Game Theory

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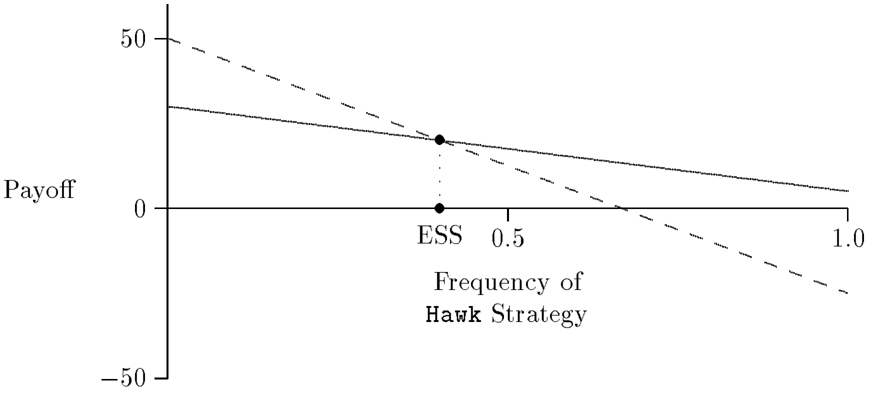

Game theory modeling: `Hawks` (dashed line) and `Doves` (solid line).

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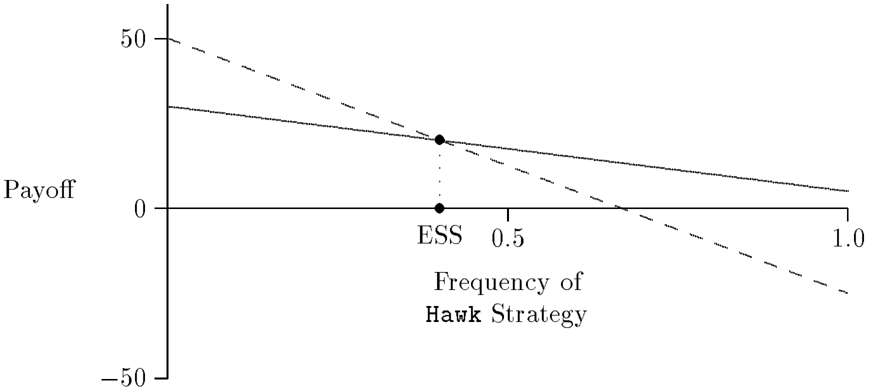

Game theory modeling: **`Hawks`** (dashed line) and **`Doves`** (solid line).

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Contents

Chapter 1

Modeling Behavior: Game and Optimality Theory

Synopsis: *This chapter presents a general overview of the use of models in evolutionary biology. The differences between adaptational and neutral models are briefly discussed. The bulk of the material deals with an overview of two types of adaptationalist models—optimality and game theory (especially optimality theory) and ends with a comparison between them. Later chapters will present a more detailed explanation of game theory.*

1.1 Adaptation versus Neutral Models of Evolution

Adaptational Models: Following the success of Darwin and Wallace's theory of natural selection, most modern biologists believe that most of the aspects of the morphology, behavior and physiology of an organism represent **adaptations**. That is, these aspects of the phenotype exist in a population because in the recent past they allowed their possessors to reproduce more successfully than individuals with alternative traits.

Neutralist Models: However, one must keep in mind that adaptation is often only an assumption. In the 1930s Sewell Wright [1931] developed the main theoretical underpinnings of an alternative means of accounting for evolution based on **genetic drift**, a process which works well in small populations especially when competing traits confer little relative survival advantage over each other (these traits are said to be **adaptively neutral**).

Extending Wright's work, others have shown that the particular traits found in a population can be the result of historical accidents. For instance, Ernst Mayr (certainly an adaptationalist) pointed out that a population's characteristics could have much to do with the genetic makeup of a small number of progenitors or **founders** [Mayr, 1954]. More recently, Stephen Jay Gould has written extensively about the role of history and accident (**contingency**) in determining the present phenotypes of members of a population and for that matter the actual range of organisms that exist at a given time [Gould, 1990].

It is fair to say that much of the value of the work of Gould and others has been to force biologists to acknowledge that all aspects of the phenotype need not represent specific adaptations—that the phenotype is in part accident, not an ideal design, and in many cases a number of competing versions of a phenotype might all do equally well, especially given the nature of environmental change. Thus, one should gain evidence that a particular phenotypic feature represents an adaptation. One should not simply make up circular “just-so” stories that purport to show adaptation by assuming it and then spinning out an explanation based on the (untested) assumption of adaptation.

1.2 Mathematical Models and Rigorous Science

Mathematical models are abstractions that an investigator hopes will, to varying degrees of precision, have predictive power. Models represent the scientist’s best (most informed) guess as to:

- the identity and function of important variables,
- the ways these variables interact with each other.

Mathematical models are useful because of the very fact that they take a scientist’s ideas and produce a more complex abstraction (since a model consists of parts and their interaction). Complex, multi-element models often yield new insights and novel predictions. Mathematical models have the advantage that they yield **quantitative predictions**. Quantitative predictions are often less ambiguous than other types of predictions. Since tests of hypotheses are attempts to show the predictions are incorrect (tests attempt to falsify the model) quantitative predictions are usually easier to test—did the model behave exactly as predicted or not? If not how different was it from prediction? How could the model be modified to make it more consistent with the results and then re-tested?

Inability to falsify the model does not validate it. Inability to falsify means nothing more than that. Not showing that a model is wrong means only **tentative acceptance**, not proof of its truth. A model that has not been falsified is nothing more than a useful working hypothesis. For example, a telling observation was made by Dr. David Norman about restoration mounts of dinosaurs (these mounts are, of course, nothing more than hypotheses) when he wryly observed, “We’ve got it right—for now.” Much of the formalism of testing and describing the scientific process can be traced to the work of the English philosopher Sir Karl Popper [1972]. (For a reference to Ernst Mayr’s extended and fascinating treatment of biological methodology, see [Mayr, 1982]).

Most commonly, models are modified as the result of (i) experimental falsification of one or more of their components or (ii) independent refinements in our understanding of the variables and interactions that already make up a model or that should be added to the model. You have probably noticed that the same process is normally followed throughout the scientific process; the main difference if any is that hypotheses in the form of mathematical models are often more concrete and quantitatively predictive than are other types of hypotheses. However, keep in mind that working with experimentally supported quantitative models is fraught with the same dangers as with less quantitative models—like any hypothesis models should always be viewed with skepticism and only trusted to the extent that they have been strongly tested.

One other note about mathematical models in evolutionary biology: they can spring from either an **adaptationalist** or a **neutralist** view point. Two important types of mathematical adaptation-based models are **optimality** and **game theory models**. The next two sections compare these two approaches. Since both are adaptation models, both will look for behavioral characteristics that maximize an individual’s reproductive success or some related variable.

1.3 Optimality Models

Often a behaviorist is interested in predicting the **best way** (in terms of its fitness consequences) for a particular animal *to behave irrespective of what other individuals are doing.* To illustrate, suppose we are trying to understand how loudly an animal should make an advertisement call (one designed to attract a mate). Thus, we are looking at a general behavior (producing an advertisement call) and we are trying understand the selective forces that determine the best way to perform a particular part of the behavior—in this case its loudness. In this particular example (and in all optimality models) we start from the *assumption that the loudness of other callers has nothing to do with predicting the loudness of a given individual.* So we might imagine a situation where an animal calls without others nearby (as would be the case in many species of crickets).

Optimality theory is adaptational: thus it springs from the theory of natural selection which predicts that an animal should behave so as to **maximize its fitness**. All behaviors can be viewed as having both **fitness benefits** and **fitness costs**. Since optimality models are quantitative, a first step will be to establish the relationships between the variable of interest (the **decision variable**) and the associated costs and benefits. **Benefits** (B) and **costs** (C) are kept strictly separate (just as is practiced in business bookkeeping) and thus two separate relationships (benefit versus the decision variable and cost versus the decision variable) are implicitly part of the process of setting up an optimality model. Notice that since we assume that the behavior (decision variable) has consequences on fitness, the behavior is the independent variable for each of these relationships with benefit or cost being the dependent variables. Now, since the fitness consequence of behavior is

$$\text{Net Change in Fitness} = \text{Benefit} - \text{Cost}, \tag{1.1}$$

the **solution** to an optimality model is to find the point where $B - C$ is maximized.

In principle this formulation is easy to understand. However, in practice, it can be more complex. Let's return to our example of call loudness to illustrate the process of constructing and solving a simple optimality model.

In acoustic communication, producing a loud call is energetically expensive [Prestwich, 1994]. However, louder calls tend to attract more mates, (for example, see [Forrest and Green, 1991]). We want to construct an optimality model in order to try to predict how loudly to call with the "goal" of maximizing lifetime fitness.

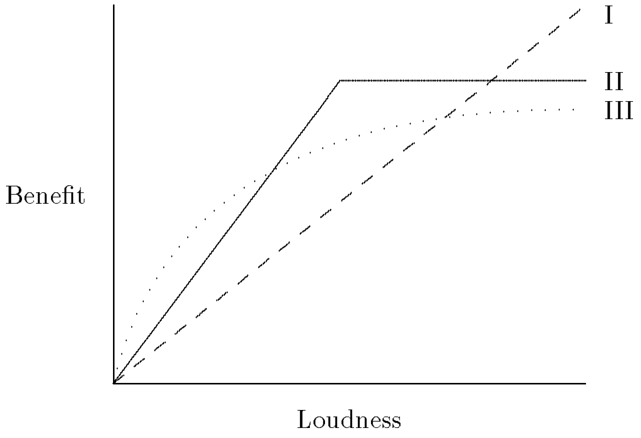
Let's start with the benefits of calling more loudly for a certain period of time. In theory there are a number of possible relationships between loudness and benefit. One would be linear—get louder and proportionately more mates will come (graph I, **Figure 1.1**). A little reflection would suggest that this cannot go on forever—at some point increasing loudness brings in so many mates that the focal animal can't handle all of them and so there is no further increase in fitness with loudness (Graph II, below). Alternately, one might assume that the rate at which matings increase drop off before finally reaching a maximum (graph III, below)—i.e., because of other things the caller has to attend to, as the number of mating opportunities increase, the percentage that are actually consummated becomes less:

There are several things to note about these plots:

- Each represents a distinct hypothesis as to the relationship between benefit and loudness;
- Beyond their general shapes, more specific adjustments could be made. For instance in an environment such as one that is heavily vegetated, sound would be heavily attenuated and the slopes of all of the graphs would probably decrease.
- Notice that the fitness measure used here (number of matings) is rather straightforward and probably easily related to relative reproductive success. That is not always the case as we will see below.

Costs Curves: It is logical to assume that loud calling will have consequences on fitness since it costs considerable amounts of energy and therefore could weaken the caller. This leads directly to

Figure 1.1: Three possible relations between loudness of call and benefit.



expressing cost as energy loss which can be measured directly and relatively easily). But absolute energy terms such as calories or joules may not be the most relevant way to measure the energy portion of the cost of calling. For instance, if the cost of getting louder is viewed relative to energy stores, low cost calls might have little impact on reserves and therefore,up to a point, increasing loudness might have little accompanying increase in cost. However, when the energy demands of making louder calls increases beyond a certain point, they may significantly affect an animals energy reserves and therefore force it to either call for a shorter time period (perhaps thereby lowering its fitness) or eat less (also lowering its fitness). Notice that once again, the exact position and shape of the curve would depend on many factors—for instance size of food reserves and the ease with which they are replaced relative to the incremental costs of louder calls.

Moreover, another important cost of calling is increased chance of falling victim to **predation** (see Mike Ryan's [1985] work on bats preying on calling frogs). What units do you use to measure this cost? The cost could be expressed as the chance of being killed, or injured or something else, or better yet, the number of future matings or future offspring lost as result the chance of injury of death associated with a certain loudness of call.

Let's assume that we believe there are just two important costs to calling—energy and risk. We need to combine them into one cost relationship. Both are already related to the same decision variable (loudness) but these two types of costs are usually expressed in units that are different from each other (for example, joules for energy and chance of death for predation risk).

If we want to combine all costs into one curve we need to put them into a common unit of measurement (a common **currency**). This currency must also be the same one used in the benefits function. This can be very difficult but lets say that we have found a way to express both energy and predation risk as lost future matings. And let's say that our best understanding is that weak calls do not attract predators at all and confer no additional feeding demands. However, eventually a point is reached where predation starts to increase and eventually also that significant increases in feeding must occur. **Figure 1.2** shows a graphical example of our costs hypothesis.

Now let's complete and solve our model. Let's say that we decide that benefits model III is the best one to use. If we now express benefits and costs of call loudness in a currency of matings, then we can superimpose the benefit and costs plot on the same axis and then solve for the loudness that gives the greatest increase in fitness as measured by the greatest number of matings (**Figure 1.3**).

Notice that the model predicts that the best loudness to call is not the loudest (which is what

Figure 1.2: A possible relation between Loudness of call and Cost (in lost matings).

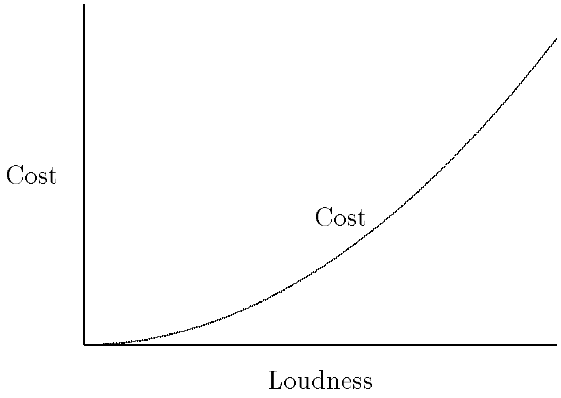
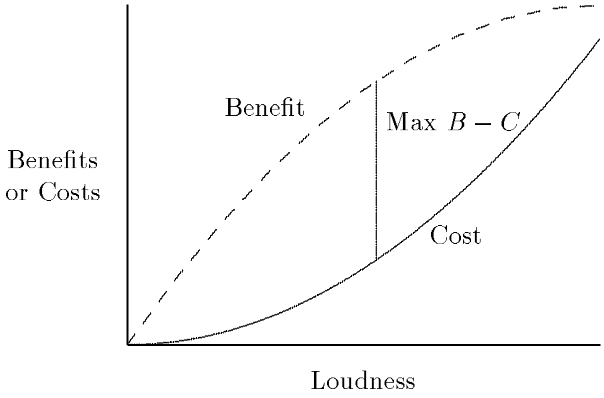


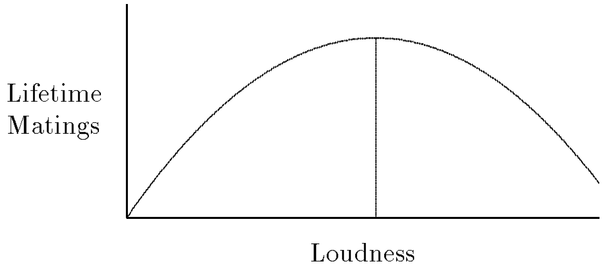
Figure 1.3: Graph of the differences between Benefits and Costs versus loudness.



you would predict if only benefits of loudness had been considered). Notice also that in this case, the model does not keep costs to an absolute minimum.

We can use the B and C curves (above) to make another graph in **Figure 1.4**, this time of $B - C$ versus loudness to illustrate the optimum another way:

Figure 1.4: Graph of $B - C$ versus loudness.



This type of depiction clearly shows that the greatest lifetime fitness in our hypothetical situation is achieved by calling with some type of intermediate loudness.

Finally, realize that the model is nothing more than an integrated set of hypotheses that together attempt to predict the best loudness to call, irrespective of what others are doing. As we saw above, this prediction will need to be tested (for instance by attempting to determine the lifetime mating curve for animals of different loudness). In practice, this essential step is often very difficult (think how hard it would be to determine the curve given above for some type of animal) and much of the art and hard work of behavioral science lies in these tests of the models.

1.4 A Brief Introduction to Game Theory

OK, we just went through a long introduction to an important topic in behavior, physiology, and ecology: optimality theory. But you thought this chapter was about game theory. It is. The stuff on optimality (above) was important because you need to know something about optimality theory to understand game theory and especially to understand which technique to use when trying to understand animal behavior.

So, what is game theory? In optimality theory it is assumed that we can predict the best behavior for a particular (focal) animal irrespective of what others are doing. However, the frequency with which others are performing a particular behavior is often highly relevant to the fitness consequences of acting a certain way. Thus, the crucial aspect of game theory is that *selection among alternative behaviors depends to a large degree on what others are doing.* A behavior that works very well when rare in a population (for instance, some type of deception) may not be nearly as advantageous to its actors when it becomes common. Thus explorations of game theory involve studies of a form of **frequency-dependent selection**.

Here's a brief example. Let's return to calling behavior. Let's assume that females are attracted to calling males and travel to them to mate. But let's also assume that arriving females are not infallible in spotting the male that actually was making the call to which they were attracted. Or, females may be intercepted by males as they approach and sometimes the intercepting males were not the ones that attracted the female in the first place.

What's the best thing for a male to do? If no one is calling, it is probably best to *call* and become conspicuous to females interested in mating. However, if there are many callers, it might be best to keep quiet (avoiding energy and predation risk costs) and try to intercept females as they approach the calling male. Such a male is termed a *satellite*.

As a strategy satellite could well be as or more fit than calling, depending on its frequency relative to callers. Thus, even though a satellite might (per day) have fewer opportunities for mating (lower benefit), the fact that his costs are less means that he might have as many if not more lifetime opportunities for mating. However, as should be obvious, his relative success does not simply reduce to costs and benefits as in optimality theory–instead, his fitness depends very much on the frequency of callers (versus satellites) in the population. If few others call, satellite is probably not a good strategy and relatively speaking, calling is an excellent strategy (or taking it to an extreme, if no one is calling, satellite (simple silence) makes very little sense since females are attracted to calling males). On the other hand, as more and more callers are present, satellite works better and at some frequencies might, over a lifetime payoff better than calling. Thus, frequency dependence distinguishes this example from simple optimality.

Note: Don't get the idea that I am arguing here that satellite is generally a more or less fit strategy than the alternative, call. Depending on conditions, at any moment in time all of these are possible. Later we will consider the most interesting outcome of evolutionary games, an evolutionary stable strategy (ESS). We will see that one type of ESS (mixed ESS) predicts that both strategies would coexist at constant relative proportions to each other and at these frequencies the fitness of individuals of each strategy are equal.

Summary

Notice the similarities and differences between optimality and game theory. Both deal with the benefits and costs of a behavior. In situations where optimality theory is applicable, that is all that is needed. However, as in the example above, there are many cases where the fitness associated with a particular behavior depends on what others are doing, that is, fitness is frequency-dependent. Thus, what is best will depend on what everyone else in the population is doing (and therefore on the likelihood of certain types of interactions with certain types of fitness consequences).

You now have a basic idea about the uses of mathematical modeling in studies of behavioral evolution. You should also be familiar with the basics of game and optimality models. You may now continue on to a more detailed introduction to game theory especially in regards to an important concept, the evolutionary stable strategy, or you may continue reading this chapter and learn a bit about the history of game theory.

1.5 A Brief Sketch of the History of Game Theory

Game theory is equally useful in studies of learned and innate behavior. In fact, when originally developed by von Neumann and Morgenstern [1953] during the mid 20th century, it's primary purpose was to understand the most rational way for humans to make decisions between alternative courses of action, in particular as they applied to economics.

However, any technique that will allow us to study the payoffs of a learned behavior can be used equally well to study innate behavioral strategies. John Maynard Smith [1982] points out that the idea of rational interest in economics is simply replaced by the concept of fitness. He traces the use of game theory in biology first to the work of Lewontin [1961] and later Slobodkin and Rapoport [1974]. These workers applied game theory to situations of "species or group survival" (Did you ever play the board game "Extinction"). The present mainstream of game theory began with Hamilton [1967] and then a few years later with Maynard Smith and Price [1972] and then Maynard Smith [1974]. In the intervening years, game theory has been adapted by a number of biologists to examine evolutionary problems—hardly an issue of *Animal Behaviour* passes when one does not see an article using game theory.

Perhaps the best thorough introduction to the use of game theory in biology is by one of the pioneers in applying it to biology—John Maynard Smith [1982]. The interested and mathematically inclined student is urged to read his classic introduction to the field. This unit is based largely on the material in the first few chapters of his book.

Chapter 2

Game Theory and Evolutionary Stable Strategies

Synopsis: *This chapter introduces the central concept of the application of game theory to evolutionary biology—the Evolutionary Stable Strategy. You will learn the basic terminology of and techniques for solving evolutionary games with two strategies. After completion of this chapter, you will move on to solving a classic two strategy game (*`Hawks` *and* `Doves`*) and then to simulations and more complex games.*

2.1 Introduction: Behavioral Strategies and Games

Why call it game theory?

In the previous section, *Modeling Behavior: Game and Optimality Theory*, we learned that competition was an important feature of game theory.[1] Thus, the analogy between human behavior and game theory is of competitors (players) seeking to win something through some sort of competition (contest or the game itself). Note that in game theory, as in human games, the outcome of a contest to a particular player is shaped by both the actions of the focal player and her/his opponent. And both human and evolutionary games can have different structures. For instance, the outcome can be determined as the sum of a series of one-on-one encounters between the players or it can involve a contest where each player is working more or less against everyone else at once. And clearly, in both of these cases, the outcome will depend on the behavior(s) of the players.

Some Definitions and Caveats

OK, so we understand why these are called games, although from the point of view of the animals, they are deadly serious. Let's see how we formally analyze a game—how we make theoretical calculations of relative fitness that are based on benefits, costs and frequencies of various types of outcomes.

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[1] About competition: Obviously, competition is also involved at some level in optimality models. Animals that "discover" the best way to perform a particular behavior in situations where the payoffs are frequency-independent are still competing with others, albeit highly indirectly. Perhaps a good way to think about competition, in the sense it is used in game theory, is that the competition is more direct. It involves something that we might analogize to human contests, although those contests could be the either one-on-one affairs we usually think of as competition or one against everyone else playing the field.

Contests and Games: Let's get a few conventions out of the way. First, we are only going to look at one general model of competition—what Maynard Smith termed **pairwise competition**. In pairwise competition, each **contest** involves two individuals **players** competing with each other at a time. Just as importantly, pairwise models view the fitness consequences of a particular contest as summing over time (as more contests occur). This type of model is quite useful in animal behavior since there are many situations where we can see two individuals interacting over some resource. Furthermore, we can see that the consequences of these interactions seem to sum in determining the fitness of the players.[2]

Strategies: The particular behavior or suite of behaviors that a player uses is termed a **strategy**.[3] Strategies can be behaviors that are on some continuum (e.g., how long to wait or display) or they may represent distinctly different behaviors (e.g., display, fight, or flee). Sometimes the terms pure strategy and mixed strategy are used. (Do not confuse these with the terms Pure ESS and Mixed ESS—it can be easy to do.) A **pure strategy** is a strategy that is not defined in terms of other strategies present in game. Examples of pure strategies that we will consider later are "`Hawk`" and "`Dove`"—they represent very different ways of trying to obtain resources—fighting and displaying. On the other hand, sometimes strategies are mixes of others. An example of a **mixed strategy** is when one individual plays a mix of "`Hawk`" and "`Dove`" with a certain probability. As we will see later, pure and mixed strategies are not necessarily ESSs—just keep all of this in the back of your mind, you'll be reminded about it later on!

One more point about **players** (contestants, whatever) and **strategists**. Players are individuals who use (play) a certain pure or mixed strategy. When we look at a game, one way is to consider the fitness consequences of contests on an individual who plays a certain strategy. However, we will more commonly look at the game from a population viewpoint. The players in a game become the strategies themselves (or the genes that encode these strategies). The game will then consider the overall fitness effects on each strategy after all possible contests are played in proportion to their likelihood. (Trust me, this will make more sense in a moment). Notice that this sort of treatment owes much to population genetics where genes (alleles) are commonly viewed in competition with each other. However, please note that this in no way implies any sort of group selection—allele or strategy competition models can be viewed as some thing and its copies (regardless of whether or not these are genes or learned behaviors) competing with some other thing (and its copies) where the winners make the most additional copies of themselves.

Asexual Models

Finally, to make the games simple, *we assume that reproduction is asexual, or, if learned, the behavior is simply copied by the offspring.* Thus, there are no complications relating to genetic interactions between the alleles producing different strategies, no need to worry about small population effects, etc. Maynard Smith and others have produced many games where sex is a factor. The interested reader is urged to look at Chapter 4 in Maynard Smith [1982] for an introduction to these models. Notice also that assuming asexual reproduction makes it easy to adapt these models to transmission by learning (assuming that no modification occurs in the process).

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[2] A more common type of game is probably playing the field [Maynard Smith, 1982], but we will not consider this model.

[3] Note that in evolutionary studies, the word **strategy** does not imply conscious choice or planning on the part of the actor. We use the term as a shorthand to describe what is happening in terms of our own experience. But we are aware that in most cases the animal is behaving by some sort of instinctual, heritable rules for behavior. Thus, the strategy is probably not planned out in the sense that human strategy is planned.

2.2 Formal Analysis of a Pairwise Game

Part 1: Contests and Payoffs

As stated above, when we talk about strategies in the context of pairwise competition in game theory, we will be interested in the outcomes of many **contests**. A contest occurs when two individuals interact within the context of the game. That is, they compete for some sort of resource using the behavioral strategies under consideration by the game theorist (remember that these games are artificial constructs to allow us to understand what the animals are doing). Contests can occur between individuals that use the same behavioral strategy (e.g., display for a lenght of time t_1 versus display for time t_1) or they may occur between individuals with different strategies (e.g., display for time t_1 versus display for time t_2).

Let's make this a bit more concrete using **Example 1** about satellite behavior. We have two different strategies, **call** and **satellite**.[4] The potential contests are:

- Caller versus Caller,
- Satellite versus Caller,
- Satellite versus Satellite.

What are the evolutionary significances of these contests? Put in the terms of an evolutionary game, we would like to know the fitness (or some stand-in for fitness) consequences on the actors of each type of contest. We usually refer to these fitness consequences as **payoffs**.

In games involving non-continuous behavioral strategies we usually start with the construction of a **payoff matrix**. The matrix in **Table 2.1** lists all the possible contests and their associated payoffs.

Table 2.1: The general payoff matrix for a two strategy game.

	Opponent	
Focal Stragey	Call	Satellite
Call	$E(C, C)$	$E(C, S)$
Satellite	$E(S, C)$	$E(S, S)$

There is a formalism to its construction:

- Typically the left column (labeled *Focal Strategy*) lists the strategies in the game.
- These strategies are also listed as the heads of the center and left columns (both labeled *Opponent*).
- Now notice that the remaining cells, identified by row and column, represent every possible type of contest in this particular game. I'll refer to them collectively as the **contest** or **payoff cells**. If you've learned any basic genetics, this payoff matrix should remind you of a *Punnet square* (since it is the same thing).

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[4] These strategies could be viewed as being either on a continuum of calling or as totally different behaviors, the distinction is largely semantic in this case.

- The row headed by a particular strategy then lists all possible contest types for that strategy.
  - Thus, the in matrix above, the third row shows the two possible contest types that Call strategists would experience.
  - The bottom row does the same for Satellite strategists.
  - Thus, a Caller can compete with another Caller (center cell, labeled $E(C, C)$) or a Caller can compete with a Satellite (rightmost cell, labeled $E(C, S)$). A similar arrangement is used for a Satellite (bottom row).
- The payoffs are listed in each of the contest cells. When not given explicitly, they are often abbreviated. For instance, the abbreviation for the payoff to the strategy Call in a contest with another Caller is $E(C, C)$ where:
  - E stands for **payoff** or expectation, and
  - the first strategy within the parentheses refers to the strategy whose payoff is being calculated and
  - the second strategy in the parentheses refers to the other strategy in the contest.
- Thus, $E(C, C)$ is the payoff to a Call strategist[5] when engaged in a contest with another Call strategist; $E(S, C)$ is the payoff to a Satellite strategist when in a contest with a caller.

Notice that the payoff matrix is a bit more complicated than was the simple list of contests. In the caller versus satellite game, there were three general types of contests but the payoff matrix lists four payoffs. Why is this? The reason is that the payoff matrix lists the consequences to a strategy for each possible type of contest. It thus becomes obvious that the strategy "call" experiences a certain type of payoff whenever two callers compete, $E(C, C)$, and also whenever a caller competes against a satellite, $E(C, S)$. Likewise, the strategy satellite experiences one type of payoff when pitted against call, $E(S, C)$, and another when pitted against another satellite, $E(S, S)$).

Part 2: Calculating Payoffs to a Strategy in a Particular Contest

Now, lets see how to calculate each payoff.[6]

- First we will need a complete description of the strategy—how does it behave in regards to other known strategies?
- Next, we will need to convert this description into payoffs. To do this, we will need to factor in:
  - the value of the resource,
  - chances of winning a resource
  - less any costs involved in winning
  - the costs of losing and finally
  - the chance of a loss.

---

[5] About payoffs to strategies and strategists: One can just as well think about this in terms of payoffs to the strategy (or the strategy's gene)—but no group selection is implied.

[6] More fussy notes about payoffs: Realize that payoffs are given as exact amounts in this game when in fact they are averages; likewise chances of victory are averages—in a real situation some animals would clearly be more competent in competitions than others. But we want to keep this simple.

Thus, all payoff calculations will have the general form:

$$\text{Payoff(to Strategy 1, when versus Strategy 2)} = \text{(Benefit from win)} - \text{(Cost of loss)} \tag{2.1}$$

Since these are contests, procuring a benefit or paying a cost depends on a number of factors. Thus, we must factor in the chance of winning a resource of some value and the chance of paying a cost in losing. So we expand (2.1) to

$$\begin{aligned}\text{Payoff(to Strategy 1, when versus Strategy 2)} &= \text{(chance of win)} \times \text{(resource value)} \\ &\quad + \text{(chance of loss)} \times \text{(cost of loss)} \end{aligned} \tag{2.2}$$

Even (2.2) is probably not sufficient since (2.2) states that winning has no costs. However, in many contests there is a cost paid by the winner. Good examples might be energetic or time costs of displays; these can be seen as lowering the value of winning. Thus, (2.2) might be expanded to:

$$\begin{aligned}\text{Payoff(to 1, when vs. 2)} &= \text{chance of win} \times \text{(resource value} - \text{cost of win)} \\ &\quad + \text{(chance of loss)} \times \text{(cost of loss)} \end{aligned} \tag{2.3}$$

We now have a good generalized equation. Notice that any of the terms in (2.3) can be made to drop out simply by setting them to zero. Thus, in a particular type of contest if the strategy under consideration incurs no cost to winning and there is no chance of losing (the chance of winning becomes 1.0), then the entire equation for payoff reduces to the value of the resource.

Here are few important considerations about calculations of payoffs

- In game simulations it is common to assign benefits and costs using some type of *relative but arbitrary scale of value.* Thus, the benefit of obtaining the resource might be assigned a value of 1.0 and the cost of a typical display might be assigned a value of −0.1. What these assignments really say is that the resource is worth about 10 times the cost of a typical display. *Selection of these relative values is extremely important—as you will demonstrate to yourself when you use the simulations, different values of benefits and costs can result in very different outcomes.*
- As in the optimality example, these arbitrary units must be a **common currency**.
- About signs:
  - Benefits are usually given positive values.
  - Costs may be assigned either positive or negative values depending on the form of the payoff equation.
    - Thus, when costs are given negative values they are added to the benefits (as was shown in the general equation for calculation of payoffs at the start of this section).
    - When positive values are used for costs, they are usually subtracted from benefits.

  Obviously the effect is the same; the only thing that matters is that the game theorist is consistent.
- Finally, since game models are abstractions, it is quite common to ignore certain costs or benefits or sometimes roll them together. For instance, in the games we will run as simulations, you will see that some costs are ignored or are expressed implicitly.

Part 3: Calculation of the Fitness of Each Strategy

Neither the payoffs for a contest, e.g., the value of $E(C, C)$, nor the simple sum of all types of payoffs to a strategy, e.g., the payoff row for the C-strategy: $E(C, C) + E(C, S)$, from the matrix in **Table 2.1** will give the fitness of a strategy. Recall that *in games, fitness also depends on the frequency of other behaviors.*

A moment's reflection will will reveal that the frequency of each type of interaction is a vital part of any fitness calculation—if satellites are very rare then the fitness consequences of interacting with a satellite are relatively small as compared to if they were more common. So, if fitness is denoted by W, then the overall fitness consequences to a particular strategist in a particular type of contest, for example a caller versus caller contest, are given as:

$$\text{Change in } W(\text{Strategy } 1) = E(\text{to Strategy } 1, \text{ versus Strategy } 2) \times \text{frequency}(\text{encounter}) \qquad (2.4)$$

Since our example game only considers two strategies (call and satellite), if we denote the frequency of caller as c and the the frequency of satellite as s, then

$$\text{Frequency of Caller} = c. \qquad (2.5)$$

If there are only two frequencies, they must sum to 1, so

$$\text{Frequency of Satellite} = s = 1 - c. \qquad (2.6)$$

Thus, in this game the fitness consequences to call, $W(C)$, are the sum of the payoffs for each type of interaction times the frequency of that interaction: Fitness of Call Strategy = Fitness Change Due to Interaction with other Callers + Fitness Change Due to Interaction with Satellites, or symbolically as

$$W(C) = E(C, C) \cdot c + E(C, S) \cdot s. \qquad (2.7)$$

More usefully, if we substitute $1 - c$ for s:

$$W(C) = E(C, C) \cdot c + E(C, S) \cdot (1 - c). \qquad (2.8)$$

A similar calculation can be made for the fitness of satellite:

$$W(S) = E(S, C) \cdot c + E(S, S) \cdot (1 - c). \qquad (2.9)$$

You have now learned the basic formalisms to setting up one especially useful type of game theory simulation. In the next section, we will look at one of the most important outcomes in evolutionary game theory—the Evolutionary Stable Strategy (ESS).

Problem

1. Notice that these last three equations (2.7)–(2.9) quantify fitness as some sort of number. One might think that the larger (more positive) the number given by either equation, the more successful the strategy in this evolutionary competition. But is that really correct? Here's your question: Is it correct to talk about the fitness of either strategy in isolation, that is, if only one strategy is present in the population, do the "fitness values" calculated by the equations above have any real meaning?

2.3 Stasis: Evolutionary Stable Strategies

One of the most important consequences of game theory is that it can be used to predict situations where:

- one behavior is more fit than all known alternatives
- or alternately, a specific mix of behaviors where no one behavior is more fit than any other.

In both cases, the result is **evolutionary stasis** with respect to the behaviors being considered; there is no change in relative frequency of strategies over time. These situations are termed **evolutionary stable strategies** or **ESSs**. There are two types of ESS:

1. **Pure ESS**: where one strategy totally out-competes all others. That means that regardless of its frequency, it is always more fit than any known alternative. A strategy that is a pure ESS is *immune to invasion by other known strategies.* Thus, any alternative that appears by mutation or immigration will not be able to increase and will eventually go extinct.
2. **Mixed ESS**: where two strategies permanently coexist. For a given set of payoffs, there will be one set of frequencies where this mix is stable. A mixed ESS can be achieved if individuals either
   - play one strategy all of the time in a population where the two strategies are at the equilibrial frequencies. For example, 60% of the individuals always call and 40% always act as satellites. Or
   - all individuals play a mixed strategy where each of the behaviors in the mix is performed at the equilibrial frequency. For example, all individuals call 60% of the time and act as satellites 40% of the time.

   In either mixed ESS case, *at the ESS, all individuals have the same fitness* regardless of their strategy.[7] At any other frequencies there will be fitness differences. For example, if a new individual enters the population (e.g., a new caller or someone who calls 70% and satellites 30% of the time), the fitness of all individuals with this behavior are lower than the alternative.

   - For the example of an extra caller, all of the callers would have lowered fitness relative to satellite.
   - For the example of the mixed strategy (70% caller: 30% satellite) invader, it will have a lower fitness than every animal that adopts the mixed ESS mixed strategy of 60:40.

As noted above, *at a mixed ESS, the pure strategies exist at the frequencies where their fitnesses are equal.* It is very important to realize that *equal fitnesses do not imply equal frequency in the population!* As we will soon see, the frequencies will depend on the payoff matrix. We will see a number of examples of mixed ESSs later and you will be able to simulate them—but you will seldom find one where the two frequencies are equal.

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[7] About fitness: Remember that all of these discussions only relate to the traits under consideration in the game. Not all the individuals have the same overall fitness but these differences are not correlated with the strategy being used and so at this equilibrium there is no difference in fitness of either of the two strategies and therefore no change in either of their frequencies.

Other Points About ESSs

In two strategy games, there will always be a pure or mixed ESS:

- It should be obvious why some sort of ESS must occur when there are only two strategies: The pure ESS case is self explanatory. The pure ESS strategy will totally dominate the population except for occasional migrants, mutants, or individuals temporarily trying to gain any fitness they can.
- However, if there is no pure ESS why must there be a mixed ESS? Recall that fitness is frequency-dependent. Thus, as long as the two strategies do not have identical payoffs[8] then at some frequencies one will be more fit while at others the other will be more fit. (Again, if one is always more fit, it is a pure ESS). Since one is not always more fit than the other then there must be a point where the two have equal fitnesses. The frequency where that happens is the mixed ESS.
- In games where three or more strategies play, it is possible to have a situation where there is no ESS. We'll discuss this at a more advanced part of this unit.

A Couple of Notes

If the preceding paragraphs confuse you, *courage mes amis*, we'll look at these concepts in more detail below and then you'll have a chance to investigate them with the aid of models.

Note that when we say an ESS (whether mixed or pure) cannot be invaded we mean that it cannot be invaded by any other *known strategy.* ESSs are always defined against other known alternative behavioral strategies. An ESS is always potentially vulnerable to any new strategy that might come along. We will see examples of this when we go from a two to a three strategy game.

Problems

2. What is the meaning of $E(B, A)$?

3. Assume that two alternative strategies make up a mixed ESS at frequencies of 0.8 for strategy A and 0.2 for strategy B. Furthermore, assume that all individuals practice both A and B. Describe each individual's behavior.

4. Explain the differences between a **pure strategy** and a **pure ESS**. Between a **mixed strategy** and a **mixed ESS**.

2.4 Pure ESSs in Two Strategy Games

In two strategy games it is a relatively simple matter to determine if one of the strategies is a pure ESS, provided certain very reasonable assumptions are met. In this section, we will review the procedure for making this determination and the logic behind this procedure.

Recall that a *pure ESS is a strategy that is unbeatable by other known strategies.* This means that:

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[8] I guess it should be mentioned that if both strategies somehow always have exactly the same fitness, then a situation has been produced where change is possible through mutation or migration (or in non-genetic models, learning). Notice that this would not be an ESS since the changes would not cause fitnesses to be unequal and thereby favor a shift back to the previous frequencies.

- a pure ESS is *immune to invasion* by any other known strategy.
- and, a strategy that is a pure ESS is also *capable of invading and displacing* other known strategies.

If we can show that either of the statements above is true, then we have shown that the strategy is a pure ESS (either one is fine, they are essentially equivalent as far as the mathematics of the game is concerned).

We can use the payoff matrix and a simplifying assumption to make the determination. Let's get away from the caller/satellite model and instead define two abstract strategies: A and B. The purpose of this switch is simply to get you more used to manipulating and using the payoff matrix.

As always, the matrix lists the relative payoffs to each strategy for each type of encounter. In this example we will assign a value to each payoff. See **Table 2.2**.

Table 2.2: Assigning payoffs to the A versus B stategies.

	Opponent's Strategy	
Focal Stragey	A	B
A	$E(A, A) = 0$	$E(A, B) = 1$
B	$E(B, A) = -0.5$	$E(B, B) = 0.5$

Let's assume that:

- The population *initially consists entirely of individuals who use strategy A.*
- A *very small number of strategy B invaders* appear. In the simplest case, this could be a single individual invading a large group of A strategists. This invasion could be the result of mutation, learning, or immigration.
- Meetings that lead to *contests between different individuals occur at random.* Thus, there is no tendency for individuals to collect by strategy in certain places and increase certain types of interactions over what would happen by chance encounter.

What types of interactions occur and how frequent are they? *The most common contests will involve A strategists.* Why is this the case? The answer is that nearly everyone is an A strategist and that meetings and conflicts with an alternative strategy are directly related to the frequency of that strategy. Thus:

- A versus A conflicts will be the most common for A strategists and will therefore largely determine the fitness of A strategists. From the point of view of A, these occur at the frequency of A.
- B versus A conflicts are the most common for B strategists and therefore will largely determine the fitness of B strategists. In the most extreme case where there is a single B invader, B versus A will be the only type of encounter that matters with respect to its fitness.

Any B versus A conflict can also be viewed as an A versus B conflict! Put another way, such a conflict involves payoffs to both strategies, $E(B, A)$ to strategy B and $E(A, B)$ to strategy A. Notice however, that *from the point of view of A, interactions with B are extremely rare* as compared to those with A. Thus, *we will assume that we can ignore the fitness contribution of A versus B interactions to the overall fitness of strategy A.* You will have a chance to look at this assumption in more detail later on.

A Note of Warning

Remember that we are attempting to calculate strategy fitnesses. Thus, we are interested in the frequency of certain types of interactions from the point of view of the strategy. Since we are considering pairwise contests, the frequencies of each contest from the point of view of one contestant (strategist) will be equal to the frequency of the opponent in the contest.

Sometimes students who are familiar with basic probability and population biology assume that the frequency of a particular payoff equals a term in a binomial expansion of the strategy frequencies. For example, if a is the frequency of strategy A and b is the frequency of strategy B, then $(a+b)^2$ is expanded to predict that:

- A versus A conflicts would occur at the frequency a^2,
- A versus B conflicts at $2ab$, and
- B versus B conflicts at b^2.

This sort of formulation is *true if one wants to estimate the rate of occurrence of these interactions in the whole population.* But *it is not correct when we are only interested in the frequency of interactions from the point of view of a particular strategy!*

Now, if we consult the payoff matrix, we can see how this invasion turns out. In our example:

- The payoff to strategy A when it is an A versus A contest is 0. (Our convention is that this means that the interaction has no fitness consequences—it neither increases nor decrease reproduction).
- What about strategy B? All (if a single invader) of the contests it faces are B versus A. From the matrix, we see that the payoff to strategy B in contests versus strategy A is -0.5. That is, B loses some fitness as a result of this interaction.
- It should now be rather obvious that B cannot invade A.

From the situation we just considered, we can construct a general rule to determine whether or not a two strategy game contains a pure ESS: If $E(A,A) > E(B,A)$ (the most common encounter for each strategy), then A is **stable** versus B (it is a pure ESS versus B).

You may be wondering what would happen if the fitness consequences of the most common types of interactions are equal, i.e., $E(A,A) = E(B,A)$. Does that mean that neither is stable against the other? Not necessarily. In this one case, there is an additional test that must be performed before concluding whether or not there is a pure ESS.

If there is more than one B invader, there may also some **rare interactions**, with payoff $E(B,B)$. Also, in this particular situation, the payoff $E(A,B)$ starts to matter, even though it is still extremely rare.

Why now but not before? In the previous example, the A versus B interaction was very rare in comparison with the common A versus A contests. Thus, any effects on the overall fitness of A due to interactions with B were so small as to probably not matter. However, in the case we are now considering $E(A,A) = E(B,A)$. Thus, the common A versus A conflict confers no relative advantage or disadvantage. (The same logic applies to the most common contest B experiences, B

versus A). So the remaining interactions will decide whether or not there is a pure ESS. Thus, if $E(A,B) > E(B,B)$, then A must still have an advantage over B and therefore it will be stable!

To review this, consider the following scenario. A population of A strategists is invaded by a small number of B strategists. In the most common types of contests for each strategy the payoffs $E(A,A)$ and $E(B,A)$ are equal. Thus, neither strategy is competitively aided or hindered by these contests. However, in the rare contests, A is doing better than B since $E(A,B) > E(B,B)$ and so A will eventually out-compete B.

Summary of Rules for Finding a Pure ESS in a Two Strategy Game

Assumption: One strategy is very rare compared to the other. In this example, let A be the common strategy. It is immune from invasion by B if

Rule 1 either $E(A,A) > E(B,A)$

Rule 2 or $E(A,A) = E(B,A)$ and $E(A,B) > E(B,B)$.

Another good way to think about **Rule 1** is think of it as the "equilibrium property," a term used by Riechert and Hammerstein [1983] to indicate that the best strategy to face strategy A is also strategy A. The equivalence between this last statement and **Rule 1** should be quite evident since **Rule 1** says that the payoff to A versus A is greater than what B would get against A.

Riechert and Hammerstein refer to **Rule 2** as the "stability property." The reasoning here is that if B does just as well A against as does A itself, then A will only be stable if it does better against B than B does against itself.

You may be uneasy about **Rule 1**. Mathematically you can vaguely imagine cases where $E(A,A)$ is greater than $E(B,A)$ yet A is not stable against B! *These situations require more than one B strategy invader* so that all the payoffs *might* matter. Since more than one invader is not an unreasonable scenario, you become suspicious that game theorists are either intellectually shallow or are trying to sweep things under a rug.

Problems

5. A quick review on notation: What does $E(B,A)$ mean?

6. The following simple problems illustrate the assumptions we made about the frequency of various contests in our population mainly composed of A strategists. Assume that the frequency of strategy A is 0.9999. Calculate:

- **a)** the frequency of strategy B.
- **b)** the frequency of A versus A interactions.
- **c)** the frequency of B versus B interactions.
- **d)** the frequency of A versus B interactions where the payoff is to A, i.e., $E(A,B)$.
- **e)** the frequency of B versus A interactions where the payoff is to B , i.e., $E(B,A)$.
- **f)** Will the proportion of the total number of payoffs to A when versus B be any different than the proportion of the total number of payoffs to B when versus A?

7. Write the expression for determining whether or not strategy B is a pure ESS against A.

8. Using the expression for B versus A that you just wrote and the matrix in **Table 2.2**, explain whether or not B is stable against invasion by A.

9. Assume that $E(A,A) = E(B,A)$. What if $E(B,B) > E(A,B)$? Does that mean that B is now stable against A?

10. If a strategy is not a pure ESS, does that mean that the opposing strategy is a pure ESS?

11. When using Maynard Smith's shortcut method to find a pure ESS, what is the hypothesized situation with respect to the frequencies of each strategy?

12. In a three or more strategy game, will failure to find any pure ESS strategy mean that the remaining strategies form a mixed ESS?

2.5 Mixed ESSs for a Two Strategy Game

What if neither strategy is a pure ESS? *If there are only two strategies, then there must be a mixed ESS.* The reason why a mixed ESS is required in this situation is easy to understand. Imagine a situation where neither A nor B is a pure ESS:

- A population that is composed entirely of members of one strategy, A for example, is invaded by the other. The fact that B can invade A means that at least at low frequencies, B is more fit than A.
- But let's turn this around. Since B is also not a pure ESS, a population of B strategists could be invaded by A. Thus, at low frequencies A is more fit than B!
- What does this mean? It means that as either strategy increases from being rare, its relative fitness must begin to decrease and eventually, by the time it is very common, it must be less than the fitness of the other strategy.
- Thus, there must be some intermediate point where both have the same fitness. The frequencies at this point are the mixed ESS.
- Notice that if either strategy increases above its equilibrium frequency, it becomes relatively less fit. Thus, we have a true equilibrium since the strategy frequency will tend to return to its original value!

So, let's see how to find a mixed ESS mathematically. We will use this solution in the simulation as an aid in visualizing mixed and pure ESSs. Let there be two strategies, A and B at respective frequencies a and b. We have already seen the expressions for calculating the fitness of each strategy. For A:

$$W(A) = E(A,A) \cdot a + E(A,B) \cdot b \tag{2.10}$$

and for B

$$W(B) = E(B,A) \cdot a + E(B,B) \cdot b \tag{2.11}$$

Now, to achieve and equilibrium, the *fitnesses must be equal.* If not, one strategy will be increasing relative to the other. Thus:

$$\begin{aligned} W(A) &= W(B) \\ E(A,A)\cdot a + E(A,B)\cdot b &= E(B,A)\cdot a + E(B,B)\cdot b. \end{aligned} \tag{2.12}$$

Substituting $1-a$ for b and rearranging, we can solve for the frequency of strategy A where its fitness is equal to B, i.e., for the frequency of A at the mixed ESS:

$$\frac{a}{1-a} = \frac{E(B,B)-E(A,B)}{E(A,A)-E(B,A)}. \tag{2.13}$$

We can now use a to find b at the mixed ESS.

This solution can be visualized graphically. If we write both (2.10) and (2.11) in the form $y = mx + b$ where y is fitness and x is the frequency of strategy A, then:

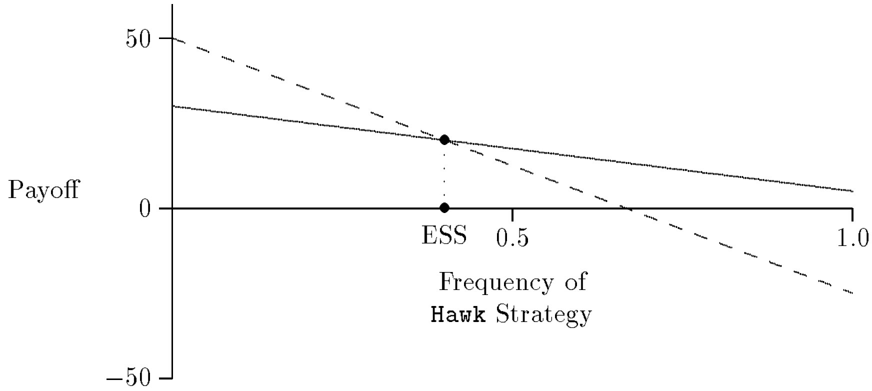
$$W(A) = [E(A,A) - E(A,B)]\cdot a + E(A,B) \tag{2.14}$$

and

$$W(B) = [E(B,A) - E(B,B)]\cdot a + E(B,B). \tag{2.15}$$

If we plots these, we get two straight lines that intersect at some frequency of strategy A that depends on the values in the payoff matrix. **Figure 2.1** shows an example from the `Hawks` and `Doves` game that we will look at next. Please note that fitness is being expressed in "payoff units" and be aware that the slopes, intercepts, etc., will be different with different payoff matrices.

Figure 2.1: Game theory modeling: `Hawks` (dashed line) and `Doves` (solid line).



Notice that *the intersection is a stable evolutionary equilibrium* since the addition of individuals of either strategy lowers the average fitness of all members of that strategy.

- Thus, an increase in `Hawks` results in moving to the right along the `Hawk` (dashed) line to a lower fitness than that of `Dove`; that is, away from equilibrium.
- Likewise, addition of `Doves` (movement to the left along the `Dove` (solid) line since their frequency is $1-h$ lowers their fitness relative to `Hawk`.
- In both cases, the lowered fitness results in reduction of their numbers back to the equilibrium point.

2.6 Can Different Strategies Co-Exist Without an ESS?

At this point you might expect that whenever two strategies persist in a population that they would always form a mixed ESS. This is not true. They are *only a mixed ESS if their fitnesses are equal.* You might ask how both strategies could possibly persist in the same population if their fitnesses were not equal. What follows is a non-exhaustive list of realistic alternatives to a mixed ESS.

Disequilibrium: In a disequilibrium, one strategy is more fit but there has not yet been sufficient time to reach equilibrium. Disequilibrium could be maintained by a number of processes, for instance the arrival of migrants who exhibit the less fit strategy (although presumably it is quite fit in the population they originated from). Genetic drift could also contribute to disequilibrium as could genetic linkages.

Changing Environments: An extension of the idea above. Here, an equilibrium is not reached because the environment changes and favors one and then the other strategy. There are many examples in evolution of this sort of cyclical variation and the disequilibrium that results and it has been a hot area of research in population genetics.

Coping or Making the Best of the Situation: Let's say that a certain strategy is a pure ESS. And let's say that animals have a choice about whether or not to exhibit this strategy. One might think that an animal would always exhibit the pure ESS strategy. But this is not necessarily so. What if the strategy is very costly and not likely to succeed for an individual who is in a certain condition? It may be that the alternative behaviors (to the pure ESS) available to an individual are of demonstrably lower fitness (e.g., they all yield lower chances of mating in the present).

Let's illustrate this by returning to the caller-satellite situation. So far we have treated these two strategies as if they were part of a mixed ESS. In fact, some studies of anurans have supported the notion that the fitnesses of caller and satellite are equal. However, what if they were not equal? If we start with the logical assumption that *call is more fit than satellite*, then we would expect to see satellite disappear. Or would we? We have already considered that calling is costly. What if, on a particular night, a male did not have sufficient energy to call and have a good chance of attracting a mate? As long as there was some chance that satellites gain mates, even if fewer than callers, it would pay a "weak" male to satellite or engage in some other less energetically expensive way to obtain a mate (e.g., searching). Satellite behavior would not disappear but would remain at a low frequency and would tend to be practiced by individuals when their energy reserves were low. When they were in better condition, they could call. But even thought both strategies persist, they are not a mixed ESS.

Another way to look at this sort of coping behavior is as an optimization problem—will engaging in lower fitness behavior at certain time increase my lifetime fitness by giving me some gains now and perhaps greater gains later?

Testing these ideas

In all of these cases, a decision about whether or not the behaviors were an ESS would require data on relative fitness and their persistence over a number of generations. The important thing to realize is that simply finding alternative strategies in a population does not prove that a mixed ESS exists anymore than finding a single strategy proves a pure ESS exists.

OK, you are now familiar with the basics of pairwise games. We will now move onto a series of simple games that will help you to understand how games work, their implications for behavior, and perhaps also help you see how to apply abstract games to the behaviors of real organisms.

Chapter 3

`Hawks and Doves`

Synopsis: *Here you will have a chance to apply what you have learned about games and their solution to a classic two strategy game—*`Hawks` *and* `Doves`*. You will be introduced to to these strategies which have utility in understanding how fighting and display strategies could co-exist in a population. After this introduction, you will be guided through the construction of a payoff matrix which you will use to determine whether or not* `Hawk` *or* `Dove` *are pure ESSs. You will also be introduced to a graphical depiction of evolutionary games. This chapter marks the end of your "basic training" in game theory and is the gateway to using the simulations that will be provided.*

3.1 Introduction

In the last section, we learned the basics of setting up and solving a two strategy game. However, we did not actually construct and solve a game. In this section, we will construct a classic but very simple game known as `Hawks` and `Doves`. These two simplified behavioral strategies employ very different means to obtain resources—fighting in `Hawks` and display in `Dove`.[1] These differences in behavior have marked consequences on the chance of winning and of paying certain types of costs. This leads to very different payoffs.

Use the `Hawk` and `Dove` example in this chapter to solidify your understanding of basic game theory. Your fundamental goal should be to feel thoroughly comfortable with the basic concepts of evolutionary game theory and with solutions to two strategy games. In addition, as you study the material:

- Think hard about species where strategies like `Dove`, `Hawk`, or a mix might occur. Try to move beyond the game to application to real animals.
- One of the most important things you should do is to think about how the relative values of the factors that determine the payoffs ultimately affect the equilibrial point of the `Hawks` and `Doves` game. An important part of your use of the accompanying simulations will be test out your ideas about how setting different benefits and costs will change the equilibrial point of a two strategy game.

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[1] Note that the `Hawk` and `Dove` refer to two different behavioral strategies adopted by members of the same species. We are not pitting two different species against each other.

- Think about the limitations of simple models like **`Hawks`** and **`Doves`**, yet at the same time be sure to think about the insights it has given you.

3.2 Evolutionary Stable Strategies: An Example

As with any game model, our central question is whether or not **`Dove`** and **`Hawk`** can coexist and if so, at what frequency. Here is a description of the two alternative behaviors:

`Hawk`: very aggressive, **always fights** for some resource.

- Fights between **`Hawks`** are brutal affairs with the loser being the one who first sustains injury. The winner takes sole possession of the resource.
- Although **`Hawks`** that lose a contest are injured, the mathematics of the game requires that they not die and in fact are fully mended before their next expected contest.[2]
- For simplicity, we will assume that all **`Hawks`** are equal in fighting ability, that is, each **`Hawk`** has a 50% chance of winning a **`Hawk`**–**`Hawk`** conflict. Another way of saying this is that **`Hawk`** versus **`Hawk`** contests are symmetrical.

`Dove`: **never fights** for a resource—it displays in any conflict and if it is attacked it immediately withdraws before it gets injured.

- Thus, in any conflict situation, **`Dove`** will always lose the resource to a **`Hawk`**, but it never gets hurt (never sustains a decrease in fitness) when confronting a **`Hawk`** and therefore the interactions are neutral with respect to the **`Dove`**'s fitness.[3]
- A corollary to this rule is that **`Doves`** do not display for very long against **`Hawks`**. After starting their displays, they immediately recognize that their opponent is a **`Hawk`** and they withdraw without paying a meaningful display cost.
- On the other hand, if a **`Dove`** meets a **`Dove`** there will be a period of displaying with some cost (time, energy for display) but no injury. We assume that all **`Doves`** are equally good at displaying and and they adapt a strategy of waiting for a random time period (see **Chapter 5**, *Wars of Attrition*) therefore when two **`Doves`** face off, each has a 50% chance of winning.
- Notice that both **`Doves`** will pay essentially the same display cost in any contest. The winner is the individual willing to pay more. However, note that the winner quits displaying essentially at the same time as the loser withdraws (see *Wars of Attrition*).

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[2] Why can't **`Hawks`** die or get permanently knocked out of action? Why must they be miraculously restored to health? The reason is very simple. If this were not the case, then in any population containing more than one **`Hawk`**, **`Hawk`** versus **`Hawk`** contests would cause the frequency of **`Hawk`** to decrease. The more **`Hawks`**, the more **`Hawk`** versus **`Hawk`** contests and the faster freq(**`Hawk`**) will decrease! Notice that the equations we learned earlier for finding the fitness of the strategy all implied a constant frequency of the strategy. Thus, the bad things that happen in **`Hawk`** versus **`Hawk`** contests should be seen as changing (in this case lowering) the general fitness of **`Hawk`** individuals in the population without changing their frequencies.

[3] There are a couple of things to notice here. First, no **`Doves`** get killed. To reiterate the material about freq of **`Hawk`** and injury, notice that if injured **`Hawks`** did drop out, the freq. of **`Dove`** would increase. Also notice the difference in the payoff (according to the descriptions of H and D that you have just read or in the same example payoff matrix that we considered with **`Hawk`**)—negative payoffs tend to mean lowered fitness as a result of the contest but not death and payoffs of 0 (the payoff to **`Dove`** versus **`Hawk`** in this example) mean no effect on fitness—the **`Dove`** goes on as before.

Notice that we have assumed there are **asymmetries** within a strategy—all `Hawks` are equally good at fighting and all `Doves` are equally good at displays. An animal that wins one contest is just as likely to win or to lose the next. Thus, in any contest between members of the same strategy, either contestant has an equal chance of winning—there is no correlation with past success, condition, whatever. This is clearly not a very reasonable assumption, but we're just starting out so let's keep things simple.

There are two other important assumptions.

- Assume that the attacking animal (the one that either starts first to physically attack or to display) has no knowledge of the strategy that its opponent will play.
- Assume that these interactions increase or decrease the animal's fitness from some baseline fitness. In other words, these interactions simply modify an animal's fitness up or down—winning a contest does create fitness. This assumption is associated with our convention that injuries and display costs will be assigned negative scores—losing animals do not have negative fitnesses.[4]

3.3 Preliminary (Qualitative) Exploration

Let's start by making an qualitative analysis of the game. Then we'll use game theory to make a much more quantitative prediction (as was discussed in the introductory material dealing with games). Let's start with the following question: Are either of the two strategies by themselves impervious to invasion? That is, does either represent a pure ESS?

To most people it immediately appears that `Dove` is not a pure ESS. Imagine a population entirely of `Doves`. It is probably a very nice place to live and everyone is doing reasonably well without injuries when it comes to conflicts over resources—the worst thing that happens to you is that you waste time and energy displaying. But that is OK because on the average you win 50% of the encounters and therefore on the average you will come out ahead provided the display costs are not large compared to the resource value.

Now, imagine what happens if a `Hawk` appears by mutation or immigration. The `Hawk` will do extremely well relative to any `Dove`—winning every encounter and, initially at least, suffering no injuries. Thus, its frequency will increase at the expense of `Dove`. Thus, `Dove` *is not a pure ESS.* If `Dove` is not an ESS, what about `Hawk`?

Let's do the analysis again, this time starting with a population made entirely of `Hawks`. This would be a nasty place, an asphalt jungle, that you wouldn't like to live in with lots of injurious fights. Although these fights don't kill you, they tend to lower everyone's fitness. Yet, just like with the `Dove` population, no `Hawk` is doing better than any other and the resources are getting divided equally.

Could a `Dove` possibly invade this rough place? It might not seem so since they always lose fights with `Hawks`. Yet think about it:

- `Doves` *don't get hurt.* The best way to think about this is that they do not pay high costs in fitness for losing a contest. While they never beat a `Hawk` they don't get hurt because they flee the moment they realize they are in a contest with a `Hawk`. The result is that, unlike `Hawk-Hawk` contests, a `Dove`'s fitness is not lowered by a conflict with a `Hawk` (i.e., it is the same

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[4] The important idea here is that the animal must be able to reproduce even if it loses all of the contests it engages in. If not, you might as well count the animal as dead with the same consequences as outlined in the discussion of injuries. Again, the important consequence of the game is contests may alter the fitness of individuals but not kill (or essentially kill) the individual.

as if no contest at all had occurred—remember that we assume a certain baseline of fitness independent of the outcome of contests—contests only increase or decrease this amount).

- `Doves` are winners 50% of the time against other `Doves` and they probably lose little in such contests.

Thus, if a mutant appears in the form of a `Dove` or one wanders in from elsewhere, it will do quite well relative to `Hawk` and increase in frequency. Thus, `Hawk` *is also not a pure ESS.*

Notice that in all of the arguments above, we made implicit assumptions about the relative values of the resource and the costs of injury and display that are consistent with the behavioral descriptions. You probably realize that if we changed some of these assumptions of relative value, the game might turn out differently—perhaps `Hawk` or `Dove` could become an ESS. Moreover, even if we stick to the qualitative values and to our conclusion that there is no pure ESS, the technique we have just used will not allow us to predict the frequencies of `Dove` and `Hawk` at the mixed ESS. As was stated earlier, the best models make quantitative predictions since these are often most easily tested.

Thus, in the next section we will use the rules and techniques we previously learned to quantitatively analyze the `Hawks` and `Doves` game.

3.4 Formal Analysis of the `Hawk-Dove` ESS

The first step of our analysis is to set-up a payoff matrix. Recall that the matrix lists the payoffs to both strategies in all possible contests (see**Table 3.1**).

Table 3.1: The `Hawk` versus `Dove` payoff matrix.

	Opponent	
Focal Stragey	`Hawk`	`Dove`
`Hawk`	$E(H, H)$	$E(H, D)$
`Dove`	$E(D, H)$	$E(D, D)$

We need to make explicit how we arrive at each payoff. Recall that the general form of an equation used to calculate payoffs is

$$\begin{aligned}\text{Payoff(to Strategy 1, when vs. Strategy 2)} &= \text{(chance of win)} \times \text{(resource value)} \\ &\quad + \text{(chance of loss)} \times \text{(cost of loss)}\end{aligned} \tag{3.1}$$

We will use the descriptions of the strategies given previously to write the equations for each payoff. But first, let's assign some benefits and costs (we could do this later, but let's do it now so that we can calculate each payoff as soon as we write its equation).

The rationale for the values in **Table 3.2** is as follows. For "gain resource," it is self-explanatory; for "lose resource," nothing is gained. For "injury to self," the cost of an injury is large (risky) if it is assumed that there are likely to be chances in the future to gain the resource again—injury now tends to preclude gain in the future. This might appear quite different however if there is only one chance—does injury matter (as compared to winning) if you are forced into a contest to have any chance at all to gain a resource? For "cost of display," displays generally have costs although how

Table 3.2: The payoff values for `Hawk` and `Dove`.

Action	Benefit or Cost (arbitraty units)
Gain Resource	+50
Lose Resource	0
Injury to Self	−100
Cost to Display Self	−10

high they are varies—clearly they have variable costs in terms of energy and time and they may also increase risk of being preyed upon. All of these type of measurements, in theory at least, can be translated into fitness terms.

Note: All of these separate payoffs are in units of fitness (whatever they are!). You will see shortly that the values that are assigned to each payoff is crucial to outcome of the game—thus accurate estimates are vital in usefulness of any ESS game in understanding a behavior.

Calculation of the Payoff to `Hawk` when versus `Hawk`

Relevant variables (from (3.1)).

- chance of winning (50%—i.e. the contests are symmetrical)
- resource value (see **Table 3.2**)
- chance of losing (50%)
- costs of losing—in this case, the cost is an injury cost (see **Table 3.2**)
- notice that no costs are paid in winning

Thus:

$$E(H,H) = (0.5 \cdot 50) + 0.5 \cdot (-100) = 25 - 50 = -25. \tag{3.2}$$

Note: The costs of losing are added in our model since we gave the costs a negative sign to emphasize that they lowered the fitness of the loser.

Calculation of the Payoff to `Hawk` when versus `Dove`

- chance of winning 100%—i.e., the contests are asymmetrical
- resource value (see **Table 3.2**)
- no costs to the `Hawk` since (a) they never lose and (b) since the `Dove` immediately retreats once it recognizes the `Hawk`

Thus:

$$E(H,D) = 1.0 \cdot 50 - 0 = +50. \tag{3.3}$$

Calculation of the Payoff to `Dove` when versus `Hawk`

- chance of winning 0%—i.e., the contests are asymmetrical and `Doves` always lose
- no costs to the `Dove` since it immediately retreats once it recognizes the `Hawk`

$$E(D, H) = 0 \cdot 50 + 1.0 \cdot 0 = 0. \tag{3.4}$$

Calculation of the Payoff to `Dove` when versus `Dove`

- chance of winning (50%—`Dove` versus `Dove` contests are symmetrical
- resource value (see **Table 3.2**)
- display cost paid in winning—both animals will display essentially the same amount of time. The one that wins is the one that is willing to display for a longer period of time this particular time (see *Wars of Attrition*).
- chance of losing (50%)
- costs of losing—as with the winner, the loser also pays a display cost and it is the same as what the winner pays (see **Table 3.2**)
- no injury cost—no violence please, we're `Doves` for heaven's sake!

$$E(D, D) = 0.5 \cdot (50 - 10) - 0.5 \cdot (-10) = +15. \tag{3.5}$$

So for this particular version of the `Hawk` versus `Dove` game (defined by these payoffs), the pay-off matrix is:

Table 3.3: A particular `Hawk` versus `Dove` payoff matrix.

	Opponent	
Focal Stragey	`Hawk`	`Dove`
`Hawk`	−25	+50
`Dove`	0	+15

Problems

1. In the list of cost and benefits in **Table 3.2**, it is assumed that injury costs are large compared to the payoff for gaining the resource. Give a situation where this relative weighing might accurately reflect the forces acting on an animal.

2. Does it seem reasonable that `Hawks` pay no cost in winning? Also, does it seem reasonable that the loser only pays an injury cost? Think about what animals do and about simplifications of models.

3. Using the matrix in **Table 3.3**, see if the `Hawk` and `Dove` game above meets the criteria for a pure ESS. Hint: Review the rules for a pure ESS and then arbitrarily define H as A and test to see if H is a pure ESS with payoffs listed above (Do this for both strategies—use H and then D as strategy A. Should you get the same results each time?)

3.5 The Fitness of Each Strategy and Mixed ESSs

If you did the last problem above, you will realize that neither `Hawk` nor `Dove` are pure ESSs given the payoffs calculated from the equations and values for benefits and costs presented above. (When you use the simulation, you will see that certain benefits and costs can be used to make either of the strategies pure ESSs, although these might seem to involve unreasonable assumptions).

It is good to keep in mind the fact that the rules you used to determine that neither strategy was a pure ESS require some reasonable assumptions. If we have no pure ESS, we know that in a two strategy game there will be a mixed ESS which is defined as the frequency of the strategies where both have equal fitness. Recall that the fitness of a strategy is the sum of the payoffs times the frequency of their occurrence

$$W(\text{strategy}) = \sum_{\text{contest}} E(\text{ contest}) \cdot \text{frequency}(\text{contest}). \tag{3.6}$$

Thus, if we assume that

$$\text{frequency}(\texttt{Hawk}) = h, \tag{3.7}$$

then

$$\text{frequency}(\texttt{Dove}) = 1 - h. \tag{3.8}$$

Thus, the fitness of `Hawk`, $W(H)$, is

$$W(H) = h \cdot E(H,H) + (1-h) \cdot E(H,D) \tag{3.9}$$

and the fitness of `Dove`, $W(D)$ is

$$W(D) = h \cdot E(D,H) + (1-h) \cdot E(D,D). \tag{3.10}$$

Notice that *each of the equations for strategy fitness yields a straight line* when solved for a series of frequencies.

Now since *in a mixed ESS both strategies must have the same fitness*, we can determine the equilibrial mix by setting the fitnesses of the two strategies equal to each other, $W(H) = W(D)$. For our game,

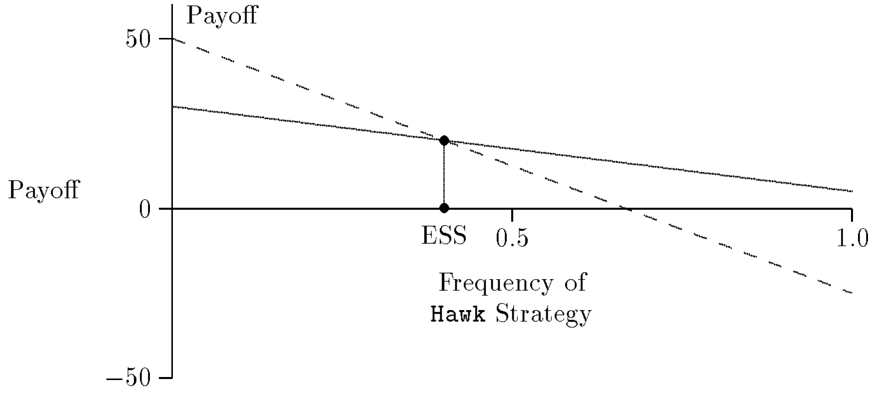
$$h \cdot E(H,H) + (1-h) \cdot E(H,D) = h \cdot E(D,H) + (1-h) \cdot E(D,D) \tag{3.11}$$

If we now solve for the frequency of `Hawk` at this equilibrium, we obtain

$$\frac{h}{1-h} = \frac{E(D,D) - E(H,D)}{E(H,H) - E(D,H)}. \tag{3.12}$$

We can understand the solution more clearly if we graph (3.8) and (3.9), as in **Figure 3.1** where the solid line is for `Dove` and the dashed line is `Hawk`. The intersection of the `Hawk` and `Dove` plots represents the frequency of one strategy (in this case `Hawk`) where the fitnesses of both strategies are equal in terms of payoff units.

Figure 3.1: Game theory modeling: `Hawks` (dashed line) and `Doves` (solid line).



Remarks About the Graphical Results the `Hawk` versus `Dove` Game

Figure 3.1 points up a number of interesting things.

- Note that at the equilibrial point, the addition of individuals of either strategy lowers the relative fitness of all members of that strategy.
  - Thus, an increase in `Hawks` results in moving to the right along the `Hawk` line to a lower fitness than that of `Dove`—away from equilibrium.
  - Likewise, addition of `Doves` (movement to the left along the `Dove` line since their frequency is $1 - h$ lowers their fitness relative to `Hawk`.
  - In both cases, the lowered fitness will eventually result in a reduction of their numbers and a return to the equilibrium frequency.
- Also note that the *addition of any* `Hawk` *overall lowers everyone's absolute fitness*!—both curves have negative slopes.
- And, the graph provides another way to see that neither `Hawk` nor `Dove` are pure ESSs:
  - `Hawk` does very poorly when in high frequency compared to when it is rare. Thus, it is easily invaded by what might seem to be the most improbable of invaders, the pacific `Dove`.
  - On the other hand, `Dove` is not stable since `Hawks` do extremely well when entering the population.
  - Thus, although it is obvious that any `Hawks` would always be "bad for the species," they cannot be kept out once they appear (so much for group selection being a common phenomenon). For this particular set of payoffs, `Dove` is not an ESS any more than `Hawk` is.

At this point you know how to set up and solve a simple game and you have a basic familiarity with the `Hawks` and `Doves` game. So, you are now ready to explore the `Hawks` and `Doves` game in detail using Prestwich's simulation that will allow you to alter payoffs by changing benefits and costs. The simulation will provide you with a visual representation of the solution, using the same techniques you have just learned (except the computer will now do the computational work for you).

And, you'll get to see something new—you'll be able to set the frequencies of the two strategies and then see how a population with a given payoff matrix will evolve over time.

Problem

4. Calculate the mixed ESS frequencies of `Hawk` and `Dove` using the payoff matrix in **Table 3.3**.

Chapter 4

The `Hawks` and `Doves` Simulation

> Synopsis: *This chapter describes how to use the Java simulation of the* `Hawks` *and* `Doves` *game. This game was explained in detail previously; you will not get much out of this simulation unless you already thoroughly understand the* `Hawks` *and* `Doves` *game.*

Computer simulations are useful in that they allow you:

- to explore a large number of situations in a short time thereby providing a means to quickly test your understanding of the system being modeled and
- visualize how the system acts.

However, it cannot be emphasized too strongly that simply playing with the simulation without understanding what it does and without relating the inputs and outputs to some biologically meaningful situation is largely, if not entirely, a fruitless exercise.

4.1 What the Simulation Does

The material below will give you an overview of the simulation. Please take the time to read it so that you have some basic familiarity with what it does and how it works.

When you launch the simulation a panel will appear like that in **Figure 4.1**. At the bottom of the panel are two buttons:

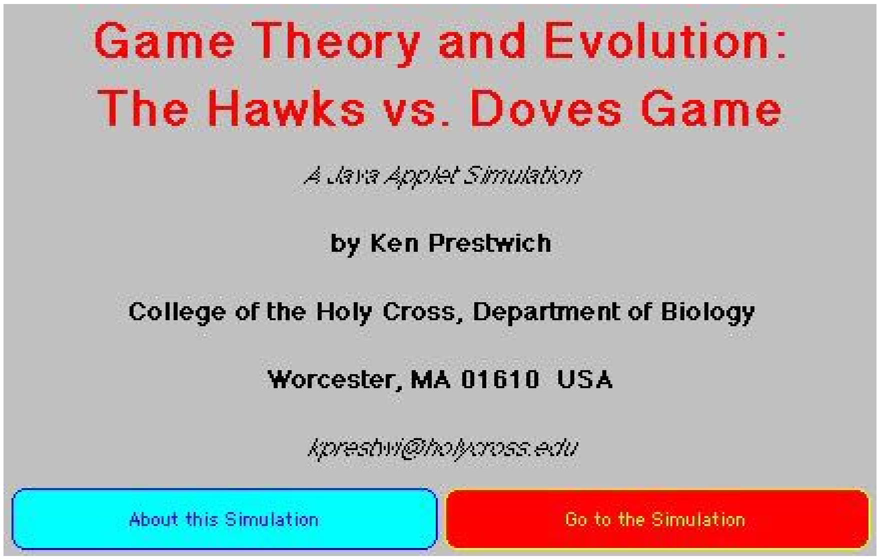
- The blue button will bring up a window that gives you general information about the simulation—copyright, acknowledgments, etc. Close this window using the normal close box after you read it.
- The red button will take you to another screen to set up the game.

Note: If you are using the Applet (web-based) version, this first screen must remain opened the entire time you use the simulation. Closing it will close the simulation.

The **Set-Up Window** (see **Figure 4.2**) will allow you to alter the payoffs by changing the benefits and costs to the `Hawk` and `Dove` strategies. You will not be able to change the ways the payoffs to the strategies are calculated, you can only change the parameters used to make these calculations.

Here's a brief outline of the set-up screen:

Figure 4.1: When you launch the simulation a panel will appear like this one.



Game Theory and Evolution:
The Hawks vs. Doves Game

A Java Applet Simulation

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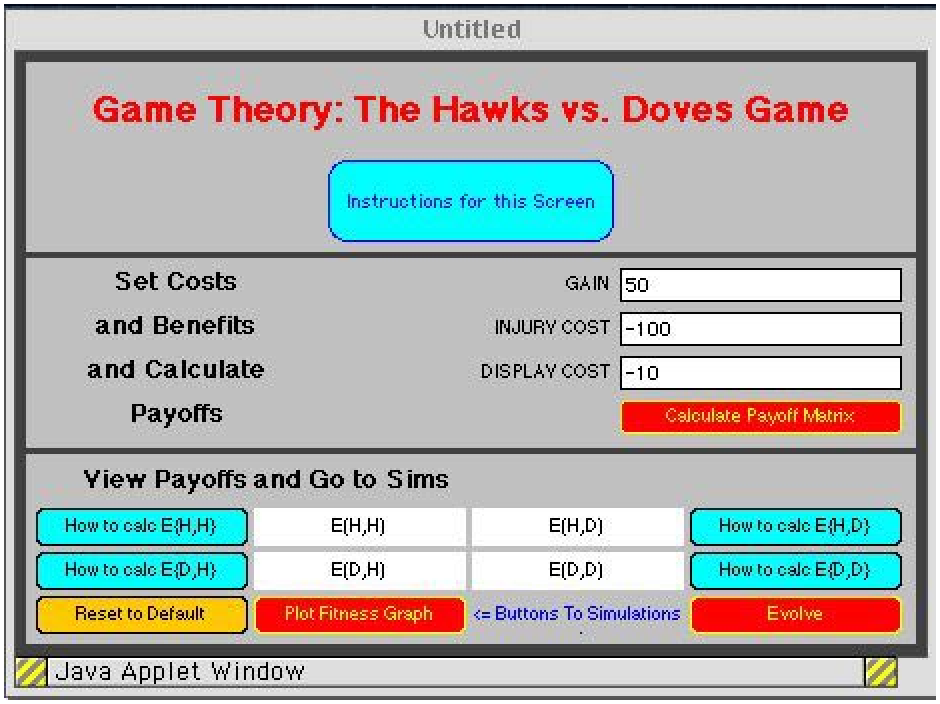
- The top panel gives general information about using the setup screen—it is more detailed that what is presented here (since only an over view is presented here).
- The middle panel has three text fields and a button (see **Figure 4.2**). When you first run the simulation at any session, the text fields will contain default values (shown), which are the same numbers we used when we considered the `Hawks` and `Doves` game. However, *you can change any of these values by simply dragging the mouse across them and then typing in the new value* or you can position the insertion point and use your delete key.

  Note 1: I must emphasize that this is the only way that you will be able to alter the payoffs.

  Note 2: Also, please note that simply typing in a new value will not alter the payoff matrix. You must press the red and yellow button labeled "Calculate Payoff Matrix" to recalculate with the new values. This also applies to using the default values.

- The bottom panel (see **Figure 4.2**) has a number of important features.
  - The first two rows are the **game payoff matrix**.
    - The blue buttons will bring up windows that explain how a given payoff is calculated.
    - Adjacent to each blue button is the associated payoff. When you first open this page, the payoffs will not be given; you need to press the red button ("Calculate Payoff Matrix") in the middle panel to get a display.
  - The last row of the bottom panel has three buttons (see **Figure 4.2**).
    - On the left is a gold "Reset" button—pressing it restores the benefits and costs to their original values.
    - The button labeled "Plot Fitness Graph" makes a plot of the fitness of H and D versus the frequency of H using the current payoff values. **Figure 4.3** shows the plot for the default values (you saw this graph when we first learned about mixed ESSs).

Figure 4.2: The Set-Up Window consists of three panels separated by horizontal lines.



GAIN 50

INJURY COST -100

DISPLAY COST -10

There are a couple of things to notice about the plot. First, fitness on the y-axis is expressed relatively. Thus, it always has a value between zero and 1.0.

Secondly, be aware that there are some slight rounding errors. For instance, the fitness of the `Hawk` line does not start exactly at 1.0 on the y-axis nor does it end exactly on the x-axis at a frequency of 1.0 as it should. But the errors are not large.

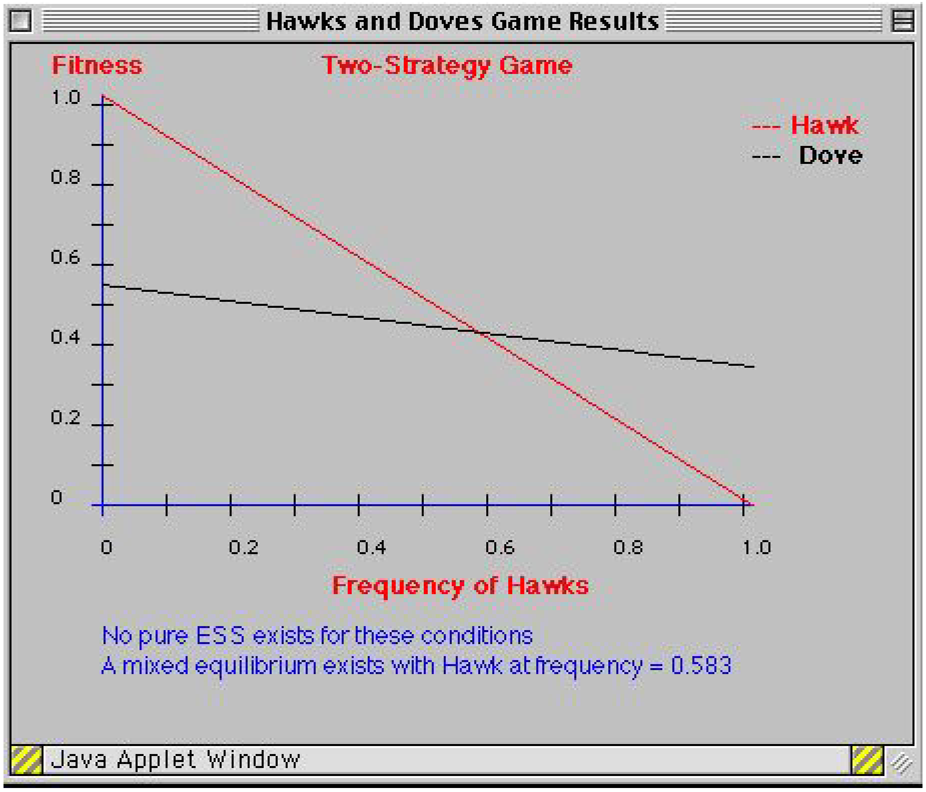
Thirdly, below the graph, a text print-out will tell you whether or not there is a pure or mixed ESS and if mixed, what the equilibrial frequency will be. It uses the rules given in previous sections to determine whether there is a pure or mixed ESS and if a mixed one, it uses the technique we learned earlier to find the value of that mix.

∗ The last yellow button, labeled “Evolve” will take you to another set-up page. This page is used to set up a simulation that shows the change in strategy frequencies and relative fitness over time given the current payoff matrix and an initial frequency of `Hawk`, which you set. See **Figure 4.4**.

Notice that this window has three panels:

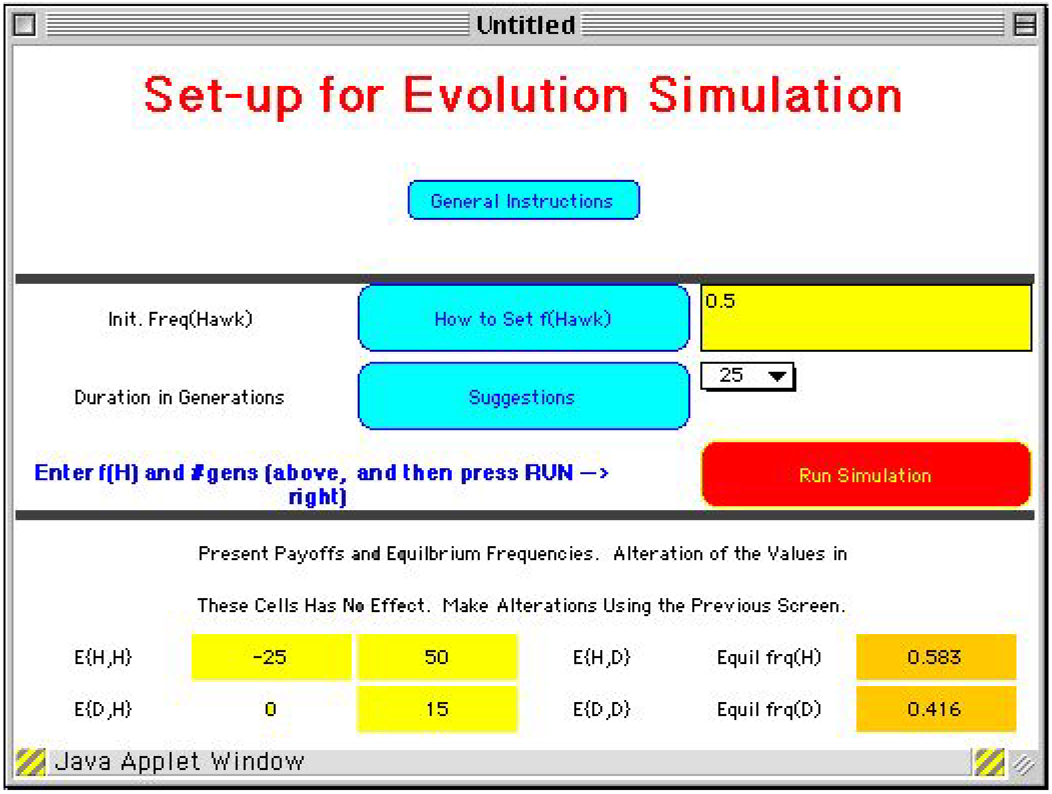
- General instructions can be obtained from the blue button on the top panel.
- The bottom panel is for reference. It contains a display of the present payoff matrix and predicted strategy equilibrial frequencies. Note that you will not be able to change any of these values—the only way to alter them is to go back to the previous window and change the values of the benefit and cost.
- The middle panel is where the action is! Here you can:

Figure 4.3: The Fitness Graph window for the `Hawks` and `Doves` Game.



No pure ESS exists for these conditions
A mixed equilibrium exists with Hawk at frequency = 0.583

Figure 4.4: The Set-up for Evolution Simulation window.



Init. Freq(Hawk) 0.5

Duration in Generations 25

Enter f(H) and #gens (above, and then press RUN —> right)

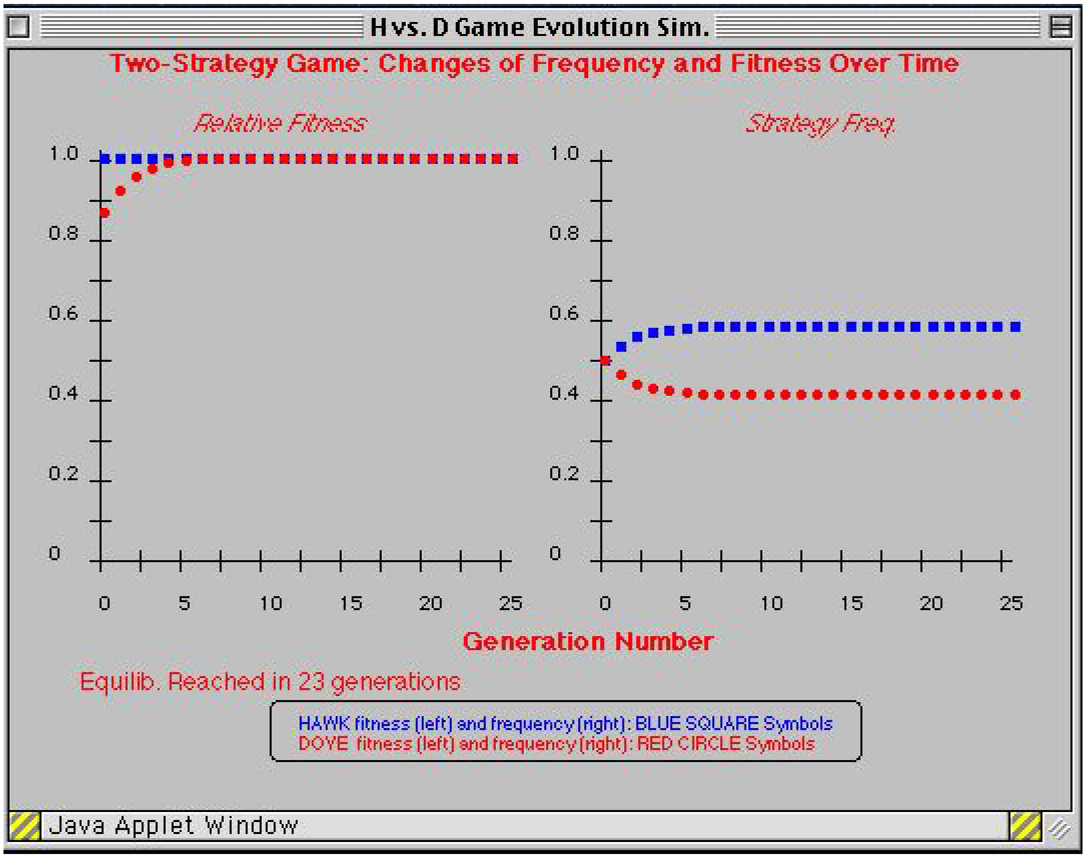
Present Payoffs and Equilbrium Frequencies. Alteration of the Values in

These Cells Has No Effect. Make Alterations Using the Previous Screen.

E{H,H}	-25	50	E{H,D}	Equil frq(H)	0.583
E{D,H}	0	15	E{D,D}	Equil frq(D)	0.416

- Use the top (yellow) text field to set the initial frequency of the `Hawk` strategy and thereby also set the freq(`Dove`) since it equals 1 − freq(`Hawk`). You should enter an initial value for the frequency of the `Hawk` strategy by typing in a value in the yellow textfield next to the text about "Initial Freq(Hawk)." Since mutation and migration do not occur, be sure to pick a value greater than 0 and less than 1 otherwise you are guaranteed stasis.
- Use the middle gold pulldown menu to set the number of generations (it has a default value of 25 generations).
- When these are set, use the red button to run the simulation. When you press "Run Simulation" you will get a graph like the one in **Figure 4.5**.

Figure 4.5: The Changes in Frequency and Fitness window.



Equilib. Reached in 23 generations

HAWK fitness (left) and frequency (right): BLUE SQUARE Symbols
DOVE fitness (left) and frequency (right): RED CIRCLE Symbols

Notice that there are two graphs with two plots on each: one each for the frequency of each strategy and one for the relative fitness for each strategy. Below the graphs, there is a text message that will tell you the number of generations required to reach a new equilibrium, if at all. Please note that, biologically-speaking, equilibrium would probably occur at a different, earlier number of generations. The program does not assign equilibrium until the frequency of H remains constant to 38 places for two successive generations!

If you want to review the concepts of fitness and frequency and especially if you want see an example of how the evolve graph is calculated, see the **Appendix** at the end of this chapter.

4.2 Differences Between the Applet and Application

There are a few differences between the stand-alone application and the web-based applet. Here they are.

- Launching:
  - **Applet**: Simply press the appropriate link.
  - **Application**: First download the application and be sure that it is unpacked. Your web browser should do this automatically, but follow the instructions that can be found on the download window. Once it's unpacked, double click on it and it'll launch (provided you have a Java interpreter installed in your OS—if you use some version of Windows 32 this may be a bit more complicated; see notes on the download page).
- Quitting:
  - **Applet**: Simply close all windows, this will exit you from the simulation.
  - **Application**: Go to the File menu and select "Quit" (Mac) or "Exit" (Windows).

4.3 Questions to Address and Things to Try

Try to answer all of the questions below. Discussion material is provided for some of the questions in the **Appendix** at the end of the text. If you have trouble answering other questions, ask about them in class.

1. **Payoffs and pure versus mixed ESSs.**
   a) Try altering the payoffs and see how this affects the equilibrium of the mixed ESS.
   b) Find the values of gain, loss, and display that produce a pure ESS for both H and D. You should probably look at them as ratios or in relative terms.
   c) What generalizations can you make?
   d) If you produce a pure ESS, are the relative payoffs that you are using still realistic? Can you use realistic numbers to produce a pure `Hawk` ESS? Pure `Dove`? Or are totally unbelievable numbers required?

2. When there is a pure ESS, where do the fitness lines for H and D converge relative to the frequency of `Hawk`?

3. Using the insights you gained from trying the previous set of questions, alter all values of costs and benefits but keep them constant in terms of ratios with respect to each other.
   a) If the ratios remain the same, does it make any difference in the equilibrial frequencies?
   b) Should it—is ratio what matters or is it absolute difference that matters?
   c) Would you expect the relative fitnesses of the two strategies to be equal or different (and if so, how different) when a mixed equilibrium is reached? How about a pure ESS? Try it and see.

4. Why is it that the *relative fitness* of H does not change (up or down) in simulations when H increases in frequency? Recall that we learned earlier that the absolute fitness of both H and D decrease as the frequency of H increases.

  a) What does this tell you about measures of relative fitness?

  b) Do you still think that relative fitness is a good measure to use in evolutionary studies?

  c) Why should there should be cases where the fitness of a strategy increases as its frequency decreases?

5. Imagine a situation where losing a fight causes severe injury but that fighting is the *only way to procure a critical resource, without which reproduction is impossible.*

  a) In this situation, what is the fitness of an individual playing a strategy that *does not fight and therefore does not obtain the resource but lives a long time?*

  b) Compared to the individual just discussed, what would be the average relative payoff to an individual playing *an alternative strategy that fights for the resource.* Assume that most individuals of this strategy die in fights without procuring the resource. However, some of them are successful and leave offspring.

  c) If death occurs in a fight, is it appropriate to use sequential contest games like `Hawk` and `Dove`?

  d) There are many cases where there are highly escalated contests leading to serious fights that might cause the death of one of the contestants. For example, male elephant seals engage in such contests over sections of a beach and "breeding rights" with the females in this area. Does that mean that males that lose such fights or that do not engage in fighting have no fitness? What does this tell you about simple games like `Hawk` and `Dove`?

4.4 Appendix: The Concept of Fitness

While the unit of evolution is the population, nevertheless, selection occurs between individuals bearing alternative phenotypes (which for our purposes will mean individuals using different genetically based behavioral strategies). Since different phenotypes spring partially from alternative alleles, selection can also be seen as a competition between alternative alleles. There are a number of ways to measure the success of different individuals or alleles. All involve the fitness concept.

The term **fitness** comes from Darwin and Wallace's idea that animals that survived (i.e., were most fit) were most likely to leave a greater number of offspring. While the notion of survival primarily has to do with what they termed "natural selection," we will also to include the effects of sexual selection on an individual's reproduction when we discuss fitness.[1]

Simply put, *fitness is a measure of the number of copies of an individual's genes*, or if we are considering a single genetic locus, *the number of copies of an allele, that are put into the next generation.*

Actually to get around some of the problems that can arise when an individual's offspring (F1 generation) are infertile (F2 generation), the most formal analyses count the number of grandchildren (F2). There are well-known examples of this sort of thing, termed **hybrid sterility**—think of donkey and horse cross. It yields a vigorous, valuable F1 (mule) but no F2—mules are sterile. Nevertheless, in cases where there is no reason to suspect hybrid sterility, it is common practice simply to count the numbers of offspring.

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[1] For the purposes of our present discussion, we will leave out concepts of indirect and inclusive fitness.

Fitness is denoted by W with some other notation that usually explains whose fitness is being considered (e.g., W(`Hawk`) for the fitness of the strategy `Hawk`). Simply counting the number of offspring or grandchildren gives a measure that can be called **absolute fitness**.

Evolution is a numbers game and so what really matters in generational competition is not the number of offspring (provided it is more than 0) but how many an individual produces relative to its competitors. The simplest way to make this comparison is to just compare how many copies of each allele are produced—for example, strategy A (associated with allele A) produces and average of 1.7 offspring while strategy B produces 2.2. One can easily see that strategy B is doing better. But how much better?

Humans have a very good understanding of proportional measurements—where 1.7 versus 2.2 tells us something, saying that strategy A is only 77% as successful as strategy B usually tells us something that we understand better when we are considering the outcome of competition. Using measures of **relative fitness** do just this sort of thing. They arbitrarily define the most successful type as having the reference fitness. All others are measured as a proportion of this reference value. Thus,

$$\text{Fitness} = W = \frac{\text{average number of offspring by any strategy}}{\text{average number of offspring of most fit strategy}}$$

and for the example we just considered,

- strategy B had the greater absolute fitness at 2.2; it becomes the reference;
- the relative fitness of strategy A is therefore $1.7/2.2 = 0.77$;
- and to be complete, the relative fitness of the reference strategy is $2.2/2.2 = 1.0$ (of course, it will always be 1.0).

Problem

6. Assume that a population of asexually reproducing organisms possess two genetically determined behavioral strategies, A and B. Assume that, taken as groups, A and B strategist's fitnesses differ only as a result of how their behavior affects their ability to reproduce (in other words, they differ only in regards of being A or B strategists). These animals live one year and the average number of offspring left by an A strategist is 0.85 and for a B strategist it is 1.05. At the start, there are 850 individuals of strategy A and 125 of strategy B.

a) What are the frequencies of strategies A and B?

b) What are the relative fitnesses of strategy A and B?

c) What will be the frequencies of the two strategies in the next generation?

d) At present, is the population size as a whole increasing, declining, or steady?

e) If evolution continues and if the relative fitnesses of the two strategies remain the same, predict what will happen to the population as a whole—will it increase, decrease or remain the same?

Chapter 5

Conflict and Ownership: The `Bourgeois` Strategy

Synopsis: *This chapter assumes that you have thoroughly investigated the* `Hawks` *and* `Doves` *game, that you understand those strategies, that you can calculate payoff matrices, and that you understand pure and mixed ESS.*

Building on this foundation, we will now consider a new strategy, `Bourgeois`*, whose central feature is that ownership of a resource determines the behavior used in a particular contest. If a* `Bourgeois` *strategist owns, it will defend its ownership with* `Hawk`*-like ferocity; if* `Bourgeois` *does not own, it will attempt to obtain the resource using display but it will not escalate to fighting.*

You will get a chance to calculate a payoff matrix for a three strategy game and then use this to consider whether `Bourgeois` *is stable against either* `Hawk` *or* `Dove`*. This will prepare you to use to the next simulation which looks at evolution in a population containing these three strategies.*

5.1 Introduction

Using the `Hawks` and `Doves` simulation you examined the solutions to a simple game involving two strategies. You have learned that this game usually yields a mixed ESS but under certain circumstances can give a pure ESS for `Hawk`. On the other hand, pure `Dove` ESSs involved unacceptable assumptions.

In the `Hawks` and `Doves` game, each contest involved situations where the competing individuals either:

- did not possess the resource prior to the contest
- and/or acted as if previous ownership had no effect on the outcome of a game.

Recall that the concept of ownership was not part of the definition of either strategy. Now, there are certainly situations where ownership is irrelevant for a number of reasons. However, in numerous cases animal do possess resources which others may sometimes attempt to wrest from them. In other cases, animals seem to respect ownership of a resource—they do not bother to attempt to take it from another individual. Are they simply being nice or is this respect the result of an evolutionary calculation based on the benefits and costs of respect for ownership?

We can certainly use game theory to see if there situations where strategies that respect ownership are stable or form a mixed ESS with other strategies such as `Hawk` and `Dove`. In this section we will define such a strategy, which has been named `Bourgeois` by Maynard Smith and consider it in games with `Hawk` and `Dove`. This addition to our `Hawks` and `Doves` population will

- allow us to examine a strategy that introduces some of the behaviors associated with possession of resources,
- give us a chance to see what happens to population when a new (previously unknown) population arrives by mutation or immigration, and
- it will introduce us to some of the evolutionary intricacies that occur when more than two strategies are competing against each other.

5.2 Definition of the `Bourgeois` Strategy

`Bourgeois` is a strategy *associated with respect for "ownership" (i.e., possession) of a resource.* `Bourgeois` strategists *fight to hold on to resources they already own* (i.e., act like a `Hawk`) and they *display over resources that they do not own.* In our simple example, we will therefore define `Bourgeois` as having either `Hawk`-like or `Dove`-like behavior contingent on whether it or the other contestant owns the resource. To recapitulate, if `Bourgeois`, then

- when an owner, fight like a `Hawk` to hold territory and be willing to risk serious (fitness-lowering—not death-causing) injury;
- when not an owner, do not risk injury and act like a `Dove`.

This is in contrast with both `Hawk` and `Dove` strategists who always play the same strategy regardless of whether or not they or their opponent own a resource.

Problem

1. Does ownership imply territoriality?
2. Does `Bourgeois` seem to you like a behavioral strategy that an animal might really employ? Critique the strategy.

5.3 Payoffs for the `Bourgeois`, `Dove`, and `Hawk` Game

We will define B very simply in light of H and D strategies. We will assume that B has a 50% chance of owning a resource in any contest. Thus, in any contest with B, there is a 50% chance that it will act like `Hawk` (owns) and a 50% chance that it will be a `Dove` (doesn't own). To continue to keep things simple, we will assume that as in the H and D contest, you don't know who you are playing against till it starts (else `Hawks` could avoid `Hawks`, for instance and they would be a pure ESS). See **Table 5.1** for the general payoff matrix.

If we insert the same default payoffs to `Hawks` and `Doves` as used were used in the previous example into the equations in the matrix above, then the payoff matrix for our three strategy game is found in **Table 5.2**.

Table 5.1: The general payoff matrix for the `Bourgeois`, `Dove`, and `Hawk` game.

	`Hawk`	`Dove`	`Bourgeois`
`Hawk`	$E(H,H)$	$E(H,D)$	$\frac{1}{2}[E(H,H) \pm E(H,D)]$
`Dove`	$E(D,H)$	$E(D,D)$	$\frac{1}{2}[E(D,H) \pm E(D,D)]$
`Bourgeois`	$\frac{1}{2}[E(H,H) \pm E(D,H)]$	$\frac{1}{2}[E(H,D) \pm E(D,D)]$	$\frac{1}{2}[E(H,D) \pm E(D,H)]$

Table 5.2: A particular payoff matrix for the `Bourgeois`, `Dove`, and `Hawk` game.

	`Hawk`	`Dove`	`Bourgeois`
`Hawk`	-25	$+50$	$+12.5$
`Dove`	0	$+15$	$+7.5$
`Bourgeois`	-12.5	$+32.5$	$+25$

5.4 Is `Bourgeois` a Pure ESS?

Notice that there is no simple way to answer this question since the rules we learned earlier for comparing the payoffs of different encounters were for two-strategy games. However, a three-strategy game can be broken down into simpler two-strategy contests. Since we already know the outcome of `Hawk` versus `Dove` (for these payoffs), the contests of interest are `Hawk` versus `Bourgeois` and `Dove` versus `Bourgeois`. If in both of these separately `Bourgeois` is a pure ESS, then it is reasonable to conclude that `Bourgeois` is a pure ESS versus a mix of `Hawk` and `Dove` since it can invade both and cannot be invaded by either.

- For B versus H: $E(B,B)$ is greater than $E(H,B)$ (i.e., $+25$ is greater than $+12.5$). Thus, for any frequency, when B interacts with B the fitness consequences to B are better than what H receives when H interacts with B (both interactions will occur at the same frequency). If, for completeness, we turn this around: $E(H,H) = -25$ which is less than $E(B,H) = -12.5$. Thus, B is stable against H.

- For B versus D: $E(B,B) = +25$ which is greater than $E(D,B) = +7.5$; if turned around, $E(D,D) = +15$ which is less than $E(B,D)$ which equals $+32.5$.

Thus, `Bourgeois` is stable against both `Hawk` and `Dove`.

You'll be able to confirm this result for these benefits and costs by using an appropriate accompanying simulation. You will also have the chance to try to find sets of benefits and costs where B is not a pure ESS. And you will be able to deepen your understanding of how a population might evolve when three strategies are present.

Chapter 6

A Three Strategy Simulation

Introduction

Synopsis: *This chapter contains a description of how to use the simulation of the Bourgeois versus Hawks and Doves game. Do not attempt this game until you thoroughly understand the (see Chapter 3) and you are familiar with the basic operation of the Hawks and Doves simulation (see Chapter 4.* This simulation has many similarities. Also be sure that you understand the "new" strategy `Bourgeois` in the previous chapter. Take the time to review the materials first or you will not get much out of this simulation and you will probably have trouble answering the questions.

One major difference between this simulation and the `Hawks` versus `Doves` simulation is that there is no plot of fitness versus frequency. With three strategies, such a plot is difficult to make (requiring either three axes or fixation of the frequency of one strategy) but more importantly, unlike a two strategy game, there may be no pure or mixed ESS outcome. Depending on the initial conditions (payoffs, frequencies) a number of outcomes are possible—pure, mixed or no ESS! So, we will only look at the result in terms of evolution.

A Note from the Programmer: Maynard Smith and many other game theorists usually plot three strategy game evolution results as barycentric plots. While very elegant, these take some getting used to and so I have decided to use the more intuitive plots of frequency versus time.

6.1 About the Simulation

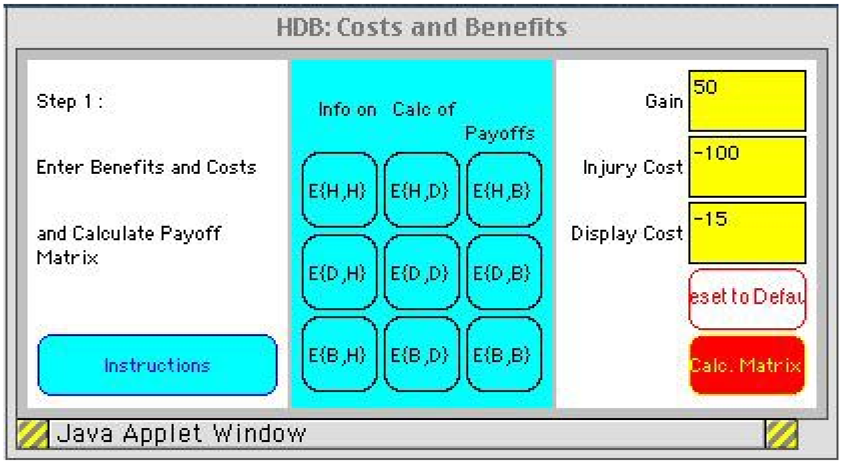
Once you have loaded the simulation and have moved from the introductory window, a new window like **Figure 6.1** will appear.

This window is divided into three sections:

- The left panel contains a button, "Instructions," which explains how to use the window.
- The central panel, "Info on Calc. of Payoffs," has nine buttons each labeled with the symbolic notation for a particular payoff. Pressing one of these buttons will tell you how a particular payoff is calculated.

  Note: As with the `Hawks` and `Doves` simulation, you will not be able to alter the actual definition of any strategy nor can you modify the formulae used to calculate the payoffs for a

Figure 6.1: The set-up panel for the costs and benefits in the `HDB` simulation.



HDB: Costs and Benefits

Step 1 :

Enter Benefits and Costs

and Calculate Payoff Matrix

Gain: 50

Injury Cost: -100

Display Cost: -15

particular contest. As in the `Hawk` and `Dove` simulation, the only way that you will be able to modify the payoffs is by changing the Benefits and Costs.

- The right panel contains controls for changing benefits and costs. As usual, simply enter the values you wish for the resource value (GAIN) and two types of costs. You should use the same conventions for assigning values to Gain, Injury, and Display as with `Hawks` and `Doves` since both of these strategies are found in this game and `Bourgeois`. is combination of the two strategies.

  The button labeled “Reset to Default” will set the gains and costs back to their initial values which are the same default values that we used in the `Hawks` and `Doves` game.

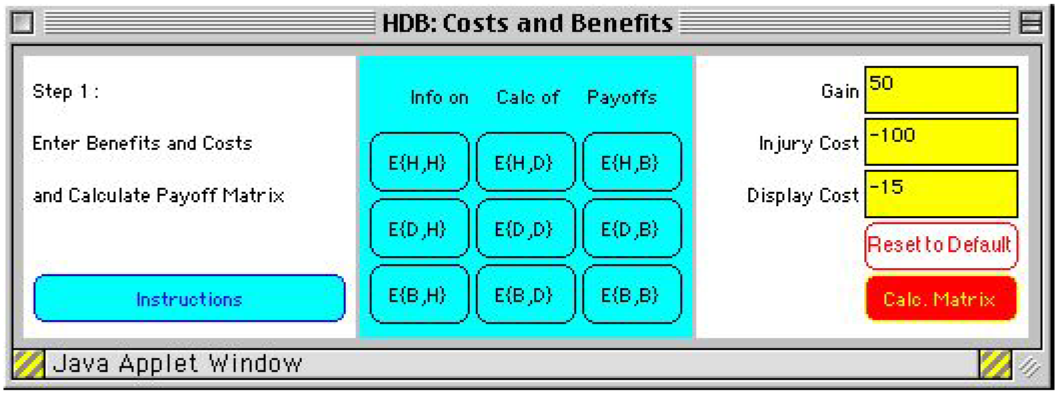
  Finally, pressing the red “Calc. Matrix” will send you on to the next window and will calculate the payoff matrix.

  Use the same conventions as before to assign benefits and costs: Benefit ≥ 0 and Costs ≤ 0.

Once you are satisfied with the benefits and costs, press the red button and you will see the next window **Figure 6.2** which reviews the payoff matrix.

- The left panel gives three buttons
  - information about using the page;
  - a button that will take you back to the previous window to revise the payoff matrix by changing the benefits and costs;
  - A red button labeled “Continue—Set Freqs and Run”—which takes you to the next window.
- The right panel contains the payoff matrix (gold) calculated using the Benefits and Costs you set on the last page. The blue button above each payoff can be pressed to give you the formula used to calculate each payoff.

Figure 6.2: The payoff matrix for the `HDB` simulation.



HDB: Costs and Benefits

Step 1 :

Enter Benefits and Costs

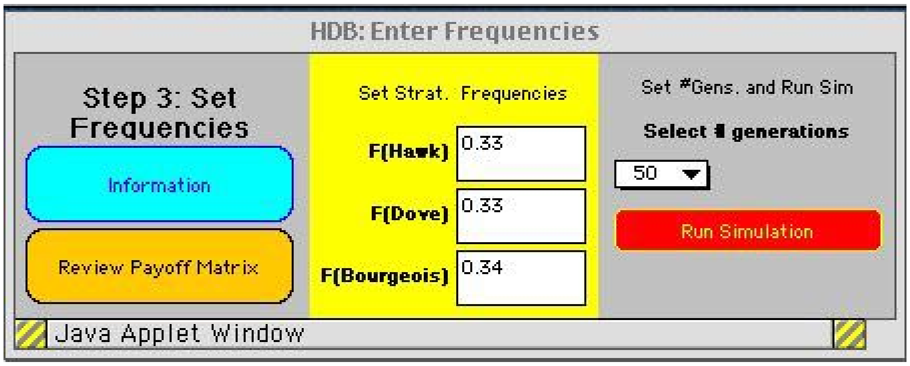
and Calculate Payoff Matrix

Gain: 50

Injury Cost: -100

Display Cost: -15

Figure 6.3: The panel for setting the initial frequencies of the strategies.



HDB: Enter Frequencies

Step 3: Set Frequencies

Set Strat. Frequencies

F(Hawk): 0.33

F(Dove): 0.33

F(Bourgeois): 0.34

Set #Gens. and Run Sim

Select # generations: 50

When you are satisfied, press the red button which takes you to the next window, **Figure 6.3**.

Once again this window is a “tryptic” (apologies to all of those great painters for appropriating the term):

- The left panel has two buttons,
  - information on using the page and
  - a button that will allow you to go back to review the last window in case you want to see the payoff matrix before you set strategy frequencies (from the previous window, you will be able to reset the benefits and costs and thereby change the payoffs as was noted above).
- The center panel contains three text fields for entering the frequencies of each of the strategies:
  - Be certain that the frequencies add to 1.0. If they do not add to 1.0 or if you enter non-numerical data, you will see a warning window which you should close and then re-enter your data.
  - If you wish to run a two strategy game (e.g., H versus B), enter a value of 0.0 for the strategy you wish to exclude but be sure that the other two add to 1.0.
- Finally, the right panel contains two controls,
  - a pull-down menu that allows you to set the number of generations in the evolution simulation. The default is 50, but experience will show that in some cases you may want to use fewer generation (to get a better view of the changes) or more generations (when equilibrium has not yet been reached)
  - and a red button that when pressed will take you to the evolution simulation.

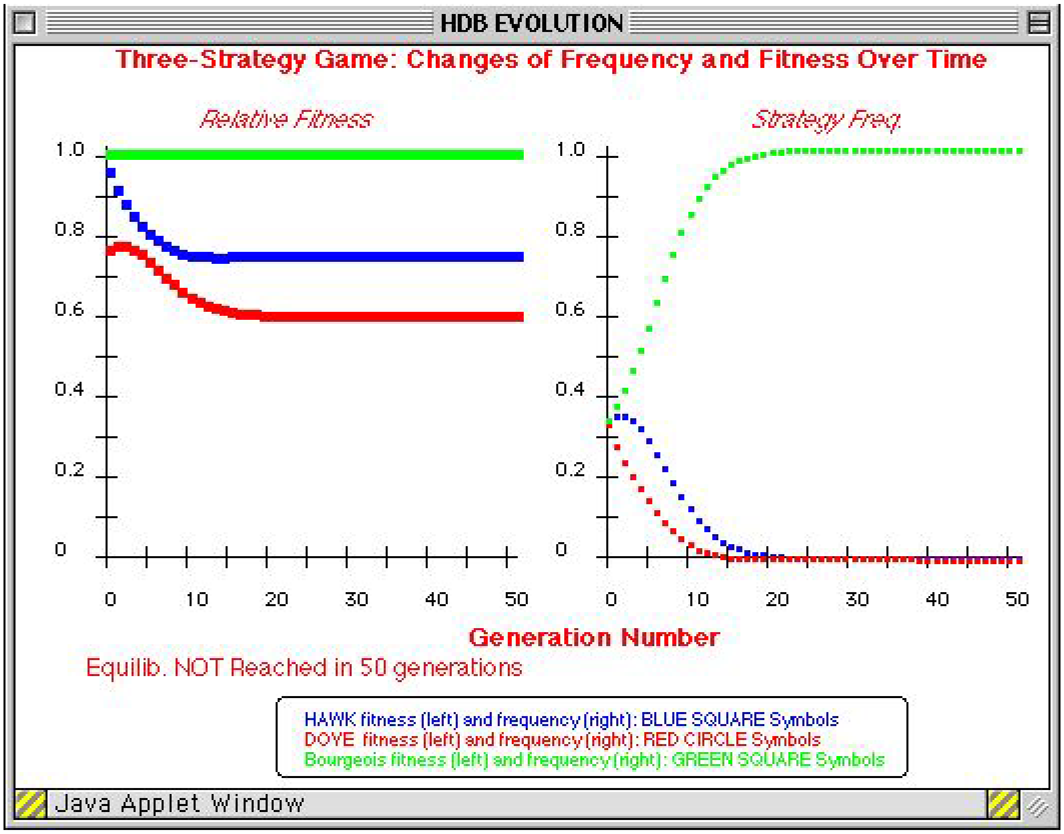
As with the evolution simulation in the `Hawks` and `Doves` Game, there are two plots, see **Figure 6.4**. The left is a plot of the relative fitnesses and the right is a plot of the strategy frequencies.

A key at the bottom gives the color and symbol labels for each strategy and a message will tell you how many generations were required to reach equilibrium (if at all).

A few things to remember when viewing the plot: As with the `Hawk` and `Dove` game, there are a couple of things to notice about the plot.

- First, fitness is expressed relatively. Thus, it always has a value between zero and 1.0.
- Second, be aware that there are some rounding errors and so the graph and hash marks on the axes have some slight errors. For instance, the fitness of the `Hawk` line does not start exactly at 1.0 on the y-axis nor does it end exactly on the x-axis at a frequency of 1.0 as it should. Nonetheless, the errors are not large.
- Third, below the graph, a text print out will tell you whether or not there is a pure or mixed ESS and if mixed, what the equilibrial frequency will be. Unlike the `Hawks` and `Doves` game, this program determines equilibrium has occurred when there is no change in two successive generations in the frequencies of all three strategies. Please note that biologically-speaking, equilibrium would probably occur at a different, earlier number of generations. The program does not assign equilibrium until the frequency of H remains constant to 38 places for two successive generations!
- Finally, please note that when the game is only played with two strategies, e.g., H and B, the relative fitnesses of all three strategies are still displayed. This is simply to help you envision what would happen if the third strategy was added.

Figure 6.4: Relative fitness and strategy frequency plots.



Equilib. NOT Reached in 50 generations

HAWK fitness (left) and frequency (right): BLUE SQUARE Symbols
DOVE fitness (left) and frequency (right): RED CIRCLE Symbols
Bourgeois fitness (left) and frequency (right): GREEN SQUARE Symbols

6.2 Differences Between the Applet and Application

There are a few differences between the stand-alone application and the web-based applet. Here they are.

- Launching:
  - **Applet**: Simply press the appropriate link.
  - **Application**: First download the application and be sure that it is unpacked. Your web browser should do this automatically, but follow the instructions that can be found on the download window. Once it's unpacked, double click on it and it'll launch (provided you have a Java interpreter installed in your OS—if you use some version of Windows 32 this may be a bit more complicated; see notes on the download page).
- Quitting:
  - **Applet**: Simply close all windows, this will exit you from the simulation.
  - **Application**: Go to the File menu and select "Quit" (Mac) or "Exit" (Windows).

6.3 Questions to Address and Things to Try

The speed of this simulation will allow you to answer all of these questions rapidly—take the time to consider each in detail and record your answers or thoughts and questions in your course notes for discussion in class.

Try to answer all of the questions below. Discussion material is provided for some of the questions in the **Appendix** at the end of the text. If you have trouble answering other questions, ask about them in class.

1. a) See how `Bourgeois` does against just `Hawk`, just `Dove`, and finally against both. Use default payoff values and set frequencies either at $50 : 50$ or $0.33 : 0.33 : 0.33$.

b) Could you use the rules presented earlier to determine a pure ESS with all three strategies at once? [Ref xxxx]

2. In a systematic manner, start with initially different frequencies of H, D, and B.

a) For example, try H at 0.9, D at 0.09 and (therefore) B at 0.01.

b) Reverse the frequencies of H and D.

c) Try nearly equal frequencies of H and D and low B.

d) Satisfy yourself that in each case B is still an ESS—can you alter the values of winning the resource, injury and display costs in any meaningful way to prevent B from being a pure ESS? Use the same sorts of modifications that you made in the H and D game to make one or the other (in one case, unrealistically) a pure ESS.

3. **More about frequencies**: Review the situation with the default payoff matrix and with H at 0.9, D at 0.09, and (therefore) B at 0.01.

- **a)** Set the number of generations to 10. Describe what happens to H, D and B over this time.
- **b)** Set the number of generations to 50. Describe what happens to H, D and B between generation 10 and 50.
- **c)** Set the number of generations to 150. Describe what happens to H, D and B between generation 50 and 150.
- **d)** Repeat this experiment with the initial frequencies of H and D reversed (and therefore the same initial frequency of B).
- **e)** Between generations 10 and 50, what were the approximate frequencies of H and D?
- **f)** Were they the same regardless of whether or not you started with H or D at 0.9?
- **g)** Have you observed these frequencies before?
- **h)** What is going on here?
- **i)** If B is a pure ESS why does it take so long for it to fix?
- **j)** What would you need to do to make B fix faster, (given a starting frequency)?

4. Which strategy could you monitor in this game to tell when the ESS is reached?

Chapter 7

Wars of Attrition: Fixed Cost Strategies

Synopsis: *In the games we have considered previously, we examined strategies that used fighting (i.e., contests that potentially involved injury) to settle symmetrical contests (e.g.,* `Hawk` *and sometimes* `Bourgeois`*). We also considered the strategy* `Dove` *(and* `Bourgeois` *when it did not "own") which settled contests with other* `Doves` *through display. In displays there is no chance of injury although there certainly are costs in terms of energy, time, or risk of being preyed on (injury from a non-contestant).*

In this chapter we will look at how simple symmetrical contests between individuals that only display might be settled without resort to fighting. These contests are referred to as "symmetrical wars of attrition."

We will first examine the question of whether or not any fixed cost display can be evolutionarily stable. We will show that fixed cost strategists are not evolutionarily stable. This will lead us to a consideration of a mixed ESS solution in the next section.

7.1 Introduction

There are situations where fighting does not occur in a contest over a resource. How then could ownership be settled?

- One rule would be simply to cooperate: *split the encounters*. However, this might only seem reasonable when the contestants knew each other and kept track of their contests so that divisions would be equal (fair). This is not something that most animals could or would do. We humans could do this, but what if you were unlikely to ever encounter the same opponent again? Game theory modeling of cooperative behavior like this can be done using the "prisoner's dilemma" game. What other possibilities are there?

- Another solution would be to *settle the contest by some asymmetry*, usually detectable in a display. However, this sort of settlement probably only works if there was some back-up to the display. Thus, this leaves the chance for **escalation**. What if the loser (the one with the supposedly inferior display) calls the winner's bluff? So, if we allow asymmetries, we are left with a model that may require fighting either as a result of the inability of the parties to discern the winner of an evenly matched contest or to back up the "honesty" of the winner's display.

- Is there another way to decide without resorting to fighting or sharing? One simple and time honored (not to make a joke) solution is a **waiting game** or **war of attrition**. We have seen an example of this in `Dove`. Recall that `Dove` strategists settle conflicts either by immediate withdrawal or by unescalated displaying contests. Thus, wars of attrition include the means `Doves` use to settle contests against other `Doves` (but not against `Hawks`!).

In this section, we will review some of the ideas about settling contests with displays.

7.2 Waiting Games and their Currencies

In a waiting game, the contestant who is willing to wait the longest wins. Think of the silly, often tragic dramas of people (often poor and desperate) who enter marathon dance contests (did you ever see the classic movie *They Shoot Horses, Don't They?*) to win prize money or those who try to win a car by keeping their hands on it, remaining awake, and standing longer than any other contestant.

Such waiting games have also been dubbed **wars of attrition**, although they do not need to be strictly analogous to the horrible "real" war of attrition where the winning side is the one whose armies, cities, and populations haven't been unacceptably decimated. In our analysis of wars of attrition, we will be concerned with individuals (acting as proxies for strategies) competing against each other. We will not be interested in societal or other group competition as in the military concept (although this analysis could also be used with groups). Types of wars of attrition that are meaningful to a behaviorist include contests that are settled

- purely by **waiting** (or some other type of **time-dependent display**) or
- by **depletion of resources** such as energy. The assumption is usually made that while costs are involved in waiting, injury (in the conventional sense) is not—animals drop out of contests before they are seriously harmed.

Currencies for Waiting Games

The fundamental currency of waiting games is, of course, fitness. But as we discussed earlier, fitness consequences, measured as changes in numbers of grandchildren, are usually hard to assess for simple behaviors such as displays.

To save time, we use some other function such as net benefit or net value (gain after all costs are factored in). Recall that to find the net value, we need to have some measure of the value of the resource and a measure of the costs associated with competing for the resource. In waiting games, these costs are absorbed by both the winner and loser.

Costs as time or energy: Obviously, costs and benefits must be enumerated the same way; they must have a **common currency**. Let's start our consideration with costs. In a waiting game, the only costs are display costs. Thus, there is no escalation to fighting and no injury.

What are these costs? Anytime an animal is doing one thing, such as displaying, it is not doing something else that might be helping its fitness. The more time it displays, the less time it might have for looking for food. There may also be costs due to exposure – animals that are displaying are often far more visible to their predators or other potential enemies.

However, we will consider display costs as the extra energy (compared to doing nothing) that an organism uses to perform the display. As was discussed in the section on optimality (review), these costs are usually a function of time. So, we can make the simple assumption that cost and time are related ("time is money"):

$$\text{Costs} \propto t, \tag{7.1}$$

where t is time. For our purposes we will *assume that costs increase linearly with time.* SO

$$\text{Costs} = kt \tag{7.2}$$

where k is a proportionality constant equaling the energy cost (x) of the use of one unit of time (t). A linear relation between energy cost and time is probably the general rule in animal repetitive animal displays. A good example is calling insects and frogs [Forrest and Green, 1991]. However, note that there are cases where cost is not a linear function of time, but we'll keep things simple and stick with (7.2).

An example: Let's look at an example of human behavior to understand the idea of contests and costs. Suppose you are hiking and you are looking for a suitable shelter to spend the night. If you arrive at a shelter that is already occupied either by some critter – let's say a bear or a rattlesnake, or you and another hiker arrive at the same time, a contest starts over who gets the shelter. These contests are settled by displays—no killings, snakebites or maulings allowed. You try to scare out the bear or snake while keeping a respectful distance or you do the typical human things to try to get the other hiker to leave (but let's not be too human—no fights!).

Let's focus on the contest with another human since the costs are most likely to be symmetrical and since games are usually (but not always) considered as costs between conspecifics. The cost of the contest is your time and patience as you discuss or posture over who is going to get to stay. Eventually one you quits. You have both paid the same cost in the contest. And we could have measured this cost either in terms of time or energy. See (7.2).

Now, what about benefit? Since we measured cost as time or energy, we need a reasonable way to evaluate the shelter in one of these currencies. Assume the shelters are equally spaced in terms of the time it takes to reach them. Occupying a shelter means that you have avoided the cost of having to walk to the next shelter. So in a simplistic but useful sense, *the value of a shelter equals the cost you would have paid to hike to the next shelter.* A famous quote from the venerable Ben Franklin crystallizes this idea: "a penny saved is a penny earned".

Avoid the error of thinking about the costs of searching as contest costs. The costs are only those associated with the actual contest—they involve the time and energy and perhaps risk involved in giving the "evil eye" to the bear, rattlesnake, or other hiker. Search costs are used only to obtain a reasonable, easily measured value of the shelter. Notice that the actual search occurs outside of the contest—the contest starts when the search ends.

7.3 Is there an ESS for a War of Attrition?

To answer this question, we will make the following assumptions (identical to those we assumed for `Dove` earlier):

- We will assume that there are *no asymmetries in the contestants* beyond the fact that one might be prepared to wait or display longer or, expend more energy (these are all related, as we saw earlier). Thus, animals do not give up because they perceive that their opponent is stronger as a result of the display. So we will refer to these contests as **symmetrical wars of attrition** or **symmetrical waiting games**.

- We will assume that animals have *no knowledge of how long their opponents are going to display*—strategies are set at the start of the game and played out.
- They simply *wait or display up to a certain period of time or burn up to a certain amount of energy.*
  - If a focal animal's opponent has not yet quit when the focal animal reaches its limit, it loses.
  - If the opponent quits before the limit is reached, the focal animal wins.
  - Since both animals quit at essentially the same time (determined by the loser since the winner is prepared to go on longer), *both will pay the same cost in the contest* (although for the winner it was less than it was willing to pay).
  - This means that the *value of the resource is discounted to the winner by the cost of displaying for it.* We have discussed this idea earlier when we developed a general formula for determining payoffs in a contest (see (2.1)).

For further information on these assumptions, the interested and mathematically inclined individual should consult [Bishop and Cannings, 1978].

The analysis of this game is rather complicated mathematically. The interested reader is advised to consult [Smith, 1974 and 1982] and [Bishop and Cannings, 1978] for elegant, detailed explanations of the problem. What follows is a synopsis of their work with commentary and expansion designed to aid a student who is new to game theory and mathematical modeling. I have dealt with the mathematics by presenting both the calculus equations (with a explanations and in some cases, derivations) and a parallel set of discrete solutions which my be more comfortable to students who are not familiar with calculus. They have the added advantage that a student can easily use them on a spreadsheet to find answers that approximate those given by the calculus.

7.4 Can a Fixed Waiting Time Strategy be a Pure ESS?

Costs and Benefits

First, let's define the costs and benefits:

- The **contested resource** has a certain absolute or gross value which we will call V (following Maynard Smith). Since I like to think of things in terms of energy, let's say that it is a certain value in joules.
- We will use two symbols for cost.
  - Any cost is symbolized as x. These accumulate according to some function of time (see (7.3) immediately below).
  - The cost that each contestant has paid at the moment the contest ends is m. This cost is determined by the loser, but both pay it.
- We will assume that display costs, x, increase in a linear manner:

$$\text{Display Costs} = kt \tag{7.3}$$

  Caution: Following Maynard Smith, we will consider costs as positive values and subtract them from the gross resource value. This is a different convention then we used in the `Hawks`, `Doves`, and `Bourgeois` games but the final mathematics are the same.

- Thus, if we have two contestants, A and B who are willing to display for times $t(A)$ and $t(B)$, then we can define their display costs as:

$$x(A) = kt(A) \qquad \text{and} \qquad x(B) = kt(B) \tag{7.4}$$

The gain to the winner of any contest will be the value of the resource V diminished by the cost of getting it. Remember that we will symbolize the cumulative cost paid at the termination of the contest as m:

$$\text{Net Gain} = V - m. \tag{7.5}$$

Now, recall that the loser pays the same display cost as the winner since the loser determines when the contest will end, i.e., when he quits $x = m$ and so the loser pays:

$$\text{Loss } = -m, \tag{7.6}$$

Payoffs

We can now construct a list of payoffs for different contests. This is not the same as the payoff matrices we have seen before, but we will use the information in it to construct similar matrices a bit later.

Table 7.1: Payoffs for various contests.

Strategy and Outcome	Change in fitness for A	Change in fitness for B
$m(A) > m(B)$, therefore A wins	$V - m(B)$	$-m(B)$
$m(A) < m(B)$, therefore B wins	$-m(A)$	$V - m(A)$
$m(A) = m(B)$, therefore **Stalemate** Resource possession is decided randomly, each wins half of the time	$0.5V - m(B)$ or equivalently $0.5V - m(A)$	$0.5V - m(B)$ or equivalently $0.5V - m(A)$

Hopefully, **Table 7.1** makes sense. Each row corresponds to the payoffs for players A and B for a given cost (length of display) that the contestants are willing to pay.

- Thus, in the first row strategy A is willing to pay more (display longer). A will win every contest.
- The cost that A pays in winning (and B in losing) is determined by B. Thus, both contestant's costs are $-m(B)$.

The second row is simply the converse—here B wins by being willing to display for a longer period of time and now the cost that is paid is what A was willing to pay. The third row—a tie, is the only one with any new tricks in it. What if both strategies A and B pick the same time (cost) to pay? For the sake of simplicity (but not reality as he pointed out), Maynard Smith stipulated that the winner will be determined at random. Thus, each contestant would win 50% of the time. In every contest both the winner and loser will pay the cost $m(A) = m(B)$. Substituting into the formula for assigning payoffs that we learned earlier,

$$\begin{aligned}\text{payoff if both display the same} &= 0.5(V - m(A)) - 0.5m(A)\\ &= 0.5V - 0.5m(A) - 0.5m(A)\\ &= 0.5V - m(A)\end{aligned}$$

which is the expression given in **Table 7.1**.

Analysis of a Game Between Fixed Cost Strategies

OK, let's construct the payoff matrix to see if a certain strategy is a pure ESS. We will use our usual procedure of assuming that one strategy is established and the other invades in very low numbers.

Situation 1: An invader willing to pay more arrives!

Define two strategies, A and B. Let B be willing to pay a slightly higher cost than A, i.e.,

$$m(B) = m(A) + \Delta m \tag{7.7}$$

where Δm is the small additional cost that B is willing to pay. Thus,

$$m(B) > m(A) \tag{7.8}$$

Make A the common strategy and B a rare invader. Notice that this is exactly the same scenario we have always discussed in determining whether or not a strategy is a pure ESS. Thus,

- nearly all of strategy A's interactions are with other A strategists while
- nearly if not all of strategy B's interactions are with A strategists.

Let's construct a payoff matrix using the formulae in **Table 7.1** above.

- When either A meets A or B meets B, contests are settled at random since both contestants are willing to pay either $m(A)$ or $m(B)$, respectively.
- B always beats A in their contests, thus, $E(A, B) = 0$ and $E(B, A) = V - m(A)$.

The payoff matrix is given in **Table 7.2**.

Table 7.2: Payoff matrix for an Invader B willing to pay more than A.

	A	B
A	$0.5V - m(A)$	0
B	$V - m(A)$	$0.5V - m(B)$

Using **Rule 1** for finding A pure ESS[1], we see than A cannot resist invasion by B and therefore A is not A pure ESS. Looking at the matrix above, you may briefly be tempted to conclude that B is an ESS. But look closer.

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[1] See Chapter 2, Section 4.

Situation 2: Same old same old: An invader willing to pay more arrives!

OK, assume that B has taken over and is very common. Now the big question: What if another strategy (we'll call it C) that waits just a bit longer than B shows up? The answer, of course, is that we will have a repeat of the situation when B invaded A! Thus, C will now successfully invade B and so B is not a pure ESS. If you continue to follow this logic, you may come to the conclusion that a strategy that is willing to pay an infinite cost would be a pure ESS. Not so fast.

Situation 3: These Queues are Getting Too Long!

Imagine that our population continues to be invaded by individuals that are willing to wait longer to win. According to (7.3), the costs are increasing with longer waits, but the value of the resource is still the same. Thus, the *net gain for winning is becoming less and less* the longer one waits to win.

Imagine that we finally get to a waiting time that is so long that it is greater than half the value of the resource, i.e.,

$$m(\text{Long}) \geq 0.5V. \tag{7.9}$$

Now, this is still a winning value with respect to taking the resource compared to any time that is shorter than it is. Let's say a new mutant appears that does not wait or display at all.

Problems

Answer these questions before going on:

1. Construct a payoff matrix for a game of long wait (where $m(\text{Long Wait}) \geq 0.5V$) versus no display. Explain how you worked out each payoff, referring to the payoffs in **Table 7.2** when appropriate.

2. Explain whether $E(\text{Long, Long})$ will be positive or negative number.

Back to the future

A version of the payoff matrix that you should have gotten is in **Table 7.3**.

Table 7.3: Payoffs for Long wait versus No Display when $m(\text{Long}) > 0.5V$.

	Long	No Display
Long	< 0 (negative)	V
No Display	0	$0.5V$

OK, now if Long represents a strategy where display times are more costly than $0.5V$, will it be stable against invasion by individuals who simply do not display? Once again, Long is common, No Display is rare. Looking down the first column of **Table 7.3** which shows the most common interactions for each strategy, *we can see that No Display can invade once the displays get costly (long) enough.*

One other point about No Display. Notice that if $0.5V \geq m(\text{Display})$, then the matrix looks like **Table 7.4** instead and A population of No Display can be invaded!

Table 7.4: Payoffs for Display wait versus No Display when $m(\text{Display}) < 0.5V$.

	Display	No Display
Display	> 0 (positive)	V
No Display	0	$0.5V$

Conclusions

This exercise has shown us that there is no pure ESS in the waiting game. We have seen that no displays can be invaded by increasingly more lengthy (costly) displays until the point where the cost of the display exceeds 0.5, the resource value at which point no display can invade again!

Rock, Scissors, Paper

It is often pointed out that the outcome we have just seen has certain similarities to the child's game Rock, Paper, Scissors. Recall that in that game (which you may have played) there are three pure strategies (rock, paper, or scissors). Here are their definitions:

- Rock breaks Scissors: $E(R,S) = +1$, $E(S,R) = -1$, and $E(R,R) = 0$.
- Scissors cuts Paper: $E(S,P) = +1$, $E(P,S) = -1$, and $E(S,S) = 0$.
- Paper covers Rock: $E(P,R) = +1$, $E(R,P) = -1$, and $E(P,P) = 0$.

The payoff matrix is given in **Table 7.5**.

Table 7.5: Payoffs for Rock, Paper, Scissors.

	Rock	Scissors	Paper
Rock	0	+1	−1
Scissors	−1	0	+1
Paper	+1	−1	0

As with the waiting times we have just investigated, clearly none of these strategies are pure ESSs (use the "look down the column" rule. Do you remember (from your childhood) the best way to win or at least survive in this game? We'll come to it in a moment.

7.5 A Mixed ESS Solution to the Waiting Game

So, how about our "war of attrition" game? From the previous section it should be clear to you that there are situations where any pure waiting time (pure strategy) can beat any other (but not all others). Thus, there is no pure ESS solution to the war of attrition. However, could there be a mixed ESS?

For an overview of the answer to this question, let's start out with the Rock, Scissors, Paper game. Its solution will have some parallels the one for our war of attrition which we will see on the next page. But it will also have one very important difference, which we will explain in the next section. Nevertheless, let's continue with Rock, Scissors, Paper.

If you played Rock, Scissors, Paper, as a child, you may remember that you could not win if your opponents knew which strategy you were going to pick. For example, if you pick Rock consistently, all your opponent would need to do is pick Paper and s/he would win. A child discovers quickly that if she or he doesn't know what the opponent will pick, then the best strategy is to pick Rock, Paper, or Scissors at random. In other words, the player selects Rock, Paper, or Scissors with a probability of $\frac{1}{3}$. This was probably how you consistently beat inexperienced, younger players (who tend to employ the same pure strategy repeatedly until they catch on).

It should be obvious that *if you do know what your opponent is likely to do*, then picking a strategy at random with a probability of $\frac{1}{3}$ is not be the best thing to do (unless that is the strategy your opponent is using!).

If you played Rock, Scissors, Paper with a probability of $\frac{1}{3}$ strategy as a child, you may remember that when you played the game against another savvy player, you only won half the time. But the other player did not win any more often and if someone else tried a different strategy, he or she did not do as well. Playing either Rock, Paper, or Scissors at random with a probability of $\frac{1}{3}$ in each game is a mixed ESS. It is mixed since it involves playing three different strategies at a fixed (equilibrial) probability. It is an ESS since it is both of higher fitness than any alternative pure or mixed strategy.

Now back to our waiting game. Unlike Rock, Scissors, Paper, potentially there are an infinite number of pure strategies (each a different waiting time) instead of just three. Nevertheless, in the next section we will see that the solution has one important parallel to Rock, Scissors, Paper in that the solution requires a mixed strategy.

Chapter 8

A Mixed ESS Solution to the War of Attrition

Synopsis: *This chapter will show that a particular mixed strategy that is composed of all possible acceptable costs, each to be played at a unique frequency is evolutionarily stable in the symmetrical war of attrition against any pure strategy (unique maximum cost) or other mix of pure strategies. We will term the stable mixed strategy* **var**. *We will see that* **var** *is characterized by:*

- *a constant probability of continuing (or quitting) from one cost to the next,*
- *the probability of continuing is governed by the value of the contested resource,*
- *the result of a constant rate of continuing (or quitting) is a negative exponential distribution of quitting costs—most* **var** *strategists quit at relatively low costs.*

The approach in this chapter will be to

- *first review the idea of a mixed ESS,*
- *then show (using some simple and fully explained calculus) how we discover an equation that describes an equilibrial mix of all possible maximum costs.*
- *Finally, using the basic rules we learned earlier to determine an ESS and some simple calculus and graphs, we will show that this equilibrial mix is also evolutionarily stable.*

Please note: *This is the most mathematical chapter of the text. It must be so because we will need to derive an equation that describes potentially an infinite number of behaviors (an infinite number of different maximum acceptable costs). In finding this equation and later in showing that* **var** *is an ESS, we will make use of simple differential and integral calculus. I have tried to explain why these techniques are used and further, to explain how they are used so that any interested student, regardless of whether or not they are familiar with calculus, should be able to follow the arguments.* As importantly, I hope to convince students of the benefits to any biologist gained by understanding basic calculus.

8.1 The Basics of a Mixed ESS in the War of Attrition

In the previous chapter we saw that in the symmetrical war of attrition, *each unique cost x* that an animal is prepared to pay (or time it is willing to display) *is a pure strategy.* Thus, there are *potentially an infinite number of pure strategies each defined by a different cost x.* We also learned that *no pure strategy is an ESS in the war of attrition.* Given this, could there be a mixed ESS?

In looking for this mixed ESS, we must realize that *any pure strategy is a candidate for inclusion in the mixed ESS.* In fact, we expect that *every possible pure strategy should belong to the* **mix** (i.e., all possible maximum acceptable costs should support the **mix**). The reason for this is simple—we learned earlier that under the right circumstances, any **fix**(cost) strategy can increase and/or mixes of these strategies can appear—it's just that none of these are evolutionarily stable. So, we expect that any stable mix will contain all possible strategies as supporting strategies.

Definitions:

A **pure strategy** is defined as some unique maximum acceptable cost between zero and infinity. **Supporting strategies** are all pure strategies that are members of an equilibrial mix. See [Bishop and Cannings, 1978]. A synonym for supporting strategy is **component strategy**.

In characterizing a **mix**, *we must know the likelihood that a given player might encounter each of these supporting strategies.* While it is possible that these frequencies are the same for each supporting strategy, it would seem far more likely that many, if not all, supporting strategies would occur at their own unique frequencies. The only rules are that

- all of these frequencies must add up to 1.0 (since they form the whole population)
- and of course, the frequencies for each supporting strategy are such that each ends up with the same fitness.

Thus, we can summarize the **mix** as

$$\mathbf{mix} = \text{prob}(\text{cost}(a_1)) + \text{prob}(\text{cost}(a_2)) + \cdots + \text{prob}(\text{cost}(a_n)) = 1 \tag{8.1}$$

where each a_i is a supporting strategy and $\text{prob}(\text{cost}(a_i))$ is either the frequency of the strategy in the population or the probability that a mixed strategist "adopts" that particular cost in a given contest.

Notice the last point—as we learned earlier when we considered the `Hawks` and `Doves` game, there are two ways to produce an equilibrial mix. To this list, we'll add a third. A population that is evolutionarily stable could be

- a population of **pure strategists**, each pure strategy is at its appropriate equilibrial frequency, or
- a population of **mixed strategists**, each of whom can potentially play all strategies of the equilibrial mix at the appropriate frequencies. Thus, in a given contest a mixed strategist uses some mechanism to adopt a particular maximum acceptable cost at the correct frequency. What it adopts in one contest in no way influences what it will do the next time, or
- a population that is a mix of supporting pure strategists (each at the appropriate equilibrial frequency) and mixed strategists (since they play each supporting cost at the equilibrial frequency). To take this a step further, the mixed strategists could even be "incomplete mixes" so long as they complemented each other and the net result was that ¡B¿in the population as a whole, the chance of any individual being in a contest with any strategy supporting the **mix** was always the equilibrial value for that strategy.

This last point is very important, so let's make it one more time. All that matters *for a population to be evolutionarily stable* is that

- the fitnesses of each supporting strategy must be equal. As always, isofitness in no way requires that each supporting strategy actually has the same frequency!
- the **mix** is immune from invasion.

It doesn't matter how the appropriate mix is obtained—whether it is from mixed strategy individuals, pure strategy individuals in the correct frequencies, or some combination of the two.

8.2 Supporting Strategy Probabilities at Equilibrium

As we start to look for a way to describe the **mix**, we seem to face a daunting task. We expect all possible costs to be members of this **mix**. Thus, there are an infinite number of supporting strategies each potentially at its own unique frequency. So, we will not be able to use the simple technique to find the **mix** that we learned with `Hawks` and `Doves`. Instead of only needing a couple of linear equations to find two frequencies, *we need a function that can give us the correct frequency for an infinite number of different supporting strategies!* What follows is a general description of the methods used by Maynard Smith [1974] to find this function.

Please read this section carefully. It sets the foundation, establishes terminology, and reviews the mathematics used throughout the rest of our treatment of the war of attrition.

We shall use the payoff that a specific supporting strategy expects to receive when competing against the **mix** to find the function that gives us the equilibrial frequency of each strategy supporting the **mix**. So, we start with a pure strategy that is a member of the **mix**.

- This **focal supporting strategy** is willing to pay up to cost $x = m$.
- So, we'll refer to it as $\mathbf{fix}(x = m)$.

Now, imagine that $\mathbf{fix}(x = m)$ is about to play a series of contests at random against other individuals (supporting strategies) from that mix. So, $\mathbf{fix}(x = m)$'s opponent in any contest can be understood to be **mix** itself.

Remember, it doesn't matter whether $\mathbf{fix}(x = m)$'s opponent is a pure or mixed strategist: in either case we know the result is that only one strategy can be played by an opponent in a given game and the chance that a particular strategy (maximum cost) will be faced is given by the characteristics of the equilibrium.

Let's find an equation for the payoff $\mathbf{fix}(x = m)$ receives against any other supporting strategy in the **mix**, $E(\mathbf{fix}(x = m), \mathbf{mix})$. Starting, in general terms

$$\begin{aligned} E(\mathbf{fix}(x = m), \mathbf{mix}) = {} & \text{Lifetime Net Benefits to Focal Strategy in Wins} \\ & - \text{Lifetime Costs to Focal Strategy in Losses} \end{aligned} \tag{8.2}$$

A reminder, gentle reader: Remember our purpose in writing equations for lifetime net benefit and cost will be to extract a function that predicts the frequency of each component strategy of the **mix**.

In finding these equations, let's make one other important assumption: *the resource has a constant value in any given contest.* You may think that it is obvious that a resource value should be constant in any contest. There certainly are many if not most situations where this is true. But, think for a moment and you'll realize that it is quite possible for a resource to become depleted during a contest. For example, individuals may be contesting a resource that one of them already is using or that naturally depletes in value over time independent of anything the contestants are doing. Or, while two individuals contest for a resource, it is possible that another individual, perhaps a member of a different species depletes it. So, while reasonable for most situations, the assumption that for a contest V is a constant may not always be justified.

Finding Expected Lifetime Net Benefits

Benefits are only obtained by the focal strategist when she wins—i.e., when the focal strategist is willing to pay a higher cost than her opponent from the **mix** ($x < m$, where m is the cost the focal strategist will pay).

$$\text{Net Benefit to } \mathbf{fix}(x = m) \text{ in a win} = V - x, \tag{8.3}$$

where V is the resource value and x is the cost the opponent from **mix** is willing to pay.

Unfortunately, (8.3) is not sufficient for our needs. The complexity of the war of attrition intervenes! Recall that the mix is composed of an infinite number of component strategies. **fix**($x = m$) only faces one of these supporting strategies in any given contest. Thus, (8.3) only describes the net gain in one specific contest. You should realize that this particular contest will probably be quite rare given the many different strategists that **fix**($x = m$) could face from the mix. Thus, one particular contest and its benefits will have little if any important *lifetime effect* on **fix**($x = m$)'s fitness. Single contests cannot describe the net benefit that the focal supporting strategy expects to gain from a large number (a lifetime) of contests.

To get an accurate measurement of lifetime net gains, we need to take into account all types (costs) of contests that **fix**($x = m$) will win (i.e., those where the opposing strategy x is at most m) and the probability of each.

$$\text{Net Benefit} = \sum_{0 \le x \le m} [(V - x) \times (\text{Probability of facing } x)]. \tag{8.4}$$

Note that this is an infinite sum because there are an infinite number of different costs (strategies) x between 0 and m. To handle this type of sum, we will need to use calculus, which we now briefly consider. We will return the question of lifetime net benefits once we have introduced the appropriate calculus techniques.[1]

8.3 An Introduction to Integration

The probability of facing a particular strategy x is determined by a **probability density function** or **pdf**. We will illustrate the idea by examining a number of different situations.

Situation 1:

Suppose that there are an infinite number of strategies x that players adopt with $0 < x \le 1$. Assume further that each strategy x with $0 < x \le 0.5$ is just as likely to occur as any other in this interval. Finally, assume that each strategy x with $0.5 < x \le 1$ is *twice* as likely to occur as any strategy x with $0 < x \le 0.5$. If we assign a positive probability p to any strategy x in $(0, 0.5]$, then since there are an infinite number of other equally likely startegies, they, too, would have probability p. But then summing these probabilities would produce an infinitely large value, not 1. For this reason, the probability that any particular strategy x is encountered must be 0.

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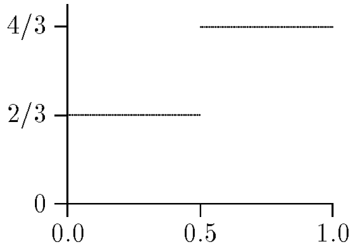
[1] Material in the next section was written by Kevin Mitchell; don't blame Kenneth Prestwich.

A better question to ask is what the probability is of facing a strategy x that falls within a certain interval. For example, let p denote the probability of encountering a strategy x that lies in the interval $(0, 0.5]$. I claim that $p = 1/3$. Here's why:

- The strategies in $(0.5, 1]$ are twice as likely to be encountered as those in $(0, 0.5]$, so they have a total probability $2p$, i.e., twice the probability of those in $(0, 0.5]$.
- But since the only strategies are those between 0 and 1, we must have $1 = p + 2p = 3p$, or $p = 1/3$.

Suppose, next, that we wanted to know the probablity of encountering a strategy x with $0 < x \leq 0.25$? Well, since all the strategies in $(0, 0.5]$ are equally like, and since their total probability is $p = 1/3$, and since $(0, 0.25]$ is exactly half the interval $(0, 0.5]$, we conclude that the probablity that $0 < x \leq 0.25$ must be half of p, that is $p/2 = 1/6$. In the same way you should be able to show that the probablity that $0.75 < x \leq 1$ is $1/3$.

Figure 8.1: A geometric realization or probability density function $p(x)$ for situation 1.



The function $p(x)$ in **Figure 8.1** gives a geometrical representation of situation 1. It has the following properties.

- $p(x_1) = p(x_2)$ for any two strategies x_1 and x_2 in $(0, 0.5]$ because they are equally likely.
- $p(x_1) = p(x_2)$ for any two strategies x_1 and x_2 in $(0.5, 1]$ because these, too, are equally likely.
- But $p(x_2) = 2p(x_1)$ for any strategy x_2 in $(0.5, 1]$ and x_1 in $(0, 0.5]$ because strategy x_2 is *twice* as likely as x_1.
- The region under the graph of $p(x)$ on the interval from 0 to 0.5 is rectangle whose area is $\frac{1}{2} \cdot \frac{2}{3} = \frac{1}{3}$ Which is the probablity that x is in $(0, 0.5]$.
- The region under the graph of $p(x)$ on the interval from 0.5 to 1 is rectangle whose area is $\frac{1}{2} \cdot \frac{4}{3} = \frac{2}{3}$ which is the probablity that x is in $(0.5, 1]$.
- The region under the graph of $p(x)$ over the entire interval from 0 to 1 is $\frac{1}{3} + \frac{2}{3} = 1$ which is the probablity that x is in $(0, 1]$.
- More generally, the area under $p(x)$ on the interval $[a, b]$ represents the probability of a strategy x where $a \leq x \leq b$.

The function $p(x)$ is an example of a **probability density function** or pdf. Such functions must satisfy two conditions:

1. $p(x) \geq 0$ for all x,

2. the total area under $p(x)$ must be 1.

For a given x the function $p(x)$ measures the *comparitive* or *relative likelihood* of strategy x. This is why the graph of p is twice as high on $(0.5, 1]$ as it is on $(0, 0.5]$.

Siutation 2:

Assume that the only strategies x are those such that $0 \le x \le 2$ and that all of these strategies are equally likely. Since they are all equally likely, $p(x)$ must be constant on $[0, 2]$, so that the region under the graph is a rectangle. Since the area under the pdf over $[0, 2]$ must be 1, the the constant height (for the rectangle) must be $\frac{1}{2}$ because the base is 2 (see **Figure 8.2 (a)**).

Figure 8.2: (a) The probability density function $p(x)$ when all strategies between 0 and 2 are equally likely. The area under the graph from a to b is $\frac{1}{2}(b-a)$.

Since all strategies are equally likely, the probability that a particular strategy x lies in $[0, 1]$ is just $\frac{1}{2}$ or half the total probablity. Of course this corresponds exactly to the area under $p(x)$ in **Figure 8.2 (a)** over the interval $[0, 1]$: it is a $1 \times \frac{1}{2}$ rectangle. In fact, if b is any number in $[0, 2]$, then the probability of encountering a strategy x in the interval $[0, b]$ is the area under the curve from 0 to b, that is, $b \times \frac{1}{2} = \frac{b}{2}$. The probablity that one encounters a strategy with waiting time less than or equal to x is called the the **cumulative probability distribution of quitting times**, and is denoted by $P(x)$. Note the uppercase P for the cumulative function and the lowercase p for the density function. In this example, $P(x)$ is just the area of the rectangle from 0 to x with height $\frac{1}{2}$, so

$$P(x) = x/2, \qquad 0 \le x \le 2.$$

If we want to find the probability of encountering a strategy x between a and b, we could find the area of the rectangle from a to b. Its base would be $b - a$ and the height $\frac{1}{2}$, so its area is $\frac{b-a}{2}$. But this probablity can be expressed more generally using $P(x)$. The probability we want is just the area from 0 to b minus the area from 0 to a as in **Figure 8.2 (b)**. But this is just

$$P(b) - P(a) = \frac{b}{2} - \frac{a}{2} = \frac{b-a}{2}.$$

Situation 3:

Suppose again that the only possible strategies x are those such that $0 \le x \le 2$ and that the pdf is $p(x) = x/2$. Notice that this is a legitimate pdf since $p(x) \ge 0$ and the region under the graph of p is a triangle whose area $\frac{1}{2} \cdot 2 \cdot 1 = 1$ (see **Figure 8.3 (a)**).

What is the cumulative distribution $P(x)$ for this situation? Well, $P(x)$ is just the area under p from 0 to x which is just a triangle with base x and height $p(x)$ (see **Figure 8.3 (b)**). Thus,

$$P(x) = \frac{1}{2} \cdot x \cdot p(x) = \frac{1}{2} \cdot x \cdot \frac{x}{2} = \frac{x^2}{4}.$$

Figure 8.3: (a) The probability density function $p(x) = x/2$ for $0 \leq x \leq 2$. (b) $P(x) = x^2/4$ is the area under p from 0 to x.

For example, the probability that a strategy x lies in the interval $[0, 0.5]$ is

$$P(0.5) = \frac{(0.5)^2}{4} = \frac{0.25}{4} = 0.0625,$$

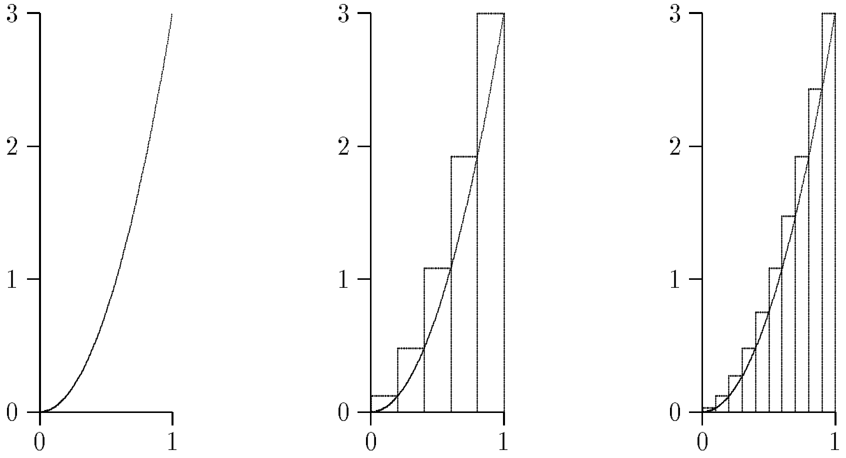
while the probability that x is in the interval $[0.5, 1.5]$ is

$$P(1.5) - P(0.5) = \frac{(1.5)^2}{4} - \frac{(0.5)^2}{4} = \frac{2.25}{4} - \frac{0.25}{4} = 0.5.$$

Situation 4:

Suppose now that the possible strategies are restricted to $0 \leq x \leq 1$ and that $p(x) = 3x^2$ (see **Figure 8.4 (a)**). Clearly $p(x) \geq 0$, so to show that $p(x)$ is a pdf, we need to show that the area under this curve is 1. But how do we find the area of a curved region?

Figure 8.4: (a) The probability density function $p(x) = 3x^2$ for $0 \leq x \leq 1$. (b) $P(x)$ is the area under p from 0 to x.



We can't directly use the area formula of a rectangle to determine the area, but we can use it indirectly to *approximate* the area under the curve. Suppose we divide the interval $[0, 1]$ into five subintervals of equal width

$$\Delta x = \frac{1 - 0}{5} = 0.2.$$

Approximate the area under the curve on each subinterval by using a rectangle whose height is determined by evaluating p at the right-hand endpoint of the subinterval (see **Figure 8.4 (b)**). These five right-hand endpoints will be $x_1 = 0.2$, $x_2 = 0.4$, $x_3 = 0.6$, $x_4 = 0.8$, and $x_5 = 1$. So in this case, the five heights would be $p(x_1) = p(0.2)$, $p(x_2) = p(0.4)$, $p(x_3) = p(0.6)$, $p(x_4) = p(0.8)$, and $p(x_5) = p(1)$. Thus, approximate area is

$$\begin{aligned}\sum_{k=1}^{5} p(x_k)\Delta x &= p(0.2)\cdot 0.2 + p(0.4)\cdot 0.2 + p(0.6)\cdot 0.2 + p(0.8)\cdot 0.2 + p(1)\cdot 0.2\\ &= 0.2[p(0.2)+p(0.4)+p(0.6)+p(0.8)+p(1)]\\ &= 0.2[3(0.2)^2+3(0.4)^2+3(0.6)^2+3(0.8)^2+3(1)^2]\\ &= 0.2[0.12+0.48+1.08+1.92+3]\\ &= 0.2(6.6)\\ &= 1.32.\end{aligned}$$

If we used ten rectangles instead each with width $\Delta x = 0.1$ (see **Figure 8.4 (c)**), the approximation is even better. This time, the area is

$$\begin{aligned}\sum_{k=1}^{10} p(x_k)\Delta x &= p(0.1)\cdot 0.1 + p(0.2)\cdot 0.1 + \cdots + p(0.9)\cdot 0.1 + p(1)\cdot 0.1\\ &= 0.1[p(0.1)+p(0.2)+\cdots+p(0.9)+p(1)]\\ &= 0.1[3(0.1)^2+3(0.2)^2+\cdots+3(0.9)^2+3(1)^2]\\ &= 0.1(11.55)\\ &= 1.155.\end{aligned}$$

The same process using one-hundred rectangles (no drawing for this!) yields an approximation of 1.01505 and with one-thousand rectangles the approximation is 1.0015005. It appears that these approximations are getting close to 1 as the number of rectangles gets large.

Mathematicians define the *exact* area under the curve to be the limit of this rectangular approximation proccess as the number of rectangles n becomes infinitely large,

$$\lim_{n\to\infty} \sum_{k=1}^{n} p(x_k)\Delta x.$$

We denote the limit of this summation process more compactly as

$$\int_0^1 p(x)\,dx.$$

This is read as, "The integral of $p(x)$ from 0 to 1." The integral sign, $\int$, is an elongated S, a reminder to us that an integral is really a sum. The lower and upper limits of integration (here 0 and 1, respectively) are the beginning and ending points of the interval where the sum is taking place. The expression $p(x)dx$ is meant to remind us of $p(x)\Delta x$, the area of a rectangle of height $p(x)$ and width Δx. Think of $p(x)dx$ as being the area of infinitesimally thin rectangle of height $p(x)$.

In our particular case, with $p(x) = 3x^2$, it appears that

$$\int_0^1 3x^2\,dx = 1,$$

and this is, in fact, correct. The Fundamental Theorem of Calculus tells us that under certain circumstances such integrals can be easily evaluated using functions called antiderivatives. In fact, the cumulative distribution function is just an antiderivative of $p(x)$. In this particular situtation using calculus, $P(b)$, that is, the area under $p(x) = 3x^2$ over the interval from 0 to b, is given by the formula

$$P(b) = \int_0^b 3x^2\, dx = b^3.$$

Since $P(b) = b^3$, then the cumulative distribution function is $P(x) = x^3$, which calculus students will recognize as an antiderivative of $p(x) = 3x^2$. Using methods developed in integral calculus, such antiderivatives can be found for a wide variety of functions.

Using the notation of integrals, we can express the probability of encountering a strategy x in the interval $[a, b]$. This is just the area under the curve $p(x)$ on this interval, or $\int_a^b p(x)\, dx$. But we saw that earlier that this is just the area from 0 to b minus the area from 0 to a (as in **Figure 8.2 (b)**) so,

$$\int_a^b p(x)\, dx = \int_0^b p(x)\, dx - \int_0^a p(x)\, dx = P(b) - P(a). \tag{8.5}$$

It is customary to use the symbol $P(x)\Big|_a^b$ to denote the difference $P(b) - P(a)$. So we would write

$$\int_a^b p(x)\, dx = P(x)\Big|_a^b.$$

In the case of situation 4, with $p(x) = 3x^2$ and $P(x) = x^3$, the probability that x lies in the interval $[a, b]$ is

$$\int_a^b 3x^2\, dx = x^3\Big|_a^b = b^3 - a^3.$$

For example, the probability that x lies in the interval $[0.2, 0.8]$ is

$$\int_a^b 3x^2\, dx = \int_{0.2}^{0.8} 3x^2\, dx = x^3\Big|_{0.2}^{0.8} = (0.8)^3 - (0.2)^3 = 0.512 - 0.008 = 0.504.$$

A more realistic situation:

Generally speaking, strategies are not restricted to finite intervals such as we have used in the previous examples. That is, x can take take on any nonnegative real value, $x \geq 0$. That means that a pdf $p(x)$ must be defined on the infinite interval $[0, +\infty)$, not just some finite interval such as $[0, 1]$ or $[0, 2]$. On the other hand, the area under this curve must still be 1 since it represents the probability of encountering some strategy, that is,

$$\int_0^\infty p(x)\, dx = 1.$$

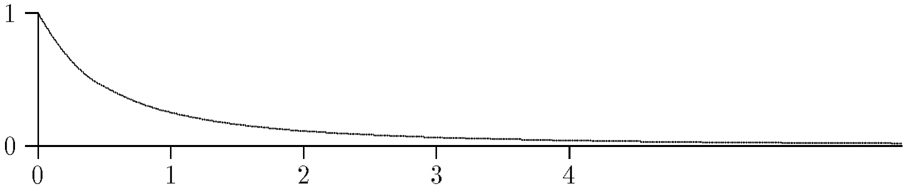
Such expressions are evaluated using limits. We first evaluate the expression $\int_0^b p(x)\, dx$. Then we see what happens to this expression as b gets infinitely large. The notation for this is

$$\lim_{b \to \infty} \int_0^b p(x)\, dx.$$

Here's a simple example: Suppose that the pdf was $p(x) = 1/(x+1)^2$ for $x > 0$. To show that this is a pdf, we need to show that the area under the curve (see **Figure 8.5**) is 1. That is we need to show that

$$\int_0^\infty \frac{1}{(x+1)^2}\,dx = 1.$$

Figure 8.5: The probability density function $p(x) = 1/(x+1)^2$ for $x \geq 0$. The total area under this infinitely long curve is 1.



It turns out that the cumulative distribution function (or in calculus terms, an antiderivative[2] for $p(x)$ is $P(x) = 1 - \frac{1}{x+1}$. Using this and limits to evaluate the integral above.

$$\int_0^\infty \frac{1}{(x+1)^2}\,dx = \lim_{b\to\infty}\int_0^b \frac{1}{(x+1)^2}\,dx = \lim_{b\to\infty} 1 - \frac{1}{x+1}\Big|_0^b \tag{8.6}$$

$$= \lim_{b\to\infty}\left(1 - \frac{1}{b+1}\right) - \left(1 - \frac{1}{0+1}\right). \tag{8.7}$$

Now as b gets large $\frac{1}{b+1}$ approaches 0. So

$$\int_0^\infty \frac{1}{(x+1)^2}\,dx = \lim_{b\to\infty}\left(1 - \frac{1}{b+1}\right) - \left(1 - \frac{1}{0+1}\right) = (1-0) - (1-1) = 1$$

as expected.

Our excursion to calculus is now complete and we return to the discussion of lifetime benefits.

Finding Expected Lifetime Net Benefits, Continued

Before our calculus interlude, we were attempting to get an accurate measurement of lifetime net gains, we need to take into account all types (costs) of contests that **fix**$(x = m)$ will win and the probability of each. Let m be the specific maximum cost that our focal contestant (**fix**$(x = m)$) will pay. Then our focal contestant only wins those constests in which the opponent's strategy x is between 0 and m. So

$$\text{Net Benefit} = \sum_{0\leq x\leq m}[(V - x)\times(\text{Probability of facing } x)]. \tag{8.4}$$

We saw that we could approximate such sums by dividing the interval $[0, m]$ up into n pieces each of width Δx, so (8.4) becomes

$$\text{Net Benefit} = \sum_{k=1}^{n}(V - x_k)p(x_k)\Delta x.$$

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[2] Calculus students note that the general antiderivative for $p(x) = \frac{1}{(x+1)^2} = (x+1)^{-2}$ is $P(x) = -(x+1)^{-1} + c$. We must choose c so that $P(0) = 0$, because the probability that an opponent quiting at cost less than 0 is 0.

Here, as in our earlier situations, $p(x_k)\Delta x$ represents the approximate probability of encountering opponent strategies willing to pay roughly cost x_k. This probability is multiplied by $V - x_k$ to obtain the net benefit accruing from such an encounter. To get the exact net benefit, we take the limit as the number of subintervals n becomes infinitely large.

$$\lim_{n\to\infty} \sum_{k=1}^{n} (V - x_k)p(x_k)\Delta x.$$

From our calculus excursion, we recognize this limit is an integral. So we can re-express (8.4), the equation for the net benefit to focal supporting strategy versus the equilibrial mix as

$$\text{Net Benefit} = \int_0^m (V - x)p(x)\,dx. \tag{8.8}$$

Expected Lifetime Costs for Losses

Benefits were the hard part of the E(focal supporting strategist, **mix**) equation. Now, the much simpler equation for **lifetime costs** to focal strat **fix**($x = m$) in contests it loses to the **mix** (i.e., a mixed strategy opponent).

As before, the logic is simplE:c **fix**($x = m$) loses whenever x, the cost the opponent from **mix** in any particular contest is willing to pay, is greater than m. All of these contests end with a cost of m. Therefore, for any one losing contest,

$$\text{Cost to } \mathbf{fix}(x = m) \text{ of a Loss} = -m. \tag{8.9}$$

So, unlike the equation for net benefit, the costs in any loss are always the same. But, we're not done because as with net benefits, we need to take into account the proportion of the time **fix**($x = m$) encounters an opponent that (in this case) it loses to in the **mix**. So

$$\text{Cost of Losses} = m \times \text{probability of losing to strategies with } x \geq m$$

Since loses occur whenever **fix**($x = m$) encounters a strategy x with $x > m$, then the probability that **fix**($x = m$) loses is

$$Q(m) = \int_m^\infty p(x)\,dx.$$

Thus, the lifetime costs of losing to the **mix**, i.e., losing to a mixed strategist is

$$\text{Cost of Losses} = mQ(m) = \int_m^\infty p(x)\,dx, \tag{8.10}$$

where m is the maximum cost that our focal supporting strategy will pay and the function $Q(x) = \int_m^\infty p(x)\,dx$ gives the lifetime proportion of times that **fix**($x = m$) loses to another member of the **mix**. Notice that as with net benefits, the function $p(x)$ is central.

Expected Lifetime Payoff

So, to get the expected lifetime payoff to **fix**($x = m$) vsersus the equilibrial mix, we simply substitute the equations for net benefit, (8.8), and cost, (8.10), and obtain

$$E(\mathbf{fix}(x = m), \mathbf{mix}) = \left(\int_0^m (v - x)p(x)\,dx\right) - mQ(m). \tag{8.11}$$

OK, we have the payoff and cost equations, (8.8) and (8.10), that contain the pdf function $p(x)$. How does one find the correct function $p(x)$ for the war attrition? It is not terribly difficult, but then neither is it central to our story. If you are interested, you should take a look at the **Appendix** at the end of this chapter. It is a beautiful application of a number of ideas from calculus. But for the moment, we'll proceed directly to the next section where we'll introduce the result that Maynard Smith obtained for $p(x)$ and we'll discuss it in considerable detail.

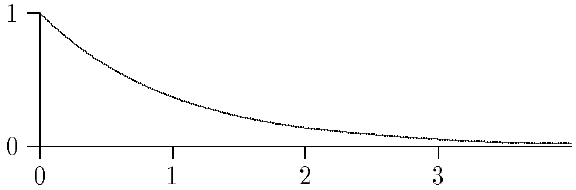
8.4 The Mathematics of the Mixed Equilibrium

Maynard Smith's goal was to find a function, $p(x)$, that would supply the frequencies of each supporting strategy (i.e., cost, x) for an equilibrium in the war of attrition. To get $p(x)$ he used (8.11) and obtained the following result,

$$p(x) = \tfrac{1}{V} e^{-x/V}, \tag{8.12}$$

where $p(x)$ is the probability density function (dimensions of probability per unit cost), x is cost, V is resource value, and e is the base of the natural logarithm function[3] ($e \approx 2.713$). See **Figure 8.6**. Negative exponential funcitons are an example of a very important group of functions called **Poisson distributions**[4].

Figure 8.6: The probability density function $p(x) = \frac{1}{V} e^{-x/V}$ when $V = 1$. The area under this curve from 0 to ∞ is 1.



If you've taken calculus the following sort of argument will be familiar; if not, just get the idea that we apply appropriate antiderivative and limit rules to get the expected result. From calculus,

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[3] Remember that $e^{-x/V} = \frac{1}{e^{x/V}}$. Negative exponents are the same thing as the multiplicative inverse of the expression.

[4] Poisson distributions are mathematical descriptions of large numbers of random events. Starting from a few simple equations that describe random events, these equations generate predictions for the large scale patterns that would result. These resulting distributions have a number of different shapes that are determined by the type of process that is being modeled.

One example of a natural phenomenon that can be modeled using a Poisson distribution is radioactive decay. We know is that there is a certain chance that an unstable nucleus of a certain type will emit energy each moment in time. Thus, decays appear to be random events that have a certain chance of happening each unit of time. Using a type of Poisson distribution known as an exponential decay, which is in form identical to (8.12) (the basis for our description of the behavior of the stable mixed strategy **var**), we can either: predict the probability that a given nucleus will decay after some starting time or, if we have a population of nuclei, we can predict the number of decays that should occur per unit time.

Closer to home, the distribution of quitting costs used by a **var** strategist will also have a negative exponential decay. And that is because just like the radioactive nuclei, there is a certain probability of continuing (quitting) for each increment of cost.

Poisson distributions are extremely important in science in general and in biology in particular. Other versions of the distribution, for example, form the basis for determining whether or not patterns we observe in nature are random as compared to grouped.

an antiderivative (read cumulative distribution function[5]) for $p(x) = \frac{1}{V}e^{-x/V}$ is just

$$P(x) = 1 - e^{-x/V}.$$

Now we can show that the total area under the density function $p(x) = \frac{1}{V}e^{-x/V}$ is 1. First use limits to express the infinitely long interval of integration and then use the antiderivative of p,

$$\int_0^\infty p(x)\,dx = \lim_{b\to\infty}\int_0^b \tfrac{1}{V}e^{-x/V}\,dx = \lim_{b\to\infty} 1 - e^{-x/V}\Big|_0^b.$$

Next do the evaluatoin,

$$\lim_{b\to\infty} 1 - e^{-x/V}\Big|_0^b = \lim_{b\to\infty} 1 - e^{-b/V} - (1 - e^{0/V}) = \lim_{b\to\infty} 1 - \frac{1}{e^{b/V}}.$$

Now as the exponent b gets infinitely large, the entire denominator gets infinitely large forcing the fraction to approach 0. So

$$\lim_{b\to\infty} 1 - \frac{1}{e^{b/V}} = 1 - 0 = 1.$$

Putting this all together,

$$\int_0^\infty p(x)\,dx = \lim_{b\to\infty}\int_0^b \tfrac{1}{V}e^{-x/V}\,dx = 1.$$

Let's also see how to integrate (8.12) to get an expression that tell us the chance that an individual plays up to a certain time. First, let's find an expression for the total proportion of individuals in the mix who are expected to have quit between costs between zero and cost $x = m$. This of course is the same as giving the chance that a mixed strategist will quit by cost m. This is the **cumulative probability distribution of quitting times** $P(x)$ that we saw earlier. In this case, when $x = m$, the probability we seek the area under the probability density curve $p(x) = \frac{1}{V}e^{-x/V}$ between 0 and m, or

$$\begin{aligned} P(m) = \int_0^m p(x)\,dx = \int_0^m \tfrac{1}{V}e^{-x/V}\,dx &= 1 - e^{-x/V}\Big|_0^m \\ &= 1 - e^{-m/V} - (1-1) \\ &= 1 - e^{-m/V}. \end{aligned} \tag{8.13}$$

To reiterate: When we evaluate (8.13) for any particular cost x, the result will be the total proportion of a population of mixed strategists who would have quit as of cost x. That is, $P(m) = 1 - e^{-m/V}$ includes those quitting at cost $x = m$ and all that have quit before cost m.

Figure 8.7 shows plots of $P(x)$ for three resource values (V) over a range of costs between $x = 0$ and $x = 10$. Notice that in all cases the chance of having quit is (of course) initially zero. As contest costs accumulate, it becomes more likely that one will have quit since costs start to exceed the maximum different supporting strategies are willing to pay. Note: We have talked about individuals who quit at cost 0; assume that what really happens is that they quit after an infinitesimally small cost, $0 + dx$, is paid).

Another way to think about these plots is to imagine 1000 identical **mix** strategists starting a display game. At time zero, all are playing so zero have quit. A short time later some have quit, as

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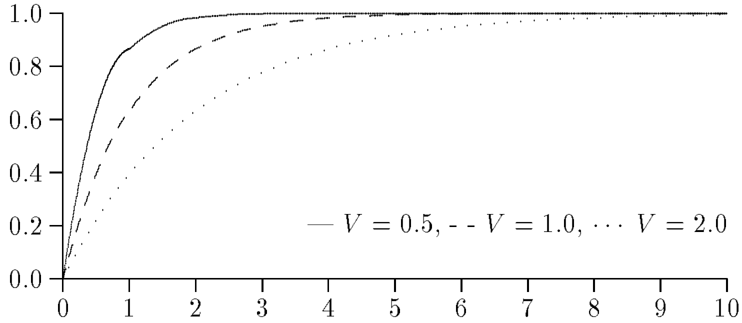
[5] The general anitderivative of $p(x) = \frac{1}{V}e^{-x/V}$ is just $P(x) = -e^{-x/V} + c$, but to account for the fact that $P(0) = 0$, we must set $c = 1$ in the cumulative distribution.

Figure 8.7: $P(x)$ for three resource values (V) over a range of costs between $x = 0$ and $x = 10$.



time goes on a greater and greater proportion have quit and so the overall chance that an individual who started the game will have quit gradually increases.

The other thing to note is the effect of V on quitting. As V gets larger, individuals quit at lower rate (fewer quit per increase in cost x). This should make sense—a contestant should be less likely to give up over a valuable resource. In fact, the rate of quitting is proportional to $1/V$; more about this below.

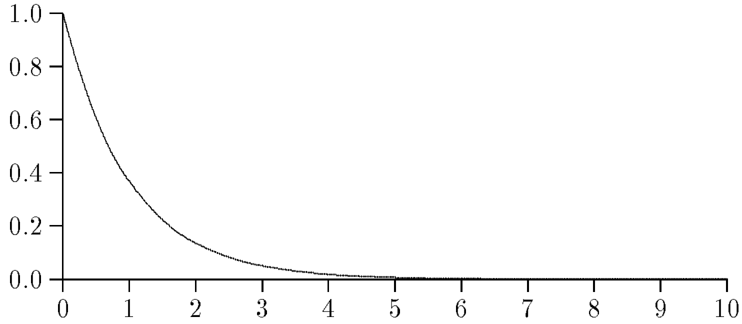
Hopefully this is all starting to make a lot of sense. Now let's look at the converse of the cumulative probability of having quit as cost x (alternately—the total frequency of quitters as of cost x). The converse would be the cumulative probability of those who have not quit as of cost x. Equivalently, this is the probability of not having quit, or the **probability of enduring to a certain cost** x. We call this $Q(x)$ and we saw it earlier in (8.10) for net cost to any supporting strategy versus **mix**.

OK, if $P(x)$ is the cumulative chance that an individual will have quit as some cost, then the probability of enduring up to a certain cost x is

$$Q(m) = 1 - P(m) = 1 - (1 - e^{-m/V}) = e^{-m/V}, \tag{8.14}$$

where we have used (8.13) for $P(m)$. We could, of course, find $Q(m)$ by integrating p from m to infinity. (Try it!) See **Figure 8.8** for a plot of Q.

Figure 8.8: A graph of $Q(x)$, the probability of enduring, when $V = 1$.



Problems

Before going any further, let's be sure that you can calculate the cumulative probability distribution equation $P(x)$. To solve this problem, you will need a calculator or spreadsheet with natural exponential function (exponentiation of e, often called *exp*) or a log table.

1. What is the cumulative chance of quitting between a cost of 0 and infinity if $V = 1$? $V = 5$? $V = 0.5$?

2. What is the cumulative chance of quitting between a cost of 0 and 0.6 if if $V = 1$? $V = 5$? $V = 0.5$?

3. As with $P(x)$, if we evaluate $Q(x)$ in (8.14) for a series of values of costs we can get a plot of the cumulative chance of enduring (not quit) as of any cost x. Reconsider the plot for $P(x)$ in **Figure 8.6**. How must this graph altered to form $Q(x)$?

Cumulative Probability over an Interval

Now, for our last equation before we use everything we've learned to summarize the characteristics of our mixed strategy (i.e., the stable mix). Notice that (8.13) and (8.14) both give **cumulative probabilities**. This means that both give frequencies/probabilities starting at zero up to some cost x. Thus, if that cost x is infinite, then the cumulative chance of having quit by that cost is 1.0 and the cumulative chance of not having quit is 0.

But what if we simply want to know the probability that an individual will quit over some specific cost range—for example, between cost $x_1 = 0.50000$ and cost $x_2 = 0.50001$. This is especially useful in understanding how a computer solves the war of attrition such as in the war of attrition simulation that accompanies this page.

- All we need to do is subtract the cumulative function ($P(x)$ or $Q(x)$) values for two different costs. We will call this probability $\Delta P(m)$ or $P(m_1 \leq x \leq m_2)$, that is, the probability of quitting between the specific costs m_1 and m_2.

- We can also get $\Delta P(m)$ by simply integrating between any two limits. (We already saw this idea in (8.5).)

$$\begin{aligned} \Delta P(m) = P(m_1 \leq x \leq m_2) &= \int_{m_1}^{m_2} \tfrac{1}{V} e^{-x/V}\, dx \\ &= -e^{-x/V}\Big|_{m_1}^{m_2} = -e^{m_2/V} - (-e^{-m_1/V}) = e^{-m_1/V} - e^{m_2/V}. \end{aligned} \tag{8.15}$$

Notice that using (8.13) gives the same expression,

$$\Delta P(m) = P(m_2) - P(m_1) = (1 - e^{m_2/V}) - (1 - e^{-m_1/V}) = e^{-m_1/V} - e^{-m_2/V}.$$

So, we have now gone over the equations that can give us various probabilities or frequency distributions in the war of attrition. And most importantly, all of these are the "children" of (8.12), the probability density function that Maynard Smith derived starting with (8.11). We will use these functions in the discussions below.

In the next section, we will discuss what (8.12) really means: what does it say about mixed strategies in the war of attrition. After we have a full description of this mix, we will turn to our final task—proving that the **mix** is an ESS.

Problems

4. Name the probability distributions that we saw earlier that give

  a) the probability of continuing to a certain cost;

  b) the probability of quitting as of a certain cost.

5. If (8.15) gives the chance of continuing for a unit of cost, find an expression that gives the chance of quitting per unit cost.

8.5 A Description of the Mixed Equilibrium

We are now at a point where we can understand the characteristics of the mixed equilibrium. As mentioned previously, this equilibrium could consist of either

- *a mix of individuals* who played different *pure strategies* (single maximum costs) but where the frequency of each pure strategy type was **equilibrial** (as ultimately described by (8.12),
- *a population consisting entirely of mixed strategists*—that is, individuals who were capable of playing any strategy in a given contest so long as the probability of playing a particular maximum cost was ultimately given by by (8.12), or
- *some mix of the two above*, including perhaps alternative versions of mixed strategists so long as the overall frequency of each supporting strategy in the population as a whole was in line with (8.12).

Thus, (8.12) has a key role in describing the equilibrium. In this section we will focus on the characteristics of the equilibrium. How should members of a population at this equilibrium act?

Important Convention: For convenience we are going to think about our population in terms of the second possibility just discussed—we will regard the equilibrial population as consisting entirely of mixed strategists, all of whom are capable of playing any maximal cost with a probability ultimately described by (8.12). Since other mixes are possible we'll give this particular mix a name **var** for **variable cost strategist**.

A Note About Strategy Names

Some of this is reiteration of what was just said but please glance over it so that you are familiar with the strategy names and definitions we will use from here on out.

The names and symbols we will use for the strategies are a bit different than those used by Maynard Smith [1974] and Bishop and Cannings [1978]. They are meant to be more descriptive and therefore easier for someone to remember; hopefully this use will not result in any confusion. to those familiar with these author's work. I do this with some reluctance but have found that my students seem to have an easier time this way as compared to using symbols such as I and J or **mix**. So:

- As just mentioned, we'll call the evolutionarily stable mix discovered by Maynard Smith **var** for variable display cost. **var** consists of all possible costs played at frequencies determined by the probability density function, (8.12). **var** will be the center of most of our discussion.
- The term **mix** will apply to any mixed strategy—i.e., a strategy that conforms to (8.1).

- The name **fix**(x) will apply to any strategy whose players select a fixed maximum display cost (time) x. Thus, there are potentially an infinite number of versions of **fix**(x), each characterized by different maximum costs but all sharing the characteristic that over a lifetime they have but one maximum cost (in contrast to **var**). We have previously considered **fix**(x) in detail in the previous chapter and shown why they are not evolutionarily stable.

- For the rest of our treatment of the war of attrition, we will regard **fix**(x) strategists not as supporters of the **var** equilibrium but instead as competitors, i.e., potential invaders. Just think of them as attempting to invade a population consisting entirely of mixed strategists; the addition of any **fix**(x) strategist will have the effect of changing the frequency of a particular maximum acceptable cost (which can be generated by either a **var** strategist or this **fix**(x) invader) from the equilibrial value given by (8.12). We're going to learn whether or not this alteration will be permanent.

The characteristics of the mixed strategy var

1. Like other strategies, **var** is highly secretive! *There can be no information transfer from* **var** *to its opponent that might signal when* **var** *will quit.*

    - Thus, the opponent of a **var** (variable display cost strategist) never knows nor never can know exactly when the **var** strategist will quit. No factor (e.g., physiological condition or some intention movement) can be allowed that might tip off the opponent as to **var**'s intentions.
    - Obviously, if such information transfer occurred, it would be easy to create a strategy against **var** (out-wait **var** in any contest up to $m \geq V/2$, quit at $m = V/2$).
    - This is one of the few important characteristics of **var** that is not subsumed by (8.12). But note that it is also a characteristic that any strategy should possess. For instance, if a **fix**(x) strategist tips its hand, it would also place it at a disadvantage.

2. **var** strategists may potentially play any cost—from no cost to (theoretically) an infinite cost. We discussed the reasons for this in the introduction to this chapter.

3. **var** strategists have a constant rate of continuing over each unit of cost. *The chance of continuing is proportional to* $1/V$. This quantity is also known as the **rate constant**.

$$\text{Probability of Continuing Per Unit Cost } x = e^{-1/V}. \tag{8.16}$$

    This is the function $Q(x)$ in (8.14) with $x = 1$. Thus, with regard to the chance of **var**'s continuing of a display:

    - the exponent x/V of e in (8.12), (8.13), (8.14), and (8.15) is nothing more than a cost/benefit ratio. Looking at cost and benefits separately is also instructivE:c
        - The larger x/V is (the cost/benefit ratio), the smaller the chance of continuing. (This should be clear because the exponent x/V occurs with a negative sign in the expression $e^{-x/V}$.)
        - So, since the chance of quitting is the inverse of continuing, the larger x/V is (the cost/benefit ratio), the greater the chance of quitting.
    - Thus:

  - the chance of continuing is *directly proportional* to the resource V. This should make good intuitive sense—the more valuable the resource the less likely a contestant should be to quit in a given increment of cost.
  - The chance of continuing is *inversely proportional* to the cost or cost increment—the greater the cost, the lower the probability of continuing.

4. Now, since the behavior of a **var** strategist is determined by a certain chance of quitting with each unit of cost, and since **var** never tips its hand, you should realize that an opponent will never know exactly when a **var** strategist will quit—anymore than you, me or anyone can always correctly guess when a "fair" coin will turn up "heads." Thus, knowing when something will happen is quite different from knowing the chance of some event. This is the essence of the problem **var**'s opponents face!

5. Another result of a constant chance of continuing per unit cost (i.e., a constant chance of quitting per cost) is that the chance of accepting greater costs (i.e., of playing from the start through to cost x) decreases exponentially (for any value of V less than infinity, i.e., for any $e^{-x/V} \leq 1.0$). The effect of this is that there is virtually no chance that a **var** strategist will be willing to pay a cost that is very large compared to V.

   - What this means is that even though the chance of remaining or quitting is always the same for those who are still playing the game, the number of players will drop most rapidly at the start and then more gradually as the number of players approach zero. We have already seen this in **Problem 3** in the plot of $Q(x)$ (the chance of playing from the start to a particular cost x) vsersus cost. (See also **Figure 8.8**.)
   - As mentioned earlier, we call this type of plot an **exponential decay**. Examples of exponential decay include probability density in (8.12), $Q(x)$ in (8.14), and $\Delta P(x)$ in (8.15).

6. So, to summarize, the opponent:

   - can have a general idea of what a **var** strategist will do in a contest for a given resource if it has a knowledge of the distribution of **var** strategists willing to pay different maximum costs, $Q(x)$.
   - However, the opponent can never consistently predict **var**'s actions in any particular contest. That is because **var**'s actions at any cost are totally independent of anything that it did in previous games—whether it continues from one moment to the next is simply a matter of a constant chance factor.
   - Thus, **var** is "predictably unpredictable."

   The last statement is perhaps the most crucial in understanding the behavior of **var** strategists. Central to it are the ideas of constant probability of continuing the game and independence of decisions from one moment (cost) to the next. You will also explore this in great detail when you run the simulations.

Problems

6. Compare what a contestant sees when it confronts a population consisting entirely of **var** strategists as compared to a population that is an equilibrial mix of pure supporting **fix**(x) strategies. Would the contestant see any difference in these two situations?

7. How would you express the idea of constant rate of quitting with respect to a population of pure strategists who together produce an equilibrium?

8. Why is it crucial that no information as to **var**'s intention to continue or quit a contest be passed on to its opponent?

9. How do you estimate the probability that a **var** strategist will win a contest of cost x?

10. How do you estimate the probability that a **var** strategist will lose a contest of cost x?

11. How do you estimate the probability that a **var** strategist loses by paying a cost between x and $x + \Delta x$?

12. These final questions call for solutions to equations derived from (8.12), the probability density function that describes **var**. You will need a calculator or spreadsheet.

- **a)** Should the chance of encountering a member of the "stable mix" with a quitting cost between 0.60 and 0.61 be greater or less than encountering an individual with a quitting cost between 0.60 and 0.62? Explain.
- **b)** What is the chance of encountering a member of the stable mix with a quitting time between a cost of 0.60 and 0.61 if $V = 1$? $V = 0.5$? Compare these answers with the next question.
- **c)** What is the the chance of encountering a member of the **mix** who quits between a cost of 1.0 and 1.01 if $V = 1$? $V = 0.5$? Compare these answers with the last answers. Why the difference—the size of the cost interval is the same?

8.6 Proving that var is Evolutionarily Stable

Requirements of Proof

We now know the general characteristics of the mixed strategy we call **var**—the range of its maximum display costs, the probability of playing each of these costs and their relationship of these probabilities to the resource, etc. And we know that the equation (8.12) which describes **var**'s behavior sprung from the assumption that

$$E(\text{any fix}, \mathbf{var}) = E(\text{any mix}, \mathbf{var}) = E(\mathbf{var}, \mathbf{var}) = \text{a constant}$$

Finally, we know that Bishop and Cannings [1978] have shown that this assumption must be correct for any ESS in the symmetrical war of attrition (see Bishop-Cannings theorem).

However, simply showing that the **var** strategy has some behavior consistent with being an ESS is not the same thing as showing that it is an ESS. Recall the two general rules for finding ESSs we learned about earlier. **var** is an ESS (cannot be invaded if sufficiently common) if

Rule 1. Common interactions: $E(\mathbf{var}, \mathbf{var}) \geq E(\mathbf{fix}(x), \mathbf{var})$.

Rule 2. Common interactions): **a)** If $E(\mathbf{fix}(x), \mathbf{var}) = E(\mathbf{var}, \mathbf{var})$, then (rare interactions): **b)** $E(\mathbf{var}, \mathbf{fix}(x)) \geq E(\mathbf{fix}(x), \mathbf{fix}(x))$.

Now, in the case of **var** we are only interested in Rule 2 since we already know that Rule 2 a): $E(\mathbf{fix}(x), \mathbf{var}) = E(\mathbf{var}, \mathbf{var})$ is true. **var** is derived from this! And of course Rule 2 is not consistent with Rule 1. But just because **var** is derived from Rule 2 a) does not mean that it must be consistent with Rule 2 b). And if **var** versus any **fix**(x) is not consistent with Rule 2 b), then **var** is not an ESS .

If var were not an ESS, what would It be? If **var** versus any $\mathbf{fix}(x)$ is only consistent with Rule 2 a), it is **equilibrial**. This is because if $E(\mathbf{var}, \mathbf{fix}(x)) \geq E(\mathbf{fix}(x), \mathbf{fix}(x))$ is false, then the only interpretation that is also consistent with Rule 2 a) is that $E(\mathbf{var}, \mathbf{fix}(x)) = E(\mathbf{fix}(x), \mathbf{fix}(x))$. So, the common interactions would have the same fitness consequences on each party (no advantage to either) and the rare interactions would also give no advantage to either strategy. Note that the payoffs in common versus rare interactions would not have to equal each other, the only equality needed is that common are equal for both as are the rare. The result is that selection could not change the strategy frequencies and we would say that the population was equilibrial.

So, to show that **var** is an ESS all we need to do is to show that Rule 2 b) holds, i.e., $E(\mathbf{mix}, \mathbf{fix}(x)) \geq E(\mathbf{fix}(x), \mathbf{fix}(x))$.

What will follow is a mathematical proof that Rule 2 b) is, in fact, true and therefore that **var** is an ESS in the war of attrition. Once again, there will be a bit of calculus to enhance the argument but anyone should be able to follow at least the outline of the proof. As before the calculus is all explained, furthermore, much of it is very similar to what we have seen earlier. And, to make the concepts clearer, graphs will be presented.

The Proof

Once again, to show that **var** is an ESS requires that:

Rule 2 b) $E(\mathbf{mix}, \mathbf{fix}(x)) \geq E(\mathbf{fix}(x), \mathbf{fix}(x))$

is true. So, we will need to find expressions for $E(var, \mathbf{fix}(x))$ and $E(\mathbf{fix}(x), \mathbf{fix}(x))$ and determine whether or not the difference between the two is always a positive number, i.e.,

$$E(\mathbf{mix}, \mathbf{fix}(x)) - E(\mathbf{fix}(x), \mathbf{fix}(x)) \geq 0. \tag{8.17}$$

Now, recall from (8.2) that the payoff to a given strategy in a certain type of contest is always

$$\begin{aligned} E(\mathbf{fix}(x = m), \mathbf{mix}) = {} & \text{Lifetime Net Benefits to Focal Strategy in Wins} \\ & - \text{Lifetime Costs to Focal Strategy in Losses.} \end{aligned} \tag{8.2}$$

So, let's find the net benefit and cost equations for $E(\mathbf{mix}, \mathbf{fix}(x))$ and $E(\mathbf{fix}(x), \mathbf{fix}(x))$ and then substitute them into (8.2) before finally solving to see if we have an ESS. We'll use the same general symbols and operations that we used in finding $E(\mathbf{fix}(x), \mathbf{var})$ earlier.

Part One: Calculation of Net Benefits

Benefits needed to calculate these payoffs are easy to find and so they represent a good place for us to start. First, recall that we assume that the value of the resource is constant in any given contest; further we assume that it has the same value to both contestants. As usual, we will symbolize it as V. Here are the net benefits for each type of interaction.

Net benefits to varin contests versus $\mathbf{fix}(x)$ Remember that **var** does not enter a contest possessing a particular maximum cost that it is willing to pay (as does a $\mathbf{fix}(x)$ strategist). Instead, at each instant it has a constant probability of quitting proportional to $1/V$. Thus, it is *unpredictable* as to exactly when it will quit.

Recall that in wars of attrition, winners, like losers, pay costs. These costs lower the net (realized) value of the resource to the winner. We'll call the maximum cost the $\mathbf{fix}(x)$ strategist is willing to pay m. So, against a given $\mathbf{fix}(x = m)$ strategist, **var** wins whenever it is willing to pay more (i.e., whenever it continues to play after **fix**$(x = m)$ quits. Thus, when **var** wins, it will always win $V - m$. But remember that it is not certain that **var** will play to a higher (winning) cost than **fix**$(x = m)$ since var uses a probability function to determine when to quit. So, **var** expects to get

$$\text{Net Benefit} = \sum_{0 \leq x << \leq m} [(V - m) \times (\text{Probability of facing } x)](8.4)$$

Recall from earlier that the chance that **var** has not quit as of paying any cost $x = m$ (i.e., the chance that **var** has continued long enough so that the cost it is willing pay, m, is greater than its opponent) is

$$Q(m) = \int_m^\infty p(x)\, dx. \tag{8.18}$$

The equation says to find the chance that **var**has not quit as of cost m by adding up all of the probabilities of **var** quitting at costs greater m. Obviously, this sum is the total proportion of times when **var** had not quit as of a given cost m. We saw this equation for $Q(x)$ earlier.

So, since for any contest that ends at a cost of m that **var** wins, **var** will receive $V - m$. And, **var** will win at a frequency given by (8.18). Thus, the benefit to **var** is

$$\text{Benefit} = (V - m) \int_m^\infty p(x)\, dx. \tag{8.19}$$

Notice that $V - m$ is outside of the integral because in the case of **var** against a given **fix**$(x = m)$, **var** can never expect to win anything except $V - m$. So, $V - m$ is a constant for a contest that can last up to a given cost m. And **var** only wins when it has not quit as of m. **var** will of course quit displaying when it wins at cost m. Remember this when you see (8.23) for the cost **var** pays in losses—there may only be one way to win against a given **fix**$(x = m)$ but are many ways for **var** to lose. In that case, the cost will remain within the integral.

Substituting (8.18) into (8.19) yields

$$\text{Benefit} = (V - m)Q(x). \tag{8.20}$$

and by (8.14), $Q(m) = e^{-m/V}$, so

$$\text{Benefit} = (V - m)e^{-x/V}. \tag{8.21}$$

Net benefits in fix(x) versus fix(x) contests In this contest we have two identical **fix**(x) strategists facing each other. Thus, they play to exactly the same cost $x = m$. Since we assume no other asymmetries, then it is best to assume that two identical individuals will each win 50% of the time—they will in effect split the net benefits. Thus,

$$\text{Benefit for } \mathbf{fix}(x) \text{ versus } \mathbf{fix}(x) = 0.5(V - m) = 0.5(V - x) \tag{8.22}$$

Part Two: Calculation of the Cost of Losing

Calculation of cost to var strategists in losses to fix(x) For contests involving var, the calculations will be a bit more complicated than those for net benefit. As mentioned above, the reason is that **var** can lose to a given **fix**$(x = m)$ many ways! Here's an example.

- Suppose that a **var** strategist repeatedly plays a **fix**$(x = m = 1)$ strategist in contests where $V = 1$. What happens in terms of costs?

  - We know that **var** loses anytime it quits before paying a cost slightly greater than 1.
  - There are many ways that a **var** strategist can lose to a **fix**$(x = 1)$ strategist over a repeated number of games because **var** can play a potentially infinite number of losing costs (i.e., costs between 0 and 1) against **fix**$(x = 1)$.
  - There is a distinct probability associated with each of these losing gambits (costs).

- So, over a lifetime, the cost that a **var** strategist expects to pay when it selects a losing cost will be equal to the *sum of the product of each unique losing cost times the probability of playing that losing cost.*

This idea is expressed mathematically using integration:

$$\text{Cost to } \mathbf{var} \text{ Losing to } \mathbf{fix}(x = m) = \int_0^m xp(x)\,dx. \tag{8.23}$$

Let's be sure we understand what (8.23) means:

- x is the cost **var** paid as of the moment of quitting, and
- $p(x)dx$ is the chance of quitting between cost x and the next infinitesimally small increment in cost. Thus,
- the product of x and $p(x)dx$ is the expected lifetime cost to **var** of playing to a particular cost x and then quitting.
- Now, since there are many ways to lose, therefore we must
- sum (integrate) the values expected for each contest cost $xp(x)dx$ between $x = 0$ and $x = m$, the cost the **fix**$(x = m)$ opponent is willing to pay.
- This sum is the the lifetime cost **var** expects to pay in losing contests where the opponent is willing to pay a certain amount m.

We can solve (8.23) by inserting (8.12) for $p(x)$ and integrating[6],

$$\text{Cost to } \mathbf{var} \text{ Losing to} \mathbf{fix}(x = m) = \int_0^m xp(x)\,dx = \int_0^m x\tfrac{1}{V}e^{-x/V}\,dx = V - e^{-m/V}(V + m). \tag{8.24}$$

Calculation of cost to fix(x) strategists when versus fix(x) Once again, this is a very easy calculation. The contestants are identical, both are willing to pay cost $x = m$. As we said in our consideration of benefits, we simply assume that each individual wins 50% of the time. So, half the time they lost and pay cost $x = m$

$$\text{Cost paid by } \mathbf{fix}(x = m) \text{ in losing to } \mathbf{fix}(x) = 0.5x = 0.5m. \tag{8.25}$$

---

[6] Calculus students will recognize that this is an integration by parts problem, since

$$\int x\tfrac{1}{V}e^{-x/V}\,dx = -xe^{-x/V} + \int e^{-x/V}\,dx = -xe^{-x/V} - Ve^{-x/V}.$$

Part Three: Payoff Equations

Section A: $E(\mathbf{fix}(x=m),\mathbf{fix}(x=m))$ We'll reverse things now and start with $\mathbf{fix}(x)$ contests that end in ties (since they're easy). Now, recall from (2.1)

$$\text{Payoff(to Strategy 1, when versus Strategy 2)} = \text{(Benefit from win)} - \text{(Cost of loss)}. \quad (2.1)$$

If we simply substitute the equations for benefit in winning (8.22) and cost in losing (8.25) into (2.1) we obtain

$$E(\mathbf{fix}(x=m),\mathbf{fix}(x=m)) = 0.5V - m. \quad (8.26)$$

Section B: $E(\mathbf{var},\mathbf{fix}(x=m))$ This time we substitute (8.19) and (8.23) into (2.1)

$$E(\mathbf{var},\mathbf{fix}(x=m)) = \text{Benefit} - \text{Cost} = (V-m)\int_m^\infty p(x)\,dx - \int_0^m xp(x)\,dx. \quad (8.27)$$

If we integrate this equation we obtain as in (8.21) and (8.24), then

$$E(\mathbf{var},\mathbf{fix}(x=m)) = 2Ve^{-m/V} - V. \quad (8.28)$$

The Mixed Strategy var is Evolutionarily Stable

Recall from above that to prove that **var** is evolutionarily stable that we need to show that Rule 2 b) is correct.

Finding an equation for the difference in payoffs Starting with Rule 2 b), we must show that

$$E(\mathbf{mix},\mathbf{fix}(x=m)) \geq E(\mathbf{fix}(x=m),\mathbf{fix}(x=m)).$$

or equivalently, we must show that

$$E(\mathbf{var},\mathbf{fix}(x=m)) - E(\mathbf{fix}(x=m),\mathbf{fix}(x=m)) \geq 0.$$

Now

$$E(\mathbf{fix}(x=m),\mathbf{fix}(x=m)) = 0.5V - m$$

and from (8.28)

$$E(\mathbf{var},\mathbf{fix}(x=m)) = 2Ve^{-m/V} - V.$$

So we must show

$$E(\mathbf{var},\mathbf{fix}(x=m)) - E(\mathbf{fix}(x=m),\mathbf{fix}(x=m)) = 2Ve^{-m/V} - V - 0.5V - m \geq 0.$$

This simplifies to showing that

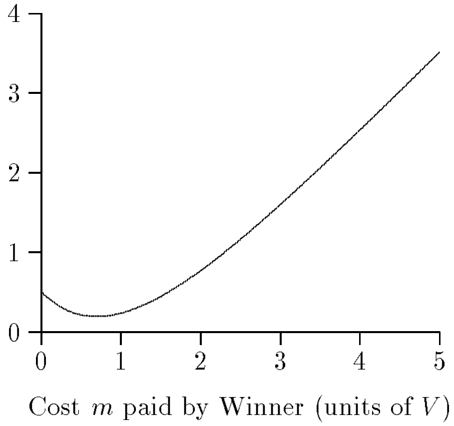
$$E(\mathbf{var},\mathbf{fix}(x=m)) - E(\mathbf{fix}(x=m),\mathbf{fix}(x=m)) = 2Ve^{-m/V} - 1.5V + m \geq 0. \quad (8.29)$$

Now the big question—is (8.29) always positive as it must be if **var** is an ESS? We could start out by simply graphing it. If we do so for $V=1$ we will see that there is no place where $E(\mathbf{var},\mathbf{fix}(x)) - E(\mathbf{fix}(x),\mathbf{fix}(x)) \geq 0$. See **Figure 8.9**.

Thus, it would appear that **var** is stable. But not so fast—this is for only one value of V. Is it possible that there are values of V where **var** is not evolutionarily stable? After all, V does affect **var**'s behavior.

As with finding the frequency of each maximum acceptable cost (when we looked for $p(x)$), solving for every possible V might appear to be a difficult problem (and approached that way, it is!). However, once again a bit of elementary calculus can come to our aid and comfort.

Figure 8.9: The graph of $E(\mathbf{var}, \mathbf{fix}(x)) - E(\mathbf{fix}(x), \mathbf{fix}(x))$ is always positive when $V = 1$. (Looks like the "swoosh" doesn't it!)



Mathematical Proof

To show that no point on (8.29) is less than or equal to zero, we need to find the minimum value of (8.29). This occurs where the slope of the graph is zero (the flat part of the graph above; on that graph it happens at a value somewhere near cost $m = 0.7$).

- To find this point for any V, we use the calculus technique of **differentiation**. It will give us an equation for the slope at every point of a plot of (8.29).
- If we then solve this "equation of slopes" for the cost m where the slope equals zero we find that this always occurs at $V \ln 2 \approx 0.693V$.
- Now, all that remains to do is to substitute the value $0.693V$ back into (8.29) and solve for $E(\mathbf{var}, \mathbf{fix}(x = m)) - E(\mathbf{fix}(x = m), \mathbf{fix}(x = m))$. The result is the that *minimum difference* is always $(\ln 2 - 0.5)V \approx 0.193V$.

Thus, **var** is an ESS!

Graphical Illustration of the Proof

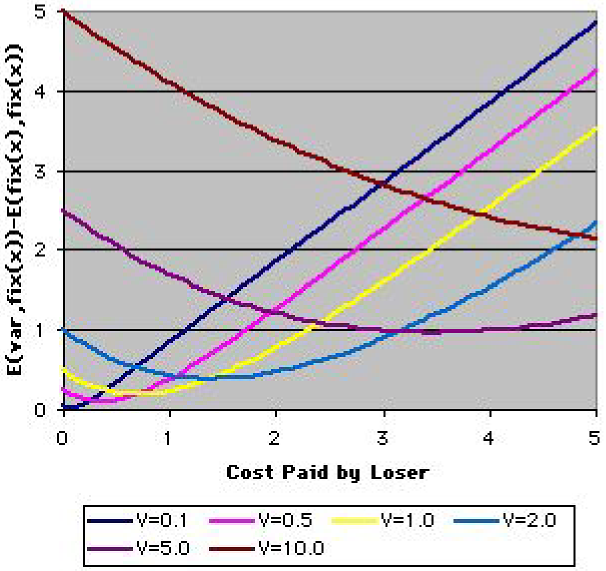
If you are not fully confident that you understand the proof, you will probably be reassured if you look at the graphs below of (8.29) for different values of V. Remember, the minimum difference in fitness will always be approximately $0.193V$ and will always occur at cost $m \approx 0.693V$. Thus, as V gets larger the minimum difference between the two payoffs increases.

For any cost m paid by the winner, $E(\mathbf{var}, \mathbf{fix}(x)) - E(\mathbf{fix}(x = m), \mathbf{fix}(x = m)) > 0$. Consequently, $E(\mathbf{var}, \mathbf{var}) = E(\mathbf{fix}(x), \mathbf{var})$ and **var** is evolutionarily stable against any $\mathbf{fix}(x)$!

Problems

13. Write an expression for the lifetime cost to a **var** strategist of quitting at a cost of exactly x.

Figure 8.10: The evolution of a population.



14. Write an expression for the lifetime cost to a **var** strategist for losing contests where the winner was willing to pay m?

15. What is $E(\mathbf{var}, \mathbf{fix}(0))$ in the case of a tie?

Things to Remember About the var Strategy

Perhaps the most striking thing about the **var** strategy is that its opponent never can know when it will quit. We have seen that the overall pattern of quitting is described by an exponential decay type of Poisson distribution with a rate constant equal to $1/V$. Thus, an opponent could learn[7] in general terms what its **var** opponent would do. It could "know" that it was most likely to quit early in a contest and that the chance of quitting per unit of contest display cost is $e^{-1/V}$. From this, it is possible to calculate (or learn from experience) the *expected* outcome of contests of various costs. Even if it knew these things, it could never know whether or not **var** really would quit with the next increment of cost. Thus, no amount of experience with **var** strategists will allow an opponent any edge over it.

The other thing to reiterate about **var** is that there is a logic to its quitting. It is tied to the resource value—the greater that value, the less likely that **var** will quit at any particular cost and as a consequence it is potentially willing to accept a higher cost contest. Also, since **var** always quits most frequently early in contests, the chance that it will pay large costs relative to a resource value are low.

Problem

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[7] I use the term learn loosely—it could mean "learn" in the usual sense of learning and memory or it may be that we are simply talking about making an appropriate evolutionary response—selection for responses that work against a fixed wait time. In either case, an appropriate response arises to a particular fixed strategy.

16. "Are You Feeling Lucky, Punk?" In the classic Clint Eastwood thriller, *Dirty Harry*, the Eastwood character asks a naer-do-well to predict the future and guess whether or not there bullets left in Eastwood's gun. So what do you think? Are you feeling lucky? The chance of getting killed in a scheduled commercial airline crash is roughly on the order of one in several million. About the same chance the earth has of being hit by a large meteor, small asteroid, or comet. Discuss whether or not someone who flies commercial airlines daily (e.g., a flight attendant or pilot) for years is more likely on her or his next flight to be in a fatal accident. Likewise, the earth has not been hit by a really big one for about 65 million years. Are we more likely to be hit now than we were say 60 million years ago (5 million after the last one). Are you more likely to win on your next lottery entry (tax on stupidity) if you haven't won in the past and less likely if you have won? What does all of this have to do with the war of attrition?

Testing to see if Animals are Using a var-like Strategy

There are a number of famous examples of animals that appear to be playing simple waiting games. We will not go into them here because they are well presented both in the literature and in just about every animal behavior text book. Perhaps the classic is the dung fly, *Scatophaga stercoraria*, studied heavy by Parker [1970a,b] and Parker and Thompson [1980]. The interested reader is urged to consult these papers or any number of behavioral ecology texts. We will finish this page, however, with the following question (which was addressed by Parker and Thompson).

Problem

17. Suppose that someone demonstrated that animal waiting times corresponded to those predicted by (8.14). Does that constitute sufficient proof that a mixed ESS described by (8.14) exists? Explain.

Chapter 9

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Chapter 10

Glossary

Adaptation. An aspect of the phenotype, whether behavioral or morphological that is heritable and that confers a reproductive advantage on its possessor(s) as compared to some alternative trait(s). Thus, the amplification of the genes partially responsible for these traits is due to Darwinian evolution. Traits that are relatively disadvantageous are termed **non-adaptive** or **maladaptive**. Note that the term non-adaptive is also often used for traits that have no significant advantage or disadvantage with respect to each other as occurs in Wrightian evolution (genetic drift). Perhaps a better adjective for these traits is **neutrally adaptive**.

Asymmetry. Where there are differences in the competitiveness of the players. Thus, the outcome of a contest is not simply a matter of chance. Asymmetries can be due to many factors, for instance different ability, experience, motivation, present ownership, and/or condition.

Boundary. In the mathematical sense used in a number of models in this text, a boundary is a frequency above or below which selection forces change from favoring some trait to favoring an alternative.

Contest. The game theory term for the competitive interaction that occurs when two or more individuals attempt to obtain the same resource item.

Continuous variable. A variable with the property that between any two values, there are an infinite number of other values. Synonym—**analog variable**.

Cooperative communication:. Where action by the receiver of a signal increases the fitness of both the signaler and receiver. Also see *honest communication*.

Currency. Units that either directly or indirectly measure fitness, examples are grandchildren, offspring, eggs, energy, time, chance of death, etc. In both games and optimality models, benefits and costs must be stated in a **common currency** and that currency must used throughout the model. Attempting to find the correct currency is one of the most important aspects of modeling.

Cumulative probability distribution. Examples: $Q(x)$ or $P(x)$. The cumulative chance of some event with respect to the independent variable. For example, if the independent variable is cost, then $P(x)$ might indicate the total proportion of times (or individuals) who have quit as of a certain cost. Thus, this would vary between zero (no one has yet quit) and 1.0 (everyone has quit).

$\Delta Q(x)$. For our purposes, the probability that a mix strategist such as **var** will pay a particular cost x and then quit. It can be computed by determining the probability of paying cost x ($Q(x)$) and cost $x - \Delta x$ (where Δx is some small increment of x) using the cumulative probability function. The difference $Q(x - \Delta x) - Q(x)$ is $\Delta Q(x)$ and is equal to the chance that an individual paid cost x and quit.

Discrete variable. A variable that can only possess certain exact values—intermediate values are not possible and are rounded to the nearest permitted value or in rare cases are simply ignored. Synonym: "digital" value.

Dishonest communication. Where action by the receiver of a signal decreases the receivers fitness but increases the sender's fitness. Please note that dishonest is used as a shorthand; no ethical or moral dimensions are necessarily part of this definition. Synonyms: deceit, non-cooperative.

Display. A behavior that has been modified to serve as a form of communication; usually no direct physical contact is involved and if there is such contact it is highly controlled and is short of fighting.

e**.** The base of the of natural logarithm function, approximately equal to 2.7183.

Equilibrial Strategy. In our context, a strategy that is NOT increasing relative to any other as a result of selection. Thus, all equilibrial strategies within a population must have the same fitness. Equilibrial strategies may or may not be evolutionarily stable.

Equilibrium. In evolution, constancy, stasis. A population is in equilibrium when there is no change in the frequency of occurrence of competing phenotypes (e.g., behavioral strategies) or alleles in a population, measured over generational time.

Escalate. When a conflict moves to increasingly direct confrontation and perhaps fights. An often cited example of an escalated conflict occurs in red deer—two well-matched males initially display acoustically by roaring, this may be followed by visual displays typified by parallel walks and may finally escalate into fights with antlers.

Evolutionary stable strategy (ESS). A strategy that cannot be displaced by any other known strategy. Put another way, when its frequency is 1.0 other strategies cannot enter the population and in situations where it appears as a mutant, it increases to fixation. It is a static condition. ESS's can come in two general types—pure and mixed.

$\exp(x)$**.** The natural exponential function: $\exp(x) = e^x$, where $e \approx 2.7183$.

Exponential decay distribution. A distribution that results from applying a constant rate of continuing to the members of some initial population. So, for each value of x, the chance that an individual will chose to continue is constant. Now, since not all continue from one value of x to the next (those that don't continue quit and are no longer in the population of players), the population decreases with x. Since the population is decreasing and since each member of it always has the same chance of continuing, the greatest number quit at first, with fewer at each subsequent step. See **Figure 8.8**.

Fitness. The sum of direct and indirect fitness. For our purposes, it is largely direct fitness which is usually defined as the number of grandchildren. However, many other definitions or stand-ins for fitness are often used – for example, fecundity, number of mates, number of eggs, territory size, territory quality, etc.

Fixed. A population genetics term—a strategy and the "gene" that causes it are said to be fixed when their frequencies are 1.0 (i.e., no alternatives exist in the population).

fix(x)**.** A fixed cost (or fixed display time) strategist equivalent to the fixed cost strategies Maynard Smith [1982] termed a,b,c, ... , etc. In the notation we are using here x refers to the cost that **fix** is willing to pay (its value of m). Thus, x can have any value but when contests are written as **fix**(x) versus **fix**(x) assume that x has the same value for each contestant (i.e., each has the same m).

Frequency-dependence. When the relative fitness of some phenotypic trait such as a behavioral strategy *depends on how commonly certain events or interactions occur.* In the context of games, these events would be certain types of contests. Imagine that an animal with a particular behavioral strategy (focal animal) can experience two particular type of interactions. Further, imagine that one of these interactions is beneficial to focal animal while the other is detrimental. Clearly the fitness of the focal individual will depend on the relative frequencies of each type of interaction—this is frequency dependence.

Game. A series of contests between all strategies in proportion to their frequency. The summed outcome of these contests determines the outcome of a game; a game could be viewed as the interactions that occur over one generation although other definitions are certainly possible.

Honest communication. A shorthand for cooperative communication, please note that intent and morality are not implied.

m. Some maximum cost that a contestant is willing to pay. Thus, it is a specific value of x (cost) or t (time). On many occasions m is used simply to symbolize the maximum cost that some arbitrary focal individual in a given contest will accept. That is the definition we use on this page—most commonly as a maximum cost that a pure strategy is willing to pay as compared to what a variable cost (mix) strategist might pay. It is used inconsistently in the literature—often m is the cost paid at the termination of a contest. Thus, since contests terminate when the cost exceeds what one player is willing to pay by a tiny amount (dx), then this cost (which represents the maximum acceptable cost to the loser) becomes m. Sorry for the confusion.

Mixed ESS. An ESS where individuals either (a) play different strategies a fixed portion of the time (e.g., `Hawk` 60% and `Dove` 40%—termed a **mixed strategy**) such that no other mix would be any more successful or where (b) certain portions of individuals play one strategy all the time (e.g., always `Hawk` or `Dove`) such that the fitness of practitioners of each strategy is equal. Also see *pure strategy*.

Mixed strategy. When an individual plays two or more behavioral strategies, usually as a matter of probability. Thus, selecting a random amount of time to display is an example of a mixed strategy. By contrast, a **pure strategy** involves selecting a particular strategy, for example, always "display for time t."

Optimality. An optimal behavior is one that *maximizes the difference between benefit and cost in some common currency*—for instance fitness, energy, time, rate, etc. Optimality theory is used to predict the best way to perform a behavior for a given set of environmental and physiological conditions, it makes predictions that are independent of the behaviors being used by other individuals.

Pairwise contests. Maynard Smith [1982] wrote about pairwise contests as games where two individuals face off against each other over some resource. The outcomes of these contests, if an individual engages in more than one, have additive effects on the individuals fitness. The games considered in this text involving sequential interactions of `Hawk`, `Dove` and `Bourgeois` are pairwise contests. The rules for determining whether or not an ESS exists in pairwise contests are somewhat different than those of a another model of interaction "playing the field."

Payoff. The net benefit of payoff of single type of contest or interaction. In the honest versus dishonest communication, the payoffs to the receiver were either B or C while in the `Hawk` versus `Dove` each strategy (`Dove` or `Hawk`) had two possible payoffs (one when playing against the same strategy, e.g., D versus D, and the other against the opposite strategy, e.g., D versus H. Multi-strategy games have even more payoffs, their number depending on the number of strategies being played. In the case of waiting games the payoff depends on the time spent waiting and what others do.

Player. In games theory, an individual engaged in a contest, sometimes used broadly as a synonym for a strategy in a contest.

Playing the field. Maynard Smith used this term to describe situations where an individual is not engaged at a certain moment in a contest with just one other individual (who employs a certain strategy) as in pairwise contests, but instead with many individuals. A good example, Maynard Smith points out, is a plant that competes not usually with one other plant but with many neighbors, simultaneously. The rules for discovering whether or not there is a pure ESS for an example of this type of contest are somewhat different than for pairwise contests. This text does not consider playing the field models, the interested reader is urged to consult Maynard Smith [1982] as a starting point.

Pseudorandom number. The result of a "random" number generation by a computer. The computer uses an algorithm to generate a numbers; numbers generated by this means fit models for randomly distributed numbers. However, since a defined set of mathematical operations produce these "random" numbers, they are not random in the truest sense of the term. Many mathematicians and computer scientists have pointed out that there are subtle differences between numbers generated by computer algorithms and those generated by, for instance, observing motion of molecules (or even mixing balls in a lottery machine!). However, for our purposes, pseudorandom numbers are just fine—we will never notice the difference. The term is used simply to remind you that computer generated random numbers are not truly random!

Pure ESS. An ESS where one strategy is fixed and all known alternatives are unable to invade since they have lower fitnesses (see *mixed ESS*).

$p(x)$. The probability density function of cost (x). The function that can be used to find the probability of any supporting strategy in the mix; finding this function was Maynard Smith's main task in describing a mixed ESS to the symmetrical war of attrition. Important Note: this function gives the probability per unit cost and must not be confused with a function that gives probability *per se*. In the war of attrition, a probability density function is used as a central element of the description of a variable cost strategist.

$P(x)$. The cumulative probability distribution function of cost (x). This gives the cumulative probability of some event (for example, quitting display) as a function of some independent variable, in this case, cost (x). It is calculated as the integral of the probability density function. We use $P(x)$ to indicate the cumulative proportion of a population who have quit as of some cost x.

$Q(x)$. The cumulative proportion of individuals who have not quit (are continuing in the contest) as of some cost x.

Rate constant. A constant in the exponent of an equation of exponential decay that determines the how fast the dependent variable (for example, chance of quitting) changes with respect to the independent variable (for example cost). For the var strategist, the rate constant is $1/V$ so the larger the value of the contested resource (V), the smaller the rate constant and therefore the less the independent variable (e.g., probability of quitting) changes per unit time. Thus, for cumulative probability distribution $P(x) = 1 - e^{-\text{rate constant} \cdot x}$ and since in this case the rate constant is $1/V$ then $P(x) = 1 - e^{-x/V}$.

Resource. Any environmental feature (biotic or abiotic) of importance to an organism's fitness. Examples include food, nesting sites, shelter, mates, symbionts, or specific places in the environment that are favorable physiologically or for behavioral reasons. Contests are waged over resources.

Satellite. Usually used in discussions of sexual selection in regards to advertisement behaviors (generally by males). The classical example is from acoustic signaling where satellites are individuals who remain silent but take up a positions (usually hidden) near an actively advertising individuals. They attempt to intercept females that approach the caller. Thus, they do not pay as large costs as do the advertisers. Satelliting may be an evolutionary stable strategy (where at some frequency it produces the same lifetime reproductive success as alternative strategies such as advertisement) or a simple contingent behavior induced by, for example, poor physiological state.

Stasis. Equilibrium, no generational change in allele (or the phenotype determined by the alleles) frequency.

Strategy. A behavior or set of behaviors used by an individual to deal with an important life-history problem (for example finding a mate, rearing young, obtaining food, etc.). As with other definitions, the human term strategy that implies conscious thought is used as a shorthand; no conscious planning is required, even though it might appear that the behaviors are rational and planned in the human sense. The use of the word "strategy" is simply a shorthand that expresses the appearance of the result of some behaviors. It is generally assumed that in most species strategies are largely innate, are produced by the usual genetic and developmental mechanisms, and are acted on by natural selection. However, strategies can also be learned, even in relatively simple animals.

Supporting strategy. Any pure strategy (unique cost in the war of attrition) that is a member of the mixed ESS. Alternatively, it is any unique cost (in the war of attrition) that a mixed strategist plays. A good synonym is component (of the mix) strategy. For example, in the `Hawks` and `Doves` game, if injury cost is greater than V, a mix with supporting (component) strategies `Hawk` and `Dove` results.

Symmetry. Equality with respect to competitive ability as defined in a particular type of contest. An unlikely situation. In most of the models we consider, we assume symmetry as a simplification. If contestants are truly of equal ability, we assume that each has a 50chance of winning the conflict with no resort to further escalation. In real situations, the closer the competitive abilities of two contestants, the more likely that a highly escalated conflict will occur.

t **(time).** A cost measured in terms of time spent displaying. When the symbol t is used, it is meant to refer to a universe of possible values of display times. A given t (e.g., t_1) refers to a specific time. A useful metric since display time is easy to measure and understand and since fitness costs (x) are usually a simple function of time.

x **(cost).** Any display cost in some sort of units that can be converted to fitness. Normally used interchangeably with time of display (t) since $x = f(t)$, where $f(t)$ can be any function that converts time to cost. We always assume that cost is a linear function of time ($x = mt + b$ where m is the slope and b the y-intercept) but there is no reason to assume that this will always be so.

V**.** The value of the contested resource; its reciprocal equals the rate constant in the probability density function and cumulative probability distributions for **var**.

var. A variable cost (variable display time) strategist equivalent to the mixed strategy Maynard Smith [1982] termed I. It is composed of all possible costs (equivalent of all possible fixed cost strategies) each played with frequency determined ultimately by a probability density function.

Zero-sum game. When there is a finite resource that different strategies compete for; it is divided between all competitors according to their competitive ability. While there certainly are many examples of what are essentially zero sum situations, there are also cases where one alternative behavior allows its possessors to exploit a resource not previously available (i.e., not available to alternative strategies) in which case it is a non-zero sum game.

Chapter 11

Appendix: Discussion and Selected Answers

11.1 Problems from Chapter 2

1. Recall that fitness is a relative measure—these games have to do with competing strategies and so it makes no sense to even consider a situation where both are not at least potentially present. Remember that fitness is a relative measure because over the long run, individuals (strategies, genes) that leave more offspring (copies, whatever) of themselves come to dominate the population. If everyone has the same strategy, then, with respect to the evolution of this strategy, they enjoy equal fitness benefits or decrements and so there is no evolution with respect to this strategy. Thus, the fitnesses calculated from the payoff matrix and frequency of different strategies only have meaning in the context of competition. If you have problems with this, review the sections of fitness and competition.

One additional point however. It would be correct to assume that the smaller the fitness value calculated by either of these equations, the smaller the number of offspring to that strategy. Likewise, if the fitness calculation yielded a negative number, that would mean that the strategy would be declining from one generation to the next. While negative fitnesses could not go on indefinitely, if one strategy's fitness was less negative than the other, it would increase relative to the other even though overall, numbers are dropping!

2. The payoff to an individual playing B against one playing strategy A.

3. Each individual plays A 80% of the time and B 20% of the time.

4. A pure strategy is a set of behaviors that an individual will employ in a given set of circumstances. A pure ESS is a single strategy that cannot be invaded by any other known strategy.

A mixed strategy is one composed of several pure strategy components. Maynard Smith [1982] states that there is a random component in the organism's behavior (in terms of which behavioral component it will employ in a given situation). We saw examples of mixed strategies in two-strategy games that had no pure ESS and in the "war of attrition." By contrast, a mixed ESS involves more than one behavior making up an equilibrium. This could a mixed strategy or an equilibrium between individuals of different strategies.

5. **a)** The frequency of strategy B is $B = 1.0 - a = 1.0 - 0.9999 = 0.0001$.

b) The frequency of A versus A interactions in the entire populaton is $a^2 = 0.9999^2 = 0.9998$. From the point of view of an A strategist, the frequency is $a = 0.9999$.

c) The frequency of B versus B interactions is $b^2 = 0.0001^2 = 0.00000001$. From the point of view of a B strategist, the frequency is $b = 0.0001$.

d) The frequency of A versus B interactions $E(A, B)$ is $ab = 0.9999 \cdot 0.0001 = 0.0000999$.

e) The frequency of B versus A interactions is the same: $ba = 0.0001 \cdot 0.9999 = 0.0000999$.

f) From the last two calculations above, you can see that the total frequency of those payoffs in the entire population is equal. But that is not what matters when considering whether or not A or B are pure strategies. We need to know how common each particular interaction is. And that is simply given by the frequency of the strategy with which the focal strategy interacts.

OK, let's see what this means: For payoffs to A: 99.99% of them will be **with other** A **strategists** and 0.01% will be with B strategists. Thus, 9999 tiems more interactions will occur against A; the B interactions would not seem to be very important. For payoffs to B: Once again, 99.99% of them will be with other A strategists and 0.01% will be with B strategists.

Thus, the important payoffs for calculating the fitness of A and B respectively when B is rare are $E(A, A)$ and $E(B, A)$ which account for 99.99% of the interactions for both strategists!

6. $E(B, B) > E(A, B)$ or if $E(B, B) = E(A, B)$ then $E(B, A) > E(A, A)$.

7. From the payoff matrix, $E(B, B) = 0.5$ and $E(A, B) = 1.0$. Thus, B is not stable to invasion by A.

8. Yes, provided that $E(A, A) = E(B, A)$.

9. Absolutely not. Remember that a pure ESS is not inevitable. In a two strategy game, if one strategy is not a pure ESS then you must test to see if the other is as well. If it isn't, then the solution is a mixed ESS. We will later see in three strategy games that if no pure ESS is found using the rules we have just learned then either a mixed ESS or no ESS at all are the possible solutions.

10. Probably not. No costs would seem to imply a very brief contest with injuries only going to the loser. That implies a contest that is probably very asymmetrical—the winner is able to quickly impress its superiority on the loser. Yet hawk vs. hawk contests are supposed to be symmetrical. It has frequently been documented (in many game theory based studies) that animals that are evenly matched tend to fight longer and injury is more likely to occur. In such cases, at least minor injuries would be expected even to the winner. Then there are energy, time and perhaps even predation costs that would be expected to be incurred. For instance in my lab, I have found that the costs of struggles in spiders are very high, especially when compared to walking or other more routine activities that might closely approximate displays. Moreover, these struggles involve anaerobic metabolism (which takes spiders a long time to recover from) and depletion of stores of compounds very important to rapid motion. And sometimes struggles can last for a considerable period of time.

11. For H: $E(A, A)$ is $E(H, H) = -25$. $E(B, A)$ is $E(D, H) = 0$. $E(H, H) < E(D, H)$, therefore H is not an ESS. For D: $E(D, D) = +15$ and $E(H, D) = +50$, therefore D is not an ESS since $E(D, D) < E(H, D)$. There is no pure ESS

12. If the animal has a reasonable expectation of continued reproduction, if it passes by the present fight for this particular resource, and if injuries are likely to be severe and lower significantly its future fitness, then C would be large compared to benefit. A young male elephant seal with little prospect of actually holding a section of beach occupied by females and great chance of injury against a larger experienced male would be a decent example of this sort of situation where $C > B$.

13. The frequency of Hawk is $h = 0.58$. Thus, the he frequency of Dove is $d = (1 - h) = 0.42$.

11.2 Problems from Chapter 4

1. d) One situation to look at is where the payoff to winning the resource is less than zero. But you need to ask yourself the question, "Would any animal work for a such a payoff since it lowers its fitness from what it would get without exhibiting the behavior?" Another situation would be to set the injury or display costs to a low (near zero) value. Think about what these sorts of payoffs mean—could you translate any of them into situations we have talked about in class that deal with the behaviors of real animals?

2. At values greater 1.0 or less than 0.0—in other words, at impossible frequencies!

4. a) It tells you that measures of relative fitness are just that—relative. Evolution is a game of relative advantage (assuming that there is at least enough reproduction so that there is another generation!). In this two strategy game, whenever `Hawk` is more fit than `Dove`, it has a relative fitness of 1.0 (and the same is true of `Dove`). Also, either strategy can maintain a relative fitness of 1.0 even though its absolute fitness decreases with a change in its frequency (for example, the absolute fitness of `Hawk` decreases with increasing numbers of `Hawks`). All that has to be true is that it is more fit than the alternative. Thus, using the default payoffs, H will increase at low frequencies even though whenever it increases it actually results in a lowering of the average reproduction of the next generation of `Hawks`.

c) If the strategy is at a greater frequency than its equilibrium, its fitness is lowered as a result of a relatively large number of unfavorable interactions—for instance, using default payoffs, H versus H interactions are highly unfavorable to H. Thus, as the frequency of H decreases and fewer of these contests occur, the fitness of H increases (proportionately it has more favorable interactions with `Doves`). The value where relative fitness stops increasing is the mixed ESS point—in the case of `Hawk`, the problems with running into other `Hawks` are exactly balanced by the benefits of intimidating `Doves`!

5. a) This individual will have a fitness that is a very, very negative number. It doesn't matter how long an individual lives, if it doesn't reproduce (or somehow gain indirect fitness which is a separate issue), its fitness is zero. Notice that this is a `Dove`-like strategy that cannot work! It is also not a very realistic one since there are usually plenty of ways for an animal to gain a critical resource short of fighting, even when fighting is common.

Notice also that we are in a bit of a mathematical quandary here. By adopting the convention that benefits are positive numbers and costs negative, we cannot easily assign this strategy the fitness it deserves—zero. Recall that in the system we are using, a payoff of zero simply means no effect on fitness, not zero fitness. Zero fitnesses are payoffs that are infinitely negative. This problem is obviated somewhat by using some positive number as a baseline fitness and assigning benefits in addition to that number and costs as values below it with zero as the zero fitness point. But, if you think about it a moment, you'll see that now the problem exists in assigning costs which are now constrained between 0 and the baseline positive value for fitness.

b) This is a `Hawk`-like strategy. There are some problems with the math in this case (see the next part below) but let's use it to make an important point. Death does not matter to the allele responsible for the strategy so long as someone carrying the allele succeeds in reproducing and does so at as least of good of a rate as the alternatives. So, as long as some individuals do win and reproduce, even thought the costs are high, this payoff will be higher than the payoffs to those who never fight and never reproduce.

c) Generally, no. The mathematics of the game assumes that individuals fight a number of sequential contests. If they die in the contests, then their strategy's frequency decreases over time. So, in our `Hawk` and `Dove` game, if `Hawks` kill each other, the frequency of `Dove` (and therefore contests involving `Dove`) will increase over time during the game. Notice that when we determined the fitness of a strategy, we multiplied the payoff of each type of encounter by the frequency of the encounter, which we took to be constant. Thus, the game assumes that no one dies. Injury just lowers success at reproduction.

Now, there is one way that death can be allowed in a game, short of recalculating strategy frequencies after every contest. If everyone simply engages in one contest with an opponent picked at random and if no further contests occur after (so that strategy fitnesses are the aggregates of these one time encounters), then individuals can die and the game will still work. In this case, death is simply equates to a fitness of zero (or since not everyone dies, a very, very high injury cost). Alternatively, the number of living individuals could be used to recalculate the strategy frequencies after each contest, but that is not how we set up the mathematics of the game.

d) In a simple world where fighting was the only way to gain access to a mate, then males that lose or do not engage in fights would have no fitness. If we defined two strategies, "fight" (`Hawk`-like) and display or "don't fight" (`Dove`-like) the payoffs for the "don't fight" strategy would truly be zero or, using the numeration scheme we have selected, the benefit would be zero and the costs (exclusion from mating) infinitely large and negative. Most of the fighters would not succeed and we could define the costs of losing as large. But the benefits to winning would be immense and "fight" would be a pure ESS since $E(\text{fighter vs. fighter})$ would be greater than $E(\text{don't fight vs. fight})$.

However, it should be easy to envision a strategy could invade a population of fighters. They could also eschew all fighting but try to sneak matings. As long as they were successful sometimes, even though the benefits they received would be different than those of the fighter, nevertheless they would not suffer any injuries and they might be able to invade.

In northern elephant seals things like this happen. Large males do defend sections of the beach using displays and fights that can escalate to death. However, other males will try to sneak matings, at least during certain parts of their lives. Now, as to whether or not this sneaking strategy is an ESS or simply a matter of trying to do the best you can given that you don't own the beach will depend on whether or not the fitnesses are equal. Compared to our simple `Hawk` and `Dove` game, this situation is much more complex and if it were an ESS (no one has looked at it, to my knowledge) it might well involve mixes of strategies over a lifetime (not one or the other for an entire lifetime, although this probably happens in some other species such as salmon) that were conditional on an animal's size, age, and general physical condition. So simple games like `Hawk` and `Dove` may help us to learn about some of the factors involved with animal contests, but they need lots of refinement before we can really understand the often highly sophisticated behavior of animals.

6. a) There are 850 individuals of strategy A and 125 of strategy B at the start for a total population size of $850 + 125 = 975$. As with any calculation of frequency,

$$\text{frequency of some group} = \frac{\text{number of members of the group}}{\text{total population size}}$$

so

$$\text{frequency of strategy } A = 850/975 = 0.872$$

and since there are only two strategies, then

$$\text{frequency of strategy } B = 1.0 - \text{frequency of strategy } A = 1.0 - 0.872 = 0.128.$$

Checking using the formula above, frequency of strategy $B = 125/975 = 0.128$.

b) Strategy B leaves an average of 1.05 offspring versus only 0.85 for strategy A. Thus, using the formula for relative fitness,

$$\begin{aligned} \text{relative } W(A) &= 0.85/1.05 = 0.81 \\ \text{relative } W(B) &= 1.05/1.05 = 1.00 \end{aligned}$$

c) Since we know the average number of offspring produced asexually by members of each strategy, we simply multiply that number times the number of individuals to get the number in the next generation. For stratege A

$$\text{absolute } W(A) \times (\text{number of} A \text{ parents}) = 0.85 \times 850 = 722.$$

For strategy B

$$\text{absolute } W(B) \times (\text{number of} B \text{ parents}) = 1.05 \times 125 = 131.$$

The total offspring (size of F1 generation) is $722 + 131 = 853$. Therefore,

$$\text{new freq}(A) = 722/853 = 0.846$$

and

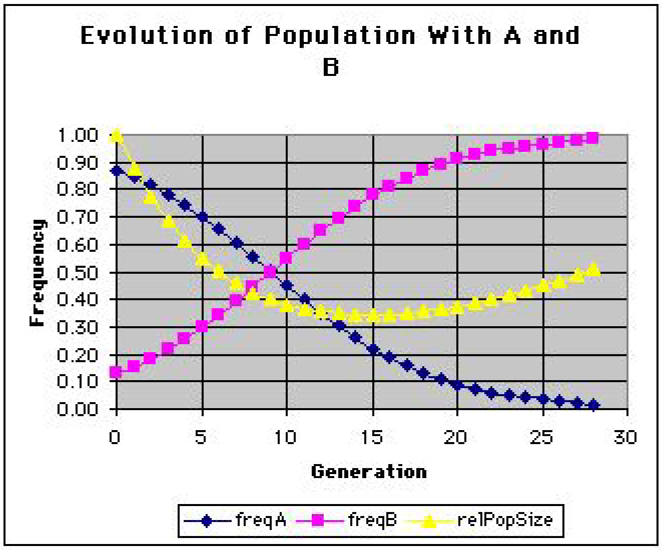
$$\text{new freq}(B) = 1.0 - 0.846 = 0.154;$$

B is increasing and A decreasing (no surprise—after all A is less fit).

d) The population is declining—from 975 to 853. While the population is declining, at the same time it is evolving more towards strategy B!

e) The population will continue to decline until most A strategists are gone (since they only leave 0.85 offspring), When the frequency of strategy B (which leaves 1.05 offspring) reaches a certain point the population will begin increasing again. In our example, this happens at about generation 15. (See **Figure 11.1**. Note in this graph, the total population size is expressed relatively to the first generation.)

Figure 11.1: The evolution of a population.



Note that this particular pattern is not required for evolution to work—it is possible that a population could be increasing the entire time one strategy was out-competing another!

11.3 Problems from Chapter 5

1. Ownership is a broader and different concept than is territory. The exact meaning of territory is muddied and beyond the scope of this discussion. For our purposes, let's just say that territory implies ownership or predominant use (something less than ownership) of some physical space of the environment. It also implies ownership or predominant use of at least some of the resources in this space (resources are defined with reference to individuals needing to make use of them). However, an animal can "own" a resource without holding what is usually construed as a territory. One example might be a male guarding its mate, for instance through prolonged copulation as is common in insects.

When discussing the `Bourgeois` strategy it is common to use the words territory and ownership interchangeably although they are not really exactly the same thing.

2. *Are the Bourgeoisie sophisticated?* With apologies to Virginia Woolf and leaving discussions of high, low, and middle brow aside, we can ask the question of whether or not `Bourgeois` represents a reasonably sophisticated (i.e., realistic) behavioral strategy.

   `Bourgeois`, like the behaviors on which it is based, `Hawk` and `Dove`, is a rather simple-minded strategy. For instance, an individual practicing `Bourgeois` decides whether or not to fight entirely on whether or not it owns the resource under contention. `Bourgeois` has the property of being an **uncorrelated asymmetry**. The asymmetry in a contest traces to the fact it either owns or does not own (the opponent owns) a resource. The strategy is uncorrelated since condition, fighting ability, and likelihood of victory have nothing to do with the decision of whether or not to fight. The decision is based entirely by whether or not the individual owns the resource.

   This is fine as far as it goes—animals that hold a resource are more likely to fight. But it is not uncommon for an animal to consider the likelihood that it will prevail in a given contest. Fights are most often escalated affairs that follow considerable amounts of assessment—it has been repeatedly documented that the most serious fights occur when the parties are evenly matched. Thus, a more sophisticated treatment would correlate likelihood of escalation to a fight and continued fighting with factors like the value of the resource and likelihood of injury (which is determined in large part by assessment of the fighting abilities of both contestants).

   Nevertheless, even though it is simple-minded, it still is an advance over simple `Hawk` and `Dove` strategies—animals that own resources often are more likely to fight and those that do not are often more likely to display or avoid an escalated fight with an owner.

11.4 Problems from Chapter 6

1. No, but you can consider all the possible combinations (`Hawk` versus `Dove`, `Hawk` versus `Bourgeois`, `Dove` versus `Bourgeois`). In any case, if one strategy is stable against several other known strategies in pairwise competition, then by definition it cannot be invaded by any of them and it can invade all of them. Thus, it is a pure ESS with respect to these strategies. You should satisfy yourself that `Bourgeois` beats both `Hawk` and `Dove` according to the standard criteria, at least with the payoffs that we have described, and then try playing the simulation all possible ways.

2. **A brief discussion of simulations using initially different frequencies of H, D and B:** For any reasonable set of payoffs, `Bourgeois` is a pure ESS versus `Hawk` and `Dove`. The initial frequencies have nothing to do with whether or not a strategy is a pure (or for that matter a mixed) ESS—when dealing with an ESS the initial frequencies only dictate how long it might take to get to equilibrium. They also might cause some interesting strategy fluctuations in getting to the ESS.

   For instance, you should have noted situations where `Bourgeois` and one of the other strategies (which one depends on the payoff matrix you are using) initially both increase as the other decreases. Sometimes the changes in frequency vary over time. An especially interested example of this occurs with the default matrix starting with $f(\texttt{Dove}) = 0.9$ and $f(\texttt{Hawk}) = 0.09$. However, eventually in every case `Bourgeois` wins out—after all, that is the definition of a pure ESS.

3. a–g) You should notice that if you used the default payoff matrix, `Hawk` and `Dove` quickly come to frequencies that are near those of a mixed `Hawk/Dove` ESS that we studied earlier.

h) What is going on here? Regardless of whether you start with a high frequency of H or D, the same approximate equilibrium is reached. This shouldn't surpise you—B is at such a low frequency initially that it is simply not a player—thus the values of $f(B) \cdot E(H, B)$ and $f(B) \cdot E(D, B)$ are nearly negliable (H and D hardly ever encounter the rare B) and therefore a pseudo mixed ESS is reached between those two. However, note that B is still more fit than either (see fitness curve) and it continued to increase at a steady rate, eventually removing both H and D with D disappearing first.

Carefully examine the fitness changes that occur in the first few generations and how they happen when you start with either `Hawk` high or `Dove` high.

i) There are three parts to the answer to this question. (i) `Bourgeois` is very rare initially and even if it is doubling each generation, doubling something extremely rare it still remains rare. (ii) Since `Bourgeois` is so rare, `Bourgeois`'s relative fitness is not initally very much greater than the other two strategies, mainly because after a few generations `Bourgeois` still hardly encounters itself (a good payoff) while `Doves` (also a good payoff) quickly become rarer than `Hawks` (a bad payoff). And (iii) since B is a hybrid of `Hawk` and `Dove`, its payoffs are not very different than theirs.

j) There is little you can do: B is a hybrid stategy and anything that helps it will help one of its competitors (try it!!). But it still always wins out!

4. Anytime one strategy is known to be a pure ESS, its the only one you need to monitor. So in this case, monitoring B will tell you when equilibrium is reached, whilst monitoring H or D could be deceptive – one might go extinct while the other continues and therefore never reach equilibrium.

11.5 Problems from Chapter 8

1. It makes no difference what the value of V is in this case. As x becomes infinitely large, so does $e^{x/V}$ and consequently its inverse, $e^{-x/V}$ becomes zero. That is, in the language of limits,

$$\lim_{x \to \infty} P(x) = \lim_{x \to \infty} 1 - (1/e^{x/V}) = 1 - 0 = 1.$$

Therefore $P(x) = 1.0$ in all cases.

2. For $V = 1$: $P(x) = 1 - e^{-0.6} \approx 1 - 0.55 = 0.45$. For $V = 5$: $P(x) = 1 - e^{-0.6/5} = 1 - e^{1-0.03} \approx 1 - 0.89 = .11$. For $V = 0.5$: $P(x) = 1 - e^{0.6/0.5} = 1 - e^{-1.2} \approx 1 - 0.30 = 0.7$.

1. $Q(x)$ and $P(x)$, respectively.

2. $1 - e^{-1/V}$. Recall that the chance of quitting, (8.13), is nothing more than $1 - Q(x)$. Now since (8.14) is essentially the same as (8.16), then $1 - e^{-1/V}$ gives us the chance of quitting. So, for example, if $V = 1$, chance of quitting per unit cost is 0.632.

3. No, they are equivalent. In both cases, the contestant has no idea which maximum cost it is facing (provided that encounters with different **fix**(x) supporting strategies are random in the mixed population and that in neither case the maximum cost is tipped before being reached).

4. One way would be to say that in any contest with members of this population, there is a constant chance per increment of cost that one' s opponent will quit. This corresponds to the idea that one's chance of opposing a given type of supporting strategist (maximum x) would be equal to its frequency in the population (as determined by integrating (8.12)). Supporting strategies with low maximum x values would be more common so you would be more likely to face them.

5. If the opponent has some reason to know **var**'s intentions, there will be strong selective pressure for it to act in a way that thwarts **var** and serves its own best interests. For instance, if it is certain that **var** will not quit before reaching the opponent's max cost, it will pay the opponent to quit immediately and cut its losses. Likewise, if **var** is certain to quit on the next move or over the next bit of cost, it will pay the opponent to wait **var** out and gain the resource (as compared to **var** who in this case gains nothing).

6. This is equal to $Q(x)$ since $Q(x)$ gives the chance that **var** has not quit as of cost x.

7. This is equal to $P(x)$ since $P(x)$ gives the cumulative chance that **var** has already quit as of some cost x.

8. This is equal to $\Delta P(x)$ since $\Delta P(x)$ gives the chance that **var** has endured to cost x without quitting but will quit before paying cost $x + \Delta x$ where Δx is some additional cost. It should be less for the smaller range of costs—i.e., less in 0.60 to 0.61 than in 0.60 to 0.62. In this case, all we have done is make a cost interval larger by 0.01. So, there are more quitting times in this larger interval and therefore a greater total probability that an individual **var** will quit within this interval.

9. **a)** For $V = 1$: $\Delta P(x) = e^{-0.60} - e^{-0.61} \approx 0.00546$. For $V = 0.5$: $\Delta P(x) = e^{-0.60/0.5} - e^{-0.61/0.5} \approx 0.00596$.

b) For $V = 1$: $\Delta P(x) = e^{-1.0} - e^{-1.01} \approx 0.00366$. For $V = 0.5$: $\Delta P(x) = e^{-1.0/0.5} - e^{-1.01/0.5} \approx 0.00268$.

c) Notice that the chance of quitting within a specific cost interval $\Delta P(x)$ of a constant range (0.01) decreases as the average cost of the interval increases. This is not because the chance of quitting per 0.01 increment in cost has changed. Indeed, it is always proportional to $1/V$, regardless of the interval. So why the difference? The difference reflects the lower chance that an individual will actually have played to the higher cost. Thus, the chance of actually having played to $x = 0.60$ is $P(0.6) = 0.549$ but the chance of playing all the way to $x = 1$ is $P(1) = 0.368$. If you apply a constant chance of remaining over the next $0.01x$ to each of these numbers (if $V = 1.0$, it is 0.99) you will see that fewer actually quit in the second interval (because there are fewer there to quit!).

10. This is given by $p(x)dx$ and it is a very small number.

11. **var** loses any contest that costs less than m. There are lots of ways this can happen—each losing cost has a unique probability of occurrence based on **var**'s probability density function. Thus

$$\text{Cost to } \mathbf{var} \text{ Losing to } \mathbf{fix}(x = m) = \int_0^m x p(x)\, dx.$$

12. Following our usual rule, each side wins 50% of the time. Since there is a 100% chance that **var** will play at time 0 and the cost equals 0, then

$$E(\mathbf{var}, \mathbf{fix}(0)) = 0.5[(V - m) - x] = 0.5[(V - 0) - 0] = 0.5V.$$

13. All of these chances are independent. In these cases, there is a more or less constant probability per flight of a disaster (this might be the worst example of the three since clearly a poor pilot, bad weather, poor maintenance or whatever could change your odds). What happens on other flights does not affect the next one you get on. The same with asteroids and lottery tickets. As with **var**, a constant probability means that it can happen any time or maybe even not at all. The main difference between these examples and the war of attrition is that in the "war" we are concerned with the distribution of quitting costs while in the other examples the emphasis is on the constant probability of some event.