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A Cooperative Species

> How selfish soever man may be supposed, there are evidently some principles in his nature, which interest him in the fortunes of others, and render their happiness necessary to him, though he derives nothing from it, except the pleasure of seeing it.
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> Adam Smith, *The Theory of Moral Sentiments* (2000[1759]) p. 3.

Is our conscience nothing but "the inner voice that tells us that somebody might be looking," as the jaundiced H. L. Mencken (1949) put it? Or did the 20th century American essayist overlook humanity's penchant genuinely to care for others, including total strangers, and to act morally, even when nobody is looking? But if Adam Smith's affirmation of humanity's moral sentiments is more nearly correct than Mencken's skepticism, how could this oddly cooperative animal, *Homo sapiens*, ever have come to be?

In the pages that follow we advance two propositions.

First, people cooperate not only for self-interested reasons but also because they are genuinely concerned about the well-being of others, try to uphold social norms, and value behaving ethically for its own sake. People punish those who exploit the cooperative behavior of others for the same reasons. Contributing to the success of a joint project for the benefit of one's group, even at a personal cost, evokes feelings of satisfaction, pride, even elation. Failing to do so is often a source of shame or guilt.

Second, we came to have these "moral sentiments" because our ancestors lived in environments, both natural and socially constructed, in which groups of individuals who were predisposed to cooperate and uphold ethical norms tended to survive and expand relative to other groups, thereby allowing these prosocial motivations to proliferate. The first proposition concerns proximate motivations for prosocial behavior, the second addresses the distant evolutionary origins and ongoing perpetuation of these cooperative dispositions.

Cooperation was prominent among the suite of behaviors that marked the emergence of behaviorally modern humans in Africa. Those living 75–90,000 years ago at the mouth of what is now the Klasies River near Port Elizabeth, South Africa, for example, consumed eland, hippopotamus, and other large game. The image of hunters and their prey on the cover of this book is from the nearby Drakensberg Mountains. Among the slaughtered remains found there is a now-extinct giant buffalo *Pelovoris antiquus* that weighed almost 2000 kilograms and whose modern day (smaller) descendant is one of the most dangerous game animals in Africa (Milo 1998). The Klasies River inhabitants, and their contemporaries in other parts of Africa, almost certainly cooper-

ated in the hunt and shared the prey among the members of their group. Even earlier evidence of trade in exotic obsidians extending over 300 kilometers in East Africa is another unmistakable footprint of early human cooperation.

Like those living at Klasies River mouth, other "hunting apes" quite likely cooperated in the common projects of pursuing large game, sharing the prey and maintaining group defense. Both *Homo neanderthalensis* and the recently discovered *Homo floresiensis* survived well into the *Late Pleistocene* (about 126,000 to 12f,000 years before the present) and hunted large game, the latter targeting the pygmy (but nonetheless substantial) elephants that had evolved on the island environment of Flores, off the coast of Indonesia.

Other primates engage in common projects. Chimpanzees, for example, join common boundary patrols and some hunt cooperatively. Male Hamadyras baboons respect proximity-based property rights in food and mates. Many species breed cooperatively, with helpers and babysitters devoting substantial energetic costs to the feeding, protection and other care of non-kin (Hrdy 2009). Social insects, including many species of bees and termites, maintain high levels of cooperation, often among very large numbers of individuals. Other common forms of cooperation among non-human animals, summarized by Kappeler and van Schaik (2006), are "grooming and other forms of body care, alarm calling, predator inspection, protection against attacks by predators or conspecifics, supporting injured group members... [and] egg-trading among hermaphrodites."

While cooperation is common in many species, *Homo sapiens* is exceptional in that in humans cooperation extends beyond close genealogical kin to include even total strangers, and occurs on a much larger scale than other species except for the social insects.

In the pages that follow we will examine the cultural, biological and other processes that explain how humans became this exceptionally cooperative species.

By *cooperation* we mean engaging with others in a mutually beneficial activity. Examples include the joint pursuit of political and military objectives as well as the more prosaic foundations of everyday life: collaboration among employees in a firm, exchanges between buyers and sellers, and the maintenance of local amenities among neighbors.

Cooperative behavior may confer benefits net of costs on the individual cooperator, and thus may be motivated entirely by self-interest. Market exchange is an example. In this case, cooperation is a form of *mutualism*, namely an activity that confers net benefits both on the actor and on others. But cooperation may also impose net costs upon individuals in the sense that not cooperating would increase their fitness or other material payoffs. In this case cooperative behavior constitutes a form of altruism (see A1).

The evolution of cooperation that is mutualistic or that involves only close family relatives is easily explained. Cooperation among close family members could have evolved by natural selection because the benefits of cooperative actions are conferred on the close genetic relatives of the cooperator, thereby helping to proliferate alleles ("genes") associated with the cooperative behavior. Cooperation could also have evolved because one individual's costly contribution to the welfare of another individual is reliably reciprocated at a future date, thereby making cooperation mutualis-

tic. Models of altruism toward close family members and reciprocal altruism (which really should be called "enlightened self-interest") are popular among biologists and economists alike and explain many forms of human cooperation, particularly those occurring in families or in frequently repeated dyadic (two-person) or other very small group interactions.

But these models fail to explain two facts about altruistic cooperation: that it takes place in groups far larger than the immediate family, and that both in real life and in laboratory experiments, it occurs in interactions that are unlikely to be repeated, and where it is impossible to obtain reputational gains from cooperating.

The most parsimonious proximal explanation of cooperation, one that is supported by extensive experimental and other evidence, is that people gain pleasure from or feel morally obligated to cooperate with like-minded people. People also enjoy punishing those who exploit the cooperation of others, or feel morally obligated to do so. Free-riders frequently feel guilty, and if they are sanctioned by others, they may feel ashamed. We term these feelings *social preferences*. Social preferences include a concern, positive or negative, for the well being of others, as well as a desire to uphold ethical norms.

In many human groups, these motives are sufficiently common to sustain social norms that support contributions to projects of common benefit, even when cooperators bear costs in order to benefit others. The forms of cooperation and the behaviors that elicit punishment by peers differ from society to society, but the critical role of social preferences in sustaining altruistic cooperation is ubiquitous.

Because we are convinced that most people enjoy cooperating at least in some situations and dislike people who do not, the task we will set for ourselves is not that typically addressed by biologists and economists, namely to explain why people cooperate despite being selfish. Rather, we seek to explain why we are not purely selfish—why the social preferences that sustain altruistic cooperation are so common. Proximate answers to this question are to be found in the way that our brains process information and induce the behavioral responses that we term cooperation. But how did we come to have brains that function in this manner?

Early human environments are part of our answer. Our Late Pleistocene ancestors inhabited the large-mammal-rich African savannah and other environments in which cooperation in acquiring and sharing food yielded substantial benefits at relatively low cost. The slow human life-history with prolonged periods of dependency of the young also made the cooperation of non-kin in child rearing and provisioning beneficial. As a result, members of groups that sustained cooperative strategies for provisioning, child-rearing, sanctioning non-cooperators, defending against hostile neighbors, and truthfully sharing information had significant advantages over members of non-cooperative groups.

In the course of our subsequent history we created novel social and physical environments exhibiting similar, or even greater, benefits of cooperation, among them the division of labor coordinated by market exchange and respect of rights of property, systems of production characterized by increasing returns to scale (irrigated agriculture, modern industry, information systems with network externalities), and warfare. The impressive scope of these modern forms of cooperation was facilitated by the emer-

gence in the last seven millennia of governments capable of enforcing property rights and providing incentives for the self-interested to contribute to common projects.

But prior to the emergence of governments and since, cooperation has been sustained also by motives that led some people to bear costs on behalf of others, contributing to common projects, punishing transgressors, and excluding outsiders. In the pages that follow we will advance three reasons why these altruistic social preferences supporting cooperation outcompeted unmitigated and amoral self-interest.

First, human groups have devised ways to protect their altruistic members from exploitation by the self-interested. Prominent among these is the public spirited shunning, ostracism, and even execution of free-riders and others who violate cooperative norms. Other group activities protecting altruists from exploitation are leveling practices that limit hierarchy and inequality, including sharing food and information.

Second, humans adopted prolonged and elaborate systems of socialization that led individuals to internalize the norms that induce cooperation, so that contributing to common projects and punishing defectors became objectives in their own right rather than constraints on behavior.Together, the internalization of norms and the protection of the altruists from exploitation served to offset, at least partially, the competitive handicaps born by those who were motivated to bear personal costs to benefit others.

Third, between-group competition for resources and survival was and remains a decisive force in human evolutionary dynamics. Groups with many cooperative members tended to survive these challenges and to encroach upon the territory of the less cooperative groups, thereby both gaining reproductive advantages and proliferating cooperative behaviors through cultural transmission. The extraordinarily high evolutionary stakes of intergroup competition and the contribution of altruistic cooperators to success in these contests meant that sacrifice on behalf of others, extending beyond the immediate family and even to virtual strangers, could proliferate. Modern-day nationalism is an example.

This is part of the reason why humans became extraordinarily group-minded, favoring cooperation with insiders and often expressing hostility toward outsiders. Boundary-maintenance supported within-group cooperation and exchange by limiting group size and within-group linguistic, normative and other forms of heterogeneity. Insider favoritism also sustained the between-group conflicts and differences in behavior that made group competition a powerful evolutionary force.

In short, humans became the cooperative species that we are because cooperation was highly beneficial to the members of groups that practiced it, and we were able to construct social institutions to share food and to socialize new members, and to make war, all of which minimized the disadvantages of those with social preferences in competition with fellow group members, while heightening the group-level advantages associated with the high levels of cooperation that these social preferences allowed. These institutions proliferated because the groups that adopted them secured high levels of within-group cooperation, which in turn favored the groups' survival as a biological and cultural entity in the face of environmental, military and other challenges.

Early humans were not alone in occupying territory and a feeding niche that made cooperation among group members highly advantageous. Indeed our ancestors competed with lions, hyenas, wild dogs and possibly other hominid cooperative hunters for the very same ungulates and other large mammals. Nor were our ancestors exceptional

in the kinds of group competition for territory and other valued resources that made cooperation so essential to survival. Chimpanzees, too, engage in lethal contests between troops where winners gain territory and reproductive advantages. The same is true of species as diverse as meerkats and fire ants. Nor are humans exceptional in constructing our own physical and social environments. Beavers build dams, birds build nests, and burrowing animals build underground catacombs. Why then did humans, rather than chimps, lions, or meerkats, develop such exceptional forms of cooperation?

Central to our reply are the human cognitive, linguistic and physical capacities that made us especially good at all of the above, and more. These capacities allow us to formulate general norms of social conduct, to erect social institutions regulating this conduct, to communicate these rules and what they entail in particular situations, to alert others to their violation and to organize coalitions to punish the violators. No less important is the psychological capacity to internalize norms, to experience such social emotions as shame and moral outrage, and to base group membership on such non-kin characteristics as ethnicity and language, which in turn facilitates costly conflicts among groups. Equally essential was the developmental plasticity of humans and our long period of maturation, the latter initially a result of the particular feeding niche that early humans occupied. Also important is the unique human capacity to use projectile weapons, a consequence of which is to lower the cost of coordinated punishment of norm violators within a group, to reduce the costs of hunting large animals, with concomitant benefits accruing to groups with widely endorsed sharing norms, and to render intergroup conflicts more lethal. A result was to elevate group-level competition to a more powerful evolutionary force.

These exceptional aspects of human livelihoods and social interactions, we will show, have favored the evolution of an individual predisposition to cooperate with others and to punish those who exploit the cooperation of others. But more than individual-level motivation is involved. The regulation of social interactions by group-level institutions plays no less a role than altruistic individual motives in understanding how this cooperative species came to be. Institutions affect the rewards and penalties associated with particular behaviors, often favoring the adoption of cooperative actions over others, so that even the self-regarding are often induced to act in the interest of the group. Of course it will not do to posit these institutions *a priori*. Rather, we will show that the could have coevolved with other human traits in the relevant ancestral ecologies and social environments.

Had we chosen *A Colluding Species* as our title, it would not be necessary to point out that cooperation is not an end, but rather a means. In some settings, competition, the antithesis of cooperation, is the more effective means to a given end. Similarly, the individual motives and group-level institutions that account for cooperation among humans include not only the most elevated, including a concern for others, fair-mindedness, and democratic accountability of leaders, but also the most wicked, such as vengeance, racism, religious bigotry, and hostility toward outsiders.

Price-fixing by cartels and other baleful economic effects of collusion motivated Adam Smith to advocate a competitive economic system under which such forms of antisocial collusion would unravel. In its stead he advocated "an invisible hand" that would guide the efforts of countless self-interested producers to coordinate a modern division of labor in the interest of all, a stunning example of mutualistic cooperation.

But if the late 18th century gave us this evocative metaphor for the beneficial effects of the pursuit of individual gain, the mid-20th century invented two no less riveting metaphors for the dark side of self-interest: the prisoner's dilemma and the tragedy of the commons. Their logic inverted Adam Smith's invisible hand, showing that even where cooperation was essential to the pursuit of common ends, it would falter in the face of self-interest. Garrett Hardin's tragedy of the commons was rapidly assimilated by scholars, as it embraced a model of self-interest already well established in both economics and the neo-Darwinian synthesis in biology.Social preferences, Hardin made clear, were powerless to counter the "remorseless" degradation of the environment:

> The tragedy cannot be solved by an appeal to conscience, for those who heeded the appeal would have fewer children, and by the heritability of capacity of conscience, this would lead to a less moral population. (p. 1246)

Because "freedom in a commons means ruin for all" (p. 1244), he advocated a modern version of Thomas Hobbes' *Leviathan* that he termed "mutual coercion mutually agreed upon" (p. 1247). Hardin termed his contribution a "rebuttal to the invisible hand" (p. 1244). In like manner, Mancur Olson's no less ineluctable"logic of collective action" in n-person prisoner's dilemmas demonstrated the inevitability of a passive citizenry and the impossibility of cooperation, due to ubiquitous free-riders. (Olson 1965)

But, as the prisoner's dilemma and the tragedy of the commons were becoming staples of undergraduate instruction, field evidence from anthropologists and micro-historical studies of social movements pointed in an entirely different direction. Herders in high Alpine and Andean common summer pastures had averted tragedy without government regulation for centuries, possibly millennia (Netting 1989). Workers and democrats had for centuries risked their lives in collective actions that plainly defied Olson's logic (Moore 1978, Hobsbawm 1983). The work of Elinor Ostrom and her collaborators documented literally hundreds of decentralized tragedy-averting commons governance systems around the world, bringing to a head this collision of empirical observation and the logic of self-interest (Ostrom 1990).

The tension between the relentless logic of self-interest and the ubiquity of collective action in real-world settings was eventually resolved by a series of experiments by psychologists and economists, most notably by Ernst Fehr and his colleagues (Fehr and Gächter 2000a, Herrmann et al. 2008). The experiments confirmed that self-interest is indeed a powerful motive, but also that other motives are no less important. Even when substantial sums of money are at stake, many, perhaps most, experimental subjects were found to be fair-minded, generous toward those similarly inclined, and nasty toward those who violate these prosocial precepts. In light of these results, the evidence that the tragedy of the commons is sometimes averted and that collective action is a motor of human history is considerably less puzzling. The puzzle, instead, is how humans came to be like this.

The growing interest in generous and civic-minded predispositions in the social sciences has been paralleled in biology, where the evolution of cooperative behavior, in the opinion of the editors of *Science*, is one of the top 25 questions facing scientists today (Kennedy et al. 2005). Biological classics such as Konrad Lorenz (1963), *On Aggression* and Richard Dawkins (1976) *The Selfish Gene* have now been joined by

works whose titles signal the shift in attention: *Good Natured*, by Frans de Waal (1997), *Mother Nature*, by Sarah Hrdy (2000), *The Moral Animal*, by Robert Wright (1995), *Origin of Virtue*, by Matt Ridley (1998), *Unto Others*, by Elliot Sober and David Sloan Wilson and Elliott Sober (1998), *Altruistically Inclined?* by Alexander Field (2004), *The Genial Gene: Deconstructing Darwinian Selfishness* by Joan Roughgarden (2009), and *Moral Origins: Social Selection and the Evolution of Virtue, Altruism, and Shame*, by Christopher Boehm (2011).

These recent works are reminiscent of Pyotr Kropotkin's *Mutual Aid* a century earlier, a book that had advanced a kinder, gentler view of the evolutionary process in opposition to the then popular dog-eat-dog Social Darwinist claims about what natural selection entails for human behavior. The moral, generous, and civic-minded predispositions documented in these works and in the pages that follow show that evolution can not only foster self-interest but also promote the generous and ethical behaviors that help us escape the prisoner's dilemma and avert the tragedy of the commons, and permit us to sustain the hope for a society committed to freedom and justice for all. However, we will see that this is true not despite, but in important measure because, evolutionary processes are "red in tooth and claw," in Alfred, Lord Tennyson's famous words.