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The Evolution of Generosity: How Natural Selection Builds Devices for Benefit Delivery

WHY DO WE CELEBRATE DARWIN DAY BUT NOT ARISTOTLE DAY OR Newton Day or Descartes Day? The reason Charles Darwin is special enough to deserve a toast every February 12, quite simply, is because he came up with what philosopher Daniel Dennett has called "the single best idea anyone has ever had" (1995: 21): a purely naturalistic means of explaining why living things bear features that make them appear as if they had been *designed* (West, Griffin, and Gardner 2007). Darwin's fundamental contribution to science was to identify a mindless, physical process that could produce complex, functional design, which he called *natural selection*.

To understand natural selection, it is useful to think of genes as replicating entities that, through repeated generational cycles of replication, mutation, and selection for variants that confer beneficial fitness effects on their bearers, come to build "devices" around themselves. These phenotypic design features, which are "devices" in the sense of having a complex ordering of interrelated and hierarchically organized parts that cooperate to efficiently and elegantly accomplish some task, are how genes "take action" in the world, which eventuates in their increased reproductive success. And, it is through the increased reproductive success of the genes that produce these design features that those features become species-typical (West, Griffin, and Gardner 2007; Dennett 1995; Dawkins 1976).

The reality of natural selection as a biological process means that genes (or combinations of genes) that cause organisms to build traits that increase those genes' rates of replication—so-called *adaptations* (Williams 1966)—themselves will become increasingly common in any population of genes. Consequently, organisms will, through the process of natural selection, come to bear traits that appear as if they were designed to increase the organism's reproductive success.

NATURAL SELECTION AND THE EVOLUTION OF BENEFIT-DELIVERY DEVICES

One of the perennial sources of fascination for evolutionary biologists is the realization that even though genes are "selfish" (in the sense that natural selection causes them to come to encode recipes for traits that cause the organisms in which they reside to act in ways that benefit the genes' own replication), the traits they create need not be (Dawkins, 1976): natural selection's action on genes can cause the evolution of traits that cause organisms to interact with other organisms in cooperative, generous, and even self-sacrificial ways. This is because there are many ways that delivering benefits to other individuals in the world ultimately boost the replication rates of the genes that create these forms of generosity. Here we use the term *benefit-delivery devices* to refer to the class of biological systems that evolved through natural selection, at least in part, because of the benefits they caused organisms to deliver to other organisms.

WHY BENEFIT DELIVERY IS AN EVOLUTIONARY PROBLEM

Benefit-delivery devices pose a problem for evolutionary theory because organisms that possess such devices should, all else being equal, experience less reproductive success than an organism that does not possess such devices. This is because delivering benefits to other individuals prevents the benefit deliverer from using those resources to advance its own reproductive efforts. Consequently, it should be impossible for mutant genes that cause organisms to deliver benefits to others to overtake a population of genes that do not create such benefit-delivery devices; furthermore, even if a species did acquire a gene that caused it to deliver benefits to others, that gene would easily be overtaken by a new mutant gene that prohibited its bearer from doing so.

Nevertheless, it is self-evident that many organisms (including humans) *do* possess devices for benefit delivery (including the cognitive ones that motivate us to care about other individuals), so a cardinal task for evolutionary science, at least as far as cooperation is concerned, is “explaining how the actual is possible” (Rosenberg 1992, 19). Evolutionary scientists who study cooperation try to determine how natural selection builds benefit-delivery devices, which usually involves trying to identify the routes by which the genes that give rise to those benefit-delivery devices are “rewarded” through enhanced reproductive fitness. In general, evolutionary biologists divide the fitness benefits that enable mechanisms for cooperation to evolve through natural selection into two broad types: direct fitness benefits (that is, the organism enjoys better reproductive success because of an allele [variant of a gene] that causes it to deliver benefits to others), and indirect fitness benefits (that is, the organism’s direct reproductive success is reduced by possessing an allele that causes it to deliver benefits to others, but the reproductive success of other individuals who also share the same allele increases, thus promoting the replication of the allele overall). The sum of direct and indirect fitness benefits is referred to as *inclusive fitness* (Hamilton 1964). In the remainder of this article we will describe first some of the direct fitness benefits, and then the indirect ones, that can lead to the natural selection of benefit-delivery devices. We also describe what is currently known (or conjectured) about the circuit logic governing the operation of naturally selected cognitive mechanisms that regulate benefit deliver. We close with a brief treatment of the concept of group selection and its value for social research on the evolution of benefit-delivery devices in humans.

NATURAL SELECTION OF BENEFIT-DELIVERY DEVICES THROUGH DIRECT FITNESS BENEFITS

In evolutionary biology, a behavior is "social" when the mechanisms that motivate it evolved in part because of the effects of its behavioral outputs on other organisms. When genes give rise to benefit-delivery systems that motivate generosity because those systems boosted the replication rates of the ancestral copies of the genes that govern their assembly and operation, evolutionary biologists talk about *mutually beneficial* cooperative traits. Mutually beneficial traits evolve by natural selection because the beneficial effects of those traits on other individuals in turn cause (by virtue of second-order effects) an increase in the reproductive success of the genes that build the trait within actors. It is worthwhile here to distinguish between systems that evolved for the function of delivering benefits to others (that is, systems whose function is to increase others' reproductive fitness) and systems that evolved for other functions, but which cause benefits to flow to other individuals incidentally in the course of executing their evolved functions. For example, elephants make available to dung beetles a substance that dung beetles recognize as a benefit—elephant dung—but it would be silly to conclude from this observation that elephants defecate for the purpose of delivering benefits to dung beetles. Instead, the benefit is a benefit only because dung beetle's evolved to make the most of elephants' waste products (West, Griffin, and Gardner 2007).

Thus, it is wise to restrict our definition of benefit-delivery devices to those that have been designed via natural selection specifically *for* the beneficial effects they deliver to others (West, Griffin, and Gardner 2007). That is, some behaviors that are often mistaken as examples of "cooperation" or "generosity" or "altruism" in human behavior might merely reflect (a) actors' pursuit of their own direct fitness interests without regard to their effects on others' fitness, and (b) others' opportunism in reaping fitness benefits for themselves from the actors' behavioral by-products. Following someone home when you have become disoriented is a costless enterprise for the person whom you follow back to camp, for instance. She pursues her own self-interest by getting herself back to camp—without regard to your welfare—while you pursue yours by following the path she takes. Thus, readers will do well to stay mindful of the fact that some apparent examples of benefit delivery are not produced by benefit-delivery devices at all. Here, we hold such by-product examples of "benefit delivery" aside and focus instead on some of the ways in which benefit-delivery devices can be explained in terms of the direct fitness benefits they secure for the genes responsible for building them. These include reciprocity, the extensions to reciprocity that might have emerged from humans' specialization in the cognitive niche, and group augmentation.

Reciprocity

The most commonly studied route by which benefit-delivery devices could have evolved in humans via natural selection is reciprocity (Trivers 1971). The Prisoner's Dilemma, in which two players are presented with a choice to cooperate with, or defect against, each other, nicely illustrates how reciprocity can generate benefits. If both players cooperate, they each receive a moderate payoff; if both defect, they each receive a small payoff; if one player defects and the other cooperates, the defector receives a large payoff and the cooperator receives the smallest possible payoff (the "sucker's payoff"). Due to this payoff structure, defection always yields the highest average payoff in a one-shot interaction (that is, an interaction that will not be repeated). However, if the game consists of multiple rounds of iterated play, mutual cooperation can lead to higher average payoffs than mutual or alternating defection (Axelrod and Hamilton 1981; Trivers 1971). When one thinks about these payoffs in the currency of "lifetime reproductive success," we can see how the prisoner's dilemma also illustrates how reciprocity might cause the evolution of benefit-delivery devices via natural selection.

Axelrod and Hamilton (1981) demonstrated that the iterated prisoner's dilemma provides a game-theoretic model for the evolution of direct reciprocity. Mechanisms that deliver benefits to others via direct reciprocity (as modeled in the iterated prisoner's dilemma) can evolve by natural selection when the probability of a successive round of interaction between two individuals (that is, the probability that two individuals will interact again in the future) exceeds the ratio of the lifetime fitness cost of the benefit delivery to the donor divided by its lifetime fitness value to the recipient. Results from more recent models suggest that a bias to cooperate, even when one faces cues of an interaction being one-shot, should be expected to co-evolve with reciprocity. This is because mistaking a one-shot interaction for a repeated interaction is a less costly error than the reverse—that is, it is much more costly to miss out on the long-term benefits that can be obtained through repeated gains in trade than it is to be exploited in a single interaction (Delton et al. 2011).

With a few possible exceptions, reciprocity appears relatively unimportant for understanding cooperation in most nonhuman animals (Clutton-Brock 2009; West, Griffin, and Gardner 2007). However, reciprocity is arguably very important for understanding the evolution of human cooperation because much of human social interaction involves long-term relationships among nonrelatives (such as in the contexts of hunting, foraging, territory defense, dwelling construction, food preparation, and child care). For example, pooling risk and effort for hunting by sharing the spoils with others, on the condition that recipients of benefits at one point in time reciprocate in the future, is much more efficient than solitary hunting to provision only oneself and one's close kin. This is because hunting is a relatively high-variance method of food acquisition: among extant hunter-gatherer groups, individual probabilities of failed hunts on any given day range from 40 percent to 96 percent (Gurven et al. 2012). Reciprocal cooperation in such circumstances can reduce or eliminate the variance in individual food availability, leading to direct benefits for recipients (through immediate acquisition of food) and benefactors (by motivating reciprocal help at a later date).

Although reciprocity can provide mutual direct benefits through gains in trade, it also exposes cooperators to the possibility of exploitation—that is, to interacting with individuals who will take benefits without reciprocating them at a later time (Cosmides 1989; Trivers 1971). The dangers of exploitation may be particularly acute in humans, for humans possess zoologically unusual cognitive capabilities such as language, mental time travel, the ability to infer others' goals and psychological states, and the ability to infer the social consequences of their (and others') actions. These cognitive capacities might make it easier for humans to evolve mechanisms for exploiting other individuals' cooperative dispositions.

Were such exploitive abilities to evolve, they would set the stage for evolutionary arms races in which natural selection might consequently favor the evolution of mechanisms that implement defensive tactics for resisting or deterring exploitation. To the extent that natural selection has indeed produced adaptations for exploitation and counter-exploitation in reciprocal interaction, all neurologically intact humans can be expected to possess the full suite of exploitive and counter-exploitive mechanisms. Such subsidiary cognitive mechanisms might include perceptual systems that identify likely reciprocators (for example, kin detection; Lieberman, Tooby, and Cosmides 2007) that inhibit individuals from helping likely nonreciprocators (Cosmides 1989), and that motivate the punishment or termination of interactions with nonreciprocators (West, Griffin, and Gardner 2007). Additional mechanisms might include capacities for remembering the outcomes of cooperative interactions (for example, classifying those actions with respect to whether they violated social contracts), as well as motivational systems for impelling cooperation, reciprocal return of benefits, and the punishment of cheaters (Trivers 1971).

It is worth keeping in mind that the prospect that a given benefit-delivery system evolved via reciprocity (that is, by virtue of the fact that benefit/cost ratio exceeded the probability of repeat encounters between the actors in the environment in which the mechanism evolved) tells us nothing, in and of itself, about how the resultant cognitive mechanisms implement their functions. A reciprocity-based benefit-delivery system could (theoretically) simply entail, for instance, a cognitive system that compares one's own language or accent to the language or accent of a potential reciprocity partner—since facility with the same language was likely very highly correlated with geographic locale, and thus, the likelihood of meeting again (Pagel and Mace 2004)—and that motivates benefit-delivery toward individuals whom one determines to speak in a language or with an accent that is suitably similar to one's own (Nettle and Dunbar 1997). It is the job of evolutionary behavioral scientists to empirically determine the circuit logic that governs the operations of these systems; the theories of social evolution do not themselves prescribe how they should be cognitively or neurally instantiated (Scott-Philips 2007).

OCCUPYING THE COGNITIVE NICHE FAVORS THE EVOLUTION OF INDIRECT RECIPROCITY

Tooby and DeVore (1987) proposed that humans evolved to exploit a "cognitive niche"—that is, a way of life for which natural selection resulted in problem-solving mechanisms that enable organisms to formulate in real time (rather than over evolutionary time) novel strategies for surmounting the fixed defenses of other organisms (for example, the toxins in otherwise edible plants or the defensive weaponry of potentially edible animals), and in so doing, extract resources from them. Pinker (2010), in particular, proposed that humans succeed in exploiting the cognitive niche due to a suite of zoologically exceptional cognitive adaptations that include technological problem-solving and grammatical language. With these adaptations in place, new adaptive space opens up in which new variations on reciprocity can plausibly evolve.

For example, once language has evolved, information about third parties' previous cooperative behaviors can be efficiently transmitted orally from someone who has acquired direct (or even indirect) knowledge bearing on this issue ("Maggie is just so stingy . . .") to third parties who lack such knowledge. If people subsequently were to come to possess, via natural selection, psychological mechanisms that motivated them to adjust their cooperative behavior on the basis of such reputational information, they could avoid the costs associated with providing benefits to nonreciprocators. Indeed, people do use third-person information to preferentially cooperate with those who have cooperated with others, but only when they lack first-person experience (once first-person experience is acquired, third-party information becomes irrelevant; Krasnow et al. 2012). This sets the stage for the evolution of so-called indirect reciprocity (Nowak and Sigmund 1998), which results in individuals who appear as if they are motivated to *reward* individuals for their previous cooperative behavior toward other beneficiaries—when what they are really doing is streamlining their own efforts to benefit from reciprocal interaction by directing benefits toward individuals who have proven themselves to be trustworthy reciprocators.

GROUP AUGMENTATION

In some animal species, members of stable social groups provide care (that is, deliver benefits) to offspring that are neither their own offspring nor the offspring of close genetic relatives (Clutton-Brock 2002). Although such behavior at first seems puzzling, a closer look at the consequences of reproductive support reveal several routes by which the genes that build the mechanisms that motivate such behaviors could be favored by natural selection. First, providing reproductive support can increase helpers' direct fitness by increasing their chances of survival (Grinnell, Packer, and Pusey 1995) or yielding allies if they migrate from their natal groups to begin their reproductive careers elsewhere (Clutton-Brock 2002). Second, by contributing to group survival, nonreproductive members can increase the likelihood that helpers will be available to aid their own reproductive efforts if they should ever become one of the group's reproductive members (Clutton-Brock 2002).

Humans are not cooperative breeders, of course: ancestral human societies are not characterized by castes of nonreproductive helpers. Even so, group size itself might nevertheless have been an important source of direct fitness benefits for ancestral humans. For example, studies with nonhuman animals suggest increases in group size can increase the fitness of all group members because larger groups can be better at obtaining (and retaining) food (Clutton-Brock 2002), spotting and defending against predators (Clutton-Brock 2002), defending breeding sites against takeovers (Port, Kappeler, and Johnstone 2011), and rearing offspring. Because of the direct benefits to individuals in the group that might accrue simply by virtue of the group's expanding, it can be beneficial for helpers to provide care for unrelated offspring in order to help in increasing the size of the group. In addition to direct benefits from so-called group augmentation, provisioning benefits to young can also be repaid via "delayed reciprocity," or benefits provided to the helper by offspring who have reached adulthood. Although the importance of group augmentation as an evolutionary route to the evolution of humans' cooperative instincts is currently unknown, it has received less attention than it merits (Port, Kappeler, and Johnstone 2011).

NATURAL SELECTION OF BENEFIT-DELIVERY DEVICES THROUGH INDIRECT FITNESS BENEFITS

The classical Darwinian notion of natural selection has seen only one major theoretical refinement. This refinement resulted from efforts by biologists to understand how traits that reduce their bearers' direct reproductive success can evolve. The existence of sterile worker castes, for example, along with less extreme instances of organisms that pay fitness costs in order to provide fitness benefits to others, caused evolutionists to eventually realize that the scope of natural selection was broader than they had originally realized: natural selection's partiality for a gene is determined not only by how that gene affects the reproductive success of the individual organism in which it resides, but also by how it affects the reproductive success of replicas of itself that are locked inside *other* organisms—namely, genetic relatives of the donor individual. Decades later, Hamilton (1964) showed mathematically that natural selection builds complex functional design by favoring mutant genes that cause traits that boost those genes' *inclusive fitness*, which is the sum of *direct fitness* (a genetic variant's success in creating replicas of itself) and *indirect fitness* (its success in assisting other copies of itself—

located inside offspring and siblings and cousins and other relatives—to replicate).

Hamilton's major insight—later dubbed *Hamilton's rule*—was that a new genetic mutant that reduces its bearers' direct reproductive success can evolve by natural selection if the lifetime reproductive benefit b it confers to all recipients, discounted by the average degree of relatedness r between the actor and all recipients (which is really shorthand for "the probability that the recipients of the benefit share the new genetic variant that is responsible for causing the benefit-delivery"), exceeds the lifetime reproductive cost c that the trait imposes upon the actor—that is, when $rb - c > 0$. Traits that evolve by adhering to Hamilton's rule can be said to have evolved through "kin selection," as common ancestry (kinship) is the most common reason why two individuals share a genetic variant. Because they evolve through the accumulation of genes that cause organisms to provide benefits for other individuals that the donors could otherwise use to pursue their own reproductive agendas (with benefits and costs referring to *lifetime* fitness consequences), kin-selected traits can rightly be said to evolve through an "altruistic" pathway of natural selection (West, Griffin, and Gardner 2007).

Adaptations for Parental Care as Altruism Devices

Some of the clearest illustrations of altruistically designed biological devices are adaptations for parental care (Dawkins 1979, 1976), and here we dwell on them in some detail. "Parental care" refers to the full suite of anatomical, physiological, and behavioral adaptations whose function is to cause parents to invest in the fitness of their offspring (Clutton-Brock 1991). For many biologists who study parental care, it seems intuitively wrong to think of adaptations for parental care as "altruistic." They often argue that when an organism provides parental care it is simply pursuing the maximization of its own direct fitness, with direct fitness being defined as the number of the organism's offspring that reach reproductive maturity. Nevertheless, evolutionary geneticists have good reasons to think that the production of zygotes (the cell that results from the union of egg and sperm) is a better measure of an individual's fitness than is the number of their offspring that make it to maturity (Hunt and Hodgson 2010). As a side benefit, we find it is clarifying to count fitness in zygotes rather than in sexually mature adults because it is a less parento-centric view of sexual reproduction. Most organisms do not provide any parental care, and relatively few provide more than humans do. Consequently, one should not be surprised if adaptations for parental care require a special kind of biological explanation. We think that explanation is the altruistic route to complex functional design.

In this way of thinking, mammalian lactation is an iconic example of an altruistically designed benefit-delivery device (Oftedal 2012). Human mothers, for instance, whose infants (in traditional societies and, one presumes, ancestral societies) feed exclusively on breast milk, must increase their caloric intake by 670 kilocalories per day because of the high metabolic costs of milk production (Dewey 1997). In addition, there are opportunity costs: breastfeeding stimulates the production of prolactin, a hormone that both stimulates milk production and prevents the release of the hormones (called gonadotropins) that cause women's menstrual cycles to resume. Thus, while human infants are nutritionally dependent on their mother's milk (a period that lasts between 2 and 3 years among women from nonindustrial societies; Sellen 2001), women are typically not ovulating, which is to say, they are delaying the pursuit of increasing their direct reproductive success.

Moreover, it is insufficient merely to *produce* milk: mammalian mothers also must have a behavioral repertoire that makes them both able and willing to transfer that milk to their offspring. There is an important but often underappreciated behavioral component to success in breastfeeding, which includes learning to read infants' signals that they are ready to eat, specialized learning systems that stimulate milk let-down in response to infants' cries, developing skill with stimulating babies who are too sleepy to eat and soothing babies who are too fussy to eat, and others (Mulford 1992). And ideally, all of this learning should happen very soon after the infant is born. For this reason, natural selection, through the altruistic design route, plausibly led to the evolution of specialized learning mechanisms, physically instantiated through a complex network of neural and endocrine pathways, whose function is to enable mothers to become proficient at breastfeeding quickly.

Milk delivery is only one element of parents' food provisions for their offspring (in modern and traditional societies alike, parents subsidize their offspring's caloric intake throughout adolescence; Kaplan et al. 2000), and food provision itself is merely the tip of the parental care iceberg. For example, the anthropologist Melvin Konner (2010) has enumerated many additional evolved functions of human motherhood. These include temperature homeostasis; protection from predators, enemies, and organisms such as insects, scorpions, and snakes; transfer of specific immunity; and the nongenetic transmission of behavioral and psychological dispositions. Parents also invest in their children's reproductive success by helping them to acquire the human capital—specialized storehouses of knowledge, skill, or expertise—that will make them valuable to potential mates, potential friends and allies, and members of the wider community (Geary 2010). The cognitive mechanisms that enable mothers (and fathers) to provide these benefits to offspring require natural selection explanations every bit as much as adaptations for food delivery do.

Kin Discrimination Systems

The high degree of relatedness between mothers and their offspring means that it is relatively easy for natural selection to build altruistic adaptations for maternal care, but another important factor is the high availability of so-called kin discrimination cues, which enable altruistic genes to "know" (in a purely metaphorical sense) where to direct their help. Kin discrimination—the ability to recognize (nonconsciously, of course) one's own relatives and then regulate behavior in response to that recognition—is a feature of human nature that is so thoroughly taken for granted (because language enables us to label certain individuals as our fathers, mothers, siblings, grandparents, and so forth) that we fail to recognize that altruistically designed systems for caring—in humans and many other species—often rely deeply on a network of kin-discrimination cues to regulate their operation. By relying on such cues, evolving altruistic systems can reduce the costs of parental care per unit of benefit transferred to offspring, which, per Hamilton's rule, enhances evolvability (West, Griffin, and Gardner 2007).

Many cues for offspring recognition are available to mothers. As a soon-to-be-born mammal descends through its mother's birth canal, for instance, the stretch of the muscle fibers that line the uterine wall send a volley of neural signals to the brain that stimulate the pituitary gland to release prolactin and oxytocin. These hormones, in turn, not only stimulate the further progress of labor and delivery, but also the activation of milk production and the brain's behavioral parenting circuits (Russell and Leng 1998). After infants are born, human mothers almost instantaneously appear to begin making use of visual, auditory, and even olfactory cues to their offspring (some of which can be updated as children age and develop) for the purpose of kin recognition (Tal and Lieberman 2007). It is also likely that humans, like many other mammals (and birds and fish), come to recognize offspring on the basis of co-residence—perhaps mediated by cognitive systems that implement the logic "any young in my nest are mine" (Penn and Frommen 2010, 64).

In discussing altruism thus far, we have focused mainly on mother-child relationships, but altruistic benefit-delivery systems have very likely also evolved to regulate benefit-delivery from fathers, siblings, grandparents, aunts and uncles, and other relatives (Sear and Mace 2008; Gurven et al. 2012). In most animals, mothers have a distinct advantage over fathers and other relatives in offspring recognition because of their heavy physiological investments in the growth and development of the offspring following egg fertilization. These investments make available to mothers (but not fathers and other kin) a variety of kin discrimination cues that maternal altruistic benefit-delivery systems can put to use. Although some evidence suggests that fathers assess kinship by relying on visual or olfactory cues of genetic similarity (Alvergne, Fauire, and Raymond 2009), it is also possible that fathers possess computational neurocircuitry that solves offspring-recognition problems in a different way.

Holding aside the wonders of modern fertility medicine, men cannot be the fathers of the children of women with whom they did not have sex, so a reasonable first step for simplifying the offspring recognition problem would be for men to rule out of further consideration all women with whom they have never had sex. Second, because ancestral men cannot be fathers of children who are not *also* the children of women with whom they had sex, they might also observe the relations between the women with whom they have had sex and the young children in their midst. Young children who receive maternal care from a woman with whom the man had sex approximately 10 months prior to the infants' births are likely (holding aside other considerations such as the woman's likelihood of having had sex with other men, which might also be relevant) to be the man's children (Lieberman, Tooby, and Cosmides 2007; Tal and Lieberman 2007).

Similarly, children apparently recognize their siblings based largely on environmental cues acquired during childhood experience, including the number of years of co-residence and (for older siblings) watching one's own mother provide maternal care to another individual (Tal and Lieberman 2007; Lieberman, Tooby, and Cosmides 2007).

DOES GROUP SELECTION EXPLAIN ADAPTATIONS FOR BENEFIT DELIVERY?

Group selection is the idea that natural selection can work by enhancing the fitness of groups of individuals rather than acting exclusively on individuals. In the scientific literature, some scholars present group selection as an alternative to standard inclusive fitness maximization models of natural selection in order to explain the evolution of mechanisms for human benefit delivery (Fehr and Fischbacher 2003; Sober and Wilson 2011). Current group selection theorists recognize that inclusive fitness models are necessary in general and that they explain many cooperative phenomena, but these scholars also maintain that inclusive fitness theory cannot account for all of the types of cooperation found in humans. For instance, group selection has been invoked to explain cooperation in one-shot interactions (interactions that will not be repeated and hence cannot be reciprocal; Gintis 2000), costly punishment in public goods scenarios (Fehr and Gächter 2002), costly punishment by third-party witnesses of unfairness (Fehr and Fischbacher 2004), and even costly punishment of an individual who has directly harmed the punisher (Fehr and Fischbacher 2003).

In all of these cases, proponents of group selection models argue that the behaviors in question provide benefits to others (for example, punishment deterring a transgressor from harming a stranger in the future) at a net cost to the individual performing them (for example, punishment is inherently costly to the punisher as it takes time, energy, and could incite retaliation) and thus cannot evolve through the standard Darwinian design pathways. Importantly, group selection proponents also tend to be skeptical of claims that behaviors like these would have been adaptive for individuals under ancestral (though not modern) conditions, or that they would reveal themselves to be adaptive even today if the fitness benefits were reckoned over the course of a lifetime (rather than over the course of a one-hour laboratory session), or that their salutary effects on others are by-products rather than evolved functions (Chudek, Zhao, and Henrich in press). Space limitations prevent formal consideration of these specific empirical claims, so we limit our attention here to describing the various ways in which group selection is invoked and some of the limitations of these usages.

Types of Group Selection

It is important to note that group selection is not a singular, formal theory. Rather, the term has been applied to several different processes that can usefully be classified as examples of either "old" group selection or "new" group selection (West, El Mouden, and Gardner 2011). Old group selection models propose that group-level adaptations would result from differential survival among groups—that is, that traits would be selected to maximize group success (West, El Mouden, and

Gardner 2011). For example, Wynne-Edwards (1962) argued that groups of organisms that sought solely to maximize their own individual interests would exhaust ecological resources and therefore face extinction, whereas groups of organisms that exercised restraint in pursuing their individual interests would not deplete their resources, and thus would be more likely to survive. Through a persistent process of differential group success on the basis of individual restraint, Wynne-Edwards argued, behaviors could evolve that benefitted the group as a whole even if costly to the individual. Old group selection models therefore rely on the proposition that groups of individuals, and not merely individuals, can be the vehicles on which natural selection acts.

The theoretical and empirical work that emerged in the wake of Wynne-Edwards's proposal showed that old group selection, while possible in theory, could only work under a very narrow range of conditions, and thus was very likely to be unimportant in explaining adaptation (and basically impossible in humans; Williams 1966; West, El Mouden, and Gardner 2011). For example, group-level adaptations can be favored by natural selection when all of the individual organisms within a group are genetic clones, which can occur when relatedness among group members is high (that is, migration is essentially zero) and there is complete suppression of reproductive competition within groups (West, El Mouden, and Gardner 2011; Gardner and Grafen 2009). Because these conditions are rarely fulfilled in nature—and not at all in the case of humans—group-level adaptation is rarely invoked intentionally in the contemporary literature, although confusion arising from "new" group selection models does sometimes result in researchers rehashing some old group selection ideas (West, El Mouden, and Gardner 2011).

Unlike old group selection models, "new" group selection models do not focus on group-level adaptations. Rather, new group selection models propose that natural selection operates at multiple levels, and that traits can be selected for if their benefits at the level of the group (between-group level) outweigh the benefits at the level of the individual (within-group level) (Sober and Wilson 2011, 1998). Some models also posit that direct competition between groups results in selection for cooperative behaviors, such as when groups battle for territories (that is, groups with a greater number of cooperators are expected to outcompete groups with fewer cooperators; West, El Mouden, and Gardner 2011). Other models that can be categorized as new group selection models incorporate culture to explain differential success of groups, whereby groups that express a particular cultural trait outcompete groups that do not (Boyd and Richerson 2005; West, El Mouden, and Gardner 2011). These various new group selection models, collectively, are featured prominently in the current literature on the evolution of benefit delivery in humans.

Is Group Selection Useful?

Group selection models *can* provide a tenable selectionist logic by which some adaptations for benefit delivery evolve (Gardner in press). So why do most evolutionary biologists resist using group selection models? There are four reasons. First, group selection models do not provide any explanatory power above and beyond the power that is already built into standard inclusive fitness theory (that is, accounting for direct and indirect benefits). More strongly, new group selection models *already are incorporated* into standard inclusive fitness theory—though they rely on different mathematical expressions of natural selection, they yield identical predictions (Gardner in press; Gardner and Grafen 2009).

Second, despite many claims to the contrary, no one has proposed an empirical or theoretical example of a benefit-delivery system that can be shown to evolve by multi-level selection and that cannot also be shown to evolve through standard inclusive fitness considerations (for a list of examples, see table 5 of West, El Mouden, and Gardner 2011). The converse is not true: some benefit-delivery systems that are explicable with an inclusive fitness maximization approach to understanding natural selection cannot be explained using the analytical tools associated with multi-level selection. Third, the mathematics required to analyze the evolution of biological phenomena with group selection models tends to be much more unwieldy than the math that is required to analyze them with inclusive fitness models.

Fourth, and perhaps most important, even when using group selectionist models to explain the evolution of benefit-delivery systems, one reaches the conclusion that organisms still evolve in such a way as to pursue their inclusive fitness interests. That is, even when one uses the (often) cumbersome group selection approach to modeling the selection dynamics that lead to benefit-delivery devices, those devices still reside in individuals who will appear as if they are designed to optimize their inclusive fitness. Group selection may provide an alternative view of selection, but it does not lead to new understandings of what results from natural selection. This is one source of the elegance of inclusive fitness theory: it seamlessly bridges the process of natural selection (genes acting in the world to create phenotypes that boost their own rates of replication will increase in the population) and the product (individual organisms that appear designed to pursue the enhancement of their own inclusive fitness). Group selection views do not unite process and product in such an elegant fashion (Gardner in press).

CONCLUSION

Human generosity is not an illusion, and much of the generosity that we see between individuals and within societies today is motivated by biological systems that plausibly evolved by natural selection through the causal pathways we have outlined here. But is evolution the only game in town for explaining human generosity? Far from it. Much of the generosity we see in the contemporary world is probably caused not by biological systems designed for generosity acting alone. Instead, these mechanisms often interact with unique innovations that have arisen in the modern world—for example, laws, charitable organizations, taxation, and social insurance—that were intentionally designed to goad humans into greater generosity than could be leveraged on the basis of naturally selected benefit-delivery devices alone. Some of these innovations might not even require the action of naturally selected benefit-delivery mechanisms at all. All they might require, instead, is for humans to apply their capacities for abstract reasoning (Singer 1981) and their evolved inclinations to avoid sticks (such as the formal penalties associated with tax dodging or failing to return found property; West 2003; Webber and Wildavsky 1986), pursue carrots (as societies grow larger, and as communication goes from oral to written to electronic, the potential reputational benefits of generosity increase exponentially), and follow fashionable social trends (note the rise of charitable voluntary associations in Victorian England; Himmelfarb 1991). A complete understanding of human generosity in the modern world, therefore, will require not only the careful application of the insights of evolutionary science, but also a careful inspection of the insights that can come from history, political science, economics, and the other social sciences.

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