CULTURAL TRANSMISSION, DISPROPORTIONATE PRIOR EXPOSURE, AND THE EVOLUTION OF COOPERATION

NOAH P. MARK
Stanford University

Why is human cooperation so prevalent? This paper identifies one potential reason for the prevalence of cooperation in human populations. People acquire social behaviors—cooperative or exploitative—from other people through cultural transmission. There is a previously unrecognized characteristic of cultural transmission—disproportionate prior exposure—that creates an evolutionary force toward cooperation: Individuals who have acquired a cooperative or exploitative behavior through cultural transmission tend disproportionately to have been targets of that behavior prior to acquiring it. Thus, individuals who have acquired cooperative behavior through cultural transmission have disproportionately benefited from the cooperative behavior of others, while individuals who have acquired exploitative behavior through cultural transmission have disproportionately been hurt by the exploitative behavior of others. Because the benefits of being a target of cooperative behavior tend to make a person more influential as a behavioral model (i.e., tend to increase that person's cultural fitness), the disproportionate prior exposure inherent in cultural transmission creates an evolutionary force toward cooperation. A simple formal analysis reveals an evolutionary force toward cooperation under a minimal set of conditions previously believed to make the evolution of cooperation impossible—one-shot prisoner's dilemmas with no option to exit played between strangers in a large, randomly mixing population. Attention to this evolutionary force is likely to advance our understanding of the prevalence of cooperation.

COOPERATION is understood to be the basis for human societies (Axelrod 1984; Carneiro 1998; Durkheim [1893] 1984; Lenski, Nolan, and Lenski [1970] 1995; Spencer [1882] 1916). In economic, political, civic, and private life, people interact for their mutual benefit; they exchange goods, services, and information, informally as well as in formal economies and illegal economies. Business organizations and their products are consequences of cooperation. People cooperate to wage war, to create peace, and to honor gods. People even cooperate to produce healthy, productive, and *cooperative* people (Clinton 1996; Folbre 1994). I identify one potential reason for the prevalence of cooperation in human populations.

Cooperation receives attention from social scientists not only because of its essential role in shaping our social world, but because social dilemmas that would seem to deter cooperation are pervasive. Although two individuals can often improve their welfare through cooperation, in many situations each individual could improve his or her own welfare even more by accepting the help of the other without returning the favor. There-

Direct all correspondence to Noah P. Mark, Department of Sociology, Stanford University, Stanford, CA 94305-2047 (nmark@stanford.edu). I thank Paul Allison, Robert Axelrod, Paula England, Mark Granovetter, Michael Hechter, Douglas Heckathorn, Michael Macy, Douglas McAdam, Miller McPherson, James Montgomery, Susan Olzak, Cecilia Ridgeway, Nobuyuki Takahashi, participants in the culture workshop at Stanford University, and the Editors, a Deputy Editor, and reviewers at *ASR* for helpful comments and discussion.

fore, scholars have found cooperation a challenge to explain.

Although attempts to explain cooperation have been dominated by rational choice (Luce and Raiffa 1957), backward-looking learning (Macy 1991), and genetic evolutionary approaches (Axelrod 1984; Trivers 1971), some argue that recognizing the human capacity for cultural transmission is essential to developing an adequate explanation for human cooperation (Allison 1992a, 1992b; Boyd and Richerson 1982; Campbell 1975; Macy 1996; Simon 1990). Following these proponents of a cultural explanation, I call attention to a fundamental but previously overlooked characteristic of cultural transmission that distinguishes it from the prevailing approaches and that has important implications for the evolution of cooperation: Individuals who have acquired a social behavior—cooperative or exploitative—through cultural transmission tend disproportionately to have been targets of that behavior prior to adopting it. This characteristic of cultural transmission—*disproportionate prior exposure*—creates a cultural evolutionary force toward cooperation.

To illustrate how cultural transmission creates this evolutionary force and to demonstrate the potential power of a cultural evolutionary explanation for cooperation, I conduct a formal theoretical analysis of the cultural evolution of cooperation under conditions thought to make the evolution of cooperation impossible: Individuals are drawn from a large population and encounter randomly selected strangers in one-shot prisoner's dilemmas with no option to exit. While cultural transmission is not the only process that determines people's behaviors, the results of this analysis suggest that explicit recognition of the role of culture in the evolution of cooperation will be important to developing a more robust explanation for cooperation and to understanding the prevalence of this type of behavior.

THE PRISONER'S DILEMMA

When individuals have the opportunity to benefit themselves and each other through cooperation, there is often a tension between individual and collective interests. The prisoner's dilemma formalizes this tension and is used widely to facilitate the study of cooperation (e.g., Axelrod 1984; Macy and Skvoretz 1998; Trivers 1971). Figure 1 shows a payoff matrix that captures the essential characteristics of a prisoner's dilemma (Luce and Raiffa 1957). Each of two actors has the opportunity to cooperate with or defect against the other actor. Mutual cooperation produces the best collective outcome (2 points for each actor), and mutual defection produces the worst collective outcome (just 1 point for each actor). However, given either action by a person's partner, the person's own payoff is higher if she or he defects than if she or he cooperates. Therefore, defection is expected, and cooperation is hard to explain.

		ACTOR B	
		Cooperate	Defect
ACTOR A	Cooperate	2, 2	0, 3
	Defect	3, 0	1, 1

Figure 1. Example of a Prisoner's Dilemma Reward Structure

WHY A MORE ROBUST EXPLANATION IS NEEDED

Cooperation is prevalent, but the prevailing theoretical approaches predict that cooperation occurs only under special circumstances. The prevalence of cooperation is revealed in naturally occurring social phenomena, especially phenomena involving forms of social organization that rest on cooperation, such as families, states, armies, firms, and educational institutions (Boyd and Richerson 1982; Campbell 1975). The prevalence of cooperation is also indicated by laboratory research (Frank, Gilovich, and Regan 1993). Cooperation even occurs despite active attempts to stop it, for example, cooperation between enemy soldiers to reduce casualties on both sides (Ashworth 1980, cited in Axelrod 1984), cooperation between cheating students, cooperation to illegally transport people from one country to another, illegal cooperation between firms (i.e., "anti-competitive" practices and agreements), and many other forms of organized crime.

THE PREVAILING VIEW: COOPERATION OCCURS ONLY UNDER SPECIAL CIRCUMSTANCES

Despite the prevalence of cooperation, the three major theoretical approaches adopted by scholars who seek to explain cooperation—utility/rational choice theory (Luce and Raiffa 1957), backward-looking learning (Macy 1991), and genetic evolutionary models (Axelrod 1984; Trivers 1971)—predict defection in their most basic form. In a large population in which individuals are randomly paired in one-shot games with no option to exit, each of these approaches predicts that cooperation will not occur or will be rare and fleeting. This prediction that little to no cooperation will occur under this minimal set of conditions has provided the baseline for comparison and evaluation of potential explanations for cooperation (Axelrod 1984; Luce and Raiffa 1957; Macy 1991; Trivers 1971). The prevailing strategy for the development of such explanations has been identification of special circumstances that are predicted to promote cooperation.

Research shows that iteration of the prisoner's dilemma game between the same two players promotes cooperation (Luce and Raiffa 1957). If the prisoner's dilemma game is iterated, cooperation can evolve in a large population if there is clustering in the social structure such that cooperators tend to encounter cooperators and defectors tend to encounter defectors (Axelrod 1984) or if the benefit that defectors derive from defection is negatively related to the number of defectors in the population (Peck and Feldman 1986). Frank (1988) and Orbell and Dawes (1991,1993) have identified other conditions that make the evolution of cooperation possible even if the above identified conditions are not met. It is possible for cooperation to evolve between strangers in one-shot games in large populations with little or no internal clustering when an option to exit the game is combined with an ability for cooperators to detect defectors (Cosmides 1989; Frank 1988; Frank et al. 1993; Macy and Skvoretz 1998; Mealey, Daood, and Krage 1996) or with a tendency for actors to project their own intention onto their partners (Orbell and Dawes 1991,1993). Sober and Wilson (1998) show that cooperation between strangers in one-shot prisoner's dilemmas with no option to exit can evolve given sufficient clustering in the social structure.

This impressive literature shows convincingly that cooperation is not an anomaly from a rational choice, backward-looking learning, or genetic evolutionary perspective. Yet, because each of the explanations offered from these perspectives rests on a special set of circumstances, and because each of these explanations predicts the extinction of cooperation when players are strangers, randomly selected from a large population, who meet in a one-shot game with no option to exit, none of these explanations offers an ideal account for the *prevalence* of cooperation in human populations. Noting this important limitation, some scholars have turned to the uniquely high human capacity for cultural transmission as a potential explanation for the prevalence of human cooperation (Allison 1992a, 1992b; Boyd and Richerson 1982; Campbell 1975; Macy 1996; Simon 1990).

CULTURAL EXPLANATIONS FOR COOPERATION

CULTURAL TRANSMISSION. Cultural transmission is the transmission of characteristics (e.g., behavioral characteristics, beliefs, opinions, tastes) between individuals through imitation or instruction (Boyd and Richerson 1985; Cavalli-Sforza et al. 1982; Macy 1996).[1] Thus, what makes a characteristic

[1] Some students of culture emphasize that cultural transmission is the transmission of information that affects an individual's characteristics rather than the transmission of the characteristics directly (Boyd and Richerson 1985; Lenski et al. [1970] 1995; Lumsden and Wilson 1981; Wilson 1998). Lenski et al. ([1970] 1995) further limit the definition of cultural transmission to transmission of information through symbolic communication (i.e., transmission through simple imitation is not considered cultural). Although

cultural is not the nature of the characteristic itself, but how individuals acquire the characteristic. For example, the language a person speaks is a cultural characteristic because people learn language from other people they interact with. The language a bee uses to communicate however, is not a cultural characteristic but a genetic one, because bees acquire their language through their genes, not by interacting with other bees from whom they learn the language (Lenski et al. [1970] 1995). In addition to the language a person speaks, technological knowledge, religion, occupation, leisure activity, beliefs, values, opinions are all commonly understood to be characteristics that humans acquire through cultural transmission.

Because the process of *transmission*, essential to both cultural and genetic explanations for cooperation, clearly distinguishes these theoretical approaches from rational choice and backward-looking learning, differences between genetic and cultural transmission and between the evolutionary forces produced by these modes of transmission are given special attention by cultural evolutionary theorists.

PAYING ATTENTION TO MODE OF TRANSMISSION. Although the idea that people learn most behaviors from other people is accepted by many social scientists (Bandura 1986; Harris and Johnson 2000; Lenski et al. [1970] 1995), some scholars argue that genetic evolutionary models capture the essentials of a cultural evolutionary process sufficiently well for their analysis to produce valuable theoretical knowledge (Axelrod 1986; Macy and Skvoretz 1998). Others advocate for explicit attention to the fact that the mode of transmission through which most human behaviors are acquired is cultural (Allison 1992a, 1992b; Boyd and Richerson 1982; Cavalli-Sforza and Feldman 1981; Macy 1996; Simon 1990). The structures through which cultural transmission occurs differ from those through which genetic transmission occurs (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981). A person acquires genetic traits at conception from two parents and never acquires another genetic trait; however, a person can acquire cultural traits throughout his or her life from a large number of other individuals, including one's genetic parents, other individuals older or younger than oneself, and individuals of one's own generation. Structures of cultural and genetic transmission also differ in that the traits a person acquires through genetic transmission do not change during the course of the person's life, but the traits acquired through cultural transmission *can* (Macy 1996). For example, some people who used to wear jackets with 20 zippers don't wear them anymore. Because cultural transmission occurs through structures that differ from the structures through which genetic transmission occurs, cultural transmission can generate evolutionary forces that differ from those generated by genetic transmission (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981). That is, a behavior that would not increase in prevalence if transmitted genetically could increase in prevalence if transmitted culturally (e.g., celibacy, sky diving [Cavalli-Sforza and Feldman 1981]).

HOW CULTURAL TRANSMISSION PROMOTES COOPERATION. Each of the cultural explanations for the evolution of cooperation offered by Boyd and Richerson (1982), Allison (1992a), and Macy (1996) identifies some way in which the structures of cultural and genetic transmission differ and shows that this aspect of the structure of cultural transmission creates an evolutionary force toward cooperation. Boyd and Richerson (1982) and Allison (1992a) build on the fact that an individual may acquire cultural characteristics from more than two individuals. Under some conditions, this property of cultural transmission creates the possibility for group selection to produce a strong evolutionary force toward cooperation (Boyd and Richerson 1982). Allison (1992a), also noting that a person can have more than two cultural parents, shows that levels of cultural relatedness within a population can be substantially higher than levels of genetic relatedness. Extending arguments from Hamilton's (1964) genetic evolutionary theory of kinship altruism to the process of cultural evolution, Allison

these distinctions are important for many analyses, they are not relevant to the simple analysis presented here. I model cultural transmission as the simple imitation of the two distinct behaviors available in a prisoner's dilemma—cooperation and defection.

(1992a) shows that these relatively high levels of cultural relatedness make possible levels of cooperation that are higher than those generated by genetic evolution. Macy (1996) shows that cultural transmission can promote the evolution of cooperation when actors encounter others in iterated prisoner's dilemmas because, unlike genetically acquired strategies of play, which remain fixed throughout an actor's life, culturally acquired strategies of play can change as one gradually adopts a strategy similar to the strategy of one's interaction partner.[2]

Although cultural explanations advance our understanding of cooperation, as is the case with rational choice, backward-looking learning, and genetic evolutionary explanations, there are important limitations on the sets of circumstances under which these previous cultural explanations predict cooperation. These explanations predict the evolution of cooperation only when exogenous factors cause cooperation to be prevalent in multiple subpopulations (Boyd and Richerson 1982), levels of contact between subpopulations are low (Allison 1992a; Boyd and Richerson 1982), interaction within prisoner's dilemmas is iterated (Macy 1996), actors can select interaction partners (Allison 1992b), or no culturally transmissible exploitative behavior has been introduced into the population (Simon 1990).

Room for Improvement

Although the achievements of rational choice (Luce and Raiffa 1957), backward-looking learning (Macy 1991), genetic (Axelrod 1984; Trivers 1971), and cultural (Allison 1992a; Boyd and Richerson 1982; Macy 1996) explanations for cooperation are important, there is room for a more robust explanation. As stated above, there are important limitations on the circumstances under which previous explanations predict cooperation.[3] A robust explanation for cooperation (i.e., for cooperation with a randomly selected stranger in a one-shot game with no option to exit—behavior empirical research shows to be prevalent [Frank et al. 1993]) has yet to be achieved.

Macy and Skvoretz (1998) draw heavily on the literature identifying cooperation-promoting circumstances in an attempt to explain cooperation in one-shot prisoner's dilemmas. Their model provides actors with an option to exit, possibilities for projection and cheater-detection to evolve, and a clustered social structure. Even in the presence of these favorable circumstances, Macy and Skvoretz (1998) comment on the difficulty of explaining the evolution of cooperation:

> In certain conditions, cooperation between strangers can evolve. . . . A caveat is in order, however. We do not claim that this finding is robust across other specifications of the chromosome structure or network structure in this experiment. On the contrary, the evolution of cooperation between strangers is exceedingly fragile. It is trivial to introduce changes in the player architecture and social structure that will preclude cooperation outside the neighborhood, regardless of the exit payoff. Our cumulative research experience shows overwhelmingly how extraordinarily difficult it is for cooperation between strangers to survive the relentless evolutionary pressure to "hit and run." The difficulty of evolving cooperation in a one-shot game makes this demonstration of a logically feasible evolutionary path all the more noteworthy. (Pp. 650–51)

A CULTURAL EXPLANATION FOR COOPERATION BASED ON DISPROPORTIONATE PRIOR EXPOSURE

A cultural explanation for the evolution of cooperation based on disproportionate prior exposure rests on three ideas that appear ex-

[2] See Allison (1992b) and Simon (1990) for discussions of other ways in which cultural transmission promotes the evolution of cooperation.

[3] My argument is not that the cooperation-promoting circumstances identified seem implausible, or even rare. Indeed, all of these circumstances are likely to have played roles in producing the cooperation observed in the natural world. Nevertheless, whether these circumstances in combination with previous explanations adequately account for the prevalence of human cooperation remains in question. For this reason, identification of a previously unrecognized characteristic of cultural transmission that creates an evolutionary force toward cooperation when none of the above cooperation-promoting circumstances is present is important.

plicitly or implicitly in past research. The first is the empirically substantiated assumption that people acquire cooperative and exploitative behaviors through cultural transmission. The second is a logical implication of the first: Individuals who have acquired a (cooperative or exploitative) behavior through cultural transmission were disproportionately exposed to that behavior prior to acquiring it. The third is the assumption, also supported by empirical research, that disproportionate prior exposure to the cooperative behavior of others increases one's cultural fitness, and disproportionate prior exposure to the exploitative behavior of others decreases one's cultural fitness.

CULTURAL TRANSMISSION OF COOPERATIVE AND EXPLOITATIVE BEHAVIOR

The idea that people acquire cooperative and exploitative behaviors through cultural transmission is central to some of the most promising explanations for cooperation (Allison 1992a, 1992b; Boyd and Richerson 1982; Campbell 1975; Macy 1996). Although the cultural transmission of cooperative and exploitative behavior in one-shot prisoner's dilemmas has not been explored empirically, empirical research does support the assumption that people learn cooperative and exploitative behaviors from other people. In addition to a large body of evidence that individuals acquire a wide variety of behaviors, beliefs, opinions, and tastes through cultural transmission (Bandura and Walters 1963; Boyd and Richerson 1985; Carley 1986; Cavalli-Sforza et al. 1982; Jacobs and Campbell 1961), research focusing on altruism suggests that altruistic and selfish behaviors are also acquired through cultural transmission (for a review, see Rushton 1980:94–109).[4] Experimental studies show that children exposed to an adult model who behaves altruistically (e.g., gives money to charity) behave more altruistically (e.g., give more money to charity) than do children exposed to a selfish adult model (Harris 1970, 1971; Lipscomb et al. 1982). Experimental studies also provide some evidence suggesting that children (Harris 1971) and young adults (Berkowitz and Daniels 1964) who were targets of altruistic behavior behave more altruistically toward third parties than do children and young adults who were not targets of altruistic behavior. Research on blood donation suggests that individuals who have received a blood transfusion or who know someone who has are more likely to give blood than are other individuals (Healy 2000; Lee, Piliavin, and Call 1999; Piliavin and Callero 1991). Complementing empirical findings on the cultural transmission of altruistic behavior, experimental research shows that children who observe an aggressive adult model will behave more aggressively than children not exposed to an aggressive model (Bandura and Walters 1963).[5]

[4] Research on altruism is especially relevant to the empirical basis for my argument because cooperation in a one-shot prisoner's dilemma, the behavior I explore, is a form of altruism. Considering a precise definition of altruism clarifies this connection. Because I develop a cultural evolutionary argument, a cultural evolutionary definition of altruism is appropriate. This definition, which is the cultural analog of the standard genetic evolutionary definition of altruism (Boorman and Levitt 1980:12), rests on the concept of cultural fitness, the cultural analogue of genetic fitness (p. 12). Boyd and Richerson (1985:255) define an individual's "cultural fitness . . . [as] the probability that [that] . . . individual . . . becomes a model" for another individual (also see Allison 1992a; Macy 1996; Macy and Skvoretz 1998). A behavior is defined as altruistic if person A's performance of that behavior increases the cultural fitness of person B, but lowers the cultural fitness of person A. Notice that while conditional cooperation in an iterated prisoner's dilemma, also known as reciprocal altruism (Trivers 1971) and achievable through the strategy labeled tit-for-tat (Axelrod 1984), does not meet the above definition of altruism, cooperation with a stranger in a one-shot prisoner's dilemma with no option to exit in a large, randomly mixing population does. In the one-shot game, regardless of one's partner's behavior, cooperating benefits one's partner at one's own expense.

[5] The assumption that people acquire cooperative and exploitative behaviors through cultural transmission is not only suggested by empirical evidence, but has a logical basis in genetic evolutionary theory. The capacity in humans (and in some other animal species) to acquire behaviors through cultural transmission is understood to

Of course, cultural transmission does not occur every time a person is exposed to a behavior that is different from one's own. In fact, studies exploring social influence within iterated prisoner's dilemmas find that competitive individuals paired with cooperative individuals rarely adopt their partners' cooperative strategy (Kelley and Stahelski 1970a, 1970b). While cooperative individuals paired with competitive individuals tend to adopt their partner's competitive strategy for the duration of their interaction with that partner, when subsequently paired with cooperative individuals, these initially cooperative individuals returned to cooperative behavior. Thus, although there is strong evidence that cultural transmission does occur, there are circumstances that limit the tendency toward cultural transmission.[6]

Cultural Transmission Implies Disproportionate Prior Exposure

Following the strategy employed by Boyd and Richerson (1982), Allison (1992a), and Macy (1996), I consider the logical implications of a difference between the structures of genetic transmission and cultural transmission. While cultural transmission occurs through social interaction between the transmitter and the receiver of the characteristic transmitted,[7] genetic transmission does not.[8] The empirically substantiated assumption that cultural transmission occurs through social interaction between transmitter and receiver implies that *individuals who have acquired a characteristic through cultural transmission were disproportionately exposed to that characteristic prior to acquiring it.* As examples below reveal, this claim is neither strong nor controversial and may even be considered a statement of the obvious. I present this claim because it has an important and previously unrecognized logical implication for the evolution of cooperation.

I begin with examples of disproportionate prior exposure that do not explicitly involve cooperative or exploitative behaviors to help isolate the logic of how cultural transmission generates disproportionate prior exposure. The languages people speak provide a useful example. People fluent in English were disproportionately exposed to English (i.e., spoken to in English) prior to becoming fluent. To see this, imagine a comparison between all people fluent in English and all people not fluent in English. Probably every person who is fluent in English was spoken to in English before acquiring fluency.[9] However, many people who are not fluent in English have never been spoken to in English. In other words, 100 percent of English speakers have had prior exposure to English, but substantially less than 100 percent of non-English speakers have prior exposure to English.[10] Any other natural spoken human

have been selected for in a genetic evolutionary process (Boyd and Richerson 1985; Flinn and Alexander 1982).

[6] Future empirical research should explore the potential for cultural transmission in one-shot prisoner's dilemmas. Future theoretical research should explore how different tendencies toward behavioral stability and susceptibility to social influence promote or impede the evolution of cooperation and how cultural transmission might (or might not) promote the evolution of cooperation when individuals meet in situations that differ from one-shot prisoner's dilemmas.

[7] Cultural transmission, as defined above, can occur through processes other than social interaction. One such process is communication via the mass media. Another is direct observation of individuals with whom one is not interacting. Nevertheless, social interaction (between parents and children, siblings, friends, teachers and students, and coworkers) continues to be an extremely important avenue for cultural transmission.

[8] While genetic transmission often involves social interaction in the form of mating behavior, this social interaction is not between the transmitter and the receiver of the characteristic transmitted. This social interaction involves only parents (i.e., transmitters of the characteristic) as interactants; the genetic offspring (i.e., the receivers of the genetic characteristic) are not participants in the social interaction that genetically transmits characteristics to them.

[9] The qualifier "probably" is conservative, but I do not know for certain that there is not some very talented person who acquired fluency in English purely through written material, language tapes, and the mass media.

[10] Alternatively, the reader can replace the dichotomous definition of the variable exposure employed above with a continuous definition (e.g., amount of time spoken to in English) to see the same relationship: The average amount of

language as well as almost any other cultural characteristic (e.g., praying, driving a car) provides a similar example.[11]

Although cultural transmission of almost any characteristic produces disproportionate prior exposure to that characteristic,[12] the importance of this implication here is limited to cases in which the characteristic in question is a cooperative or exploitative behavior. Individuals who have acquired a social behavior—cooperative or exploitative—through cultural transmission were disproportionately exposed to that behavior prior to acquiring it. As long as some of the exposure people have to cooperative and exploitative behaviors occurs in social interactions in which they are targets of these behaviors and as long as this exposure has the potential of resulting in cultural transmission,[13] *individuals who have acquired a social behavior—cooperative or exploitative—through cultural transmission were disproportionately targets of that behavior prior to acquiring it.*

Although past work does not explicitly call attention to the fact that cultural transmission logically implies disproportionate prior exposure, empirical (and theoretical[14]) studies illustrate this logical connection. For example, in an experimental study by Harris (1970), of the 103 subjects who behaved altruistically, 88 (85 percent) were either targets of altruism (42) or third-party witnesses to altruism (46) prior to behaving altruistically. However, of the 65 subjects who did not behave altruistically, only 24 (40 percent) were either targets of altruism (14) or third-party witnesses to altruism (10) prior to behaving selfishly.[15]

---

time people fluent in English were spoken to in English prior to becoming fluent is greater than the average amount of time people not fluent in English have been spoken to in English.

[11] A number of special cases in which cultural transmission does not imply disproportionate prior exposure can probably be identified. For example, if it is normative for only males to initiate heterosexual relationships, then the individuals who have the characteristic of initiating heterosexual relationships (i.e., males) will have been exposed to such initiations less than the individuals who do not have the characteristic (i.e., females).

[12] A reader may wonder how a process (e.g., cultural transmission) could "produce" a pattern involving exposure that occurs prior to the process that produces the pattern. Accordingly, it is worth noting that the way cultural transmission produces disproportionate prior exposure is completely consistent with temporal rules of causality. The first event is exposure to a culturally transmissible characteristic (possibly a behavior). Some individuals are exposed while others are not. The second event is acquisition of the characteristic. Those exposed to the characteristic may acquire the characteristic through cultural transmission, but those not exposed will not. Thus, those who ultimately hold the characteristic were disproportionately exposed to the characteristic prior to acquiring it. That is, *all* of the individuals who hold the characteristic were exposed to it prior to acquiring it; however, only *some* (and possibly none) of the individuals who do not hold the characteristic have been exposed to it. In other words, cultural transmission produces a relationship between individuals' initial influential exposure to a characteristic (exposure that occurs prior to acquisition of the characteristic) and the characteristic individuals eventually acquire and hold. I call this relationship *disproportionate prior exposure.*

[13] These qualifications will be met in any natural setting. Nevertheless, the logical necessity of these qualifications calls attention to the difference between influential exposure to cooperative and exploitative behaviors as a target of those behaviors and influential exposure to cooperative and exploitative behaviors as a third-party observer of those behaviors. For example, if *all* exposure to cooperative and exploitative behaviors occurred through the mass media, then the disproportionate prior exposure implied by cultural transmission would not imply disproportionate prior exposure to these behaviors as targets of these behaviors. Future research should explore potential attenuation of the effect of disproportionate prior exposure by third-party exposure.

[14] Careful consideration of the cultural model developed by Macy and Skvoretz (1998) reveals not only that cultural transmission implies disproportionate prior exposure, but how this idea in combination with the idea that the benefits one acquires in social interaction affects one's cultural fitness (see definition below) could create an evolutionary force toward cooperation. (Note that although Macy and Skvoretz [1998] do not identify their model as a cultural evolutionary model but as a general evolutionary model, for the purpose of this paper I identify their model as cultural because actors acquire characteristics by interacting with other actors who already have those characteristics.)

[15] Given that there were 28 subjects in each of

Note that genetic transmission does not disproportionately expose a person to a behavior prior to the person's acquisition of the behavior (or more precisely, prior to the person's acquisition of the gene or genes that determine or influence that behavior). By the time an individual is a target of any social behavior, that individual's genetic characteristics have already been determined.[16] This fact is reflected in genetic models of the evolution of cooperation (Axelrod 1984,1997a; Macy 1996; Peck and Feldman 1986).[17]

Benefits Acquired in Social Interaction Positively Affect Cultural Fitness

The third idea on which the proposed explanation rests is that the benefits one acquires in social interaction with one individual (e.g., in a prisoner's dilemma) may positively affect the probability that one will be imitated by *some other individual* [18] at some future time (i.e., may positively affect one's cultural fitness; see Allison 1992b; Boyd and Richerson 1985:255; Macy and Skvoretz 1998). For example, acquiring benefits from one person may increase one's wealth or status, thus increasing one's attractiveness to others as a cultural model (Rogers and Shoemaker 1971; Tarde [1890] 1962).[19]

Empirical research indicates that characteristics of an individual, including such characteristics as wealth and status, affect the probability that the individual's behaviors will be imitated by others (for reviews, see Boyd and Richerson 1985, chap. 8; Rushton 1980:103–105). Lefkowitz, Blake, and Mouton (1955) find that more pedestrians imitate a model's violation of a "don't walk" signal when the model is dressed in a freshly pressed suit, tie, and shined shoes than when the model is dressed in scuffed shoes, soiled and patched pants, and an unpressed denim shirt. Bandura, Ross, and Ross (1963) find that a child is more likely to imitate a model who possesses rewarding power than a model who does not.[20] Eisenberg-Berg and Geisheker (1979) find that children exposed to a competent altruistic model behave more altruistically than do children exposed to an incompetent altruistic model (or to a selfish model). Studies of naturally occurring cul-

the experiment's six conditions, these numbers can be calculated from the percentages reported by Harris (1970) in her Table 3.

[16] Accordingly, the only way cooperation can evolve under genetic transmission is if individuals who already are cooperators (i.e., who already acquired the "cooperator gene" or genes) are disproportionately targets of the cooperative behaviors of others. Selective cooperation is one of the best known ways that individuals who have acquired a cooperative behavior through genetic transmission can disproportionately be targets of the cooperative behaviors of others. Such selectivity is the basis for the genetic theory of kinship altruism (Hamilton 1964). Under this theory, altruists were disproportionately exposed to altruism in the past because their parents and other kin behaved more altruistically toward them than toward other individuals.

[17] Analyses of other genetic evolutionary models limit consideration to a single generation (Frank 1988; Kollock 1993). These analyses implicitly reflect the fact that genetic transmission does not produce disproportionate prior exposure.

[18] As addressed in greater detail below, this assumption is essential to the cultural explanation for cooperation I develop here. If the benefits received in social interaction with one individual affect the probability that one will be imitated *only by the person from whom one received those benefits*, cooperation will not evolve under the very hostile conditions explored here. Nevertheless, the promise of a cultural explanation for the evolution of cooperation based on disproportionate prior exposure is suggested by the fact that many (and possibly most) benefits that an individual receives in social interaction with one individual (e.g., food, property, money, training, self-esteem) affect characteristics (e.g., health, wealth, status, competence, displays of confidence) that can be observed by many other individuals.

[19] Scholars argue that a tendency to imitate individuals who appear to be more successful is likely to have been adaptive and selected for in a genetic evolutionary process (Boyd and Richerson 1985; Flinn and Alexander 1982).

[20] Two aspects of the experimental procedure indicate that these results are not explained by strategic behavior to secure rewards by pleasing the model with rewarding power. First, the models gave no indication that they desired to be imitated. Second, the models were not present to observe the child when the child had the opportunity to behave as the powerful or nonpowerful model had, and the child was aware of each model's absence.

tural change suggest that individuals of high status within a local social context are more influential as cultural models than are other individuals in the same local context (Boyd and Richerson 1985:245–47; Katz and Lazarsfeld 1955; Labov 1972,1980; Rogers and Shoemaker 1971).

EVOLUTIONARY FORCE TOWARD COOPERATION

Together, these ideas imply an evolutionary force toward cooperation. Because individuals who have acquired cooperative behavior through cultural transmission were disproportionately targets of cooperative behavior before, and as they learned to cooperate, cooperators tend disproportionately to have benefited from cooperation. Likewise, because individuals who have acquired exploitative behavior through cultural transmission were disproportionately targets of exploitative behavior before and as they learned to exploit, exploiters tend disproportionately to have been hurt by exploitation. If the benefits of being a target of cooperation increase one's cultural fitness and if the costs of being exploited decrease one's cultural fitness, there is an evolutionary force toward cooperation that is not present when behavior is acquired through mechanisms that do not produce disproportionate prior exposure (i.e., genetic transmission, rational calculation, and backward-looking learning).

A FORMAL ANALYSIS OF THE CULTURAL EVOLUTION OF COOPERATION

I now develop and analyze a simple formal model of the cultural evolution of cooperation and defection in prisoner's dilemmas. This model is not intended to be an accurate description of the numerous processes that have contributed to the evolution of cooperation in humans in the natural world. The model illustrates how the disproportionate prior exposure inherent to cultural transmission logically implies an evolutionary force toward cooperation under the conditions considered most hostile to the evolution of cooperation—one-shot prisoner's dilemmas between randomly selected strangers with no option to exit.

THE MODEL

I examine the case in which individuals are paired in the prisoner's dilemma reward structure represented by Figure 1. Each person is characterized by two variables: behavior and fitness level. Behavior has two values: cooperate and defect. A person may be a cooperator (C): A cooperator cooperates every time she or he interacts. Or a person may be a defector (D): A defector defects every time she or he interacts.[21] A person's fitness takes one of four levels: 0, 1, 2, 3.[22] A person's behavior and/or fitness level can change as a result of interactional outcomes as described below. The model is iterative, and each iteration, or round, is composed of 5 steps.

Step 1: Individuals paired. The model assumes that a process of unbiased random mixing assigns pairs of individuals to one-shot prisoner's dilemmas. Each round, each person in the system is paired with exactly one other person in the system.

Step 2: Comparison of fitness levels. Each person compares his or her partner's fitness level to his or her own and determines whether the partner's fitness level is higher than his or her own.

Step 3: Interaction and payoff determination. Cooperators cooperate, and defectors defect. Individuals' payoffs are determined by the prisoner's dilemma reward structure (see Figure 1). A cooperator whose partner defects gets 0 points; a defector whose partner defects gets 1 point; a cooperator whose partner cooperates gets 2 points; a defector whose partner cooperates gets 3 points.

[21] This assumption constitutes an extreme simplification of human behavior. Scholars have explored a wide variety of more complex strategies and decision-making processes (Axelrod 1984; Hayashi and Yamagish 1998; Kollock 1993; Macy 1996) as well as mechanisms for detecting cheaters (Cosmides 1989; Frank 1988; Frank et al. 1993; Macy and Skvoretz 1998; Mealey et al. 1996). Exploration of how disproportionate prior exposure combines with these other processes is left for future work.

[22] This specification of fitness captures the essential feature of the concept of cultural fitness as defined above. As becomes clear below, the greater one's fitness level, the greater is the probability that one will be imitated by one's interaction partner.

Table 1. Consequences of Behaviors and Fitness Levels of Interactants at Time *t* for Behaviors and Fitness Levels of the Same Individuals at Time *t* + 1

	Defector		
Cooperator	D0 at time *t*	D1 at time *t*	D3 at time *t*
C0 at time *t*	C0, D3 at time *t* + 1	D0, D3 at time *t* + 1	D0, D3 at time *t* + 1
C2 at time *t*	C0, C3 at time *t* + 1	C0, C3 at time *t* + 1	D0, D3 at time *t* + 1
C3 at time *t*	C0, C3 at time *t* + 1	C0, C3 at time *t* + 1	C0, D3 at time *t* + 1

Note: Cooperators who encounter a cooperator at time *t* will be C2 at time *t* + 1 regardless of their fitness levels at time *t*. Defectors who encounter a defector at time *t* will be D1 at time *t* + 1 regardless of their fitness levels at time *t*. Behavior-fitness categories C1 and D2 do not appear because, according to the model, no individual can enter or remain in either of these behavior-fitness categories (see footnote 23).

Step 4: Behavior switching. A person whose behavior is different from her or his partner's behavior switches to the partner's behavior if (and only if) the partner's fitness level is higher than the person's own.

Step 5: Determination of fitness level for next round. The fitness level of each person for the next round is the payoff he or she received this round.

ANALYSIS OF THE MODEL

The purpose of the analysis is to determine what the model implies concerning the number of cooperators relative to the number of defectors over time. Determining the trajectories of these proportions requires keeping track of the proportions of each type of person as identified by the combination of behavior and fitness level. There are eight categories of person, each identified by a unique combination of behavior and fitness level—C0, C1, C2, C3, D0, D1, D2, D3. Consideration of the model indicates which of these categories will actually be occupied by individuals. We know the categories C0, C2, D1, and D3 may be occupied by individuals. These categories are occupied by individuals who did not switch behavior in the previous round. Any C who interacts with a D and does not switch behavior will be C0 in the next round. Any C who interacts with another C will be C2 in the next round. Any D who interacts with another D will be D1 in the next round, and any D who interacts with a C and does not switch will be D3 in the next round.

The more interesting categories are C1, C3, D0, and D2. A person can be C3 in round $t+1$ if she or he is a defector in round t, meets a cooperator in that round, and switches to cooperation. Likewise, a person can be D0 in round $t+1$ if he or she is C in round t, meets a defector, and switches to defection. On the other hand, it is impossible for a person to interact with another person and become or remain C1 or D2. A person cannot become C1 because the only way to have a fitness level of 1 in round $t+1$ is to be a D who meets another D in round t. Such a person (D in round t) cannot be C in round $t+1$ because she or he encountered no C to imitate. Similarly, a person cannot become D2 because to have a fitness level of 2 in round $t+1$, a person must be a C who interacts with another C in round t. Such a person cannot switch to D in round t. Table 1 summarizes how the behavior and fitness level of a person at time $t+1$ is determined by the combination of the person's own behavior and fitness level at time t and the behavior and fitness level of the person's partner at time t. To read Table 1, consider the cell corresponding to row C0 and column D0. If a person who is C0 meets a person who is D0 at time t, then at time $t+1$, the person who was initially C0 will still be C0 and the person who was initially D0 will be D3. In the analysis that follows, I focus on the six categories that are relevant under the assumptions of the model—C0, C2, C3, D0, D1, and D3.[23]

[23] Including the categories C1 and D2 would be straightforward but would add unnecessary complication. The only cases in which these categories might be occupied by individuals would be in initial conditions. According to the model,

I analyze the model as a dynamic system (Drazin 1992; Fararo 1989; Luenberger 1979). The system of difference equations implied by the model indicates the proportions of people with different combinations of behavior and fitness level. Given any distribution of people across the six combinations of behavior and fitness level, the difference equations tell us the expected proportions of people in each of these categories in the next round. There is one equation in the system for each of the six categories of people.

The equation for the i^{th} category tells the proportion of people expected in the i^{th} category at time $t+1$ based on the proportions of people in each of the six categories at time t. Consider the category C0. The equation for C0 tells us the proportion of people in this category at the beginning of round $t+1$ based on the proportions of people in different categories at the beginning of round t. To discover the form of this equation, I ask: What kinds of people at time t can have a fitness level of 0 at time $t+1$? The answer is that only people who are C0, C2, or C3 at time t can have a fitness level of 0 at time $t+1$ because only cooperators can get a payoff of 0; defectors always get at least 1. Next, I ask for each of the categories I have just identified: What proportion of people in this category will be C0 at time $t+1$—that is, will receive a payoff of 0 in round t and will not switch behavior to defection? For each of the categories C0, C2, and C3, the answer is the proportion of people in this category at time t ($p\mathrm{C0}_t$, $p\mathrm{C2}_t$, and $p\mathrm{C3}_t$, respectively) who meet a defector whose fitness is not greater than that of the cooperator category in question. Under the model's assumption of unbiased random mixing, these proportions are the proportion of people in category D0 at time t ($p\mathrm{D0}_t$) for the category C0, $p\mathrm{D0}_t + p\mathrm{D1}_t$ for the category C2, and $p\mathrm{D0}_t + p\mathrm{D1}_t + p\mathrm{D3}_t$ for the category C3. Accordingly, the proportion of all people in the system who are C0 at time t and will be C0 at time $t+1$ is $p\mathrm{C0}_t(p\mathrm{D0}_t)$; the proportion who are C2 at time t and will be C0 at time $t+1$ is $p\mathrm{C2}_t(p\mathrm{D0}_t + p\mathrm{D1}_t)$; the proportion who are C3 at time t and will be C0 at time $t+1$ is $p\mathrm{C3}_t(p\mathrm{D0}_t + p\mathrm{D1}_t + p\mathrm{D3}_t)$. The sum of these products is the proportion of all people in the system who will be cooperators with fitness level 0 at time $t+1$:

$$\begin{aligned} p\mathrm{C0}_{t+1} &= p\mathrm{C0}_t(p\mathrm{D0}_t) \\ &\quad + p\mathrm{C2}_t(p\mathrm{D0}_t + p\mathrm{D1}_t) \\ &\quad + p\mathrm{C3}_t(p\mathrm{D0}_t + p\mathrm{D1}_t + p\mathrm{D3}_t). \end{aligned}$$

Similar reasoning indicates that the difference equations for the other five categories are the following:

$$p\mathrm{C2}_{t+1} = (p\mathrm{C0}_t + p\mathrm{C2}_t + p\mathrm{C3}_t)^2,$$

$$p\mathrm{C3}_{t+1} = (p\mathrm{D0}_t + p\mathrm{D1}_t)(p\mathrm{C2}_t + p\mathrm{C3}_t),$$

$$\begin{aligned} p\mathrm{D0}_{t+1} &= p\mathrm{C0}_t(p\mathrm{D1}_t + p\mathrm{D3}_t) \\ &\quad + p\mathrm{C2}_t(p\mathrm{D3}_t), \end{aligned}$$

$$p\mathrm{D1}_{t+1} = (p\mathrm{D0}_t + p\mathrm{D1}_t + p\mathrm{D3}_t)^2,$$

$$\begin{aligned} p\mathrm{D3}_{t+1} &= (p\mathrm{D0}_t + p\mathrm{D1}_t)p\mathrm{C0}_t \\ &\quad + p\mathrm{D3}_t(p\mathrm{C0}_t + p\mathrm{C2}_t + p\mathrm{C3}_t). \end{aligned}$$

For any initial distribution of people across these six categories, the system of difference equations gives the trajectory of the model through its state space. I begin by calculating the trajectories for three initial conditions that seem especially informative. Then I present the results from analyzing a random sample of initial conditions.

First, consider a system initially composed of half cooperators and half defectors. Because I explore the model under conditions of unbiased random mixing, it seems reasonable to suppose in this initial condition that half the Cs are C0, and half are C2. Also, in this initial condition, half the Ds are D1, and half are D3.[24] Table 2 illustrates how these proportions change with time according to the system of equations. After an early and short-lived increase in the proportion of defectors (resulting from the fitness advantage

after one round of interaction, these categories will always be empty. A C1 who continues to be a cooperator into the next round will be C0 or C2; a D2 who continues to be a defector into the next round will be a D1 or D3.

[24] For a system that is half Cs and half Ds, this distribution of individuals across behavior-fitness categories would occur under the assumption of random unbiased mixing if there were no behavior switching.

Table 2. Trajectory of System through State Space

	Proportion of Population at Beginning of Round								
Behavior-Fitness Category	Initial State $t = 0$	Round 1	Round 2	Round 3	Round 4	Round 5	Round 10	Round 20	Round 100
C0	.25	.06	.16	.15	.16	.16	.13	.06	.01
C2	.25	.25	.14	.19	.23	.27	.49	.75	.96
C3	.00	.06	.14	.13	.13	.13	.11	.06	.01
D0	.00	.19	.07	.09	.09	.09	.08	.05	.01
D1	.25	.25	.39	.32	.28	.23	.09	.02	.00
D3	.25	.19	.10	.12	.12	.12	.10	.06	.01
C, any fitness level	.50	.38	.44	.47	.52	.56	.73	.88	.98
Mean fitness of cooperators	1.00	1.83	1.58	1.62	1.63	1.66	1.79	1.92	1.99
Mean fitness of defectors	2.00	1.30	1.22	1.27	1.31	1.34	1.47	1.52	1.51

of defectors in the initial condition), the proportion of cooperators increases monotonically as the system moves toward the state in which every person is a cooperator with fitness level 2. This result indicates a evolutionary force toward cooperation when behaviors are transmitted culturally.

Table 2 suggests that the state in which every person is a cooperator (and has fitness level 2) is an attractor—systems move from other states toward all-C, and systems near or at all-C do not move away from all-C. However, the above analysis is not the strongest possible test of the model's tendency toward cooperation because it is limited to an initial condition in which half the people are cooperators. What would happen if there had been a lower proportion of cooperators and a higher proportion of defectors in the initial condition? What would happen if the mean fitness levels in the initial condition favored defectors even more strongly than in the analysis above? In such cases, is it possible that the system would move toward the state of all-D and even farther from the state of all-C? In the language of dynamic systems, these are questions about whether all-D is an attractor or a repellor. These are also questions about the boundaries of the basin of attraction that surrounds all-C and about the boundaries of the basin of attraction that surrounds all-D if that state is an attractor. Table 3 identifies three different initial conditions (including the initial condition described above), the attractor corresponding to each initial condition (i.e., the state the system approaches from the indicated initial condition), a state "close" to the attractor, and the number of rounds it takes the system to reach that state close to the attractor from the indicated initial condition. (I consider the number of rounds until a system reaches a state "close" to the attractor for the following reason: When analyzed as a dynamical system, a system that is approaching an attractor never actually reaches the attractor, although the distance between the system's state and the attractor approaches zero.)

Table 3 shows that the basin of attraction for all-C is very large. It also appears that all-D is a repellor. As indicated by the bottom panel of Table 3, even if 99 percent of the people in a system are defectors with fitness level 3 and 1 percent are cooperators with fitness level 0—an extremely hostile initial condition for the evolution of cooperation—the system still moves toward all-C, becoming "close" by the 99,579th round.

I perform one additional analysis to confirm that: (1) All-D is a repellor; (2) all-C is the only attractor; (3) any system with an initial proportion of cooperators greater than 0 converges on all-C. I randomly select 100

Table 3. Three Initial States and Corresponding Attractor

Behavior-Fitness Category	Initial State (Proportion in Category)	State Approached	State Close to Attractor Occupied by Indicated Time	Number of Rounds
C0	.25	All-C	.0001118158	8,955
C2	.25		.9995527867	
C3	.00		.0001117908	
D0	.00		.0001117658	
D1	.25		.0000000500	
D3	.25		.0001117908	
C0	.09	All-C	.0001118136	9,022
C2	.01		.9995527958	
C3	.00		.0001117886	
D0	.00		.0001117636	
D1	.81		.0000000500	
D3	.09		.0001117886	
C0	.01	All-C	.0000111804	99,579
C2	.00		.9999552790	
C3	.00		.0000111801	
D0	.00		.0000111799	
D1	.00		.0000000005	
D3	.99		.0000111801	

initial conditions and repeatedly apply the system of difference equations to each initial condition until it converges on some state. For each initial condition in the sample, the system converges on all-C.

DISCUSSION

This analysis shows that the defined cultural model predicts an evolutionary force toward cooperation. This force's effects are observed under conditions considered most inhospitable for the evolution of cooperation—one-shot prisoner's dilemmas with no option to exit played between strangers selected by an unbiased random process from a large system.

This analysis also reveals the substantive reason cultural transmission favors the evolution of cooperation. An important clue is that three different fitness levels that a cooperator can have (0, 2, 3) are, on average, higher than the three fitness levels that a defector can have (0, 1, 3). This difference arises from the model's implication that any defector who becomes a cooperator will be C3, and any cooperator who becomes a defector will be D0. For a defector to become a cooperator, he or she must interact with a cooperator and be influenced to switch to cooperation. This process involves benefiting from interacting with a cooperator. That is, becoming a cooperator involves benefiting from another person's cooperative behavior. Likewise, for a cooperator to become a defector, she or he must interact with a defector and be influenced to switch to defection. This process involves being hurt by interacting with a defector. That is, becoming a defector involves being hurt by another person's exploitative behavior.[25] This differ-

[25] These implications about the past experience of any person who has learned to cooperate from another person and the past experience of any person who has learned to defect from another person are the implications of the model that call attention to the general substantive argument in-

ence results in the mean fitness of cooperators being greater than the mean fitness of defectors, as illustrated in Table 2.[26]

Alternative Specifications of Cultural Transmission Process

Considering alternatively specified cultural models and determining whether they also imply an evolutionary force toward cooperation can move us toward two goals. One is isolating what it is about cultural transmission and disproportionate prior exposure that implies an evolutionary force toward cooperation. The other is identifying the circumstances under which cultural transmission will *not* result in the evolution of cooperation. Although an extensive analysis of potential alternative specifications is beyond the scope of this paper, I summarize the results and implications of some initial steps.

I label the model I explore above the "compare-play model" because interactants compare fitness levels before playing the prisoner's dilemma game. In one alternative specification, the "observe-play model," individuals simply observe their partner's fitness level instead of comparing their partner's fitness level with their own. In this specification, a person whose partner's behavior is different from his or her own switches to the partner's behavior with probability equal to 1/3 of the partner's fitness. Thus, when a person's partner's behavior is different from her or his own, the probability that she or he will switch behavior is 0 when the partner's fitness level is 0, 1/3 when the partner's fitness level is 1, 2/3 when the partner's fitness level is 2, and 1 when the partner's fitness level is 3. This model implies an evolutionary force toward cooperation: All-C is an attractor; all-D is a repellor; the basin of attraction for all-C consists of all states other than all-D.

In another specification, the "play-compare model," a person whose partner's behavior is different from his or her own switches behavior if and only if the partner's payoff in the present round is greater than his or her own. In other words, individuals play with each other before comparing their most recent levels of success. In stark contrast to the other specifications (and as many readers would infer), this specification implies an evolutionary force toward defection: All-D is an attractor; all-C is a repellor; the basin of attraction for all-D consists of all states other than all-C.

Considering how payoffs affect cultural fitness in each of these models indicates the logical sources of these similarities and differences in their implications. The two models that predict the evolution of cooperation (compare-play and observe-play) are also similar in that their assumptions imply that the payoff one acquires in social interaction with one individual positively affects the probability that one will be imitated by the next individual she or he encounters. In contrast to the models that predict the evolution of cooperation, the play-compare model does not imply that the payoff one acquires in social interaction with one individual positively affects the probability that one will be imitated by any future interaction partner. Although future research should explore the limitations on the tendency for cultural transmission to promote the evolution of cooperation, the similarities and differences among these models suggest the following tentative conclusion: The disproportionate prior exposure inherent in cultural transmission promotes the evolution of cooperation only if the benefits of being a target of cooperation and the costs of being exploited affect one's attractiveness as a model to individuals other than those from whom one learned to cooperate or defect and from whom one did or did not receive the benefits of being a target of cooperation. In other words, the theoretical assumption that the benefits a person

---

troduced above. Cultural transmission implies disproportionate prior exposure: Individuals who have acquired a social behavior—cooperative or exploitative—through cultural transmission were disproportionately targets of that behavior prior to acquiring it.

[26] Recognition of this fact differs from what Sober and Wilson (1998) call the "averaging fallacy," which would involve concluding from this difference that cooperating benefits the person who cooperates and defecting hurts the person who defects. The difference in fitness levels is produced by disproportionate prior exposure even though cooperating is always costly to the person who cooperates and defection is always beneficial to the person who defects.

acquires in social interaction with one individual positively affects the probability that the person will be imitated by *some other individual* in the future appears to be essential to a cultural explanation for the evolution of cooperation based on disproportionate prior exposure. (An appendix reporting these analyses in detail is available from the author on request.)

DEPARTURES FROM REAL-WORLD DESCRIPTION AND A SUBSTANTIVE LESSON

Readers will note that aspects of the formal model run counter to assumptions of backward-looking learning and rational action. Specifically, the idea that a defector would switch to cooperation after having received the highest possible payoff is at odds with principles of backward-looking learning, and under no circumstances is it rational to cooperate in a one-shot prisoner's dilemma. The purpose of this analysis is not to argue that individuals never learn on the basis of rewards they have received in associations with their own actions, nor is it to argue that individuals never make a decision based on rational calculation. My argument is about what happens when people learn behaviors from other people (Bandura 1986; Boyd and Richerson 1985). I seek to advance our knowledge about the implications of cultural transmission in its purest and most basic form. I leave for future work the exploration of how the effects of cultural transmission combine with the effects of other processes that shape human behavior.

In addition to abstracting the process of cultural transmission from other processes that shape human behavior, the compare-play model is an extreme simplification of real processes of cultural transmission. Indeed, a single interaction may not be sufficient to determine whether a person will be a cooperator or a defector (see Kelley and Stahelski 1970a, 1970b). Likewise, a person's cultural fitness (e.g., wealth or status) is not wholly determined by the last time he or she interacted with another person. Sometimes a person can be influenced to become a defector without being impoverished, and sometimes a person can be influenced to become a cooperator without being made wealthy. Future research should explore how variations in the process and structure of cultural transmission could attenuate the tendency for cultural transmission to create an evolutionary force toward cooperation.

Nevertheless, the simplicity of this model calls attention to an important implication of cultural transmission: Individuals who have acquired cooperative behavior through cultural transmission disproportionately were targets of and disproportionately benefited from cooperative behavior by others before and as they learned to cooperate. Individuals who have acquired exploitative behavior through cultural transmission disproportionately were targets of and disproportionately were hurt by exploitative behavior by others as they learned to exploit.[27] If, as past theoretical and empirical research suggests, the benefits individuals receive in social interaction increase their attractiveness as cultural models to others they encounter in the future, and the costs individuals incur in social interaction decrease their attractiveness as cultural models to others they encounter in the future, then the disproportionate prior exposure that is implied by cultural transmission will create an evolutionary force toward cooperation. To be of value, the formal model that calls attention to this idea does not need to be an accurate description of the empirical world. Understanding the logical argument revealed by the model, we can see how the evolutionary force implied by cultural transmission—attenuated by some real-world conditions and opposed by some real-world forces excluded from the analy-

[27] One qualification should be noted. Under some empirically unrealistic but logically important circumstances, cooperators and defectors will not necessarily differ in these ways. Consider the circumstances in which individuals are influenced to adopt cooperative or exploitative behaviors only by exposure to these behaviors as third-party observers, rather than sometimes being influenced to adopt a behavior when one is exposed to that behavior as a target of that behavior. In this case, it may not be true that cooperators will disproportionately have benefited from the cooperative behaviors of others and defectors will have disproportionately been hurt by others' exploitative behaviors.

sis—is still likely to be important in helping account for the prevalence of human cooperation in the real world.

Strengths of a Cultural Explanation for Cooperation

Some scholars argue that attention to cultural evolution will contribute greatly to explaining the prevalence of human cooperation (Allison 1992a, 1992b; Boyd and Richerson 1982; Campbell 1975; Macy 1996; Simon 1990). The discovery of the disproportionate prior exposure inherent to cultural transmission and the evolutionary force toward cooperation generated by this characteristic of cultural transmission strengthens this argument. As demonstrated, explicit recognition of the disproportionate prior exposure inherent to cultural transmission brings the evolution of cooperation between randomly selected strangers in one-shot games with no option to exit into the realm of theoretical possibility. Neither genetic evolution (Axelrod 1984; Trivers 1971), rational calculation (Luce and Raiffa 1957), nor backward-looking learning (Macy 1991) can produce cooperation under these circumstances. Given the favorable prospects for culture as a basis for understanding the prevalence of human cooperation, I note here some specific strengths of a cultural explanation for the evolution of cooperation, especially of a cultural explanation that takes disproportionate prior exposure into account.

Social organization of human populations. Scholars note the tremendous difference in levels of cooperation and social organization between human populations and populations of other species of animal, and these scholars argue that humans' uniquely high capacity for cultural transmission is essential to an account for this difference (Boyd and Richerson 1982; Campbell 1975; Lenski et al. [1970] 1995). Hopefully, recognition and further exploration of the role that disproportionate prior exposure plays in the cultural evolution of cooperation will improve our understanding of how cultural transmission helps to account for the extraordinary differences between human populations and populations of other species of animal in levels of cooperation and social organization.

Cooperation in cultural theoretical context. Advancing a cultural explanation for cooperation is important because of the relationship of such an explanation to other social scientific knowledge. The idea that culture is an important factor shaping human social phenomena is fundamental to sociology (Blumer 1962; Bourdieu [1979] 1984; Carley 1991; Durkheim [1915] 1965; Powell and DiMaggio 1991; Stryker 1980; Swidler 1986; Weber [1904–1905] 1958) and related fields (Axelrod 1997b; Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981; Durham 1990; Geertz 1973; Kroeber and Kluckhohn [1952] 1963). A cultural explanation for cooperation is more consistent with this basic understanding than is an explanation that does not take cultural transmission into account. Thus, advancing cultural explanations for cooperation may contribute to a more unified understanding of human social phenomena.

Disproportionate prior exposure complements previous cultural explanations. Some scholars build their cultural explanations on the assumption that a population is segmented into a number of subpopulations among which movement of individuals and transmission of cultural characteristics is relatively low (Allison 1992a; Boyd and Richerson 1982; Sober and Wilson 1998). These scholars argue that when this condition is met, selection for cooperation can occur at the group level (Boyd and Richerson 1982; Campbell 1975; Sober and Wilson 1998; Soltis, Boyd, and Richerson 1995). Recognition of the disproportionate prior exposure generated by cultural transmission answers questions left unanswered by these promising explanations. First, noting that subpopulations of cooperators must exist before they can be selected for, disproportionate prior exposure helps to provide a general explanation for how cooperation could initially evolve within a subpopulation, and does so even if the subpopulation is large and randomly mixing.

Second, because these explanations (Allison 1992a; Boyd and Richerson 1982) assume that the degree to which groups are isolated from each other is substantial, they raise the question of whether the level of contact among groups has been sufficiently low to produce observed levels of cooperation. Sober and Wilson (1998) argue that the structural requirements for the evolution of cooperation at the group level may be weaker than previously thought in cases where rules for sanctioning behavior (i.e., for punishing defectors and/or rewarding cooperators) are introduced into a population along with cooperative behaviors. The reason is that engaging in sanctioning behavior may be less costly to sanctioners than cooperation is to cooperators in the case where cooperation is not enforced (Boyd and Richerson 1992; Heckathorn 1990, 1993). Like Sober and Wilson's (1998) normative explanation, disproportionate prior exposure creates an evolutionary force toward cooperation even when the structural requirements of previous group-selectionist explanations are not met. Thus, disproportionate prior exposure complements Sober and Wilson's normative explanation by providing an evolutionary pathway to forms of cooperation that are not (or are only weakly) normatively enforced.

There is another plausible answer to the question of whether populations have been sufficiently structured for cooperation to evolve at the group level. This answer is that even though there is too much contact among subpopulations in the world today for group selection to produce cooperation, in the distant past, human subpopulations were sufficiently isolated from each other for cooperation to become widespread (for a review, see Boyd and Richerson 1985:231; Sober and Wilson 1998:141).[28] In contrast to this answer, disproportionate prior exposure suggests that the cooperation observed today is not entirely an enduring consequence of a previously operating evolutionary force; instead, there may be a characteristic of cultural transmission, disproportionate prior exposure, that creates an evolutionary force toward cooperation even in the highly interconnected world of today. This view suggests that potentially observed declines in cooperation might be offset by future increases.

Third, Boyd and Richerson (1982) note that group selection not only promotes cooperation within groups, but promotes exploitation and hostility between groups. Certainly, given the observed prevalence of intergroup hostility in the world today and in the past, an explanation for this phenomenon would be of great value. Nevertheless, it is important to know whether there might be a source of cooperation that does not simultaneously promote intergroup hostility. The above analysis suggests that cultural transmission, because it generates disproportionate prior exposure, may be such a source.

Disproportionate Prior Exposure May Promote Multiple Forms of Cooperation. I have explored the evolution of cooperation in one-shot prisoner's dilemmas. Because cultural transmission that occurs within social interactional contexts other than prisoner's dilemmas also produces disproportionate prior exposure, cultural transmission and the associated disproportionate prior exposure may promote cooperation outside of prisoner's dilemma situations. One important form of cooperation that occurs outside of prisoner's dilemmas is unilateral giving within networks of genetic kinship (Hamilton 1964), networks of cultural kinship (Allison 1992a), and other networks of generalized exchange (Boyd and Richerson 1989; Nowak and Sigmund 1998; Takahashi 2000; Yamagishi and Cook 1993). Because people may learn how to behave in such networks by observing how others behave toward them, disproportionate prior exposure is expected to occur. That is, we expect that individuals who give will disproportionately be those who have been given to, and individuals who do not give will disproportionately be those who were not given to. If, as I have argued here, the benefits of having been given to increase the probability that one will be imitated by others (i.e., increase one's cultural fitness), then a cultural evolutionary force toward unilateral giving may result. One reason such an explanation would be important is that, unlike previous explanations that predict the evolution of selective giving (Allison 1992a; Boyd and Richerson 1989; Hamilton 1964; Nowak and Sigmund 1998; Takahashi 2000), disproportionate prior exposure may help explain the evolution of indiscriminant giving.

[28] See Watts (1999) on differences between past and present network structures of human populations.

A Methodological Lesson

Axelrod (1986) recommends using genetic evolutionary models to explore the implications of cultural evolution. My recommendation is different: *Scholars who wish to explore the cultural evolution of cooperation using formal models should construct models that are explicitly cultural in their specification of the transmission process.* That is, they should construct models in which individuals acquire behaviors by interacting with people who display those behaviors (also see Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981). My finding that cultural transmission creates an evolutionary force toward cooperation in one-shot prisoner's dilemmas played between randomly selected strangers with no option to exit—conditions under which the genetic evolution of cooperation is understood to be impossible (Trivers 1971)—is revealed precisely because the model I constructed and analyzed is explicitly cultural. Because this model is explicitly cultural, it captures the disproportionate prior exposure that is implied by cultural transmission and that promotes the evolution of cooperation. In contrast, genetic evolutionary models (Axelrod 1984,1997a; Frank 1988; Kollock 1993; Macy 1996; Peck and Feldman 1986) capture an important characteristic of genetic transmission, which might be called "no exposure prior to acquisition." That is, genes are acquired only at the beginning of an individual's life. Therefore, a person cannot be exposed to any cooperative or exploitative behavior prior to acquiring one or more genes that might influence or determine the person's tendencies toward cooperative or exploitative behaviors. Thus, under genetic transmission, the only way for cooperators to disproportionately benefit from the cooperation of others is if cooperation is selective (Frank 1988; Hamilton 1964), if cooperation is conditional (Axelrod 1984; Trivers 1971), or if social encounters (Sober and Wilson 1998) or decisions to interact (Orbell and Dawes 1991) are structured so that cooperators interact with cooperators more often than defectors do. The inability of genetic transmission to produce exposure to a behavior prior to acquisition of the behavior is incorrectly attributed to cultural transmission when genetic models are used to explore the cultural evolution of cooperation.

CONCLUSION

My goal here has been to call attention to a previously unrecognized characteristic of cultural transmission—disproportionate prior exposure—and to how this characteristic creates an evolutionary force toward cooperation. To do so, I have conducted a formal theoretical analysis that isolated the logic of cultural transmission. This analysis revealed an evolutionary force toward cooperation under conditions previously thought to make the evolution of cooperation impossible—individuals randomly encounter strangers in one-shot prisoner's dilemmas with no option to exit. Of course, my goal has not been to predict that in the real world every person will cooperate in every situation; some real-world conditions will attenuate this cultural evolutionary force toward cooperation. And this evolutionary force toward cooperation is not the only force that shapes people's cooperative and exploitative behaviors. Future research should look at how this cultural evolutionary force may be attenuated under various circumstances and how the effect of this force combines and/or interacts with the effects of other processes such as backward-looking learning, rational calculation, and genetic evolution. Such efforts may lead to an understanding of human social behavior that can account for exploitation, but which views the prevalence of human cooperation as a natural and expected consequence of the human capacity for cultural transmission.

***Noah P. Mark** is Assistant Professor of Sociology at Stanford University. His research focuses on social and cultural evolutionary processes. In 1999, his paper titled "Beyond Individual Differences: Social Differentiation from First Principles" (*American Sociological Review*, 1998, vol 63, pp. 309–330), won the Theory Prize of the Theory Section of the American Sociological Association. Works in progress seek to explain the emergence of status inequality, generalized exchange, and sociodemographic patterns of cultural taste and practice.*

REFERENCES

Allison, Paul D. 1992a. "Cultural Relatedness Under Oblique and Horizontal Transmission." *Ethology and Sociobiology* 13:153–69.

———. 1992b. "The Cultural Evolution of Beneficent Norms." *Social Forces* 71:279–301.

Ashworth, Tony. 1980. *Trench Warfare, 1914–1918: The Live and Let Live System.* New York: Holmes and Meier.

Axelrod, Robert. 1984. *The Evolution of Cooperation.* New York: Basic.

———. 1986. "An Evolutionary Approach to Norms." *American Political Science Review* 80:1095–111.

———. 1997a. *The Complexity of Cooperation: Agent-Based Models of Competition and Collaboration.* Princeton, NJ: Princeton University Press.

———. 1997b. "The Dissemination of Culture: A Model with Local Convergence and Global Polarization." *Journal of Conflict Resolution* 41:203–26.

Bandura, Albert. 1986. *The Social Foundations of Thought and Action: A Social Cognitive Theory.* Englewood Cliffs, NJ: Prentice-Hall.

Bandura, Albert, Dorothea Ross, and Sheila A. Ross. 1963. "A Comparative Test of the Status Envy, Social Power, and Secondary Reinforcement Theories of Identificatory Learning." *Journal of Abnormal and Social Psychology* 67:527–34.

Bandura, Albert and Richard H. Walters. 1963. *Social Learning and Personality Development.* New York: Holt, Rinehart, and Winston.

Berkowitz, Leonard and Louise R. Daniels. 1964. "Affecting the Salience of the Social Responsibility Norm: Effects of Past Help on the Response to Dependency Relationships." *Journal of Abnormal and Social Psychology* 68:275–81.

Blumer, Herbert. 1962. "Society as Symbolic Interaction." Pp. 179–92 in *Human Behavior and Social Processes*, edited by A. M. Rose. London, England: Routledge and Kegan Paul.

Boorman, Scott A. and Paul R. Levitt. 1980. *The Genetics of Altruism.* New York: Academic.

Bourdieu, Pierre. [1979] 1984. *Distinction: A Social Critique of the Judgement of Taste.* Reprint, Cambridge, MA: Harvard University Press.

Boyd, Robert and Peter J. Richerson. 1982. "Cultural Transmission and the Evolution of Cooperative Behavior." *Human Ecology* 10:325–51.

———. 1985. *Culture and the Evolutionary Process.* Chicago, IL: University of Chicago Press.

———. 1989. "The Evolution of Indirect Reciprocity." *Social Networks* 11:213–36.

———. 1992. "Punishment Allows the Evolution of Cooperation (or Anything Else) in Sizable Groups." *Ethology and Sociobiology* 13:171–95.

Campbell, Donald T. 1975. "On the Conflicts between Biological and Social Evolution and between Psychology and Moral Tradition." *American Psychologist* 30:1103–26.

Carley, Kathleen. 1986. "Knowledge Acquisition as a Social Phenomenon." *Instructional Science* 14:381–438.

———. 1991. "A Theory of Group Stability." *American Sociological Review* 56:331–54.

Carneiro, Robert L. 1998. "What Happened at the Flashpoint? Conjectures on Chiefdom Formation at the Very Moment of Conception." Pp. 18–42 in *Chiefdoms and Chieftaincy in the Americas*, edited by E. M. Redmond. Gainesville, FL: University Press of Florida.

Cavalli-Sforza, Luigi L. and Marcus W. Feldman. 1981. *Cultural Transmission and Evolution: A Quantitative Approach.* Princeton, NJ: Princeton University Press.

Cavalli-Sforza, L. L., Marcus W. Feldman, K. H. Chen, and S. M. Dornbusch. 1982. "Theory and Observation in Cultural Transmission." *Science* 218:19–27.

Clinton, Hillary Rodham. 1996. *It Takes a Village.* New York: Simon and Schuster.

Cosmides, Leda. 1989. "The Logic of Social Exchange: Has Natural Selection Shaped How Humans Reason? Studies with the Wason Selection Task." *Cognition* 31:187–276.

Drazin, P. G. 1992. *Nonlinear Systems.* Cambridge, MA: Cambridge University Press.

Durham, William H. 1990. "Advances in Evolutionary Culture Theory." *Annual Review of Anthropology* 19:187–210.

Durkheim, Emile. [1893] 1984. *The Division of Labor in Society.* Translated by W. D. Halls. Reprint, New York: Free Press.

———. [1915] 1965. *The Elementary Forms of Religious Life.* Translated by J. W. Swain. Reprint, New York: Free Press.

Eisenberg-Berg, Nancy and Elizabeth Geisheker. 1979. "Content of Preachings and Power of the Model/Preacher: The Effect on Children's Generosity." *Developmental Psychology* 15: 168–75.

Fararo, Thomas J. 1989. *The Meaning of General Theoretical Sociology.* Cambridge, MA: Cambridge University Press.

Flinn, Mark V. and Richard D. Alexander. 1982. "Culture Theory: The Developing Synthesis from Biology." *Human Ecology* 10:383–400.

Folbre, Nancy. 1994. *Who Pays for the Kids?* London, England: Routledge.

Frank, Robert H. 1988. *Passions within Reason: The Strategic Role of the Emotions.* New York: Norton.

Frank, Robert H., Thomas Gilovich, and Dennis T. Regan. 1993. "The Evolution of One-Shot

Cooperation: An Experiment." *Ethology and Sociobiology* 14:247–56.
Geertz, Clifford. 1973. *The Interpretation of Cultures*. New York: Basic.
Hamilton, William D. 1964. "The Genetical Evolution of Social Behaviour." Parts 1 and 2. *Journal of Theoretical Biology* 7:1–52.
Harris, Marvin and Orna Johnson. 2000. *Cultural Anthropology*. Boston, MA: Allyn and Bacon.
Harris, Mary B. 1970. "Reciprocity and Generosity: Some Determinants of Sharing in Children." *Child Development* 41:313–28.
———. 1971. "Models, Norms, and Sharing." *Psychological Reports* 29:147–53.
Hayashi, Nahoko and Toshio Yamagishi. 1998. "Selective Play: Choosing Partners in an Uncertain World." *Personality and Social Psychology Review* 2:276–89.
Healy, Kieran. 2000. "Embedded Altruism: Blood Collection Regimes and the European Union's Donor Population." *American Journal of Sociology* 105:1633–57.
Heckathorn, Douglas D. 1990. "Collective Sanctions and Compliance Norms: A Formal Theory of Group Mediated Social Control." *American Sociological Review* 55:366–84.
———. 1993. "Collective Action and Group Heterogeneity: Voluntary Provision versus Selective Incentives." *American Sociological Review* 58:329–50.
Jacobs, Robert C. and Donald T. Campbell. 1961. "The Perpetuation of an Arbitrary Tradition Through Several Generations of a Laboratory Microculture." *Journal of Abnormal and Social Psychology* 62:649–58.
Katz, Elihu and Paul F. Lazarsfeld. 1955. *Personal Influence: The Part Played by People in the Flow of Mass Communications*. Glencoe, IL: Free Press.
Kelley, Harold H. and Anthony J. Stahelski. 1970a. "Errors in Perception of Intentions in a Mixed-Motive Game." *Journal of Experimental Social Psychology* 6:379–400.
———. 1970b. "Social Interaction Basis of Cooperators' and Competitors' and Beliefs about Others." *Journal of Personality and Social Psychology* 16:66–91.
Kollock, Peter. 1993. "An Eye for an Eye Leaves Everyone Blind: Cooperation and Accounting Systems." *American Sociological Review* 58:768–86.
Kroeber, Alfred L. and Clyde Kluckhohn [1952] 1963. *Culture: A Critical Review of Concepts and Definitions*. Reprint, New York: Vintage.
Labov, William. 1972. *Sociolinguistic Patterns*. Philadelphia, PA: University of Pennsylvania Press.
———. 1980. "The Social Origins of Sound Change." Pp. 251–65 in *Locating Language in Time and Space*, edited by W. Labov. New York: Academic.
Lee, Lichang, Jane Allyn Piliavin, and Vaughn R. A. Call. 1999. "Giving Time, Money, and Blood: Similarities and Differences." *Social Psychology Quarterly* 62:276–90.
Lefkowitz, Monroe, Robert R. Blake, and Jane Srygley Mouton. 1955. "Status Factors in Pedestrian Violation of Traffic Signals." *Journal of Abnormal and Social Psychology* 51:704–706.
Lenski, Gerhard, Patrick Nolan, and Jean Lenski. [1970] 1995. *Human Societies: An Introduction to Macro Sociology*. Reprint, New York: McGraw-Hill.
Lipscomb, Thomas J., Julie A. Larrieu, Hunter A. McAllister, and Norman J. Bregman. 1982. "Modeling and Children's Generosity: A Developmental Perspective." *Merrill-Palmer Quarterly* 28:275–82.
Luce, R. Duncan and Howard Raiffa. 1957. *Games and Decisions: Introduction and Critical Survey*. New York: Wiley.
Luenberger, David G. 1979. *Introduction to Dynamic Systems: Theory, Models, and Applications*. New York: John Wiley and Sons.
Lumsden, Charles J. and Edward O. Wilson. 1981. *Genes, Mind, and Culture: The Coevolutionary Process*. Cambridge, MA: Harvard University Press.
Macy, Michael W. 1991. "Learning to Cooperate: Stochastic and Tacit Collusion in Social Exchange." *American Journal of Sociology* 97:808–43.
———. 1996. "Natural Selection and Social Learning in Prisoner's Dilemmas: Coadaptation with Genetic Algorithms and Artificial Neural Networks." *Sociological Methods and Research* 25:103–37.
Macy, Michael W. and John Skvoretz. 1998. "The Evolution of Trust and Cooperation between Strangers: A Computational Model." *American Sociological Review* 63:638–60.
Mealey, Linda, Christopher Daood, and Michael Krage. 1996. "Enhanced Memory for Faces of Cheaters." *Ethology and Sociobiology* 17:119–28.
Nowak, Martin A. and Karl Sigmund. 1998. "Evolution of Indirect Reciprocity by Image Scoring." *Nature* 393:573–77.
Orbell, John and Robin Dawes. 1991. "A 'Cognitive Miser' Theory of Cooperators' Advantage." *American Political Science Review* 85:515–28.
———. 1993. "Social Welfare, Cooperators' Advantage, and the Option of Not Playing the Game." *American Sociological Review* 58: 787–800.
Peck, Joel R. and Marcus W. Feldman. 1986. "The Evolution of Helping Behavior in Large, Randomly Mixed Populations." *The American*

Naturalist 127:209–21.
Piliavin, Jane Allyn and Peter L. Callero. 1991. *Giving Blood: The Development of an Altruistic Identity*. Baltimore, MD: Johns Hopkins University Press.
Powell, Walter W. and Paul J. DiMaggio, eds. 1991. *The New Institutionalism in Organizational Analysis*. Chicago, IL: University of Chicago Press.
Rogers, Everett M. and F. Floyd Shoemaker. 1971. *Communication of Innovations: A Cross-Cultural Approach*. New York: Free Press.
Rushton, Philippe J. 1980. *Altruism, Socialization, and Society*. Englewood Cliffs, NJ: Prentice-Hall.
Simon, Herbert A. 1990. "A Mechanism for Social Selection and Successful Altruism." *Science* 250:1665–8.
Sober, Elliott and David Sloan Wilson. 1998. *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Cambridge, MA: Harvard University Press.
Soltis, Joseph, Robert Boyd, and Peter J. Richerson. 1995. "Can Group-Functional Behaviors Evolve by Cultural Group Selection?" *Current Anthropology* 36:473–94.
Spencer, Herbert. [1882] 1916. *Principles of Sociology*. Vol. 2. Reprint, New York: Appleton.
Stryker, Sheldon. 1980. *Symbolic Interactionism*. Menlo Park, CA: Benjamin Cummings.
Swidler, Ann. 1986. "Culture in Action: Symbols and Strategies." *American Sociological Review* 51:273–86.
Tarde, Gabriel. [1890] 1962. *The Laws of Imitation*. Reprint, Gloucester, MA: Peter Smith.
Takahashi, Nobuyuki. 2000. "The Emergence of Generalized Exchange." *American Journal of Sociology* 105:1105–34.
Trivers, Robert L. 1971. "The Evolution of Reciprocal Altruism." *The Quarterly Review of Biology* 46:35–57.
Watts, Duncan J. 1999. "Networks, Dynamics, and the Small-World Phenomenon." *American Journal of Sociology* 105:493–527.
Weber, Max. [1904–1905] 1958. *The Protestant Ethic and the Spirit of Capitalism*. Translated by T. Parsons. Reprint, New York: Charles Scribner's Sons.
Wilson, Edward O. 1998. *Consilience: The Unity of Knowledge*. New York: Vintage.
Yamagishi, Toshio and Karen Cook. 1993. "Generalized Exchange and Social Dilemmas." *Social Psychology Quarterly* 56:235–48.