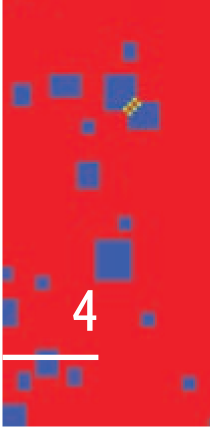


4

EVOLUTIONARY GAMES

EVOLUTIONARY GAME THEORY means that the fitness of individuals is not constant, but depends on the relative proportions (frequencies) of the different phenotypes in the population: fitness is frequency dependent. Evolutionary game theory is the generic approach to evolutionary dynamics and contains as a special case constant selection.

Game theory was invented by John von Neumann and Oskar Morgenstern. They wanted to design a mathematical theory to study human behavior in strategic and economic decisions. Von Neumann was a Hungarian-born mathematician working at the Institute for Advanced Study, where he invented and revolutionized several fields of mathematics. We have already encountered him in Chapter 3 in connection with the terms “translation” and “transcription,” which he invented when thinking about how to conceive of a machine that could reproduce itself. He built the first computer that held the program for the calculation in its memory rather than in its hardware. Incidentally, one of the first projects that this computer did in its spare time was a mathematical simulation of an evolutionary system.

John Nash came as a mathematics Ph.D. student to Princeton University with a remarkably short letter of reference: “This man is a genius.” Nash invented a simple but important concept in game theory, which is now called the “Nash equilibrium.” A Nash equilibrium is very similar to an evolutionarily stable strategy (ESS). Both concepts are important for evolutionary dynamics. Nash’s Ph.D. thesis led to a single-page paper in the *Proceedings of the National Academy of Sciences USA* (1950), which earned him a Nobel Prize in economics in 1994.

William Hamilton and Robert Trivers were among the first to use game theoretical ideas in biology, but the field of evolutionary game theory was founded by the work of John Maynard Smith and others, including Peter Taylor, Josef Hofbauer, and Karl Sigmund.

John Maynard Smith and George Price introduced game theory to evolutionary biology and population thinking to game theory in a paper published in *Nature* in 1973. Traditional game theory typically analyzes an interaction between two players, for example, you and me. The question is how you can maximize your payoff in a game, given that you do not know what I will do. The concept of rationality comes into play. You may assume that I will act in order to maximize my payoff. Given this assumption, you will then behave to maximize your payoff. But nothing guarantees that I will behave rationally, and in fact many experimental games show that humans do not behave rationally.

Evolutionary game theory does not rely on rationality. Instead it considers a population of players interacting in a game. Individuals have fixed strategies. They interact randomly with other individuals. The payoffs of all these encounters are added up. Payoff is interpreted as fitness, and success in the game is translated into reproductive success. Strategies that do well reproduce faster. Strategies that do poorly are outcompeted. This is straightforward natural selection.

In Figure 4.1 we see two phenotypes. A can move while B cannot. A pays a certain cost for the ability to move, but also gains the associated advantage. Suppose the cost-benefit analysis leads to a fitness of 1.1 for A compared to a fitness of 1 for B. In this setting, fitness is constant, and A will certainly outcompete B. But imagine that the advantage of being able to move is large when few others are on the road, but diminishes as the highways get blocked up. In this case, the fitness of A is not constant, but is a declining function

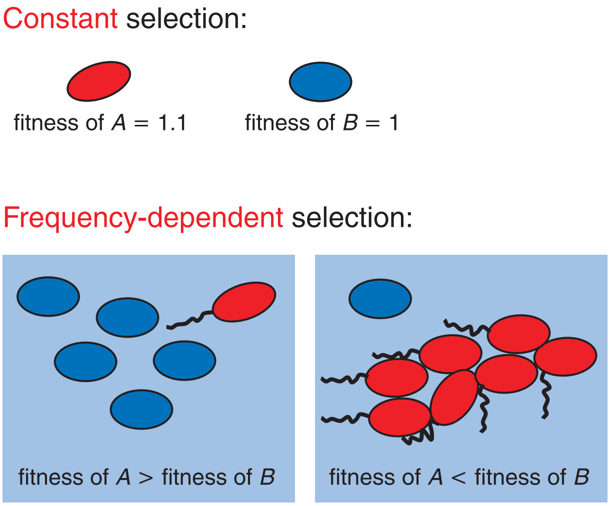


Figure 4.1 Constant selection means fitness neither depends on the composition of the population nor changes over time. For example, A has constant fitness 1.1, while B has constant fitness 1. In contrast, frequency-dependent selection means that fitness does depend on the relative abundance (= frequency) of individual types. A has the ability to move. If few other cells are moving, then A has a larger fitness than B. But if many other cells "are on the road," this fitness advantage is reversed (in this hypothetical example).

of the frequency of A. A has a higher fitness than B when A is rare, but has a lower fitness than B when A is common. What is the outcome of such a selection process?

Let us formalize the general case of frequency-dependent selection between two strategies A and B. Denote by x_A the frequency of A and by x_B the frequency of B. The vector $\vec{x} = (x_A, x_B)$ defines the composition of the population. Denote by $f_A(\vec{x})$ the fitness of A and by $f_B(\vec{x})$ the fitness of B. The selection dynamics can be written as

$$\begin{aligned} \dot{x}_A &= x_A[f_A(\vec{x}) - \phi] \\ \dot{x}_B &= x_B[f_B(\vec{x}) - \phi] \end{aligned} \tag{4.1}$$

The average fitness is given by $\phi = x_A f_A(\vec{x}) + x_B f_B(\vec{x})$.

Because $x_A + x_B = 1$ at all times, we can introduce the variable x with $x_A = x$ and $x_B = 1 - x$. We can write the fitness functions as $f_A(x)$ and $f_B(x)$.

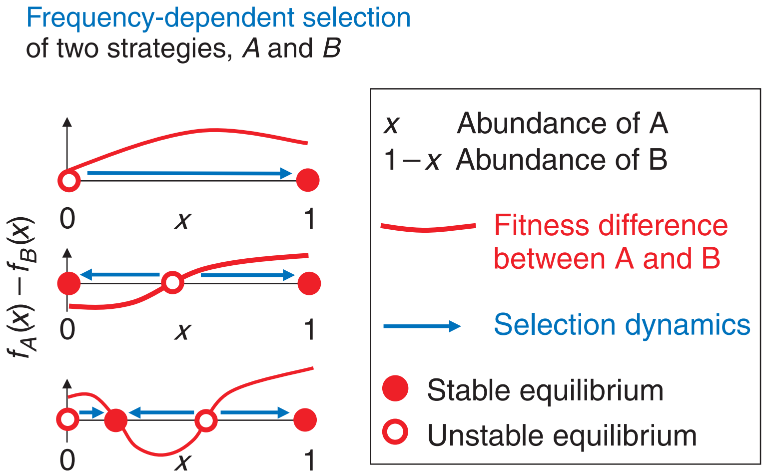
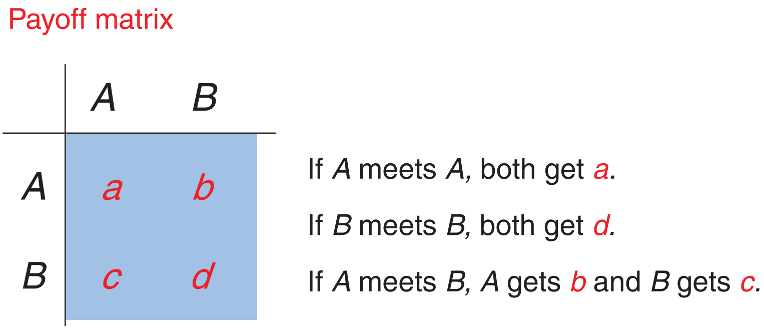


Figure 4.2 Frequency-dependent selection between two strategies can lead to multiple stable and unstable equilibria. The red curve, $f_A(x) - f_B(x)$, indicates the fitness difference between A and B as a function of the frequency, x, of A. If $f_A(x) - f_B(x) > 0$, then the frequency of A will increase, as shown by the blue arrows indicating the direction of selection dynamics. If $f_A(x) - f_B(x) < 0$, then the frequency of A will decline. Whenever $f_A(x) - f_B(x) = 0$, the frequency of A will not change. This condition characterizes an equilibrium of selection dynamics. If the slope of $f_A(x) - f_B(x)$ is positive at this point, then the equilibrium is unstable. If the slope is negative, then the equilibrium is stable. The points $x = 0$ and $x = 1$ are always equilibria. The equilibrium $x = 0$ is stable if $f_A(0) - f_B(0) < 0$. The equilibrium $x = 1$ is stable if $f_A(1) - f_B(1) > 0$.

System (4.1) leads to

$$\dot{x} = x(1 - x)[f_A(x) - f_B(x)]. \tag{4.2}$$

The equilibria of this differential equation are given by $x = 0$, $x = 1$, and all values $x \in (0, 1)$ that satisfy $f_A(x) = f_B(x)$. The equilibrium $x = 0$ is stable if $f_A(0) < f_B(0)$. Conversely, the equilibrium $x = 1$ is stable if $f_A(1) > f_B(1)$. An interior equilibrium, x^*, is stable if the derivatives of the functions f_A and f_B satisfy $f_A'(x^*) < f_B'(x^*)$. Figure 4.2 gives a graphical representation. There can be several stable and unstable equilibria in the interior of the interval $[0, 1]$.



If A meets A, both get a.

If B meets B, both get d.

If A meets B, A gets b and B gets c.

Figure 4.3 A game between two strategies, A and B, is defined by a 2×2 payoff matrix.

4.1 TWO-PLAYER GAMES

Normally, a game with two strategies, A and B, is described by a payoff matrix

$$\begin{array}{c} \\ A \\ B \end{array} \begin{array}{c} \begin{array}{cc} A & B \end{array} \\ \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array} \tag{4.3}$$

The payoff matrix is read in the following way: A gets payoff a when playing against A; A gets payoff b when playing against B; B gets payoff c when playing against A; B gets payoff d when playing against B (Figure 4.3).

The key idea of evolutionary game theory is to consider a population of A and B players and to equate payoff with fitness. If x_A is the frequency of A and x_B the frequency of B, then the expected payoff for A and B is respectively given by

$$\begin{aligned} f_A &= a x_A + b x_B \\ f_B &= c x_A + d x_B \end{aligned} \tag{4.4}$$

These equations assume that for each player the probability of interacting with an A player is x_A and the probability of interacting with a B player is x_B. Thus players meet each other randomly.

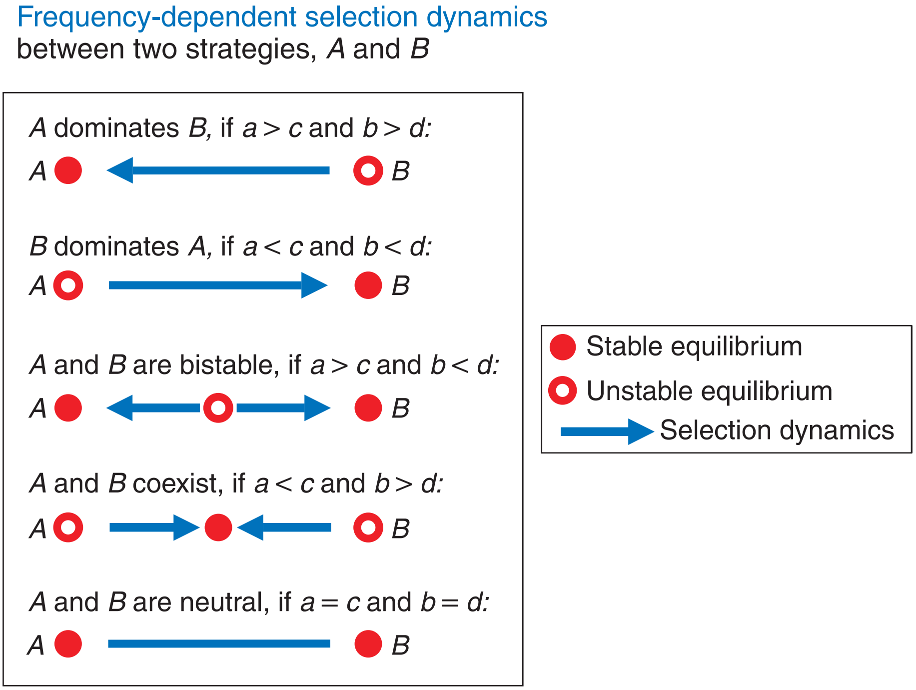


Figure 4.4 There are five possibilities for the selection dynamics between two strategies: (i) A dominates B, (ii) B dominates A, (iii) A and B are bistable, (iv) A and B coexist in a stable equilibrium, and (v) A and B are neutral variants of each other.

Let us now insert these linear fitness functions into equation (4.1). Let $x = x_A$ as before. We obtain

$$\dot{x} = x(1 - x)[(a - b - c + d)x + b - d]. \tag{4.5}$$

We want to classify the behavior of the nonlinear differential equation (4.5) depending on the ranking of the entries in the payoff matrix (4.1). There are five cases (Figure 4.4):

(i) A dominates B. This is the case if $a > c$ and $b > d$. If you were to play this game with another person, then no matter whether the other person chooses A or B it is best for you to play A. For a population of A and B players, this ranking of payoff values implies that the average fitness of A will always exceed that of B. Thus selection will favor A over B for any composition of the population. Selection will lead to the state where the whole population consists of A players, $x_A = 1$. More accurately, we say that A dominates B if $a \geq c$ and $b \geq d$, where at least one inequality must be strict.

(ii) B dominates A. This is the case if $a < c$ and $b < d$. This situation is the mirror image of case (i) with A and B exchanged. Again, more accurately, we say that A dominates B if $a \leq c$ and $b \leq d$, where at least one inequality must be strict.

(iii) A and B are bistable. This is the case if $a > c$ and $b < d$. If you were to play this game with another person, you should try to play the same choice as the other person. A is the best response for A. B is the best response for B. For the selection dynamics within a population, the outcome depends on the initial condition. There is an unstable equilibrium in the interior of the interval $[0, 1]$ given by $x^* = (d - b)/(a - b - c + d)$. If the initial condition, $x(0)$, is less than this value, $x(0) < x^*$, then the system will converge to all-B. If $x(0) > x^*$ then the system will converge to all-A.

(iv) A and B stably coexist. This is the case if $a < c$ and $b > d$. If you were to play this game with another person, you should always try to choose the opposite of what your opponent does. A is best response to B, and B is best response to A. A population of A and B players will converge to the interior, stable equilibrium

$$x^* = \frac{d - b}{a - b - c + d}. \tag{4.6}$$

(v) A and B are neutral. This is the case if $a = c$ and $b = d$. If you were to play this game with another person, then no matter what you chose you would always have exactly the same payoff as your opponent. Selection will not change the composition of the population. Any mixture of A and B is an equilibrium for selection dynamics.

4.2 THE NASH EQUILIBRIUM

The Nobel Prize–winning concept of a Nash equilibrium is defined in the following way. Imagine there is a game between two people. If both play a strategy that happens to be a Nash equilibrium, then neither person can deviate from this strategy and increase his payoff.

Consider the general payoff matrix between two strategies, A and B,

$$\begin{array}{c|cc} & A & B \\ \hline A & a & b \\ B & c & d \end{array}$$

We have the following criteria:

(i) A is a strict Nash equilibrium if $a > c$.
(ii) A is a Nash equilibrium if $a \geq c$.
(iii) B is a strict Nash equilibrium if $d > b$.
(iv) B is a Nash equilibrium if $d \geq b$.

Let us explore the following game

$$\begin{array}{c|cc} & A & B \\ \hline A & 3 & 0 \\ B & 5 & 1 \end{array} \tag{4.7}$$

If both players choose A, then one player can improve his payoff by switching to B. If both play B, then neither player can improve his payoff by switching to A. Hence B is a Nash equilibrium. Note that A is dominated by B. Note also that playing the Nash equilibrium, B, in this game leads to a lower payoff than playing the dominated strategy, A. The payoff matrix (4.7) is an example of the famous Prisoner's Dilemma game, which we will study in Chapter 5.

Consider the game

$$\begin{array}{c|cc} & A & B \\ \hline A & 3 & 1 \\ B & 5 & 0 \end{array} \tag{4.8}$$

If both players choose A, then one player can improve his payoff by switching to B. If both play B, then again one player can improve his payoff by switching to A. Hence neither A nor B is a Nash equilibrium. This is an example of a Hawk-Dove game, which will be studied in section 4.6.

Finally, consider the game

$$\begin{array}{c} \\ A \\ B \end{array} \begin{array}{c} \begin{array}{cc} A & B \end{array} \\ \begin{pmatrix} 5 & 0 \\ 3 & 1 \end{pmatrix} \end{array} \tag{4.9}$$

If both players choose A, then neither player can improve his payoff by switching to B. If both play B, then again neither player can improve his payoff by switching to A. Hence both A and B are Nash equilibria.

4.3 EVOLUTIONARILY STABLE STRATEGY (ESS)

John Maynard Smith invented the important concept of an evolutionarily stable strategy when he was unaware of the Nash equilibrium in game theory. Imagine a large population of A players. A single mutant of type B is introduced. The game between A and B is given by the general payoff matrix (4.3), and the fitness functions are given by (4.4). What is the condition for selection to oppose the invasion of B into A?

Let us assume there is an infinitesimally small quantity of B invaders. Thus the frequency of B is ϵ. The frequency of A is $1-\epsilon$. For this population, the fitness of A is greater than the fitness of B if

$$a(1-\epsilon)+b\epsilon > c(1-\epsilon)+d\epsilon. \tag{4.10}$$

Canceling the ϵ terms, this inequality leads to

$$a > c. \tag{4.11}$$

If, however, it happens that $a=c$, then inequality (4.10) leads to

$$b > d. \tag{4.12}$$

Therefore we summarize: strategy A is ESS if either (i) $a>c$ or (ii) $a=c$ and $b>d$. This definition guarantees that selection will oppose the invasion of B into A. As we will see later, this concept holds only for infinitely large populations and for infinitesimally small quantities of the potential invader.

4.4 MORE THAN TWO STRATEGIES

Let us explore games with more than two strategies. The payoff for strategy S_i versus S_j is given by $E(S_i, S_j)$.

(i) Strategy S_k is a strict Nash equilibrium if

$$E(S_k, S_k) > E(S_i, S_k) \qquad \forall i \neq k \tag{4.13}$$

The symbol ∀ means "for all." Thus $\forall i \neq k$ reads "for all i not equal to k."

(ii) Strategy S_k is a Nash equilibrium if

$$E(S_k, S_k) \geq E(S_i, S_k) \qquad \forall i \tag{4.14}$$

(iii) Strategy S_k is ESS, if $\forall i \neq k$ we have either

$$E(S_k, S_k) > E(S_i, S_k) \tag{4.15}$$

or

$$E(S_k, S_k) = E(S_i, S_k) \quad \text{and} \quad E(S_k, S_i) > E(S_i, S_i). \tag{4.16}$$

Note that ESS guarantees that selection will oppose any potential invader. The same is true for a strict Nash equilibrium, but not for a Nash equilibrium. If $E(S_k, S_k) = E(S_j, S_k)$ and $E(S_k, S_j) < E(S_j, S_j)$ then S_k is still a Nash equilibrium, but selection will favor S_j invading S_k. Thus it makes sense to add a fourth definition.

(iv) Strategy S_k is stable against invasion by selection (let us call this "weak ESS") if $\forall i \neq k$ we have either

$$E(S_k, S_k) > E(S_i, S_k) \tag{4.17}$$

or

$$E(S_k, S_k) = E(S_i, S_k) \quad \text{and} \quad E(S_k, S_i) \geq E(S_i, S_i). \tag{4.18}$$

If a strategy is a strict Nash equilibrium then it is also an ESS. If a strategy is an ESS then it is also a weak ESS. If a strategy is a weak ESS then it is also a Nash equilibrium. Thus strict Nash implies ESS implies weak ESS implies Nash:

$$\text{strict Nash} \Rightarrow \text{ESS} \Rightarrow \text{weak ESS} \Rightarrow \text{Nash}. \tag{4.19}$$

All of these concepts play important roles when studying the evolutionary dynamics of frequency-dependent selection.

The concept of an "unbeatable strategy" was introduced by William Hamilton in his work on sex ratios preceding John Maynard Smith's work on evolutionary game theory. Strategy S_k is unbeatable if $\forall i \neq k$:

$$E(S_k, S_k) > E(S_i, S_k) \quad \text{and} \quad E(S_k, S_i) > E(S_i, S_i). \tag{4.20}$$

Therefore an unbeatable strategy dominates every other strategy. An unbeatable strategy is certainly a strict Nash equilibrium. An unbeatable strategy is the most you can ask for, but usually you are asking for too much. Unbeatable strategies are rare.

4.5 REPLICATOR DYNAMICS

Peter Taylor and Leo Jonker were the first to introduce a differential equation for evolutionary game dynamics. They were quickly followed by Christopher Zeeman (Warwick) as well as Peter Schuster, Josef Hofbauer, and Karl Sigmund (all three in Vienna).

Given what we have seen so far in this book, the equation that we will write down now is an obvious next step. Consider the interaction among n strategies. The payoff for strategy i when interacting with strategy j is given by a_{ij}. The $n \times n$-matrix $A = [a_{ij}]$ is called the "payoff matrix." Let x_i denote the frequency of strategy i. The expected payoff of strategy i is given by $f_i = \sum_{j=1}^{n} x_j a_{ij}$. The average payoff is given by $\phi = \sum_{i=1}^{n} x_i f_i$. Equating payoff with fitness, we obtain the replicator equation (Figure 4.5)

$$\dot{x}_i = x_i(f_i - \phi) \qquad i = 1, \ldots, n \tag{4.21}$$

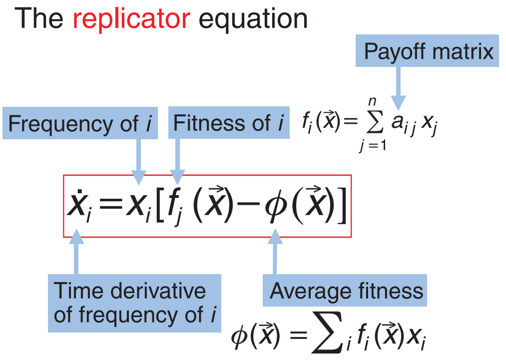


Figure 4.5 The replicator equation is the cornerstone of evolutionary game dynamics. It describes frequency-dependent selection among n different phenotypes (strategies) in an infinitely large population without mutation. In general, the fitness, f_i, of the phenotype, i, depends on the composition of the population, $\vec{x} = (x_1, \ldots, x_n)$. Usually f_i is a linear function of the frequencies x_j, and the coefficients of this function are the entries of the payoff matrix $A = [a_{ij}]$. The entry a_{ij} denotes the payoff for strategy i interacting with strategy j.

The difference between (4.21) and (2.16) is frequency-dependent as opposed to constant selection. The fitness values are linear functions of the frequencies.

Equation (4.21) is defined on the simplex S_n, which is given by $\sum_{i=1}^{n} x_i = 1$. We note that the interior of the simplex is invariant: if a trajectory starts in the interior, it will always remain in the interior; it might converge to the boundary, but it will never actually reach the boundary. Moreover, we note that each face of the simplex is invariant. A face is a subset of the simplex where at least one strategy has zero frequency. A strategy which is not there will not appear.

Replicator dynamics describe pure selection without mutation. Often, however, we ask the question whether a new strategy, which is not present in the population, could invade the population and increase in frequency. Thus, while not explicitly modeled, mutation is on the mind of the analyst.

The corners (vertices) of the simplex are fixed points of the replicator dynamics. Depending on the payoff matrix, A, there can be fixed points in the interior and in every face of the simplex.

4.5.1 Two Strategies

For $n = 2$, we have already derived a complete classification of all possible evolutionary dynamics in section 4.2. The simplex S_2 is the closed interval $[0, 1]$. The corner points, $x_1 = 0$ and $x_1 = 1$, are always fixed points of the replicator dynamics. In the interior, there can be at most one isolated fixed point. Such a fixed point exists if $(a_{11} - a_{21})(a_{12} - a_{22}) < 0$. This condition ensures that neither A dominates B nor B dominates A. Instead A and B can either be bistable or coexist. The interior fixed point is stable if A and B coexist which is the case for $a_{11} < a_{21}$ and $a_{12} > a_{22}$.

The neutral case, $a_{11} = a_{21}$ and $a_{12} = a_{22}$, implies that every point of the interval $[0, 1]$ is an equilibrium point. In this case, the replicator dynamics do not move. The strategies A and B have identical fitness for any composition of the population. In such a case, we would say that replicator dynamics do not adequately describe the biological behavior. For any finite population size, the relative proportions of A and B will drift until eventually one strategy becomes extinct. We will discuss the evolutionary dynamics of finite populations in Chapter 6.

Constant selection between A and B is obtained as a special case of the replicator equation if $a_{11} = a_{12} \neq a_{21} = a_{22}$. Thus evolutionary game dynamics is the generic description of natural selection, with constant selection being a special case.

4.5.2 Three Strategies

For $n = 3$, interesting new dynamical features are possible. The phase space is the simplex S_3, which can be represented by a triangle with identical sides. There is a complete classification of all possible phase portraits.

Of special interest is the case where A is dominated by B, B is dominated by C, and C is dominated by A. This is the so-called Rock-Paper-Scissors game. In this well-known children's game, rock beats scissors which beat paper which beats rock.

Any 3 × 3 payoff matrix with cyclic domination of the three strategies characterizes a Rock-Paper-Scissors game. The analysis of the evolutionary game dynamics can be simplified by a trick that is applicable to any replicator equation: the dynamics of the replicator equation (4.21) remain unchanged if an arbitrary constant is added to each entry in a column of the payoff matrix. Thus by subtracting the diagonal element from each column, we can transform every payoff matrix into a payoff matrix that has only zero entries in the diagonal.

For example, the payoff matrix

$$A = \begin{array}{c} \\ R \\ S \\ P \end{array} \begin{array}{c} \begin{array}{ccc} R & S & P \end{array} \\ \begin{pmatrix} 4 & 2 & 1 \\ 3 & 1 & 3 \\ 5 & 0 & 2 \end{pmatrix} \end{array}$$

can be transformed to

$$A = \begin{array}{c} \\ R \\ S \\ P \end{array} \begin{array}{c} \begin{array}{ccc} R & S & P \end{array} \\ \begin{pmatrix} 0 & 1 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \end{pmatrix} \end{array} \tag{4.22}$$

Both payoff matrices lead to identical replicator dynamics.

The payoff matrix (4.22) defines the symmetric Rock-Paper-Scissors game. The interior of the simplex S_3 contains a unique equilibrium point given by (1/3, 1/3, 1/3). This point is stable, but not asymptotically stable. There are infinitely many periodic orbits surrounding this center. In fact all other points in the interior are on periodic orbits. The time average of each cycle is given by (1/3, 1/3, 1/3). This situation is not generic: small deviations from the symmetry of A will change the phase portrait.

Note that payoff matrix (4.22) describes a zero-sum game. For a zero-sum game we have $a_{ij} = -a_{ji}$. The gain of one player is the loss of another; the average fitness of the population is always zero, $\phi = 0$. Thus the replicator equation becomes $\dot{x}_i = x_i f_i$ for all $i = 1, \ldots, n$.

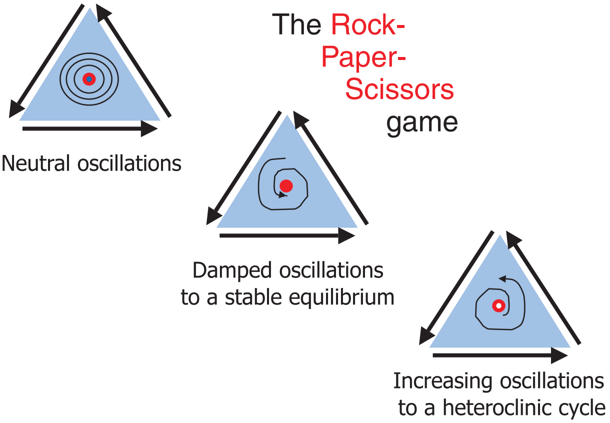


Figure 4.6 In the Rock-Paper-Scissors game, there is cyclic domination among three strategies. There is always one interior equilibrium. Depending on the payoff matrix, this interior equilibrium is (i) a center surrounded by neutral oscillations, (ii) a stable equilibrium that is approached in damped oscillations, or (iii) an unstable equilibrium, in which case there are oscillations of increasing amplitude converging to the boundary of the simplex.

The general Rock-Paper-Scissors game is given by the payoff matrix

$$A = \begin{pmatrix} 0 & -a_2 & b_3 \\ b_1 & 0 & -a_3 \\ -a_1 & b_2 & 0 \end{pmatrix} \tag{4.23}$$

There are two possibilities.

(i) if the determinant of A is positive (which is the case for $a_1a_2a_3 < b_1b_2b_3$), then there exists a unique interior equilibrium that is globally stable. The trajectories of the replicator dynamics starting from any interior initial condition will converge to this equilibrium in an oscillatory manner (Figure 4.6).

(ii) if the determinant of A is negative (which is the case for $a_1a_2a_3 > b_1b_2b_3$), then there exists a unique interior equilibrium that is unstable. The trajectories of the replicator dynamics starting from any interior initial condition will converge to the boundary of the simplex in oscillations with increasing amplitude. The boundary of the simplex is a heteroclinic cycle that is an attractor for all trajectories starting in the interior (a heteroclinic cycle is an invariant set containing saddle points on trajectories connecting them). For the differential equation, the oscillations will converge to the heteroclinic cycle without ever reaching it. For practical purposes, one of the three strategies will eventually become extinct, either by a rounding error of the computer program or by a random fluctuation in nature. Then only two strategies are left, and one will outcompete the other, leaving a single strategy in the end. It cannot be predicted which strategy will win. Thus the attracting heteroclinic cycle reveals a kind of deterministic unpredictability that is of a different type than chaos.

4.5.3 More than Three Strategies

For four species, the replicator dynamics are defined on the simplex S_4 given by a tetrahedron. This is the minimum number of dimensions that are needed for the replicator equation to allow limit cycles and chaotic attractors.

Finally, let us state some important results that hold in any dimension.

(i) An interior equilibrium of the replicator dynamics is given by the solution of the linear system of equations

$$f_1 = f_2 = \cdots = f_n \quad \text{and} \quad x_1 + x_2 + \cdots + x_n = 1. \tag{4.24}$$

Remember that $f_i = \sum_{j=1}^{n} a_{ij} x_j$. This system of n linear equations has either one or zero nondegenerate solutions. Thus there can be at most one isolated equilibrium in the interior of the simplex S_n.

(ii) If there is no equilibrium in the interior, then all trajectories converge to the boundary of the simplex. Thus there can be no chaotic attractor and no limit cycle in the interior if there is no equilibrium in the interior. This result is very helpful, because sometimes it is possible to show that a particular replicator equation admits no interior equilibrium. If this is the case, then we know that nothing more complicated can happen in the interior; coexistence of all strategies is impossible.

(iii) In degenerate cases, the replicator equation can admit a manifold of equilibria in the interior. These equilibria can be stable, but not asymptotically stable.

(iv) If a strategy is a strict Nash equilibrium or ESS, then the corner point of the simplex, which corresponds to a pure population of this strategy, is asymptotically stable.

Proofs of these assertions are given in the book by Hofbauer and Sigmund (1998).

4.6 HAWK OR DOVE?

Animals of the same species fight with each other. Conflicts arise over food, territory, or sex. Female lions fight to maintain their hunting grounds. Male chimpanzees fight for dominance of a group: the alpha male has to withstand challenges from other males, and in return gets the majority of matings. There are many examples of fierce and even deadly conflicts among animals. The human species, of course, is unsurpassed in its sad efficiency in inflicting murder, war, and genocide.

Often, however, conflicts between animals (including humans) do not escalate, but are fought out with those involved obeying certain limits. Ethology has a long-standing fascination with so-called conventional fights. A sequence of threatening signals and displays allow the contestants to assess each other's strength or determination before one of them simply walks away. Stags perform roaring matches followed by parallel walks and head pushing with interlocked antlers. Despite the lethal points of their antlers, only few contests lead to serious injury.

For a long time, biologists have accepted the following explanation: conventional fighting is frequently observed in nature because it is good for the species. Fighting that leads to serious injury is bad for the species. This argument, however, is problematic. There can certainly be selection between groups or whole species, but often stronger selection is put on the shoulders of individuals. If one individual in a population were to disobey the rules and escalate all fights by inflicting serious injury, then it might win many contests and thereby reproduce its genes more efficiently than others would.

Conventional fighting from the perspective of individual selection was first analyzed by John Maynard Smith. There are two strategies, hawks (H) and doves (D). While hawks escalate fights, doves retreat when the opponent escalates. The benefit of winning the fight is b. The cost of injury is c. If two hawks meet, then the expected payoff for each of them is $(b-c)/2$. The fight will escalate. One hawk wins, while the other is injured. Since both hawks are equally strong, the probability of winning or losing is 1/2. If a hawk meets a dove, the hawk wins and receives payoff b, while the dove retreats and receives payoff 0. If two doves meet, there will be no injury. One of them will eventually win. The expected payoff is $b/2$. Thus, the payoff matrix is given by

$$\begin{array}{cc} & \begin{array}{cc} \mathrm{H} & \mathrm{D} \end{array} \\ \begin{array}{c} \mathrm{H} \\ \mathrm{D} \end{array} & \begin{pmatrix} \frac{b-c}{2} & b \\ 0 & \frac{b}{2} \end{pmatrix} \end{array} \tag{4.25}$$

If $b < c$, then neither strategy is a Nash equilibrium. If everybody else plays "hawk," it is best to play "dove." If everybody else plays "dove," it is best to play "hawk." Thus hawks and doves can coexist. Selection dynamics will lead to a mixed population. At the stable equilibrium, the frequency of hawks is given by b/c. If the cost of injury is much larger than the benefit of winning the fight, $c \gg b$, then the equilibrium frequency of hawks will be small.

The name of the game is somewhat misleading, because normally we think of games between individuals of the same species. Moreover, real doves fight to death when confined in a cage.

4.6.1 Mixed Strategies

So far we have considered pure strategies that either play hawk all the time or play dove all the time. Let us now consider mixed strategies which play hawk with probability p and dove with probability $1-p$. There is no longer a discrete set of just two strategies but a continuous set of infinitely many strategies. The space of strategies is given by the closed interval [0, 1]. The payoff for strategy p_1 versus p_2 is given by

$$E(p_1, p_2) = \frac{b}{2}(1 + p_1 - p_2 - \frac{c}{b}p_1 p_2). \tag{4.26}$$

From this function we can infer that the strategy $p^* = b/c$ is evolutionarily stable. Note that

$$\begin{aligned} E(p^*, p^*) &= \frac{b}{2}(1 - \frac{b}{c}) \\ E(p, p^*) &= \frac{b}{2}(1 - \frac{b}{c}) \\ E(p^*, p) &= \frac{b}{2}(1 + \frac{b}{c} - 2p) \\ E(p, p) &= \frac{b}{2}(1 - \frac{c}{b}p^2) \end{aligned} \tag{4.27}$$

We see that $E(p^*, p^*) = E(p, p^*)$ for all p. Therefore p^* is a Nash equilibrium, but not a strict Nash equilibrium. Since $E(p^*, p) > E(p, p)$ for all $p \neq p^*$, it follows that p^* is an evolutionarily stable strategy.

4.7 THERE IS ALWAYS A NASH EQUILIBRIUM

Consider a game given by an $n \times n$ payoff matrix A. There are n pure strategies, $S_1, \ldots, S_n$. Depending on the details of A, there may or may not exist a Nash equilibrium among those pure strategies. There is, however, always a Nash equilibrium if one considers the set of all mixed and all pure strategies. This is a deep result in game theory.

A strategy is given by the vector $\vec{p} = (p_1, \ldots, p_n)$. Here p_i is the probability of playing S_i. Clearly $\sum_{i=1}^{n} p_i = 1$. The payoff for strategy $\vec{q}$ versus strategy $\vec{p}$ is given by

$$E(\vec{q}, \vec{p}) = \sum_{i=1}^{n} \sum_{j=1}^{n} a_{ij} q_i p_j. \tag{4.28}$$

In vector notation we can write

$$E(\vec{q}, \vec{p}) = \vec{q} A \vec{p}. \tag{4.29}$$

It can be shown that for any payoff matrix A there exists at least one strategy $\vec{q}$ with the property that

$$\vec{q}A\vec{q} \geq \vec{p}A\vec{q} \qquad \forall\vec{p} \tag{4.30}$$

Thus $\vec{q}$ is a best reply to itself, a Nash equilibrium.

4.8 CHICKEN AND SNOWDRIFT

In the Chicken game, two cars head for each other at high speed. The loser is whoever chickens out first. The winner stays on the track. If neither driver chickens out, there is the substantial cost of a collision. Consider two strategies: A means you go for it. B means you chicken out after some time. The reward for winning is b, the cost of a collision is $-c$. If both players decide to chicken out, then the chance that you will win is 1/2. Hence the payoff matrix is

$$\begin{array}{c c} & \begin{array}{cc} \mathrm{A} & \mathrm{B} \end{array} \\ \begin{array}{c} \mathrm{A} \\ \mathrm{B} \end{array} & \begin{pmatrix} -c & b \\ 0 & \frac{b}{2} \end{pmatrix} \end{array} \tag{4.31}$$

Comparing the entries in each column of the matrix leads to the same conclusion as in the Hawk-Dove game. It is always best to adopt the opposite strategy as your opponent. A mixed strategy between A and B is ESS.

In the Snowdrift game, two drivers are stuck on their way home, because the road is blocked by a snowdrift. You have a choice between cooperation and defection. Cooperation means that you get out of the car and shovel. Defection means that you remain in your car, relax, listen to music, and let the other person shovel. If both cooperate, the amount of work is only half as much. If neither cooperates, each is stuck in the snowdrift until the snowplow comes along. The benefit for getting home is b, the cost of shoveling in the cold is $-c$. The payoff matrix is

$$\begin{array}{c|cc} & \mathrm{C} & \mathrm{D} \\ \hline \mathrm{C} & b-\frac{c}{2} & b-c \\ \mathrm{D} & b & 0 \end{array} \tag{4.32}$$

If $b > c$, we have the same structure as in the Hawk-Dove game. It is best to defect when the other person cooperates. It is best to cooperate when the other person defects. If $b < c$, it is best to defect no matter what the other person does. This leads us to the Prisoner's Dilemma.

4.9 GAME THEORY AND ECOLOGY

Ecologists investigate the interaction of species and how their abundance changes over time. The logistic map, which we encountered in Chapter 2, is an important equation of ecology, demonstrating that complicated time series of species abundance can be generated by very simple rules. The fundamental mathematical approach to ecology is given by the Lotka-Volterra equation. The logistic map is a one-dimensional Lotka-Volterra equation in discrete time.

4.9.1 Predator and Prey

The hostilities between the Austrian and Italian navies during World War I disrupted fishing in the Adriatic Sea. After the war, it was observed that the number of predatory fish had increased. "Why does war favor sharks?" was the question that was posed to Italy's leading physicist of the time, Vito Volterra.

Volterra wrote down the following equations. Let x and y denote, respectively, the abundance of prey and predator fish. Prey reproduce at rate ax. They are eaten by predators at rate bxy. Predators die at rate cy and reproduce at rate dxy. Thus we have the following system of two nonlinear differential equations

$$\begin{aligned} \dot{x} &= x(a-by) \\ \dot{y} &= y(-c+dx) \end{aligned} \tag{4.33}$$

If there are no predators, $y = 0$, then the population of prey fish grows exponentially as

$$x(t) = x(0)e^{at}. \tag{4.34}$$

If there are no prey, $x = 0$, then the population of predators declines exponentially as

$$y(t) = y(0)e^{-ct}. \tag{4.35}$$

The point $x = 0$ and $y = 0$ is a saddle point of the system. There is one interior equilibrium given by

$$x^* = c/d \quad \text{and} \quad y^* = a/b. \tag{4.36}$$

A linear stability analysis reveals that this equilibrium is neutrally stable. It is surrounded by infinitely many periodic orbits. The abundance of prey and the abundance of predators oscillate indefinitely. The oscillatory period is $2\pi/\sqrt{ac}$, but the amplitude depends on the initial condition. The time averages of the oscillations are given by the equilibrium values x^* and y^*. Neutral oscillations represent an ungeneric phenomenon, because small modifications of the differential equation (4.33) can destroy neutral stability.

Volterra could now answer the question why the reduced activity of fishing during the war had favored predators. Fishing decreases the reproductive rate of prey from a to $a - k$ and increases the death rate of predators from c to $c + m$. Hence, with fishing the time averages of the oscillations are given by

$$x_F^* = (c + m)/d \quad \text{and} \quad y_F^* = (a - k)/b. \tag{4.37}$$

The relative abundance of predators is greater in the absence of fishing:

$$y^*/x^* > y_F^*/x_F^*. \tag{4.38}$$

4.9.2 Kolmogorov's Predator-Prey Theorem

The neutral stability of equation (4.33) is a consequence of the particular assumptions for the interaction between prey and predator. There have been many extensions toward increased realism, such as including maximum carrying capacities for prey and predators and saturating functional responses of predator to prey. All such extensions tend to remove the unrealistic neutral stability. Instead, the abundance of predators and prey will usually converge to either a stable equilibrium or a stable limit cycle. In contrast to neutral oscillations, a stable limit cycle is a robust phenomenon. After small perturbations, the trajectory returns to the limit cycle. The period and amplitude do not depend on the initial condition, but are entirely determined by the parameters of the equation.

In 1936 the Russian mathematician A. N. Kolmogorov wrote a general predator-prey equation in the following form

$$\begin{aligned} \dot{x} &= xF(x, y) \\ \dot{y} &= yG(x, y) \end{aligned} \tag{4.39}$$

Here F and G are continuous functions with continuous first derivatives. Kolmogorov's theorem states that equation (4.39) has either a stable limit cycle or a stable equilibrium if the following conditions hold:

(i) $\partial F/\partial y < 0$

(ii) $x(\partial F/\partial x) + y(\partial F/\partial y) < 0$

(iii) $\partial G/\partial y < 0$

(iv) $x(\partial G/\partial x) + y(\partial G/\partial y) > 0$

(v) $F(0, 0) > 0$

Furthermore, there must exist constants, $A > 0$ and $B > C > 0$, such that

(vi) $F(0, A) = 0$

(vii) $F(B, 0) = 0$

(viii) $G(C, 0) = 0$

The biological interpretation of these conditions is illuminating: (i) the per capita rate of increase of prey is a decreasing function of predator abundance; (ii) for any given ratio of the two species, the rate of increase of prey is a decreasing function of population size; (iii) the per capita rate of increase of predators is a decreasing function of their abundance; (iv) for any given ratio of the two species, the rate of increase of predators is an increasing function of population size; (v) when both populations are small, the abundance of prey can increase; (vi) there exists a predator population size sufficiently large to prevent further increase of the prey population; (vii) there exists a critical prey population size, B, beyond which it can no longer grow even if there are no predators, which means the ecosystem has a maximum carrying capacity for the prey species; (viii) there exists a critical prey population size, C, below which predators cannot grow even if they are rare.

For a thorough discussion of such issues and many additional aspects of theoretical ecology, you must seek out Robert May's classic *Stability and Complexity of Model Ecosystems,* first published in 1973.

4.9.3 The Lotka-Volterra Equation

Equation (4.33) was also studied by the American biologist Alfred Lotka in the context of chemical kinetics and, therefore, became known as Lotka-Volterra equation. The general Lotka-Volterra equation describes the interaction of n species and is of the form

$$\dot{y}_i = y_i(r_i + \sum_{j=1}^{n} b_{ij} y_j) \qquad i = 1, \ldots, n \tag{4.40}$$

The abundance of species i is given by y_i, which is a non-negative number. Hence the equation is defined on the positive orthant R^n_+, which is given by the set of all points $(y_1, y_{21}, \ldots, y_n)$ with $y_i \geq 0$ for all i. The growth rate of species i is given by r_i. The interaction between species i and j is given by b_{ij}. The parameters r_i and b_{ij} can be positive, zero, or negative.

It turns out that the Lotka-Volterra equation (4.40) and the replicator equation (4.21) are equivalent. A replicator equation with n strategies can be transformed into a Lotka-Volterra equation with $n-1$ species. The $n \times n$ matrix $A = [a_{ij}]$ defines the interaction of the n strategies in the replicator equation

$$\dot{x}_i = x_i \left(\sum_{j=1}^{n} a_{ij} x_j - \phi \right) \qquad i = 1, \ldots, n \tag{4.41}$$

The Lotka-Volterra equation

$$\dot{y}_i = y_i(r_i + \sum_{j=1}^{n-1} b_{ij} y_j) \qquad i = 1, \ldots, n-1 \tag{4.42}$$

with the parameters $r_i = a_{in} - a_{nn}$ and $b_{ij} = a_{ij} - a_{nj}$ is equivalent to (4.41).

Let $y = \sum_{i=1}^{n-1} y_i$. The equivalence can be shown with the transformation $x_i = y_i/(1 + y)$ for $i = 1, \ldots, n-1$ and $x_n = 1/(1 + y)$.

Therefore, whatever result holds for one equation will hold for the other. The equivalence of the Lotka-Volterra and replicator equations represents a beautiful bridge between aspects of theoretical ecology and evolutionary game theory.

We will see that theoretical ecology is the foundation for many studies in mathematical biology. For example, viruses and cells can behave as predator and prey. Immune cells, in turn, can "prey" on infected cells. Virus dynamics in infected hosts represent a "microecology."

SUMMARY

- Evolutionary game theory is the study of frequency-dependent selection.
- Games can be formulated in terms of a payoff matrix, which specifies the payoff for one strategy when interacting with another. Evolutionary game theory interprets payoff as fitness: successful strategies reproduce faster.
- A Nash equilibrium is a strategy with the following property: if two players adopt a Nash equilibrium, then neither player can improve her payoff by switching to another strategy.
- If an entire population (of infinite size) adopts an evolutionarily stable strategy (ESS), then no other strategy can invade.
- The replicator equation describes deterministic evolutionary game dynamics. For $n = 2$ strategies, there can be dominance, coexistence, bistability, or neutrality. For $n \geq 3$ strategies, there can be heteroclinic cycles. For $n \geq 4$ strategies, there can be limit cycles and chaos.

- In the Rock-Paper-Scissors game there can be either damped oscillations to a stable equilibrium or oscillations with increasing amplitude that eventually lead to the random elimination of two strategies.
- The Hawk-Dove game explains why many animals can resolve conflict without full-blown escalation.
- Chicken and Snowdrift are games that are similar to Hawk-Dove.
- The replicator equation is equivalent to the Lotka-Volterra equation of ecology. Evolutionary game theory and ecology have the same mathematical foundations.
- Kolmogorov's theorem specifies when a two-dimensional predator-prey system has a stable equilibrium or a stable limit cycle.