Chimpanzee Hunting Behavior and Human Evolution

Craig B. Stanford

The Hunt

In a forest in Tanzania in East Africa, a group of a dozen chimpanzees is travelling along the forest floor, stopping occasionally to scan the trees overhead for ripe fruit. The group is composed of five adult males weighing nearly one hundred pounds each, plus several females and their offspring. They come upon a tree holding a group of red colobus monkeys; these are long-tailed leaf-eating monkeys weighing about twenty-five pounds each. This group has twenty-five members, about average for the species in this forest. The male chimpanzees scan the colobus group looking for immature animals or mothers carrying small babies. The colobus, meanwhile, have heard the pant-hoot calls of the chimpanzees approaching for the past several minutes and have gathered up their offspring and positioned themselves in order to defend against a possible attack.

The chimpanzees do indeed attack, the five males—Frodo, Goblin, Freud, Prof, and Wilkie—climbing the larger limbs of the tree. They meet the male colobus, who have descended to counter-attack their potential predators. In spite of repeated lunges by the chimpanzees against the colobus group, they are turned back by the colobus' aggressive defense; at one point two male colobus even leap onto Frodo's back, trying to bite him as he runs along a tree limb, hurling them off. In the end, however, the chimpanzees prevail; Frodo scatters the male colobus and manages to pluck a newborn infant off of its mother's belly. Some of the chimpanzees continue hunting, while others gather around Frodo, begging with extended hands for scraps of meat from the baby colobus' tiny carcass. Frodo offers bits of meat to his allies and to females with whom he has a close relationship; rivals, however, are denied meat. Meanwhile, the other hunters capture the mother of the baby, who has strayed too close in her effort to rescue her now-consumed infant and has fallen from the tree to the forest floor. The mother is grabbed by a young chimpanzee, Pax, and flailed against the tree trunk until nearly dead. The alpha (dominant) male, Wilkie, promptly steals the prey from Pax, however, and a number of females and juveniles crowd around him. An hour later, the last strands of colobus meat, bone, and skin are still being consumed amid occasional outbursts of aggression by individuals who have not received the meat they desired.

THE SIGNIFICANCE OF CHIMPANZEE HUNTING BEHAVIOR TO HUMAN EVOLUTIONARY RESEARCH

Two of the most important and intriguing questions in human evolution are when and why meat became an important part of the diet of our ancestors. Physical anthropologists and archaeologists try to answer these questions using a number of techniques. The presence of primitive stone tools in the fossil record tells us that 2.5 million years ago, early hominids were using stone implements to cut the flesh off the bones of large animals that they had either hunted or whose carcasses they had scavenged.[1] The pattern of obtaining and processing meat by more recent people has been studied by examining archaeological sites in Europe and elsewhere,[2] and also by studying the hunting and meat-eating behavior of modern foraging people, the so-called hunter-gatherers.[3]

Earlier than 2.5 million years ago, however, we know very little about the foods that the early hominids ate or the role that meat may have played in their diet. We know that the earliest upright-walking (bipedal) hominids, currently classified as *Australopithecines*, evolved in Africa about five million years ago, and that they shared a common ancestor with modern chimpanzees before that time. Modern people and chimpanzees share an estimated 98.5 percent of the DNA sequence, making them more closely related to each other than either is to any other animal species.[4] Therefore, understanding chimpanzee hunting behavior and ecology may tell us a great deal about the behavior and ecology of those earliest hominids. This is the approach I have taken in my field study of the hunting behavior of wild chimpanzees; I especially focus on their relationship with the animal that is their major prey, the red colobus monkey. I am trying to answer the following questions:

1. What are the social and ecological factors that predict when chimpanzees will hunt and whether they will be successful?
2. What is the effect of chimpanzee predation on the populations of their prey animals, such as the red colobus?
3. What are the likely similarities in meat-eating patterns between chimpanzees and the earliest hominids?

In the early 1960s, when Dr. Jane Goodall began her now-famous study of the chimpanzees of Gombe National Park, Tanzania, it was thought that chimpanzees were strictly vegetarian. In fact, when Goodall first reported this behavior, many people were skeptical or claimed that meat was not a natural part of the chimpanzee diet. Today, hunting by chimpanzees at Gombe has been well documented.[5] Hunting has also been observed at other sites in Africa where chimpanzees have been studied, such as Mahale Mountains National Park,[6] also in Tanzania, and Taï National Park in Ivory Coast in West Africa.[7] At Gombe, we now know that each year chimpanzees may kill and eat more than 150 small and medium-sized animals, such as monkeys, wild pigs, and small antelopes. Because of the complex fission-fusion nature of chimpanzee society, in which there are no stable groups, only temporary subgroupings called parties that congregate and separate throughout the day, the size and membership of hunting parties vary greatly, from a single chimpanzee to as many as 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.

Studying Chimpanzee Hunting Behavior

Studying the relationship between predators and prey of any two species is always difficult, because in order to observe hunts the researcher must accustom both the hunter and the prey to his or her presence. Because the chimpanzees of Gombe are thoroughly used to being followed throughout the day by human researchers, habituating the predators to my presence was not a problem; it has been a slower process, though, to accustom two colobus groups that inhabit the territory of the Gombe chimpanzees to human observers. In addition, chimpanzees do not usually hunt every day and sometimes two weeks will pass without any hunting. During each week in the field, I follow chimpanzee parties in the hope of seeing a hunt and also observe any of several colobus groups that may become the targets of hunts. While this may sound like a chancy way to observe a hunt, in practice it has worked very well. At least one party of chimpanzees at Gombe is followed daily by researchers; at the end of each day, the chimpanzees build leafy nests in trees where they will sleep for the night. The following morning they will often head off together, giving loud pant-hoot

calls as they travel. These calls allow me to hike early in the morning to a high point in the valley above the chimpanzees' sleeping trees to listen for the direction in which they are moving. I can then walk to any colobus group that I know to be in the path taken by the chimpanzees in order to reach the colobus before the chimpanzees do. In this way I have been able to observe and record nearly one hundred encounters between chimpanzee foraging parties and colobus (from the perspective of the colobus prey) and watch the colobus' reaction to the approach of potential predators. Early morning, therefore, frequently finds me sitting atop a high point in Kakombe Valley (one of the main valleys used by the chimpanzees) called the peak. It was from this point that Jane Goodall made many of her important early observations of chimpanzee behavior many years ago, and it has served me well in my own research. It is also a beautiful vantage point for seeing the whole valley and the animals that inhabit it: chimpanzee, colobus and other monkeys, eagles soaring past, and sometimes a shy bushbuck antelope. As the chimpanzee parties around the valley awake at dawn and set off on their day of travel and feeding, they usually pant-hoot, and this tells me their direction of travel and the likelihood of their meeting a colobus group.

WHAT IS CHIMPANZEE PREDATORY BEHAVIOR?

After three decades of research on the hunting behavior of chimpanzees at Gombe and elsewhere, we already know a great deal about their predatory patterns. We know that, although chimpanzees have been recorded to eat more than twenty-five types of vertebrate animals,[8] the most important vertebrate prey species in their diet is the red colobus monkey. At Gombe, red colobus account for more than 80 percent of the prey items eaten. But Gombe chimpanzees do not randomly select the colobus they will kill; infant and juvenile colobus are caught in greater proportion than their availability[9]—75 percent of all colobus killed are immature. Chimpanzees are largely fruit eaters, and meat-eating comprises only about 3 percent of the time they spend eating overall. Adult and adolescent males do most of the hunting, making about 90 percent of the kills recorded at Gombe over the past decade.

Females also hunt, though more often they receive a share of meat from the male who either captured the meat or stole it from the captor.

One of the main recent findings about hunting by Gombe chimpanzees is its seasonality.[10] Nearly 40 percent of the kills of colobus monkeys occur in the dry season months of August and September. At Gombe, it appears that this is a time of food shortage, since the chimpanzees' body weights decline.[11] Here, the killing is actually less strongly seasonal than in the Mahale Mountains, where 60 percent of kills occur in a two-month period in the early wet season. Why would chimpanzees hunt more often in some months than in others? This is an important question, because studies of early hominid diets have shown that meat-eating occurred most often in the dry season, at the same time that Gombe chimpanzees are eating most of their meat. And the amount of meat eaten, even though it composed a small percentage of the chimpanzee diet, is substantial. I estimate that in some years the forty-five chimpanzees of the main study community at Gombe kill and consume more than 1,500 pounds of prey animals of all species. This is far more than most previous estimates of the weight of live animals eaten by chimpanzees. A large proportion of this amount is eaten in the dry season months of August and September. In fact, during the peak dry season months, the estimated per capita meat intake is about sixty-five grams of meat per day for each adult chimpanzee. This approaches the meat intake by the members of some human foraging societies in the lean months of the year. Chimpanzee dietary strategies may thus approximate those of human hunter-gatherers to a greater degree than we had imagined.

Several other aspects of hunting by Gombe chimpanzees are noteworthy. First, although most successful hunts result in a kill of a single colobus monkey, in some hunts from two to seven colobus may be killed. The likelihood of such a multiple kill is tied directly to the number of hunters in the hunting party. Interestingly, the percentage of kills that are multiple kills rose markedly in the late 1980s and early 1990s, which in turn meant that many more colobus, overall, were being eaten in the late 1980s compared to five years earlier.[12] This is most likely due to changes in the age and sex composition of the chimpanzee community. The number of adult and adolescent male chimpanzees in the study community rose from five to twelve over the 1980s due to a large number of young males who were maturing and taking their places in hunt-

ing parties. One could therefore say that the fate of the Gombe red colobus monkeys is in the hands of the chimpanzee population; this is reflected in the colobus mortality rate in relation to the number of hunters available in a given era.

Although both male and female chimpanzees sometimes hunt by themselves, most hunts are social. In other species of hunting animals, cooperation among hunters may lead to greater success rates, thus promoting the evolution of cooperative behavior. Such cooperation has also been posited as important in our own evolution.[13] Whether or not chimpanzee hunters cooperate is a question that has been debated, and the degree of cooperative hunting may differ from one forest to another.[14] In the Taï forest in the Ivory Coast, Christophe Boesch has documented highly cooperative hunting behavior and meat-sharing behavior after a kill that rewards those chimpanzees who participated in the hunt.[15] The highly integrated action by Taï hunters has never been seen at Gombe. In both Gombe and Taï, however, there is a strong positive relationship between the number of hunters and the odds of a successful hunt.[16] This points out the difficulty of interpreting cooperative behavior; even though Gombe hunters do not seem to cooperate, the greater success rate when more hunters are present suggests that some cooperation is occurring. We are still looking for measures of cooperation that can distinguish true cooperation from hunts in which some chimpanzees hunt and others follow along hoping to capitalize on the efforts of others.

Throughout years of research, Jane Goodall noted that the Gombe chimpanzees displayed a tendency to go on "hunting crazes," during which they would hunt almost daily and kill large numbers of monkeys and other prey.[17] The explanations for such binges have always been unclear. My own research has focused on the causes for such spurts in hunting frequency, with unexpected results. 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 sixty-eight days, the chimpanzees were observed killing seventy-one colobus monkeys in forty-seven hunts. It is important to note that this is the observed total, and the actual total of kills, which includes hunts at which no human observer was present, may be one-third greater. During this time the chimpanzees thus may have killed

more than 10 percent of the entire colobus population within their hunting range.[18]

To try to solve the binge question my colleagues and I examined the enormous database of hunts recorded by field assistants over the past decade to see what social or environmental factors coincided with the hunting binges. Knowing that hunting was seasonal helped, in that I expected binges to occur mainly in the dry season, which was indeed the case. But other interesting correlations leapt out as well. Periods of intense hunting tended to be times when the size of chimpanzee foraging parties was very large; this corresponded to the direct relationship between party size and both hunting frequency and success rate. Additionally, hunting binges occurred especially when there were female chimpanzees with sexual swellings (the large pink anogenital swellings that females exhibit during their periods of sexual receptivity, or estrus) travelling with the hunting party. When one or more swollen females was present, the odds of a hunt occurring were substantially greater, independent of other factors. This co-occurrence of party size, presence of swollen females, and hunting frequency led me to ask the basic question, "Why do chimpanzees hunt?"

WHY DO CHIMPANZEES HUNT?

Among the great apes (the gorilla, orangutan, bonobo, and chimpanzee) and ourselves, only humans and chimpanzees hunt and eat meat on a frequent basis. Since neither humans nor chimpanzees are truly carnivorous—most traditional human societies eat a diet made up mostly of plant foods—we are considered omnivores. Therefore, the important decisions about what to eat and when to eat it should be based on the nutritional costs and benefits of obtaining that food compared to the essential nutrients that the food provides. However, as I discussed previously, there are social influences, such as party size and composition, that also seem to play an important role in mediating hunting behavior. Understanding when and why chimpanzees choose to undertake a hunt of colobus monkeys rather than simply continue to forage for fruits and leaves—even though the hunt involves risk of injury from colobus canine teeth and a substantial risk of failure to catch anything—is a major goal of my research.

In his study of Gombe chimpanzee predatory behavior in the 1960s, Geza Teleki considered hunting to have a strong social basis.[19] Some early researchers proposed that hunting by chimpanzees might be a form of social display, in which a male chimpanzee tries to show his prowess to other members of the community.[20] In the 1970s Richard Wrangham conducted the first systematic study of Gombe chimpanzee behavioral ecology and concluded that predation by chimpanzees was nutritionally based, but that some aspects of the behavior were not well explained by nutritional needs alone.[21] More recently, Toshisada Nishida and his colleagues in the Mahale Mountains chimpanzee research project reported that the alpha there, Ntilogi, used captured meat as a political tool to withhold from rivals and dole out to allies.[22] And William McGrew has shown that those female Gombe chimpanzees who receive generous shares of meat after a kill have more surviving offspring, indicating a reproductive benefit from hunting.[23]

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 in 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. That is, when is the time, energy, and risk (the costs) involved in hunting worth the potential benefits, and, therefore, when should a chimpanzee decide to join or not to join a hunting party? And how does it compare to the costs and benefits of foraging for plant foods? Because of the difficulty in learning the nutritional components of the many plant foods in the chimpanzees' diverse diet, these analyses are still underway. But the preliminary results are surprising. I expected that as the number of hunters increased, the amount of meat available for each hunter would also increase. This would explain 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 hunting success rates of lone hunters is only about 30 percent, while that of parties with ten or more hunters is close to 100 percent. As it turned out, there is no relationship, either positive or negative, between the number of hunters and the amount of meat available per

capita. This may be because even though the likelihood of success increases with more hunters in the party, the most frequently caught prey animal is a one kilogram baby colobus monkey. Whether shared among four hunters or fourteen, such a small package of meat does not provide anyone with much food.

CHIMPANZEES AND PREDATOR-PREY SYSTEMS

The October 7 Massacre

This hunting pattern and its potential effects on the colobus population are best illustrated by my observation of one of the largest colobus hunts observed in the thirty-four-year history of research at Gombe. On October 7, 1992, I located the twenty-five members of my main colobus study group feeding and socializing on a hillside in Kakombe Valley, known as Dung Hill. From 7:00 to 11:00 A.M. they moved slowly across the hill slope and into a ravine known as KK6. It was a quiet morning, and the colobus were relaxed as they munched on foliage and young fruits. But beginning about 9:00 A.M., the distant pant-hoots of one or more chimpanzee foraging parties could be heard coming from further down the valley. The male colobus gave occasional alarm calls, high-pitched bird-like calls that warn other group members of nearby danger, but the chimpanzees did not approach. Then, at about 11:00 A.M., the pant-hoots rang out in two directions at close range, coming from both north and south of the location of the colobus group and me. For several minutes these two chimpanzee parties called, then the calls converged and moved toward us. Clearly, two foraging parties had met and become one larger party that was headed in the colobus' direction. For several suspenseful minutes, the colobus and I waited to learn whether the chimpanzees were headed directly toward us.

Minutes later, the vanguard of the chimpanzee party arrived, a male named Beethoven and several of the adult females and their offspring. They were being followed that morning by two Tanzanian researchers, Msafiri Katoto and Bruno Herman. The colobus were wary and alarm calling, but such a small party was not a great risk to them. Then the main party arrived, with all

twelve adult and adolescent males and many females and juveniles—thirty-three chimpanzees in all. The hunt began, as usual, with Frodo climbing a tall emergent tree in which some of the colobus group was clustered, and for the next twenty minutes the trees shook and the foliage crashed with the sounds of leaping and calling colobus and equally frenzied chimpanzee hunters. As the hunt progressed, I felt sure that the colobus would succeed in driving the chimpanzees away, but Frodo and the other males managed to scatter the male colobus, whereupon the rest of the group fled and became easy prey. Just in front of me a young colobus whom I had watched all morning as it fed on leaves and played with other juveniles attempted to flee the chimpanzees by leaping onto a branch that unfortunately held a male chimpanzee named Atlas. Atlas quickly grabbed the young colobus and dispatched it with a bite to the skull. Within seconds, an estrous female chimpanzee named Trezia ran up to Atlas and begged for meat. Atlas held the colobus carcass away from her; she then turned and presented her sexual swelling to him, they copulated, and only then did she receive a share of the meat. A few feet away, Beethoven had caught a young infant colobus and was engaging in identical behavior with the female chimpanzee Gremlin. The number of colobus killed, however, was difficult to know because after an hour some chimpanzees were still hunting while others who had captured colobus sat on the ground over a fifty-yard circle eating and sharing meat. My reaction to seeing my colobus being killed and eaten one by one before my eyes was initially one of excitement; I was in the unique position of observing a hunt and knowing both predators and prey as individuals. The excitement paled quickly, however, when Msafiri called out through the forest that there had been at least six colobus killed (the final tally turned out to be seven). Four hours later, the chimpanzees finally finished their feast of colobus meat and the ensuing rest and socializing period and departed the scene of the kill.

A hunt like this one does not occur often at Gombe; indeed, this was only the second kill of seven colobus observed in thirty-four years. But multiple kills of two or more colobus happen more frequently—twenty-one times in 1990 alone—illustrating the powerful influence chimpanzees may have as predators on the populations of prey animals within their hunting range. I estimate that from 1990 through 1993, the colobus kills made by the male chimpanzee Frodo alone have eliminated about 10 percent of the colobus monkeys in the home range of the Gombe chimpanzees.

Effects of Chimpanzee Predation on the Colobus Population

As the above-mentioned hunt describes, one chimpanzee hunting party can decimate a group of red colobus prey in a matter of minutes. What is the likely long-term effect of intensive chimpanzee predation on the colobus population? Using information on the size, age, and sex composition of red colobus groups, combined with knowledge of the hunting patterns of Gombe chimpanzees, it is possible to estimate the impact of predation on the colobus. Based on my monitoring of five colobus groups over the past four years, plus censusing of a number of other groups that occupy the eighteen square kilometers of the chimpanzees' hunting range, I estimate there are about 500 (± 10 percent) in the chimpanzees' range. I estimate that from approximately 75 to 175 colobus are killed by chimpanzees annually; I base this estimate on those kills that have been observed, plus the expected number of kills per day in which no human observer was following them in the forest. The annual mortality rate in the colobus population that is due to chimpanzee predation is thus between 15 and 35 percent, depending on the frequency of hunting that year.[24] While 15 percent mortality due to predation has been recorded for other species of mammals, it must be noted that this figure represents predation by chimpanzees only and does not include death at the hands of other predators (leopards and eagles exist at Gombe and eat monkeys) or mortality due to disease, infanticide, or other factors. And 35 percent mortality would mean, if it happened every year, that the red colobus population would almost certainly be in sharp decline. It appears, however, that the average mortality of colobus due to predation by chimpanzees over the past decade has been about 20 percent of the population killed by chimpanzees each year; this figure is comparable to what many other populations of prey animals sustain.[25]

To understand the impact of this mortality on the colobus population, it is important to consider certain aspects of the monkey population. First, female colobus appear to give birth about every two years, and births occur in every month of the year. Since chimpanzees prey mainly upon young colobus (under two years old), female colobus that lose a baby to chimpanzee hunters are able to begin cycling again soon afterward and to produce a new offspring as soon as seven months later. These two facts, lack of breeding sea-

sonality and mortality of immatures rather than adults, may minimize the impact of predation on the colobus, in that a single infant lost is more quickly replaced than an older offspring or adult would be.

To learn whether chimpanzee predation has the potential to be a limiting factor in the size of the colobus population at Gombe, I compared the intensity of hunting by chimpanzees with the size of red colobus groups in each of the valleys of the chimpanzees' hunting range. The central valley of the chimpanzees' range (their so-called core area) is Kakombe Valley; the chimpanzees made about one-third of all their hunts there over the past decade. As one travels away from the center and toward the northern and southern borders of the chimpanzees' range, their use of the more peripheral valleys is much less frequent, and their frequency of hunting there is also less. Only about 3 percent of all hunts took place at the northern and southern edges of their range. I found that the size of red colobus groups also varied over the area of the chimpanzees' hunting range. In the core area, red colobus groups averaged only nineteen animals, little more than half the average of about thirty-four at the outer boundaries.[26] In other words, colobus groups are small where they are hunted frequently and larger where hunting is infrequent. Moreover, I found that this size difference was due largely to a difference between core area and peripheral groups in the percentage of the groups that was immature colobus. In the core area, only 17 percent of each group were infants and juveniles, while fully 40 percent of peripheral groups were immature. This is a direct demonstration of the power of predation to limit both group size and population size in a wild primate population. From now on, we must consider the possibility that in addition to their other interesting traits, chimpanzees may be among the most important predators on certain prey species in the African ecosystems where they live.

What Does Chimpanzee Hunting Behavior Suggest about Early Hominid Evolution?

Did early hominids hunt and eat small and medium-sized animals in numbers as large as these? It is quite possible that they did. We know that colobus-like monkeys inhabited the woodlands and

riverside gallery forest in which early hominids lived three to five million years ago. We also know that these earliest hominids were different from chimpanzees in two prominent anatomical features: they had much smaller canine teeth, and they had a lower body adapted for walking on the ground rather than swinging through trees. They almost certainly continued to use trees for nighttime shelter and for daytime fruit foraging, as do modern ground-living primates such as baboons. In spite of lacking the weaponry such as large canine teeth and tree-climbing adaptations that chimpanzees possess, early hominids probably ate a large number of small and medium-sized animals, including monkeys. Chimpanzees do not use their canine teeth to capture adult colobus; rather, they grab the prey and flail it to death on the ground or a tree limb. And once the prey is cornered in an isolated tree crown, group cooperation at driving the monkeys from one hunter to another would have been a quite efficient killing technique.

In addition to the availability of prey in the trees, there were of course small animals and the young of larger animals to catch opportunistically on the ground. Many researchers now believe that the carcasses of dead animals were an important source of meat for early hominids once they had stone tools to use for removing the flesh from the carcass.[27] Wild chimpanzees show little interest in dead animals as a food source, so scavenging may have evolved as an important mode of getting food when hominids began to make and use tools for getting at meat. Before this time, it seems likely that earlier hominids were hunting small mammals as chimpanzee do today, and that the role that hunting played in the early hominids' social lives was probably as complex and political as it is in the social lives of chimpanzees. When we ask when meat became an important part of the human diet, we therefore must look well before the evolutionary split between apes and humans in our own family tree

NOTES

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