
Appendices

A1 Agent-Based Models: an Introduction

Agent-based modeling is a tool for analyzing certain types of complex dynamical systems. The actors in these systems are individual agents who share many characteristics, but differ on key characteristics that affect their relative reproductive success. The agents operate semi-autonomously, but are linked through a network of structured interactions. The individual characteristics in a complex system evolve through a process of replication, mutation, and selection of relatively successful individuals. Such dynamics are recursive, meaning that changes in one period become the basis for changes in future periods, and are non-linear, with the implication that they are generally incapable of being expressed as closed-form analytical solutions to sets of equations.

For instance, the individuals may be competing for jobs, or males and females who are interested in finding a good mate, or predators trying to catch prey and prey who are trying to avoid being caught. Suppose the individuals and their environment undergo mutation and structural change, so that the resulting system is sufficiently complex that it has “emergent properties” that cannot be determined simply by aggregating individual interactions, and the mathematics of the system is too complicated to solve in analytical form. Finally, suppose that each individual history of interaction affects his play, and individuals continually adapt by taking on the behaviors of other individuals who have done especially well, in terms of fitness, material gain or some other standard, in the course of time. In such a situation, agent-based modeling is an appropriate tool for investigating the dynamics of the interactive system.

Agent-based modeling is widely used in the natural and behavioral sciences, and the growth in its use has been extremely rapid since the advent of the powerful desktop computer. Such modeling (often called ‘simulation’) lies outside the two standard methods of gaining scientific knowledge: deduction and induction. Deduction means proving theorems—showing

that certain mathematical conclusions follow from certain axioms (e.g., the Pythagorean Theorem follows from the laws of algebra). Induction means finding lots of evidence and drawing conclusions (e.g., all swans are white). Agent-based modeling is like deduction in that it starts with a rigorously specified computer program, but it is like induction in that it treats the operation of the program as a set of data points from which generalizations can be made. In particular, if a complex system has emergent properties, these can be ascertained by exhibiting an agent-based model in which these properties are seen and persist over many simulations.

We use agent based models to study the dynamics of hypothetical populations that are structured to evolve in ways that we think represent long-term human evolution. Using this method, we can generate literally thousands of artificial histories allowing us to investigate the likely effects of differences in the benefits and costs of cooperative activities, the frequency of group conflict, the structure of a group's socialization practices and other influences.

While agent-based modeling is important because many dynamic strategic settings are too complicated to admit standard mathematical analysis, it should not be thought that agent-based models are necessarily second-best. The assumptions made to permit explicit analytical solutions are often sufficiently unrealistic (e.g., continuous time, infinite numbers of individuals) that the agent-based model behaves more like the situations we are trying to model than does a tractable analytical model (Durrett and Levin 1994). Nevertheless, agent-based models require extensive experimentation to ensure that results accurately reflect the properties of the system.

The classical example of an agent-based model is Thomas Schelling's (1978) study of residential segregation. Schelling showed that if families like having at least one neighbor of the same ethnic background, but otherwise prefer diversity to uniformity in neighbors, in the long run, family relocation is likely to lead to a high degree of segregation. In this case, segregation is an emergent property of the system because no individual family wanted this or sought it, and it was not predicted as the logical consequence of the system's initial conditions using a set of differential equations. We can study residential segregation using Schelling's idea by varying the number of ethnic groups, varying the intensity of preference for uniformity and diversity, and by varying the rules of neighborhood formation and population movement. For instance, Schelling predicted the "tipping" phenomenon often found in residential dynamics: when the fraction of res-

idents of a minority group in a community reaches a certain “tipping point,” the community more or less rapidly shifts towards that group becoming a majority.

An *evolutionary* agent-based model has, in addition to a *stage game* representing the interaction of agents, has a *replication phase*, in which individuals replicate according to some updating rule, often in proportion to their average success in the stage game. As a result, old individuals disappear, and their offspring inherit their behavior, perhaps with some mutation. In an evolutionary agent-based model, the more successful strategies are permitted to increase in frequency at the expense of the less successful. Thus, evolutionary agent-based models possess the three main characteristics of Darwinian evolution: replication, mutation, and selection according to fitness.

Among the first behavioral science applications of evolutionary agent-based modeling was Joshua Epstein and Robert Axtell’s *Growing Artificial Societies* (1997), which produced a wide variety of emergent behaviors from simple rules governing individual behavior inscribed in a “chromosome” that could evolve over time much as DNA, the computer genes being used to represent different strategic behaviors. They modeled migration, environmental externalities, conflict, and even disease transmission in a population of individuals competing for food. More recently, agent-based models of political competition, stock markets dynamics and investor strategies, as well as models of parasitism and disease transmission have become standard components of behavioral research (Miller and Page 2007, Epstein 2007). Agent-based models of cooperation in biological systems For a useful overview of the application of such models to various fields in the natural and behavioral sciences, see Tesfatsion and Judd (2006).

Figure A1 shows the programming structure of a typical evolutionary agent-based model. In the figure, “Game Parameters” refer to the specifics of the stage game being simulated, including the payoffs, the probabilities with which various events occur, and the like. The “Number of Generations” specifies how many rounds of replication you want to take place. This may be as small as 10 or as large as 10,000,000. The “Number of Rounds/Generation” refers to the speed of play as compared to the speed of replication. By the Law of Large Numbers, the more rounds per generation, the more accurately the actual success of individuals reflects the expected payoff of the strategies they represent. “Group All Individuals” captures the matching phase of the simulation, as well as the notion that

a strategy in a game reflects a social practice occurring in the population, rather than the carefully thought-out optimizing strategy of classical game theory. Note that in some situations, we will want some structure to this stage of the model. For instance, “neighbors” may meet more frequently than “strangers,” or individuals who play similar strategies may meet more frequently than individuals with different strategies.

The “Individuals Replicate” box is worth a diagram of its own, which we present in Figure A2. First we set various parameters, including the rate of mutation of new individuals and the extinction rate of old individuals. We then eliminate the appropriate number of unsuccessful individuals, and make an equal number of copies of the high success individuals, giving them the same strategies as their replicators, except that we allow some mutation. Success may be measured by fitness (offspring surviving to reproductive age) or by extent to which an individual’s behavior is copied (adopted through social learning) by others.

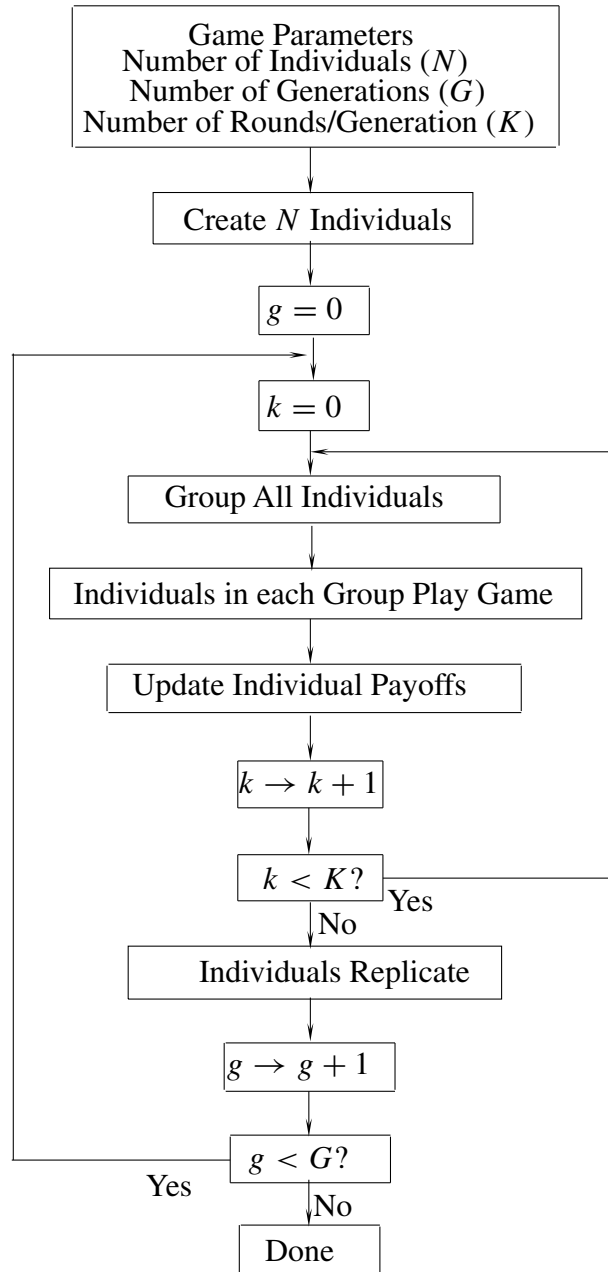


Figure A1. Structure of an Evolutionary Agent-Based Simulation

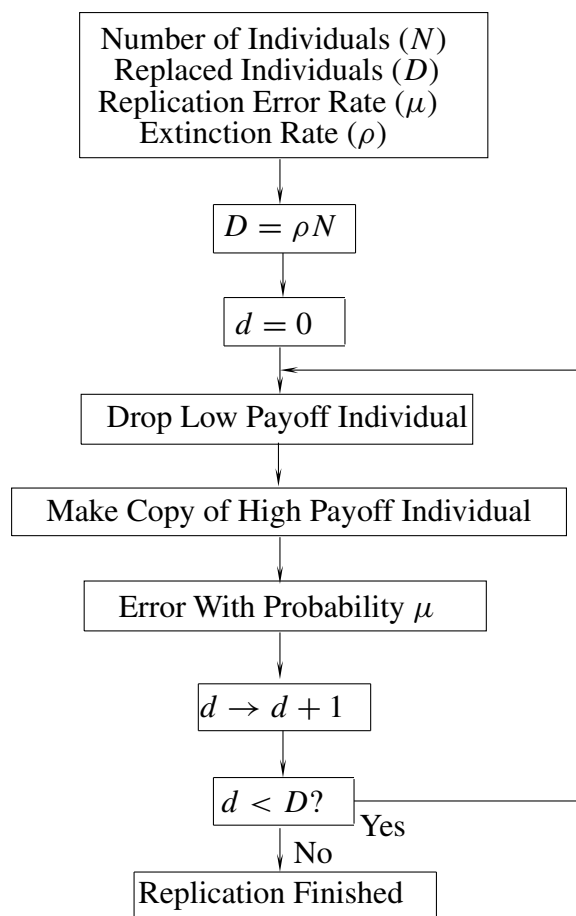


Figure A2. Structure of Replication Process

A2 Game Theory

Suppose we have a number of individuals $i = 1, \dots, n$ involved in a social interaction. Suppose each individual i has a set S_i of possible actions available to him, and each individual chooses an action $s_i \in S_i$ independently, and to each such action profile (s_1, \dots, s_n) , each individual i receives a payoff $\pi_i(s_1, \dots, s_n)$. We call the various actions s_i *pure strategies* and we call this social situation a *game in strategic form*. This definition extends readily to *mixed strategies*, where players use probability distributions over their pure strategies, but we will not need this extension in this book.

An example of a game in strategic form is the prisoners' dilemma (§4.3), in which each player $i = 1, 2$ has pure strategy set $S_i = \{H, N\}$, and $\pi_1(H, H) = b - c$, $\pi_1(H, N) = -c$, $\pi_1(N, H) = b$, and $\pi_1(N, N) = 0$. The payoffs to player 2 are $\pi_2(H, H) = b - c$, $\pi_2(H, N) = b$, $\pi_2(N, H) = -c$, and $\pi_2(N, N) = 0$.

Suppose players choose strategies (s_1, \dots, s_n) . We say s_i is a *best response* to the remaining $n - 1$ strategies of the other players if there is no strategy for player i that can give player i a payoff greater than $\pi_i(s_1, \dots, s_n)$. We say (s_1, \dots, s_n) is a *Nash equilibrium* if every player's choice is a best response to the choices of the other players. There are many cases in which we do not expect players to choose a Nash equilibrium, for example the repeated games described in Chapter 5, but in many games described in this book, it is reasonable to expect individuals to play a Nash equilibrium.

In some games, including the prisoners' dilemma described above, and its extension to an n -player game, the public goods game (§4.4), a player may have a strategy that offers higher payoff than any other strategy, no matter what the other players do. Such a strategy is called *dominant*. A player who has a dominant strategy will play it in any Nash equilibrium, because such a strategy is a best response to any configuration of strategies of the other players. In the one-shot prisoners' dilemma and public goods games, for instance, defecting is a dominant strategy for all players.

In many games, players move more than one time and do not play simultaneously. We represent such games as *extensive form games*, as in Figure 7.1. In this case we use a *game tree* consisting of *nodes* connected by *branches*. Each node represents a point in the game where a particular player gets to move, and each branch emanating from a node represents the various actions that the player has when choosing at that node. At the end of the game tree are *terminal nodes* where the payoffs to the players are exhibited. For a more complete treatment of extensive form games, consult Gintis (2000a).

We can define a Nash equilibrium for an extensive form game in a manner parallel to the definition in the previous section. Consider a choice of an action at each node of the extensive form game. We say the resulting profile of choices is a Nash equilibrium if no player can gain by changing his choice at any node where he gets to choose.

Suppose we start with a game \mathcal{G} as in the previous section, and repeat the game indefinitely, with a probability $1 - \delta > 0$ of terminating the process at the end of each period (§4.3). We then call \mathcal{G} the *stage game*, of the repeated

game. The payoff to the repeated game is just the sum of the payoffs to the various stages. Note that the payoff is finite, because the process terminates in a finite number of periods with probability one. Note also that we can include a time discount factor in δ , as explained in Chapter 4.

The most important fact about the repeated game based on stage game \mathcal{G} is that it can support cooperative equilibria in situations where \mathcal{G} cannot. Consider, for instance, the prisoners' dilemma (§4.3). The only Nash equilibrium of the stage game has both players defecting, hence earning payoff 0. But, suppose the players follow the strategy in the repeated game of cooperating until the first player defects, and then defecting forever. We call this the Grim Strategy. By following the Grim Strategy, the players earn $(b - c)/(1 - \delta)$, as analyzed in §4.7. The gain from defecting right away is b , so following the Grim Strategy is a Nash equilibrium as long as $(b - c)/(1 - \delta) > b$, which reduces to $\delta b > c$.

An *evolutionary game* is a repeated game, as in the last section. However, instead of n players, there are n *populations* of players, and in each period, many stage games \mathcal{G} are played, each consisting of one player drawn randomly from each population. Moreover, as in agent-based modeling, we assume players each play a fixed strategy rather than a best response. A running total of player's scores is kept, and periodically, the high-scoring players have their strategies copied by the low-scoring players. Moreover, we may add a bit of random mutation to the mix, so that once in a while a low-scoring agent chooses a random strategy rather than imitating a high-scoring individual.

The idea of an evolutionary game is due to the biologist Maynard Smith (1982), who applied it to animals whose limited intelligence does not allow us to assume that they play best responses. However, the concept applies just as well to humans who, while intelligent, often lack the information to choose a best response, or who are not sufficiently coordinated to choose one among the variety of best responses available to them.

The most natural dynamic to apply to an evolutionary game is the *replicator dynamic*, which we describe below. Indeed, it can be shown that every equilibrium of an evolutionary game under the replicator dynamic is a Nash equilibrium of the stage game (Nachbar 1990). This shows that the Nash equilibrium criterion remains powerful even without assuming that players are rational (i.e., that they choose best responses) or coordinated.

However, in many cases, Nash equilibria of the stage game are not stable equilibria of the corresponding evolutionary game. For this reason, Maynard

Smith developed the stronger notion of an *evolutionarily stable strategy* (ESS) for the case of a two-player stage game \mathcal{G} in which a single population of individuals play against themselves, as in the prisoners' dilemma. A strategy is an ESS if a whole population using that strategy cannot be invaded by a small group playing any other strategy defined in \mathcal{G} . It is easy to show that an ESS is always a Nash equilibrium, but the converse is false. Indeed, an ESS is always a stable equilibrium of the replicator dynamic (Gintis 2000a).

We here derive the replicator dynamic for an evolutionary game by imitation of cultural (phenotypic) traits. The derivation for genetic evolution is similar, but somewhat simpler to derive. Consider a population of individuals who play a game in which each player follows one of n pure strategies s_i for $i = 1, \dots, n$. The play is repeated in periods $t = 1, 2, \dots$. Let p_i^t be the fraction of players playing s_i in period t , and suppose the payoff to s_i is $\pi_i^t = \pi_i(p^t)$, where $p = (p_1, \dots, p_n)$. We look at a given time t , and number the strategies so that $\pi_1^t \leq \pi_2^t \leq \dots \leq \pi_n^t$.

Suppose in every time period dt , each individual with probability $\alpha dt > 0$ learns the payoff to another randomly chosen other individual and changes to the other's strategy if he perceives that the other's payoff is higher. However, information concerning the difference in the expected payoffs of the two strategies is imperfect, so the larger the difference in the payoffs, the more likely the individual is to perceive it, and change. Specifically, we assume the probability p_{ij}^t that an individual using s_i will shift to s_j is given by

$$p_{ij}^t = \begin{cases} \beta(\pi_j^t - \pi_i^t) & \text{for } \pi_j^t > \pi_i^t \\ 0 & \text{for } \pi_j^t \leq \pi_i^t \end{cases}$$

where β is sufficiently small that $p_{ij} \leq 1$ holds for all i, j . The expected fraction $\mathbf{E}p_i^{t+dt}$ of the population using s_i in period $t + dt$ is then given by

$$\begin{aligned} \mathbf{E}p_i^{t+dt} &= p_i^t - \alpha dt p_i^t \sum_{j=i+1}^n p_j^t \beta(\pi_j^t - \pi_i^t) + \sum_{j=1}^i \alpha dt p_j^t p_i^t \beta(\pi_i^t - \pi_j^t) \\ &= p_i^t + \alpha dt p_i^t \sum_{j=1}^n p_j^t \beta(\pi_i^t - \pi_j^t) \\ &= p_i^t + \alpha dt p_i^t \beta(\pi_i^t - \bar{\pi}^t), \end{aligned}$$

where $\bar{\pi}^t = \pi_1^t p_1^t + \dots + \pi_n^t p_n^t$ is the average return for the whole population. If the population is large, we can replace $\mathbf{E}p_i^{t+dt}$ by p_i^{t+dt} . Subtracting p_i^t

from both sides, dividing by dt , and taking the limit as $dt \rightarrow 0$, we get

$$\dot{p}_i^t = \alpha\beta p_i^t(\pi_i^t - \bar{\pi}^t), \quad \text{for } i = 1, \dots, n, \quad (\text{A1})$$

which is called the *replicator dynamic*. Because the constant factor $\alpha\beta$ merely changes the rate of adjustment to stationarity but leaves the stability properties and trajectories of the dynamical system unchanged, we often simply assume $\alpha\beta = 1$.

Several points are worth making concerning the replicator dynamic. First, under the replicator dynamic, the frequency of a strategy increases exactly when it has above average payoff. Second, if we add up all the equations, we get $\sum_i \dot{p}_i^t = 0$, so if $\sum_i p_i^t = 1$ at one point in time, this remains true forever. Moreover, while a particular replicator can become extinct, a replicator that is not represented in the population at one point in time will never be represented in the population at any later point in time. So, replicator dynamics deal poorly with mutation and innovation. A more general system adds a term to the replicator equation expressing the spontaneous emergence of replicators.

Book length treatments on evolutionary game theory are Gintis (2000a), Weibull (1995) and Vega-Redondo (2003). Young (1998), Bowles (2004) and McElreath and Boyd (2006) (2006) use evolutionary game theory to study the dynamics of human behavior and institutions. Applications to biology are developed in Nowak (2006).

A3 Dynamical Systems: An Introduction

We will explain two major types of dynamical systems, a continuous time system using differential equations, and a discrete time system using Markov chains. The material presented below is a condensed version of the presentation in Gintis (2000a), to which the reader should refer for additional material and references.

For ease of exposition, suppose our continuous time system has two dimensions, represented by variables x and y , the horizontal and vertical axes of the Cartesian plane. An example is the coevolution of the fraction of altruists and of parochialists in the population depicted in Figures 8.2 and 8.3. The *path* of the system in time is represented by a pair of functions $x(t)$ and $y(t)$. We assume that the rate of change of the system in the x - and y -directions are functions of the position of the system alone, so we can

write

$$\frac{dx(t)}{dt} = f(x, y) \quad (\text{A2})$$

$$\frac{dy(t)}{dt} = g(x, y). \quad (\text{A3})$$

There is a theorem that guarantees that, given an initial time $t = t_0$, if f and g are reasonably well-behaved, there is a unique solution to (A2) through $t = t_0$. This is called the *path* of the dynamical system.

An *equilibrium* of the dynamical system (A2), also called a *critical point* or *fixed point*, or *stationary point*, is a value (x^*, y^*) such that $f(x^*, y^*) = g(x^*, y^*) = 0$. Note that at an equilibrium, $dx/dt = dy/dt = 0$, so the dynamical system remains forever at (x^*, y^*) once it reaches there. Under what conditions does a dynamical system move towards an equilibrium?

Suppose that, starting from a point (x_0, y_0) , the path of the dynamical system (A2) approaches (x^*, y^*) as $t \rightarrow \infty$; i.e., $\lim_{t \rightarrow \infty} x(t) = x^*$ and $\lim_{t \rightarrow \infty} y(t) = y^*$. Then we say (x_0, y_0) is in the *basin of attraction* of the equilibrium (x^*, y^*) . If the basin of attraction of an equilibrium is two-dimensional, it must surround the equilibrium, and we say the equilibrium is *asymptotically stable*, or simply *stable*. If the equilibrium is not stable, it may be either *neutrally stable* or *unstable*. The equilibrium is unstable if, no matter how close a path starts near (but not at) the equilibrium, there is a positive distance d from the equilibrium such that the path eventually is farther than d from the equilibrium, and never gets closer than d thereafter. If the path is neither stable nor unstable, we say it is neutrally stable. In the neighborhood of a neutrally stable equilibrium, paths neither escape nor converge to the equilibrium. They are therefore themselves either equilibria, or they trace out paths around the equilibrium.

Very few dynamical systems, even simple ones in two dimensions, can be solved analytically, so the paths $x(t)$ and $y(t)$ cannot be written in closed form. Nevertheless, there are well-developed methods for determining when an equilibrium is stable, unstable, or neutrally stable, using tools from algebra and calculus.

A finite *Markov chain* is a dynamical system that can be in any of n states s_1, \dots, s_n , and if the system is in state i in time period t , it will be in state j in time period $t + 1$ with probability p_{ij} . Of course, for this to make sense, we must have $p_{ij} \geq 0$ for all $i, j = 1, \dots, n$, and $\sum_{j=1}^n p_{ij} = 1$. Statistical estimates of these probabilities, based on thousands of implementations of our model, for example, are the basis of our calculation the vector field in

Figure eightthree giving the movement of the population among the states indicating various frequencies of altruists and of parochials.

For instance, consider two urns, one filled with 10 red balls and the other with 10 white balls. In each time period, we choose one ball from each urn simultaneously and place each ball in the other urn. Let s_i be the state where the first urn has i red balls, so we start out in state s_{10} . It is easy to write down the transition probabilities if you know a little probability theory, but we will leave this exercise to the reader. It is intuitively obvious that in the long run, there will be an average of 5 white balls in the first urn, and this will be true independent of how many of the 10 white balls were in this urn when we started. When a Markov chain has this property—that the average fraction of time in each state in the long run is independent from the starting state, we say the system is *ergodic*, and we call the resulting long run distribution of probabilities the *stationary distribution* of the Markov chain. The Markov chain represented by our urn problem is thus an ergodic Markov chain. Figure 8.3 gives the stationary distribution of parochials and altruists while Figures 4.1 and 4.3 give the mean levels of net cooperation in the stationary distribution of the agent based models of cooperation, for varying group sizes and error rates.

We say the states of a Markov chain *communicate* if, for every pair of states, there is a positive probability of moving from the first state to the other and then back. If we write $p_{ij}^{(k)}$ for the probability that the Markov change moves from state i to state j in k periods, then states i and j communicate if $p_{ij}^{(k)} > 0$ and $p_{ji}^{(m)} > 0$ for some integers k and m . Let i be a state of a Markov chain, and let T_i be the set of integers k such that $p_{ii}^{(k)} > 0$. If the greatest common divisor of the integers in T_i is greater than 1, we say the state i is *periodic*. For instance, consider a Markov chain consisting of 10 points equally spaced on a circle, numbered 1 to 10, and suppose the state can move either clockwise or counter-clockwise by one position. Then, every state has period 2, because the system can only return to a state in an even number of transitions. If a Markov chain has no periodic states, we say the Markov chain is *aperiodic*.

Using these definitions, we can state the most important property of finite Markov chains. Suppose every pair of states of a finite aperiodic Markov chain communicate. Then the chain is ergodic. Clearly, this applies to the above urn problem.

An agent-based model is a finite Markov chain because there are a finite number of agents, each can only be in a finite number of states, and if there

are parameters in the model (e.g., the current weather), then these are in finite number. Moreover, a computer language can support only a finite number of real numbers without ‘overflow’, so even supposedly “real” numbers are really a finite range of integral fractions. The number of states in the resulting system can be huge, but it is a finite number. Moreover, while it may be quite impractical to calculate the probability of movement from one state to another, the probability itself is perfectly determinate. To ensure that the Markov chain represented by the agent-based model is ergodic, we always allow agents to remain in their current state with positive probability, and mutate to another state with positive probability, however small.

It follows that the ergodic theorem holds for all of the agent-based models used in this book. This means that the long-run behavior of the dynamical systems generated by our agent-based models is independent from the particular initial parameters we have chosen for our illustrative runs. Of course, the ergodic theorem cannot tell us how long it will take to “erase” the effect of our initial conditions, and the number of periods involved could be truly astronomical. Thus, we take the question of how fast a system moves to its stationary distribution to be a very important one,

It may appear that the stationary distribution of an ergodic Markov chain somehow represents a small cluster of nearby “long-run average states,” but that is not the case in some Markov chains. For instance, consider the Markov chain with two states s_1 and s_2 , where $p_{11} = 0.99$, $p_{12} = 0.01$, $p_{22} = \epsilon$ and $p_{21} = 1 - \epsilon$. If ϵ is a small perturbation, this chain spends almost all its time in state 1, but it does spend a positive amount of time, about ϵ periods, on average, in state 2. We say a state is *recurrent* if it spends a positive fraction of time in this state in the stationary distribution, so both states in this example are recurrent. However, when it enters state 1, it stays there for almost 100 periods, on average, before moving to states 2, while in state 2, it rarely stays for more than one period. We say that a state is *stochastically stable* if, under a small perturbation of size $\epsilon > 0$, the fraction of time it spends in that state is bounded away from zero as $\epsilon \rightarrow 0$. Clearly, only state 1 is stochastically stable in this case. Young (1998) uses finite Markov processes to study the long term evolution of contracts and other institutions.

A4 Altruism Defined

In Chapters 3 and 4 we provide two definitions of altruistic behavior, one concerning preferences (other-regarding or self-regarding) that motivate behavior (p. 35) and the other based on its fitness effects on the actor and others (p. 82).

Our biological definition of altruism refers to a large population composed of a large number of groups: the behaviors induced by an altruistic genotype increase the expected average fitness of members of the group of which the focal individual is a member, but the focal individual would have higher fitness were he not the bearer of the altruistic genotype. This is the definition adopted by Hamilton (1975), Grafen (1984), and others. To make this clear, following Kerr et al. (2004), suppose the expected fitness of altruists and non-altruists in a group of m members with j altruists are $w^A(j)$ and $w^N(j)$ respectively. Then our first condition, that the altruistic behavior raises the expected average fitness of members of the group, is that

$$P = \{jW^A(j+1) + (m-j-1)w^N(j)\}/m > \{jW^A(j) + (m-j)w^N(j)\}/m \quad (\text{A4})$$

and the second, that switching from an N to an A lowers the actor's fitness, is

$$w^A(j+1) < w^N(j). \quad (\text{A5})$$

These two conditions are respectively Conditions 4 and 1 of Kerr et al. (2004), which together imply their Condition 2.

There are two attractive features of this definition. First, it is the most stringent definition possible (other than definitions that preclude the evolution of altruism under any conditions). In the absence of positive assortment altruism cannot evolve under our definition. An alternative definition found in Haldane (1932), Cohen and Eshel (1976), Maynard Smith (1964) and Sober and Wilson (1998) replaces (A5) with the condition that A 's have lower fitness than N 's, or

$$w^A(j) < w^N(j). \quad (\text{A6})$$

This is less stringent because it does not preclude that $W^A(j+1) > w^N(j)$ so that an N would increase its fitness by switching to an A . This would be the case if the altruistic act cost c and conferred a benefit b on a randomly selected member of the group, and $b/m > c$. Then condition 3 would hold but condition 2 would not: by switching to A from N , the

chance that the benefit would accrue to the actor would more than offset the cost of the behavior. In this case altruism will evolve even under random assortment (Matessi and Jayakar 1976).

The second attractive feature is that the definition maps directly onto the two terms in the Price equation (A8). Recall that the β 's in the equation are partial derivatives of expected group average fitness with respect to (for β_G) the fraction of altruists in the group and (for β_i) the actor's own type (N or A). Condition 1 above requires that $\beta_G > 0$ while condition 2 requires that $\beta_i < 0$, thus defining what we have called (in Chapter 4) the "strong group selection" problem.

Our preference-based definition is that a person acts altruistically by conferring benefits on other members of one's group at a personal cost, meaning that the act would not be chosen by an individual with entirely self-regarding preferences. Strictly speaking, our definition does not require that the average well-being of the group members increase, but we are generally interested in altruistic behaviors only when in some sense this is true. The definitions are identical if the states over which the individual is choosing are fitness levels, so that an entirely self-regarding individual would never act altruistically (if condition 2 above obtained) because given 2, N is the unique best response independently of j . Because we also generally assume that b , the benefit conferred on others, exceeds c , the cost, condition 2 must obtain: an altruistic act raises the total benefit of the group. This formulation entails that the well-being of group members can be summed, if not in fitness terms, then in some other.

The attractive feature of this definition is that it allows altruistic behaviors to be motivated by preferences, thus allowing use of the term altruistic or other-regarding preferences. The alternative—to regard any preference-motivated behavior as selfish—is the equivalent in preference terms to the biological definition requiring that altruistic behaviors entail lower fitness in the population taken as a whole. The first requires that altruism be counter-preferential and hence irrational. The second precludes altruism being evolutionarily feasible.

A5 The Price Equation: An Introduction

Suppose there are groups $j = 1, \dots, m$, and let q_j be the fraction of the population in group j . Let w_j be the mean fitness of the members of group j , so $w = \sum_j q_j w_j$ is the mean fitness of the whole population. We use

the term fitness here, but as the Price equation is applicable to any system in which traits are differentially replicated over time, we could have used the more general term: number of replicas in the next period. Groups grow from one period to the next in proportion to their relative fitness, so if q'_j is the fraction of the population in group j in the next period, then

$$q'_j = q_j \frac{w_j}{w}.$$

Suppose there is a trait with frequency p_j in group j , so the frequency of the trait in the whole population is $p = \sum_j q_j p_j$. If p'_j is the mean fitness of members of group j and the frequency of the trait in group j in the next period, respectively, then $p' = \sum_j q'_j p'_j$, so

$$\begin{aligned} p' - p &= \sum q'_j p'_j - \sum q_j p_j \\ &= \sum q_j \frac{w_j}{w} (p_j + \Delta p_j) - \sum q_j p_j \\ &= \sum q_j \left(\frac{w_j}{w} - 1 \right) p_j + \sum q_j \frac{w_j}{w} \Delta p_j. \end{aligned}$$

Now writing $\Delta p = p' - p$ and multiplying the above expression by w , this becomes

$$w \Delta p = \sum q_j (w_j - w) p_j + \sum q_j w_j \Delta p_j. \quad (\text{A7})$$

Because $\sum q_j (w_j - w) p_j = 0$, from the definition of w , and noting that

$$\sum q_j (w_j - w) (p_j - p) \equiv \text{cov}[w_j, p_j]$$

and

$$\sum q_j w_j \Delta p_j \equiv \mathbf{E}[w_j \Delta p_j],$$

we can rewrite A7 as

$$w \Delta p = \text{cov}[w_j, p_j] + \mathbf{E}[w_j \Delta p_j], \quad (\text{A8})$$

where the covariance and expectations are taken with respect to the population fractions q_j . We interpret (A8) as follows. The trait measured by p will increase in frequency if the left hand side of the equation is positive. Because $w > 0$, this will occur only if the right hand side is positive. If the trait measured by p is altruistic, as in the conventional application of the Price equation, then the first term $\text{cov}[w_j, p_j]$ will be positive, because

groups with higher fractions of the trait will have supranormal average fitness of its members. But, the second term, $\mathbf{E}[w_j \Delta p_j]$, will be negative, because the altruists are disadvantaged within each group, so their within-group frequency declines, and Δp_j will be negative for all j . The trait will then spread only if the between-group advantage of the high altruism groups is sufficient to overcome the within-group disadvantage of the altruists.

In chapter 6 we apply the above equation to the case of Nonpunishing Cooperators, who may be considered within-group parasites rather than altruists, because they free ride on the punishment meted out by strong reciprocators against selfish individuals. In this case, the term $\text{cov}[w_j, p_j]$ may be negative, because groups with higher fractions of Cooperators may have been invaded by selfish individuals and hence have below average fitness, unless the fraction of Cooperators is very high. Within groups the situation is inverted. As long as there is a sufficient number of strong reciprocators and sufficiently few selfish individuals, the term $\mathbf{E}[w_j \Delta p_j]$ will be positive, because the Cooperators are advantaged within each group. The reason is that they are never punished and do not bear the costs of punishing others. As a result, they are advantaged within each group, so their within-group frequency increases. The parasitic trait will then spread as long as the between-group disadvantage of the high Cooperator groups is insufficient to overcome the within-group advantage of the Cooperators. For very high or very low fractions of Cooperators in the population, of course this situation would not obtain. But the accounting of the within and between group effects in figure 4.4 shows that for the simulations we have studied, our interpretation of the parasitic nature of Cooperators is indeed true.

In Section 4.7, we apply the Price equation to altruism in a social dilemma, where altruists supply a benefit b to other members of the group at a cost c to themselves. In this case, adding (4.10) over all i in group j , of which there are $q_j N$, where N is total population size, and dividing by N , we get

$$q_j w_j = q_j \beta_o + q_j p_j \beta_g + q_j p_j \beta_i. \quad (\text{A9})$$

Adding this equation over all groups and dividing by N gives

$$w = \beta_o + p \beta_g + p \beta_i. \quad (\text{A10})$$

This allows us to rewrite the group effect, the covariance term, in the Price equation above as the between-group variance multiplied by the total derivative of expected group size with respect to the fraction of altruists in a group,

namely $\beta_g + \beta_i$:

$$\begin{aligned}
\text{cov}[w_i, p_i] &= \sum_j q_j (w_j - w)(p_j - p) \\
&= \sum_j q_j (w_j - w) p_j \\
&= \sum_j q_j (p_j - p)(\beta_i + \beta_g) p_j \\
&= \sum_j q_j (p_j - p) p_j (\beta_i + \beta_g) \\
&= \sum_j q_j (p_j - p)^2 (\beta_i + \beta_g) \\
&= \text{var}(p_j) (\beta_i + \beta_g). \tag{A11}
\end{aligned}$$

The second equality follows from the fact that $\sum_j q_j (w_j - w) p = 0$ by the definition of w . The third follows by subtracting (A10) from (A9), simplifying, and substituting in the equation. The fourth equation is an algebraic rearrangement. The fifth equation follows from the fact that $\sum_j q_j (p_j - p) = 0$, which follows from the definition of p .¹ To evaluate $\mathbf{E}[w_j \Delta p_j]$, we note that

$$\begin{aligned}
p'_j - p_j &= \sum_i q'_j p'_{ji} - \sum_i q_j p_{ji} = \sum_i q_j \frac{w_{ji}}{w_j} p_{ji} - \sum_i q_j p_{ji} \\
&= \frac{1}{w_j} \sum_i q_j (w_{ji} - w_j) p_{ji},
\end{aligned}$$

so

$$\begin{aligned}
\mathbf{E}[w_j \Delta p_j] &= \sum_i q_j (w_{ji} - w_j) p_{ji} = \beta_j \sum_i q_j (p_{ji} - p_j) p_{ji} \\
&= \beta_j \mathbf{E}[\text{var}(p_{ji})]. \tag{A12}
\end{aligned}$$

Thus, substituting equations A11 and A12 into the Price equation, we have

$$w \Delta p = \text{var}(p_j) \beta_G - \beta_i \mathbf{E}[\text{var}(p_{ij})]. \tag{A13}$$

¹More generally, if x and y are random variables and $y = a_0 + a_1 x$ is the regression equation of x on y , then $\text{cov}(x, y) = a_1 \text{var}(x)$.

Substituting the costs and benefits of the altruistic behavior for the β 's in this equation we have

$$w\Delta p = \text{var}(p_i)(b - c) - c\mathbf{E}[\text{var}(p_{ji})]. \quad (\text{A14})$$

where, as before, w is the population-wide average of the number of replicas (which we normalize to unity) and the expectation operator \mathbf{E} indicates a weighted average over groups (the weights being relative group size).

For an example of using the Price equation, suppose a population is composed of two groups that in a given period are of equal size, with the fractions of altruists in each, $p_1 = 3/4$ and $p_2 = 1/4$, so $p = 1/2$. To find the values of b and c such that p will be stationary, we need to equate the average fitness of the two types. Writing w_{ij} for the fitness of type i in group j ($i = A, N$, $j = 1, 2$) and w_i for the population average fitness of type i , and ignoring β_o , we have

$$w_A = p_1 w_{A1} + p_2 w_{A2} = (1 - p_1) w_{N1} + (1 - p_2) w_{N2} = w_N, \quad (\text{A15})$$

or, using the payoff table in the text, the average fitness of A's and N's is the weighted average of their respective fitnesses in the two groups so the condition for p to be stationary, is given by

$$\begin{aligned} w_A &= \frac{3}{4} \left(\frac{3}{4}b - c \right) + \frac{1}{4} \left(\frac{1}{4}b - c \right) \\ &= \frac{1}{4} \left(\frac{3}{4}b \right) + \frac{3}{4} \left(\frac{1}{4}b \right) = w_N. \end{aligned} \quad (\text{A16})$$

Solving, we find the values of b and c for which $\Delta p = 0$, namely, $c/b = 1/4$. This means that, given the assumed distribution of A's and N's in the two groups, the population frequency of A's will be stationary if the cost of performing the altruistic act is one fourth the benefit. If we add the further requirement that the size of the total population be constant, so $w_A = 1 = w_N$ and assuming $\beta_o = 0$, we have $b = 8/3$ and $c = 2/3$.

An equivalent method is simply to use equation (A14), along with the facts that $\text{var}(p_{ij}) = p_j(1 - p_j) = 3/16$ for $j = 1, 2$ and $\text{var}(p_j) = 1/16$, so, using (A14), we have from the Price equation 4.11

$$w\Delta p = (b - c)/16 - 3c/16,$$

which, for $w \neq 0$, gives $c/b = 1/4$ as a condition for $\Delta p = 0$, reproducing the above result.

Further, reproducing the condition for the stationarity of p , given by (4.17), and using the empirical values from the example gives us:

$$\frac{c}{b} = F = \frac{\text{var}(p_j)}{\text{var}(p_{ij}) + \text{var}(p_j)} = (1/16)/(3/16 + 1/16) = \frac{1}{4}, \quad (\text{A17})$$

as we would expect.

Thus, for values of $b > 4c$, the frequency of the altruistic trait will grow, exceeding one half in the next period. This occurs because the relative size of the more altruistic group grows, offsetting the decline in the fraction of altruists in each group.

The proliferation of the group-beneficial but individually-costly trait is explained by the group structure of the population, which accounts for the fact that altruists tend to be paired with other altruists more frequently than the population average, despite random pairing within groups. Thus, the probability of meeting an altruist conditional on being an altruist is

$$P(A|A) = p_1^2 + p_2^2 = 5/8.$$

This follows from the fact that a fraction p_1 of all A's are in group 1 in which the likelihood of being paired with an A is p_1 , and analogously for the fraction p_2 of A's in group 2. Non-altruists meet altruists with probability

$$P(A|N) = (1 - p_1)p_1 + (1 - p_2)p_2 = 3/8.$$

The difference between these two conditional probabilities, $1/4$, is a measure of the degree of positive assortment in this population, and it is the expected advantage enjoyed by the altruistic trait by dint of its favored distribution among groups. Thus, reproducing (4.15) and (4.17), we have an equivalent way of representing (A17):

$$\frac{c}{b} = P(A|A) - P(A|N) = \frac{1}{4}. \quad (\text{A18})$$

A6 Pleistocene Warfare

How are we to estimate the fitness advantage of the winners and the disadvantages of the losers? There are cases in the ethnographic record of virtually all members of a band being killed in a single decisive conflict, as when in 1849 a group of 52 Assiniboin encountered a much larger Blackfoot

war party and was annihilated (Keeley 1996):194. But, much more common are accounts of on-going low-level conflicts in which a few fatalities occur. Losing a conflict may reduce reproductive success in two ways: those killed in conflict leave no or fewer offspring; and those who survive the conflict may have reduced reproductive success either because they are displaced to less favorable environments, or they are assimilated by the winners or some other group in which they occupy socially inferior positions, at least for a few generations. Keeley (1996):198 reports the percentage gains or losses of territory among five hunter-gatherer groups (Walbiri, Ingalik, Wappo, Kutchin, and Comox) averaging 16 percent per 25 years. Gains and losses among pastoralists and horticulturalists are considerably greater.

Suppose groups compete in every generation and one group is the winner, the other the loser, and further that due to the carrying capacity of the sites they jointly occupy, the change in population from one generation to the next is the proportional to change in territory each commands minus the losses due to conflict. If, on the basis of the above estimates, we conclude that those lost in combat represent 0.005 of the adult population per year, that deaths are four times as numerous among losers as among winners, and that groups are initially of the same size, then losers lose 0.008 of their population from warfare annually, and winners lose 0.002. Ignoring the possibly considerable indirect loss of life among the losers due to hazardous relocation or subjugation by winners, and abstracting from territorial losses and gains, the winners would thus lose 5 percent per (25-year) generation and the losers would lose 22 percent.

What would be the impact on expected deme size of these contests taking place every generation? Let δ be the difference in expected deme size conditional on the deme being a winner or loser. Using the above data we estimate under two assumptions: δ^0 includes both the change in territory and the mortalities occasioned by the conflict, while δ^1 takes account of territorial changes only. In the first case the expected size of the winning deme after a generation (25 years) is $(1.15)(0.95)$ and of the losing deme is $(0.85)(0.78)$ so the difference, $\delta^0 = 0.43$. Ignoring wartime mortality differences the same calculation $\delta^1 = 0.3$. A contest that creates a per-generation difference in expected deme size of conditional on winning or losing is equivalent to a contest resulting in either the elimination or doubling of the deme occurring each generation with probability δ^2 , which is thus our estimates of κ (namely, 0.215 and 0.15, the latter ignoring wartime deaths) This suggests that continuous low level conflict might have effects similar

to a single decisive conflict (the losers being annihilated the winning deme doubling in size) occurring at the rate of once every $4.7 = 1/0.215$ or $6.7 = 1/0.15$ generations. Figure 8.1 is based on the lesser of the two estimates of κ (rounded), such that decisive conflicts take place every 7 generations (i.e. $\kappa = 0.142$).

A7 Social Emotions

We have

$$a_i^{\text{Nash}} = 1 - \frac{c\chi\xi_j + 2v_j\xi_i}{\lambda_j(4v_1v_2 - c^2\chi^2)}. \quad (\text{A19})$$

From (A19) and the definition of ξ_i and ξ_j we calculate that

$$\frac{da_i^{\text{Nash}}}{d\gamma_i} = \frac{2cv_j}{\lambda_j(4v_1v_2 - c^2\chi^2)^2}, \quad (\text{A20})$$

which is positive, so an increase in guilt increases i 's contribution in the Nash equilibrium. Also,

$$\frac{da_i^{\text{Nash}}}{dv_i} = \frac{4v_j(2v_j\xi_i + c\chi\xi_j)}{\lambda_j(4v_1v_2 - c^2\chi^2)^2}, \quad (\text{A21})$$

which is also positive, so an increase in i 's shame parameter increases his contribution in the Nash equilibrium. We also have

$$\frac{da_i^{\text{Nash}}}{d\lambda_j} = \frac{c(\chi\xi_j + 2v_j(1 - \gamma_i - \chi))}{\lambda_j^2(4v_1v_2 - c^2\chi^2)} \quad (\text{A22})$$

so an increase in j 's level of reciprocity leads to an increase in i 's contribution in the Nash equilibrium.

We can indeed show that under favorable conditions, and increase in an increased sense of shame may enhance ones own payoffs: i.e., $d\pi_i^{\text{Nash}}/dv_i > 0$. For ease of exposition, after taking this derivative, we will set $v_i = v_j = v$ and $\lambda_i = \lambda_j = \lambda$ for ease of exposition, and then let $v = c\chi/2 + \epsilon$ for small $\epsilon > 0$. Note that this is possible provided ξ_1 and ξ_2 are suitable small, so that $0 < \alpha_i^*, \alpha_j^* < 1$ and the stability conditions remain satisfied. In this case, algebraic manipulation shows that for sufficiently small ϵ ,

$$\text{sign} \frac{d\pi_i^{\text{Nash}}}{dv_i} = \text{sign} 2c^3\lambda\chi^3(2\lambda - c(2 - \gamma_1 - \gamma_2 - 2\chi))^2, \quad (\text{A23})$$

which is positive.

Table of Symbols

| Symbol | Chapter | Meaning |
|-----------------|---------|--|
| n | | Number of individuals |
| r | 4 | Genetic Relatedness |
| δ | | Continuation Probability |
| D | 4 | Duration of an Interaction |
| v | 4 | Value of Cooperating in Repeated Interaction |
| k | 4 | Periods of Defection Following A Defection |
| N | 4,5 | Number of Groups |
| d | 4 | Number of Stage Game Repetitions |
| t | 4,5 | Cooperates if t Members Cooperated Last Period |
| ϵ | | Execution or Perception Error Rate |
| v_g | 4 | Value of Being in Good Standing in a Population of Cooperators |
| v_b | 4 | Value of Being in Bad Standing |
| q | 4 | Quality of Signal |
| i, j | | Indices for Individuals and/or Groups |
| ∂_{ij} | 4 | Probability Individual i in Group j is an Altruist |
| w_{ij} | 4 | Fitness of Individual i in Group j |
| w | 4 | Average Fitness |
| w_j | 4 | Average Group j Fitness |
| p_j | 4 | Fraction of Group j who are Altruists |
| β_o | 4,9 | Baseline Replication Rate |
| β_g | 4 | Effect of p_j on w_{ij} |
| β_i | 4 | Effect of p_{ij} on w_{ij} |
| β_G | 4 | $\beta_i + \beta_g$ |
| F | 4 | Wright's Variance Ratio |
| λ_A | 4 | Marginal Effect of Altruism on Group Survival |
| γ | 4,9 | Rate of Conversion of Altruists to Selfish Types by Socialization |
| t_g | 5 | Focal Rule Minimum Cooperate |
| c_p | 5,6 | Cost of Punishing |
| m | 6,7,8,9 | Migration Rate |
| w_o | 6 | Fitness in pool |

| Symbol | Chapter | Meaning |
|-------------------------|---------|--|
| ϕ | 6 | Fraction of Population in Pool |
| s | 6,9 | Fitness Cost |
| σ, σ_s | 6 | Average and Selfish Shirking Rates |
| f^s, f^c, f^r | 6 | Frequency of Selfish, Cooperator, and Reciprocator |
| $\lambda(1 - \sigma_s)$ | 6 | Cost of Working |
| $g(\sigma_s)$ | 6 | Cost of Effort |
| κ | 7 | Conflict Probability |
| λ | 7 | Deme Survival Probability |
| τ | 7 | Reproductive Leveling |
| ω | 7 | Gains/Losses from Conflict |
| ζ | 7 | Segmentation Rate |
| Δ | 8 | Probability Hostile Interaction Results in War |
| λ | 8 | Probability of Winning a Conflict |
| h^{ij} | 8 | Probability that an Interaction between Groups i and j is Hostile |
| f_i^T | 8 | Fraction Tolerant in Group i |
| f_e | 8 | Fraction of Population Eliminated From Losing Group |
| t, u | 9 | Fitness Costs and Benefits |
| f_A | 9 | Fraction of Altruists |
| η | 9 | Imitation Rate |
| $P(\cdot)$ | 9 | Probability |
| p_A, p_S | 9 | Frequency of a -Individuals of Phenotype A and S |
| s_{\min}, s_{\max} | 9 | Maximum and Minimum Fitness Costs |
| a | 10 | Contribution to a Public Good |
| χ | 10 | Efficiency of Public Good |
| μ_{ij} | 10 | Penalty |
| γ | 10 | Guilt |
| ρ | 10 | i 's Degree of Reciprocity |
| β_{ij} | 10 | i 's Valuation of Material Payoff Received by j |
| v_i | 10 | i 's Susceptibility to Shame |
| γ_i | 10 | i 's Susceptibility to Guilt |
| ψ_i | 10 | i 's Unconditional Generosity or Spite Towards Others |

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