Module 783

Game Theory Models of Animal Behavior

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INTERMODULAR DESCRIPTION SHEET: UMAP Unit 783

TITLE: Game Theory Models of Animal Behavior

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MATHEMATICAL FIELD: Game theory

APPLICATION FIELD: Biology

TARGET AUDIENCE: Students in either a game theory course or an introductory course on animal behavior.

ABSTRACT: This unit is an introduction to elementary game theory and some of its applications to evolutionary biology. The concept of an evolutionary stable strategy (ESS) is defined and its consequences are explored in several two- and three-person games. References are made throughout to examples of contests between animals in the wild. The unit concludes with a detailed application of this theory to male elephants and their mating strategies, using data from research studies.

PREREQUISITES: None.

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MODULES AND MONOGRAPHS IN UNDERGRADUATE
MATHEMATICS AND ITS APPLICATIONS (UMAP) PROJECT

The goal of UMAP is to develop, through a community of users and developers, a system of instructional modules in undergraduate mathematics and its applications, to be used to supplement existing courses and from which complete courses may eventually be built.

The Project was guided by a National Advisory Board of mathematicians, scientists, and educators. UMAP was funded by a grant from the National Science Foundation and now is supported by the Consortium for Mathematics and Its Applications (COMAP), Inc., a nonprofit corporation engaged in research and development in mathematics education.

Paul J. Campbell
Solomon Garfunkel
Editor
Executive Director, COMAP
1. Introduction

1.1 Animals Playing Games

As cooler temperatures descend on the Rocky Mountains during the fall, male elk (*Cervus elaphus*) enter a state of heightened sexual activity referred to as “rut.” A rutting male spends considerable time calling to attract females into a harem that the male defends from other males. When another male attempts to mate with a female from the harem, the harem holder races in to drive off the interloper. In some cases, these disputes lead to fighting between the two rival males, and the loser may be wounded during the contest. Even the winner may fare poorly in the long run, as the constant battles to protect his harem often leave him weak and in poor condition at the onset of winter [McCullough 1969].

Animal conflicts also occur over access to food resources. A group of vultures feeding on a dead wildebeest, for example, squabble with one another over access to the carcass. In this case, the resource being contested is food and not access to females, but the rules of the contest are essentially the same. At first, it might seem that we could apply optimality models to animal conflicts by determining the costs and benefits and solving for the optimal strategy. Unfortunately, this is not possible, because the optimal strategy for one individual depends on the behavior of its competitors in the population.

Evolutionary game theory is adapted from economic theory, except that the currency is Darwinian fitness and not money [von Neumann and Morgenstern 1944; Maynard Smith and Price 1973; Maynard Smith 1982]. Game theory is similar to optimization theory (e.g., the study of optimal foraging) in that it attempts to identify the best strategy based on the costs and benefits of some required resource. There are, however, important differences. Unlike optimization theory, where an individual’s reproductive success depends only on its own behavior, game theory involves more than one contestant and a contestant’s success depends on the behavior of all the other players.

1.2 Rules of the Game

In the simplest terms, economic game theory deals with two or more players each attempting to select the best response to the anticipated strategy of their opponents. Evolutionary game theory, however, tends not to focus on individual players, but on strategies available to different categories of individuals (i.e., male vs. females, dominants vs. subordinates, experienced vs. inexperienced, etc.). Each type of player has a set of strategies that it can adopt in response to its opponent’s anticipated strategy. Players that adopt the best strategies contribute more offspring to future generations and therefore by definition have higher reproductive fitness. If the best strategy is also heritable, it will become the dominant strategy for this category of player over evolutionary time. In
theory, the game stabilizes when all categories of players have adopted their best response to each of their opponents.

As Mesterton-Gibbons and Adams [1998] point out, in evolutionary game theory the “best” solution to the contest is the strategy that can be expected to evolve by natural selection. In other words, any possible alternative behavior would yield lower reproductive fitness or else it would have already spread throughout the population. This “best” solution is termed an evolutionary stable strategy (ESS). Informally, an ESS is a strategy that cannot be replaced by any (rare) alternative strategy that appears in the population (i.e., a mutant strategy). An ESS may be pure (consist of a single strategy) or mixed (consist of several strategies in a stable equilibrium).

The fitness of a genotype (sometimes) depends on the genetic composition of the population (it is “frequency-dependent”). In the language of game theory, this means that the payoff from a particular strategy depends on the strategies of the other players, so multiplayer game models are needed. In most cases, evolutionary games are played within a single species by a local population in a specific environment. In addition, game theory models allow an individual to play more than one strategy over time. Multiple strategies allow animals to modify their behavior in different conditions. A harem-holding male elk, for example, would behave differently if it were displaced and had to take on the role of intruder.

1.3 Types of Evolutionary Games

A game is a model describing the behavioral interactions of two or more individuals whose interests may conflict. In order to model the potentially conflicting interactions between players, we must be precise about

- who is involved in the game,
- what “moves” are possible, and
- how one player’s success depends on the behavior (moves) of the other players in the game [Hammerstein 1998].

In other words, a game has

- a set of players or categories of players;
- a strategy set—a list of alternative behaviors or morphologies that each category of player could use; and
- a set of payoffs (in terms of evolutionary fitness) for each possible combination of strategies.

Virtually all evolutionary games can be classified based upon four criteria. Different combinations of these four criteria yield different types of games each with its own set of assumptions, methods, and ESSs [Bradbury and Vehrencamp 1998]. The four criteria are:
• type of strategy set,
• type of player symmetry,
• number of opponents at one time,
• the number of sequential decisions in the game.

A strategy set can include discrete strategies (e.g., fight or flee), continuous strategies (e.g., vary the frequency of a call over a range of possible frequencies), or some combination of behaviors (e.g., produce pheromone A 30% of the time and pheromone B 70% of the time). If the strategy contains only one behavior, it is called a pure strategy. When a player (or category of players) performs a combination of alternative strategies, the combination is called a mixed strategy. For example, male frogs often call to attract mates. Suppose there are two genotypes for calls and 75% of male frogs always give call A (one genotype) while 25% percent of males always give call B (second genotype). In a second species of frogs, each male can perform each call type and each male uses call A 75% of the time and call B the remaining 25% of the time. Both are examples of a mixed strategy (in each case, females encounter a 3:1 ratio of calls).

Games can also be classified by the type of player symmetry. If the game is symmetrical, then all players use identical strategy sets and players are essentially interchangeable. Two male warblers of identical age and size displaying over access to a suitable nest site would be playing a symmetrical game if each could use the same set of display behaviors. Asymmetrical games, however, are probably more common in animal populations. Asymmetrical games have at least two categories of players, with each category having “access to different alternative strategies, different probabilities of winning with a given strategy, different payoffs when they win with a given strategy, or some combination of these conditions” [Bradbury and Vehrencamp 1998]. Interactions between dominant and subordinate individuals within a social group, or between males and females, are asymmetrical, because the players are not likely to use the same strategy set and there are different fitness payoffs to each type of contestant.

A simple contest involves a player and a single opponent at a time, such as two male yellow warblers disputing the boundaries of a territory. In contrast, n-person games or scrambles involve more than two players at once. Imagine a harem-holding bull elk defending his harem against a series of bachelor males. Here the possible payoffs to the bull depend on the frequency with which alternative strategies are used by the bachelor males. If all bachelors elect to fight, the payoffs are different than if only 40% elect to fight and the other 60% elect a strategy of sneaking copulations when the harem master is otherwise occupied. In other words, payoffs for n-person games are frequency-dependent.

A discrete symmetric contest requires a different model from an asymmetric n-person game. For each type of game, there are unique assumptions, different sets of ESSs possible, and different ways of finding those ESSs. In this article, we discuss contests involving two players.
2. Two-Strategy Games

We denote the expected payoff to a contestant playing strategy $A$ against another playing strategy $B$ by $E(A, B)$. Note that in general $E(A, B) \neq E(B, A)$, since the payoffs to different strategies are likely to be different. Ordinarily this information is presented in a matrix (see Table 1) that gives the fitness payoffs for each cell in the matrix.

Table 1.
The payoff matrix for Player 1 in a two-strategy game.

<table>
<thead>
<tr>
<th></th>
<th>Player 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
</tr>
<tr>
<td>A</td>
<td>$E(A, A)$</td>
</tr>
<tr>
<td>B</td>
<td>$E(B, A)$</td>
</tr>
</tbody>
</table>

The “best” course of action depends on what the other players are doing. A gull, for example, might feed itself by two strategies: Catch its own fish or steal a fish from another gull. If almost all gulls forage by catching their own fish, then it pays to be a thief as there are many potential victims. If most of the gulls are playing the thief strategy, then it may not pay to steal food.

2.1 Discrete Symmetric Contests:
The Game of Chicken

Most readers are familiar with the game of Chicken, at least from the movies. In our version, two players bet a certain amount of money and then drive their cars towards each other. There are two strategies. A Chicken will swerve at the last second to avoid an accident, but in the process will lose the bet. A player who is Not Chicken will not swerve out of the way and will crash into the other player if that player also does not swerve.

Clearly the payoff to each player (strategy) depends on the opponent’s strategy. To calculate the payoff in a contest, we need to know:

- the value of the prize or resource,
- the cost of winning,
- the probability of winning,
- the cost of losing, and
- the probability of losing.
The payoff to strategy \( A \) when playing against strategy \( B \) is given by

\[
E(A, B) = (\text{probability that } A \text{ beats } B) \times (\text{value of resource} - \text{cost of winning})
- (\text{probability that } A \text{ loses to } B) \times (\text{cost of losing})
\]  

(1)

Suppose that each player bets $100 on the race and that it takes $10 to get the car ready for the race. Suppose further that it costs $1000 to repair a car in the event of a crash. Let \( C \) denote the Chicken strategy and \( N \) the Not Chicken strategy.

When two Chickens race against each other, we assume that there is a 50% chance that either contestant swerves first and thus loses. The value of the contest is $200, the amount of money in the pool. It costs each contestant $100 that they bet and $10 to prepare the car, for a total of $110 whether the contestant wins or loses. Thus, using (1), we have

\[
E(C, C) = 0.5 \times (200 - 110) - 0.5 \times (110) = -10.
\]

This makes sense, since \( C \) wins half the time and it always costs $10 to prepare the car. In a Chicken vs. Not Chicken contest, the Chicken always loses, so

\[
E(C, N) = 0 \times (200 - 110) - 1 \times 110 = -110.
\]

In a Not Chicken vs. Chicken contest, Not Chicken always wins, so its payoff is

\[
E(N, C) = 1 \times (200 - 110) - 0 \times 110 = 90.
\]

When two Not Chickens play each other, neither swerves and an accident results. We'll assume that each gets their $100 back, but it still cost $10 to prepare the car and $1,000 to repair the car. Therefore,

\[
E(N, N) = 0 \times (200 - 110) - 1 \times (10 + 1000) = -1010.
\]

It is convenient to gather these payoffs into a single matrix, as in Table 2, which shows the payoffs for Player 1. Notice that \( E(N, C) \neq E(C, N) \): The first quantity is the payoff to an \( N \) when playing a \( C \) and the second is the payoff to a \( C \) when playing an \( N \); there is no reason that they should be the same.

<table>
<thead>
<tr>
<th>Player 1</th>
<th>Player 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Chicken</td>
</tr>
<tr>
<td>Chicken</td>
<td>-10</td>
</tr>
<tr>
<td>Not Chicken</td>
<td>90</td>
</tr>
</tbody>
</table>

Table 2.
The payoff matrix for Player 1 in the game of Chicken.

In this game, there are two pure strategies, namely, always play Chicken (swerve) or always play Not Chicken (never swerve). But some contestants
might play a *mixed strategy*, that is, a mixture of the Chicken and the Not Chicken strategies. The choice of which strategy to play might depend on peer pressure, the reputation of the opponent, whether or not the car belongs to one’s parents, and so on. While Table 2 gives the payoffs for pure strategies only, with a bit of algebra it can be used to calculate the payoffs for mixed strategies.

Suppose that $A$ represents a mixed strategy that plays Chicken with probability $p$ and Not Chicken with probability $1 - p$. We denote this by the linear combination

$$A = pC + (1 - p)N.$$ 

Similarly, let $B$ be a second mixed strategy such that

$$B = qC + (1 - q)N.$$ 

If we assume that $A$ and $B$ choose their strategies independently in each encounter, then the probabilities of the various strategic encounters are multiplicative. There will be a Chicken vs. Chicken encounter with probability $pq$, a Chicken vs. Not Chicken encounter with probability $p(1 - q)$, a Not Chicken vs. Chicken encounter with probability $(1 - p)q$, and a Not Chicken vs. Not Chicken encounter with probability $(1 - p)(1 - q)$. Each of these probabilities must be multiplied by the expected payoff for the corresponding encounter and then added to give the total payoff $E(A, B)$. Thus, to evaluate $E(A, B)$, we simply expand the expression as if it were a product of factors:

$$E(A, B) = E(pC + (1 - p)N, qC + (1 - q)N)$$


(2)

For example, if $A$ plays Chicken 60% of the time (so $p = 0.6$) and $B$ plays Chicken 20% of the time (so $q = 0.2$), then using (2) and the values in Table 2, we have

$$E(A, B) = (0.6)(0.2)(-10) + (0.6)(0.8)(-110) + (0.4)(0.2)(90) + (0.4)(0.8)(-1010) = -370.$$ 

Which strategy is best? The answer depends on the population of opponents. If a town consisted of almost all Chickens, then a Not Chicken would win most contests. On the other hand, if a town consisted of almost all Not Chickens, the Chicken strategy would be more prudent; while it would not win many contests, it would never result in an accident costing $1,010. Intuitively, we might expect that there is some mix of Chicken and Not Chicken such that the average payoff to each strategy is precisely the same. That is, there should be some stable mixture of strategies so that any player would be disadvantaged by switching from one strategy to the other.
**Definition 1** A strategy \( S \) is an evolutionary stable strategy (ESS) if for every strategy \( T \neq S \) we have

\[
E(S, S) \geq E(T, S)
\]

and if \( E(S, S) = E(T, S) \), then

\[
E(S, T) > E(T, T).
\]

This definition was originally given by Maynard Smith [1974]. For \( S \) to be an ESS, the first condition says that no strategy has a higher payoff against \( S \) than \( S \) itself. When there is a strategy \( T \) that has the same payoff as \( S \) does against \( S \), then the second condition says that \( S \) has an advantage over \( T \) when playing \( T \). In evolutionary terms, the strategy \( S \) can invade any population, since it will out-compete any other strategy \( T \). Moreover, no strategy \( T \) can invade a population of \( S \), since \( S \) will out-compete it. In this sense, a population of \( S \)-strategists is stable. Chicken is not an ESS, because

\[
E(C, C) = -10 < 90 = E(N, C).
\]

But neither is Not Chicken an ESS, because

\[
E(N, N) = -1010 < -110 = E(C, N).
\]

Is there some mixture of the Chicken and Not Chicken strategies that is stable? How to find such mixtures is the subject of the next section.

**Exercises**

1. **a)** What is the value of \( E(B, A) \) in the payoff matrix in **Table 3**?

<table>
<thead>
<tr>
<th></th>
<th>Player 1</th>
<th>Player 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>B</td>
</tr>
<tr>
<td>A</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>B</td>
<td>-3</td>
<td>4</td>
</tr>
</tbody>
</table>

**b)** Is either strategy an ESS?

2. Suppose in a game of Chicken that it costs \( x \) dollars to get the car ready for the race, that each player bets \( y \) dollars, and that it costs \( z \) dollars to repair the car in case of accident. Write out the general payoff matrix for this game.
2.2 ESSs and Two-Strategy Games

We now consider a general two-strategy game. We show that such a game always has an ESS. Denote the two strategies by $X$ and $Y$. Table 4 shows the payoffs for this general situation. We assume that the strategies are distinct, that is, we do not have both $a = c$ and $b = d$.

It is easy to check for pure ESSs: $X$ is pure ESS if either $E(X,X) > E(Y,X)$ or if both $E(X,X) = E(Y,X)$ and $E(X,Y) > E(Y,Y)$. Using the payoff matrix, this is equivalent to either $a > c$ or $(a = c$ and $b > d)$. Similarly, $Y$ is an ESS if either $d > b$ or $(d = b$ and $c > a)$. Consequently, there is no pure ESS only when both $c > a$ and $b > d$.

Now suppose that there is no pure ESS. We will (eventually) show that there must be a mixed strategy $S = pX + (1-p)Y$ that is an ESS, where $p$ denotes the probability with which strategy $X$ is played and $1-p$ the probability with which strategy $Y$ is played. We first examine the properties that any such mixed ESS must have.

**Theorem 1** Let $S = pX + (1-p)Y$ be a mixed ESS, where $X$ and $Y$ are pure strategies. Then the payoff to $X$ or to $Y$ against $S$ is the same as the payoff to $S$ against itself. That is,


Moreover, if $T = qX + (1-q)Y$ is any mix of the $X$ and $Y$ strategies, then

$$E(T, S) = E(S, S).$$

**Proof.** First, we have


From (2), we get

$$E(S, S) = p^2E(X, X) + p(1-p)E(X, Y) + (1-p)pE(Y, X) + (1-p)^2E(Y, Y)$$

$$= p[pE(X, X) + (1-p)E(X, Y)] + (1-p)[pE(Y, X) + (1-p)E(Y, Y)]$$


Table 4.

The payoff matrix for a general two-person game.

<table>
<thead>
<tr>
<th>Player 1</th>
<th>Player 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$X$</td>
</tr>
<tr>
<td>$X$</td>
<td>$a$</td>
</tr>
<tr>
<td>$Y$</td>
<td>$c$</td>
</tr>
</tbody>
</table>
But $S$ is an ESS, so $E(S, S) \geq E(X, S)$ and $E(S, S) \geq E(Y, S)$, so (3) becomes


Since the first and last terms are equal, the middle relation must also be an equality. Consequently, $E(S, S) = E(X, S)$ and $E(S, S) = E(Y, S)$. Using these equalities, we get


(4)

**Corollary 1** Let $X$ and $Y$ be any pure strategies and let $S = pX + (1 - p)Y$ be any mixed strategy such that $E(X, S) = E(Y, S)$. Then


**Proof.** As in (3) in the proof of Theorem 1,


But since $E(X, S) = E(Y, S) = E(S, S)$, then


By Theorem 1, if $S = pX + (1 - p)Y$ is a mixed ESS, then $E(X, S) = E(Y, S)$, that is, $pE(X, X) + (1 - p)E(X, Y) = pE(Y, X) + (1 - p)E(Y, Y)$. Using the payoffs in Table 4, this means

$$pa + (1 - p)b = pc + (1 - p)d.$$

Collecting the terms involving $p$ yields

$$b - d = p(b + c - a - d),$$

(5)

so that

$$p = \frac{b - d}{b + c - a - d}.$$  

(6)

Since we have assumed that there is no pure ESS, $c > a$ and $b > d$. So $0 < p < 1$, in other words, $p$ is a legitimate probability.

Conversely, if there is no pure ESS and $p = (b - d)/(b + c - a - d)$, then

$$E(X, S) = pE(X, X) + (1 - p)E(X, Y)$$
\[ = pa + (1 - p)b = \frac{(ab - ad) + (bc - ab)}{b + c - a - d} = \frac{bc - ad}{b + c - a - d}. \]

Similarly, we have

\[ E(Y, S) = pE(Y, X) + (1 - p)E(Y, Y) = pc + (1 - p)d = \frac{bc - ad}{b + c - a - d}. \]

That is, with \( p \) chosen as in (6), \( E(X, S) = E(Y, S) \).

The theorem and corollary assume that we are given mixed strategies that are ESSs. Now we finally show that a mixed ESS must exist if no pure ESS exists in a two-strategy game. Let \( S = pX + (1 - p)Y \) now denote the mixed strategy with \( p \) chosen as in (6). We show that \( S \) is an ESS.

Let \( T = qX + (1 - q)Y \) be any strategy other than \( S \), with \( 0 \leq q \leq 1 \). (If \( q = 1 \) or \( q = 0 \), then \( T \) is the pure strategy \( X \) or \( Y \), respectively.) Given our choice of \( p \), we have \( E(X, S) = E(Y, S) \), by Corollary 1 \( E(S, S) = E(X, S) = E(Y, S) \). So just as in (4) in the proof of Theorem 1, \( E(T, S) = E(S, S) \). So to show that \( S \) is an ESS, we must show that \( E(S, T) > E(T, T) \). But using the payoffs in Table 4, we get

\[ E(S, T) = pqa + p(1 - q)b + (1 - p)qc + (1 - p)(1 - q)d = d + (c - d)q + p[b - d + (a + d - b - c)q]. \]

Similarly, we may determine \( E(T, T) \) by just substituting \( q \) for \( p \) in (7),

\[ E(T, T) = d + (c - d)q + q[b - d + (a + d - b - c)q]. \]

To show that \( E(S, T) > E(T, T) \), it suffices to show that \( E(S, T) - E(T, T) > 0 \). But by (7) and (8), we have

\[ E(S, T) - E(T, T) = (p - q)[b - d + (a + d - b - c)q]. \]

Adding \( (a + d - b - c)q = -q(b + c - a - d) \) to (5), we obtain

\[ b - d + (a + d - b - c)q = (p - q)(b + c - a - d). \]

Substituting this into (9), we find

\[ E(S, T) - E(T, T) = (p - q)^2(b + c - a - d) > 0, \]

where the inequality follows because we have assumed there is no pure ESS, so \( c > a \) and \( b > d \). Thus, we have shown the following.

**Theorem 2** In a two-person game with payoff matrix

<table>
<thead>
<tr>
<th>Player 1</th>
<th>Player 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>X</td>
</tr>
<tr>
<td>X</td>
<td>a</td>
</tr>
<tr>
<td>Y</td>
<td>c</td>
</tr>
</tbody>
</table>
there is always an ESS. If there is no pure ESS, then $S = pX + (1 - p)Y$ is a mixed ESS with

$$p = \frac{b - d}{b + c - a - d}.$$ 

Let’s apply Theorem 2 to the game of Chicken in Table 2. Since there is no pure ESS, there must be a mixed ESS where the proportion of Chicken strategists is

$$p = \frac{b - d}{b + c - a - d} = \frac{-110 - (-1010)}{-110 + 90 - (-10) - (-1010)} = 0.90.$$ 

That is, there is a mixed ESS in which the Chicken strategy is played 90% of the time and Not Chicken is played 10%. This can happen in a variety of ways: 90% of the population might be “pure” Chickens and 10% “pure” Not Chickens, or each individual might be a mixed strategist playing Chicken 90% and Not Chicken 10%, or individuals might play each of the strategies with varying percentages but the overall play in the population is 90% Chicken and 10% Not Chicken.

Even very simple games like this are found in nature. Eagles often engage in spectacular aerial dogfights in which opponents fly at each other, lock their talons together, and fall in a spiral toward the earth. Just before they reach the treetops, the two eagles let go of each other and pull out of the dive. In these contests, the loser is the eagle that lets go first.

**Exercises**

3. Revise the game of Chicken so that

- each player now puts $200 into the pot,
- it still costs $10 get the car ready, and
- it still costs $1000 to repair in case of an accident.

a) Fill in the following table of payoffs to Player 1 for each possible contest.

<table>
<thead>
<tr>
<th>Player 1</th>
<th>Player 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Chicken</td>
</tr>
<tr>
<td>Chicken</td>
<td></td>
</tr>
<tr>
<td>Not Chicken</td>
<td></td>
</tr>
</tbody>
</table>

b) Determine the ESS for the game.
4. Revise the game of Chicken so that
   • each player puts $100 into the pot,
   • it still costs $1000 to repair in case of an accident, and
   • it does not cost anything to get the car ready.

   a) Fill in the following table of payoffs to Player 1 for each possible contest.

<table>
<thead>
<tr>
<th>Player 1: Chicken</th>
<th>Player 2: Chicken</th>
<th>Player 1: Not Chicken</th>
<th>Player 2: Not Chicken</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

   b) Determine the ESS for the game.

5. Consider the following two payoff matrices. Does either game have a pure ESS? If not, find the mixed ESS. Explain.

   \[
   \begin{array}{c|cc}
   \text{Player 1} & A & B \\
   \hline
   A & 0 & 2 \\
   B & -3 & 1 \\
   \end{array}
   \hspace{1cm}
   \begin{array}{c|cc}
   \text{Player 1} & A & B \\
   \hline
   A & 4 & 3 \\
   B & 4 & -1 \\
   \end{array}
   \]

6. In a game of Chicken assume that it costs $10 to get the car ready and $1,000 to repair it. How much money would each player have to put in the pot for there to be a mixed ESS in which the proportion of Chicken strategists in the population is \( p = 2/3 \)?

7. a) Return to the game in Problem 2. Assume that \( x < y < z \). Find the ESS for this game.
   
   b) What happens to the ESS as \( z \), the cost of repairs, increases?
   
   c) What happens to the ESS as \( y \), the amount bet, increases?
   
   d) What happens to the ESS as \( x \), the cost of preparing the car, increases?

3. **Hawk and Dove: A Discrete Symmetric Contest**

   The classic Hawk and Dove game involves two discrete strategies. Those individuals playing a Hawk strategy always fight to injure or kill their opponent. Individuals employing the Dove strategy always display and never escalate the
contest to serious fighting. (It is important to remember that these two strategies are being played by contestants of the same species.) If two individuals meet and both adopt the Hawk strategy, at least one will be seriously injured in the contest. Likewise, if two players both adopt the Dove strategy, there is some cost to continued displaying. When one player adopts a Hawk strategy and the other plays Dove, the Hawk wins the contested resource (i.e., food, territory, mates).

We now carry out an analysis of Hawk vs. Dove game. First we list, in general terms, the costs and benefits associated with the various strategies.

<table>
<thead>
<tr>
<th>Action</th>
<th>Benefit or Cost (arbitrary units)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gain resource</td>
<td>$v$</td>
</tr>
<tr>
<td>Lose resource</td>
<td>0</td>
</tr>
<tr>
<td>Injury to self</td>
<td>$i$</td>
</tr>
<tr>
<td>Cost to display self</td>
<td>$t$</td>
</tr>
</tbody>
</table>

Here, $v$ is positive, $i$ and $t$ are nonnegative numbers, and the payoffs are in arbitrary units of fitness. We can calculate the payoffs in the various Hawk and Dove contests as was done in the game of Chicken. Hawk always beats Dove; and when the same two strategies compete, we assume that either player has a 50% chance of winning. Therefore,

\[
E(H, H) = \frac{1}{2}v - \frac{1}{2}i, \\
E(H, D) = 1 \cdot v - 0 = v, \\
E(D, H) = 0 \cdot v + 1 \cdot 0 = 0, \\
E(D, D) = \frac{1}{2}(v - t) + \frac{1}{2}(-t) = \frac{1}{2}v - t.
\]

The payoff matrix for the Hawk vs. Dove game is given in Table 6.

<table>
<thead>
<tr>
<th>Player 1</th>
<th>Player 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawk</td>
<td>Dove</td>
</tr>
<tr>
<td>Hawk</td>
<td>$\frac{1}{2}v - \frac{1}{2}i$</td>
</tr>
<tr>
<td>Dove</td>
<td>0</td>
</tr>
</tbody>
</table>

### 3.1 Pure ESSs for Hawk and Dove

Recall that Hawk is a pure ESS if either $E(H, H) > E(D, H)$ or both $E(H, H) = E(D, H)$ and $E(H, D) > E(D, D)$. Using the values in Table 6, the first condi-
tion becomes

\[ E(H, H) > E(D, H) \iff \frac{1}{2}v - \frac{1}{2}i > 0 \iff v > i. \]

The second condition is equivalent to

\[ E(H, H) = E(D, H) \iff \frac{1}{2}v - \frac{1}{2}i = 0 \iff v = i \]

and

\[ E(H, D) > E(D, D) \iff v \frac{1}{2}v - t. \]

But this latter condition is always true, since \( v \) is positive and \( t \) is nonnegative. Thus, we conclude that \( \text{Hawk} \) is a pure ESS whenever \( v \geq i \), that is, whenever the value of the resource is at least as great as the cost incurred by injury.

Can \( \text{Dove} \) ever be an ESS? We just saw that \( E(H, D) > E(D, D) \), so \( \text{Dove} \) can never be a pure ESS. This makes sense, since any population of \( \text{Doves} \) can easily be invaded by \( \text{Hawks} \).

### 3.2 Mixed ESSs for \( \text{Hawk} \) and \( \text{Dove} \)

Common assumptions for this game are that the value of the resource is less than the cost of injury (this is what makes life risky) and that twice the cost of display is less than the value of the resource. That is, we assume that \( 2t < v < i \). In short, injuries are costly but displaying is inexpensive.

However, if \( v < i \), then neither \( \text{Hawk} \) nor \( \text{Dove} \) is a pure ESS. But by \textbf{Theorem 2}, there must be a mixed ESS. If \( h \) is the proportion of the \( \text{Hawk} \) strategy in such a mixed ESS, then using Table 6 and \textbf{Theorem 2} we get

\[ h = \frac{v - (\frac{1}{2}v - t)}{v + 0 - (\frac{1}{2}v - \frac{1}{2}i) - (\frac{1}{2}v - t)} = \frac{t + \frac{1}{2}v}{t + \frac{1}{2}i}, \]

or more simply,

\[ h = \frac{2t + v}{2t + i}. \]

Thus, when injury costs exceed the value of the resource (i.e., when \( i > v \)), (10) gives the proportion of the \( \text{Hawk} \) strategy in a mixed ESS as a function of the payoffs. This makes computing the equilibrium frequency a straightforward matter. For example, if the payoffs are \( v = 50 \), \( i = 100 \), and \( t = 10 \), then

\[ h = \frac{2(10) + 50}{2(10) + 100} = \frac{70}{120} = 0.583. \]

The frequency of the \( \text{Dove} \) strategy will be \( d = 1 - h = 1 - 0.583 = 0.417. \)
3.3 Two-Strategy Contests in Nature

The Hawk vs. Dove game is undoubtedly an oversimplification of the types of animal conflicts that exist in the wild. Nevertheless, these strategies represent two extremes of the possible strategies that might be played by wild animals. The model is used mainly to gain insight on how animal behavior evolves. To use game theory models to predict animal behavior, we need to know the range of possible strategies that could be played and the benefits for each. In practice it is difficult to measure costs and benefits in terms of Darwinian (reproductive) fitness. We can, however, use game theory models to make predictions about animal behavior that can be tested experimentally in the field or laboratory.

For example, in Exercise 8 you are asked to show that in a Hawk-Dove contest, as the resource value \( v \) increases, the proportion of Hawk strategists increases in the population. That is, game theory predicts that escalated contests and potentially costly fighting are selected for only if the winners leave more offspring than losers. Measuring fitness is very difficult, in part because it requires longitudinal data (i.e., data collected over several generations). Bonduriansky and Brooks [1999] carried out such a study on antler flies (Protopiophila litigata). Male antler flies compete for oviposition sites on discarded moose antlers. Female antler flies prefer to oviposit on the upward-facing surface of antlers. Male antler flies fight aggressively for access to these main oviposition sites, where females are a high-density resource. Bonduriansky and Brooks [1999] show that male antler flies holding high-quality territories are larger, tend to live longer, and have greater lifetime reproductive success. Winners of escalated contests enjoy a significantly higher frequency of mating and greater lifetime reproductive fitness.

The foraging behavior of bald eagles (Haliaeetus leucocephalus) involves multiple strategies to acquire prey. In their wintering grounds in Chilkat Valley, Alaska, bald eagles employ two basic strategies: capturing live or unclaimed prey (hunter) or stealing prey from another eagle (robber) [Hansen 1986]. By placing dead salmon on a gravel bar at intervals of approximately 4 m, Hansen [1986] created artificial food patches. Whenever two eagles interacted over a salmon carcass, Hansen recorded the number and type of display, type and duration of attack, winner and loser, injury status, and degree of hunger for each eagle.

In this two-strategy game, the payoff to the robber is frequency-dependent; the fitness of a robber is higher than that of the hunter when robbers are rare. In other words, if everybody steals, there will be no one to steal from. Game theory predicts that the frequencies of hunter and robber will eventually reach equilibrium (ESS), where the payoffs for both strategies are equal. In Hansen’s [1986] study, eagles pirated 58% of the time and hunted 42% but ultimately both types of strategists consumed similar amounts of flesh per unit time via each strategy. The risks of stealing vs. hunting were also equal, because no eagles were injured in Hansen’s study (although both behaviors are probably not really risk-free). The foraging tactics of bald eagles at Chilkat Valley appear to be an ESS.
Although displays are commonly used by robbers to steal salmon, bald eagles rarely escalate fighting to the point of injury. According to Maynard Smith and Parker [1976], competitors can use traits such as size, age, or hunger level to predict the winner without having to resort to escalated fighting. Eagles apparently use relative body size to settle disputes without escalated fighting. By careful observations, Hansen [1986] found that the larger of the pair of eagles wins 85% of the disputes.

The value of the resource may also change rapidly under certain conditions. Salmon carcasses are plentiful for short periods of time each year. When fish are plentiful (and there are few eagles in the neighborhood), the value of “owning” a fish is small, because it can easily be replaced. As fish become scarce or the cost of replacing a fish rises, the value of the resource increases. Hansen predicted that escalated fighting should increase when fish carcasses become scarce. In other words, animals should take greater risks when a contested resource becomes more valuable. As predicted, display rates, rates of retaliation of hunters against robbers, and rates of physical contact all increased when food levels were low.

One interesting outcome of Hansen’s study was the observation that a relatively constant ESS point is possible in eagle hunter-robber contests despite changes in food resource levels. Table 7 shows that the proportion of “robbers” in the population remained relatively constant despite varying amounts of food available. The “best” strategy for each eagle may depend more on its size or hunger level than on food level. Smaller (or younger) birds may be more successful as hunters, while larger birds may benefit more by stealing.

Table 7.
The frequency of bald eagle foraging strategies under different food levels during three periods of the winter (taken from Table 7 of Hansen [1986]).

<table>
<thead>
<tr>
<th>Period</th>
<th>Food Level</th>
<th>Hunter</th>
<th>Robber</th>
<th>% Robbers</th>
</tr>
</thead>
<tbody>
<tr>
<td>17 Nov–9 Dec</td>
<td>High</td>
<td>21</td>
<td>47</td>
<td>69</td>
</tr>
<tr>
<td>10 Dec–16 Dec</td>
<td>Low</td>
<td>10</td>
<td>16</td>
<td>62</td>
</tr>
<tr>
<td>17 Dec–23 Dec</td>
<td>High</td>
<td>8</td>
<td>20</td>
<td>71</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>39</td>
<td>83</td>
<td>68</td>
</tr>
</tbody>
</table>

Exercises

8. In (11), we saw that in the Hawk–Dove game, with resource value \( v = 50 \), injury cost \( i = 100 \), and display cost \( t = 10 \), there is a mixed ESS, with the equilibrium proportion of Hawks being \( h = 0.583 \).

a) Increase the resource value to \( v = 60 \). Is there still a mixed ESS? What happens to \( h \)?

b) Increase the resource value to \( v = 80 \). What happens to \( h \)?

c) Explain in one sentence why this makes biological sense.
9. a) Reset the value of \( v \) to 50 and leave \( t = 10 \). Increase the cost of injury to \( i = 120 \). What is the effect on \( h \) compared to the value of \( h \) in (11)?

b) Now increase the cost of injury further to \( i = 150 \). What is the effect on \( h \)?

c) Explain in one sentence why this makes biological sense.

10. a) Again set the value of \( v = 50 \) and \( i = 100 \). Increase the display cost to \( t = 20 \). What is the effect on \( h \) compared to the value of \( h \) in (11)?

b) Now increase the display cost to \( t = 30 \). What is the effect on \( h \)?

c) Explain in one sentence why this makes biological sense.

11. Let \( i = 100 \) and \( t = 10 \). What value of \( v \) produces a mixed ESS with a population with 50% Hawks and 50% Doves?

12. a) Assume the resource value is \( v = 100 \), the injury cost is \( i = 120 \), and the display cost is \( t = 20 \). Fill in the values in the payoff matrix below.

<table>
<thead>
<tr>
<th>Player 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawk</td>
</tr>
<tr>
<td>Dove</td>
</tr>
</tbody>
</table>

b) Why are neither pure strategies ESSs in this game?

c) Determine the mixed ESS.

d) With \( i = 120 \) and \( t = 20 \), determine the smallest value of \( v \) that makes Hawk a pure ESS.

13. a) Double the size of all the costs and benefits of the original example in the text. That is, assume a resource value of \( v = 100 \), an injury cost of \( i = 200 \), and display cost of \( t = 20 \). Fill in the values in the payoff matrix below.

<table>
<thead>
<tr>
<th>Player 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawk</td>
</tr>
<tr>
<td>Dove</td>
</tr>
</tbody>
</table>

b) Show that there is a mixed ESS and determine \( h \), the equilibrium frequency of the Hawk strategy in the mixed ESS.

c) Compare this to the equilibrium value of \( h \) in the original game (11). What is the effect of the doubling?
4. Three-Strategy Games

4.1 Asymmetries Between Players

As Hansen’s [1986] study of eagle foraging behavior demonstrates, the relative size or age of an opponent is important in determining the outcome of the game. Given that one contestant is bigger and stronger, playing Hawk against a smaller weaker opponent surely means the larger animal is less at risk of suffering an injury. A small eagle is therefore unlikely to escalate fighting against a larger or more experienced eagle. For a model to be realistic, we must take these asymmetries into consideration.

There are basically three kinds of asymmetries:

- asymmetries correlated with fighting ability,
- asymmetries correlated with resource value, and
- uncorrelated asymmetries.

When the resource is worth more to one contestant than to the other, or one contestant is more likely to win a fight because it is larger or stronger, then the contestants have asymmetries correlated with resource value or fighting ability, respectively. Uncorrelated asymmetries are unrelated to fighting ability or resource value. For example, being first to arrive at a resource may give the player an advantage over those arriving later, but the advantage is not due to fighting ability or the value of the resource.

4.2 The Hawk, Dove, Bourgeois Game

Suppose that one contestant arrived at a resource such as a nest site, territory, or harem of females and, in the absence of any opponents, took ownership of the resource. In this case, it might pay the owner to fight harder to retain the resource. The owner has information about the asymmetry that the other players do not (i.e., the owner knows that it owns the resource) and can assess which strategy to play.

Building on our previous Hawk and Dove model, we now add a third strategy that assesses and uses ownership information to decide on how to play. Call this assessor strategy Bourgeois. An individual exhibiting the Bourgeois strategy would play Hawk if it were the resource owner and Dove if it were the intruder. (The word “bourgeois” comes from the French term for middle class and is used in opposition to the proletariat or working class. The middle class enjoyed property ownership, which the lower working class did not.)

Again let $v$ denote the value of the resource contested, $i$ the cost of injury, and $t$ the display cost. As earlier, we assume that the cost of injury exceeds the value of the resource and that the value of the resource exceeds twice the cost of displaying, that is, $2t < v < i$. The payoffs in contests involving only
Game Theory Models of Animal Behavior

Hawks and Doves remain as in Table 6. We assume that Bourgeois has a 50% chance of owning a resource any time that it competes; so in any contest with Bourgeois, there is a 50% chance that it will act like a Hawk (own the resource) and a 50% chance that it will be a Dove (not own the resource). In other words, $B = \frac{1}{2} H + \frac{1}{2} D$. Therefore, the payoffs in contests involving Bourgeois are:

$$E(H, B) = \frac{1}{2} [E(H, H) + E(H, D)] = \frac{1}{2} \left[ \left( \frac{v}{2} - \frac{i}{2} \right) + v \right] = \frac{3v}{4} - \frac{i}{4},$$

$$E(D, B) = \frac{1}{2} [E(D, H) + E(D, D)] = \frac{1}{2} \left[ 0 + \left( \frac{v}{2} - t \right) \right] = \frac{v}{4} - \frac{t}{2},$$

$$E(B, H) = \frac{1}{2} [E(H, H) + E(D, H)] = \frac{1}{2} \left[ \left( \frac{v}{2} - \frac{i}{2} \right) \right] = \frac{v}{4} - \frac{i}{4},$$

$$E(B, D) = \frac{1}{2} [E(H, D) + E(D, D)] = \frac{1}{2} \left[ v + \left( \frac{v}{2} - t \right) \right] = \frac{3v}{4} - \frac{t}{2},$$

$$E(B, B) = \frac{1}{2} [E(H, D) + E(D, H)] = \frac{1}{2} \left[ v + 0 \right] = \frac{v}{2}.$$

The calculation of $E(B, B)$ requires a bit of explanation. We assume that when one of the $B$ strategists acts like it owns the resource, the other does not. Hence, $E(B, B) = \frac{1}{2} [E(H, D) + E(D, H)]$. Using the payoffs calculated above, the payoff matrix for the Hawk, Dove, Bourgeois game can be found in Table 8.

Table 8.
The payoff matrix for the Hawk, Dove, Bourgeois game.

<table>
<thead>
<tr>
<th></th>
<th>Hawk</th>
<th>Dove</th>
<th>Bourgeois</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawk</td>
<td>$\frac{v}{2} - \frac{i}{2}$</td>
<td>$v$</td>
<td>$\frac{3v}{4} - \frac{i}{4}$</td>
</tr>
<tr>
<td>Dove</td>
<td>0</td>
<td>$\frac{v}{2} - t$</td>
<td>$\frac{v}{4} - \frac{t}{2}$</td>
</tr>
<tr>
<td>Bourgeois</td>
<td>$\frac{v}{4} - \frac{i}{4}$</td>
<td>$\frac{3v}{4} - \frac{t}{2}$</td>
<td>$\frac{v}{2}$</td>
</tr>
</tbody>
</table>

4.3 Is Bourgeois a Pure ESS?

To determine whether Bourgeois is a pure ESS, we first compare the payoffs of the other pure strategies played against $B$ to how $B$ fares against itself and then compute the payoff of a general mixed strategy played against $B$. For Hawk vs. Bourgeois,

$$E(B, B) > E(H, B) \iff \frac{v}{2} > \frac{3v}{4} - \frac{i}{4} \iff \frac{i}{4} - \frac{v}{4} > 0 \iff i > v.$$ 

This last inequality is always true, since we have assumed that $i > v$. For Dove vs. Bourgeois,

$$E(B, B) > E(D, B) \iff \frac{v}{2} > \frac{v}{4} - \frac{t}{2} \iff \frac{v}{4} > -\frac{t}{2},$$

which is always true because $v$ is positive and $t$ is nonnegative.

Now let $T = qH + rD + (1 - q - r)B$ be any mixed strategy so that either $q$ or $r$ or both are not 0. Then using the previous two results, we get

$$E(T, B) = E(qH + rD + (1 - q - r)B, B)$$
Thus, by Definition 1, Bourgeois is a pure ESS if \( v < i \).

### 4.4 The Diagonal Rule

The reason why it was so easy to show that Bourgeois is a pure ESS is that in Table 8 \( E(B, B) \) is the largest payoff in the third column. More precisely, a payoff on the diagonal is the greatest element in the column of a payoff matrix. When this is so, the strategy is a pure ESS.

Let’s be completely general about this. Suppose that we have an \( n \)-strategy game with strategies \( X_1, X_2, \ldots, X_n \). Suppose that in the \( n \times n \) payoff matrix for this game, the \( i \)-th diagonal element, \( E(X_i, X_i) \) is the largest element in the \( i \)-th column. This means that \( E(X_i, X_i) > E(X_j, X_i) \) for all \( j \neq i \). Let \( T \neq X_i \) be any (mixed) strategy. We can write \( T \) as a combination of the pure strategies, \( T = p_1X_1 + p_2X_2 + \cdots + p_nX_n \), where \( p_1 + p_2 + \cdots + p_n = 1 \) and each \( p_i \geq 0 \). Then because \( E(X_j, X_i) < E(X_i, X_i) \), we have

\[
E(T, X_i) = p_1E(X_1, X_i) + p_2E(X_2, X_i) + \cdots + p_nE(X_n, X_i)
\]

\[
< p_1E(X_i, X_i) + p_2E(X_i, X_i) + \cdots + p_nE(X_i, X_i)
\]

\[
= (p_1 + p_2 + \cdots + p_n)E(X_i, X_i)
\]

\[
= E(X_i, X_i).
\]

So \( E(T, X_i) < E(X_i, X_i) \). Thus, we have proven the following result.

**Theorem 3 The Diagonal Rule.** In an \( n \)-strategy game with pure strategies \( X_1, X_2, \ldots, X_n \), if \( E(X_i, X_i) > E(X_j, X_i) \) for all \( j \neq i \), then \( X_i \) is a pure ESS.

**Exercises**

14. **a)** Let the resource value be \( v = 50 \), the injury cost \( i = 100 \), and the display cost \( t = 10 \). Determine the payoff matrix for the Bourgeois game.

**b)** Verify that the Bourgeois strategy is ESS.

15. Use the general payoff matrix for the Bourgeois game to answer the following questions.

**a)** Suppose that the cost of display is \( t = 10 \), as usual. What value of \( v \) makes \( E(D, D) = E(B, D) \)?

**b)** Does such a value of \( v \) make biological sense?

**c)** Suppose that the cost of display is \( t = 10 \) and the value of the resource is \( v = 50 \). What injury cost \( i \) makes \( E(H, B) = E(D, B) \)?

**d)** Does such a value of \( i \) make biological sense?
16. a) Suppose we set the display cost to \( t = 0 \) but leave \( v = 50 \) and \( i = 100 \) unchanged. What is the payoff matrix?

b) Because the display cost is 0, we might expect Doves to fare somewhat better? Is Dove an ESS?

17. a) Let \( v = 100 \) and \( i = 100 \) and let the display cost \( t = 10 \). What assumptions about the payoffs is no longer valid?

b) Is there a pure ESS? If so, what is it?

18. a) Can Hawk ever be a pure ESS? We might think so if the injury cost is not too large relative to the value of the resource. Use Table 8 to show that \( E(H, H) > E(B, H) \) whenever \( v > i \).

b) Set the value of \( v \) to 120. Leave the cost of injury at \( i = 100 \) (so \( v > i \)) and the display cost at \( t = 10 \). Is Hawk a pure ESS?

4.5 Bully: A More Complicated Three-Strategy Game

We now consider a second game involving assessment by players. A Bully strategist first plays Hawk, but after a brief evaluation period it then plays opposite to its opponent's strategy. In other words, if a Bully's opponent initially plays Hawk, then the Bully soon backs down and plays Dove. If a Bully's opponent initially plays Dove, then the Bully seizes the advantage and continues to play Hawk. This means that when two Bullies meet, they will both eventually adopt the Dove strategy in the contest. The payoffs in contests involving a Bully are determined by the final strategy that the Bully adopts. The payoff matrix is given in Table 9.

Table 9.
The payoff matrix for the Hawk-Dove-Bully game.

<table>
<thead>
<tr>
<th>Player 1</th>
<th>Player 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Hawk</td>
</tr>
<tr>
<td>Hawk</td>
<td>( \frac{1}{2}v - \frac{1}{2}i )</td>
</tr>
<tr>
<td>Dove</td>
<td>0</td>
</tr>
<tr>
<td>Bully</td>
<td>0</td>
</tr>
</tbody>
</table>

The advantage of the Bully strategy is that, like Hawk, it always beats Dove but does not incur the injury cost of Hawk in contests with Hawk. A Bully fares better than a Dove in all contests except those with Hawks where the two strategies fare equally well.

Are any of the pure strategies an ESS? Assume as before that the cost of injury exceeds the value of the resource and that twice the cost of displaying
is less than the value of the resource, $2t < v < i$. Then Hawk is not an ESS, because $E(H, H) = \frac{1}{2}v - \frac{1}{2}i < 0 = E(D, H)$. Dove is not an ESS because $E(D, D) = \frac{1}{2}v - t < v = E(H, D)$. Similarly, Bully is not an ESS because $E(B, B) = \frac{1}{2}v - t < v = E(H, B)$.

Is there a mixed ESS? Suppose that $S = p_1H + p_2D + p_3B$ were a mixed ESS with $p_1 + p_2 + p_3 = 1$. A mixed ESS can be composed of all three strategies (no $p_i$ is 0) or a combination of any two (exactly one $p_i$ is 0). By Corollary 1, any pure strategies that do appear in a mixed ESS must all have the same payoff when played against $S$.

We now show that no mixed ESS $S$ can have both Bully and Dove as component strategies. For if $S$ did, then both $p_2 > 0$ and $p_3 > 0$ and, consequently,

$$E(B, S) = p_1E(B, H) + p_2E(B, D) + p_3E(B, B)$$
$$= p_1 \cdot 0 + p_2 \cdot v + p_3 \left(\frac{1}{2}v - t\right)$$
$$> p_1 \cdot 0 + p_2 \left(\frac{1}{2}v - t\right) + p_3 \cdot 0$$
$$= p_1E(D, H) + p_2E(D, D) + p_3E(D, B)$$
$$= E(D, S).$$

But this conclusion contradicts the fact that $E(B, S) = E(D, S)$ if both Bully and Dove are part of the mixed ESS. This means that Bully and Dove cannot both be part of any mixed ESS. So any ESS must consist of a mixture of Hawks and Bullies or Hawks and Doves.

Next we show that there is no mixed ESS composed of only Hawks and Doves. Suppose that $S = pH + (1 - p)D$ were an ESS for some $p$ with $0 < p < 1$. Then, by Theorem 1 $E(S, S) = E(D, S)$. But

$$E(D, S) = E(D, pH + (1 - p)D) = pE(D, H) + (1 - p)E(B, D) = 0 + (1 - p)\left(\frac{v}{2} - t\right),$$

while

$$E(B, S) = E(B, pH + (1 - p)D) = pE(B, H) + (1 - p)E(B, D) = 0 + (1 - p)v.$$ 

Consequently, $E(B, S) > E(D, S) = E(S, S)$, so $S$ cannot be an ESS. This makes biological sense, because Bullies outplay Doves, so Doves should not be part of an ESS.

Is a mixed ESS of Hawks and Bullies possible? Suppose that $S = pH + (1 - p)B$ were an ESS for some $p$ with $0 < p < 1$. By Theorem 1, we must have $E(H, S) = E(B, S)$. But

$$E(H, S) = E(H, pH + (1 - p)B) = p \left(\frac{v}{2} - \frac{i}{2}\right) + (1 - p)v = v - \frac{1}{2}pv - \frac{1}{2}pi$$

and

$$E(B, S) = E(B, pH + (1 - p)B) = (1 - p) \left(\frac{v}{2} - t\right) = \frac{1}{2}v - t - \frac{1}{2}pv + pt.$$ 

\(^1\)Theorem 1 and Corollary 1 are easily generalized to $n$-person games and mixed strategies composed of more than two pure strategies.
If \( E(H, S) = E(B, S) \), then
\[
v - \frac{1}{2}pv - \frac{1}{2}pi = \frac{1}{2}v - t - \frac{1}{2}pv + pt.
\]
Collecting all the \( p \)-terms together yields
\[
p(t + \frac{1}{2}i) = t + \frac{1}{2}v.
\]
Solving for \( p \), we find
\[
p = \frac{t + \frac{1}{2}v}{t + \frac{1}{2}i},
\]
or more simply,
\[
p = \frac{2t + v}{2t + i}. \quad (12)
\]

The proportion \( p \) of Hawks in this mixed strategy is the same as in the Hawk-Dove game (see (10)). This makes biological sense. Without any Doves present, the Bullies act effectively like Doves. In every encounter (whether with a Hawk or another Bully), they will bluff first and then, having encountered Hawk-like behavior, subsequently adopt the Dove strategy.

We must still show that \( S = pH + (1 - p)B \) with \( p \) as in (12) is an ESS. By Corollary 1 \( E(S, S) = E(H, S) = E(B, S) \). Also notice that since Doves lose to Hawks and Bullies,
\[
E(D, S) = E(D, pH + (1 - p)B) = pE(D, H) + (1 - p)E(D, B) = 0. \quad (13)
\]

Now let \( T = qH + rD + (1 - q - r)B \) be any mixed strategy. We must show that \( E(S, S) > E(T, S) \) or \( E(S, S) = E(T, S) \) and \( E(S, T) > E(T, T) \). Using Theorem 1 and (13), we have
\[
E(T, S) = E(qH + rD + (1 - q - r)B, S)
= qE(H, S) + rE(D, S) + (1 - q - r)E(B, S)
= qE(S, S) + 0 + (1 - q - r)E(S, S)
= (1 - r)E(S, S)
\leq E(S, S). \quad (14)
\]
Thus, if \( r > 0 \) (i.e., Dove is part of the mixed strategy \( T \)), then \( E(S, S) > (1 - r)E(S, S) = E(T, S) \). However, if \( T \) is a mixture of Hawk and Bully only, that is, if \( r = 0 \) so that \( T = qH + (1 - q)B \), then \( E(S, S) = E(T, S) \).

So the problem has been reduced to a two-strategy game, Hawk and Bully. But as we observed earlier, without any Doves present, Bullies are reduced to Dove-like behavior. The Hawk and Bully payoffs are given in Table 10.

Since the entries in Table 10 are identical to those in the Hawk-Dove game in Table 6, so is the mixed ESS but with Bullies replacing the Doves: \( S = pH + (1 - p)B \) with \( p = 2t + v/(2t + i) \).
Table 10.
The reduced payoff matrix for Hawk vs. Bully.

<table>
<thead>
<tr>
<th>Player 1</th>
<th>Player 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Hawk</td>
</tr>
<tr>
<td>Hawk</td>
<td>( \frac{1}{2} v - \frac{1}{2} i )</td>
</tr>
<tr>
<td>Bully</td>
<td>0</td>
</tr>
</tbody>
</table>

Exercises

19. Consider a new strategy Dove. A Retaliator plays in a way exactly opposite to a Bully. It starts out playing Dove and then after a brief evaluation period it adopts the strategy of its opponent. Fill in the payoff table (\( v \), \( i \), and \( t \) have their usual meanings) for a Bully vs. Retaliator game and find the ESS(s) assuming \( 2t < v < i \). Remember: Bully starts out playing Hawk.

20. Write the payoff matrix and find the ESS for a Bully vs. Bourgeois game.

21. Write the payoff matrix and find the ESS for a Retaliator vs. Bourgeois game.

22. Write out the payoff matrix for a Dove, Bully, Retaliator game. Show that there is only one pure ESS.

23. a) Write out the payoff matrix for the four strategy game involving Hawk, Dove, Bully, and Retaliator. Is there a pure ESS?
   b) Show that the mixed strategy \( S = pH + (1-p)B \) with \( p \) chosen as in (6) is an ESS for this new game. Hint: Mimic the ideas following (12).

5. Asymmetries

All the models described so far assume that all Hawks are equally matched (symmetric), as are all Doves and Bourgeois. In the real world, this is rarely the case. Instead, contestants usually vary in one or more qualities that may have an effect on the outcome of the interaction; they have asymmetries in behavior. Given that asymmetries exist, it would make sense if the contestants could assess these asymmetries in some way and adjust their behavior to the particular situation. Play Dove when, after evaluating the asymmetries, you decide the opponent is more likely to win, and play Hawk when you decide you have the advantage. The particular asymmetry could be differences in body size, age, ownership of the disputed resource, etc. Cases where opponents can adjust the strategy they play depending on the circumstances are referred to as conditional strategies. Conditional strategies can be more successful than the mixed ESS of a randomly played Hawk-Dove game.
5.1 Asymmetries in Resource Values

A given resource may be perceived differently by two contestants. A female may be perceived as more valuable if she has not already been inseminated [Austad 1983]. Territories may be more valuable to a resident who has already learned the location of important food patches or nest sites than to an intruder [Beletsky and Orians 1987]. Likewise, an animal that is starving places a higher value on a given food item than an animal that has recently fed. As a result, the starving animal might be more willing to risk injury by adopting a Hawk strategy even in the face of a larger opponent. This prediction has been verified experimentally for common shrews (Sorex araneus) [Barnard and Brown 1984]. Shrews have very high metabolic rates and consequently must consume relatively large quantities of food per day, making food a valuable resource. Prior to each experiment, shrews were divided into two groups, those that received a high-density food supply and those that received a low density food supply. After two days, one “high-density shrew” and one “low-density shrew” were placed together in an observation arena where aggressive interactions were scored. In the second stage of the trial the diets of the shrews were reversed: “Low-density shrews” were given access to high-density food resources, “high-density shrews” foraged where prey were at low density, and the experiments were repeated (see Table 11). In both stages, shrews experiencing lower food density won the majority of the interactions. Presumably, hungrier shrews are more willing to risk injury to secure the rights to a disputed food resource.

<table>
<thead>
<tr>
<th>Prior resource experience</th>
<th>Density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Stage 1</td>
<td>85.8 (231.3)</td>
</tr>
<tr>
<td>Stage 2</td>
<td>20.4 (45.5)</td>
</tr>
</tbody>
</table>

Male damselflies (Calopteryx maculata) defend territories consisting of small patches of emergent vegetation along the water’s edge. Females come to these patches to lay eggs on the vegetation thereby providing the territory holder with an opportunity to mate. Males vigorously defend their small territories from other males by chases lasting from a few seconds to over an hour. Typically, the territory holder wins the contest. When territory holders are away feeding or chasing an intruder, the territory may sometimes be taken over by another male. When the original owner returns, territory ownership is confused and an escalated contest results [Waage 1988; Marden and Waage 1990]. The fact that territory owners tend to defeat intruders in disputes might mean that a Bourgeois strategy is being played. Alternatively, it might mean that territory owners have more to gain and are therefore prepared to fight harder or longer. If the territory is rich in high quality food patches or provides better access...
to mating opportunities, then the territory has a higher resource value to the owner, because the owner has more knowledge of the territory’s characteristics.

In cases where the value of the resource exceeds the cost of injury, we would predict Hawk-like strategies to evolve. Fierce fighting results because losers might fail to pass on any genes to future generations. When the resource value is lower or the injury cost is very high, we would predict that a Bourgeois strategy would evolve to settle disputes.

Male elephant seals (*Mirounga angustirostrus* and *M. leonina*) congregate on certain beaches each year to breed. Large, dominant males arrive first and set up territories on the beach. As females arrive on the breeding beaches, the males sequester the females into harems that are vigorously defended. All matings are performed by these harem masters who defend their females from the many late arriving bachelor males that live at the edge of the sea. Fights between elephant seal bulls are brutal and bloody. The females in the harem benefit by mating only with the largest and strongest bulls. The harem masters risk serious injury and expend so much energy defending their females that they usually retain their harems for only a year or two before dying. As a result, a harem master’s entire reproductive success may depend on retaining the harem for a single year [Le Boeuf 1974].

Game theory predicts that as the value of the resource increases, contestants will be more likely to escalate the battle. In the case of male elephant seals, the value of retaining harem ownership is very high: their one chance to breed. For the harem master, a major portion of his lifetime reproductive success is at stake and he has nothing to gain by retreating. Under conditions of extremely high resource values, interaction strategies leading to serious injury or even death can evolve.

### 5.2 Asymmetries in Fighting Ability

Even if the resource does have equal value to both contestants, not all players are created equal. Often one contestant is larger, heavier, has larger weapons, or has more experience fighting. In these cases, the contestant is said to have greater “resource holding power” (RHP). Rivals would increase their own long-term fitness by accurately assessing their opponent’s RHP and adjusting their behavior accordingly. Male deer, for example, assess the size of their opponent’s antlers, and male elk assess their opponent’s vigor by the duration and intensity of roaring contests [Clutton-Brock and Albon 1979].

In situations where animals can assess the resource holding potential of a rival, the Assessor strategy may prevail [Maynard Smith 1982]. If a contestant’s RHP is greater than its opponent’s, adopt the Hawk strategy; but if its RHP is less than its opponent’s, play Dove. This is an example of a conditional strategy.

Strategies such as Bourgeois and Bully are essentially Assessor strategies, because the decision to escalate or retreat is based on an assessment of the opponent or its strategy. How can opponents assess one another? Perhaps the most common method of assessment is based on differences in body size or
strength between opponents. If an Assessor can accurately evaluate its relative size or strength, it is likely to fare well against a Hawk or Dove strategy, because it avoids paying fighting and injury costs when it is likely to lose the contest.

Body size can be evaluated in a number of ways. Several species of frogs and toads evaluate the relative size of an opponent by the frequency range of the opponent’s calls [Davies and Halliday 1978]. The physics of sound production make it energetically less expensive for larger toads to produce low-frequency calls. Therefore, call frequency is inversely proportional to caller body size and can be readily evaluated by an opponent without direct observation. Male toads (Bufo bufo) fight over gravid females. Davies and Halliday [1978] allowed both large males and small males to amplex (mount and hold onto a female) with gravid females. Each male was temporarily muted and a series of either high or low-frequency calls was played back via a small speaker near the amplexed pair. As predicted, when a male of intermediate size was introduced, it more readily attacked the amplexed male when high-frequency croaks were played, especially if the defender was also smaller in body size. Only when the defender and the attacker were of similar body size did fights escalate. These experiments suggest that male Bufo can use a combination of visual and auditory cues to assess the fighting ability of an opponent.

In some cases, relative fighting ability is not related to body size. Briffa and Elwood [2000] studied fighting ability in hermit crabs. Hermit crabs fight by rapping their shells against those of an opponent in an attempt to evict the opponent from its shell. Once evicted, the aggressor exchanges its own shell for the newly vacant shell. The information on fighting ability is conveyed by the force and rate of shell rapping. Briffa and Elwood [2000] experimentally reduced the force with which an aggressor could rap on an opponent’s shell by painting the aggressor’s shell with a rubberized material. Hermit crabs in rubberized shells were less likely to evict (i.e., win) opponents from their shells. Presumably the force and rate of shell rapping is a more accurate signal of fighting ability than shell size, because small hermit crabs often occupy large shells and large crabs may occupy small shells.

Visual cues are often used to assess relative fighting ability. As previously described for eagles and toads, overall body size is a common method of assessing fighting ability. In other cases, dominant or more aggressive individuals often display badges of status. Many species of lizards display brightly colored throat patches (called dewlaps) when confronted by an opponent. Males with dewlaps of specific colors or patterns are significantly more likely to win disputes. Male house sparrows (Passer domesticus) exhibit a great deal of variation in the size of the dark patch of feathers on the throat. Males with the largest throat patches are socially dominant to other males, and these “badges” of status serve as effective deterrents.
6. Application: Musth in African Elephants

Female African elephants (*Loxodonta africana*) are social animals and often live in kinship groups dominated by a matriarchal female. Adolescent and adult males are excluded from these female groups, and become solitary or form loose bachelor herds. Sexually active males (usually older than 25 years of age) seek out females that are in estrus (sexually receptive). Some proportion of adult males experience episodes of *musth*, a period of heightened aggression and sexual activity brought on by elevated levels of testosterone in the blood [Vaughan, et al. 1999]. The frequency of musth and its duration is related to the age of the male. When a male enters a period of musth, it advertises its increased aggressiveness with secretions from a gland near the eye, vocalizations, and increased urine-marking [Poole 1989]. These cues should be relatively easy for other males to assess. Musth males may be signaling their intention to fight (asymmetry in fighting ability or motivation) and that they place a higher value on receptive females than non-musth males (asymmetry in resource value).

During aggressive encounters between sexually active but non-musth males, body size usually determines the outcome. In 86% of the interactions between non-musth males and those in musth, however, the musth male won the contest regardless of size. When both males are in musth, fights often escalate and can result in serious injury and even death [Poole 1989]. Escalated fights can last for several hours during the heat of the day, resulting in significant thermoregulatory costs for both contestants. In addition, musth males spend less time feeding and their overall condition over the 2–4 month musth period frequently deteriorates. The benefits to the winner are measured in terms of evolutionary fitness as the number of offspring sired per year.

According to Poole [1989], at Amosell National Park in Kenya there are approximately 30 estrus females available during the wet season and 15 during the dry season. These females represent the available resources or benefits (see Table 12). High-ranking males (H) guard and mate any receptive females they encounter, but lower-ranking males (L) can mate with only those females that are not being guarded by a higher-ranking male.

The costs of securing and defending females were estimated by Poole [1989] by using several methods to score the physical condition of each male before and after the breeding season. Physiological costs are higher during the dry season, because elephants must travel farther to water. Further, the cost of fighting is higher for lower-ranking males, because they are more likely to meet males of equal or higher rank than are higher-ranking males. Moreover, since reproductive success rises rapidly later in life, small young males have more to lose in reproductive success if they are injured or killed in a fight. Lastly, the physiological costs prevent males from being in musth continuously, which leads to three possible strategies for any higher- or lower-ranking male:
Table 12.
Costs, benefits, and payoffs for high- and lower-ranking males.
Adapted from Poole [1989], Tables III–IV.

<table>
<thead>
<tr>
<th></th>
<th>Benefits</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Wet</td>
<td>Dry</td>
<td>Full Yr</td>
</tr>
<tr>
<td>All males</td>
<td>30</td>
<td>15</td>
<td>45</td>
</tr>
<tr>
<td>Condition Costs</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All males</td>
<td>10</td>
<td>15</td>
<td>25</td>
</tr>
<tr>
<td>Fighting Costs</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Higher-ranking males</td>
<td>5</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td>Lower-ranking males</td>
<td>10</td>
<td>10</td>
<td>20</td>
</tr>
</tbody>
</table>

1. Come into musth each year but only during the wet season (W).
2. Come into musth each year but only during the dry season (D).
3. Stay in musth for a full year, but only come into musth every other year (F).

Poole was therefore able to assign qualitative scores to both fighting and condition costs for each male for each of these strategies (see Table 12).

A game theory model of this general situation has six different types of players, whose strategies consist of all possible dominance (H or L) and musth season (W, D, or F) combinations. For example, HW represents the strategy of a higher-ranking male coming into musth only in the wet season while LF represents the strategy of a lower-ranking male coming into musth for a full year but only in alternate years.

6.1 The Payoff Matrix

We now determine the entries in the payoff matrix for this six strategy game. For the sake of simplicity and clarity, we make the following assumptions.

1. Benefits consist of the total number of females available during the particular period.
2. If two elephants in musth compete, the higher-ranking male always wins; if both are the same rank, each has a 50% chance of winning.
3. Payoffs are calculated for a two-year period to accommodate the F-strategy: in musth for a full-year in alternate years.
4. In a contest between one elephant adopting a wet season musth strategy and the other a dry season musth strategy, no fighting occurs, so no fighting costs are incurred.
5. In a contest between one elephant adopting a wet (dry) season musth strategy and the other a full-year musth strategy, fighting and its costs occur only in one of the wet (dry) seasons during the two year period.

6. In any one year, only half of the F-strategists are actually in musth. Consequently, in a contest between two F-strategists, there is a 50% chance that they will be in phase (both in musth and out of musth in the same years), so fighting will occur in one of the two years. There is also a 50% chance that they will be out of phase (one in musth and one out of musth in the same years), so fighting will not occur.

Table 13.
Payoff matrix for different strategies. Key: high-ranking male (H), low-ranking male (L), in musth wet season (W), in musth dry season (D), in musth full year in alternate years (F).

<table>
<thead>
<tr>
<th></th>
<th>HW</th>
<th>HD</th>
<th>HF</th>
<th>LW</th>
<th>LD</th>
<th>LF</th>
</tr>
</thead>
<tbody>
<tr>
<td>HW</td>
<td>0</td>
<td>40</td>
<td>20</td>
<td>30</td>
<td>40</td>
<td>35</td>
</tr>
<tr>
<td>HD</td>
<td>0</td>
<td>−25</td>
<td>−12.5</td>
<td>0</td>
<td>−10</td>
<td>−5</td>
</tr>
<tr>
<td>HF</td>
<td>0</td>
<td>7.5</td>
<td>3.75</td>
<td>15</td>
<td>15</td>
<td>15</td>
</tr>
<tr>
<td>LW</td>
<td>−40</td>
<td>40</td>
<td>0</td>
<td>−10</td>
<td>40</td>
<td>15</td>
</tr>
<tr>
<td>LD</td>
<td>0</td>
<td>−50</td>
<td>−25</td>
<td>0</td>
<td>−35</td>
<td>−17.5</td>
</tr>
<tr>
<td>LF</td>
<td>−20</td>
<td>−5</td>
<td>−12.5</td>
<td>−5</td>
<td>2.5</td>
<td>−1.25</td>
</tr>
</tbody>
</table>

We won't go through all 36 payoff calculations in Table 13, but here are a few. You should try to check the values in the rest of the table.

- For $E(HW, HW)$, there’s a 50% chance of winning a wet season benefit of 30 minus the condition and fighting costs for the wet season (all times 2 years).
  \[ E(HW, HW) = 2[(0.5)30 − 10 − 5] = 0. \]

- For $E(HW, HD)$, there’s a 100% chance of winning a wet season benefit of 30 minus the condition for the wet season; no fighting cost is incurred (all times 2 years).
  \[ E(HW, HD) = 2(30 − 10) = 40. \]

- For $E(HW, HF)$, from the point of view of HW, half of the time, the HF is in musth (so fighting occurs with each having a 50% chance of victory)—this is equivalent to $E(HW, HW)$. The other half of the time no fight occurs since HF is not in musth: there’s a 100% chance of HW winning—this is equivalent to $E(HW, HD)$.
  \[ E(HW, HF) = (0.5)[E(HW, HW) + E(HW, HD)] = (0.5)(0 + 40) = 20. \]

- For $E(HW, LW)$, there’s a 100% chance of winning a wet season benefit of 30 minus the condition and fighting costs for the wet season (all times 2 years).
  \[ E(HW, LW) = 2(30 − 10 − 5) = 30. \]
Notice that $E(HW, LD) = E(HW, HD) = 40$ since no fighting occurs. $E(HW, LF)$ is the average of $E(HW, LW)$ and $E(HW, LD)$, so $E(HW, LF) = 35$. Payoffs for HD are similarly calculated.

- Full-year alternate-year payoffs are more complicated to calculate. For $E(HF, HW)$, from the point of view of HF in its musth year, fighting occurs in the wet season with a 50% chance of victory; no fighting occurs in the dry season (HF receiving the dry season benefit). HF incurs full-year condition costs, but only wet season fighting costs. In the non-musth year, no fighting occurs; there are no benefits and no costs.

$$E(HF, HW) = (0.5)30 + 15 - 25 - 5 = 0.$$  

Similarly,

$$E(HF, HD) = 30 + (0.5)15 - 25 - 5 = 7.5.$$  

- For $E(HF, HF)$, in its musth year, half the HFs encountered are also in musth, fighting occurs each with an equal chance of victory; the other HFs encountered are not in musth, no fighting occurs and the benefits accrue to the first HF. There are condition costs for the entire year. In its non-musth year, there are no benefits or costs.

$$E(HF, HF) = (0.5)[(0.5)45 - 10] + (0.5)45 - 25 = 3.75.$$  

- For $E(HF, LW)$, in its musth year, fighting occurs in the wet season with a 100% chance of victory, no fighting occurs in the dry season (HF receiving the dry season benefit). HF incurs full-year condition costs, but only wet season fighting costs. In the non-musth year, no fighting occurs; there are no benefits and no costs.


- $E(HF, LF)$ is similar to $E(HF, HF)$, except that when fighting occurs, HF is always the winner.

$$E(HF, LF) = (0.5)[45 - 10] + (0.5)45 - 25 = 45 - 5 - 25 = 15.$$  

- For $E(LW, HW)$, there’s no chance of winning a wet season benefit while incurring the condition and fighting costs for the wet season (all times 2 years).

$$E(LW, HW) = 2[(0.0)30 - 10 - 10] = -40.$$  

- For $E(LW, LW)$, there’s a 50% chance of winning a wet season benefit with condition and fighting costs for the wet season (all times 2 years).

$$E(LW, LW) = 2[(0.5)30 - 10 - 10] = -10.$$  

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• For $E(LW, LF)$, from the point of view of LW, half of the time LF is in musth (so fighting occurs with each having a 50% chance of victory)—this is equivalent to $E(LW, LW)$, the other half of the time no fighting occurs, since LF is not in musth there’s a 100% chance of winning—this is equivalent to $E(LW, LD)$.

\[
E(LW, LF) = (0.5)[E(LW, LW) + E(LW, LD)] = (0.5)(-10 + 40) = 15.
\]

• For $E(LD, HW)$, there’s no fighting cost and the dry season benefit accrues to LD.

\[
E(LD, HW) = 2(15 - 15) = 0.
\]

• For $E(LD, HF)$, when HF is in musth there’s fighting and no victory for LD, when HF is not in musth there’s no fighting cost and the dry season benefit accrues to LD.

\[
E(LD, HF) = 2(0.5)[(-15 - 10) + (15 - 15)] = -25.
\]

• For $E(LF, HF)$, in the year when LF is in musth, half the HFs encountered are in musth, there’s fighting and no victory for LF, the other half of the time there’s no fighting cost and the full season benefit accrues to LF. When LF is not in musth, there are no benefits or costs.

\[
E(LF, HF) = (0.5)(-25 - 20) + (0.5)(45 - 25) = -12.5.
\]

• For $E(LF, LW)$, in its musth year, fighting occurs in the wet season with a 50% chance of victory, no fighting occurs in the dry season (LF receiving the dry season benefit). LF incurs full-year condition costs, but only wet season fighting costs. In the non-musth year, no fighting occurs; there are no benefits and no costs.

\[
E(LF, LW) = (0.5)30 + 15 - 25 - 10 = -5.
\]

• $E(LF, LF)$ is similar to $E(HF, HF)$, except the fighting costs are higher.

\[
E(LF, LF) = (0.5)[(0.5)45 - 20] + (0.5)45 - 25 = -1.25.
\]

6.2 Strategies for High-ranking and for Low-ranking Males

From Table 13, we see that for high-ranking males, HW is a pure ESS, because for any pure strategy $X$ we have $E(HW, HW) \geq E(X, HW)$, and whenever $E(HW, HW) = E(X, HW)$, then $E(HW, X) \geq E(X, X)$. Thus, high-ranking males should come into musth only during the wet season.

But if all high-ranking males come into musth in the wet season, then this means that there will be no females available to low-ranking males during the
Table 14.
Costs, benefits, and payoffs for lower-ranking males under the assumption that all higher-ranking males come into musth in the wet season. Adapted from Poole [1989], Tables III–IV.

<table>
<thead>
<tr>
<th></th>
<th>Wet</th>
<th>Dry</th>
<th>Full Yr</th>
</tr>
</thead>
<tbody>
<tr>
<td>Benefits</td>
<td>0</td>
<td>15</td>
<td>15</td>
</tr>
<tr>
<td>Condition Costs</td>
<td>10</td>
<td>15</td>
<td>25</td>
</tr>
<tr>
<td>Fighting Costs</td>
<td>10</td>
<td>10</td>
<td>20</td>
</tr>
</tbody>
</table>

Wet season but there will be 15 available during the dry season and, consequently, only 15 available over the full year. That is, Table 13 is now modified as follows.

The costs and benefits in Table 14 may be used to construct a revised payoff matrix for lower-ranked elephants. This has been done in in Table 15. For example, for $E(LF, LW)$, in its musth year, fighting occurs in the wet season with a 50% chance of victory, no fighting occurs in the dry season (LF receiving the dry season benefit). LF incurs full-year condition costs, but only wet season fighting costs. In the non-musth year, no fighting occurs; there are no benefits and no costs.

$$E(LF, LW) = (0.5)0 + 15 - 25 - 10 = -20.$$  

The other entries are calculated similarly.

Table 15.
Two-year payoff matrix for different strategies under the assumption that all high-ranking males come into musth in the wet season.

<table>
<thead>
<tr>
<th></th>
<th>HW</th>
<th>LW</th>
<th>LD</th>
<th>LF</th>
</tr>
</thead>
<tbody>
<tr>
<td>LW</td>
<td>-40</td>
<td>-40</td>
<td>-20</td>
<td>-30</td>
</tr>
<tr>
<td>LD</td>
<td>0</td>
<td>0</td>
<td>-35</td>
<td>-17.5</td>
</tr>
<tr>
<td>LF</td>
<td>-20</td>
<td>-20</td>
<td>-27.5</td>
<td>-23.75</td>
</tr>
</tbody>
</table>

In Garrison Keillor’s fictional town of Lake Wobegon, “All the children are above average” [Keillor 1974]. The same is not true for male Amboseli elephants: Some are higher ranked and some are lower ranked. Given that the optimal strategy for the higher-ranking males is to come into musth annually only in the wet season, what is the best strategy for the lower-ranking males? We show that LD is their optimal response under some mild assumptions.

Depending on how you think about it, this might seem to be the “obvious” strategy or it might seem contradictory. It might be obvious, because lower-ranked males cannot win contests with higher-ranked males. Since the higher-ranked males are in musth only in the wet season, the lower-ranked males should avoid being in musth during this period. Therefore, they should not adopt LW, or even LF, since the latter strategy has a wet-season component.
in alternate years. This leaves LD as the only remaining strategy. But if we look back at Table 15, we see that LD is actually the worst or most costly response to itself. This means that an entire population of LD strategists could be invaded by either LF strategists or LW strategists. The problem here is that the population includes some higher-ranked males and both the LF and LW strategies are very costly in contests with HW elephants, while LD is not. Consequently, we should expect the response of the lower-ranked elephants to depend on the number of higher-ranked males in the population.

More precisely, let \( h \) denote the proportion of the male population consisting of the higher-ranked males. We regard \( h \) as some fixed but unknown constant and assume, based on earlier calculations, that these males all adopt strategy HW. Let

\[
T = pLW + qLD + rLF
\]  

(15)

denote a general strategy adopted by the lower-ranking males, where \( p, q, \) and \( r \) may vary as long as each is nonnegative and \( h + p + q + r = 1 \). In particular, \( p + q + r = 1 - h \).

Recall from Definition 1 that if for every strategy \( T \neq S \), \( E(S, S) > E(T, S) \), then \( S \) is an ESS. To determine the optimal strategy for the lower-ranking males, we extend this idea as follows. Given that the high-ranking males use strategy HW, we seek a strategy \( S \) for the low-ranking males so that for any strategy \( T \) as in (15) with \( T \neq S \), we have

\[
E(S, hHW + S) > E(T, hHW + S),
\]  

(16)

where \( S = p'LW + q'LD + r'LF \) with \( p', q', \) and \( r' \) nonnegative and \( h + p' + q' + r' = 1 \). In other words, \( S \) is the best strategy for lower-ranked elephants to adopt in a world where all the higher-ranked elephants play HW.

We show that the strategy \( S = (1 - h)LD \) satisfies (16). That is, lower-ranked elephants should adopt a strategy of coming into musth only in the dry season. Some preliminary calculations simplify the process. Using Table 15, we have

\[
E(LW, hHW + (1 - h)LD) = hE(LW, HW) + (1 - h)E(LW, LD) = -40h - 20(1 - h) = -20 - 20h.
\]

Similarly,

\[
E(LD, hHW + (1 - h)LD) = 0 - 35(1 - h) = -35 + 35h
\]

and

\[
E(LF, hHW + (1 - h)LD) = -20h - 27.5(1 - h) = -27.5 + 7.5h.
\]

Next, observe that

\[
E(LD, hHW + (1 - h)LD) > E(LW, hHW + (1 - h)LD)
\]
\[
\iffalse -35 + 35h > -20 - 20h \\
\iffalse 55h > 15 \\
\iffalse h > \frac{3}{11}. \tag{17}
\]

Similarly,
\[
E(LD, hHW + (1 - h)LD) > E(LF, hHW + (1 - h)LD) \\
\iffalse -35 + 35h > -27.5 + 7.5h \\
\iffalse 27.5h > 7.5 \\
\iffalse h > \frac{3}{11}. \tag{18}
\]

Now assume that \( h > 3/11 \approx 0.273 \). Biologically, this assumption means that high-ranking elephants compose somewhat more than a quarter of the adult male Amboseli elephant population. If \( T \neq hHW + (1 - h)LD \) is any strategy for lower-ranked males, \( T = pLW + qLD + rLF \), then, using (17), (18), and the fact that \( p + q + r = 1 - h \), we have
\[
E(T, hHW + (1 - h)LD) = E(pLW + qLD + rLF, hHW + (1 - h)LD) \\
= pE(LW, hHW + (1 - h)LD) \\
+ qE(LD, hHW + (1 - h)LD) \\
+ rE(LF, hHW + (1 - h)LD) \\
< pE(LD, hHW + (1 - h)LD) \\
+ qE(LD, hHW + (1 - h)LD) \\
+ rE(LD, hHW + (1 - h)LD) \\
= (p + q + r)E(LD, hHW + (1 - h)LD) \\
= (1 - h)E(LD, hHW + (1 - h)LD) \\
= E((1 - h)LD, hHW + (1 - h)LD). \tag{19}
\]

Thus, we have shown that \( S = (1 - h)LD \) satisfies (16) and is an uninvadeable strategy if \( h > \frac{3}{11} \).

Using the payoffs in Table 13 and Table 15, our model predicts that high-ranking males should come into musth only during the wet season and that lower-ranking males should come into musth only during the dry season. Are these predictions supported for wild Amboseli elephant populations? This is more or less what Poole observed. The high-ranking males came into musth primarily in the wet season and the lower-ranking males (Poole’s medium category), came into musth primarily in the dry season. Good! The model seems to describe observed behavior. As Poole [1989] states,

Since fights frequently lead to injury or death, thereby reducing future reproductive potential, elephants should clearly signal, by not being in musth, that they will not fight when the benefits derived from winning
are relatively less than they could achieve either at a different time of year or at a later stage of life. Since the number and fighting ability of males in musth changes frequently, males must continuously reassess their role in each asymmetry.

Exercises

24. Suppose that through hunting, all higher-ranked (larger, older) males were removed from the population. Or alternatively, suppose a population of lower-ranked males is relocated to some area (along with females) to reintroduce the species. In either case, there would be only lower-ranked males.

a) Why are the payoffs for the various strategies in the lower right corner of Table 13 and not Table 15?

b) Is any pure strategy an ESS?

c) Is there a mixed strategy ESS?

25. Poole suggests that a more realistic assumption is that when males are in musth, a confrontation between a higher- and lower-ranked male is won 93% of the time by the higher-ranked male rather than 100%. Redo the analysis in this section with that assumption.

7. Answers to the Exercises

1. a) \( E(B, A) = -3 \).

b) Both strategies are pure ESSs! \( E(A, A) = 0 > -3 = E(B, A) \) and \( E(B, B) = 4 > 2 = E(A, B) \).

2. 

<table>
<thead>
<tr>
<th>Player 1</th>
<th>Player 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Chicken</td>
</tr>
<tr>
<td>Chicken</td>
<td>(-x)</td>
</tr>
<tr>
<td>Not Chicken</td>
<td>(y - x)</td>
</tr>
</tbody>
</table>

3. a)

<table>
<thead>
<tr>
<th>Player 1</th>
<th>Player 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Chicken</td>
</tr>
<tr>
<td>Chicken</td>
<td>(-10)</td>
</tr>
<tr>
<td>Not Chicken</td>
<td>(190)</td>
</tr>
</tbody>
</table>

b) The mixed ESS has 80% Chickens.
4. a)  

<table>
<thead>
<tr>
<th>Player 1</th>
<th>Player 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chicken</td>
<td></td>
</tr>
<tr>
<td>Not Chicken</td>
<td></td>
</tr>
<tr>
<td>Chicken</td>
<td>0</td>
</tr>
<tr>
<td>Not Chicken</td>
<td>100</td>
</tr>
</tbody>
</table>

b) The mixed ESS has 90% Chickens.

5. A is a pure ESS in the first game because \( E(A, A) = 0 > -3 = E(B, A) \). A is also pure ESS in the second game because \( E(A, A) = E(B, A) \) and \( E(A, B) = 3 > -1 = E(B, B) \).

6. Each player would have to put $333.33 into the pot.

7. a) The proportion of Chickens is \( (z - y)/z \).
   b) The proportion of Chickens increases as \( z \) does.
   c) The proportion of Chickens decreases as \( y \) increases.
   d) The proportion of Chickens is independent of the cost to prepare the car.

8. a) Yes, and \( h = \frac{2}{3} \).
   b) \( h = \frac{5}{6} \).
   c) \( h \) increases as \( v \) does because it is worth fighting for a more valuable resource given that the cost of injury remains the same.

9. a) \( h = \frac{1}{2} \).
   b) \( h = \frac{7}{17} \).
   c) \( h \) decreases as \( i \) increases because it becomes more costly to fight given that the value of the resource remains the same.

10. a) \( h = \frac{9}{14} \).
    b) \( h = \frac{11}{16} \).
    c) \( h \) increases as \( t \) does because it becomes more costly to display (to be a Dove) given that the value of the resource and the cost of injury remain the same.

11. \( v = 40 \).

12. a)  

<table>
<thead>
<tr>
<th>Player 1</th>
<th>Player 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawk</td>
<td></td>
</tr>
<tr>
<td>Dove</td>
<td></td>
</tr>
<tr>
<td>Hawk</td>
<td>-10</td>
</tr>
<tr>
<td>Dove</td>
<td>0</td>
</tr>
</tbody>
</table>
b) Because

\[ E(D, H) = 0 > -10 = E(H, H) \quad \text{and} \quad E(H, D) = 100 > E(D, D) = 30. \]

c) \( h = 0.875. \)

d) \( v = 120. \)

13. a) 

<table>
<thead>
<tr>
<th>Player 1</th>
<th>Player 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Hawk</td>
</tr>
<tr>
<td>Hawk</td>
<td>-50</td>
</tr>
<tr>
<td>Dove</td>
<td>0</td>
</tr>
</tbody>
</table>

b) \( h = 0.583. \)

c) \( h \) is the same as in the original game.

14. a) 

<table>
<thead>
<tr>
<th></th>
<th>Hawk</th>
<th>Dove</th>
<th>Bourgeois</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawk</td>
<td>-25</td>
<td>50</td>
<td>12.5</td>
</tr>
<tr>
<td>Dove</td>
<td>0</td>
<td>15</td>
<td>7.5</td>
</tr>
<tr>
<td>Bourgeois</td>
<td>-12.5</td>
<td>32.5</td>
<td>25</td>
</tr>
</tbody>
</table>

b) Bourgeois is an ESS by the diagonal rule.

15. a) \( v = -20. \)

b) This does not make biological sense, since the resource should have a positive value.

c) \( i = 120. \)

d) Yes, cost of 120 units of fitness makes sense.

16. a) 

<table>
<thead>
<tr>
<th></th>
<th>Hawk</th>
<th>Dove</th>
<th>Bourgeois</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawk</td>
<td>-25</td>
<td>50</td>
<td>12.5</td>
</tr>
<tr>
<td>Dove</td>
<td>0</td>
<td>25</td>
<td>12.5</td>
</tr>
<tr>
<td>Bourgeois</td>
<td>-12.5</td>
<td>37.5</td>
<td>25</td>
</tr>
</tbody>
</table>

b) Bourgeois is still a pure ESS by the diagonal rule.

17. a) We no longer have \( v < i. \)

b) There is no longer a pure ESS, because even though the first part of Definition 1 is satisfied by both Hawk and Bourgeois, the second part is not.
18. a) If $v > i$, then $\frac{v}{2} - \frac{i}{2} = \frac{v-i}{2} > 0$. So $E(H, H) = \frac{v-i}{2} > \frac{v-i}{4} = E(H, B)$. Further, $E(H, H) = \frac{v-i}{2} > 0 = E(H, D)$. So by the diagonal rule, Hawk is a pure ESS.

b) Yes, by a).

19. Since Bully starts out Hawk-like and Retaliator starts out Dove-like, the Bully judges the Retaliator to be a Dove and so continues its Hawk-like behavior. The Retaliator does just that—retaliates—and responds with Hawk-like behavior. So Bully-Retaliator contests end up with Hawk-Hawk payoffs.

<table>
<thead>
<tr>
<th>Player 1</th>
<th>Player 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bully</td>
<td>Retaliator</td>
</tr>
<tr>
<td>Bully</td>
<td>$\frac{1}{2}v - t$</td>
</tr>
<tr>
<td>Retaliator</td>
<td>$\frac{1}{2}v - \frac{1}{2}i$</td>
</tr>
</tbody>
</table>

Both Bully and Retaliator are ESSs.

20. | Player 1 | Player 2 |
<table>
<thead>
<tr>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Bully</td>
<td>Bourgeois</td>
</tr>
<tr>
<td>Bully</td>
<td>$\frac{1}{2}v - t$</td>
</tr>
<tr>
<td>Bourgeois</td>
<td>$\frac{1}{2}v$</td>
</tr>
</tbody>
</table>

Bourgeois is a pure ESS.

21. | Player 1 | Player 2 |
<table>
<thead>
<tr>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Retaliator</td>
<td>Bourgeois</td>
</tr>
<tr>
<td>Retaliator</td>
<td>$\frac{1}{2}v - t$</td>
</tr>
<tr>
<td>Bourgeois</td>
<td>$\frac{1}{2}v - \frac{1}{4}i - \frac{1}{2}t$</td>
</tr>
</tbody>
</table>

Bourgeois is a pure ESS. Retaliator is also a pure ESS, because $i > 2t$ implies $\frac{1}{4}i + \frac{1}{2}t > t$.

22. | Dove | Bully | Retaliator |
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Dove</td>
<td>$\frac{1}{2}v - t$</td>
<td>0</td>
</tr>
<tr>
<td>Bully</td>
<td>$v$</td>
<td>$\frac{1}{2}v - t$</td>
</tr>
<tr>
<td>Retaliator</td>
<td>$\frac{1}{2}v - t$</td>
<td>$\frac{1}{2}v - \frac{1}{2}i$</td>
</tr>
</tbody>
</table>

Only Bully is an ESS. Retaliator does not satisfy the second part of the definition of an ESS.
23. a) No strategy is a pure ESS.

b) Hint: Show that $E(R, S) = \frac{1}{2}v - \frac{1}{2}i < E(S, S)$ and that $E(D, S) = 0 < E(S, S)$. Let $T = qH + rD + xB + (1 - q - r - x)R$ and argue as in (14).

24. a) The payoffs in Table 15 assume that there are no females available to low-ranking males during the wet season because of the presence of high-ranking males in musth at this time. If no high-ranking males are present at all, then the assumptions in Table 13 are valid viz., females are available to low-ranking males during the wet season.

b) No.

c) Assume that $S = p_1 LW + p_2 LD + p_3 LF$ is a mixed ESS. Using Theorem 2, then

$$E(LW, S) = E(LD, S) \implies -10p_1 + 40p_2 + 15p_3 = -35p_2 - 17.5p_3$$

$$\implies -10p_1 + 75p_2 + 32.5p_3 = 0.$$

Using this result and the fact that $p_1 + p_2 + p_3 = 1$, we have a system of two linear equations whose solutions are

$$p_2 = p_1 - \frac{13}{17}, \quad p_3 = -2p_1 + \frac{30}{17},$$

where $13/17 \leq p_1 \leq 15/17$ since each $p_i \geq 0$. A particular solution to this system is $T = \frac{15}{17}LW + \frac{2}{17}LD$. Let $S = p_1 LW + p_2 LD + p_3 LF$ be any other solution. Check that

$$E(S, S) = E(T, S) = E(S, T) = E(T, T) = -\frac{70}{17}.$$

Now by Definition 1 neither S nor T is an ESS. Consequently, there are no mixed ESSs.

25. The new payoff matrix, which is the analog to Table 13, is

<table>
<thead>
<tr>
<th></th>
<th>Hawk</th>
<th>Dove</th>
<th>Bully</th>
<th>Retaliator</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawk</td>
<td>$\frac{1}{2}v - \frac{1}{2}i$</td>
<td>$v$</td>
<td>$v$</td>
<td>$\frac{1}{2}v - \frac{1}{2}i$</td>
</tr>
<tr>
<td>Dove</td>
<td>0</td>
<td>$\frac{1}{2}v - t$</td>
<td>0</td>
<td>$\frac{1}{2}v - t$</td>
</tr>
<tr>
<td>Bully</td>
<td>0</td>
<td>$v$</td>
<td>$\frac{1}{2}v - t$</td>
<td>$\frac{1}{2}v - \frac{1}{2}i$</td>
</tr>
<tr>
<td>Retaliator</td>
<td>$\frac{1}{2}v - \frac{1}{2}i$</td>
<td>$\frac{1}{2}v - t$</td>
<td>$\frac{1}{2}v - \frac{1}{2}i$</td>
<td>$\frac{1}{2}v - t$</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>HW</th>
<th>HD</th>
<th>HF</th>
<th>LW</th>
<th>LD</th>
<th>LF</th>
</tr>
</thead>
<tbody>
<tr>
<td>HW</td>
<td>0</td>
<td>40</td>
<td>20</td>
<td>25.8</td>
<td>40</td>
<td>32.9</td>
</tr>
<tr>
<td>HD</td>
<td>0</td>
<td>-25</td>
<td>-12.5</td>
<td>0</td>
<td>-12.1</td>
<td>-6.05</td>
</tr>
<tr>
<td>HF</td>
<td>0</td>
<td>7.5</td>
<td>3.75</td>
<td>12.9</td>
<td>13.95</td>
<td>13.425</td>
</tr>
<tr>
<td>LW</td>
<td>-35.8</td>
<td>40</td>
<td>2.1</td>
<td>-10</td>
<td>40</td>
<td>15</td>
</tr>
<tr>
<td>LD</td>
<td>0</td>
<td>-47.9</td>
<td>-23.95</td>
<td>0</td>
<td>-35</td>
<td>-17.5</td>
</tr>
<tr>
<td>LF</td>
<td>-17.9</td>
<td>-3.95</td>
<td>-10.925</td>
<td>-5</td>
<td>2.5</td>
<td>-1.25</td>
</tr>
</tbody>
</table>
HW is still a pure ESS. (Why?) So high-ranking males should come into musth only during the wet season. (In fact, this is what Poole observed.) To determine the strategy for lower-ranked males, we use the analog to Table 15:

<table>
<thead>
<tr>
<th></th>
<th>HW</th>
<th>LW</th>
<th>LD</th>
<th>LF</th>
</tr>
</thead>
<tbody>
<tr>
<td>LW</td>
<td>-35.8</td>
<td>-40</td>
<td>-20</td>
<td>-30</td>
</tr>
<tr>
<td>LD</td>
<td>0</td>
<td>0</td>
<td>-35</td>
<td>-17.5</td>
</tr>
<tr>
<td>LF</td>
<td>-17.9</td>
<td>-20</td>
<td>-27.5</td>
<td>-23.75</td>
</tr>
</tbody>
</table>

We argue as before. Let $h$ denote the fixed but unknown proportion of the male population consisting of the higher-ranked males. Let $T = pLW + qLD + rLF$ denote a general strategy adopted by the lower-ranking males, where $p, q,$ and $r$ may vary as long as each is nonnegative and $h+p+q+r = 1$. We show that the strategy $S = (1 - h)LD$ still satisfies (16). Lower-ranked elephants should come into musth only in the dry season. Using the analog above to Table 15, we get

$$E(LW, hHW + (1 - h)LD) = -35.8h - 20(1 - h) = -20 - 15.8h.$$  

Similarly,

$$E(LD, hHW + (1 - h)LD) = -35 + 35h$$

and

$$E(LF, hHW + (1 - h)LD) = -27.5 + 9.6h.$$  

Next,

$$E(LD, hHW + (1 - h)LD) > E(LW, hHW + (1 - h)LD)$$

$$\iff -35 + 35h > -20 - 15.8h$$

$$\iff 50.8h > 15$$

$$\iff h > \frac{15}{50.8} \approx 0.2953. \quad (20)$$

Similarly,

$$E(LD, hHW + (1 - h)LD) > E(LF, hHW + (1 - h)LD)$$

$$\iff -35 + 35h > -27.5 + 9.6h$$

$$\iff h > \frac{7.5}{25.4} \approx 0.2953. \quad (21)$$

Now assume that $h \geq 0.30$, which means that high-ranking elephants compose at least 30% of the adult male Amboseli elephant population. If $T \neq hHW + (1 - h)LD$ is any strategy for lower-ranked males, $T = pLW + qLD + rLF$, then exactly the same argument as in (19), but using (20) and (21), shows that $S = (1 - h)LD$ satisfies (16) and is an uninvadeable strategy.
References


Game Theory Models of Animal Behavior


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This Module was developed by the authors at Hobart and William Smith Colleges for their team-taught interdisciplinary course entitled “Mathematical Models and Biological Systems.”