Exercise Set #2

Do at least two of the following three exercises

1. For a haploid population with genotypes *A* and *a*, we saw that the deterministic evolutionary dynamics of q_t, the frequency of *A* at time *t*, can be described by the recursion $q_{t+1} = q_t \dfrac{w_A}{q_t w_A + (1-q_t) w_a}$, where w_A and w_a are the fitnesses of *A* and *a*, respectively.

   (a) Show that $\Delta q_t = q_{t+1} - q_t = \dfrac{1}{\bar{w}_t} q_t (1-q_t)(w_A - w_a)$, where $\bar{w}_t = \mathrm{E}_t(w_i) = q_t w_A + (1-q_t) w_a$ is the mean fitness at time *t*.

   (b) Let g_i be the proportion of *A* alleles in genotype *i* (i.e., $g_A = 1$, $g_a = 0$). The covariance of random variables *X* and *Y* is cov(*X*, *Y*) = E(*XY*) – E(*X*)E(*Y*) where E() is expected value. Use the definition of covariance to show that at time *t*,

   $$\mathrm{cov}(g_i, w_i) = q_t(1 - q_t)(w_A - w_a)$$

   which, from (a), implies $\Delta q_t = \mathrm{cov}(g_i, w_i)/\bar{w}_t$ for asexual populations.

   (c) Let $\Delta \bar{w}_t = \bar{w}_{t+1} - \bar{w}_t$ be the change in mean fitness between successive generations. Show that $\Delta \bar{w}_t = \dfrac{q_t(1-q_t)(w_A - w_a)^2}{\bar{w}_t}$.

   (d) The variance of random variable *X* is var(*X*) = E(X^2) – [E(*X*)]^2. Use the definition of variance to show that the variance in fitness at time *t* is

   $$\mathrm{var}(w_i) = q_t(1 - q_t)(w_A - w_a)^2,$$

   which implies, from (c), that $\Delta \bar{w}_t = \mathrm{var}(w_i)/\bar{w}_t$. This is Fisher's fundamental theorem of natural selection for asexual populations.

   (e) Compare and contrast the fundamental theorems for a haploid locus and a quantitative trait (see eq. 3.16 on p. 121 of Charlesworth & Charlesworth).

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2. Write a program that iterates directional selection for a diploid population with two alleles, A_1 and A_2, using the <u>exact</u> recursion for allele frequency change (eq. B2.2.2b on p. 53 of Charlesworth & Charlesworth). Assume A_2 is favored and fitnesses are additive, i.e., that $w_{11} = 1$, $w_{12} = 1 + (s/2)$, and $w_{22} = 1 + s$, where $s > 0$; follow the evolution of q, the frequency of A_2.

(a) Use your program to compute the minimum number of generations needed to evolve from q_0 to q_1 for each of the following 4 cases:

Case	q_0	q_1	s
1	0.01	0.99	0.01
2	0.01	0.99	0.1
3	0.001	0.999	0.01
4	0.001	0.999	0.1

(b) Compare your computational results to those predicted by the approximate formula, equation (3.3) on p. 93 of Charlesworth & Charlesworth. Explain any differences between the approximations and your results.

(c) Compare your results for additive fitnesses (h = ½) to approximations (B3.2.4a) and (B3.2.4b) for, respectively, a dominant favored allele (h = 1) and a recessive favored allele (h = 0).

(d) In light of your results and computations above, discuss the relative importance of (i) the initial and final frequencies, (ii) the selection coefficient, and (iii) the dominance coefficient for the time required by a favored allele to evolve.

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3. (a) Problem 3.11 on p. 142 of Charlesworth & Charlesworth

(b) Suppose that a quantitative trait z has a normal distribution[·] with mean $\bar{z}$ and variance V_Z. The selection gradient is defined as $\beta = S/V_z$ where S is the selection differential. Assuming that fitness is "frequency independent", i.e., that the fitness of an individual with phenotype z, w(z), does not depend on $\bar{z}$, show that

(*) $$\beta = \frac{1}{\bar{w}}\frac{d\bar{w}}{d\bar{z}} = \frac{d\ln\bar{w}}{d\bar{z}}$$

where $\bar{w}$ is the expected value of $w(z)$ over the (normal) distribution of z.

(c) The mean of a quantitative trait evolves between successive generations according to the equation

$$\Delta\bar{z} = G\beta \ ,$$

where $G = V_A$ is the additive genetic variance of z (cf. eq. B3.8.1b on p. 128 of Charlesworth & Charlesworth). With this equation in mind, discuss the evolutionary implications of relation (*).

[·] The probability density function of this distribution is $\phi(z) = (2\pi V_z)^{-1/2} \exp\left[-(z-\bar{z})^2/(2V_z)\right]$