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Chapter 2

Simple Frequency Dependence

Things get interesting when the fitness of a strategy can change over time. The first chapter allowed this to happen only when the background environment changed. The rest of the book allows the fitness of each strategy to depend on its share and on the share of other strategies, which themselves change over time. When a particular strategy becomes more prevalent, it can become more fit, due to “increasing returns” or “synergy.” Another sort of strategy can become less fit, due to congestion effects.

This chapter takes a first look at such strategic interdependence, or frequency dependent selection, as it is called by biologists. To better introduce ideas, the chapter begins with linear frequency dependence between two alternative strategies in a single unified population.

The first example is the famous Hawk-Dove game, as formulated by Maynard Smith (1982). After looking at a numerical example, we analyze Maynard Smith’s two parameter version of the game, and apply discrete time replicator dynamics. As in the Chapter 1 example of sickle cell anemia, we find an interior steady state in HD games, but here it is due to strategic interaction rather than diploid genetics. It turns out that the forces of congestion prevail in HD games. We will also identify a key boundary condition ignored in previous analysis, and will see how continuous time replicator dynamics simplify the situation.

We then consider other types of games with two alternative strategies. Recent empirical work shows that RNA viruses play a Prisoner’s dilemma game. We will see that in a wider

set of games, there is a dominant strategy (DS) whose share is forced to 100% (fixation, as biologists call it) under replicator dynamics.

The next section shows that, besides HD and DS, there is only one other type of game possible in our setting with two alternative strategies. In this third type of game, called Coordination (CO), the forces of increasing returns prevail. There is an interior steady state, but it is unstable. As in the underdominance case of diploid dynamics, this steady state separates the states that evolve towards fixation on the first pure strategy from the states that evolve towards fixation on the second pure strategy.

The last three sections show how to use these simplest sorts of frequency dependence as building blocks for more complex games. One important form of complexity is nonlinear frequency dependence between two strategies. Another is linear frequency dependence among three alternative strategies, as illustrated in the famous Rock-Paper-Scissors game. The data show that male side-blotched lizards play a generalized version of this game.

2.1 The hawk-dove game

In the parlance of the Vietnam War era, Hawk refers to an aggressive but costly strategy, while Dove refers to a low-cost submissive strategy. Maynard Smith's Hawk-Dove game involves two animals (not necessarily birds) that meet at a resource. Seizing the resource adds to an individual's fitness. Each animal can adopt one of two strategies. Strategy H, or hawk, is to behave aggressively until victory or serious injury (perhaps death), while strategy D, or dove, is to display threateningly but to retreat if the opponent is aggressive.

The animals then reproduce as haploids, and in the next generation progeny follow the parental strategy. For now we assume that generations are discrete and non-overlapping; the adult population of hawks and doves dies before the progeny generation matures. Thus parental hawks and doves never play the game with the progeny generation.

2.1.1 Numerical example

An example of hawk-dove interaction is captured in the following payoff (or fitness) bimatrix:

	Player 2:	
Player 1:	H	D
H	(-1, -1)	(4, 0)
D	(0, 4)	(2, 2)

The first element of each vector is the payoff to (or fitness increment of) the row player (Player 1) while the second element is the payoff to the column player (Player 2). This game is symmetric in that the off-diagonal elements are mirror images of each other, and the vectors on the diagonal have the same elements. Consequently the payoffs to each player depend on her choice and her opponent's choice, but not on whether she is a column player or row player. If I pick H and my opponent picks D, for example, then I get 4 and my opponent gets 0, whether I am the row or the column player. This payoff symmetry arises from the fact that we are dealing with a single population. In the next chapter we will study games where row players and column players belong to separate populations, and there the payoff bimatrix need not be symmetric.

For single population games, the symmetry of payoffs makes the bimatrix redundant. We can simply show the row player's payoffs in an ordinary matrix as below, and not lose any information.

	encounter rate:	
	s_H	$1 - s_H$
Player 1:	H	D
H	-1	4
D	0	2

Here we include an extra line above the payoff matrix, which gives the population shares of H (namely, s_H) and D (s_D , written as $1 - s_H$) in the current adult cohort.

To see the decreasing returns (or congestion or negative frequency dependent) aspect of this game, notice that if everyone else is playing H, then I get payoff -1 if I also play H, but I get payoff $0 > -1$ if I instead play D. Likewise, I'm better off going against the crowd if they are all playing D: in this case I get 4 if I play H, but only $2 < 4$ if I also play D.

Can some mix of H and D persist from one generation to the next? To find out, we begin by writing out the fitnesses of the two strategies, W_H and W_D . Each strategy faces

a population that is composed of hawks with share s_H and doves with share $s_D = 1 - s_H$. Therefore, fitness (or expected payoff) to the row player is given by those shares times the corresponding entries in the matrix:

$$W_H = -1s_H + 4(1 - s_H) \quad (2.1)$$

because any H player receives payoff -1 in the fraction s_H of encounters and payoff 4 in the remaining encounters. Likewise, the fitness of any D player is

$$W_D = 0s_H + 2(1 - s_H). \quad (2.2)$$

It turns out that what really matters is the payoff difference, or relative fitness of the first strategy, denoted $\Delta W = W_H - W_D$. Thus

$$\Delta W = -s_H + 2(1 - s_H) = 2 - 3s_H \quad (2.3)$$

See Figure 2.1 for a graphs of W_H, W_D and ΔW as functions of s_H .

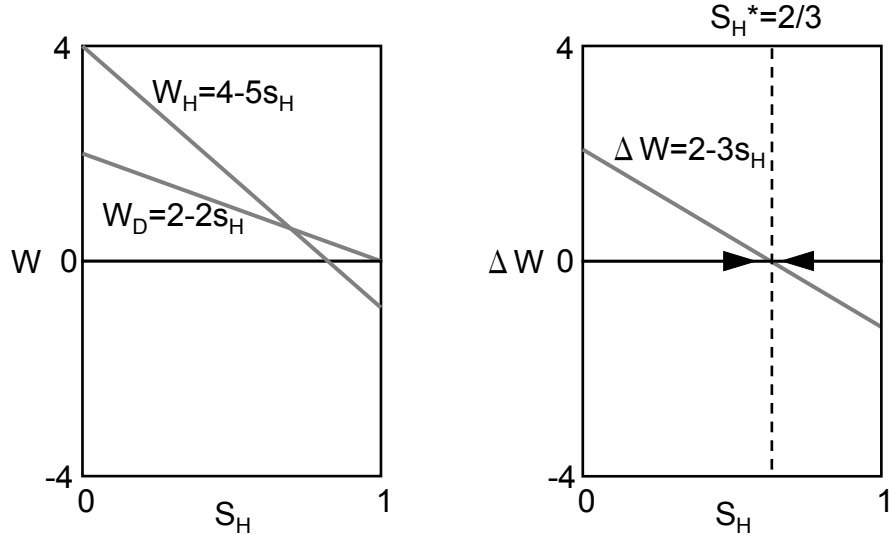


Figure 2.1: Fitness of Hawk (H) and Dove (D) in Panel A, and their difference ΔW in Panel B, as a functions of the share s_H of Hawks.

Now consider the mix s^* that gives equal payoff, $\Delta W = 0$. From (2.3) we see that $s_H^* = \frac{2}{3}$ and $s_D^* = \frac{1}{3}$. To determine whether this mix is stable as we move from one generation to the

next, we first note from (2.3) that $\Delta W > 0$ when $s_H < \frac{2}{3}$. Thus H has the higher fitness and its share s_H should increase when it is below $\frac{2}{3}$. On the other hand, if $s_H > \frac{2}{3}$ then $\Delta W < 0$, so in this case the share of H should decrease back towards $\frac{2}{3}$. It seems that, as the arrows indicate in Figure 2.7 Panel B, the $s_H^* = \frac{2}{3}$ mix is stable. In chapter 4 we will see that it is indeed a stable equilibrium known as an ESS.

2.1.2 H-D dynamics in discrete time

While numerical examples help illustrate the issues, in most applications the models are written in terms of parameters. This chapter will show how the the dynamics (and the steady states) change as we vary the parameters, and how to estimate realistic parameter values from the data.

For the HD game, there are two important parameters: the value of the resource $v > 0$ and the cost $c > 0$ of losing a battle over the resource. When two animals play H, they each (as far as one can say from the outside) have a $\frac{1}{2}$ probability of losing so the average cost is $\frac{c}{2}$. Likewise, each of them gains an average resource value of $\frac{v}{2}$. The expected payoff for each of the two H strategists thus is $\frac{v-c}{2}$. When two animals play D, neither incurs the cost and each gains on average half the resource value, so both get payoff $\frac{v}{2}$. When a H strategist meets a D, the H always seizes the resource at no cost, so the H payoff is v and D gets 0. This all is summarized in the following parametrized payoff matrix.

	encounter rate:	
	s_H	$1 - s_H$
Player 1:	H	D
H	$\frac{v-c}{2}$	v
D	0	$\frac{v}{2}$

You can see that we used $v = 4$ and $c = 6$ in the numerical example.

Row elements of the payoff matrix reflect payoffs of any individual player (labelled player 1 in the matrix and shown as the row player) against each strategy available to other players. The shares shown above the columns (here s_H and $1 - s_H$) aggregate the strategies used by all other players. Usually we assume that there are so many other players that the fractions are not affected by the choice of player 1, but this is not necessary to write the matrix.

Occasionally we will comment on what happens when the number of players is not so large.

The other implicit assumption is that the row player is equally likely to be matched with any other player, and so the payoffs from each possible strategy by other (column) players is proportional to its share. In Chapter 5, we will relax this assumption and consider games in which players can seek out and exploit other strategies at rates greater than random, so that, for example, the fraction of D encounters might be greater than s_D . But in the meantime we ignore such potential complications.

With these simplifying assumptions, the fitness of any strategy W_i for $i = H, D$ is obtained from the rate of encountering each strategy $j = H, D$ multiplied by the payoff W_{ij} from the encounter. Thus

$$\begin{aligned} W_H &= s_H W_{HH} + (1 - s_H) W_{HD}, \\ &= s_H \frac{v - c}{2} + (1 - s_H) v. \end{aligned} \tag{2.4}$$

Likewise,

$$\begin{aligned} W_D &= s_H W_{DH} + (1 - s_H) W_{DD} \\ &= s_H \cdot 0 + (1 - s_H) \frac{v}{2}. \end{aligned} \tag{2.5}$$

The payoff difference now is

$$\begin{aligned} \Delta W &= W_H - W_D \\ &= s_H \frac{v - c}{2} + (1 - s_H) \frac{v}{2} = \frac{1}{2}(v - s_H c). \end{aligned} \tag{2.6}$$

Can hawks invade a population of all doves? The question reduces to checking whether whether $\Delta W > 0$ when $s_H = 0$. From (2.6), or directly from the payoff matrix, we see that $\Delta W(0) = W_{HD} - W_{DD} = \frac{v}{2}$. This is positive since $v > 0$, by definition of resource value. So the answer to the first question is affirmative.

Can doves invade a population of all hawks? The answer is yes, as long as $\Delta W < 0$ (i.e., D is fitter) when $s_H = 1$. Clearly $\Delta W(1) = W_{HH} - W_{DH} = \frac{v - c}{2}$, which is positive iff $v > c$. In this case, D cannot invade and H can persist as a pure strategy.

The case $v < c$ is more interesting. In this case, pure H can not persist, and (as in the numerical example) a stable mixture s_H^* can be found by solving $\Delta W = 0$. Inspection of the

last expression in (2.6) reveals

$$s_H^* = \frac{v}{c}. \quad (2.7)$$

To check dynamics, recall the replicator equation from chapter 1. The shares of $i = H, D$ at time $t + 1$ are given by:

$$s_i(t + 1) = \frac{W_i}{\bar{W}} s_i(t), \quad i = H, D, \quad (2.8)$$

where

$$\bar{W} = s_H W_H + (1 - s_H) W_D \quad (2.9)$$

is average fitness in the population. It is easy to see that s_H increases whenever $\frac{W_H}{\bar{W}} > 1$, i.e., whenever H yields a higher payoff than D, i.e., whenever $\Delta W > 0$ in equation (2.6), i.e., whenever $s_H < s_H^*$. Thus in the general case, as in the numerical example, s_H increases when it is below the steady state s_H^* and decreases when it is above the steady state.

2.1.3 Zone of total destruction

There is a problem with the discrete replicator equation (2.8) applied to Maynard Smith's (1982) formulation of the Hawk-Dove game. We can get a negative value of W_H , and hence a negative value of $s_H(t + 1)$, contrary to the definition of shares and state space.

We have to decide what a negative value really means. In a biological system, W_H is a composite of reproduction and survival. One can perhaps imagine overkill, or negative survival numbers. But if no H survive, then reproduction is zero, not negative, so each W_i must be bounded below by zero. As noted in Chapter 1, it follows that \bar{W} always is greater than zero.

So we have to modify the definition of W_H when equation (2.4) goes negative. The critical value of s_H , call it s_c , is where W_H is zero:

$$W_H = v - s_c \frac{v}{2} - s_c \frac{c}{2} = 0, \quad (2.10)$$

with solution

$$s_c = \frac{2v}{v + c}. \quad (2.11)$$

Thus, if $s_H(t) > s_c$ then the unmodified replicator equation says that $s_H(t+1) < 0$. The interpretation is that hawks in this cohort keep killing one another off and have no progeny. So $s_H \in [\frac{2v}{v+c}, 1]$ is a zone of total destruction. If we ever reach that zone, then the meek (D) shall inherit the earth, i.e., $s_D = 1$ and $s_H = 0$ at time $t+1$ and forever after. In principle the HD game will not enter this zone during normal dynamics but you might start out the game within this zone (e.g., starting conditions for $s_H(t=0)$) and in this case you would observe abnormal dynamics. See the problem at the end of this chapter, and an excel spreadsheet derivation that reproduces the dynamics of the HD game.

When we use the replicator equations we have to guard against this. Negative values for W are not permissible. We either exclude that zone from the domain of the replicator equation, or else treat it as the total destruction endgame with W_H set to 0 instead of a negative number.

2.1.4 Continuous replicator

The total destruction problem does not arise for replicator dynamics in continuous time. Values of $w = \ln(W)$ can go negative, but this simply describes negative growth rates or declining frequencies. Actual shares can never go negative, as can be seen from a little algebra. Since $\bar{w} = s_H w_H + (1 - s_H) w_D$, we have

$$\begin{aligned}\dot{s}_H &= (w_H - \bar{w})s_H = (w_H - s_H w_H - (1 - s_H)w_D)s_H = (1 - s_H)(w_H - w_D)s_H \\ &= s_H(1 - s_H)\Delta w,\end{aligned}\tag{2.12}$$

where $\Delta w = w_H - w_D$. When $\Delta w < 0$, the Hawk growth rate \dot{s}_H/s_H is negative but this means that s_H shrinks towards zero while remaining positive. Likewise for Doves: for any parameter values, the growth rate $\dot{s}_D/s_D = -\dot{s}_H/(1 - s_H)$ can be negative but s_D remains positive even if it shrinks towards zero.

Equation (2.12) is interesting in its own right. It shows that the direction of change in the state (\dot{s}_H positive or negative) is the same as the sign of the fitness advantage (Δw positive or negative). Indeed, the rate of change $\dot{s}_H = -\dot{s}_D$ in the shares equal to the fitness advantage times the factor $s_H(1 - s_H)$, the binomial variance associated with the current shares. This factor goes to 0, and adjustment slows to a crawl, as we approach either

endpoint. Thus the continuous replicator equation is in many ways parallel to the version of Fisher's Fundamental equation derived near the end of Chapter 1.

2.2 The three kinds of 2x2 games

Besides convergence to an interior steady state as in the HD game, what other sorts of behavior can occur with 2x2 payoff matrices? Let's give the two alternative strategies the labels $i, j = A, B$, and explore the possibilities.

We begin with a fully parametrized version of the 2x2 payoff matrix, suitable for continuous time analysis:

	encounter rate:	
	s_A	$1 - s_A$
Player 1:	A	B
A	w_{AA}	w_{AB}
B	w_{BA}	w_{BB}

Following the analysis of earlier sections, the fitness of strategy A is

$$w_A = w_{AA}s_A + w_{AB}(1 - s_A), \quad (2.13)$$

and the fitness of the alternative strategy is

$$w_B = w_{BA}s_A + w_{BB}(1 - s_A). \quad (2.14)$$

The payoff advantage of A over B then is

$$\Delta w = (w_{AA} - w_{BA})s_A + (w_{AB} - w_{BB})(1 - s_A). \quad (2.15)$$

Equation (2.15) shows that the payoff advantage depends entirely on certain combinations of parameters, and these combinations turn out to have helpful interpretations. A biologist would describe the combination $w_1 = w_{AB} - w_{BB}$ as the fitness advantage of rare mutant strategy A when strategy B is common, while a game theorist would describe w_1 as the payoff advantage of A over B when playing against B. The analogous combination for the other strategy is $w_2 = w_{BA} - w_{AA}$, the advantage of rare mutant strategy B over common strategy A.

Using these parameter combinations, we can rewrite the payoff advantage in (2.15) as

$$\Delta w = -w_2 s_A + w_1(1 - s_A) = w_1 - (w_1 + w_2)s_A. \quad (2.16)$$

The last expression shows that the payoff advantage line has vertical intercept w_1 and slope $-(w_1 + w_2)$. By setting $\Delta w = 0$ and solving for s_A , we see that $s_A^* = w_1/(w_1 + w_2)$ is the equal fitness point.

Equation (2.16) also shows that the payoff advantage graph is the line segment that connects the point $(0, w_1)$ to the point $(1, -w_2)$ in $(s_A, \Delta w)$ -space. If this line segment crosses the horizontal axis, it does so at the point $(s_A^*, 0)$. Examples are shown in Figure 2.2.

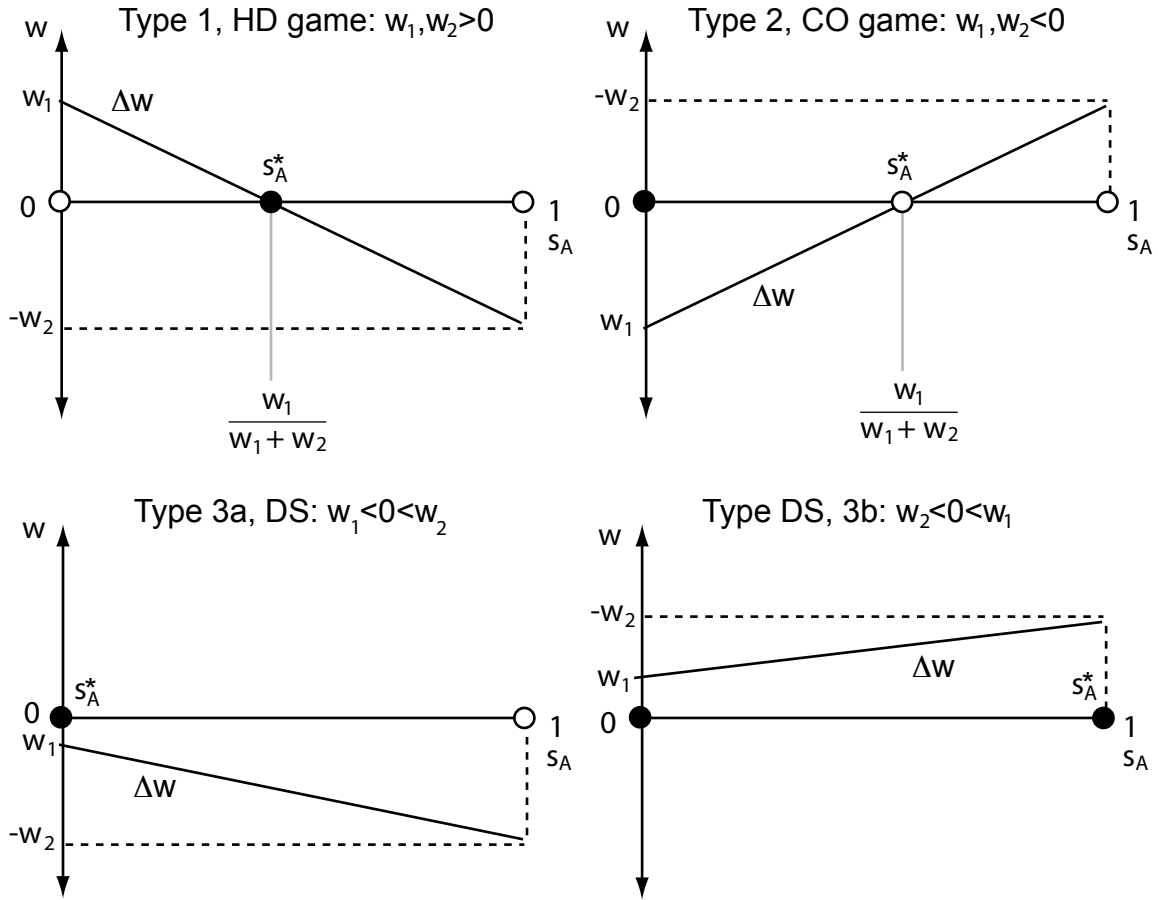


Figure 2.2: The three types of linear one-dimensional games.

Recall from section 2.1.4 above that the sign of \dot{s}_A is the same as the sign of Δw under continuous replicator dynamics. Using the current general notation, the continuous replicator equation is

$$\dot{s}_A = s_A(1 - s_A)\Delta w. \quad (2.17)$$

Taking time derivatives of the expression $s_A + s_B = 1$, we see that $\dot{s}_A + \dot{s}_B = 0$, so $\dot{s}_B = -\dot{s}_A = s_A(1 - s_A)(-\Delta w)$.

The upshot is that the signs of the w_i 's tell the whole story. The signs determine whether the fitness difference line starts out positive or negative, and whether it crosses the horizontal axis. Then replicator dynamics determine behavior.

Consequently, as shown in Figure 2.2, there are three main kinds of 2x2 matrices: Type 1 or HD, Type 2 or CO, and Type 3 or DS.

2.2.1 HD Type

When w_1 and w_2 are both positive, then mutants can invade either common type. Economists call this situation decreasing returns to scale or congestion, and biologists call it negative frequency dependence. As shown in Panel A of Figure 2.2, when both w_i 's are positive then:

- the only steady state is at $s_A^* = w_1/(w_1 + w_2)$, which is strictly between 0 and 1.
- The payoff advantage line Δw has negative slope $-(w_1 + w_2)$, and so s_A^* is a **down-crossing**. That is, $\Delta w > 0$ when $s_A < s_A^*$ and $\Delta w < 0$ when $s_A > s_A^*$.
- The steady state s_A^* is stable in the sense that all other states move towards s_A^* and converge to it under continuous replicator dynamics.

Downcrossings s_A^* are stable because the replicator equation (2.17) and the signs of Δw ensure that the state moves towards s_A^* from both sides.

We have encountered this sort of situation before, in our analysis of Hawk-Dove, so we refer to this case as HD. Now it is clear that the single, stable interior steady state is not simply a matter of having the cost of fighting greater than the value of the resource. More generally, it will occur whenever both pure strategies are invadable for any reason.

2.2.2 CO Type

What are the other possibilities? Of course, one or both of the w_i 's might be zero. The chapter-end exercises invite you to analyze these knife-edge cases yourself.

Another possibility, labeled CO (or Type 2) in Figure 2.2, is that the w_i 's are both negative. That is, neither pure strategy can be invaded. It is an important case that we have not discussed previously. Biologists call it positive frequency dependence, and economists refer to it as increasing returns to scale or synergy.

Here is an example, based on some remarks by French enlightenment philosopher Jean-Jacques Rousseau (1712-1778). The population consists of hunters in a village who seek to capture a great stag, *Cervus cervus*, a male with spectacular antlers. If the hunt is successful, everyone shares in the glory and their payoff is 10 each. But each hunter can be distracted from hunting the stag (strategy A) by hunting rabbits (strategy B). Hunting rabbits is quite reliable; no matter what other hunters do, it yields payoff 8. The stag is very good at escaping when some hunters are distracted (hunting rabbits makes a lot of noise), and so the chance of capturing it drops sharply when more hunters switch to strategy B.

This story is encapsulated in the following payoff table.

	encounter rate:	
	s_A	$1 - s_A$
Player 1:	A	B
A	10	0
B	8	8

For these payoffs we have $w_1 = w_{AB} - w_{BB} = 0 - 8 = -8 < 0$ and $w_2 = w_{BA} - w_{AA} = 8 - 10 = -2 < 0$; both are negative, as advertised. The interior rest point is $s_A^* = w_1/(w_1 + w_2) = -8/(-8 - 2) = 8/10 = 0.80$. The payoff advantage $\Delta w = 8 - 10s_A$ is negative for $s_A < s_A^*$ and positive for $s_A > s_A^*$, so s_A^* is an **upcrossing**.

This example illustrates the following general features when both w_i 's are negative:

- there are three steady states, the corners $s_A = 0$ and $s_A = 1$ as well as the interior steady state $s_A^* = w_1/(w_1 + w_2)$.
- The payoff advantage line Δw has positive slope $-(w_1 + w_2)$, and so s_A^* is a upcrossing.
- Consequently the steady state s_A^* is unstable. It separates the basins of attraction of the two pure steady states $s_A = 0$ and $s_A = 1$.

The interpretation in terms of the Stag Hunt game is that if at first a larger fraction than

$s_A^* = 0.80$ of the villagers focus on the stag, then under replicator dynamics, eventually all of them will choose strategy A, and the hunt will be successful. On the other hand, if a smaller fraction than 0.8 chooses A initially, then its support will decay and eventually everyone will end up hunting rabbits.

We refer to the general case of negative w_i 's as coordination games (CO), because they have two pure strategy stable steady states in which each player has the incentive to coordinate behavior with the other players. The incentives come from positive frequency dependence.

Two final examples illustrate the general point. Choosing computer operating systems is a coordination game — the more people who use Linux the better off are Linux users, and similarly for Windows users. Conventions like driving on the left side of the road or the right side have the same logic: you are better off doing what most other players do.

2.2.3 DS Type

When w_1 and w_2 have opposite signs, then one of the strategies can invade the other, but can't itself be invaded. That strategy always has a higher payoff, and therefore game theorists call it a **dominant strategy**. We shall refer to this case as DS for short.

We encountered DS earlier, in the general parametrized Hawk-Dove example. Hawk is a dominant strategy in the extreme case $c < v$, i.e., when the cost of fighting is less than the value of the resource.

To work out the general case, suppose that $w_1 > 0 > w_2$. Then A is the dominant strategy—it can invade B, but B can't invade it. As shown in the bottom right panel of Figure 2.2, this case has the following features:

- the only steady state is at $s_A = 1$, where everyone plays the dominant strategy A,
- the payoff advantage line Δw lies entirely above the horizontal axis, and so there is no crossing point s_A^* between 0 and 1. Consequently,
- the steady state $s_A = 1$ is stable, and its basin of attraction is the entire state space $(0, 1)$.

The other DS possibility is $w_2 > 0 > w_1$. Here strategy B is dominant, Δw lies entirely below the horizontal axis, and the steady state $s_A = 0$ is the global attractor, as shown in the bottom left panel of Figure 2.2. It really is the same as the first DS possibility with the strategy labels A and B switched.

It might seem, then, that all DS cases are essentially the same. However, a more careful analysis shows that there is a crucial distinction that gives completely different sorts of DS games. That distinction concerns the effect of the dominant strategy on mean fitness \bar{w} .

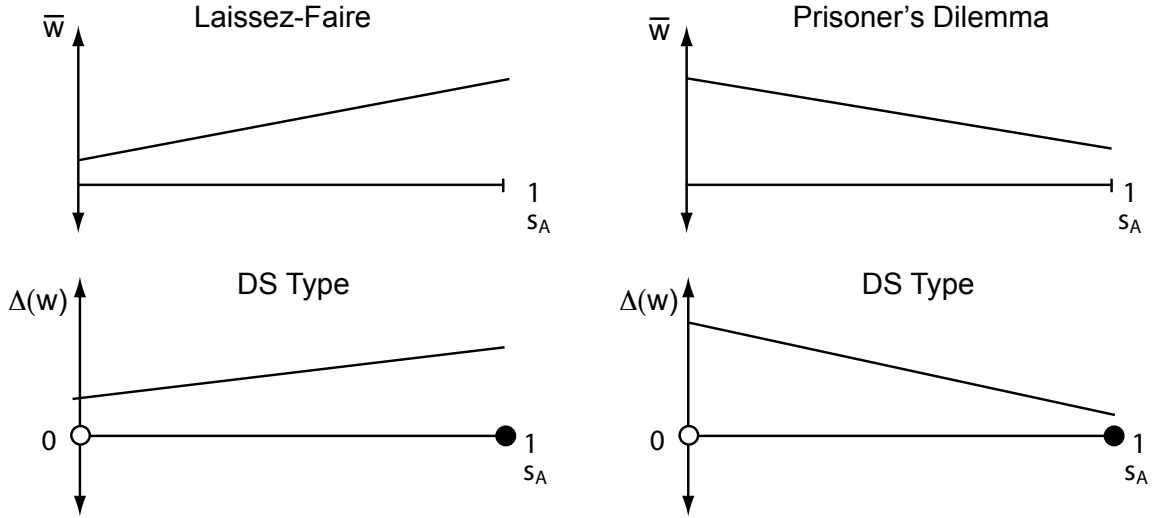


Figure 2.3: The two subtypes of DS games with dominant strategy A. In Laissez-Faire type (on the left) mean fitness \bar{w} increases as s_A goes to fixation. In Prisoners' dilemma type (on the right) \bar{w} decreases as s_A goes to fixation.

As shown on the right side of Figure 2.3, we have a *social dilemma* when \bar{w} a decreasing function of the share s_A of the dominant strategy A. The more individuals who adopt that strategy, the lower is everyone's payoff. Often this case is referred to as the Prisoner's dilemma, and it is discussed further in the next subsection.

In the other subtype of DS game, the mean payoff increases in the share of the dominant strategy. We refer to this sort of game as Laissez-Faire because since the population spontaneously evolves towards the highest mean fitness. The more individuals who adopt the dominant strategy, the better off everyone is.

2.3 Viruses play the prisoner's dilemma

The prisoner's dilemma (PD) is a famous 2x2 game. Instead of the usual contrived story about two prisoners who might or might not testify against each other, we will tell a true story involving two alternative behaviors of viruses. This example has the same strategic tensions as the standard PD, and it also illustrates how to estimate payoff matrices from biological data.

Turner and Chao (1999) investigated viruses that are parasites of bacteria. Such viruses consist of gene-carrying strands of RNA wrapped in a protein coat that protects the RNA and allows the virus to stick to and enter its next host.

The interests of cloned viruses are aligned and they replicate without conflict. However, conflict arises when two or more genetically different viruses invade the same cell. Inside the bacterial host, the two viral types compete to replicate their own type. There is a cheater strategy that relies on a co-infecting viral genotype to produce the proteins which the cheater uses to build its coat. All the cheater has to do is replicate its RNA many fold, and to grab the coat proteins created by the non-cheater viruses. When enough coat proteins are around, the cheater type can outcompete the non-cheater type that produces proteins first and then replicates its own RNA.

Thus we have two viral strategies, Defect (the cheater type), and Cooperate (the other type). Turner and Chao (1999) varied the initial infection frequency of the two types of viruses, and measured how the progeny frequency changed from the chosen initial frequency. The results are shown in Figure 2.4. Note that the data are normalized so that the fitness of Cooperate against Cooperate is $W_{CC} = 1.0$. The Figure shows that the Defect strategy always has higher fitness than Cooperate, a defining feature of PD-type games.

	encounter rate:	
	s_C	$1 - s_C$
Player 1:	Cooperate	Defect
Cooperate	1	$1 - c_C$
Defect	$1 + v_D$	$1 - c_D$

The payoff matrix above has three positive parameters to be estimated from the data. The first, v_D , represents the proportional advantage gained by D, the defector, over the

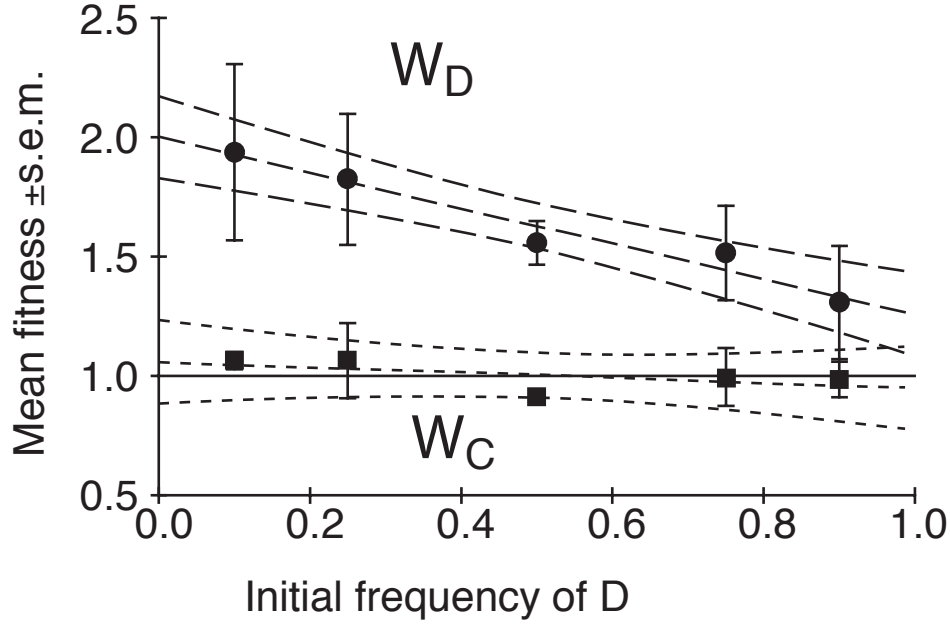


Figure 2.4: Fitness of C (squares) and D (dots) viruses as a function of $s_D = 1 - s_C$. Adapted from Turner and Chao (1999).

cooperator, i.e., $W_{DC} = 1 + v_D$. In Figure 2.4, the intercept of the upper fitted line (for D) with the vertical axis indicates $W_{DC} = 1.99$ or $v_D = 0.99$. The second parameter c_C represents the cost to the cooperator of being cheated of its proteins, i.e., $W_{CD} = 1 - c_C$. The third parameter indicates the cost to the defector of not having completely functional machinery for protein production, $W_{DD} = 1 - c_D$. The intercepts with the vertical line $w_D = 1$ in Figure 2.4 show that $W_{DD} > W_{CD}$, so $1 - c_D > 1 - c_C$ or $c_D < c_C$. This confirms that strategy D dominates C, as it must in a PD-type game. However, the normalization doesn't allow an estimate of the remaining parameter values. In a separate experiment reported in the same paper, Turner and Chao (1999) measured $W_{D,D} = 0.83$ in a population of defector viruses compared against a pure population of cooperators, and also estimated that $W_{C,D} = 0.65$. Therefore, the empirical payoff matrix is:

	Cooperate	Defect
Cooperate	1.00	0.65
Defect	1.99	0.83

This sort of game is called a social dilemma because self interest (or evolution) works against social efficiency. The highest average fitness for a population occurs when no cheaters

are present, so $\bar{W} = W_{CC} = 1$ and $s_C = 1$. However, cheaters can invade because $W_{DC} = 1.99 > W_{CC} = 1$. The invaders have a dominant strategy and so eventually the state evolves to $s_D = 1$ with lower average fitness $\bar{W} = W_{DD} = 0.83 < 1$ — exactly as shown in the right side of Figure 2.3!

2.4 Nonlinear frequency dependence

In all examples seen so far, the fitness of strategy i is given by expressions like (2.13), which are linear in the state $\mathbf{s} = (s_1, s_2)$. But sometimes fitness w_i is a nonlinear function of \mathbf{s} . An example: Friedman and Fung (1996) use the Cournot model to obtain fitness (i.e., profit) of firms pursuing alternative strategies as the quotient of fourth degree polynomials in the shares (s_1, s_2) , where the polynomial coefficients are functions of the demand and cost parameters and the number of firms. Another example: Blume and Easley (1991) model wealth dynamics in which each individual's expected wealth increment is a nonlinear function of the distribution \mathbf{s} of investment strategies.

Fitness functions that are nonlinear in \mathbf{s} create fewer technical difficulties than one might suppose. Continuing our focus in the present chapter on one-dimensional games, let $\mathbf{s} = (s_A, s_B)$ so $s_B = 1 - s_A$, and write the payoff difference between the two available pure strategies as $\Delta w(s_A) = w_A(\mathbf{s}) - w_B(\mathbf{s})$. Although the fitnesses now are nonlinear, it is still true that continuous replicator dynamic obeys equation (2.17). Thus $\dot{s}_A > 0$ (i.e., s_A increases) at interior states where $\Delta w(s_A) > 0$ and $\dot{s}_A < 0$ where $\Delta w(s_A) < 0$. Hence we have a steady state at any interior root s_A^* of the equation $\Delta w(s_A) = 0$.

By the same argument as before, the steady state s_A^* is stable if $\frac{d\Delta w(s_A^*)}{ds_A} < 0$, i.e., if it is a downcrossing so Δw is downward sloping; and is unstable if $\frac{d\Delta w(s_A^*)}{ds_A} > 0$, i.e., at an upcrossing. Also, the endpoint $s_A^* = 1$ is a stable steady state if $\Delta w(1) > 0$, and $s_A^* = 0$ is a stable steady state if $\Delta w(0) < 0$.

The logic is unchanged by the possibility that $\Delta w(s_1)$ is nonlinear. The only real novelty is that the graph of Δw can cross the s_1 -axis several times. Hence there can be several interior steady states. Of course, as in the linear case, either or both endpoints can also be stable steady states.

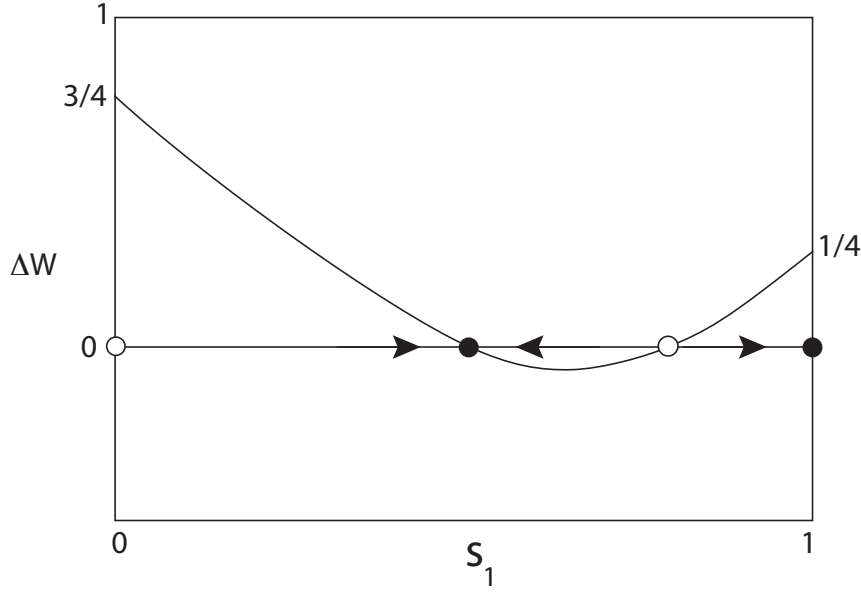


Figure 2.5: Graph of non-linear fitness advantage $\Delta w = 2(s_1 - 0.5)(s_1 - 0.75)$. The unstable steady state $s_1^* = 0.75$ separates the basins of attraction for stable steady states $s_1^* = 0.5$ and 1.0 .

For example, suppose that firms in an industry must adopt one of two alternative technologies. The first technology has decreasing returns to scale when rare and increasing returns when common; its profitability can be expressed as $w_1 = 2s_1^2 - 2s_1 + 1$, where s_1 is the fraction of industry output produced using that technology. By contrast, technology 2 has moderately decreasing returns at all scales; its profitability is $w_2 = 0.5(s_1 + 0.5)$ when $s_2 = 1 - s_1$ of the output is produced using it. Then, as shown in Figure 2.5, the fitness difference is $\Delta w(s_1) = w_1 - w_2 = 2s_1^2 - 2.5s_1 + 0.75 = 2(s_1 - 0.5)(s_1 - 0.75)$, with roots $s_1^* = 0.5, 0.75$. The steady states $s_1^* = 0.5$ and $s_1 = 1.0$ are stable because $\frac{d\Delta w(0.5)}{ds_1} = 4(0.5) - 2.5 = -0.5 < 0$ and $\Delta w(1) = 2(1)^2 - 2.5(1) + 0.75 = 0.25 > 0$. By contrast, the steady states $s_1^* = 0.75$ and $s_1 = 0$ are unstable, since $\frac{d\Delta w(0.75)}{ds_1} = 4(0.75) - 2.5 = 0.5 > 0$ and $\Delta w(0) = 2(0)^2 - 2.5(0) + 0.75 = 0.75 > 0$.

Figure 2.5 is generic for one-dimensional nonlinear dynamics in that downcrossings and upcrossings alternate. That is, the steady states are alternately stable and unstable, and the unstable steady states separate the basins of attraction of the stable steady states.

What do we mean by “generic”? The nice alternation property holds for any continuously differentiable fitness difference function Δw that has transverse crossings (i.e., $\frac{d\Delta w(s_1^*)}{ds_1} \neq 0$

at every interior root s_1^*) and non-vanishing endpoints (i.e., $\Delta w(0), \Delta w(1) \neq 0$). To be non-generic, the fitness difference function must either be tangent to the horizontal axis at an interior root, or have a root at an endpoint. Such situations are very delicate; even the slightest change to the fitness function will break the tangency or move the root away from the endpoint. On the other hand, in the generic case, a sufficiently small change in the fitness function shifts the steady states only slightly and doesn't change their number or their stability. So generic here means robust as well as typical.

2.5 RPS and the simplex.

The rest of the chapter will take a first look at what can happen when players have three alternative strategies. We focus on the famous rock-paper-scissors game, using lower case notation for continuous time games (e.g., rps with strategies r, p, s) and UPPER CASE for discrete time games (e.g., RPS with strategies R, P, S).

2.5.1 Building up from edge games

Let us begin with a very simple continuous rps game in which ties (e.g., when r meets r) get zero payoff, wins (e.g., for p when matched with r) get payoff 1, and losses (e.g., for r when matched with p) get -1. The payoff matrix for this game is:

encounter rate:	s_r	s_p	s_s
strategy :	r	p	s
r	0	-1	1
p	1	0	-1
s	-1	1	0

Recall from Chapter 1 that the state space is the simplex $\mathcal{S} = \{(s_r, s_p, s_s) \in \mathbb{R}_+^3 \mid s_r + s_p + s_s = 1\}$. The simplex is 2-dimensional because each state is pinned down by 2 of the 3 shares. For example, if $s_r \geq 0$ and $s_p \geq 0$ are known then we also know that $s_s = 1 - s_r - s_p \geq 0$. The central triangle in Figure 2.6 represents \mathcal{S} ; it is sometimes called a tenary plot, or a De Finetti diagram, or barycentric coordinates.

Note that each edge of \mathcal{S} — for example the states for which $s_s = 0$ and so $s_r + s_p = 1$ — is itself the state space of a game with only two alternative strategies. We will leverage the insights gained for such games earlier in the chapter in order to better understand behavior in the three strategy game.

In particular, the edge game of r vs. p is given by the upper left 2x2 block of the last payoff matrix:

encounter rate:	s_r	s_p
Player :	r	p
r	0	-1
p	1	0

To apply the analysis of Section 2.2 above, set $w_1 = w_{r,p} - w_{r,r} = -1 - 0 = -1$ and similarly $w_2 = w_{p,r} - w_{p,p} = 1 - 0 = 1$. Since $w_2 > 0 > w_1$, the game type is DS, with strategy p (paper) dominant over r (rock). Under replicator dynamics, paper will go to fixation at $s_p = 1$, as illustrated in the bottom line in Figure 2.6.

The edge game of p vs. s is given by the lower right 2x2 block of the rps payoff matrix:

encounter rate:	s_p	s_s
Player :	p	s
p	0	-1
s	1	0

The analysis of Section 2.2 quickly tells us that this edge game is also of type DS, with s dominant over p. Scissors will go to fixation, $s_s = 1$, as in the slanted line on the right side in Figure 2.6.

The final edge game, s vs. r, has payoff matrix obtained from the corners of the of the 3x3 rps matrix:

encounter rate:	s_r	s_s
Player :	r	s
r	0	1
s	-1	0

Once again, the game type is DS with r dominant over s. Rock will go to fixation, $s_r = 1$, as in the slanted line on the left side in Figure 2.6.

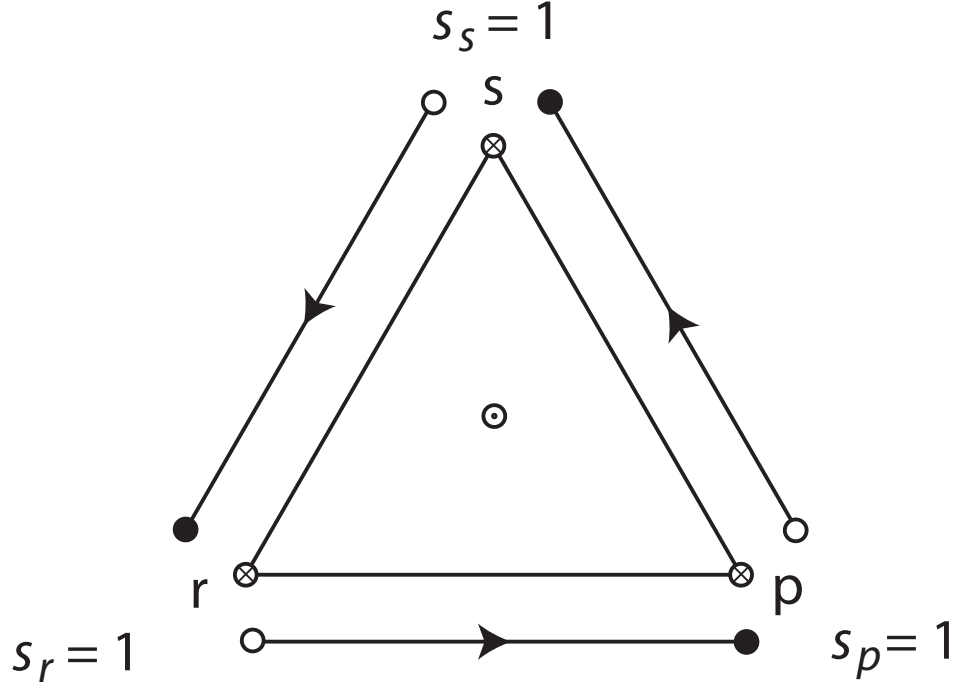


Figure 2.6: The 3-strategy simplex exploded to show the three edge games for ur-rps. Notice that each vertex is a source in one edge game and sink in another, and so each vertex in the full game is a saddle.

The payoffs in the game just analyzed are, of course, very special; there are lots of 3x3 payoff matrices $\mathbf{w} = ((w_{ij}))_{i,j=r,p,s}$ with the same basic cyclical DS structure. We will say that a 3x3 game \mathbf{w} is *ur-rps* if the following strict inequalities hold:

$$w_{s,r} < w_{r,r} < w_{p,r} \quad (2.18)$$

$$w_{p,s} < w_{p,p} < w_{s,p} \quad (2.19)$$

$$w_{p,s} < w_{s,s} < w_{r,s}. \quad (2.20)$$

That is, each strategy (when common) beats another strategy but is beaten by the remaining strategy, and the pairwise dominance relations are intransitive (i.e., cyclical).

2.5.2 Replicator dynamics for RPS

Intuitively, we can expect some sort of cycling behavior in ur-rps games. When r is common, it loses share to p , which (when it becomes common) then loses share to s , which in turn loses share to r again. But do the cycles eventually die out? Or do they settle into a moderate amplitude, or perhaps become more extreme over time?

To figure it out, we turn once more to replicator dynamics. We begin with discrete time because, as you will see in the chapter end exercises, it is easy to do such simulations with an electronic spreadsheet. Also, many organisms that express RPS dynamics actually have non-overlapping generations and for them discrete time is in fact a natural formulation.

Given a 3x3 payoff matrix $\mathbf{W} = ((W_{ij}))_{i,j=R,P,S}$, the fitness of the three strategies at a given state $\mathbf{s} = (s_R, s_P, s_S) \in \mathcal{S}$ are:

$$W_R = s_R W_{R,R} + s_P W_{R,P} + s_S W_{R,S} , \quad (2.21)$$

$$W_P = s_R W_{P,R} + s_P W_{P,P} + s_S W_{P,S} , \quad (2.22)$$

and

$$W_S = s_R W_{S,R} + s_P W_{S,P} + s_S W_{S,S} . \quad (2.23)$$

Using these fitness functions and given initial shares $\mathbf{s}(0) = (s_R(0), s_P(0), s_S(0)) \in \mathcal{S}$, discrete time replicator dynamics are defined recursively for times $t = 1, 2, \dots$ by:

$$s_i(t+1) = s_i(t) \frac{W_i(\mathbf{s}(t))}{\overline{W}(\mathbf{s}(t))}, \quad i = R, P, S, \quad (2.24)$$

where $\overline{W}(\mathbf{s}) = s_R W_R + s_P W_P + s_S W_S$.

If you try the following RPS matrix in your spreadsheet simulator for (2.24), you will see that, beginning from almost any interior state, over time the state will spiral outward until it almost reaches the edges of the simplex:

encounter rate:	s_r	s_p	s_s
Player :	R	P	S
R	1	$\frac{1}{2}$	$\frac{3}{2}$
P	$\frac{3}{2}$	1	$\frac{1}{2}$
S	$\frac{1}{2}$	$\frac{3}{2}$	1

On the other hand, if you try the following matrix, the cycle will die out and the state will spiral into the center of the simplex:

encounter rate:	s_r	s_p	s_s
Player :	R	P	S
R	1	$\frac{1}{2}$	4
P	4	1	$\frac{1}{2}$
S	$\frac{1}{2}$	4	1

We'll say more about the stability properties of steady states in the next chapter.

2.5.3 Lizard games

Male side-blotched lizards (*Uta stansburiana*) display three different mating strategies that are color coded as orange, blue and yellow, by the colors on their throats (Sinervo and Lively 1996). The orange male strategy (which we'll designate as "rock") has high levels of testosterone, aggressive, very large territories and thus a large female harem. The yellow male strategy ("paper") mimics female behavior. Therefore, when orange is common yellow males can copulate with many females in the orange male harems, by virtue of their female mimicking behaviors. The blue male strategy ("scissors") aggregates with other blue male neighbors to mutually defend adjacent territories against yellow, thereby thwarting the cheat strategy of yellow.

The side-blotched lizard is an annual with discrete one-year generation time. If we ignore genetics for the moment (and the interesting clumping behavior of blue males) and assume that the fitness of each type of lizard is due to a simple allele substitution, then we have a simple way to estimated fitness. Just measure the frequency of color alleles in each generation and use a technique called DNA paternity to figure out how many progeny were sired by each color type. Then measure fitness of each strategy each year as the number of progeny sired by that type divided by the number of adult males of that type that year.

Bleay et al. (2007) actually did this kind of genetic paternity testing, and they also tested paternity in an experiment reminiscent of Turner and Chao's work with viruses. Bleay et al. (2007) seeded a number of isolated neighborhoods (sandstone outcroppings) with lizard hatchlings with randomly assigned and quite varied initial shares of orange, blue and yellow

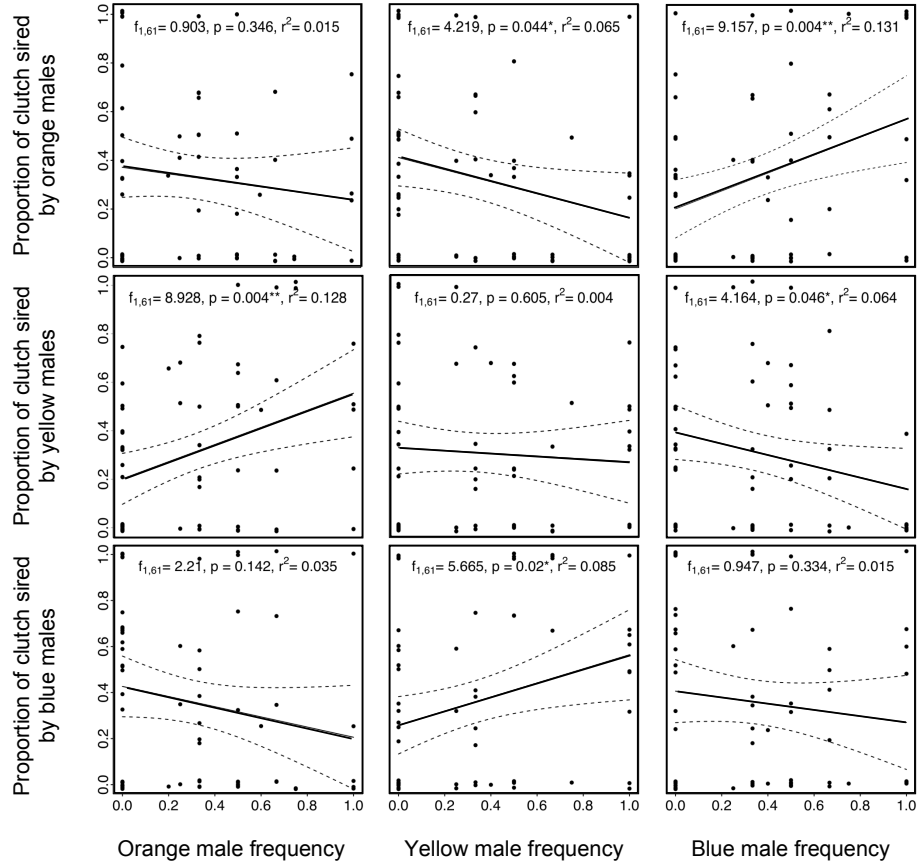


Figure 2.7: Fitness of orange, yellow and blue males measured by the average proportion of the clutch that they sire, in neighborhoods of each color allele frequency

alleles. The investigators returned the next year, obtained eggs and hatchlings from all the reproductive females, and tested their paternity. They regressed the fitness of each male type (proportion of progeny sired in a female's clutch) against the frequency of each male allele, using data from all the isolated neighborhoods.

Figure 2.7 summarizes the results. The 3x3 array of panels shows how each male color type fares in competition against the other male types. The fitted line's y-intercept on the right-hand side of each panel (at $s_j = 1$ in column j) estimates the fitness (W_{ij} , the proportion of progeny sired) of the color type in row i when color type j is common. (We discuss other methods for estimating the fitness matrix in an Appendix to Chapter 3.)

The matrix of these right-hand side y-intercepts is given by:

$$\mathbf{W} = \begin{pmatrix} W_{oo} & W_{oy} & W_{ob} \\ W_{yo} & W_{yy} & W_{yb} \\ W_{bo} & W_{by} & W_{bb} \end{pmatrix} = \begin{pmatrix} 0.22 & 0.16 & 0.58 \\ 0.56 & 0.26 & 0.17 \\ 0.20 & 0.57 & 0.26 \end{pmatrix}.$$

To get the discrete time payoff matrix, we normalize by dividing the numbers in each column by the diagonal element of that column:

$$\mathbf{W} = \begin{pmatrix} 1.00 & 0.62 & 2.23 \\ 2.55 & 1.00 & 0.65 \\ 0.91 & 2.19 & 1.00 \end{pmatrix}.$$

Taking the natural logarithm, we obtain a continuous time approximation of the game:

$$\mathbf{w} = \begin{pmatrix} w_{oo} & w_{oy} & w_{ob} \\ w_{yo} & w_{yy} & w_{yb} \\ w_{bo} & w_{by} & w_{bb} \end{pmatrix} = \begin{pmatrix} 0 & -0.49 & 0.80 \\ 0.93 & 0 & -0.42 \\ -0.09 & 0.78 & 0 \end{pmatrix}$$

Do lizards play rps? To check, let's look at the 2x2 edge games. Indeed y dominates o:

$$\begin{pmatrix} w_{oo} & w_{oy} \\ w_{yo} & w_{yy} \end{pmatrix} = \begin{pmatrix} 0 & -0.49 \\ 0.93 & 0 \end{pmatrix},$$

and b dominates y:

$$\begin{pmatrix} w_{yy} & w_{yb} \\ w_{by} & w_{bb} \end{pmatrix} = \begin{pmatrix} 0 & -0.42 \\ 0.78 & 0 \end{pmatrix},$$

and the final edge game shows that o dominates b:

$$\begin{pmatrix} w_{oo} & w_{ob} \\ w_{bo} & w_{bb} \end{pmatrix} = \begin{pmatrix} 0 & 0.80 \\ -0.09 & 0 \end{pmatrix}$$

Alternatively, one can check inequalities (2.18 - 2.20) in the estimated \mathbf{W} or \mathbf{w} matrices, relabeling strategies rps as oyb. All the inequalities satisfy an ur-rps and this generates the real-life oscillations of the rock-paper-scissors dynamic that we will analyze further in Chapter 3.

2.5.4 Payoff differences

It will turn out to be useful to generalize the payoff difference expression Δw that served us so well in 2x2 games, and apply it to rps and other 3x3 games. To begin, consider a general 3x3 payoff matrix in continuous time:

$$\mathbf{w} = \begin{pmatrix} w_{aa} & w_{ab} & w_{ac} \\ w_{ba} & w_{bb} & w_{bc} \\ w_{ca} & w_{cb} & w_{cc} \end{pmatrix}$$

As usual, the strategies have fitness given by:

$$w_a = w_{aa}s_a + w_{ab}s_b + w_{ac}s_c, \quad (2.25)$$

$$w_b = w_{ba}s_a + w_{bb}s_b + w_{bc}s_c, \quad (2.26)$$

$$w_c = w_{ca}s_a + w_{cb}s_b + w_{cc}s_c, \quad (2.27)$$

and average fitness is given by:

$$\bar{w} = w_a s_a + w_b s_b + w_c s_c. \quad (2.28)$$

Define the following pairwise payoff difference functions:

$$\Delta w_{a-b} = w_a - w_b = (w_{aa} - w_{ba})s_a + (w_{ab} - w_{bb})s_b + (w_{ac} - w_{bc})s_c \quad (2.29)$$

$$\Delta w_{b-c} = w_b - w_c = (w_{ba} - w_{ca})s_a + (w_{bb} - w_{cb})s_b + (w_{bc} - w_{cc})s_c \quad (2.30)$$

$$\Delta w_{c-a} = w_c - w_a = (w_{ca} - w_{aa})s_a + (w_{cb} - w_{ab})s_b + (w_{cc} - w_{ac})s_c \quad (2.31)$$

It is easy to confirm the following useful identities:

$$\Delta w_{a-b} + \Delta w_{b-c} + \Delta w_{c-a} = 0, \quad (2.32)$$

and

$$\Delta w_{i-j} = -\Delta w_{j-i}. \quad (2.33)$$

The continuous time replicator for this general 3x3 game reads

$$\dot{s}_i(t) = (w_i - \bar{w})s_i(t). \quad (2.34)$$

In particular, we have

$$\begin{aligned}
\dot{s}_c &= (w_c - \bar{w})s_c \\
&= (w_c - w_a s_a - w_b s_b - w_c s_c)s_c \\
&= s_c(w_c - w_c s_c - w_b(1 - s_a - s_c) - w_a s_a) \\
&= s_c(w_c - w_c s_c - w_b(1 - s_c) + w_b s_a - w_a s_a) \\
&= s_c(1 - s_c)(w_c - w_b) + s_c(w_b s_a - w_a s_a) \\
&= s_c(s_a + s_b)(w_c - w_b) + s_c s_a(w_b - w_a) \\
&= s_c s_a \Delta w_{c-b} + s_c s_b \Delta w_{c-b} + s_c s_a \Delta w_{b-a}
\end{aligned} \tag{2.35}$$

Using the identities (2.32 - 2.33) we have

$$\begin{aligned}
\dot{s}_c &= s_c s_a \Delta w_{c-b} + s_c s_b \Delta w_{c-b} + s_c s_a \Delta w_{b-a} \\
&= s_c s_a (\Delta w_{a-b} + \Delta w_{c-a}) + s_c s_b \Delta w_{c-b} + s_c s_a \Delta w_{b-a} \\
&= -s_c s_a \Delta w_{b-a} + s_c s_a \Delta w_{c-a} + s_c s_b \Delta w_{c-b} + s_c s_a \Delta w_{b-a} \\
&= s_c s_a \Delta w_{c-a} + s_c s_b \Delta w_{c-b}.
\end{aligned}$$

The same sort of algebra yields:

$$\dot{s}_a = s_a s_b \Delta w_{a-b} + s_a s_c \Delta w_{a-c} \tag{2.36}$$

$$\dot{s}_b = s_b s_a \Delta w_{b-a} + s_b s_c \Delta w_{b-c} \tag{2.37}$$

That is, with continuous replicator dynamics, the growth rate $\frac{\dot{s}_i}{s_i}$ of each strategy share in any 3x3 game is a weighted sum of its payoff advantages Δw_{i-j} and Δw_{i-k} over the alternative strategies.

2.6 Notes

The Stag Hunt is a story that became a game. The game is a prototype of the social contract. The story is briefly told by Jean-Jacques Rousseau, in A Discourse on Inequality (1754): “If it was a matter of hunting a deer, everyone well realized that he must remain faithful to his post; but if a hare happened to pass within reach of one of them, we cannot doubt that he would have gone off in pursuit of it without scruple...”

The rock-paper-scissors game has held the imagination of game theorists for decades. Maynard Smith (1982) was one of the first to point out that the rock-paper-scissors game might promote an endless cycle in the context of replicator dynamics. Actually, Sewall Wright pointed this out decades before (1968) when he described an unnamed 3x3 frequency dependent game that could cycle endlessly. Weissing (1991) provides a thorough analytical treatment of such games. On the empirical side, Buss and Jackson (1979) worked out intransitive relations in coral growth dynamics (8 different species!) and suggested ecosystem dynamics might be governed by intransitive dynamics. However, the first payoff matrix for the rock-paper-scissors game in a single population was derived for lizards in the context of mating system dynamics.

Since those early formulations, the number of natural systems in which rock-paper-scissors dynamics has been identified is growing exponentially in recent years, it is now recognized to be one of the apex social system (e.g, most complex dynamics) in many organisms including isopods, damselflies, lizards, rodents, fish, insects, bacteria and even humans (reviewed in Sinervo and Calsbeek 2006; Sinervo in prep.).

The general RPS defined above can be observed in many biological situations which are reviewed in Sinervo and Calsbeek (2006, *Ann. Rev. Ecol. Evol. Syst.*).

We work through a continuous time rps example in the R workspace "RPS rK workspace Ch01.RData", where we introduce the DE solver of the R statistical package. This workspace also gives the r-K game of Figure 1.1.

2.7 Exercises

1. Build a spreadsheet to simulate discrete replicator dynamics for general HD games. Have labelled cells near the top for entering the parameters v and c , and write formulas that display the resulting 2x2 matrix. Include another labelled cell for the initial H share. Then build up a row and column display similar to that used in the chapter 1 spreadsheet to track H and D shares for 30 or more periods. Verify that you get convergence to the interior steady state v/c for appropriate values of the parameters.
2. Build a similar spreadsheet to simulate discrete replicator dynamics for RPS and other

3x3 matrix games. Check the claims made in section 2.5.2 about stability and spiraling.

3. For the general 2x2 matrix games presented in section 2.2, what can you say about behavior when $w_1 = w_2 = 0$? How do you interpret this situation? What can you say about behavior when $w_1 > w_2 = 0$? How do you interpret this situation? What can you say about behavior when $w_1 < w_2 = 0$? How do you interpret this situation?

Remark. In a later chapter, we will discuss extensive form games. They often give rise to situations in which two or more w_{ij} 's are equal. Therefore, when the payoff table comes from an extensive form game, it is much more likely to have some $w_i = 0$.

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