the cosmological parameters with great precision (*14*). The latest cosmological-scale simulations (*15*) are providing a basis for a new round of even more ambitious semianalytic models to be compared with new multiwavelength observations.

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Supporting Online Material
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BEHAVIOR

Cooperation and Punishment

Punishment can support cooperative behavior in a group, but requires coordination.

Louis Putterman

In an era in which the "tragedy of the commons" has acquired new meaning on a global scale, social scientists are beginning to find hope in human nature. True, we are self-interested creatures capable of destroying the habitats that support us as we each focus on getting our share of the global commons before others beat us to it. Yet *Homo sapiens* could never have populated the planet and mastered complex technologies and organizational forms had nature not also made us sensitive to one another's regard. Both field studies and laboratory experiments depict humans as willing to cooperate when convinced that others are doing the same and that at least some will incur costs to sanction cheating. On page 613 in this issue, Janssen *et al.* (*1*) show that communication among members of a group is key to establishing cooperation and using punishment effectively, and on page 617, Boyd *et al.* (*2*) provide a model of how signaling (a stylized kind of communication) could have allowed punishment and cooperation to evolve.

Achieving cooperation. Coordination is key to successful cooperation. A group in rural Burkino Faso is shown.

CREDIT: CURT CARNEMARK/THE WORLD BANK (1993)

For over a century, economists and social scientists have used the "*Homo economicus*" construct to depict humans as rational beings who act entirely in their own self-interest. Populating their models with *Homo economicus* gave economists the basis for predicting efficient outcomes in market interactions, but it also implied that mutually beneficial cooperation could not occur without binding contracts or outside enforcement. In the prisoners' dilemma game, each of two players has both a cooperative and a selfish option ("defection"). While both would be better off with mutual cooperation than with mutual defection, the fact that the privately best option of each is to defect leads to the prediction of mutual defection, if the game is played once without binding agreements. Still, when real individuals are enlisted to play the game as experimental subjects, with real money at stake, substantial numbers try cooperation.

Related evidence that real individuals are not accurately depicted by the *Homo economicus* model came from experiments using the voluntary contribution mechanism, a variation on the prisoners' dilemma game, in which each individual can choose not only full cooperation or no cooperation, but also intermediate levels of cooperation in the form of contributing funds to a collectively advantageous group project. The first voluntary contribution mechanism experiments defied the *Homo economicus* prediction of universal "free-riding," finding instead that many players did contribute to the common good rather than defect by contributing nothing. But when the game was played repeatedly for a preannounced number of times, contributions fell off toward zero. However, a result frequently replicated in the last decade shows that when subjects are permitted to communicate before playing or are allowed to punish one another's actions, conditional cooperation trumps strict self-interest (and *Homo sapiens* triumphs over *Homo economicus*) (*3*).

In different ways, Janssen *et al.* and Boyd *et al.* address the same problem. Permitting costly punishment often leads to more sustained cooperation, and the willingness to incur a cost to punish is characteristic of *Homo sapiens*. But uncoordinated punish-

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ment is frequently counterproductive, and being punished for letting others do the punishing (free-riding on punishment) almost never occurs (*4*). This raises the question of why anyone incurs the cost of punishing.

The solutions that Janssen *et al*. and Boyd *et al*. propose share the common element that punishment solves the problem of cooperation efficiently only when it is coordinated. The study by Janssen *et al*. is a new-generation laboratory decision-making experiment using an interface that simulates the common pool resource problem, a cousin of the voluntary contribution mechanism, more realistically than past work. Like earlier experiments (*5*), it allows subjects either to communicate, to punish one another, or both. Both generations of experiments find that subjects engage in costly punishment, but that punishment enhances cooperation and efficiency (sustainable harvesting of the resource) only when combined with the coordinating advantages of communication. The new results are even stronger than the old, in that the opportunity to punish is found to be outright counterproductive when not combined with communication.

Boyd *et al*. were inspired in part by the mixed or negative experimental findings regarding uncoordinated punishment. They introduce coordination into a purely theoretical model of how the propensity to punish could have evolved. Their model recognizes that the anticipation of punishment for free-riding can make cooperative behavior individually beneficial, but being predisposed to letting others do the costly punishing would appear to give one's own genes an evolutionary advantage. One element of the solution discussed by Boyd and collaborators elsewhere is the idea that individual disadvantage can be outweighed evolutionarily by group advantage if the disadvantage is sufficiently small and there is sufficient separation of groups and/or barriers to mobility among groups. One possible solution (*6*) includes higher-order punishing of those who free-ride by not punishing other noncooperators. If punishing second-, third-, or still higher-order free-riding (where third-order free riding means failing to punish those who fail to punish noncooperators) were common enough, the argument is that first-order noncooperation would be so rare that true punishing types (those with a preference to punish, even if they are not punished for failing to do so) almost never incur the cost of punishing and thus suffer only a negligible individual fitness disadvantage. But retaliation for punishing is more common in the lab than is punishment for failing to punish, so the alternative solution of Boyd *et al*. appears preferable: Punishers avoid wasting resources by not punishing unless enough others will also do so, the key being the emission of credible preplay signals.

Achieving cooperation with informal methods of coordination is not a problem of primitive and small-scale societies only. Today's state and multilateral institutions function only because problems of free-riding are being solved on a day-to-day basis, in part through willingness to cooperate and inclination to punish defection. Whether humans can solve seemingly intractable problems such as those of climate change and nuclear weapons proliferation depends to a large extent on whether the human sociality that evolved in our small-group past is robust enough to overcome the ever-present temptations to free ride.

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EVOLUTION

Chimpanzee Technology

Chimpanzees are the only nonhuman animal species known to make and use a wide range of complex tools.

William C. McGrew

Almost 50 years ago, Jane Goodall watched an adult male chimpanzee in the Gombe Stream Reserve, Tanzania, make and use a blade of grass to "fish" termites from a mound for food (*1*). Her mentor, Louis Leakey, declared, "Now we must redefine 'tool,' redefine 'man,' or accept chimpanzees as humans!" (*2*). Today, we know that various vertebrates in nature have elementary technology, but chimpanzees across Africa continue to astonish us with their technical abilities. Recent findings have further blurred the boundaries between what we consider to be human versus nonhuman by showing that chimpanzees can use and combine tools in complex sequences and combinations.

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Since Goodall's discovery, scientific analyses of chimpanzee behavior have changed from natural history notes to descriptive, classifying ethnography, to theory-driven, hypothesis-testing ethnology (*3*, *4*). To systematic but serendipitous observation has been added experimentation, even with free-ranging apes (*5*, *6*). Eight populations of wild chimpanzees across Africa from Senegal to Tanzania are fully habituated (that is, they can be observed at close range from dawn to dusk). Scores more are not fully habituated, but leave behind artifacts that can be collected and analyzed.

Researchers use the term "tool kits" to describe the repertoire of tools used habitually by a group of chimpanzees (*7*, *8*). The tool kits of most chimpanzee populations consist of about 20 types of tools, which are used for various functions in daily life, including subsistence, sociality, sex, and self-maintenance. This tool-kit size is relatively constant, whether the apes live in rainforest or on savanna, with one regional exception: The tool kits of three Ugandan populations (Budongo, Kanyawara, and Ngogo), all well-habituated, are about half the usual size, for reasons as yet undetermined (*9*).

The uses to which tools are put vary across chimpanzee populations. At Goualougo, Republic of Congo, the most commonly used tools are for extractive foraging, whereas at Ngogo, they are for hygiene and courtship. However, some tools are used by all chimpanzee populations: They all make leaf sponges to obtain drinking water, show aimed throwing of missiles, and communicate by drumming on tree buttresses.

Chimpanzees also use tool sets, that is, they use two or more tools in an obligate sequence to achieve a single goal. In the most impressive example, a chimpanzee popula-