

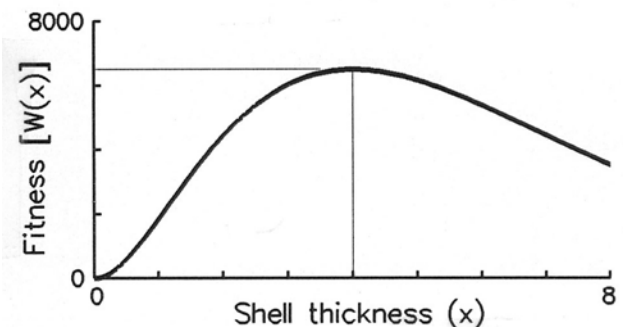
**1. Fitness differences associated with observed rates of short-term evolution.** The median rate of evolution among 54 estimates reviewed by Hendry and Kinnison (1999) is 0.03 haldanes (that is, 0.03 phenotypic standard deviations per generation). To produce such a rate of change, *how large a difference in fitness must there be, on average, between individuals one standard deviation above and below the mean phenotype?* To answer this question you must estimate the selection gradient ( $\beta$ ). Assume that a typical quantitative trait has a heritability ( $h^2$ ) of 0.5, and remember that in units of standard deviations, the phenotypic variance ( $V_p$ ) is 1.0, by definition. How does your answer change for traits evolving at rates of 0.01, 0.1, and 0.5 haldanes?

We work in (dimensionless) units of phenotypic standard deviations. On this scale of measurement, the population mean for a typical trait changes by about 0.03 per generation. We know  $R = h^2 S$ , so  $R$  is 0.03 and  $S = 0.06$ , because  $h^2 = 0.5$ .  $S$ ,  $\beta$  and  $b_{Wx}$  are all the same if  $V_p = 1$ , which is true by definition because we are measuring our traits in haldanes! So individuals one standard deviation above and below the mean will have fitnesses 6% (0.06) above and below the mean fitness, which means that they will differ in fitness by 12%, on average. This relationship simply scales up and down in proportion to  $R$ .

**2. Optimal shell thickness.** A species of marine snail is attacked by crabs that attempt to crush its shell. If it makes a thick shell it can increase its probability of surviving an attack, but at the cost of reducing its egg output. Let its expected adult lifetime be  $T(x) = 300x^2$  days, where  $x$  is shell thickness in millimeters, and let its average daily egg output be  $f(x) = 10e^{-\frac{1}{2}x}$  eggs.

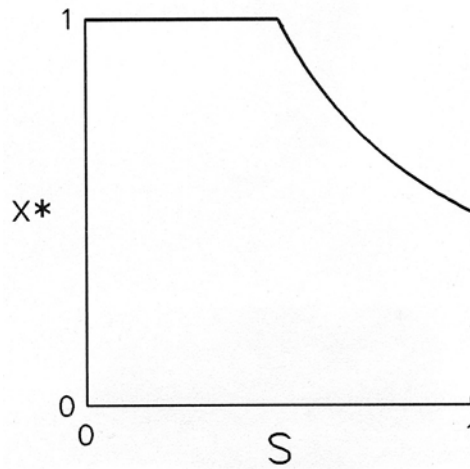
(a) Write an expression for a snail's expected lifetime reproductive success as a function of shell thickness. (b) Using calculus, find the shell thickness that maximizes this quantity. (c) To confirm and illustrate the "optimum" found in part (b), graph fitness as a function of shell thickness. (d) Explain why this optimal shell thickness is the one that would be expected to evolve, other things being equal.

Egg output decreases as shell thickness increases ( $10e^{-\frac{1}{2}x}$  eggs/day), but adult survival increases ( $300x^2$  days). A snail's lifetime fitness as a function of its shell thickness will therefore be  $300x^2 10e^{-\frac{1}{2}x} = 3000x^2 e^{-\frac{1}{2}x}$ . What shell thickness maximizes fitness? Differentiating this expression with respect to  $x$  gives  $dW/dx = 3000e^{-\frac{1}{2}x}(2x - \frac{1}{2}x^2)$ . Fitness is maximized when  $dW/dx = 0$  ( $2x = \frac{1}{2}x^2$ ); the solution is  $x = 4$  millimeters. We can confirm this conclusion by graphing the fitness function. We expect this shell thickness to evolve because individuals with 4-mm shells leave more offspring, on average, than individuals with thinner or thicker shells, and as a consequence, genotypes that give their carriers 4-mm shells become ever more common.



**3. Optimal reproductive effort.** A local biennial grass *Poa desereti* is subject to a tradeoff between first-year fecundity ( $x$ ) and second-year fecundity ( $y$ ). From experiments in the greenhouse, you estimate the relationship between second-year and first-year seed output as  $y = 1 - x^2$  (where  $x$  has been rescaled, for convenience, to fall in the interval between 0 and 1). Thus a plant that makes a relatively large reproductive effort in its first year will be able to make only a relatively small effort in its second year. (The reason turns out to be that it will have a smaller root system and fewer nutrient resources with which to make seeds in the second year, having spent so much of its resources on seeds in the first year.) (a) If each individual plant alive in the first year were certain to *survive* to reproduce again in the second year, what would be the optimal first-year fecundity  $x$ ? (b) Now suppose that the probability of survival is  $S$ , which may be less than 1. What value of  $x$  will maximize a plant's expected lifetime fitness? Graph the relationship between  $S$  and  $x^*$ , the optimal  $x$ . Interpret your result. Does it illustrate a general principle of life-history evolution?

If a plant is certain to be alive in the second year, then its fitness (total seed output) is  $W(x) = x + y = x + (1 - x^2) = 1 + x - x^2$ , which is maximized at  $x = 0.5$ . If the plant is *not* certain to be alive in the second year, then its fitness is  $W(x) = x + Sy$ . (Its seed output in the second year is *discounted* by the chance of being alive in the second year.) Then  $W(x) = x + S - Sx^2$  and  $dW/dx = 1 - 2Sx$ , so fitness is maximized when  $x = 1/2S$  (or for  $S < 0.5$ , when  $x = 1$ , since a plant cannot put more than all of its effort into first-year seed production). This relationship between survival ( $S$ ) and the optimal first-year seed output ( $x^*$ ) is graphed on the other side of the page. This general solution includes the previous one as a special case (when  $S = 1$ , then  $x = 0.5$ ). Yes, it illustrates a general principle of life-history evolution: as future survival becomes more uncertain, future reproduction is discounted more heavily relative to present reproduction.



**4. Differential costs of male and female offspring.** In an outbred population, selection favors *equal net investment* in the sexes, not an equal numerical sex ratio *per se*. Where males and females are equally costly these are the same thing, but if one sex (say, females) costs more, then we expect fewer of that sex to be produced. If the relative costs of males and females are  $1:C_f$ , then at equilibrium they should be produced in a ratio of  $C_f:1$  (males:females). Invent and explain a set of *numerical examples* that *illustrate* this principle. Assume that each parent (or pair) has an equal, fixed pool of resources (say, 24 units) that it can convert into offspring (e.g. 24 males, or  $24/C_f$  females, or any other combination that adds up to 24 units in all). **Hint:** Show that if the population is *not* at the sex-ratio equilibrium, then there will exist "mutant" sex ratios that yield *more expected grandchildren* (for the parents producing them) than does the "wild-type" sex ratio.

The solution was illustrated on the back of the problem set (from February 27) for the case in which males and females are equally costly ( $C_f = 1$ ). All you need to do differently here is adjust the "sons" and "daughters" columns to reflect the greater cost of offspring of one sex.

**5. Sibling rivalry.** Life is intense for nestling birds in most species, because they need to grow as rapidly as possible and the only available food is what their (exhausted) parents bring to the nest. The young ones therefore stand in direct competition with their siblings for vital resources. In a few species this competition sometimes culminates in siblicide, with one sibling pushing another out of the nest. The benefit to the aggressor is that it gets more food, and its direct (personal) fitness is therefore increased (let us say by  $b$  expected future offspring). But there is also an indirect cost to its inclusive fitness, through the complete loss of the reproductive success that the victim would have achieved had it not been killed (say,  $c$  offspring). If the nestlings involved are certain to be full siblings ( $r=1/2$ ), then under what values of  $b$  and  $c$  can the potential aggressor increase its inclusive fitness by carrying out such an act of siblicide? (And conversely, under what conditions should it refrain?) How does the situation change if with probability  $1/2$  the nestlings are half siblings ( $r=1/4$ )? For both cases, show the answer *graphically* as regions in the  $(b,c)$  plane.

In the first case, the aggressor is half as related to the victim's potential offspring as it is to its own offspring, so it should refrain from siblicide whenever  $2c > b$ . (That is, it values its lost nephews and nieces half as much as its own children.) In the second case, it values its sibling's lost offspring  $3/8$  as much as its own, because it is related to them by  $3/16$  (on average) rather than by  $1/2$ .

