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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.

Adam Smith, *The Theory of Moral Sentiments* (2000[1759]) p. 3.

In the pages that follow we advance two propositions. First, people cooperate and punish those who fail to cooperate not only for self-interested reasons but because they are genuinely concerned about the well being of others, care about social norms, and wish to act ethically. 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, such that groups in which most individuals were predisposed to cooperate and uphold ethical norms tended to survive and expand relative to other groups, thereby proliferating these pro-social motivations. The first proposition concerns proximate motivations for social behavior, the second addresses the distant evolutionary origins of these cooperative dispositions.

Cooperation is prominent among the suite of behaviors that mark 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. Among the 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 cooperated in the hunt and shared the prey among the members of their group. Evidence of trade in exotic obsidians extending over 300 kilometers in East Africa dating from considerably earlier, provides 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 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 among non-kin. Chimpanzees, for example, join common defensive patrols and some hunt cooperatively. Male Hamadryas baboons respect property rights in food and mates. Many species breed cooperatively, with helpers and baby sitters devoting substantial energetic costs to the feeding, protection and other care of non-kin. Social species, including many species of bees and termites, maintain high levels of cooperation. 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.”

Thus, cooperation among *Homo sapiens* is unique not because it is absent in other animals, but for the scale on which cooperation among non-kin takes place among humans, for the role of what Robert Trivers (1971) termed “moralistic aggression” in sustaining cooperation, and for the importance of cooperation in giving human society its distinctive characteristics.

In the pages that follow we will explain how humans became a uniquely cooperative species.

By cooperation we mean engaging with others in a mutually beneficial activity. Examples include the joint pursuit of political and military objectives in groups 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 by entirely self-interest. 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 incur net costs to the individual. In this case cooperative behavior constitutes a form of *altruism*. By contrast to mutualistic cooperation, altruistic cooperation would not be undertaken by an individual whose motives were entirely self-

interested and thus did not take account of the effects of one's actions on others.

Cooperation among relatives could have evolved because the benefits of cooperative actions are conferred on the genetic relatives of the cooperator, thereby helping to proliferate alleles associated with the cooperative behavior. Cooperation may 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 mutualistic. These two models, kin altruism and reciprocal altruism, are popular among biologists and economists alike, and explain how many forms of human cooperation could have evolved, particularly those occurring among relatives or in dyadic or other very small group interactions. But they fail to explain two facts about human cooperation: that it takes place in groups including substantial numbers of unrelated individuals, and that both in real life and in laboratory experiments, it occurs in interactions that are unlikely to be repeated, and is motivated by the subjects' concerns for the well-being of others and hostility towards those who violate social norms.

The most parsimonious proximal explanation of cooperation, supported by extensive experimental and other evidence, is that people enjoy cooperating with like-minded people. People also enjoy punishing those who exploit the cooperation of others. Free-riders frequently feel guilt, and if they are sanctioned by others, they feel ashamed. Cooperation is often motivated by these social preferences, to which we might add empathy, honesty, generosity and trustworthiness. In many human groups, these motives are sufficiently common to sustain socially valuable norms and contributions to projects of common benefit, even when cooperators bear costs in order to benefit others, or conform to personally costly but socially beneficial character virtues, such as honesty and personal integrity. The forms of cooperation and the behaviors that elicit punishment differ from society to society, but the critical role of social preferences in sustaining cooperation is ubiquitous.

Thus, in seeking to understand ourselves as a cooperative species, the task we will set is not that typically addressed by biologists and economists, namely to explain why people cooperate despite being selfish. Rather, we seek to explain why the social preferences that sustain altruistic cooperation are so common; why, that is, so many people care about fairness and reciprocity and value the well-being of fellow members of their groups, favoring them over 'outsiders.' 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. The question we pose is: how did we come to have brains that function in this way? Here is our answer.

Early modern humans inhabited the mammal-rich African savannah and other environments in which cooperation yielded substantial benefits at relatively low cost. As a result, members of groups that sustained cooperative strategies for provisioning, defense and predation *vis-a-vis* other groups, maintenance of social order, and information-sharing 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 generalized 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 inter-state warfare. The impressive scope of these modern forms of cooperation was facilitated by the emergence in the last seven millennia of governments capable of enforcing property rights and providing incentives for the self-interested to contribute in common projects.

But, prior to the emergence of governments and because group-level cooperative practices have been sustained in important measure by motives that led some people to bear costs on behalf of others, contributing to common projects, punishing transgressors, and excluding outsiders. Altruistic social preferences proliferated rather than being eclipsed by self-interest for three reasons.

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 practices protecting altruists from exploitation are mating customs such as monogamy that reduced reproductive inequalities, and institutions such as the egalitarian sharing of food and information.

Second, humans adopted prolonged and elaborate systems of socialization whereby members of a group internalize the norms that induce cooperation, thereby making contributing to common projects and punishing defectors objectives in their own right rather than constraints on behavior. Both the internalization of norms and the protection of altruists from exploitation relied on the uniquely human ability to formulate general rules of behavior, 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. 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. Together the internalization of norms and the protection of the altruists from exploitation were sometimes sufficient to halt entirely or even reverse within-group selection pressures operating against those who were motivated to bear personal costs to benefit others.

Third, uniquely among animals, members of human groups are often not related by recent common descent, and between-group competition for resources and survival is periodically a decisive force in evolutionary dynamics. From warfare and environmental catastrophe among hunter-gatherers to the rise and fall of modern nation states, group extinction, costly group dispersal, and ostracism from groups have been powerful mechanisms supporting the evolution of human cooperation.

This is in part the reason why humans became extra-ordinarily group-minded, often favoring cooperation with ‘insiders’ and expressing hostility towards others. This parochial aspect of human altruism is itself a puzzle, given the many opportunities for personal gain that are forgone by those who use arbitrary ethnic, racial, or other markers to limit the people with whom one is willing to interact in a cooperative manner. The most likely explanation of why this cooperative species is also parochial is that boundary-maintenance sustained within-group cooperation and exchange by limiting group size and within-group linguistic, normative and other heterogeneity while at the same time sustaining the between-group conflicts and differences in behavior that make group competition a powerful evolutionary force.

Our answer, in short, is that humans became a cooperative species because cooperation was highly beneficial to the members of groups that practiced it, and we were able to construct social institutions—to enforce norms, to share food, to socialize new members, to distinguish insiders from outsiders, to make war—that minimized the within-group selective pressures operating against those with social preferences, while heightening the group-level advantages associated with the high levels of cooperation that these social preferences allowed. Adherence to these institutions across generations was secured through the cultural transmission of the values and beliefs that favored conformity to existing norms. These institutions proliferated because cooperation enhanced the chances that a group would survive as a biological and cultural entity in the face of environmental, military and other challenges.

Central to our explanation are human cognitive, linguistic and physical capacities that allow the formulation of general norms of social conduct, the emergence of social institutions regulating this conduct, the psychological capacity to internalize norms, and to experience such “social emotions” as shame and moral outrage, and to base group membership on such non-kin characteristics as ethnicity and linguistic differences, which in turn facilitates costly conflicts among groups. Also important is the unique human capacity to use projectile weapons, a consequence of which is to lower the cost of punishing norm violators within a group, to reduce the costs of hunting large animals with concomitant benefits accruing to groups with widely endorsed sharing norms, to render intergroup conflicts more lethal, and hence to elevate group-level competition to a more powerful evolutionary force.

These unique aspects of human livelihoods and social interactions, we will show, have favored the evolution of an individual predisposition to cooperate 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 norms and institutions plays no less a role than altruistic individual motives in understanding how the cooperative species came to be. Institutions affect the rewards and penalties associated with particular behaviors, often favoring the adoption of cooperative actions over others. In the social environments common to human interactions, even the self-regarding are often induced to act in the interest of the group. Of course it will not do to posit these rules and institutions *a priori*. Rather, we show that these could have co-evolved with other human traits in a plausible representation of 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 to be valued in its own right, but rather is a means that under some conditions may contribute to human well-being. In other settings, competition—the antithesis of collusion—plays no less essential a role. Similarly, the individual motives and group-level institutions that account for cooperation among humans include not only the most elevated—a concern for others, fair-mindedness, and democratic accountability of leaders, for example—but also the most venal: vengeance, racism, religious bigotry, hostility towards “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 anti-social cooperation 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.

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 prisoners' dilemma and the tragedy of the commons. Their logic inverted Adam Smith's, showing that even where cooperation was essential to the pursuit of common ends, it would falter in the face of self-interest. Both Mancur Olson's *logic of collective action* and Garrett Hardin's *tragedy of the commons* were rapidly assimilated by scholars, as they clearly articulated the implications of the assumption of self-interest already well established in both neoclassical 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).

But, as the prisoners' 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. Workers and democrats had for centuries risked their lives in collective actions that plainly defied Olson's logic. High Alpine and Andean common summer pastures had averted tragedy without government regulation for centuries, possibly millennia. The work of Elinor Ostrom and her collaborators documented literally hundreds of decentralized 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 two would eventually be resolved by a series of experiments by psychologists and economists, most notably by Ernst Fehr and his colleagues (Fehr and Gächter 2000). 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

experimental subjects are fair-minded, generous towards those similarly inclined, and nasty towards those who violate these pro-social precepts. In light of these results, the evidence that the tragedy of the commons is sometimes averted and 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 twenty-five questions facing scientists today (Kennedy, Norman and Pennisi 2005). Biological classics such as Konrad Lorenz (1963) *On Aggression* and Richard Dawkins (1976) *The Selfish Gene* have been joined by more recent 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 Richard Wright (1995), *Origin of Virtue*, by Matt Ridley (1998), *Unto Others*, by David Sloan Wilson and Elliott Sober (1998), *Altruistically Inclined?* by Alexander Field (2004), and *Moral Minds* by Marc Hauser (2006). The moral, generous, and civic minded predispositions documented in these works imply that evolutionary processes, even those that are, as Alfred, Lord Tennyson put it, 'red in tooth and claw,' can foster not only self-interest but also the generous and ethical behaviors that may account for human capacities to sometimes escape the prisoners dilemma and avert the tragedy of the commons.

No empirical challenge to the remorseless logic of the prisoners' dilemma and tragedy of the commons is greater than the decentralized social organization of our foraging ancestors. They rejected every would-be headman and yet escaped Hobbes' dismal prognosis for a state of nature lacking centralized government. The social order of the mobile band of hunters and gatherers must rank as the most successful form of government ever, encompassing as it does the first 90 or 95 percent of the human career on earth. It is also the setting in which much of the human genetic and cultural legacy on which modern cooperation depends emerged and proliferated. It is here that will find clues to the puzzle of how we became a cooperative species.