

shown in Figure 9.5(d). In particular, they converge on the mixed Nash equilibrium.

9.5 Biological Libration

Maynard Smith's *Evolution and the Theory of Games* spotlights many interesting applications of game theory to biology. This section can do no more than indicate the flavor of the ideas. Even then, much of the savor will be lost, since only sexless reproduction will be considered.

9.5.1 Replicators

At first sight, it seems unlikely that game theory could be successfully applied in evolutionary biology. How could an insect, for example, be a player in a game? Insects cannot reason. Their behavior is instinctive. They just do what they are programmed to do.

Nevertheless, some of the most promising applications of game theory have been biological. Paradoxically, the *less* developed an organism's thinking abilities, the *better* the theory tends to work. It is sometimes even usable when the protagonists are trees or flowers. How can this be so?

The secret is that the players in the game are *not* taken to be the organisms under study. If the behavior being investigated is instinctive, then it is coded in the organism's genes. One may think of the genes as part of the hardware of a natural computer: the part where the computer's programs are stored. Some of the programs control the organism's behavior. The programs we shall be interested in are those that select a strategy for the organism in a particular game. It is these *programs* that must be seen as substitutes for players when game theory is applied.

An important property of computer programs is that they can be copied from one computer to another. "Computer viruses" copy *themselves* from one computer to another. They are *self-replicating* programs.²¹ The programs imprinted on an animal's genes are also self-replicating. But their replication is immensely complicated compared with the replication of a computer virus. Nature not only has to copy programs from one natural computer to another, she has to create a

²¹A virus is a type of self-replicating molecule. Computer viruses usually do more than replicate themselves. Those widely publicized are akin to the biological virus for the common cold in that they create mayhem inside their host.

new natural computer to which the programs may be copied. Crick and Watson's discovery of how Nature works this trick using the device of the "double helix" is one of the great scientific adventure stories. But its thrills will have to be enjoyed elsewhere. All that is important here is that we understand that *something* exists that does two things:

- It replicates itself.
- It determines strategic behavior in a game.

Such an entity will be called a *replicator*.²²

Replicators do not only arise in a biological context. Rules-of-thumb, codes-of-conduct, fashions, life-styles, creeds and scientific ideas are all replicators of a kind.²³ Their mode of replication is not biological. They spread from one human mind to another through imitation or education (as in Section 9.4). However, given our current state of knowledge, one can only speculate about the detailed mechanics of such socio-economic replication. It therefore seems wiser to stick with the biological paradigm in what follows.

All this insistence on the importance of replicators is a preliminary to a discussion of Charles Darwin's notion of *natural selection*, which the philosopher Spencer encapsulated in the phrase "survival of the fittest".

To survive, replicators need hosts in whose genes they are imprinted. If we define the fitness of a host to be some measure of how frequently it gets to reproduce its genes, then it becomes almost a tautology that replicators that confer high fitness on their hosts will come to control a larger share of hosts than those that confer low fitness. If the environment will only support a restricted number of hosts, the replicator conferring low fitness on its hosts may die out altogether. The fittest replicator will then have survived.

A kibitzer watching the situation evolve might try to make sense of what he sees by attributing a goal or purpose to a replicator: that of maximizing the fitness of its hosts. If natural selection operates for long enough in a stable

²²This follows Dawkin's usage in his magnificent book, *The Selfish Gene*. The term is not intended to denote anything physical here. A computer program should not be confused with the hardware that stores it, nor a story with the book in which it is written. Similarly, when a double helix unravels, two different molecules result whose atoms are arranged in the same pattern. Neither of these molecules is the replicator. It is their common *pattern* that is the replicator.

²³In the *Selfish Gene*, Dawkin's calls such socio-economic replicators "memes".

environment, only those replicators that are good at maximizing the fitness of their hosts will remain in existence. To the kibitzer, it would therefore seem *as though* the surviving replicators were consciously seeking to attain the goal he had assigned to them. In brief, it would seem as though a replicator were acting like a *player in a game*.

Game theory is relevant because the behavior that confers high fitness on a host will often depend on what other hosts in the population are doing. Evolution should therefore be expected to generate an *equilibrium* of some kind among the surviving replicators. In this equilibrium, each replicator will be maximizing the fitness of its hosts, given the behavior induced in other organisms in the population by the replicators they are hosting.

9.5.2 Fitness

Maynard Smith's *Evolution and the Theory of Games* uses the Hawk-Dove Game of Figure 7.3(a) to illustrate the ideas of Section 9.5.1. To make things even simpler, the special form of the Hawk-Dove Game called Chicken in Figure 7.3(c) will be used here. This is shown again in Figure 9.7(a). Recall from Section 7.1.2 that Chicken has three Nash equilibria. It has two Nash equilibria in pure strategies, (*hawk, dove*) and (*dove, hawk*). It also has a mixed Nash equilibrium in which both players use each pure strategy with probability $\frac{1}{2}$. The latter is a *symmetric* equilibrium because both players do the same thing.

Although the pure strategies are labeled *hawk* and *dove*, Chicken is *not* to be interpreted as an inter-species game between hawks and doves. Think of it in terms of conflict between different members of the *same* species. To emphasize that the example is only an illustrative parable, we shall call the animal being studied the dodo. Dodos are extinct in real life, and so we are free to follow the example of historians in inventing any facts about them that suit our convenience. In particular, our dodos are all female and so reproduce asexually.²⁴

A dodo's day is not 24 hours long, but some fraction of τ of a year. During the daylight hours, dodos search for food. All dodos are equally good at foraging, but some may be unlucky because there is only enough food to support N dodos. Those

²⁴The assumption of an all-female species is not so crazy as it may seem. Certain beetles dispense with a male sex and reproduce parthenogenetically.

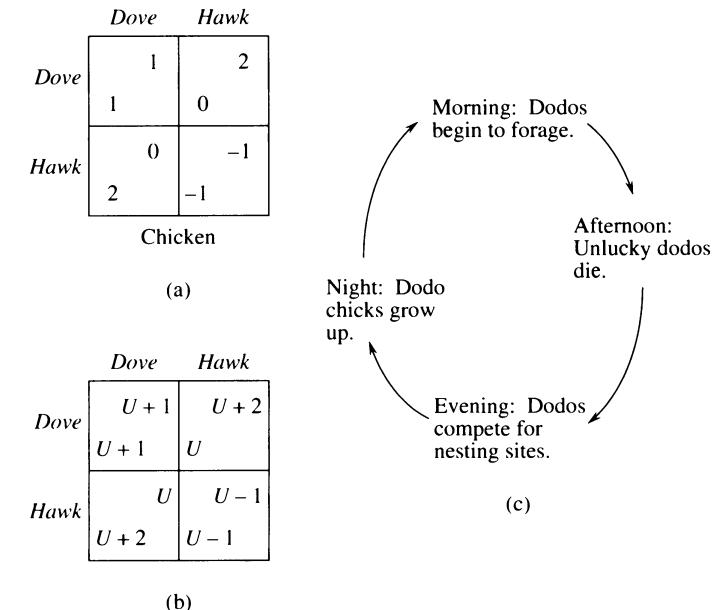


Figure 9.7 The facts of dodo life.

who fail to find food die. This is particularly tragic since a dodo that found food every day would be immortal.

In the evening, the N surviving dodos compete for favored nesting sites in the following way. Pairs of dodos chosen at random from the population are matched against each other to play Chicken. Remember that the *real* players are not the dodos, but the replicators that they are hosting. Only two types of replicator are considered at this stage: a replicator D that induces its host to play *dove*, and a replicator H that induces its host to play *hawk*.

A dodo that plays *hawk* against an opponent who plays *dove* gets exclusive possession of a favored nesting site. The opponent is excluded altogether. If both play *dove*, the site is shared. If both play *hawk*, there is a fight.

These different outcomes each affect the chances of a dodo laying an egg that evening differently. The dodo chicks that hatch out grow to maturity overnight, and are indistinguishable next morning from other dodos. Since older dodos have forgotten everything they knew the day before, they all start the new day on an equal basis. Figure 9.7(c) illustrates a dodo's daily round.

The precise fitnesses for the various possible strategy combinations for Chicken are shown in Figure 9.7(b). These are

given as the expected number of chicks a dodo will mother in a year. This means, for example, that a mother excluded altogether from a favored nesting site will expect $U\tau$ chicks on any particular evening. A mother who is sharing a site will expect $(U + 1)\tau$ chicks. A mother who has exclusive possession of a site will expect $(U + 2)\tau$ chicks. A mother who had to fight will expect $(U - 1)\tau$ chicks.

Notice that everything is stated in terms of *expected* number of chicks. We do not care about the number of chicks born to any particular dodo on any particular evening. We only care about the *total* number of dodos who will be hosting a particular replicator tomorrow.

Since reproduction is asexual, a chick's genes will be a copy of its mother's.²⁵ A chick therefore hosts the same replicator as her mother. To find the number of chicks hosting the D replicator tonight, we therefore have to add up all the chicks born to mothers hosting the D replicator. If the number of such mothers is sufficiently large, adding up the *expected* numbers of chicks and the *actual* numbers will nearly be the same thing.

This is why it is *expected* fitness that matters in biological discussions, just as it is *expected* Von Neumann and Morgenstern utility that matters in conventional game theory. In fact, nothing goes wrong if fitnesses are treated *exactly* like Von Neumann and Morgenstern payoffs. In particular, subtracting U from each entry in the fitness table of Figure 9.7(b) makes no difference to anything, as we shall see in Section 9.5.3. One therefore might as well confine attention to the regular Chicken game of Figure 9.7(a) in which the payoffs are *incremental* fitnesses.²⁶

9.5.3 The Replicator Equation

The time has now come to follow the evolution of the dodo population in detail. To this end, let $1 - p(t)$ denote the fraction of dodos hosting the D replicator who survive the daylight hours on some particular day. Let $p(t)$ denote the fraction hosting the H replicator. We shall abbreviate $p(t)$ to p in what follows, but the fact that p depends on time must not be forgotten.

²⁵Unless a mutation occurs. But this possibility is neglected for the moment.

²⁶That is, fitnesses in excess of the background level of U . In general, Nature cares nothing about absolutes. She cares only about how well one replicator does *relative* to another.

How many chicks does a mother hosting the D replicator expect *before* Chicken is played to apportion nesting sites? The answer is

$$\tau f_D(p) = \tau U + \tau(1 - p), \quad (9.5)$$

which is what the play of *dove* in Figure 9.7(b) would yield if the opponent used the mixed strategy $(1 - p, p)^T$. It is true that the opponent will not use a mixed strategy, but the effect is the same because the opponent is chosen at random from a population in which a fraction $1 - p$ play *dove* and a fraction p play *hawk*.

Since only N dodos survive until the evening, there will be $N(1 - p)$ mothers hosting the D replicator. Thus $N(1 - p)\tau f_D(p)$ chicks hosting the D replicator will be born. Since the mothers will be around in the morning too, the total number of dodos hosting the D replicator next morning is

$$N(1 - p)(1 + \tau f_D(p)).$$

The corresponding expression for the total number of dodos next morning hosting the H replicator is

$$Np(1 + \tau f_H(p)),$$

where

$$\tau f_H(p) = \tau U + 2\tau(1 - p) - \tau p. \quad (9.6)$$

Because all dodos have an equal chance of surviving the next day, the fraction $p(t + \tau)$ of dodos hosting the H replicator who make it to the next evening is necessarily the same as the fraction of dodos hosting the H replicator next morning. Thus

$$p(t + \tau) = \frac{Np(t)(1 + \tau f_H(p))}{N(1 + \tau \bar{f}(p))} = p(t) \left(\frac{1 + \tau f_H(p)}{1 + \tau \bar{f}(p)} \right)$$

where $\tau \bar{f}(p) = (1 - p)\tau f_D(p) + p\tau f_H(p)$, so that $N(1 + \tau \bar{f}(p))$ is the total number of dodos next morning.

It remains to rewrite the expression for $p(t + \tau)$ as

$$\frac{p(t + \tau) - p(t)}{\tau} = p \left\{ \frac{f_H(p) - \bar{f}(p)}{1 + \tau \bar{f}(p)} \right\}.$$

After Section 9.3.3, it will come as no surprise that the limit will now be taken as $\tau \rightarrow 0$. The result is the *replicator equation*

$$p' = p(f_H(p) - \bar{f}(p)). \quad (9.7)$$

In this differential equation, recall that $p(t)$ is the fraction of dodos hosting the H replicator. The quantity $f_H(p)$ is the

fitness²⁷ conferred on a host by the H replicator, given the current population mix. The quantity $\bar{f}(p) = (1-p)f_D(p) + pf_H(p)$ is the average fitness of the population as a whole.

The story that led us to the replicator equation is more than a little far-fetched. But it is only one of many stories that lead to the same conclusion. Other stories require less fanciful assumptions about the natural history of the organism under study, but they take longer to tell.

9.5.4 Who Survives?

Substitute (9.5) and (9.6) in the replicator equation (9.7). Notice that the background fitness U cancels out, confirming that only the *incremental* fitnesses of Figure 9.7(a) are relevant. The result is the differential equation

$$\frac{dp}{dt} = p(1-p)(1-2p). \quad (9.8)$$

This differential equation governs the evolution of the dodo population. If we could solve it, we would know the fraction of hawkish dodos at every time t . But solving complicated differential equations is a headache even for experts. Fortunately, we can evade this difficult task because we care only about what happens in the long run.

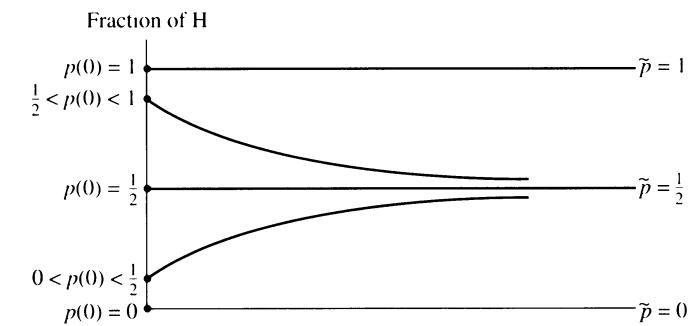
As we know from our previous study of dynamic processes, the rest points of the process are likely to be significant. The rest points for (9.8) are $\tilde{p} = 0$, $\tilde{p} = 1$ and $\tilde{p} = \frac{1}{2}$. If the process is started at one of these points, it will never move anywhere else, because the replicator equation tells us that the rate at which it starts moving is $p'(0) = \tilde{p}(1-\tilde{p})(1-2\tilde{p}) = 0$.

Our study of Shapley's Shimmy warns us not to leap to any conclusions about the convergence properties of the dynamic process when it does not start at a rest point. However, here things are easy. If $p > \frac{1}{2}$, then

$$p'(t) = p(1-p)(1-2p) < 0$$

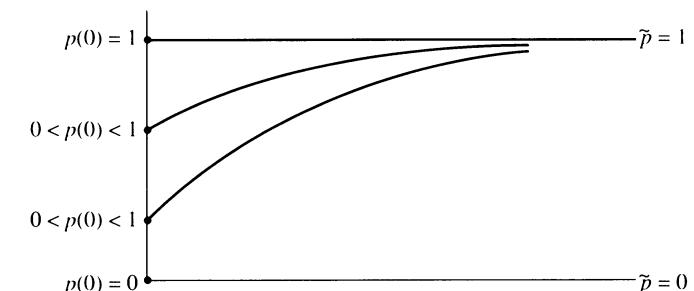
and so the function p is *strictly decreasing*. If $p < \frac{1}{2}$, then $p'(t) > 0$ and so the function p is *strictly increasing*. This tells us what the shape of the graph of p must look like. The possibilities are illustrated in Figure 9.8(a). Only $\tilde{p} = \frac{1}{2}$ is a local attractor.

Neither of the rest points $\tilde{p} = 0$ or $\tilde{p} = 1$ is stable. The first corresponds to a population in which only the H replicator is present. If no D replicator ever appears, the population just



Chicken

(a)



Prisoners' Dilemma

(b)

Figure 9.8 The evolution of dodos.

stays the way it is. But, if there should be a *mutation* that generates even a tiny fraction of dodos hosting the D replicator, then that fraction will grow over time until the numbers of dodos hosting the H and D replicators are equalized. The same goes for the rest point $\tilde{p} = 1$. A population in which only the D replicator is present is vulnerable to an invasion by a tiny fraction of H mutants. Such a tiny fraction will grow until the numbers of H and D replicators are equalized.

The only population invulnerable to such invasions is one in which half the population is hosting the H replicator and half is hosting the D replicator. This corresponds to the rest point $\tilde{p} = \frac{1}{2}$ for the replicator equation.

Recall that Chicken has three Nash equilibria. The local attractor $\tilde{p} = \frac{1}{2}$ corresponds to the *mixed* Nash equilibrium in which both players use each pure strategy with probability $\frac{1}{2}$. However, no dodo tosses any coins. We have yet another

²⁷Expressed in expected number of chicks per year.

interpretation of a mixed-strategy equilibrium in which no player actually randomizes. The randomization is done by Nature when she pairs off the dodos to play Chicken. To a kibitzer, it will seem *as though* a dodo is choosing *hawk* and *dove* with probability $\frac{1}{2}$. But this is only because the kibitzer is ignorant of the replicator the dodo is hosting. In fact, a dodo's behavior is entirely deterministic.

Biologists refer to populations in which distinct behaviors coexist together as polymorphous.²⁸ However, it will be evident that it is not only in biology that polymorphy matters. In particular, when mixed Nash equilibria are important, it will often be because the players have been randomly selected from a polymorphous population even when the context is economic or sociological.

Of the three Nash equilibria for Chicken, only the mixed equilibrium corresponds to a local attractor. What is wrong with $(\text{hawk}, \text{dove})$ and $(\text{dove}, \text{hawk})$? In brief, they are not symmetric. Nothing asymmetric can emerge from the story told about the evolution of dodos, because both player I and player II are chosen at random from the *same* population. Hence, the probability that any pure strategy is used must be the *same* for each player.

It remains to say something about Figure 9.8(b). Exercise 9.8.10 asks for the replicator equation to be obtained for the case in which Chicken is replaced by the Prisoners' Dilemma of Figure 7.3(b). Since the only Nash equilibrium of the Prisoners' Dilemma is $(\text{hawk}, \text{hawk})$, it is no surprise that the only local attractor is then $\tilde{p} = 1$, which corresponds to the case when all dodos are hosting the *H* replicator. It is true that $\tilde{p} = 0$ is also a rest point, but a population consisting of dodos hosting the *D* replicator can be invaded by a mutant *H* replicator that takes over a tiny fraction of the dodo population. The fraction of the population hosting the *H* replicator will expand over time until the *D* replicator is displaced altogether.

9.6 Evolutionary Stability

Local attractors for the replicator dynamics in Chicken and the Prisoners' Dilemma correspond to symmetric Nash equilibria. This is no accident. It is another example in which a trial-and-error adjustment process leads to the use of optimal strategies, even though nobody did any conscious optimizing. Mutations

²⁸This means “many forms”.

provide the source of new strategies to be tried,²⁹ and natural selection is the mechanism for the correction of errors.

It is tempting to seek to short-circuit the painful study of the mathematics of replication, and to leap directly to the conclusion that evolution is bound to lead to optimizing behavior in the long run. The idea of evolutionary stability is an attempt to put such intuitions into concrete form.

9.6.1 Mutant Invasions

Imagine that only one replicator is present in a population of dodos. This replicator will be denoted by *N* to indicate that it is the “normal” replicator. A new *mutant* replicator *M* now appears. At first, the fraction of the population hosting *M* is some tiny number $\epsilon > 0$. Will this mutant invasion be repelled, or will the mutant replicator establish itself permanently? The condition for *evolutionary stability* is that the mutant replicator will necessarily be driven to extinction, provided that ϵ is sufficiently small.

Figure 9.9(a) is a fitness table. For example, $f(N, M)$ is the fitness of a dodo hosting the *N* replicator when it is matched against a dodo hosting the *M* replicator. Any dodo has probability $1 - \epsilon$ of being matched against a dodo carrying the *N* replicator and probability ϵ of being matched against a dodo carrying the *M* replicator. The overall fitness of a dodo carrying the *N* replicator is therefore

$$(1 - \epsilon)f(N, N) + \epsilon f(N, M).$$

The overall fitness of a dodo carrying the *M* replicator is

$$(1 - \epsilon)f(M, N) + \epsilon f(M, M).$$

The condition that the mutant invasion be repelled is that mutant dodos be less fit than normal dodos. Evolutionary stability therefore requires that

$$(1 - \epsilon)f(N, N) + \epsilon f(N, M) > (1 - \epsilon)f(M, N) + \epsilon f(M, M), \quad (9.9)$$

for sufficiently small $\epsilon > 0$.

²⁹Here biologists have an advantage over economists. Their discipline provides them with hard information about what mutations it is sensible to include in the model. For example, the phrase “dead as a dodo” would perhaps not be in common usage if a mutant strain of evil-smelling, skunk-like dodos had appeared at the appropriate time. However, science-fiction movies to the contrary, biologists know enough about how genes work to be able to dismiss such an eventuality as absurdly unlikely. However, very little is known about how humans come up with new “mutant” ideas for making money. Economists can therefore only guess at what strategies they should include in deciding what game to study.

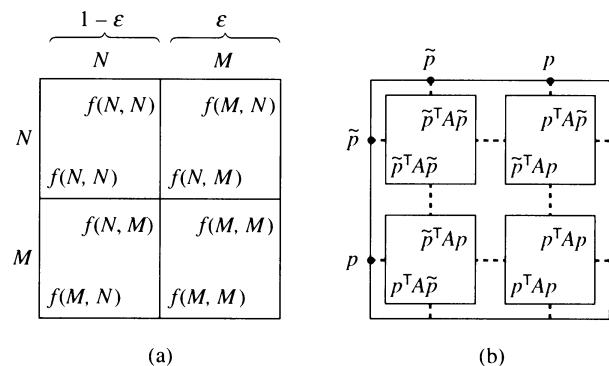


Figure 9.9 Evolutionary stability.

Evolutionary fitness in our dodo story depends on how a game is played. In Section 9.5.2, the game was Chicken. Here it will be any symmetric bimatrix game. An entry in the $n \times n$ payoff matrix A is to be interpreted as player I's incremental fitness. The game is symmetric because we are modeling a situation that looks precisely the same to both players. In algebraic terms, the requirement for symmetry is that player II's payoff matrix B be given by $B = A^\top$. Figure 9.9(b) shows what the fitnesses will be if the N replicator induces its hosts to use the mixed strategy \tilde{p} , and M induces its hosts to use the mixed strategy p .

9.6.2 Symmetric Nash Equilibria

A mixed strategy in a symmetric $n \times n$ bimatrix game is an $n \times 1$ column vector. Recall from Section 6.4.4 that player I's payoff from using mixed strategy p when player II uses mixed strategy q is $\Pi_1(p, q) = p^T A q$. Player II's payoff³⁰ is $\Pi_2(p, q) = p^T B q = q^T A p = \Pi_1(q, p)$. Section 6.5.6 gives the requirement that (\tilde{p}, \tilde{q}) be a Nash equilibrium in the form

$$\Pi_1(\tilde{p}, \tilde{q}) \geq \Pi_1(p, \tilde{q})$$

$$\Pi_2(\tilde{p}, \tilde{q}) \geq \Pi_2(\tilde{p}, q).$$

The first inequality says that \tilde{p} is a best reply to \tilde{q} since it is at least as good as any other reply p . The second inequality says that \tilde{q} is a best reply to \tilde{p} since it is at least as good as any other reply q .

³⁰Since $p^T B q$ is a scalar, it is equal to its transpose. For the reasons given in Section 4.3.1, $(p^T B q)^\top = q^T B^\top p = q^T A p$. The last step uses the symmetry of the game. Since $B = A^\top$, $B^\top = (A^\top)^\top = A$.

Only *symmetric* Nash equilibria in our symmetric game are of interest here. For a symmetric equilibrium, $\tilde{p} = \tilde{q}$. The second of the two inequalities characterizing a Nash equilibrium then becomes $\Pi_2(\tilde{p}, \tilde{p}) \geq \Pi_2(\tilde{p}, q)$, which is the same as $\Pi_1(\tilde{p}, \tilde{p}) \geq \Pi_1(q, \tilde{p})$. If q is replaced by p , this is exactly the same as the first inequality:

$$\Pi_1(\tilde{p}, \tilde{p}) \geq \Pi_1(p, \tilde{p}). \quad (9.10)$$

In brief, the condition that (\tilde{p}, \tilde{p}) be a Nash equilibrium for our symmetric game is that the inequality (9.10) holds for all mixed strategies p . This guarantees that \tilde{p} is a best reply to \tilde{p} for both players.

9.6.3 Evolutionarily Stable Strategies

Suppose that the normal replicator N induces its host to use the mixed strategy \tilde{p} , and the mutant replicator M induces its host to use the mixed strategy p .³¹ Then (9.9) translates into the requirement that, for all sufficiently small $\epsilon > 0$,

$$(1 - \epsilon)\Pi_1(\tilde{p}, \tilde{p}) + \epsilon\Pi_1(\tilde{p}, p) > (1 - \epsilon)\Pi_1(p, \tilde{p}) + \epsilon\Pi_1(p, p). \quad (9.11)$$

If this requirement holds for all mixed strategies p , then the mixed strategy \tilde{p} is said to be an *evolutionarily stable strategy*.³²

Lemma 9.6.1 A necessary and sufficient condition that \tilde{p} be an evolutionarily stable strategy is that

- (i) $\Pi_1(\tilde{p}, \tilde{p}) \geq \Pi_1(p, \tilde{p}) \quad (\text{for all } p)$
- and (ii) $\Pi_1(\tilde{p}, \tilde{p}) = \Pi_1(p, \tilde{p}) \Rightarrow \Pi_1(\tilde{p}, p) > \Pi_1(p, p) \quad (\text{for all } p \neq \tilde{p})$

Proof. To obtain necessary conditions, we begin with (9.11) and see what follows. The first step is to consider the limit as $\epsilon \rightarrow 0$. This yields (i) immediately.³³ Item (ii) is even easier

³¹For a biologist, N and M are *genotypes*. These express themselves in the *phenotype* of an animal. An animal's phenotype is the set of its observable attributes. In our case, what matters about the phenotype of a dodo is the mixed strategy it uses in the game.

³²To be precise, the requirement is that, for any p there exists $\delta > 0$ such that the inequality holds for each ϵ satisfying $0 < \epsilon < \delta$. Notice that several different replicators may induce \tilde{p} . Thus the evolutionary stability of \tilde{p} does not guarantee evolutionary stability for any particular replicator.

³³It does *not* yield the conclusion $\Pi_1(\tilde{p}, \tilde{p}) > \Pi_1(p, \tilde{p})$. For example, if $\epsilon > 0$, then $2\epsilon > \epsilon$. But we cannot take the limit as $\epsilon \rightarrow 0$ in this inequality and deduce that $0 > 0$. We can only deduce that $0 \geq 0$. If you suspect that even this is wrong (on the grounds that what is true is $0 = 0$), then consider carefully what $0 \geq 0$ means.

	<i>s</i>	<i>t</i>
<i>s</i>	0	0
<i>t</i>	1	2

(a)

	<i>Rock</i>	<i>Scissors</i>	<i>Paper</i>
<i>Rock</i>	0	-1	1
<i>Scissors</i>	1	0	-1
<i>Paper</i>	-1	1	0

(b)

	<i>Rock</i>	<i>Scissors</i>	<i>Paper</i>
<i>Rock</i>	0	1	0
<i>Scissors</i>	0	0	1
<i>Paper</i>	1	0	0

(c)

Figure 9.10 Evolutionarily stable strategies.

to deduce. Just put $\Pi_1(\tilde{p}, \tilde{p}) = \Pi_1(p, \tilde{p})$ in (9.11) and see what happens.

For (i) and (ii) to be sufficient conditions, we must be able to use them to derive (9.11). If (i) holds, then either $\Pi_1(\tilde{p}, \tilde{p}) > \Pi_1(p, \tilde{p})$ or $\Pi_1(\tilde{p}, \tilde{p}) = \Pi_1(p, \tilde{p})$. In the second case, (9.11) follows immediately from (ii). For the first case, simply note that the left side of (9.11) can be made as close to $\Pi_1(p, \tilde{p})$ as we choose by taking $\epsilon > 0$ sufficiently small. Similarly, the right side can be made as close to $\Pi_1(p, \tilde{p})$ as we choose. Thus, when $\Pi_1(\tilde{p}, \tilde{p}) > \Pi_1(p, \tilde{p})$, the inequality (9.11) must hold provided $\epsilon > 0$ is chosen to be small enough.³⁴ \square

The criteria for an evolutionarily stable strategy \tilde{p} given in Lemma 9.6.1 have a straightforward game-theoretic interpretation. Criterion (i) is identical to (9.10) and hence says that (\tilde{p}, \tilde{p}) is a Nash equilibrium. Thus \tilde{p} is a best reply to itself. But \tilde{p} need not be the only best reply to itself. Criterion (ii) asks us to consider an *alternative best reply* p to \tilde{p} . It then insists that, for \tilde{p} to be evolutionary stable, \tilde{p} must be a better reply to p than p is to itself.

Figure 9.10(a) shows a 2×2 symmetric game in which the symmetric Nash equilibria in pure strategies are (s, s) and (t, t) . Although t is evolutionarily stable, s is not. The reason is that t is an alternative best reply to s , but s is not a better reply to t than t is to itself.

³⁴Let $a = \Pi_1(\tilde{p}, \tilde{p}) - \Pi_1(p, \tilde{p})$ and $b = \Pi_1(p, p) - \Pi_1(\tilde{p}, p)$. If $b \leq 0$, any $\epsilon > 0$ will suffice. Otherwise $a > 0$ and $b > 0$, and ϵ must be chosen to satisfy $0 < \epsilon < a/(a + b)$.

9.6.4 Replicator Dynamics

Evolutionarily stable strategies were introduced in an attempt to short-circuit the difficulties involved in modeling the details of biological adaptation processes. How successful are they in this role? Our crazy model of the evolution of dodos can be used to examine this question. Its lack of realism is no handicap for this purpose because, if the ideas that led us to the concept of evolutionary stability are valid, then they would still be valid in crazy *counterfactual* worlds like that inhabited by our dodos. The use of such unrealistic, oversimplified formal models for the purpose of testing the *internal consistency* of theories that do claim to be realistic is very important indeed, although widely misunderstood.³⁵

Before discussing how evolutionarily stable strategies are related to attractors of the replicator dynamics, it is necessary to say something about mixed strategies. Animals *do* sometimes use mixed strategies, but it seems that they seldom do so in one-on-one contests. If a mixed strategy is used, it will usually be when an animal is “playing the field”. That is, when it is competing simultaneously with a large number of its fellows. So why take the trouble to define an evolutionarily stable mixed strategy? Why not stick to pure strategies? As regards the replicator dynamics, we shall do precisely that. Only replicators that induce their hosts to use pure strategies will be considered. However, in studying Chicken, we discovered that *polymorphic* populations may turn out to be stable. These are populations in which different animals may be hosting different replicators. Although we shall not study the case when any particular animal makes random choices, we shall find the idea of an evolutionarily stable mixed strategy useful in describing stable polymorphic populations.

It is not necessary to repeat the derivation of the replicator equation (9.7) from Section 9.5.3. When Chicken is replaced by a symmetric game in which player I's payoff matrix is A , it is true that things get a little more complicated. Instead of two replicators, one needs n replicators, one for each pure strategy. At any time, the *state* of the population will then be determined by a vector $p = (p_1, p_2, \dots, p_n)^\top$ that gives the

³⁵Some social scientists are touchy about the “scientific” status of their subject, and insist that a model is worthwhile if and only if it predicts actual behavior. One might characterize this attitude as “naive positivism”. Physicists, of course, know better. In particular, they understand mathematics well enough to appreciate the importance of searching for logical *counterexamples* when confronted with a conjecture.

fractions of the population hosting each replicator. If the i th replicator induces its host to play the i th pure strategy, its fitness $f_i(p)$ can be calculated from the matrix A .³⁶ The argument of 9.5.3 then yields the replicator equation in the form

$$p'_i = p_i(f_i(p) - \bar{f}(p)). \quad (9.12)$$

Let A be any symmetric 2×2 matrix whose rows are not both the same.³⁷ The replicator dynamics for such a matrix are not difficult to study. The argument of Section 9.5.4 suffices to prove part (ii) of the simple proposition stated below (Exercise 9.8.12). Part (i) is equally easy (Exercise 9.8.16).

Proposition 9.6.1 When $n = 2$,

- (i) The payoff matrix A always admits at least one evolutionarily stable strategy \tilde{p} .
- (ii) A population state \tilde{p} is an asymptotic attractor of the replicator dynamics if and only if \tilde{p} is an evolutionarily stable strategy.

When $n > 2$, the world becomes more complicated. Neither (i) nor (ii) is then true. The Rock-Scissors-Paper game of Figure 9.10(b) is a counterexample to (i). It has no evolutionarily stable strategy.³⁸ (Exercise 9.8.17). The 4×4 analog of Shapley's Shimmy given in Figure 9.10(c) is a counterexample to (ii). The population state $\tilde{p} = (\frac{1}{4}, \frac{1}{4}, \frac{1}{4}, \frac{1}{4})^\top$ is an asymptotic attractor of the replicator dynamics, but \tilde{p} is not an evolutionarily stable strategy.³⁹ However, some useful things are true in the general case. The following proposition summarizes some of these.

Proposition 9.6.2 Let \tilde{p} be an $n \times 1$ vector whose coordinates are nonnegative and sum to one. Then, for any symmetric $n \times n$ game, the following implications hold:

³⁶The fitnesses $f_i(p)$ are incremental fitnesses per unit of time. The $n \times 1$ column vector $f(p)$ is given by $f(p) = Ap$. The average fitness $\bar{f}(p)$ of a member of the population is given by $\bar{f}(p) = p^\top f(p) = p^\top Ap$.

³⁷If both rows are the same, then both pure strategies are equally good no matter what the other player does. This trivial case therefore has to be excluded (Exercise 9.8.12(c)).

³⁸The only Nash equilibrium is for each player to use the mixed strategy $\tilde{p} = (\frac{1}{3}, \frac{1}{3}, \frac{1}{3})^\top$. Both players then get zero. Anything is a best reply to \tilde{p} . In particular, *rock* is an alternative to \tilde{p} as a best reply to \tilde{p} . But \tilde{p} is not a strictly better reply to *rock* than *rock* is to itself.

³⁹This is a little troublesome to prove. Exercise 9.8.26 provides a less elegant example that is easier to analyze.

- (i) \tilde{p} is an evolutionarily stable strategy
- \Rightarrow (ii) \tilde{p} is an asymptotic attractor of the replicator dynamics
- \Rightarrow (iii) \tilde{p} is a Nash equilibrium
- \Rightarrow (iv) \tilde{p} is a rest point of the replicator dynamics.

The failure of Proposition 9.6.1 to generalize means that the idea of an evolutionarily stable strategy does not allow us to escape the painful task of studying the replicator dynamics in detail. However, it remains a useful tool. The fact that evolutionarily stable strategies sometimes fail to exist at all should not lead us to change our minds on this point.⁴⁰ Indeed, the nonexistence of an evolutionarily stable strategy may well be a useful indication in itself that the replicator dynamics need particularly careful study.

9.7 The Evolution of Cooperation

Axelrod's *Evolution of Cooperation* has been so influential a book that it is often taken for granted that the repeated Prisoners' Dilemma is the right and proper vehicle for the study of this question. However, it is complicated to study repetitions of a repeated game. Moreover, the question of how cooperative behavior may evolve becomes entangled with a second even more important question: namely, how do *learning rules* evolve? This second question is unavoidable when boundedly rational players confront each other in a *repeated* game. A replicator that did not program its host to respond to the way the opponent is playing would usually not stand much chance of surviving.

Since little seems to be known about the evolution of learning rules, it seems wiser to continue to use Chicken to illustrate how cooperation may evolve. However, it will be necessary to examine a souped-up version of Chicken with four pure strategies instead of two.

9.7.1 Chicken Soup

If two hawkish dodos are matched to play the original version of Chicken, they fight and thereby risk injury. However, in real life, contests between animals of the same species are often settled by a *ritualized* battle. Both animals begin by

⁴⁰Some game theorists make existence for all games a *sine qua non* for an equilibrium concept.