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The Cognitive Animal

Empirical and Theoretical Perspectives on Animal Cognition

Edited by: Marc Bekoff, Colin Allen, Gordon M. Burghardt

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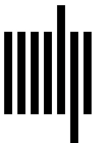
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The belief that hunting animals tend to be clever is very deeply held in our culture. Our images of predators, from lions to eagles, portray them in positions of power, both physical and intellectual. Whether there is truth in this portrayal depends very much on one's definition of intelligence. If we employ two commonly used criteria—that intelligent animals typically use their cognitive abilities for environmental problem-solving and that being smart allows them to adjust quickly and frequently to novel situations—we find that most species of predators are not necessarily very intelligent. Many employ a highly evolved set of weapons and a few, such as lions and wolves, also use cooperation to kill their prey. Without the weapons of teeth and claws, even the most cooperative wolf hunt would be unsuccessful.

Humans are an exception. The idea that hunters are smart comes mainly from human subsistence hunting, in which outwitting one's quarry is more important than possessing the best weapon. Hunting for a living is still practiced by some traditional foraging societies, and in these societies meat is by far the favored food source (Cordain et al. 2000). The notion that hunting places a natural selection pressure on the evolution of intelligence acquired a bad name during the 1970s and 1980s, owing to a now-infamous body of theory often labeled "Man the Hunter." Sherwood Washburn and Chet Lancaster (1968) hypothesized a crucial role for hunting in the evolution of the human intellect because of the natural selection pressure placed upon coordination and communication during the hunt. This placed the evolution of the human mind in the brain of males, who hunted, rather than females, who tended not to hunt. In the early 1970s, other anthropologists pointed out that Man the Hunter neglected the role of the human female in the evolutionary process, citing data from a variety of traditional societies showing that women are responsible for procuring most of the protein

calories for the family group. In spite of the attention paid to male hunting behavior, these critics claimed that gathering by females was nutritionally more important. These criticisms led to a dismissal of theories about hunting and the early human diet (Tanner and Zihlmann 1976).

Through the 1980s, theories of early human foraging behavior focused mainly on scavenging rather than hunting (Blumenshine 1987). In the past decade, the pendulum has swung back to the importance of hunting, in part owing to field data on chimpanzee behavior. The primacy of high-quality foods such as meat is again at the center of hypothesized links between hunting and brain size (see Kaplan et al. 2000).

There is one nonhuman animal that is both our close relative and a predator in social groups, much like traditional foraging people. Chimpanzees are related closely enough to humans and also cognitively similar enough to them to suppose that the evolutionary pressures on their encephalization may have been similar to our own. In order to learn more about the role of cognition in hunting behavior, I turned to the predatory behavior of wild chimpanzees. In the early 1960s, when Jane Goodall began her now famous study of the chimpanzees of Gombe National Park, Tanzania, it was thought that chimpanzees were strictly vegetarian. Today, hunting by chimpanzees at Gombe has been well documented (Teleki 1973; Goodall 1986; Stanford 1998), and hunting patterns have been reported from most other sites in Africa where chimpanzees have been studied. These include Mahale National Park in Tanzania (Uehara et al. 1992), Kibale National Park in Uganda (Mitani and Watts 1999), and Tai National Park in the Ivory Coast (Boesch and Boesch 1989; Boesch 1994).

Chimpanzee society is described as fission-fusion because there is little cohesive group structure apart from mothers and their in-

ants; instead, temporary subgroupings called “parties” come together and separate throughout the day. These parties vary in size in relation to the abundance and distribution of the food supply and the presence of estrous females, who serve as a magnet for males. Thus the size and membership of hunting parties vary greatly, from one to thirty-five. The hunting abilities of the party members as well as the number of hunters present can thus influence when a party hunts as well as whether it will succeed in catching a colobus.

Chimpanzee Predatory Behavior

After four decades of research on chimpanzees at Gombe, we know a great deal about their predatory patterns. A community of chimpanzees may kill and eat more than a hundred small- and medium-sized animals such as monkeys, wild pigs, and small antelopes each year. The most important vertebrate prey species in their diet, however, is the red colobus monkey. At Gombe, red colobus account for more than 80 percent of mammalian prey. Infant and juvenile colobus are caught in greater proportion than their availability (Stanford et al. 1994a); 75 percent of all colobus killed are immature.

Chimpanzees are largely fruit eaters, and meat consumption takes up only about 3 percent of the time they spend eating overall, which is less than in nearly all human societies. Adult and adolescent males do most of the hunting, making about 90 percent of the kills. Females also hunt, although more often they receive a share of meat from the male who either captured the meat or stole it from the captor. Although lone chimpanzees, both male and female, sometimes hunt, most often hunts are social. In other hunting species, cooperation among hunters yields greater success rates. In both Gombe and in the Tai Forest in the Ivory Coast, there is a strong positive relationship between the number of hunters and the odds of a successful hunt (Boesch and Boesch 1989; Stanford et al. 1994b). Although

most successful hunts result in a kill of a single colobus monkey, in some hunts from two to seven colobus may be killed.

In her early years of research, Jane Goodall (1986) noted that the Gombe chimpanzees tend to hunt in binges, during which they would hunt almost daily and kill large numbers of monkeys and other prey. The explanation for such binges has always been unclear. My own work focused on the causes for such spurts in hunting frequency, with unexpected results (Stanford 1998). The explanation for sudden changes in frequency seems to be related to whatever factors promote hunting itself; when such factors are present to a high degree or for an extended period of time, frequent hunting occurs. For example, the most intense hunting binge we have seen occurred in the dry season of 1990. From late June through early September, a period of 68 days, the chimpanzees were observed to kill 71 colobus monkeys in 47 hunts. It is important to note that this is the observed total; the actual total that includes hunts at which no human observer was present may be one-third greater. During this time the chimpanzees may have killed more than 10 percent of the entire colobus population within their hunting range (Stanford 1998).

Hunting and Intelligence

Every researcher has his or her own revealing anecdotes about some clever tactic employed by a hawk or a leopard to catch prey. It appears, however, that chimpanzees respond to myriad hunting scenarios just as they respond to other social situations, with highly flexible and context-dependent tactics for achieving their goal. I have seen male chimpanzees corner male colobus monkeys on narrow tree branches, then grab the limb with their hands and whip it up and down until the colobus were forced to leap off, allowing the hunters to rush in and capture babies from the group. I once saw the male chimpanzee Frodo attack a colobus group huddled in the top of a palm tree. He approached from beneath,

then pulled a palm frond down, creating a temporary bridge over which the group tried to escape the tree. Frodo's hand holding the frond remained unseen until the last moment, when he lunged for (and missed) a mother colobus and her baby crossing to safety. Frodo appeared to set a trap for the colobus, one that nearly worked.

Both humans and chimpanzees are omnivores, eating a diet that is high in plant foods. The important decisions about when to eat meat are based on the nutritional costs and benefits of obtaining prey compared with the essential nutrients that the food provides relative to plants. However, social influences such as party size and composition seem to play an important role in mediating hunting behavior as well. A major goal of my research was understanding when and why chimpanzees decide to hunt colobus monkeys rather than forage for fruits, even though the hunt involves the risk of injury from colobus canine teeth and a substantial risk of failure to catch anything.

In his study of Gombe chimpanzee predatory behavior in the 1960s, Geza Teleki (1973) considered hunting to have a strong social basis. Other early researchers had said that hunting by chimpanzees might be a form of social display, in which a male chimp tries to show his prowess to other members of the community (Kortlandt 1972). In the 1970s, Richard Wrangham conducted the first systematic study of chimpanzee behavioral ecology at Gombe and concluded that predation by chimps was nutritionally based, but that some aspects of hunting behavior were not well explained by nutritional needs alone.

More recently, Toshisada Nishida and his colleagues in the Mahale Mountains chimpanzee research project reported that the alpha male there, Ntilogi, used colobus carcasses for political gain, withholding meat from rivals and doling it out to allies (Nishida et al. 1992). William McGrew (1992) has shown that those female Gombe chimps who receive generous shares of meat after a kill have more surviving offspring, indicating a reproductive benefit tied to meat eating.

My own preconception was that hunting must be nutritionally based. After all, meat from monkeys and other prey would be a package of protein, fat, and calories hard to equal from any plant food. I therefore examined the relationship between the odds of success and the amount of meat available with different numbers of hunters in relation to each hunter's expected payoff in meat obtained. When are the time, energy, and risk (in other words, the costs) involved in hunting worth the potential benefits, and therefore when should a chimp decide to join or not join a hunting party? And how do the costs of hunting compare with the costs and benefits of foraging for plant foods?

The results were surprising. I expected that as the number of hunters increased, the amount of meat available for each hunter would also increase. This would have explained the social nature of hunting by Gombe chimpanzees. If the amount of meat available per hunter declined with increasing hunting party size (because each hunter got smaller portions as party size increased), then it would be a better investment of time and energy to hunt alone rather than join a party. The success rate of lone hunters was only about 30 percent, while that of parties with ten or more hunters was nearly 100 percent. However, there was no relationship between the number of hunters and the amount of meat available per capita. This is because even though the likelihood of success increases with more hunters in the party, the most frequently caught prey animal is a 1-kg baby colobus monkey. Whether it is shared among four hunters or fourteen, such a small package of meat does not provide anyone with much food or incentive to hunt. The decision to join a hunting party therefore is based on some calculation of expected returns by potential hunters.

Whether intelligence is an important factor in hunting tactics by chimpanzees is a key issue because of the putative importance of hunting to the evolution of human intelligence. If intelligent hunters succeed more often than less intelligent hunters, and if the capture of meat has some

survival value to the animals, then natural selection should have favored those chimpanzees who employed clever hunting tactics. If females prefer to mate with the best hunters, perhaps because the females benefit nutritionally from gifts of meat, then hunting performance would be subject to sexual selection as well.

Since there is little evidence that chimpanzees set off each morning with the intention of finding meat, optimizing their foraging routes to take advantage of the likely locations of colobus monkeys is probably not part of a chimpanzee hunting strategy. Many animal species, from bumblebees to hummingbirds, forage efficiently without any semblance of higher intelligence, since natural selection may program the ability to optimize travel routes to locate a maximum number of quality food sources per unit of area. A leopard needs extraordinarily evolved sensory capabilities and the weaponry to stalk and kill prey, but perhaps not the higher cognitive function that lies at the basis of the evolution of the human brain.

In many mammalian predators, however, hunting tactics and the expected behavior of the prey species must be learned. This is true for solitary hunters like leopards as well as for social hunters like lions and wolves. It reaches a peak in humans in traditional hunting and gathering societies, who spend years learning to be good hunters. Some anthropologists have even argued that the long human maturation period is evolutionarily related to the need to learn the skills for obtaining the highest quality foods—namely meat (Kaplan et al. 2000). Skills that might be important to making a kill, such as the flexibility to respond strategically to rapidly changing circumstances, should also be selected for and enhanced.

Conclusions

There are many reasons why chimpanzees hunt, and they vary according to season, group com-

position, and individual personalities (Stanford 1998). Future research in this area should be able to establish further the why and wherefore of hunting and sharing. Although most researchers (e.g., Boesch 1994) have drawn comparisons between chimpanzee hunting behavior and that of social carnivores such as wolves and lions, much more apt comparisons are to be found with human hunter-gatherers. In both humans and chimpanzees, meat is only a part of the diet, and decisions on whether to hunt must be made on an hourly basis. People forage for meat and also gather plant foods. Chimpanzees forage mainly for ripe fruit and hunt opportunistically when they happen to encounter prey. Their meat-sharing patterns are also more systematic and more nepotistic than those that researchers see in wild baboons, capuchin monkeys, and any other nonhuman primate. Whether intelligence is crucial to hunting and sharing in humans seems indisputable; its role among chimpanzees is likely to be only marginally less so.

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