

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 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. People punish those who exploit the cooperation 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 are 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 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. 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 even earlier trade in exotic obsidians extending over 300 kilometers in East Africa, 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 (about 126,000 to 11,000 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 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 (Hrdy 2009). Social insects, 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 not unique because it is absent in other animals, but for other reasons: the extension of human cooperation beyond close family members to include even total strangers, the scale on which cooperation among non-kin takes place among humans, the role of what Robert Trivers (1971) termed “moralistic aggression” in sustaining cooperation, and the importance of cooperation in giving human society its distinctive characteristics.

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

The evolution of cooperation that is mutualistic or involving 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 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 mutualistic. Models of altruism towards close family members and reciprocal altruism are popular among biologists and economists alike and explain many forms of human cooperation, particularly those occurring among close kin or in dyadic or other very small group interactions.

But these models fail to explain three facts about human 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 behaving prosocially. This cooperation 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 participating in punishing those who exploit the cooperation of others. Free-riders frequently feel guilt, and if they are sanctioned by others, they may feel ashamed. Cooperation is often motivated by these social preferences, to which we might add empathy and such character virtues as honesty, generosity, trustworthiness, considerateness, loyalty, and personal integrity. In many human groups, these motives are sufficiently common to sustain socially valuable norms that support contributions to projects of common benefit, even when coop-

erators 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.

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 do 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. How did we come to have brains that function in this manner? 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, sanctioning non-cooperators, defending against hostile neighbors, and sharing truthfully transmitted 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 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 to common projects.

Both prior to the emergence of governments and since, however, 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. These altruistic social preferences supporting cooperation out-competed unmitigated self-interest and proliferated 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 pub-

lic spirited shunning, ostracism, and even execution of free-riders and others who violate cooperative norms. Other group activities protecting altruists from exploitation are levelling practices that limit hierarchy and inequality, including monogamous mating practices that prevent dominant males from monopolizing reproduction and the sharing of food and information.

Second, humans adopted prolonged and elaborate systems of socialization that lead individuals to 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. 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, between-group competition for resources and survival was a decisive force in human evolutionary dynamics. Groups with many cooperative members tended to survive these challenges and to occupy the territory of the less cooperative groups, thereby both gaining reproductive advantages and proliferating cooperative behaviors through cultural transmission. 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. 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.

This is part of the reason why humans became extraordinarily group-minded, often favoring cooperation with ‘insiders’ and expressing hostility towards others. 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 op-

erating 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 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 linguistic differences, 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, 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, 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 rules and institutions *a priori*. Rather, we show that these could have co-evolved 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 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 cooperation, 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 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.

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 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 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). 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.

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 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 remorseless theoretical logic of self-interest and the ubiquitous nature of collective action and other forms of cooperation in real world settings 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, perhaps most, 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 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 twenty-five 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 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 show that evolution can foster not only self-interest but also

promote the generous and ethical behaviors that may account for human capacities to sometimes escape the prisoners dilemma and avert the tragedy of the commons, and to sustain the hope for a society committed to freedom and justice for all. We will see that is true not despite but in important measure because evolutionary processes are “red in tooth and claw,” as Alfred, Lord Tennyson put it.