

GAMES IN FINITE POPULATIONS

7

IN CHAPTER 4, we discussed the traditional approach to evolutionary game dynamics via the replicator equation, which describes deterministic evolution in infinitely large populations. All of our understanding of frequency-dependent selection comes from this approach. We will now develop a framework for studying evolutionary game dynamics in finite populations. Finiteness requires stochasticity. The interplay of random drift and frequency-dependent selection will determine the outcome of evolutionary games. We will calculate fixation probabilities to decide whether selection favors one strategy over another. In a game between two strategies, A and B , the fixation probability of A is given by the probability that a single A player in a population of $N - 1$ B players generates a lineage of A that does not become extinct but instead takes over the whole population. If the fixation probability of A is greater than $1/N$, then selection favors A replacing B .

The intensity of selection plays an important role for game dynamics in finite populations. The game under consideration can have a strong or weak influence on the overall fitness of an individual. If the payoff makes a small contribution to fitness, then selection is weak. If the payoff makes a large contribution to fitness, then selection is strong. Some of our results only hold in

the limit of weak selection. In the traditional replicator equation, in contrast, any parameter that describes the intensity of selection cancels out.

Biologists are interested in the concepts of a strict Nash equilibrium or an evolutionarily stable strategy, because natural selection protects populations of such strategies against invasion by mutants. We will see, however, that this implication only holds for deterministic dynamics of infinite populations. For stochastic dynamics of finite populations, we have to derive new conditions for evolutionary stability.

Risk dominance is an important concept in game theory, defined as follows: if two strategies, A and B , are best replies to themselves, then the risk-dominant strategy has the larger basin of attraction. We will see that in finite populations, however, the risk-dominant strategy need not have the larger fixation probability. Instead, we will encounter a $1/3$ law. If the basin of attraction of strategy B is less than $1/3$, then selection will favor the fixation of strategy A for sufficiently large N and weak selection.

7.1 ONE BASIC MODEL AND ONE-THIRD

Consider a game between two strategies, A and B , with payoff matrix

$$\begin{matrix} & \begin{matrix} A & B \end{matrix} \\ \begin{matrix} A \\ B \end{matrix} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{matrix} \quad (7.1)$$

The total population size is N . The number of A individuals is i . The number of B individuals is $N - i$. For each individual, there are $N - 1$ other individuals. For each A individual, there are $i - 1$ other A individuals. For each B individual, there are $N - i - 1$ other B individuals. The probability that an A individual interacts (plays the game) with another A individual is given by $(i - 1)/(N - 1)$. The probability that an A individual interacts with a B individual is given by $(N - i)/(N - 1)$. The probability that a B individual interacts with another B individual is given by $(N - i - 1)/(N - 1)$. The probability that a B individual interacts with an A individual is given by $i/(N - 1)$. Hence, the expected payoff for A and B is, respectively, given by

$$\begin{aligned}
 F_i &= \frac{a(i-1) + b(N-i)}{N-1} \\
 G_i &= \frac{ci + d(N-i-1)}{N-1}
 \end{aligned}
 \tag{7.2}$$

The index i indicates that these quantities represent the expected payoff in a population that contains i many A individuals.

In the traditional framework of evolutionary game dynamics, the expected payoff is interpreted as fitness. Individuals reproduce, either genetically or culturally, with a rate that is proportional to their payoff. Let us introduce a parameter w that measures the intensity of selection. The fitness of A and B is given by

$$\begin{aligned}
 f_i &= 1 - w + wF_i \\
 g_i &= 1 - w + wG_i
 \end{aligned}
 \tag{7.3}$$

The intensity of selection, w , is a number between 0 and 1. If $w = 0$, the game does not contribute to fitness. Strategies A and B are neutral variants. If $w = 1$, selection is strong; the fitness is entirely determined by the expected payoff. The limit $w \rightarrow 0$ characterizes the case of weak selection, where the payoff provides only a small contribution to fitness. Figure 7.1 illustrates the basic model of evolutionary game dynamics in finite populations.

It is important to note that the parameter w , which quantifies the intensity of selection, cancels out in deterministic replicator dynamics of infinite populations, but plays a crucial role in the stochastic process describing finite populations. We will obtain elegant results in the limit of weak selection.

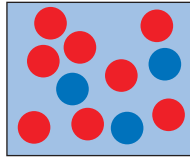
Consider a Moran process between A and B . The frequency-dependent fitness values are given by equation (7.3). The state variable, i , denotes the number of A individuals. The probability to move from i to $i + 1$ is given by

$$p_{i,i+1} = \frac{if_i}{if_i + (N-i)g_i} \frac{N-i}{N}.
 \tag{7.4}$$

The probability to move from i to $i - 1$ is given by

$$p_{i,i-1} = \frac{(N-i)g_i}{if_i + (N-i)g_i} \frac{i}{N}.
 \tag{7.5}$$

Games in finite populations



There are i players of type A and $N - i$ players of type B

The fitness of A is: $f_i = 1 - w + w \frac{a(i-1) + b(N-i)}{N-1}$

The fitness of B is: $g_i = 1 - w + w \frac{ci + d(N-i-1)}{N-1}$

The parameter w denotes the intensity of selection

Figure 7.1 We can study evolutionary game dynamics in finite populations of size N . Each individual can interact with $N - 1$ other individuals. The expected payoff for each individual is determined from these interactions. The parameters a , b , c , and d represent the entries of the payoff matrix. The parameter w , a number between 0 and 1, denotes the intensity of selection. If $w = 1$, then the fitness of an individual is identical to its payoff. If $w = 0$, all individuals have the same fitness. Small w denotes the case of weak selection: the game under consideration makes only a small contribution to the total fitness of an individual. In any one time step, one individual is chosen for reproduction proportional to fitness, while a second individual is chosen for elimination at random. The total population size is constant.

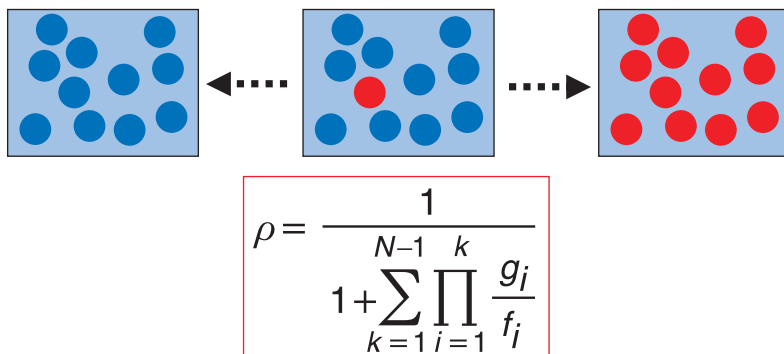
The probability that the process remains in state i is simply

$$p_{i,i} = 1 - p_{i,i+1} - p_{i,i-1}. \quad (7.6)$$

All other transitions have zero probability.

Note that $p_{0,0} = 1$ and $p_{N,N} = 1$. Therefore the process has two absorbing states, $i = 0$ and $i = N$. If the population has reached either one of these states, then it will stay there forever. Any mixed population of A and B will eventually end up in either all- A or all- B . We want to calculate the fixation probabilities of A and B (Figure 7.2).

Fixation probability of strategy *A*



If $\rho > 1/N$, then selection favors *A* replacing *B*

If $\rho < 1/N$, then selection opposes *A* replacing *B*

Figure 7.2 The fixation probability, ρ , of a strategy under frequency-dependent selection can be calculated. For a neutral mutant, $\rho = 1/N$. Selection favors the fixation of the invading strategy if $\rho > 1/N$. Selection opposes the fixation of the invading strategy if $\rho < 1/N$.

For the backward to forward transition ratio, we obtain

$$\frac{p_{i,i-1}}{p_{i,i+1}} = \frac{g_i}{f_i}. \quad (7.7)$$

Using equation (6.13) of Chapter 6, the fixation probability of *A* is given by

$$\rho_A = 1 / \left(1 + \sum_{k=1}^{N-1} \prod_{i=1}^k \frac{g_i}{f_i} \right). \quad (7.8)$$

The ratio of the fixation probabilities is

$$\frac{\rho_B}{\rho_A} = \prod_{i=1}^k \frac{g_i}{f_i}. \quad (7.9)$$

For **weak selection** . . .

$$\rho > 1/N$$

is equivalent to

$$a(N-2) + b(2N-1) > c(N+1) + d(2N-4)$$

for $N=2$: $b > c$
 $N=3$: $a + 5b > 4c + 2d$
 $N=4$: $2a + 7b > 5c + 4d$
 $N=5$: $3a + 9b > 6c + 6d$
 . . .
 large N : $a + 2b > c + 2d$

Figure 7.3 In the limit of weak selection, $w \rightarrow 0$, the condition $\rho > 1/N$ is equivalent to a simple inequality that is linear in N . For any given population size, therefore, a simple condition determines whether or not selection favors the fixation of a strategy.

Let us consider the limit of weak selection. A Taylor expansion of equation (7.8) for $w \rightarrow 0$ leads to

$$\rho_A \approx \frac{1}{N} \frac{1}{1 - (\alpha N - \beta)w/6}. \quad (7.10)$$

Here $\alpha = a + 2b - c - 2d$ and $\beta = 2a + b + c - 4d$.

If $\rho_A > 1/N$, then selection favors the fixation of A . From equation (7.10), we see that $\rho_A > 1/N$ is equivalent to $\alpha N > \beta$. This condition can be written as

$$a(N-2) + b(2N-1) > c(N+1) + d(2N-4). \quad (7.11)$$

For a population of only two individuals, $N = 2$, we have

$$b > c. \quad (7.12)$$

This result makes sense: in a mixed population of one A and one B individual, the former has payoff b and the latter has payoff c ; hence if $b > c$, then A is more likely to become fixed than B (Figure 7.3).

For large population size, inequality (7.11) leads to

$$a + 2b > c + 2d. \quad (7.13)$$

The **1/3 law**:

If $x^* < 1/3$ then $\rho > 1/N$
for large N and weak selection

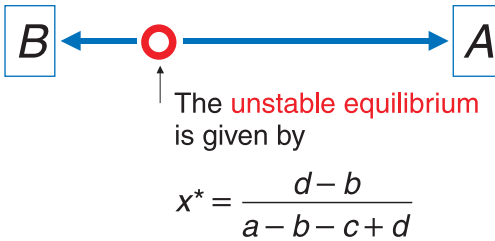


Figure 7.4 There is a surprising 1/3 law for evolutionary games in finite populations. Consider two strategies A and B in a bistable relationship, $a > c$ and $b < d$. The unstable equilibrium (of the replicator equation) occurs at a frequency of A given by $x^* = (d - b)/(a - b - c + d)$. For finite population dynamics, we find that selection favors strategy A , which means $\rho_A > 1/N$, if $x^* < 1/3$. In other words, a strategy has a fixation probability greater than $1/N$, if it has a higher fitness at frequency $1/3$. This simple condition holds for weak selection and large population size.

How can we interpret this condition?

Consider a game with $a > c$ and $b < d$. Both A and B are best replies to themselves. Consider the limit of large population size. If the frequency of A is high, then A has a larger fitness than B . If the frequency of B is high, then B has a larger fitness than A . There is a point where the two fitnesses are equal. This point can be calculated by setting $F_i = G_i$ in equation (7.2). For large N , this equilibrium point is reached at a frequency of A given by

$$x^* = \frac{d - b}{a - b - c + d}. \quad (7.14)$$

In the replicator equation, this expression denotes the unstable equilibrium between A and B .

Inequality (7.13) leads to

$$x^* < 1/3. \quad (7.15)$$

Therefore, if the unstable equilibrium occurs at a frequency of A which is less than $1/3$, then in a large finite population of size N , in the limit of weak selection, the probability that a single A mutant takes over the whole population is greater than $1/N$. In this case, selection favors the fixation of A in B . The condition $x^* < 1/3$ also means that the basin of attraction of B is less than $1/3$ (Figure 7.4).

If A dominates B , then $a > c$ and $b > d$. In this case, $x^* < 0$ and inequality (7.13) always holds. Therefore, if A dominates B , then selection will favor the fixation of A and oppose the fixation of B in a sufficiently large population. But the dominated strategy, B , can still be favored in a small population if $b < c$. In this case, there will be a critical population size, N_c . If $N < N_c$, then selection might favor the dominated strategy B . If $N > N_c$, selection will favor the dominant strategy A .

7.2 EVOLUTIONARY STABILITY IN FINITE POPULATIONS

These results have immediate consequences for the concept of evolutionary stability. The well-known definition of an evolutionarily stable strategy is motivated by selection dynamics in infinite populations. For payoff matrix 7.1, strategy B is ESS if either (i) $d > b$ or (ii) both $d = b$ and $a < c$. These conditions imply that selection opposes the spread of infinitesimally small fractions of A in infinitely large populations of B .

For finite population size N , we propose that B is an evolutionarily stable strategy, ESS_N , if two conditions hold: (i) selection opposes A invading B , which means that a single mutant A in a population of B has a lower fitness; and (ii) selection opposes A replacing B , which means $\rho_A < 1/N$, for any $w > 0$ (Figure 7.5).

The first condition is equivalent to

$$b(N - 1) < c + d(N - 2). \quad (7.16)$$

The second condition, for small w , is equivalent to

$$a(N - 2) + b(2N - 1) < c(N + 1) + d(2N - 4). \quad (7.17)$$

For $N = 2$, both conditions reduce to $b < c$. For large populations, the two conditions lead to $b < d$ and $x^* > 1/3$, respectively. Hence for small populations the traditional ESS concept is neither necessary nor sufficient; for large populations, it is necessary but not sufficient (Figure 7.6). If we consider a game with many different strategies, then the two conditions must hold in pairwise comparison with every other strategy.

Evolutionary stability in finite populations

	A	B
A	a	b
B	c	d

B is ESS_N if

1. Selection opposes A invading B:

$$b(N-1) < c + d(N-2)$$

2. Selection opposes A replacing B:

$$a(N-2) + b(2N-1) < c(N+1) + d(2N-4)$$

Figure 7.5 There are two logical requirements for evolutionary stability in finite populations. Selection has to protect an evolutionarily stable strategy (ESS) against the invasion and fixation of a mutant strategy. If the fitness of a single mutant is less than the fitness of the resident, then selection opposes invasion. If the fixation probability of the mutant is less than $1/N$, then selection opposes fixation. The first condition is always a simple linear inequality in N . The second condition is a simple linear inequality in N for weak selection.

For small N ($N=2$)

B is ESS_N if

- | | |
|------------|----------------------------------|
| 1. $b < c$ | Traditional ESS condition is |
| 2. $b < c$ | neither necessary nor sufficient |

For large N

B is ESS_N if

- | | |
|----------------|------------------------------|
| 1. $b < d$ | Traditional ESS condition is |
| 2. $x^* < 1/3$ | necessary but not sufficient |

Figure 7.6 The smallest possible population size for an evolutionary game is $N = 2$. In this case, both conditions for evolutionary stability reduce to $b < c$. For large N , the invasion condition is $b < d$ and the fixation condition is $x^* < 1/3$. Hence for small finite populations, the traditional ESS concept is neither necessary nor sufficient to confer protection by selection. For large finite populations, the traditional ESS concept is necessary but not sufficient.

Two examples

	<i>A</i>	<i>B</i>
<i>A</i>	20	0
<i>B</i>	17	1

A is ESS_{*N*} for $N > 12$

B is ESS_{*N*} for $N < 53$

	<i>A</i>	<i>B</i>
<i>A</i>	1	28
<i>B</i>	2	30

A is ESS_{*N*} for $N < 22$

B is ESS_{*N*} for $N > 17$

Figure 7.7 Whether one or the other strategy is ESS_{*N*} depends on the population size. Two interesting examples are shown. In the first case, both *A* and *B* are strict Nash equilibria. In finite populations, however, *B* is the only ESS_{*N*} for $N = 2, 3, \dots, 12$, both strategies are ESS_{*N*} for $N = 13, \dots, 52$, and *A* is the only ESS_{*N*} for $N \geq 53$. In the second example, *B* dominates *A*. In finite populations, however, *A* is the only ESS_{*N*} for $B \geq 2, 3, \dots, 17$, both strategies are ESS_{*N*} for $N = 18, \dots, 21$, and only *B* is ESS_{*N*} for $N \geq 22$.

The motivation of the ESS_{*N*} concept is as follows. If a strategy is ESS_{*N*}, then a single mutant of any other strategy must have a lower fitness. Therefore selection opposes the initial spread of any other strategy. As we have seen, however, in a finite population it is possible that the fixation of a strategy is favored by selection although its initial increase is opposed by selection. Thus the second condition demands that a strategy is only ESS_{*N*} if the fixation probability of every other strategy is less than the neutral threshold, $1/N$. In summary, we simply require that a homogeneous ESS_{*N*} population be protected by selection against invasion and replacement. These requirements represent a natural extension of the original ESS concept formulated by John Maynard Smith for infinitely large populations and deterministic evolutionary dynamics. Two specific examples are discussed in Figure 7.7.

If $d > b$, then *B* is both a strict Nash equilibrium and an ESS in comparison with *A*. A strict Nash equilibrium implies protection by selection against replacement in the following sense: for a given payoff matrix (7.1), with $d > b$ and for any given intensity of selection, $0 < w \leq 1$, we have $\rho_A \rightarrow 0$ as

$N \rightarrow \infty$. For every finite population size, N , however, selection can favor the fixation of strategy A .

7.3 RISK DOMINANCE

Sometimes it is of interest to ask whether A is more likely to replace B than vice versa. Let ρ_A and ρ_B denote the respective fixation probabilities. In the case where both A and B are best replies to themselves and in the limit of weak selection and large population size, we find that $\rho_A > \rho_B$ is equivalent to

$$a + b > c + d. \quad (7.18)$$

This condition means that A is risk dominant. If both A and B are best replies to themselves, $a > c$ and $b < d$, then the risk-dominant strategy has the larger basin of attraction. Inequality (7.18) can be written as $x^* < 1/2$.

Let ρ_A denote the probability that a single A player reaches fixation in a population of B . Let ρ_B denote the probability that a single B player reaches fixation in a population of A . We have

$$\frac{\rho_A}{\rho_B} = \prod_{i=1}^{N-1} \frac{f_i}{g_i}. \quad (7.19)$$

For weak selection (small w) we find

$$\frac{\rho_A}{\rho_B} = 1 + w \left[\frac{N}{2}(a + b - c - d) + d - a \right]. \quad (7.20)$$

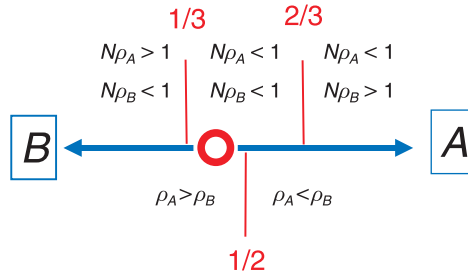
This equation can also be obtained from equation (7.10) and its symmetric counterpart, $\rho_B = (1/N)/[1 - (\alpha'N - \beta')w/6]$, where $\alpha' = -2a - b + 2c + d$ and $\beta' = -4a + b = c + 2d$.

It follows that $\rho_A > \rho_B$ is equivalent to

$$(N - 2)(a - d) > N(c - b). \quad (7.21)$$

For large N , this means $a - c > d - b$. Hence if both A and B are strict Nash equilibria, then the risk-dominant equilibrium has a higher fixation probability. For general N and w , however, risk dominance does not decide

Risk dominance and the 1/3 law



... for weak selection and large population size

Figure 7.8 The figure illustrates the relationship between the 1/3 law and risk dominance. The fixation probabilities of strategies A and B are given by ρ_A and ρ_B . The unstable equilibrium, x^* , is illustrated by the red circle. If $x^* < 1/3$, then $N\rho_A > 1 > N\rho_B$; selection favors A and opposes B . If $x^* > 2/3$, then $N\rho_B > 1 > N\rho_A$; selection favors B and opposes A . If $1/3 < x^* < 2/3$, then both $N\rho_A$ and $N\rho_B$ are less than one; selection opposes the fixation of both strategies. Risk dominance is determined by x^* being greater or less than $1/2$. If $x^* < 1/2$, then strategy A is risk-dominant; it has the larger basin of attraction. If $x^* > 1/2$, then strategy B is risk-dominant. For evolutionary game dynamics in finite populations, we find that $x^* < 1/2$ is equivalent to $\rho_A > \rho_B$, while $x^* > 1/2$ is equivalent to $\rho_A < \rho_B$. All these relationships hold in the limit of large population size and weak selection. In general, however, risk dominance does not determine the ranking of the fixation probabilities.

whether ρ_A is greater than ρ_B . Figure 7.8 shows the relationship between risk dominance and the 1/3 law.

Note that both ρ_A and ρ_B can be less than $1/N$. In this case, selection opposes replacement in either direction. It is also possible to find conditions where both ρ_A and ρ_B are greater than $1/N$. In this case, selection favors replacement in either direction.

7.4 TIT-FOR-TAT CAN INVADE “ALWAYS DEFECT”

In the nonrepeated Prisoner’s Dilemma, cooperators are dominated by defectors. In the repeated PD, the same two players meet more than once, and there are many conceivable strategies that allow cooperative behavior which can-

not be invaded by defectors (see Chapter 5). One such strategy is Tit-for-tat, which cooperates in the first round and then does whatever the opponent did in the previous round. If the number of rounds is greater than a critical value, then neither “Always defect” (ALLD) nor TFT can be invaded by the other. If everybody plays ALLD, then TFT has a lower fitness. If everybody plays TFT, then ALLD has a lower fitness. Thus TFT can maintain cooperation, but likewise ALLD can maintain defection. The question is, How can cooperation get established?

The notion that ALLD resists invasion by TFT is derived from concepts of evolutionary stability and game dynamics of infinite populations. If everybody in an infinitely large population uses ALLD, then a small fraction of TFT players have a lower payoff. Therefore every invasion attempt by TFT is eliminated by natural selection.

The payoff matrix for TFT and ALLD in a Prisoner’s Dilemma that is repeated for m rounds, on average, is given by

$$\begin{array}{cc} & \begin{array}{cc} \text{TFT} & \text{ALLD} \end{array} \\ \begin{array}{c} \text{TFT} \\ \text{ALLD} \end{array} & \left(\begin{array}{cc} mR & S + (m - 1)P \\ T + (m - 1)P & mP \end{array} \right) \end{array} \quad (7.22)$$

Recall that the Prisoner’s Dilemma is defined by $T > R > P > S$. If the average number of rounds, m , exceeds a critical value,

$$m > \frac{T - P}{R - P}, \quad (7.23)$$

then ALLD does not dominate TFT. Each strategy is stable against invasion by the other strategy.

Let us now study the evolutionary game dynamics of TFT and ALLD in finite populations. We can use the payoff matrix (7.22) together with equation (7.8) to calculate the fixation probability, ρ , of a lineage starting from a single TFT player in a population of ALLD. Figure 7.9 shows that $N\rho$ is a one-humped function of N . For a wide choice of parameter values, there is an intermediate range of population sizes, N , where selection favors TFT. Thus

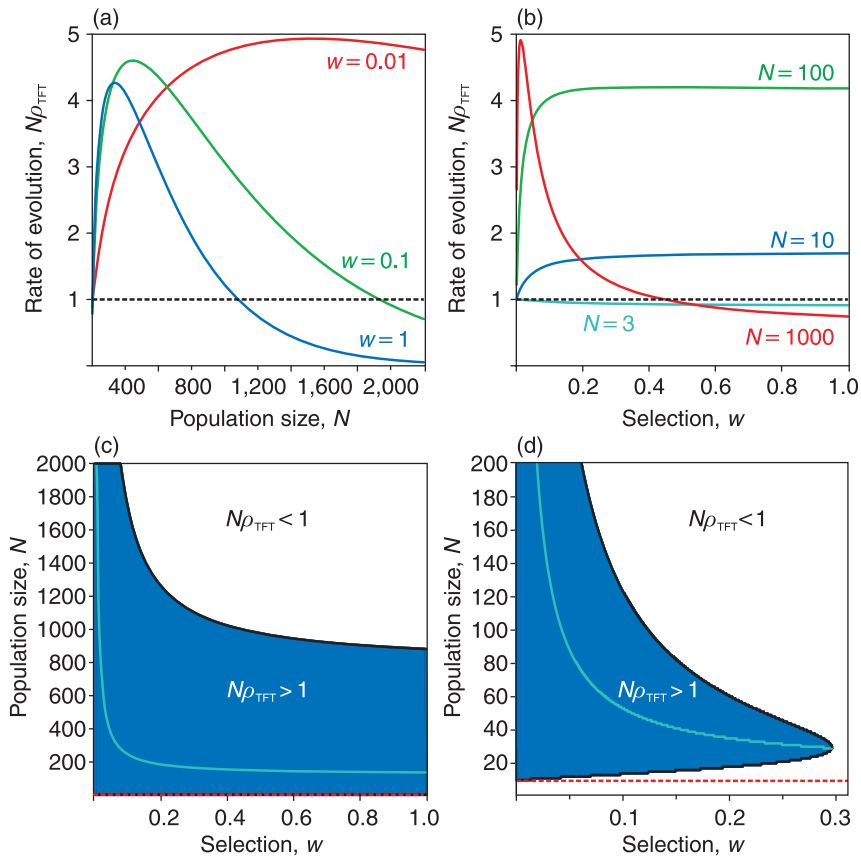


Figure 7.9 Selection can favor the replacement of ALLD by TFT in finite populations. (a) The rate of evolution, $N\rho_{\text{TFT}}$, is a one-humped function of population size N . There is an intermediate range of N that leads to positive selection of TFT, $N\rho_{\text{TFT}} > 1$. (b) $N\rho_{\text{TFT}}$ is shown as function of w , the intensity of selection. For small N , we have $N\rho_{\text{TFT}} < 1$ for all w . For larger N we have $N\rho_{\text{TFT}} > 1$ for all w . For even larger N we have $N\rho_{\text{TFT}} > 1$ as long as w is below a certain threshold. (c, d) The blue-shaded region indicates the parameter region where $N\rho_{\text{TFT}} > 1$. The light blue line shows the optimum value of N for given w maximizing $N\rho_{\text{TFT}}$. The broken red line indicates $N_{\text{min}} = (2a + b + c - 4d)/(a + 2b - c - 2d)$, which is the predicted minimum population size required for positive selection of TFT in the limit of weak selection. Parameter choices: $R = 3$, $T = 5$, $P = 1$, $S = 0$; $n = 10$ rounds for (a–c) and $n = 4$ rounds for (d).

Selection can favor TFT replacing ALLD

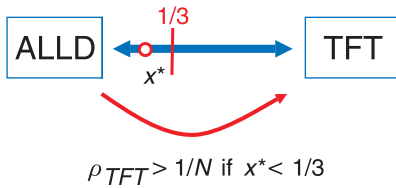


Figure 7.10 In a finite population, the fixation probability of a single TFT mutant in a population of ALLD can be greater than $1/N$. This is the case if the unstable equilibrium (the invasion barrier) is less than $1/3$, a condition that can be easily fulfilled in the repeated Prisoner's Dilemma.

the invasion and replacement of ALLD by TFT, starting from a single individual of TFT, can be favored by natural selection. Interestingly, there are critical minimum and maximum population sizes that allow positive selection of TFT. In very small populations, there is a strong effect of spite: helping another individual leads to a significant disadvantage; in a population of size $N = 2$, TFT always has a lower fitness than ALLD. In very large populations, it is too unlikely that TFT will reach the invasion barrier, x^* , when starting with a single player. Thus neither small nor large but intermediate population sizes are optimum for initiating cooperation.

Combining the payoff matrix (7.22) and condition (7.11) we obtain

$$m > \frac{T(N + 1) + P(N - 2) - S(2N - 1)}{(R - P)(N - 2)}. \quad (7.24)$$

This inequality determines the minimum number of rounds required for selection to favor TFT replacing ALLD for a given population size N . Note that we need at least a population size of $N = 3$. For a large population size, we obtain the condition

$$m > \frac{T + P - S}{R - P}. \quad (7.25)$$

This inequality ensures that the basin of attraction of ALLD is less than $1/3$.

Let us consider the payoff values $R = 3$, $T = 5$, $P = 1$, and $S = 0$ as a numerical example. For $N = 3$, we need $m > 10.5$ rounds. For $N = 4$, we need $m > 6.75$ rounds. For large N , we only need $m > 3$ rounds.

SUMMARY

- ◆ The Moran process can be extended to study evolutionary game dynamics in populations of finite size.
- ◆ The intensity of selection is of crucial importance. The game's payoff can make a large contribution to fitness (strong selection) or a small contribution (weak selection).
- ◆ The fixation probabilities determine whether selection favors the replacement of an existing strategy by an incoming mutant.
- ◆ Natural selection favors A replacing B in a sufficiently small population provided $b > c$.
- ◆ Natural selection favors A replacing B in a sufficiently large population and for weak selection (small w) provided $a + 2b > c + 2d$. If A and B are best replies to themselves, then this inequality means that the basin of attraction of B is less than $1/3$.
- ◆ The analysis leads to natural conditions for evolutionary stability in finite populations. These conditions specify whether a given resident strategy is protected by selection against invasion and replacement by any mutant strategy.
- ◆ The traditional ESS and Nash conditions are neither necessary nor sufficient to imply protection by selection in finite populations.
- ◆ Even if A is risk dominant over B , then B can have a greater fixation probability than A . Only in the limit of weak selection and large population size does risk dominance determine the ranking of the fixation probabilities.
- ◆ In a finite population, natural selection can favor the replacement of "Always defect" by a cooperative strategy (such as Tit-for-tat), when starting from a single individual using that strategy.