

The Evolutionary Psychology of Prosocial Behavior

It is ironic that although most people view evolution as a process that selects selfish traits, evolutionary theory has gone further than any other theory to explain why animals behave in prosocial ways. The chapters in this section discuss advances in the evolutionary psychology of cooperation, helping, altruism, and morality. Evolutionary theorists do not always agree with one another. An important controversy is explicated in chapters 16 and 17.



15

How Selfish by Nature?

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The idea that all animals, including humans, are selfish by nature has a long history in theology, philosophy, and the social sciences. It appears to have been endorsed by scholars who are in the best position to evaluate it—evolutionary biologists. In *Descent of Man*, Charles Darwin(1884) wrote, Q1

It is extremely doubtful whether the offspring of the most sympathetic and benevolent parents, or of those which were the most faithful to their comrades, would be reared in greater number than the children of selfish and treacherous parents of the same tribe. He who was ready to sacrifice his life..., rather than betray his comrades, would often leave no offspring to inherit his noble nature. (p. 163)

Following the publication of *Descent of Man*, Thomas Huxley (1893) considered the moral implications of Darwin's theory of evolution and concluded that if "brought before the tribunal of ethics, [nature] might well stand condemned" (p. 59). More than a century later, Williams (1989) evaluated Huxley's (1893) conclusions in light of refinements in the theory of evolution and found it "indecisive and disappointing" (p. 180). After considering the evidence, Williams (1989) reached the following decisive conclusion:

There is no encouragement for any belief that an organism can be designed for any purpose other than the most effective pursuit of...self-interest (p. 197). Nothing resembling the Golden Rule or other widely preached ethical principles seems to be operating in living nature. It could scarcely be otherwise, when evolution is guided by a force that maximizes genetic selfishness. (p. 195) Q2

In his highly influential book, *The Selfish Gene*, Dawkins (1989) popularized William's position:

I think “nature red in tooth and claw” sums up our modern understanding of natural selection admirably....If you look at the way natural selection works, it seems to follow that anything that has evolved by natural selection should be selfish....Be warned that if you wish, as I do, to build a society in which individuals cooperate generously and unselfishly toward a common good, you can expect little help from biological nature. (pp. 2–4)

In this chapter, I will evaluate the idea that the process of natural selection has rendered all beings selfish by nature and find it wanting. I will begin by spelling out the logic that has induced evolutionary theorists to conclude that all evolved behavioral dispositions are selfish, then go on to argue that because the genetically selfish dispositions favored by natural selection do not equate to biologically or psychologically selfish dispositions, the latter can evolve. In the remainder of the chapter, I will review evidence suggesting that both selfish and unselfish dispositions have evolved in a variety of social species, including our own.

THE SELFISHNESS OF EVOLVED DISPOSITIONS

The reason why evolutionary theorists hold that all evolved behavioral dispositions are selfish is because they define selfishness in terms of behaviors that enhance animals’ fitness relative to, or at the expense of, the fitness of other animals. As expressed by Sober and D. S. Wilson (2000), “By definition altruists have lower fitness than the selfish individuals with whom they interact. It therefore seems inevitable that natural selection should eliminate altruistic behaviour, just as it eliminates other traits that diminish an individual’s fitness” (p. 186). (Sober & D. S. Wilson also argue that altruistic traits can evolve through group selection.)

The ultimate measure of fitness lies in the propagation of genes. Dawkins (1989) suggested that it is appropriate to label genes that are selected and transported to future generations selfish, because, in an environment with a limited carrying capacity, such genes increase their welfare, or frequency, at the expense of the welfare, or frequency, of their alleles. As expressed by Nesse (2000),

It is correct beyond question that genes shape brains that induce individuals to do whatever best gets copies of those genes into future generations. This principle follows from the logic of how natural selection works, and is not an empirical issue. When this is combined with our intuitive notion that altruism consists of costly acts that benefit others, and genes are seen as the ultimate currency, then altruism [seems] impossible. (p. 228)

As defined by evolutionary biologists, a disposition or trait qualifies as *genetically selfish* when it induces those who possess it to behave in ways that have the consequence of increasing the number of replicas of their genes in the population. Genetic selfishness equates to success at genetic replication.

Although it may be appropriate to define all evolved behavioral dispositions as genetically selfish, it is important to recognize the constraints on this definition. First, it pertains only to the environment in which the dispositions were selected, in a post hoc manner (see Crawford, this volume; Gangestad, this volume). In a book called *Mean Genes*, Burnham and Phelan (2000) review evidence demonstrating that mechanisms governing hunger, thrill seeking, greed, and sexual relations that were fitness enhancing (and therefore genetically selfish) in the environments in which they were selected now dispose people to behave in fitness-reducing (i.e., genetically unselfish) ways in current environments. Troisi (this volume) explains how maladaptive behaviors and disorders such as obesity, drug addiction, and alcoholism originate from a mismatch between modern environments and the environments in which the mechanisms that give rise to them were selected (for a more detailed account of the evolution or maladaptations, see Crespi, 2000).

Second, the genetic selfishness of social dispositions may vary with their frequency in the population (Axelrod, 1988; Maynard-Smith, 1982). The same disposition could be genetically selfish in

one social environment and genetically unselfish in another social environment. For example, the disposition to reciprocate could pay off genetically in an environment replete with reciprocators, but prove genetically costly (genetically altruistic) in an environment replete with cheaters.

Third, evolved mechanisms that, on balance, enhance the fitness of those who inherit them may be designed in adaptively imperfect ways, which may induce individuals to emit some genetically unselfish behaviors. Simon (1990) has argued that the adaptive benefits of susceptibility to social influence (“docility”) outweigh the genetic costs of the altruistic acts that the mechanisms occasionally produce. An important implication of this argument is that members of groups may be manipulated into behaving altruistically (William, 1989). Williams has suggested that cognitive mechanisms that enable people to reap adaptive benefits from reason may incidentally induce them to derive moral judgments that dispose them to behave in fitness-reducing ways.

Finally, it is important to note that genetic forms of selfishness do not necessarily pertain to the physical welfare of individuals; they pertain to the effect of individuals’ behavior on the number of replicas of their genes they contribute to future generations. Following Dawkins (1989), it is appropriate to view genes as entities that use individuals as vehicles to propagate themselves.

BIOLOGICAL SELFISHNESS

One of the biggest obstacles to scholars’ abilities to determine whether humans and other animals are selfish by nature is the pervasive tendency for people to use the word *selfishness* to refer to quite different phenomena. Those who take different sides on the issue often engage in futile debates in which they use the word selfish in quite different ways, while assuming that they are talking about the same thing. Little is gained by arguing that one’s preferred definition of selfishness is the only valid definition. It is more constructive to acknowledge that there are different forms of selfishness than to examine the relations among them. To this end, I believe it is useful to distinguish between genetic selfishness and another form of selfishness with which it is often confused—a form that I will label *biological selfishness*.

Evolutionary theorists define selfish behaviors as those that “confer a fitness benefit on the actor, while placing a fitness cost on the recipient” (Kurland & Gaulin, 2005, p. 448), which they contrast with (a) altruistic behaviors, which confer a fitness benefit on the recipient at a cost to the actor and (b) cooperative behaviors, which purvey “mutual fitness benefits for both actors” (p. 448). Ultimately, fitness is defined in terms of the propagation of genes. However, as indicated in the quote from *Descent of Man* at the beginning of this chapter, fitness also may be defined in terms of survival and reproductive success. In these terms, a disposition, trait, or behavior is *biologically selfish* when it enhances the biological welfare (i.e., the survival and reproductive success) of actors at the expense of the biological welfare of recipients.

Biologically selfish and unselfish forms of conduct are similar to their genetic counterparts in that they usually help individuals get replicas of their traits into future generations. However, the two forms of selfishness differ in terms of what is replicated and of the types of costs and benefits that they bestow. The costs and benefits of genetically selfish behaviors are defined in terms of the effect of actors’ actions on the number of *replicas of their genes* they contribute to future generations relative to the number of alleles of these genes contributed by others. In contrast, the costs and benefits of biologically selfish and unselfish forms of conduct are defined in terms of the effect of actors’ actions on the probability that they (the *individuals*—the vehicles—carrying the genes) will survive and produce other individuals (vehicles) like them (i.e., who share some of their traits).

Although evolutionary theorists might argue that it is misguided to attend to the survival and reproductive success of individuals because, in the end, all that counts is the fate of the genes that they transport, distinguishing between biological and genetic forms of selfishness is helpful in explicating the nature of selfishness and exploring its implications for human nature. Indeed, it is helpful to distinguish between the kinds of biologically selfish dispositions that enhance survival

and the kinds that enhance reproductive success. Survival affects evolution only as a prerequisite for reproduction and other means of genetic propagation (see Scheyd, Garver-Apgar, & Gangstad, this volume). Reproductive selfishness is more closely related to genetic selfishness than survival selfishness is. However, behaviors that enhance individuals' survival seem more selfish than those that enhance individuals' reproductive success. Characterizing mating and offspring-supporting behaviors as selfish is neither as connotatively comfortable nor as theoretically appropriate as characterizing survival behaviors as selfish. When individuals seek to foster their own survival, they benefit themselves, but when they seek to foster their reproductive success, they bestow biological benefits on the most direct recipients of their reproductive behaviors—their mates and offspring.¹

PSYCHOLOGICAL SELFISHNESS

Laypeople rarely use the word “selfish” in the way in which evolutionary biologists use it in their disciplines. When people characterize a behavior, disposition, or person as selfish, they mean, “[D]eficient in consideration for others, concerned chiefly with one’s own profit or pleasure” (Oxford Dictionary, XXXX); “seeking or concentrating on one’s own advantage, pleasure, or well-being without regard for others” (Funk & Wagnalls, XXXX); “regarding one’s own interest chiefly or solely” (Webster, XXXX); or “concerned only to satisfy one’s own desires and prepared to sacrifice the feelings and needs etc. of others to do so” (Webster’s Encyclopedia, XXXX). Note the implicit association between selfishness and immorality in these definitions. Most people believe that it is right to show consideration for others, and wrong for people to sacrifice others’ feelings and needs to satisfy their own desires. People define altruism, which is commonly considered good, as the opposite of selfishness.

In this paper, I will define psychological selfishness and psychological altruism in the way in which it is implicitly defined by most laypeople, and explicitly defined by the psychologists and philosophers who have considered the concept most extensively, Batson (1991) and Sober and D. S. Wilson (2000), in terms of the motives that are reflected in the proximate terminal goals (ends) that individuals seek to achieve. A motive or desire is *psychologically selfish* when its aim (terminal goal) is to benefit the actor, especially by increasing his or her “profit,” “pleasure,” “well-being,” and “advantage,” without regard for others. By implication, a behavior is psychologically altruistic when its terminal goal is to benefit a recipient, as an end in itself (rather than as a means of benefiting the actor).

Many researchers, especially economists and social exchange theorists, define selfishness, altruism, and fairness in terms of how people choose to distribute material resources. Selfishness is defined operationally as taking more than one’s share; altruism is defined as giving more than one’s share; and fairness and equity are defined as giving people what they deserve. As discussed in other chapters of this volume (e.g., Gintis, Bowles, Boyd, & Fehr, this volume; Johnson Price, & Takezawa, this volume; Kenrick & Sundie, this volume), a great deal of recent research has challenged the classic “homo economicus” conception of human nature by demonstrating that people often refrain from making instrumental self-serving “rational choices” when they allocate resources, opting instead to distribute resources in more equitable ways (see also Lerner, 2003; Miller, 1999).

I will accommodate to economic definitions of selfishness and altruism when I review relevant research later in this chapter, evaluating it on its own terms. However, it is important to recognize that economic definitions fail to meet the criteria of selfishness and altruism employed by Batson (1991) and Sober and D. S. Wilson (1998) because they fail to establish that the choices in question reflect the terminal goals that those who make them are attempting to achieve. Although studies

¹ On the other side of the coin, evolutionary biologists such as A. Zahavi and A. Zahavi (1997) have labeled dispositions to sacrifice one’s prospects of surviving in order to optimize one’s prospects of reproducing “altruistic.”

that employ economic definitions of selfishness and altruism may control such terminal goals as currying favor and making a good impression (e.g., by permitting participants to make only one choice, by using strangers as recipients, and by making choices anonymous; see Gintis et al., this volume; Johnson et al., this volume), they rarely attempt to establish that participants are not making fair and altruistic choices in order, for example, to make themselves feel good; that is, participants are not, in effect, sacrificing their profits in order to increase their pleasure.

Psychological selfishness and unselfishness differ from their evolutionary (genetic and biological) counterparts in two related ways. First, psychological forms of selfishness and altruism are defined in terms of the *motivational states* individuals are in, as reflected in the kinds of goals that they pursue. In contrast, evolutionary forms of selfishness and altruism are defined in terms of the ultimate *effects* they have on animals' *fitness*, relative to the fitness of other animals affected by the behaviors (recipients). When we ask whether a behavior is psychologically selfish, we are asking how the proximate mechanisms that generate it are designed. When we ask whether a behavior is biologically or genetically selfish, we are asking about its effects on the biological or genetic success of those who emit it. It follows that psychological selfishness and unselfishness pertain to the nature of the *vehicles* created by natural selection (and the mechanisms and adaptations the vehicles contain), whereas biological and genetic forms of selfishness and unselfishness pertain to what ultimately happens to the vehicles as they pursue their proximate goals—whether they survive, produce offspring, and propagate their genes.

Defined strictly, actual effects and consequences of any kind—even profit, pleasure, advantage, and well-being—are irrelevant to psychological selfishness and altruism, except as goals. A psychologically altruistic act could end up benefiting people and making them feel good, and a psychologically selfish act could end up harming people and making them feel bad. To quote Batson (1998), “[T]he pleasure obtained [from a psychologically altruistic behavior] can be a consequence of reaching [the] goal [of benefiting another rather than oneself] without being the goal itself” (p. 300). The behaviors directed at achieving psychologically selfish goals remain psychologically selfish even when they fail to produce the desired results. Behaviors that stem from psychologically selfish motives could end up harming actors and benefiting recipients, and behaviors that stem from psychologically altruistic motives could end up benefiting actors and harming recipients. For example, a coward who fled from battle might be killed, yet distract the enemy to the benefit of his comrades, and a hero who tried to rescue his comrades, but failed, might win a medal of honor.

The second way in which psychological and evolutionary forms of selfishness differ pertains to the types of interests individuals (attempt to) advance. Whereas the interests that evolutionarily selfish behaviors promote are restricted to biological and genetic interests, the interests that psychologically selfish behaviors are directed at promoting are defined more broadly in terms of anything that individuals believe will benefit them. As indicated in dictionary definitions, psychologically selfish behaviors are aimed at accruing such physical, material, and psychological benefits as “profit,” “pleasure,” “well-being,” and “advantage.” Whether the benefits that people seek for themselves end up enhancing their biological and genetic welfare is an open question.

To classify a behavior or form of conduct as psychologically selfish or altruistic, we must decipher the motivational state of the individuals emitting it. This could be accomplished directly by assessing their physiological or neurological reactions, or indirectly by identifying the terminal goals that they are trying to achieve. Deciphering individuals' motivational states is a very difficult undertaking because actors may be in more than one motivational state at the same time and because they may use the same behavior to achieve more than one goal. For example, individuals could be motivated to bestow benefits on both themselves and others. In addition, individuals may use unselfish behaviors to achieve selfish goals (and vice versa). For example, as I will discuss more fully later, individuals may help others instrumentally, as a means of achieving the terminal goal of gaining recipients' approval, impressing observers, relieving vicariously experienced distress, or

elevating their self-esteem. In many contexts, it is difficult to identify the terminal goal of a behavior or choice. You observe one individual helping another; is the helper trying to enhance the welfare of the recipient as an end in itself, or is the helper using the seemingly altruistic behavior instrumentally to achieve some selfish goal? If you scratch an altruist, will you see a hypocrite bleed?

POSSIBLE RELATIONS AMONG GENETIC, BIOLOGICAL, AND PSYCHOLOGICAL FORMS OF SELFISHNESS AND UNSELFISHNESS

As outlined in Figure 15.1, there are eight possible relations among psychological, biological, and genetic forms of selfishness and unselfishness. There is a pervasive tendency to assume that, if an evolved disposition is genetically selfish (or unselfish), it also is biologically and psychologically selfish (or unselfish). This tendency is understandable on conceptual and theoretical grounds. Conceptually, it is natural to assume that selfish is selfish. It seems incongruent or contradictory to characterize the same behavior as both selfish and unselfish. Theoretically, there are good reasons to expect natural selection to produce a correspondence among the different forms of selfishness. We would expect a positive relation between biologically and genetically selfish behaviors because the most direct way for members of sexually reproducing species to propagate their genes is to survive and maximize the number of offspring they contribute to future generations. In addition, as implied in the quotation from *Descent of Man* at the beginning of this paper, it makes sense to expect animals that are psychologically disposed to benefit themselves without regard for others to fare better biologically (and genetically) than animals that are motivated to help others without regard for their own welfare.

The expected correspondences notwithstanding, the three forms of selfishness (and unselfishness) need not *necessarily* be related (Batson, 2000; Dawkins, 1989; Nesse, 2000; Sober & D. S. Wilson, 2000). To quote Sober and D. S. Wilson (1998)

The automatic assumption that individualism in evolutionary biology and egoism in the social sciences must reinforce each other is as common as it is mistaken. More care is needed to connect the behaviors that evolved...with the psychological mechanisms that evolved to motivate those behaviors. (p. 205)

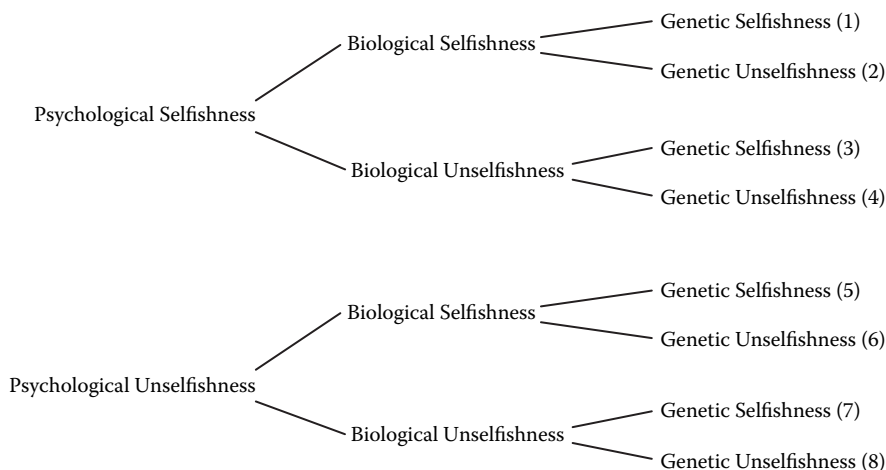


Figure 15.1 Possible relations between genetic, biological, and psychological forms of selfishness.

Whether individuals who seek to obtain benefits for themselves without regard for others fare better biologically and contribute more copies of their genes to future generations than those who behave in less psychologically selfish ways is an open question. They might, or they might not. Certainly, nothing in the process of natural selection dictates that individuals who are motivated to behave in psychologically selfish ways will prevail in the struggle for existence and reproduction.

On the other side of the coin, there is no logical inconsistency in the assertion that behaving in psychologically unselfish ways may pay off biologically and genetically in the end. Cooperative individuals motivated to benefit both themselves and others, and altruistic individuals motivated to help others as an end in itself, could end up being more likely to survive, to produce offspring, and to propagate their genes than individuals who were motivated to help themselves at the expense of others².

Finally, biologically selfish dispositions need not necessarily be genetically selfish. As Dawkins (1989) has explained, “[T]here are special circumstances in which a gene can achieve its own selfish goals by fostering a limited form of altruism at the level of individual animals” (p. 6). Individuals can propagate their genes by sacrificing their survival and reproductive interests for the sake of those who possess copies of their genes.

Conclusions

We can safely conclude that the assertion that all evolved dispositions are selfish is at best valid—or more exactly, true by definition—with respect to genetic forms of selfishness in the types of environment in which they were selected. Changes in environments can render dispositions that were genetically selfish when they were selected genetically unselfish (i.e., maladaptive) when emitted by descendants of those in whom they originated. Because biologically and psychologically unselfish dispositions may be genetically selfish, they can evolve. Genetic benefits trump biological benefits and psychological motives in the evolution of social behavior.

Establishing that animals need not necessarily be selfish by nature does not equate to establishing that they are not, in fact, selfish by nature. Establishing that mechanisms that dispose animals to behave in biologically and psychologically unselfish ways *can* evolve does not equate to establishing that they *have* evolved. It raises a question. What kinds of mental mechanisms enabled the ancestors of humans and members of other social species to solve the adaptive problems they encountered and to propagate their genes most effectively in the social and physical environments in which the mechanisms evolved—mechanisms that enabled or motivated them to benefit themselves at the expense of others, mechanisms that enabled or motivated them to benefit both themselves and others, or mechanisms that enabled or motivated them to benefit others at their own expense. I believe that the answer to these questions is “all of the above mechanisms,” depending on the conditions. I turn now to a consideration of the evidence relevant to first, the evolution of biologically selfish and unselfish dispositions, then to the evolution of psychologically selfish and unselfish dispositions.

² Indeed, psychologically unselfish dispositions could also maximize individuals’ net *psychological* gains. For example, individuals who were motivated to enhance the profit and pleasure of others without consideration for their own profit and pleasure could, over the long run, end up experiencing more *net* profit and pleasure than individuals who possessed more psychologically selfish dispositions. As demonstrated by Rachlin (2002), and others, individuals who make immediately unselfish choices may end up with greater net benefits than those who make immediately selfish choices, because the long-term benefits of moderation and cooperation may exceed those of short-sighted selfishness. Even though the long-term psychological benefits may reinforce the strategies or dispositions that give rise to the unselfish choices, the reinforcement does not render the motivational states or immediate goals of those invoking them psychologically selfish, as long as the individuals who invoke or are guided by them are not motivated to help others as a means of enhancing their own personal welfare when they make the choices in question.

THE EVOLUTION OF BIOLOGICALLY SELFISH AND UNSELFISH DISPOSITIONS

The Selection of Dispositions to Behave in Biologically Selfish Ways

There is no denying the potential in biologically selfish dispositions to help animals propagate their genes. In support of his case for the evolution of selfishness and his case against the evolution of morality, Williams (1989) offered “obvious examples of the pursuit of self-interest as practiced in the biological cosmos,” noting that, “I will need no theoretical subtleties to show their gross selfishness and moral unacceptability” (p. 197). Included in these examples were tendencies for offspring to attempt to obtain more than their share of resources from parents, for males to rape females, and for females to cuckold males: “Recent accounts of reproductive behavior in wild animals are tales of sexual intrigue full of deception, desertion, double-dealing, and sometimes lethal violence” (p. 198). In addition, Williams argued, “[T]he killing of other members of the same species is a frequent phenomenon in a wide variety of forms and contexts” (p. 202). Clearly, humans also behave in the morally repugnant ways described by Williams.

When Williams (1989) adduced evidence that animals behave in ways that seem both psychologically selfish and morally repugnant to support his contention that all evolved dispositions are genetically selfish, he performed a little slight of hand. There are three problems with this tactic. First, even if the morally unacceptable forms of conduct he described were biologically and genetically selfish in the environments in which they were selected, they may not be biologically or genetically selfish in modern environments. Whether individuals who are disposed to take more than their share, steal, cheat, assault, rape, cuckold their mates, and murder members of their groups are more likely than those who behave in more morally acceptable ways to survive, produce more offspring, and propagate their genes is an open question. Behaviors that people consider selfish and morally repugnant—suicide, sloth, and uncontrolled aggression, for example—could diminish individuals’ chances of surviving and reproducing (and therefore qualify as biologically unselfish).

Second, some biologically selfish behaviors are morally acceptable. Consider the often cited mating behaviors of scorpion flies, for example. Although male scorpion flies may resort to rape, they also may foster their reproductive success by giving gifts to potential mates. When they work, both tactics are biologically selfish. Or consider prudential and temperate behaviors such as working hard, delaying gratification, and consuming resources in an optimally healthy manner. Even though these types of behavior may increase the survival and reproductive success of those who emit them relative to (therefore at a cost to) the survival and reproductive success of other members of their groups, they do not seem selfish or morally repugnant. Finally, evidence that some evolved dispositions are biologically selfish does not establish that all evolved dispositions are biologically selfish. Biologically unselfish dispositions could have evolved as well.

The Selection of Dispositions to Behave in Biologically Cooperative Ways

There is no question that cooperative dispositions have evolved in a wide array of social species (Dugatkin, 1997). There is compelling evidence that animals are disposed to coordinate their efforts to solve adaptive problems (mutualism), to exchange goods and services (reciprocity), and to invest in members of their groups (long-term social investments). Let us consider each form of cooperation in turn.

Mutualism. Members of many social species join forces and coordinate their efforts to accomplish such tasks as mating, caring for offspring, increasing status, grooming, hunting large game, attacking competing groups, defending territory, and protecting their groups (for reviews, see Alcock, 2004; Kurland & Gaulin, 2005). The magnitude of mutualism in the human species is unprecedented in the animal kingdom. It takes thousands of people coordinating their efforts to

create a city or to build a dam. Although the biological benefits that those who join forces extend to others may be incidental by-products of efforts to enhance their own biological welfare, this does not render their efforts biologically selfish as long as they have the consequence of increasing the survival and reproductive success of others as well as themselves.

Social exchange. More than three decades ago, Trivers (1971) explained how dispositions to reciprocate could evolve through gains in trade, and he offered evidence that they have evolved in a selection of species. The title of Trivers' (1971) seminal piece on the evolution of reciprocity is "The Evolution of Reciprocal Altruism." Clearly, Trivers was not using the word altruism to refer to biological or genetic forms of altruism. The point of Trivers' paper was to explain how dispositions to exchange goods and services could pay off biologically and genetically under some conditions. Although particular acts of giving and repaying could be viewed as (temporarily) biologically altruistic if they enhanced the biological welfare of recipients at a cost to the biological welfare of donors, these acts become biologically cooperative when recipients reciprocate. "Reciprocal altruism" is a form of biological cooperation.

It is well-established that dispositions to reciprocate evolved in relatively small groups through individual selection in the way described by Trivers (1971). There is, however, considerable controversy about whether the forms of cooperation displayed by humans living in large groups can be accounted for by selection at the level of individuals. On one side, theorists such as Johnson et al. (this volume) argue that reciprocity can evolve in large groups if those who are disposed to cooperate interact selectively with other cooperators. On the other side, theorists such as Richerson and Boyd (2005) and Gintis et al. (this volume) argue that it is not possible to account for the kind of large-scale cooperation displayed by humans without appealing to gene-culture coevolution.

Social investments. Enhancing the biological welfare of mates may help individuals increase their reproductive success because they need them in order to reproduce. In addition, it may be in the adaptive interest of mates to join forces to preserve their mutual biological interests in their offspring. Inasmuch as the biological benefits that members of pair bonds reap are dependent on the welfare of their partners, it may be in their biological interest to foster the welfare of their partners over long periods in order to foster their own ultimate reproductive success (Ellis, 1998).

It also may pay off biologically for members of groups to form long-term, mutually supportive relationships with individuals other than their mates. Several investigators have pointed out that exchanges among friends rarely conform to the principles of concrete reciprocity (Clark & Mills, 1993; Janicki, 2004; Nesse, 2001; Shackelford & Buss, 1996; Tooby & Cosmides, 1996). People do not keep track of every favor they do for their friends, and people are disposed to help their friends when their friends are in need, without expectation of immediate repayment. Tooby and Cosmides have argued that it could be in individuals' ultimate biological interest to contribute to the biological welfare of their friends over long periods if such acts increased the probability that their friends would contribute to their biological welfare when it was in serious jeopardy. In effect, it could pay for people to invest in their friends as insurance policies to foster their long-term security.

In a recent paper, S. L. Brown and M. Brown (2006) reviewed evidence demonstrating that humans are disposed to form affectively laden social bonds with members of their groups, which dispose them support them over long periods, at costs to themselves. S. L. Brown and M. Brown argued that these mechanisms were selected because it is in the ultimate genetic interest of individuals to form relationships with, and feel motivated to support, those on whom their fitness is dependent, whether offspring, parents, mates, friends, or members of one's in-group. Although S. L. Brown and M. Brown consider such social support "altruistic" because at a phenotypic level it involves costs to donors and benefits to recipients, it would qualify as biologically altruistic only if it ended up enhancing the survival and reproductive success of recipients at a cost to the survival and reproductive success of donors. Although this is plausible with respect to social support for kin,

as discussed in the following section, it is not plausible with respect to social support for nonkin, because the biological costs suffered by individuals who help nonkin tend to be outweighed by the biological benefits of sustaining relationships with them, or even simply having them around. As explained by Flack and de Waal (2000),

Inasmuch as every member [of a group] benefits from a unified, cooperative group, one expects them to care about the society they live in, and to make an effort to improve and strengthen it similar to the way the spider repairs her web, and the beaver maintains the integrity of his dam. Each and every individual has a stake in the quality of the social environment on which its survival depends. In trying to improve this quality for their own purposes, they help many of their group mates at the same time. (p. 95)

- Q7 More generally, Laland (2000) has suggested that organisms should be prepared to cooperate with other organisms when the other organisms niche construct in ways that increase their fitness.

In conclusion, there is no question that biologically cooperative dispositions have evolved in humans and other social species. Individuals may increase their chances of surviving and reproducing by joining forces with others to achieve biologically beneficial goals, by initiating and sustaining the exchange of biologically beneficial goods and services, and by investing in those on whom their fitness is dependent. Some behaviors that appear to be altruistic, because they bestow physical and material benefits on others without any immediate return, turn out to be biologically cooperative, because they enhance the biological welfare of both donors and recipients.

The Selection of Dispositions to Behave in Biologically Altruistic Ways

Members of virtually all mammalian species are disposed to help their offspring at costs to themselves. The prolonged dependency of human infants has led to the selection of mechanisms that dispose parents to invest a great deal in their offspring (Flinn & Low, 1986; J. B. Lancaster & C. S. Lancaster, 1987; MacDonald, 1997). Although parental investment is most appropriately classified as biologically cooperative because helping one's offspring contributes to one's own reproductive success as well as to the reproductive success of the recipients—one's offspring—, it seems altruistic when assessed in terms of the willingness of parents to sacrifice their survival interests (most extremely, their lives) for the sake of their offspring. The significance of parental investment is easy to overlook. It provides clear and pervasive proof that dispositions to sacrifice one's own physical and material welfare for the sake of other individuals have evolved in many species.

Kin selection of biologically altruistic dispositions. In an insight that had a profound effect on our understanding of the evolution of altruism, Hamilton (1964) explained that dispositions to help others could evolve if the fitness costs of the behaviors were less than the fitness benefits they bestowed on recipients, weighted by their degree of relatedness ($c < rb$). In effect, Hamilton's rule explicates the "if" conditions built into an evolved strategy. Helping kin (other than offspring) qualifies as biologically altruistic when it reduces actors' survival and reproductive success relative to the survival and reproductive success of recipients.

There is no question that biological forms of altruism can evolve through kin selection, and there is a great deal of evidence that biologically altruistic dispositions have evolved through this process in many species (Kurkland & Gaulin, 2005; Sachs, Mueller, Wilcox, & Bull, 2004; West, this volume). Ethnographic and experimental research on humans has revealed strong positive correlations between degree of relatedness and the probability of engaging in a variety of helping behaviors, including—indeed especially—those that are very costly and life threatening to the helper (Burnstein, 2005; Kurkland & Gaulin, 2005). There is, however, some question about the extent to which such biologically altruistic dispositions can be evoked by nonkin.

The expansion of kin-selected altruism. To help one's kin, one must be able to distinguish them from nonkin, and to accomplish this, animals must rely on kin recognition cues such as familiarity, proximity, and phenotypic similarity (Johnson et al., this volume; Porter, 1987). Early imprinting-like familiarity and facial resemblance appear to constitute especially important cues in humans (Burstein, 2005). There is evidence that nonkin who emit such cues—either incidentally or as a form of manipulation—are able to activate kin-selected altruistic dispositions, thus expanding the range of recipients (see Park, Schaller, & Van Vugt, in press, for a review of relevant literature). The more imprecise the mechanisms of kin recognition are, the more we would expect them to misfire in modern environments, the larger the circle of recipients we would expect to activate them, and the more biologically (and genetically) altruistic we would expect the behaviors to be (cf. Johnson et al., this volume; Krebs, 1987, 1998).

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Although we would expect natural selection to refine kin-recognition mechanisms in ways that decrease fitness-reducing mistakes, the process of refinement would take time. Some theorists (e.g., Johnson et al., this volume; Trivers, 2004) argue that the kin-recognition mechanisms inherited by contemporary humans dispose them to help a large array of nonkin. Theorists such as Gintis et al. (this volume) are skeptical.

Even if animals possessed kin-recognition mechanisms that were perfectly precise, the best most mammals could do is direct their altruism toward recipients who had a 50% probability of sharing their genes. If the process mediating kin selection of altruism involves individuals fostering the fitness of other individuals who possess copies of their genes, why limit it to kin? It would be more efficient for individuals to be able to detect the presence in other individuals of the genes that dispose them to behave altruistically and direct their altruism toward them, whatever their degree of relatedness. Any phenotypic quality that enabled altruistic individuals to identify other individuals who possessed copies of the genes that disposed them to behave altruistically could mediate the evolution of selectively altruistic dispositions³.

Phenotypic manifestations of altruism may supply a more reliable indicator of altruistic dispositions than kinship does. The strategy “if you are disposed to help others, select as recipients of your altruism those who also are disposed to help others” could evolve if there were a reliable relation between the shared genes and shared dispositions in question. As with the evolution of strategies that induce cooperators to cooperate with cooperators, the key to the evolution of such strategies is discrimination in favor of those who adopt similar strategies and possess similar genes.

Group-level selection of biologically altruistic dispositions. Sober and D. S. Wilson (1998) have explained how, in certain conditions, altruistic strategies can evolve through selection at the level of groups. These theorists make the plausible assumption that groups of altruists fare better than groups of selfish individualists, just as pairs of cooperators fare better than pairs of defectors in prisoner's dilemma games. Sober and D. S. Wilson explain how, if groups of altruists were sufficiently large, if the between-group variance in altruism were greater than the within-group variance, and if groups integrated at optimal points in time, the proportion of altruistic genes in the population could increase even though it decreased within all subgroups that make up the population. Although Sober and D. S. Wilson acknowledge that the conditions necessary for between-group selection for altruism to outpace within-group selection for selfishness may be rare in the animal kingdom, they argue that these conditions might well have existed in the human species, augmented by cultural evolution (see also Gintis et al., this volume). Altruistic behaviors that stem from mechanisms designed by group selection qualify as genetically altruistic when they are directed toward selfish members of one's group.

³ It is theoretically possible for a gene to be selected that enabled animals to recognize replicas of itself in others and disposed them to behave altruistically toward those who carried them (the Green Beard Effect); however, most theorists agree that there are significant obstacles to the evolution of such genes (Dawkins, 1989; Kurkland & Gaulin, 2005).

THE EVOLUTION OF PSYCHOLOGICALLY SELFISH AND UNSELFISH DISPOSITIONS

Having adduced evidence that animals that are disposed to behave in biologically selfish ways also may be disposed to behave in biologically cooperative and altruistic ways, I turn to a different question, pertaining to the ways in which the mechanisms that give rise to social behaviors are designed. I ask whether mechanisms have evolved that dispose individuals (a) to seek to benefit themselves without regard for others, (b) to seek to benefit both themselves and others, and (c) to seek to benefit others as an end in itself. In contrast to biological questions about the consequences of social behaviors, psychological questions pertain to the nature of the motivational states generated by evolved mechanisms and the types of goals they induce people to pursue.

The Selection of Psychologically Selfish Dispositions

If people were asked to give examples of psychologically selfish behaviors, they probably would list the kinds of behaviors described by Williams (1989) as evidence of the “triumph of selfishness”—behaviors that stem from motivational states such as those that define the seven deadly sins (i.e., wrath, lust, gluttony, envy, sloth, pride, and greed). There is no denying that humans and other animals are sometimes driven by morally repugnant motives that induce them to seek to benefit themselves without consideration for others. However, there is more to human nature (and to the nature of other animals) than dispositions to behave in nasty and brutish ways. Although there are contexts in which individuals who seek to maximize their benefits without regard for others fare better biologically and genetically than those who behave in less psychologically selfish ways, the adaptive potential in short-sighted, unrestrained, and unconditional selfishness is limited in several ways.

Adaptive Limitations of Short-Sighted Selfishness

The unmitigated pursuit of pleasure may be dangerous to one's health. For example, gluttony and the unconstrained consumption of alcohol and drugs may jeopardize people's survival and reproductive success (Burnham & Phelan, 2000; Crawford, this volume). Unrestrained promiscuity may jeopardize animals' reproductive success (see Gangestad, this volume; Lack, 1954). Individuals who resist the temptation to maximize their pleasure without consideration for others may fare better biologically than those who behave in self-indulgent and hedonistic ways.

An important limitation of selfish behaviors—especially those that people consider morally repugnant—is that they tend to evoke costly reactions from others. Two animals bent on maximizing their profit by taking more than their share of resources or by exploiting one another could end up in a conflict that diminished their survival and reproductive success—an outcome that is modeled in prisoner's dilemma games in which two players making selfish choices gain fewer points than two players making cooperative choices (Axelrod & Hamilton, 1981). In addition, animals that try to maximize their benefits at the expense of others may provoke their intended victims and other members of their groups to punish them—by refusing to help them when they are in need (Nowack & Sigmund, 1998), by inflicting physical and material sanctions on them (Gintis et al., this volume), by turning others against them, and by ostracizing them from their group (Alexander, 1987).

More indirectly, selfish motives to maximize one's benefits without regard for others may destroy beneficial relationships, undermine coalitions, and diminish the welfare of one's group as a whole, thereby jeopardizing the social environment that one needs to survive and reproduce. In contrast, less selfish motives to help one's friends and other members of one's group may help preserve valuable resources, and therefore pay off physically, materially, biologically, and genetically in the end.

Further, it is important to remember that the evolutionary consequences of motivational states, decision-making strategies, and forms of conduct are a function of the net genetic costs and benefits

to the actor and to everyone else affected by the actor's behavior, including those with the same genes. Although we would expect psychologically selfish motives to be selected when they induced individuals to behave in ways that helped them propagate their genes at the expense of those who possessed alleles of their genes, we would not necessarily expect them to be selected when they induced individuals to behave in ways that jeopardized the genetic success of those who possessed copies of their genes.

The adaptive limitations of psychologically selfish forms of conduct open the door for the selection of dispositions to behave in psychologically unselfish ways. Although the biological benefits that animals behaving in biologically cooperative and altruistic ways bestow on others could be by-products of their desire to benefit themselves, this is neither the only, nor the most plausible, possibility. If we assume animals that benefit themselves biologically are motivated to benefit themselves, why not assume animals that benefit others are motivated to achieve this goal?

In conclusion, although psychologically selfish forms of conduct may be adaptive in some conditions, they are limited in other conditions. For this reason, we would expect the mechanisms regulating selfish (and unselfish) forms of conduct to be designed in terms of "if-then" types of decision rules. The key to understanding human nature and the nature of other animals lies in deciphering the design of these mechanisms, mapping the ways in which they are shaped during development, and identifying the internal and external stimuli that activate them in everyday life.

The Selection of Psychologically Cooperative Dispositions

Cooperative social exchanges may produce three beneficial consequences: benefiting actors, benefiting recipients, and benefiting the partnership or group involved in the exchange. Identifying the motives of those involved in cooperative exchanges is challenging because individuals may employ seemingly altruistic and cooperative tactics to achieve selfish goals. Although those who engage in social exchanges may sometimes—perhaps even often—seek to maximize their net gains without regard for others, there is evidence that they also may be motivated (a) to maximize the joint gains of their partners and themselves, (b) to repay those who have helped them, and (c) to foster fair outcomes, as ends in themselves.

Seeking to Maximize Mutual Benefits

If people were driven by selfish motives, we would expect them to try to obtain as much as possible for themselves and to give as little as possible in return, either on individual exchanges or over the long run. However, many studies have found that in some contexts individuals choose to take less than they could for themselves in order to maximize the net benefits of everyone involved in the exchange, even when they engage in such behaviors anonymously and never expect to see their exchange partners again. As one example, Fehr and Gächter (2002) found that when game players were given an opportunity to contribute some of their winnings anonymously to a common pool that was doubled by the experimenter and shared equally among members of their group regardless of their contributions, players tended to contribute approximately half of their earnings, even though they could have maximized their gains by contributing nothing (for additional examples, see Gintis et al., this volume; Johnson et al., this volume).

Those who seek to maximize joint gains rather than their own gains may be driven either by the desire to be fair, which I will discuss in the following section, or by the desire to enhance the welfare of a unit with which they identify. Social psychologists have found that people are disposed to identify with those with whom they have formed social bonds, view themselves in terms of units that contain both themselves and others—whether it be a partnership, a team, or an in-group—and feel motivated to promote the welfare of the unit, as an end in itself (A. Aron & E. N. Aron, 1986; Cialdini et al., 1976; Richerson & Boyd, 2001; Schaller & Neuberg, this volume; Tajfel & Turner, 1985). In such cases, people view their outcomes in terms of how "we" fare against "them," instead of how "I" fare against "you." Although the motivation that drives people to help the groups with

which they identify could be considered selfish (a) because the individuals view themselves in terms of their groups and seek to benefit this aspect of their sense of self or (b) because they are motivated to help their groups in order to foster their own welfare, studies have found that members of groups often choose to uphold the interests of their groups at a cost to themselves (see Gintis et al., this volume; Johnson et al., this volume).

Seeking to Reciprocate

Social psychologists have concluded that receiving assistance from others may evoke two qualitatively different affective reactions—feelings of indebtedness and a sense of gratitude. Feeling indebted is unpleasant. It motivates people to pay others back as a means of reducing aversive arousal (Greenberg, 1980). In contrast, feelings of gratitude are pleasant. They motivate people not to help not only those who benefited them but also third parties (McCullough, Kilpatrick, Emmons, & Larson, 2001). Helping behaviors that stem from feelings of gratitude would qualify as psychologically unselfish if their terminal goal were to benefit recipients, or to benefit third parties, even if the behaviors had the incidental effect of increasing recipients' or observers' desire to proffer additional assistance to those who expressed gratitude.

If those who engage in reciprocal exchanges were motivated to maximize their own gains, we would expect them to be more concerned about being paid back than about paying back, and we might expect them to overestimate the value of the goods they give to others and underestimate the value of the goods they receive in return. However, studies on social exchange between friends have found the opposite. For example, Janicki (2004) found that participants underestimated the costs of giving to their friends and overestimated the value of the benefits they received. In addition, they reported feeling more upset when they failed to pay their friends back than they did when their friends failed to pay them back.

Seeking to Foster Fair Outcomes

When people reciprocate, they are, in effect, making things even—balancing the scales. More generally, justice involves ensuring that people get what they deserve. Social psychologists have attempted to determine whether people possess a “justice motive” that disposes them to promote equity and fairness, as an end in itself, even when it is costly for them to do so. Many studies have found that people who are given the choice between maximizing their own immediate gains and distributing resources in a fair and equitable manner opt for the latter (Greenberg & Cohen, 1982). The question is are people motivated to uphold justice as an end in itself or are they motivated to use justice instrumentally as a “tool of self-interest” (Lerner, 2003, p. 388). Research on equity, retribution, and third-party punishment suggests that people may be intrinsically motivated to uphold justice.

Seeking equity. Research aimed at identifying the motives that induce individuals to promote equitable outcomes has produced mixed results. Compare, for example, studies by Adams (1963) and Rivera and Tedeschi (1976). Adams found that workers performed better when they were paid more than they deserved and concluded that the workers were motivated to bring about a fair outcome rather than to maximize their own gains. In contrast, Rivera and Tedeschi found that although workers who publicly evaluated payments that they and others received after doing the same amount of work reported feeling more pleased with fair outcomes than with outcomes that favored them, workers who evaluated the payments in private, when hooked up to a lie detector, said they felt happier when they received more than their share.

In a recent paper, Lerner (2003) offered an explanation for the inconsistencies in the findings on research on equity and justice. Lerner adduced evidence that when people are faced with

high impact contexts: those situations involving serious deprivation, suffering, loss of esteem, humiliation, or significant amounts of desired resources...the awareness of an injustice can elicit several emotions: anger, guilt, shame, disgust, contempt, sadness...[and that] people are impelled to act on those emotions and are motivated to eliminate or rectify the injustice. (p. 394)

In contrast, in low-impact contexts in which people have the opportunity to reflect before passing judgment or making a decision, they may behave in more rationally self-serving ways. Note that in contrast to cognitive-developmental theorists, such as Gibbs (2006), who argue that justice-upholding behaviors stem from uniquely human, sophisticated forms of moral reasoning, the data that Lerner (2003) adduces suggest that justice-upholding behaviors are the product of phylogenetically primitive affective reactions shared by humans and other animals (cf. Frank, this volume; Haidt, 2001; Krebs, 2007; Krebs & Denton, 2005).

Seeking retribution. An important implication of the idea that people are motivated to uphold justice is that they will be motivated to redress injustices. We know that people feel angry and indignant when others exploit them and that they may seek to get even. The immediate aim of vengeful behavior may be to hurt the exploiters or to repair a damaged reputation, which seems psychologically selfish. However, retribution also could be a means to a less selfish end, namely restoring balance and upholding justice by evening the score.

Seeking to punish wrongdoers. Researchers have adduced an impressive array of experimental and naturalistic evidence that people possess an other regarding “predisposition to cooperate with others, and to punish those who violate the norms of cooperation, at personal cost, even when it is implausible to expect that these costs will be repaid” (Gintis, Bowles, Boyd, & Fehr, 2003, p. 153)—a phenomenon Gintis et al. call “strong reciprocity.” For example, game theorists have found that in ultimatum games in which one player decides how to divide a pot of money and another decides whether to accept the division or to return all the money, players reject unfair offers (which punishes the player making the offer) even though it costs them to do so (see Gintis et al., this volume, for additional examples). Consistent with these findings, Lerner (1983) found that participants chose to forgo opportunities to make money in order to punish an individual who had abused their (fictitious) partner. As pointed out by Gintis (in press), such behaviors defy rational choice theory only if we assume that people’s preferences are narrowly self-regarding. It is rational to behave fairly if one’s goal is to be fair.

The Selection of Psychologically Altruistic Dispositions

If natural selection designed mechanisms equipped to generate psychologically altruistic motives, the mechanisms that dispose animals to help their offspring and other kin seem like the most promising candidates. Although animals may enhance their inclusive fitness by helping their kin, they are not aware of this ultimate goal, nor do they seek to pursue it as an end in itself. Animals, in effect, do not say to themselves, “I will try to maximize the number of genes I contribute to future generations by helping those who possess copies of my genes.” Although animals may sometimes feel good about helping their kin, Sober and D. S. Wilson (1998) have argued that it would have been more efficient for natural selection to have designed a psychological system that motivates animals directly to help their kin than to design a psychological system that motivates them help their kin in order to maximize their pleasure. Animals may be willing to suffer significant pain and even death to assist their kin.

Although psychologically altruistic motivational states could be generated in humans from higher order cognitive processes such as moral reasoning, altruistic states could not be generated by these processes in other animals, because they do not possess them. In humans and in other

animals, psychologically altruistic motives appear to stem primarily from mental mechanisms that give rise to affective states such as those we call love, loyalty, sympathy, empathy, and so on. As implied in the earlier discussion of biological altruism, after a psychological system that motivates individuals to help their kin evolved, it could have been activated by those who resemble kin. In support of this possibility, studies have found that humans are disposed to empathize with, feel loyalty to, and love those whom they view as similar to them, those with whom they grew up, those with whom they identify, those with whom they have formed affectionate bonds, and so on (Batson, 1991; Decety, 2005; Fischer, 2004; Richerson & Boyd, 2001).

It is well-established that individuals are disposed to help those who evoke affective states such as love and empathy (Batson, 1998). Psychologists have attempted to determine the nature of the motives generated by these affective states. Do these affective states dispose individuals to help others as an end in itself, or do they dispose individuals to help others as a means to other ends, such as promoting their long-term interests or making themselves feel good? This question has been addressed most extensively with respect to the motivational state generated by empathy.

Empathically-Induced Altruistic Motives

Batson (1991) and his collaborators hypothesized that empathy triggers an altruistic motivational state that induces people to want to help those with whom they empathize, as an end in itself, as opposed to wanting to help them instrumentally in order to achieve egoistic goals. To test the “empathy-altruism hypothesis,” Batson and his colleagues designed more than two dozen experiments, some of them quite ingenious, in which they induced groups of participants to empathize with victims (e.g., by inducing them to take their perspective or by leading them to believe they were similar to them), then provided them with ways of achieving a variety of egoistic goals in less costly ways than by helping the victims.

Q11 Consider some examples. To determine whether those who empathize with others help them in order to gain social approval or to avoid disapproval, Batson and his colleagues compared the amount of helping in public and private conditions. To determine whether high-empathy participants help in order to reduce their own vicariously experienced aversive arousal, Batson and his colleagues offered them an opportunity to reduce their arousal by terminating their exposure to the victim or by leaving the experiment. To determine whether empathizing people help in order to avoid self-censure, Batson and his colleagues offered them personally and socially acceptable reasons and justifications for not helping. To determine whether those in empathic states help in order to feel good about themselves, Batson and his colleagues, assessed the mood of participants after they learned that third parties helped victims. Without exception, the studies conducted by Batson and his colleagues supported the empathy-altruism hypothesis.

Q12 Batson and his colleagues challenged skeptics to demonstrate that those who empathize with others will choose to pursue self-serving goals rather than to help victims when given the opportunity or that they will help victims only when this option provides the most effective way of achieving self-serving goals. Researchers such as Cialdini et al. (1987) and Schaller and Cialdini (1988) claim to have met this challenge, adducing evidence that people help distressed victims with whom they empathize in order to relieve the negative state of sadness that they experience, but Batson and his colleagues (e.g., Batson et al., 1989) have disputed their conclusions (see also Dovidio, Allen, & Schroeder, 1990). Although Batson and his colleagues have been remarkably successful at rejecting hypotheses pertaining to the most plausible sources of selfishness, no one will ever be able to prove that empathically aroused people are not motivated to achieve some subtle selfish goal not assessed by the experimenter.

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CONCLUSION

What, then, is the answer to the question addressed in this chapter: How selfish are humans and other animals by nature? The answer implied by my analysis of the nature of selfishness and the evolution of social dispositions is, more or less, depending on the type of selfishness in question and the extent to which individuals are exposed to the conditions in which it is activated. All dispositions that help individuals propagate their genes are genetically selfish by definition. However, individuals may inherit dispositions that, though genetically selfish in the environments in which they were selected, may misfire in modern environments, produce unselfish by-products, and give rise to maladaptive, genetically unselfish behaviors.

Because natural selection tends to design animals to behave in ways that foster their survival and reproductive success, most evolved dispositions are biologically selfish. However, dispositions to behave in cooperative ways that foster others' biological success in addition to one's own also have evolved in many social species. Cooperative dispositions probably played a pivotal role in the evolution of the human species (Leakey & Lewin, 1977; Tooby & DeVore, 1987). In addition, the evidence strongly suggests that biologically altruistic dispositions have evolved through kin selection, perhaps augmented by selection at the level of groups; and that these dispositions may be activated by nonkin.

When it comes to questions about human nature, people are rarely concerned about biological and genetic forms of selfishness. What they want to know is whether humans and other animals are naturally disposed to advance their own profit, pleasure, well-being, and advantage without consideration for others. That people are disposed to behave in ways that propagate their genes and foster their biological welfare is only tangentially relevant to this question. What is relevant is how the mechanisms that dispose people to behave in fitness-enhancing ways are designed, and how people go about achieving fitness-enhancing goals. The evidence establishes unequivocally that, in conducive conditions, people are motivated (a) to divide resources in fair and equitable ways, even when they could take more than their share without adverse physical, material, or social costs; (b) to reciprocate, even when they end up giving more than they receive; (c) to punish those who violate norms of fairness, at a cost to themselves; and (d) to help their relatives, friends, and in-group members over long periods without tangible compensation. The evidence also clearly establishes that in conducive conditions, people are disposed to suffer considerable pain, and even death, in order to help those for whom they care and with whom they empathize.

It remains unclear whether people who sacrifice their interests for the sake of others are driven by the desire to achieve internally rewarding goals such as allaying their sadness, making themselves feel good about themselves, upholding their values, and behaving in ways that are consistent with their identity; but with regard to judgments about human nature, does it really matter? Although there is theoretical and practical value in mapping the motivational states and identifying the terminal goals that drive prosocial and altruistic behaviors, establishing that people help others in order to uphold their identity or their values would not detract significantly from the nobleness of human nature. Even if, on a strict definition, such motives turned out to be psychologically selfish, virtually no one would consider those who are driven by them selfish in any morally deficient way.

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