

1. Fitness differences associated with observed rates of short-term evolution. The rapid evolution of beak depth in Darwin's medium ground finch may be the most famous observation of ongoing evolution in nature, but it is not the only one! Hendry and Kinnison (*Evolution* **53**:1637-1653, 1999) reviewed the rates of evolution observed for 54 different quantitative traits in scores of studies on more than a dozen different species of animals and plants. To make these estimates comparable, H&K converted the observed rates of change into standard units called "haldanes" (after the British evolutionist J.B.S. Haldane). A trait evolving at a rate of 1 haldane would change by one *phenotypic standard deviation* in one *generation*. The 54 traits reviewed by H&K changed at rates ranging from zero to about 0.5 haldanes; the average was 0.03 haldanes (that is, 0.03 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 (β). 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?

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 $f(x) = 10e^{-1/2x}$ 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.

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 have estimated 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 *P. desereti* 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. Now 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?

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. You will find some helpful notes on the next page. There's also a text box on page 462 of Freeman & Herron.

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.

About the sex ratio

In a sexually reproducing species, everyone has exactly one father and exactly one mother. It follows that the *sum total* of male reproductive success (RS) must exactly equal the sum total of female reproductive success in every generation. This is ultimately why the expected RS of individual offspring is inversely related to their relative abundance. Members of the under-represented sex will have more children, on average, than members of the over-represented sex, and so *their* parents will have more grandchildren than parents who produced offspring of the other (over-represented) sex.

Suppose males and females each cost one unit of investment to produce, and each parent (or pair of parents) has four units to invest (can make four offspring). Suppose in addition that for some reason most parents made 3 sons and 1 daughter. If the mating system is monogamous, then two thirds of the males will remain unmarried, so a typical male will get, in effect, 1/3 of a mating. This is true regardless of the mating system. For example, under monogamy, all of the females would be mated, but only 1/3 of the males. Alternatively, under polyandry all the males could be mated, but on average each male would share his mate with two other males, so he would be expected to father only 1/3 of his mate's offspring. Thus, no matter how you distribute parentage, the *average* sex-specific relative reproductive success is the inverse of the sex ratio. In the present case, we can calculate the payoffs (*in expected numbers of grandchildren*) to parents producing any of the possible offspring sex ratios as follows.

Offspring ("clutch") sex ratio		"payoff" in total grandchildren	** = wild type
sons	daughters		
0	4	$(0)(1/3)(4) + (4)(1)(4) = 0 + 16 = 16$	
1	3	$(1)(1/3)(4) + (3)(1)(4) = 4/3 + 12 = 13.333$	
2	2	$(2)(1/3)(4) + (2)(1)(4) = 8/3 + 8 = 10.333$	
3	1	$(3)(1/3)(4) + (1)(1)(4) = 4 + 4 = 8$	**
4	0	$(4)(1/3)(4) + (0)(1)(4) = 16/3 + 0 = 5.333$	

In this population, all offspring sex ratios more female biased than the wild type do better (for the parents that produce them) than the does the wild-type sex ratio. Likewise, a sex ratio even *more* male biased than the wild type does even worse (4 and 0). Thus any alleles that inclined their bearers to produce a relative excess of females would be expected to increase in frequency, and as they did so, the sex ratio would *evolve* in the direction of a greater number of females. When males and females were being produced in equal numbers, over the population as a whole, there would be *no* advantage or disadvantage associated with the production of any given sex ratio, so any genes that affect sex allocation would cease to change in frequency under the force of selection.
