Exercise Set #3

Do at least one of the following two multi-part exercises

1. Quantitative geneticists are often interested in understanding variation in two or more traits simultaneously (e.g., height *and* weight or metabolic rate *and* body size). The overall variability of such "multivariate" traits includes the variance of each component trait as well as the covariances between all pairs of traits. Like variances, these covariances can be partitioned into genetic and environmental components. In this exercise you will derive this partition as well as the "cross-variance" between parent and offspring, parallel to what Gillespie does for a single trait.

   Consider two traits X and Y expressed by a single offspring of two parents. Following Gillespie, suppose that $P_{\mathrm{X}} = X_{\mathrm{m}} + X_{\mathrm{p}} + \mathcal{E}_{\mathrm{X}}$ for trait X and $P_{\mathrm{Y}} = Y_{\mathrm{m}} + Y_{\mathrm{p}} + \mathcal{E}_{\mathrm{Y}}$ for Y.

   a. Using arguments similar to Gillespie's for a single trait (1st ed p., 107/2nd ed., pp. 142–3), show that

      $C_{\mathrm{P}} = C_{\mathrm{A}} + C_{\mathrm{E}}$,

      where $C_{\mathrm{P}} = \mathrm{Cov}(P_{\mathrm{X}}, P_{\mathrm{Y}})$ is the "phenotypic covariance," $C_{\mathrm{A}} = 2\mathrm{Cov}(X_{\mathrm{m}}, Y_{\mathrm{m}}) = 2\mathrm{Cov}(X_{\mathrm{p}}, Y_{\mathrm{p}})$ is the "additive covariance," and $C_{\mathrm{E}} = \mathrm{Cov}(\mathcal{E}_{\mathrm{X}}, \mathcal{E}_{\mathrm{Y}})$ is the "environmental covariance." *Important: in your derivation, be sure to include the justifications for setting any terms equal to zero.*

   b. The additive covariance, C_{A} , can be estimated using the parent-offspring "cross-variance," which is the covariance between X in a parent and Y in the offspring (or vice versa). Use arguments parallel to those in Gillespie (1st ed pp., 108-9/2nd ed., p. 144) to show that

      $C_{\mathrm{A}} = 2\mathrm{Cov}(P_{\pi\mathrm{X}}, P_{\mathrm{OY}})$,

      where $P_{\pi\mathrm{X}}$ is the phenotypic value of X in the parent and P_{OY} is the phenotypic value of Y in the offspring. *Be sure to justify setting any terms equal to zero in your derivation.*

   c. It can be shown[†] that if $C_{\mathrm{A}} \neq 0$ then selection on trait X alone will cause a change in Y and vice versa. Use your intuition to discuss possible consequences of selecting up or down on X alone if $C_{\mathrm{A}} < 0$ or if $C_{\mathrm{A}} > 0$. What do you think would happen if $C_{\mathrm{A}} = 0$?

[†] The derivation, which uses concepts and results from multiple linear regression and linear algebra, is slightly beyond of scope of this course. See me if you're interested in the details.

2. Write a program that iterates the two-locus selection model described in §4.2 of Gillespie, 2nd edition. Your script should track the evolution of the gamete frequencies x_1, x_2, x_3, and x_4 over generations. Use the equations on p. 108 to project frequencies for the next generation in terms of the current ones. That is, use the recursion equations $x_1' = x_1 + \Delta x_1$, $x_2' = x_2 + \Delta x_2$, $x_3' = x_3 + \Delta x_3$, and $x_4' = 1 - x_1' - x_2' - x_3'$ each generation. (Careful: be sure your program uses only the current frequencies x_1, x_2, x_3, and x_4 when calculating Δx_1, Δx_2, and Δx_3 each generation.)

   Adapt your script to analyze the selective sweep phase of genetic draft (§4.3). Specifically, use the hitchhiking fitnesses at the foot of p. 108 with $h = ½$ and $s = 0.2$. Assume the pre-mutation frequency of neutral allele B_1 is $p_2 = 0.3$ and that the new advantageous mutant A_1 appears in a diploid population of size $N = 50$.

   a. Assume that the new mutation appears on a B_1 background, i.e., initially $x_1 = \frac{1}{2N} = \frac{1}{100} = 0.01$, $x_2 = 0$, $x_3 = p_2 - \frac{1}{2N} = 0.3 - 0.01 = 0.29$, and $x_4 = 0.7$. What is the initial value (including the sign) of the disequilibrium D in this case?

      - Set the recombination rate $r = 0.1$ and iterate your recursions until A_1 has nearly completed its selective sweep to fixation, i.e., until $p_1 = x_1 + x_2 \approx 1$. (1000 generations should suffice.) Record the final frequency of B_1, $p_2 = x_1 + x_3$

      - Repeat the steps above to compute the final frequencies of B_1 for recombination rates $r = 0.075$, $r = 0.05$, $r = 0.025$, and $r = 0$

   b. Compute the five final values comparable to those you found in part a but assume that the new mutation first appears on a B_2 background, i.e., initially $x_1 = 0$, $x_2 = \frac{1}{2N} = 0.01$, $x_3 = 0.3$, and $x_4 = q_2 - \frac{1}{2N} = 0.7 - 0.01 = 0.69$. What is the initial value of D in this case?

   c. Discuss how your results relate to those shown in Figure 4.4 on p. 110 of Gillespie