39 EVOLUTIONARILY STABLE STRATEGIES AND GROUP VERSUS INDIVIDUAL SELECTION

Objectives

- Understand the concept of game theory.
- Set up a spreadsheet model of simple game theory interactions.
- Explore the effects of different strategies on animal fitnesses.
- Understand the concept of an evolutionarily stable strategy.
- See how the concept of an evolutionarily stable strategy is a strong argument against group selection.

INTRODUCTION

Evolutionary biologists have long been interested in behavioral interactions between animals and how these interactions affect evolutionary fitness. One approach has been to model interactions using **game theory**. Game theory in its broadest sense is the mathematical analysis of conflict, and it has been applied to interactions between countries, business firms, individual humans, and animals. This exercise follows John Maynard Smith's (1976) model of behavioral interactions between animals and leads to his concept of an evolutionarily stable strategy (ESS). We will apply this model to the question of individual selection versus group selection—that is, the question of whether natural selection can act on groups as well as on individuals.

In our context, we will imagine that animals engage in contests over resource items, such as food, nest sites, or mates. We will assume that in each contest, there is only one winner, and the winner takes all of the contested resource item. Bear in mind, however, that animals engage in repeated contests, and any given animal may win on one occasion and lose on another. Our model makes several assumptions:

- We assume that winning a resource item increases an animal's fitness (in the evolutionary sense) by some amount, which we will symbolize as V (for victory).
- We assume that if an animal sustains an injury in a contest, that reduces its fitness by some amount, symbolized as W (for wound).
- Finally, we assume that if a contest continues too long, it costs both participants some amount of fitness, T (for time), representing the metabolic energy expended during the contest, and forgone opportunities to garner other resource items.

We will also assume, at least to begin with, that each animal always employs the same behavioral strategy in these contests. We will relax this assumption later.

Doves versus Hawks

By calling these behaviors "strategies," we do not necessarily imply any conscious decision-making by the animals. The word strategy in this context simply means a rigid, predictable set of behaviors that always occur in response to certain stimuli. To make this clear, we will define two strategies, called "Dove" and "Hawk" (Maynard Smith 1976). A Dove begins a contest by making a threat display but never backs up its threat with real violence. If its opponent displays, a Dove continues to display, but if its opponent attacks, a Dove retreats immediately. A Hawk wastes no time on display, but attacks immediately.

A contest between two Doves becomes a drawn-out battle of displays, with no injuries but much wasted time. In a contest between a Dove and a Hawk, the Dove retreats immediately when the Hawk attacks, and thus loses the resource item, but avoids injury. A contest between two Hawks is a violent affair, in which one party is always injured and retreats from the fray, leaving the resource item to the uninjured victor.

We can translate these descriptions into mathematical expressions using the fitness values defined above. A Dove contesting with another Dove will win half the contests and lose half, but it will always pay the time cost, T, of extended display. Thus, on average, the payoff to Doves contesting with other Doves will be $(V/2) - T$. A Dove contesting with a Hawk will always lose, but will not spend time or suffer injury. Thus, the mean payoff to Doves contesting with Hawks is zero. A Hawk will always win immediately against a Dove, and so the mean payoff to Hawks contesting with Doves is V. Finally, a Hawk fighting a Hawk will win half the time, and enjoy a fitness payoff of V, but it will also lose half the time, at a cost of W. So, the mean payoff to Hawks fighting Hawks is $(V/2) - (W/2)$, which we can simplify to $(V - W)/2$.

We can conveniently represent these outcomes in a payoff matrix in which we show all possible encounters and the fitness implications for the participants (Table 1). The payoffs are for the player on the left.

Table 1. Payoff matrix for Hawks versus Doves.

	Hawk	**Dove**
Hawk	$\frac{V-W}{2}$	V
Dove	0	$\frac{V}{2}-T$

We want to know which strategy confers higher fitness. To find out, we need to calculate the mean fitness of Doves and Hawks in a mixed population. Let us represent the frequency of Hawks by H, and the frequency of Doves by D. These are relative frequencies, and therefore lie between 0 and 1, and sum to 1 (i.e., $H + D = 1$).

Let us assume that encounters occur at random. If we consider all the encounters of an average Dove, the proportion of them that will involve another Dove will be D, and the proportion that will involve a Hawk will be H, or $1 - D$. The frequencies of encounters will be the same for the average Hawk.

To calculate the mean fitness of Doves, we must weight the payoffs of each kind of encounter by its frequency: the mean fitness of Doves is

$$0H + \left(\frac{V}{2} - T\right)D \qquad \text{Equation 1}$$

By the same logic, the mean fitness of Hawks is

$$\left(\frac{V-W}{2}\right)H+VD \qquad \text{Equation 2}$$

If we start with a population consisting of some mixture of Hawks and Doves, which strategy will prevail? The answer is not obvious. Hawks always win encounters with Doves, but Doves are never injured. We can approach the question by determining whether Hawk or Dove is an **evolutionarily stable strategy**, or **ESS**. An evolutionarily stable strategy is one that cannot be successfully invaded by any of the other strategies in the game.

Let us imagine a population consisting entirely of Doves. Could Hawks successfully invade? The concept of invasion in this context includes not only immigration, but also the appearance of mutations within the population. In other words, Hawks may move into the Dove population, or a genetic mutation may cause some Dove offspring to behave as Hawks.

In either case, a few invading Hawks would mean that $D \approx 1$ and $H \approx 0$. The mean fitness of Doves, Equation 1, would then be approximately

$$0(0)+\left(\frac{V}{2}-T\right)(1) \quad \text{or} \quad \frac{V}{2}-T$$

Analogously, the mean fitness of Hawks, Equation 2, would be approximately

$$\left(\frac{V-W}{2}\right)(0)+V(1) \quad \text{or} \quad V$$

Provided V and T are both greater than 0 (which is implicit in the definitions), V will be greater than $(V/2)-T$, and Hawks will increase in numbers. This is a successful invasion, and therefore Dove is not an evolutionarily stable strategy against Hawk.

PROCEDURES

But is Hawk an evolutionarily stable strategy against Dove? Could a few Doves successfully invade a population of Hawks? We will find the answer using a spreadsheet model, and it may surprise you. As always, save your work frequently to disk.

INSTRUCTIONS	ANNOTATION

A. Game Theory Model

1. Open a new spreadsheet and set up titles and column headings as shown in Figure 1. Enter only the text items for now.

These are all literals, so just select the appropriate cells and type them in.

	A	B	C	D	E	F	G	H	I
1	***Evolutionarily Stable Strategies***								
2	Based on John Maynard Smith's model of Hawks and Doves								
3	All costs and benefits are expressed in "fitness points."								
4	Model assumes that the probability of winning a fair encounter (i.e., Hawk vs. Hawk or Dove vs. Dove) is 0.50.								
5	It also assumes that a Hawk always wins against a Dove.								
6									
7	Outcome	Fitness points		Payoff matrix (payoffs to player on left)				Equilibrium mix	
8	Victory	0.50			Hawk	Dove		Proportion of Doves	
9	Wound	1.00		Hawk				Proportion of Hawks	
10	Time	0.10		Dove					
11								Fitness matrix	
12	Proportion		Fitness					Population composition	Mean fitness
13	Doves	Hawks	Doves	Hawks	Population			All Hawks	
14	0.0	1.0						All Doves	
15	0.1	0.9						Equilibrium mix	
16	0.2	0.8							

Figure 1

2. Enter the values shown in Figure 1 for V, W, and T.

In cells B8, B9, and B10 enter the values 0.50, 1.00, and 0.10, respectively. These are the values in fitness points of victory, a wound, and time lost.

3. Enter formulae to calculate values of the payoff matrix.

In cell E9, enter the formula **=0.5*(B8-B9)**. This corresponds to $(V - W)/2$, the payoff to a Hawk in an encounter with another Hawk.
In cell E10, enter the value 0. This is the payoff to a Dove in an encounter with a Hawk.
In cell F9, enter the formula **=B8**. This is the payoff to a Hawk in an encounter with a Dove. Use a formula rather than entering the value V, so that when you change V in cell B8, the change will automatically occur in cell F9 as well.
In cell F10, enter the formula **=0.5*B8-B10**. This corresponds to $(V/2) - T$, the payoff to a Dove in an encounter with another Dove.

4. Create a series in column A to represent various frequencies of Doves in the population.

In cell A14 enter the value 0.
In cell A15 enter the formula **=A14+0.1**. Copy the formula into cells A16 through A24.

5. Create a series in column B to represent various frequencies of Hawks in the population.

In cell B14 enter the formula **=1-A14**. Copy the formula into cells B15 through B24. Note that the frequency of Doves plus the frequency of Hawks must equal 1.

6. Calculate the mean fitness of Doves in a population of all Hawks.

In cell C14 enter the formula **=$E$10*B14+$F$10*A14**.
This corresponds to, Equation 1

$$0H + \left(\frac{V}{2} - T\right)D$$

and calculates the mean fitness of Doves in a population having the proportion of Doves and Hawks shown to the left in the same row.

We include **$E$10*B14** (i.e., $0H$) in the formula in case you want to change the payoff in cell E10 later in the exercise.

7. Calculate the mean fitness of Hawks in a population of all Hawks.

In cell D14 enter the formula **=$E$9*B14+$F$9*A14**.
This corresponds to Equation 2

$$\left(\frac{V - W}{2}\right)H + VD$$

and calculates the mean fitness of Hawks in a population with the same proportion of Doves and Hawks.

8. Calculate the mean fitnesses of Doves and Hawks at each of the population ratios in columns A and B. Save your work.

Copy the formulae from cells C14 and D14 into cells C15 through D24.

9. Graph the mean fitness of Doves and Hawks against the proportion of Hawks in the population.

Select cells B14 through D24 and make an XY graph. Edit your graph for readability. It should resemble the one in Figure 2.

10. Answer questions 1–5 at the end of the chapter.

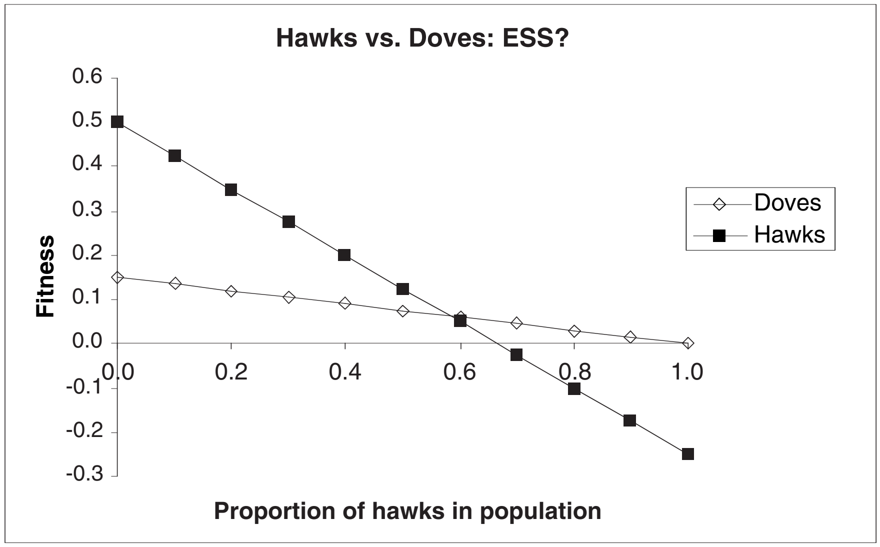

Figure 2

Equilibrium Solutions

In answering questions 1–5 at the end of the chapter, you should have discovered that if $V < W$, neither strategy is an ESS, and the equilibrium population will consist of a mixture of Hawks and Doves. In the first section of this exercise, we spoke of these strategies as being fixed patterns of behavior. However, the model may still apply even if behavior is not so rigid. We may suppose that a given animal behaves as a Hawk in some encounters and as a Dove in others. This changes our interpretation of the equilibrium result somewhat. Now we may conceive of the equilibrium as representing the optimal split in each animal's behavior. For example, if the equilibrium is 0.60 Dove and 0.40 Hawk, that would indicate that an animal achieves the greatest fitness by acting like a Dove in 60% of its encounters, and like a Hawk in 40%.

As you discovered graphically above, if wounds cost more than victory pays (i.e., if $W > V$), then neither Hawk nor Dove is an ESS. In such cases, the equilibrium population will consist of some mixture of Hawks and Doves. Can we determine what this equilibrium mixture will be?

We can, if we begin with an insight from Figure 2, our graph of fitness of Hawks and Doves at various frequencies of the two strategies. When the two strategies are at their equilibrium frequencies, their mean fitnesses are equal. This must be so, because if either strategy had a higher mean fitness, its frequency would increase, and therefore the population would not be at equilibrium.

So, if we represent the equilibrium frequency of Hawks as H_{eq} and the equilibrium frequency of Doves as D_{eq}, we can write

$$0H_{eq} + \left(\frac{V}{2} - T\right)D_{eq} = \left(\frac{V-W}{2}\right)H_{eq} + VD_{eq}$$

Because H_{eq} and D_{eq} are relative frequencies, they must add up to 1. Therefore, we can rewrite H_{eq} as $1 - D_{eq}$, and substitute:

$$0(1-D_{eq}) + \left(\frac{V}{2} - T\right)D_{eq} = \left(\frac{V-W}{2}\right)(1-D_{eq}) + VD_{eq}$$

If we eliminate the zero term on the left, and multiply both sides by 2, we get

$$(V - 2T)D_{eq} = (V - W)(1 - D_{eq}) + 2VD_{eq}$$

Carrying out the multiplications gives us

$$VD_{eq} - 2TD_{eq} = V + WD_{eq} - W - VD_{eq} + 2VD_{eq}$$

Canceling and rearranging terms yields

$$-2TD_{eq} = V + WD_{eq} - W$$

Collecting terms, we get

$$D_{eq}(2T + W) = W - V$$

and dividing both sides by $(2T + W)$ gives us the solution

$$D_{eq} = \frac{W - V}{2T + W} \qquad \text{Equation 3}$$

This equation agrees with our graphical analysis: If $W = V$, then the equilibrium frequency of Doves is zero; if $W > V$, then D_{eq} is between 0 and 1. In the numerator W has a positive number (V) subtracted from it, and in the denominator it has a positive number ($2T$) added to it, so D_{eq} must always be less than 1. Therefore, Dove is not an ESS against Hawk, regardless of the values of V, W, and T—as long as all are greater than zero.

If $W < V$, then the equation appears to predict a negative equilibrium frequency for Doves. This makes no sense, so we interpret it to mean that the frequency of Doves will decline (from any starting value) until it reaches zero. In other words, if $W < V$, then Hawk is an ESS against Dove.

For the sake of completeness, we can calculate the equilibrium frequency of Hawks as $1 - D_{eq}$, or

$$H_{eq} = 1 - \frac{W - V}{2T + W}$$

Substituting $\frac{2T + W}{2T + W}$ for 1 gives us

$$H_{eq} = \frac{2T + W}{2T + W} - \frac{W - V}{2T + W}$$

Combining the fractions, we get

$$H_{eq} = \frac{2T + W - W + V}{2T + W}$$

$$H_{eq} = \frac{2T + V}{2T + W} \qquad \text{Equation 4}$$

Although it is not as obvious, this equation makes the same predictions as Equation 3. That is, if $W = V$, then Hawk is an ESS against Dove; if $W > V$, Hawk is not an ESS against Dove (but remember, Dove is never an ESS).

Group Selection versus Individual Selection

These equilibrium solutions may not seem very interesting in themselves, but we can use them to arrive at some interesting conclusions. People often argue that some physical or behavioral trait exists because it benefits the species (or the population, or some other group). For instance, it is often said that humans (and many other animals) display cooperative behavior because cooperative groups are better at gathering food or fending off predators, or for other reasons have higher odds of survival. Such arguments are called group selection arguments, because they claim that natural selection operates on the group as a whole. **Group selection** argues that natural selection will favor a trait that confers higher fitness on the group, even if it reduces the fitness of the individuals that make it up.

The contrasting position, **individual selection**, claims that natural selection operates on individuals, not groups. Individual selection arguments predict that natural selection will favor a trait that confers higher fitness on individuals, even if it reduces the fitness of the group to which they belong.

We will use the equations for mean fitness of Doves and Hawks, and their equilibrium solutions, to investigate the contrast between group selection and individual selection. We will show that if a population consisted entirely of Doves, it would have a higher mean fitness than a population consisting entirely of Hawks or of any mixture of Hawks and Doves. A group selectionist would therefore expect the frequency of Doves in a population to increase, because that would benefit the group. However, as we will see, individual Hawks have higher fitness than individual Doves (at least when Hawks are rare). An individual selectionist would therefore expect natural selection to favor Hawks over Doves (at least when Hawks are rare), even if that reduces the fitness of the group as a whole.

PROCEDURES

Our strategy to test these ideas has five components:

- Calculate the mean fitness of the entire population, across the range of all mixtures of Hawks and Doves, from $D = 0$ and $H = 1$ to $D = 1$ and $H = 0$.
- Graphically estimate the mixture of Hawks and Doves that produces the maximum mean population fitness.
- Calculate the equilibrium mix of Doves and Hawks.
- Calculate the mean fitness of a population consisting of the equilibrium mix.
- Compare the maximum possible mean fitness of the population to its mean fitness at equilibrium.

We will repeat these steps for various values of V, W, and T, and compare the calculated values of mean fitness. We will see that this game theory model supports individual selection.

As always, save your work frequently to disk.

INSTRUCTIONS	ANNOTATION
B. Group selection versus individual selection.	
1. On the spreadsheet you prepared earlier (see Figure 1), change the values of V and W to 1, and the value of T to 0.	Enter these values into cells B8, B9, and B10, respectively.
2. Add a column heading for mean fitness of the entire population.	In cell E13 enter the label “Population.”
3. Calculate the mean fitness of the entire population for each mixture of Doves and Hawks in cells A14 through B24.	In cell E14 enter the formula **=C14*A14+D14*B14**. Copy this formula into cells E15–E24. This formula multiplies the mean fitness of Doves by their frequency and the mean fitness of Hawks by their frequency, then adds the two products together. When you have finished, your spreadsheet should resemble Figure 3.

	A	B	C	D	E	F
7	Outcome	Fitness points		Payoff matrix (payoffs to player on left)		
8	Victory	1.00			Hawk	Dove
9	Wound	1.00		Hawk	0.00	1.00
10	Time	0.00		Dove	0.00	0.50
11						
12	Proportion		Fitness			
13	Doves	Hawks	Doves	Hawks	Population	
14	0.0	1.0	0.000	0.000	0.000	
15	0.1	0.9	0.050	0.100	0.095	
16	0.2	0.8	0.100	0.200	0.180	
17	0.3	0.7	0.150	0.300	0.255	
18	0.4	0.6	0.200	0.400	0.320	
19	0.5	0.5	0.250	0.500	0.375	
20	0.6	0.4	0.300	0.600	0.420	
21	0.7	0.3	0.350	0.700	0.455	
22	0.8	0.2	0.400	0.800	0.480	
23	0.9	0.1	0.450	0.900	0.495	
24	1.0	0.0	0.500	1.000	0.500	

Figure 3

4. Set up labels in column H and in cell I12, as shown in Figure 4.

These are all literals, so just select the appropriate cells and type them in.

	H	I
7	Equilibrium mix	
8	Proportion of doves	
9	Proportion of hawks	
10		
11	Fitness matrix	
12	Population composition	Mean fitness
13	All hawks	
14	All doves	
15	Equilibrium mix	

Figure 4

5. Calculate equilibrium frequencies of Doves and Hawks.

In cell I8, enter the formula =**IF((B9-B8)/(2*B10+B9)>0,(B9-B8)/(2*B10+B9),0)**.
In this formula, **(B9-B8)/(2*B10+B9)** corresponds to Equation 3:

$$D_{eq} = \frac{W - V}{2T + W}$$

However, this equation can predict negative equilibrium frequencies for Doves, given some parameter values. We use the **IF()** function to restrict Dove frequencies to non-negative values. If D_{eq} is negative, we set it to zero.

In cell I9, enter the formula **=1-I8**.
This is the spreadsheet equivalent of $1 - D_{eq}$. Because $H_{eq} + D_{eq} = 1$, we do not need to use Equation 4 to calculate the equilibrium frequency of Hawks. You can, if you prefer, enter the spreadsheet equivalent of Equation 4; it should yield the same result.

6. Calculate mean fitness of a population consisting entirely of Hawks.

In cell I13 enter the formula **=E9**.
In an all-Hawk population, all encounters will be Hawk against Hawk. Therefore, all members of the population will receive the same payoff, $(V - W)/2$, which is calculated in cell E9.
You can arrive at the same result using Equation 2 to calculate the mean fitness of Hawks, bearing in mind that $H = 1$ and $D = 0$.

7. Calculate mean fitness of a population consisting entirely of Doves.

In cell I14 enter the formula **=F10**.
In an all-Dove population, all encounters will be Dove against Dove. Therefore, all members of the population will receive the same payoff, $(V/2) - T$, which is calculated in cell F10.
You can arrive at the same result using Equation 1 for mean fitness of Doves, bearing in mind that $H = 0$ and $D = 1$.

8. Calculate mean fitness of a population consisting of the equilibrium mixture of Hawks and Doves.

In cell I15 enter the formula **=$E$9*I9+$F$9*I8**.
This is the spreadsheet version of Equation 2 for the mean fitness of Hawks, this time using the equilibrium values of *D* and *H*, as calculated in cells I8 and I9. Remember that, at equilibrium, the mean fitnesses of Hawks and Doves are equal, so this is equivalent to calculating the mean fitness of all members of the population, regardless of strategy.

9. Add the data for population fitness to your existing graph.

Select the graph by clicking once anywhere in it and selecting Open Chart | Add Data. In the dialog box that appears, enter the cell addresses E13– E24. Be sure to include the label in cell E13, so that it will appear in the figure legend. Edit your graph for readability. It should resemble Figure 5.

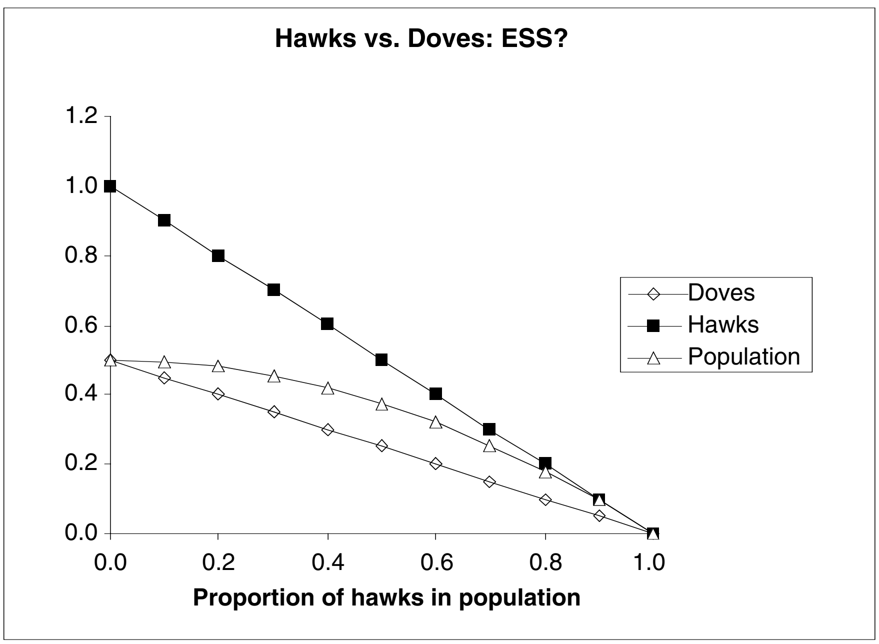

Figure 5

10. Answer questions 6 and 7 at the end of the chapter.

Conclusions

The upshot of this part of the exercise is strong support for individual selection. In every case where group and individual selection hypotheses predict different outcomes, the model produces the individual selection outcome.

One may argue, however, that this result does not prove that group selection cannot occur, only that it does not operate in this model. On the other hand, it is clearly the case that a pure population of Doves has the highest fitness in most scenarios, and yet Doves are displaced by Hawks. The matter comes down to the problem of cheaters. If everyone in the population "agrees" to behave as a Dove, the group as a whole will benefit. But if anyone "cheats" on the pact, and behaves as a Hawk, he or she will reap greater benefits than anyone behaving as a Dove. Hawkish behavior will spread through the population, either by genetic heritage, or by other Doves defecting as they see cheaters prospering. As the frequency of Hawks goes up, the fitness of each drops, because there are fewer Doves left to exploit. Even so, it still pays better to be a Hawk than a Dove. The result will be a population of Hawks, but each with lower fitness than he or she would have enjoyed if only everyone had remained a Dove. The language of "agreeing" and "cheating" should be understood metaphorically; there need be no conscious decision-making involved.

Another way to state the problem is in terms of individual interests versus group interests. If the interests of the individual are opposed to the interests of the group, individual interests are likely to dominate. Most evolutionary biologists are convinced that group selection, if it operates at all, can have noticeable effects only under very narrowly circumscribed conditions.

QUESTIONS

1. Is Dove an ESS against Hawk?
2. In the Introduction, we found the same answer without giving explicit values to V, W, or T. We implied that Dove was not an ESS against Hawk with any values of V, W, or T, as long as all are greater than zero. Can you support this conclusion using your spreadsheet?
3. Is Hawk an ESS against Dove?
4. Are there values of V, W, and T that would make Hawk an ESS against Dove?
5. Can you find what relationship among these parameters is necessary to make Hawk an ESS?
6. With the given parameter values, what is the equilibrium mixture of Hawks and Doves?
7. What does this result imply about individual versus group selection? Is this conclusion general, or does it depend on choosing parameter values carefully?

LITERATURE CITED

Maynard Smith, J. 1976. Evolution and the theory of games. *American Scientist* 64: 41–45.