Answers to Exercise 39

Evolutionarily Stable Strategies and Group versus Individual Selection

The answers to questions 1–5 refer to values given in the spreadsheet shown in Figure 1, p. 501, and to the graph in Figure 2.

1. With the values of V, W, and T given in Figure 1, Dove is not an ESS against Hawk You can see this by examining Figure 2, the graph of mean fitness of Doves and Hawks against the proportion of Hawks in the population. When there are few Hawks present (look at the left-hand side of the graph), Hawks have a higher mean fitness than Doves. Therefore, their frequency in the population will increase. This constitutes a successful invasion of a population of Doves by Hawks, and shows that Dove is not an ESS against Hawk.

2. Simply plug in any values greater than 0 for V, W, and T and you should see that the fitness of Hawks is always higher than the fitness of Doves when Hawks are rare. This is what is required for Hawks to invade Doves, and demonstrates that Dove cannot be an ESS against Hawks regardless of the values of V, W, or T.

3. With the values of V, W, and T given in Figure 1, Hawk is not an ESS against Dove. Again, examine your graph of mean fitness (Figure 2) of Doves and Hawks against the proportion of Hawks in the population. When Doves are rare (on the right-hand side of the graph), their fitness is higher than that of Hawks. Therefore, Doves can invade a population of Hawks, and Hawk is not an ESS against Dove.

   Another way to think about this is to continue the scenario of Hawks invading Doves. At first Hawks are rare and have higher fitness than Doves. Their frequency increases, and we move toward the right along the horizontal axis. As we do so, the mean fitness of Hawks decreases. The mean fitness of Doves also decreases, but more slowly. As a result, the two fitness lines cross at about a 60:40 mix of Hawks and Doves. If Hawks continue to increase in frequency, we continue to the right, and the fitness line for Hawks dives below that of Doves. This reasoning implies that Hawks and Doves should come to some equilibrium mixture, such that both strategies are present in the population.

   An important point to note is that at this equilibrium, Hawks and Doves have equal fitness. We will use this fact to calculate the equilibrium frequencies for any values of V, W, and T.

4. Yes. Try, for example, $V = 1.00$, $W = 0.50$, and $T = 0.25$. Your graph should show that Hawks have higher fitness than Doves in all mixtures of Hawks and Doves. The only equilibrium is a population composed entirely of Hawks. In other words, regardless of the starting mixture, Hawks will increase in frequency until they drive

Doves to extinction.

5. Try various values for V, W, and T. In order for Hawk to be an ESS, $V \geq W$. The value of T is irrelevant (as long as it is ≥ 0). Try increasing the value of W given above (0.50) by small increments to V (1.00). You should see the fitness line for Hawks slope downward more and more steeply, until at $W = V$ it meets the Dove line at $H = 1$. If $W > V$, the two lines cross, indicating an equilibrium with both strategies present.

   Thus, for all values of $V \geq W$, Hawk is an ESS against Dove. For $V < W$, neither strategy is an ESS, and the equilibrium population will contain some of both.

The answers to questions 6 and 7 refer to values given in the spreadsheet shown in Figure 3, p. 506, and to the graph in Figure 5.

6. The equilibrium is a population consisting entirely of Hawks. You can see this in Figure 5. Note that Hawks have higher mean fitness at all frequencies, and would therefore eliminate Doves from the population. You can also inspect the curve of mean population fitness (Figure 2). It is highest when the proportion of Hawks is zero (i.e., a pure population of Doves). You can also compare the mean fitness values calculated in cells I13–I15 of Figure 3. A population of Doves has a mean fitness of 0.50, whereas a population of Hawks (which is also the equilibrium mix) has a mean fitness of 0.00.

7. The case in this exercise gives an example of individual selection overwhelming group selection. The population would have the highest mean fitness if it consisted entirely of Doves. However, the equilibrium mixture, which results from individual selection, has the lowest mean fitness of any mixture of Hawks and Doves. Thus, group selection would predict that the population should evolve toward 100% Doves, but the model shows it moves in the opposite direction, as predicted by individual selection.

   This result is fairly general. You will have to look hard to find parameter values that do not produce an equilibrium population with lower mean fitness than some other mixture of Hawks and Doves. In other words, most parameter values support individual selection over group selection. You *can* find parameter values in which the equilibrium population has the highest fitness of any mixture, but the values seem unreasonable. For example, if you make victory worthless ($V = 0$), and time the most expensive commodity ($T > W$ and $T > V$), then the equilibrium population will have the highest fitness.

   However, this result does not indicate that group selection overwhelms individual selection. Rather, it describes a situation in which both group and individual selection make the same prediction. Therefore, it is not a test of either hypothesis. In this model, no set of parameter values will support group selection over individual selection.