product rule with $F(x) = x^{1/3}$, $G(x) = x^{2/3}$ and hence $F(x)G(x) = x$,

$$\begin{aligned}\frac{d}{dx}\{x\} &= \frac{d}{dx}\left\{x^{1/3}\cdot x^{2/3}\right\}\\ &= \frac{d}{dx}\left\{x^{1/3}\right\}x^{2/3} + x^{1/3}\cdot\frac{d}{dx}\left\{x^{2/3}\right\}.\end{aligned}$$

From the product rule with $F(x) = x^{1/3} = G(x)$ and hence $F(x)G(x) = x^{2/3}$,

$$\begin{aligned}\frac{d}{dx}\left\{x^{2/3}\right\} &= \frac{d}{dx}\left\{x^{1/3}\cdot x^{1/3}\right\}\\ &= \frac{d}{dx}\left\{x^{1/3}\right\}x^{1/3} + x^{1/3}\cdot\frac{d}{dx}\left\{x^{1/3}\right\}\\ &= 2x^{1/3}\cdot\frac{d}{dx}\left\{x^{1/3}\right\}.\end{aligned}$$

So

$$\begin{aligned}\frac{d}{dx}\{x\} &= \frac{d}{dx}\left\{x^{1/3}\right\}x^{2/3} + x^{1/3}\cdot\frac{d}{dx}\left\{x^{2/3}\right\}\\ &= \frac{d}{dx}\left\{x^{1/3}\right\}x^{2/3} + x^{1/3}\cdot 2x^{1/3}\frac{d}{dx}\left\{x^{1/3}\right\} = 3x^{2/3}\frac{d}{dx}\left\{x^{1/3}\right\},\end{aligned}$$

implying

$$\frac{d}{dx}\left\{x^{1/3}\right\} = \frac{1}{3x^{2/3}}\frac{d}{dx}\{x\} = \frac{1}{3x^{2/3}} = \frac{1}{3}x^{-2/3}.$$

Substituting above,

$$\frac{d}{dx}\left\{x^{2/3}\right\} = 2x^{1/3}\cdot\frac{d}{dx}\left\{x^{1/3}\right\} = 2x^{1/3}\cdot\frac{1}{3x^{2/3}} = \frac{2}{3}x^{-1/3}$$

17.10 From the product rule with $F(x) = x^{2/3}$, $G(x) = x$ and hence $F(x)G(x) = x^{5/3}$,

$$\frac{d}{dx}\left\{x^{5/3}\right\} = \frac{d}{dx}\left\{x^{2/3}\cdot x\right\} = \frac{d}{dx}\left\{x^{2/3}\right\}x + x^{2/3}\cdot\frac{d}{dx}\{x\}$$
$$= \frac{d}{dx}\left\{x^{2/3}\right\}x + x^{2/3} = \frac{5}{3}x^{2/3},$$

by Exercise 8.

17.13 $u^* = 1/2$

17.14 In place of (25) and (26) we find $d\{(1-u)^{1/4}\}/du = -(1-u)^{-3/4}/4$ and $p'(u) = \frac{1}{4}(1-u)^{-3/4}\left\{4-5u\right\}$, so that $u^* = 4/5$ and $\square = 1/2$, because $c = 1/2$ in (33).

17.15 Go to http://www.math.fsu.edu/~mm-g/QuizBank/mac3311.s97.html (Second Test, #2)

17.16 Go to http://www.math.fsu.edu/~mm-g/QuizBank/mac3311.s97.html ((Mock Test 2), #3)

17.17 (i) By the rule for the derivative of a sum of multiples, we have $P'(x) =$

$$\frac{d}{dx}\left\{8-2x-x^2\right\} = \frac{d}{dx}\{8\} - \frac{d}{dx}\{2x\} - \frac{d}{dx}\left\{x^2\right\} = 0-2-2x = -2(1+x).$$

(ii) By the product rule, $P'(x) = F'(x)F(x) + F(x)F'(x) = 2F(x)F'(x)$, implying

$$F'(x) = \frac{P'(x)}{2F(x)} = \frac{-2-2x}{2\sqrt{8-2x-x^2}} = -\frac{1+x}{\sqrt{(4+x)(2-x)}}.$$

(iii) By the product rule,

$$G'(x) = \frac{d}{dx}\left\{xF(x)\right\} = \frac{d}{dx}\{x\}F(x) + x\frac{d}{dx}\{F(x)\} = F(x) + xF'(x),$$

implying $G'(0) = F(0) = \sqrt{8} = 2\sqrt{2}$.

17.18 (i) By the rule for the derivative of a sum of multiples, we have $P'(x) =$

$$\frac{d}{dx}\left\{9x-x^3\right\} = 9\frac{d}{dx}\{x\} - \frac{d}{dx}\left\{x^3\right\} = 9-3x^2 = 3(3-x^2).$$

(ii) By the product rule, $P'(x) = F'(x)F(x) + F(x)F'(x) = 2F(x)F'(x)$, implying

$$F'(x) = \frac{P'(x)}{2F(x)} = \frac{3(3-x^2)}{2\sqrt{9x-x^3}} = \frac{3(3-x^2)}{2\sqrt{x(3-x)(3+x)}}.$$

(iii) By the product rule,

$$G'(x) = \frac{d}{dx}\left\{xF(x)\right\} = \frac{d}{dx}\{x\}F(x) + x\frac{d}{dx}\{F(x)\} = F(x) + xF'(x),$$

implying $G'(1) = F(1) + F'(1) = \sqrt{8} + 3/\sqrt{8} = 11\sqrt{2}/4 \approx 3.89$.