Chimpanzee Technology
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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-

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tion in Gabon uses a tool set of five objects—pounder, perforator, enlarger, collector, and swab—to obtain honey (*10*). Other tool sets are used to fish for termites or dip for army ants. All these tool sets must be used in the correct functional order to be successful. Some primatologists have argued that this necessity for sequential order is a sign of complex cognitive processes.

Another way of using tools is as a tool composite, that is, two or more objects are used simultaneously and complementarily to achieve a goal. Tool composites long used by humans include bow-and-arrow and mortar-and-pestle, but such composites are virtually unknown in other species. In chimpanzees, the main example is the use of stones or clubs as hammers to crack nuts on anvils of stone or wood (see the photo). This impressive technology provides access to embedded, high-calorie nut meat, with less expenditure of energy and less risk to the consumer's teeth. At Bossou, Guinea, chimpanzees have favorite combinations of hammer and anvil stones, which they use again and again (*11*).

Less common are compound tools, in which two or more components are combined as a single working unit. Human examples are commonplace, including hafted spears (with shaft, point, and adhesive) and bead necklaces (with beads, string, and knot). Compound tools used by chimpanzees include the leaf sponge: Several fresh leaves are compressed into a single absorbent mass that allows water to be extracted from inaccessible tree holes (*12*). Another example is the wedge stone, which chimpanzees insert under a stone anvil to level its working surface, thus making it more efficient. Finally, to make their sleeping platforms (beds or nests), great apes daily interweave various branches, twigs, and leaves to make a frame, mattress, lining, and even a pillow (*13*).

How long have chimpanzees and their ancestors been making such complex tools? Chimpanzee tool use often modifies the raw materials (even stones), making them distinguishable from natural damage (*14*). Systematic excavation, radiometric dating, organic residues, wear patterns, actualistic experimentation (in which archaeologists seek to model past processes by recreating them in the present), and even museum studies have now been applied to the stone artifacts generated by ape tool users (*15*, *16*). The search is on for diagnostic wear patterns that allow the stone artifacts of the chimpanzee ancestors to be distinguished from those of early humans. Using apes as models may allow us to identify the precursors of the oldest known human tools by focusing on percussive technology, such as pounding tools, before the onset of Oldowan industries 2.6 million years ago.

Learning to use tools. Chimpanzee mother, juvenile, and infant at Bossou, Guinea. While the mother cracks oil palm nuts, the juvenile pays attention and the infant plays with nuts.

Of the other living great apes, two taxa—bonobo and gorilla—show no habitual tool use in nature, which is puzzling given that laboratory studies show that their intelligence is comparable to that of chimpanzees. The fourth taxon—orangutan—shares many of the attributes of chimpanzees; for example, orangutan tool kits vary across populations. However, their largely arboreal lifestyle curtails their technical expression. (Most chimpanzees use tools while on the ground.) Among other animals, species such as the Galapagos woodpecker finch, California sea otter, and Egyptian vulture are specialists at a single kind of tool use. Of the birds, the impressive New Caledonian crow lags far behind the apes with regard to the types of elementary technology described above. New Caledonian crows make tools in the wild and in captivity, but only for extractive foraging. It is the only species of corvid habitually to make tools in nature. Of the other primates, the bearded capuchin monkeys top the tool use list: Their only well-established tool use is the use of hammer-and-anvil to crack nuts, but they also use stone tools to dig up roots at one site.

Among all animals, only chimpanzees appear to be able to use one type of raw material to make many kinds of tools (e.g., leaf as sponge, napkin, or fishing probe), or make one kind of tool from many raw materials (fishing probe from grass, bark, vine, and twig). Only chimpanzees have been shown to vary in their tool use at a multitude of levels, from individual, family, community, and population to subspecies. Chimpanzees also continue to yield new forms of tool use from continuing study (*17*, *18*): In the Nimba Mountains of Guinea, they "cleave" fibrous, basketball-sized fruits into manageable smaller pieces, using hammers and anvils (*19*); this is unlike nut-cracking, for example, which cracks open natural containers to get at the goal item inside.

With each passing day, the number of wild chimpanzees declines, with advancing deforestation and expansion of the bush-meat trade. Whole groups of chimpanzees already have been exterminated, and with them, their technological heritage, which probably will never be recovered. If we value the technology of our nearest living relations, in its own right or to help in understanding our ancestors, then we must not allow the apes to go extinct.

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