Hominization in the Rainforest: The Chimpanzee's Piece of the Puzzle

HEDWIGE BOESCH-ACHERMANN AND CHRISTOPHE BOESCH

Many models of human evolution propose that key behavioral innovations were involved in the divergence of the human line from the ape line. An ecological reason, the shift from dense forests to a more open habitat, is suggested as the basis for these innovations. Primate models can be useful to our understanding of how environmental factors can affect such key behaviors. New results on forest chimpanzees demonstrate that for most patterns of behavior considered to favor a savanna model, the environmental influences are in opposition to the expectations. A new evaluation of the environmental influences on human evolution is required. We propose that either patterns of key human behaviors were inaccurately distinguished or that the hominization process started while the common ancestor of the chimpanzee and man was alive.

How did human evolution take place? What makes humans different from their closest living relatives? These questions are not only central to most anthropological quests, but have directed major speculation about the numerous fossil excavations of the last decades. However, fossil remains can provide only limited information on the behavior abilities of a presumed species.

All theories of human evolution, from Man the Hunter[1] to Man the Scavenger[2] and from Woman the Gatherer[3] to "Homo faber,"[4] as well as those that focus on food sharing,[5] reproductive strategy,[6] and meat trading,[7] center on the uniqueness of humans with respect to cooperation, food sharing in conjunction with tool use, division of labor, and bipedalism.

Hedwige Boesch-Achermann and Christophe Boesch started the Taï chimpanzee project in Côte d'Ivoire in 1979. They lived for 12 years in this tropical rainforest to follow the chimpanzees. They are presently at the University of Basel, where Christophe Boesch is an assistant professor. The chimpanzee project is still being actively pursued by many students from different countries. The evolution of cooperation and sociality, as well as cultural aspects of the chimpanzees, are the most recent research topics.

Key words: hominization, chimpanzee, tool, hunting, culture

There is no agreement about the respective influence of these factors on hominid evolution. For clues, one usually relies on today's dwindling hunter-gatherer societies and on information from studies of great apes.

In an effort to explain why these factors influenced the evolution of early hominids and not that of other primates, Raymond Dart[1] was the first to propose that it was habitat that had the key function: our ancestors lived in the savanna, whereas the ape ancestors remained in the forest. According to the savanna model, the development of human-like behaviors is related to a radical change in the habitat of early hominids from the forest to the more open savanna-woodland east of the Rift Valley in East Africa, which compelled our ancestors to find new solutions in order to survive. This model, which is still central to most theories of human evolution, is supported in part by the lack of convincing ethnographic and archeologic evidence of pure foragers in undisturbed tropical rain forests[8] and the fact that no hominid fossil remains have been found in present forest regions.

Due to the limited information provided by paleontological discoveries, study of the great apes rapidly became the focus of attention in efforts to obtain information on behavioral perspectives. This approach was not new. In the second half of the nineteenth century, Huxley and Haeckel had compared humans and living apes and Darwin had anticipated the discovery of fossils that would fill in the gap between great apes and hominids. Almost a century later, in the early 1960s, as it became increasingly obvious that the great apes, particularly the chimpanzee, were the surviving source that might shed light on the wealth of fossils that had been found at various sites in East and South Africa, Louis Leakey initiated the first long-term studies of chimpanzees, gorillas, and orangutans in the wild. These included the pioneering studies done by Jane Goodall, Dian Fossey, and Biruté Galdikas.

Taï chimpanzees and a detailed comparison with chimpanzee populations living in more open environments revealed that...forest chimpanzees use more tools, make them in more different ways, hunt more frequently and more often in groups, and show more frequent cooperation and food sharing.

TABLE 1. Types of Tool-Use by Wild Chimpanzees in Different Habitats

	Savannah-Woodland		Rainforest
Tool-use Activity	**Gombe[24]**	**Mahale[32]**	**Taï[15,31]**
Insert	Termites (1sp) Ants (1sp) Bees (1sp)	Termites (2sp) Ants (4sp) Honey	Ants (2sp) Bees (1sp) Honey (4sp) Bone marrow Brain Eyes Nuts (4sp) Grubs Larvae Mushroom
Probe	Termite nests Tree holes Feared objects Other bodies	Ant nests Tree holes Feared objects	Bee nests Tree holes Feared objects Wounds Under bark Other bodies
Clean	Sponging Wounds Dirt Brushing Catching	Ants Dirt	Sponging Wounds
Display	Aimed throwing Throwing Dragging Hitting Play	Aimed throwing Throwing Dragging Hitting Leaf-clipping	Aimed throwing Throwing Dragging Hitting Play Leaf-clipping Weapon Insect
Pound			Nuts (5sp)
Combined			Pound + insert

In line with the savanna model, the emphasis in chimpanzee studies was placed on populations living in open environments. Thus, for two decades all new data on wild chimpanzees came from Gombe and Mahale, both located in savanna-woodland habitats near Lake Tanganyika. The discovery in those populations of some so-called proto-human behaviors such as tool use, hunting, and food sharing supported the supposition that man's evolution took place in a savanna-like habitat. However, most chimpanzees live in the tropical rain forest, not in the savanna. Their way of life had been ignored by the scientific world at that time, except for scarce anecdotal reports. When these hypotheses were built, it was commonly acknowledged that forest chimpanzees simply do not exhibit all the proto-human activities that had been observed at the two Tanzanian sites. This was the situation when, in 1979, we started one of the first long-term projects on forest chimpanzees, in the Taï forest, Ivory Coast.[9] At about the same time, two other studies on chimpanzees in forest environments were started, one in Guinea[10] and one in Central Africa that focused on bonobos (*Pan paniscus*).[11]

The savanna model has now been challenged from three different directions. First, a close look at the anatomy of some *Australopithecus afarensis* skeletons showed that this species was at least a part-time climber[12] and that the forest might have played a much greater role in its life than had been suspected. Second, recent reevaluations of the environment in which the *Australopithecus* species were supposed to have lived revealed a much more forested habitat than had previously been assumed. For example, a study of the habitat of *Australopithecus africanus* of about 3 million years old in northern Transvaal[13] provided an image of wet forests and woodlands rather than bush and grassland. Third, our study of the Taï chimpanzees and a detailed comparison of this population with chimpanzee populations living in more open environments revealed a trend that differs from the one expected under the savanna model. Specifically, forest

TABLE 2. Comparison of Tool Making by Chimpanzees in Different Habitats

	Savannah-Woodland		Rainforest
Type of Tool Making	**Gombe**	**Mahale**	**Taï**
Cutting at right length (grass, sticks, twigs, stone)	Breaking with hands Cutting with teeth	Breaking with hands Cutting with teeth	Breaking with hands Cutting with teeth Pulling while standing on it Hitting against a hard surface
Shaping (twigs, sticks)	Removing leaves or bark	Removing leaves or bark	Removing leaves or bark Sharpening ends with the teeth

Figure 1. An adult female chimpanzee, Héra, cracks hard *Panda* nuts with a granite hammer. This female has been observed to crack nuts for more than five hours without interruption, including while nursing her baby.

chimpanzees use more tools, make them in more different ways, hunt more frequently and more often in groups, and show more frequent cooperation and food sharing.[14,15] Thus, behavioral observations of our closest living relative strongly contradict the savanna model and raise questions about the causative mechanism of human evolution.

TOOL USE AND TOOL MAKING IN WILD CHIMPANZEES

The savanna model predicts that savanna chimpanzees will make and use more tools than will their forest counterparts. We were able to test this prediction by comparing the tool repertoire of chimpanzees living in the woodland-savanna of Gombe and Mahale National Parks with that of chimpanzees in the tropical rainforest of the Taï National Park. This comparison is restricted to these three populations because they are the only ones that have been observed for more than ten years, which allows us to be fairly certain about their tool repertoire. Table 1 shows the types of tools used by the three chimpanzee populations; Table 2 shows the types of tools made. Clearly, these observations contradict the predictions of the savanna model. Taï chimpanzees make and use more kinds of tools than do chimpanzees in more open environments. In addition, Taï chimpanzees tend to perform all modifications on their tools before use, as well as to transport them more frequently and over longer distances.[15,16] One striking point is that Taï chimpanzees use different types of sticks to eat various insect species, which they seem to exploit more systematically than their woodland-savanna counterparts. Taï chimpanzees also consistently use tools to pound nuts (Fig. 1). During the *Coula* nut season, which lasts from November to March, they use natural hammers for more than two hours a day. They may even combine the use of two kinds of tools to gain access to all the content of a single nut. This behavior has not been observed elsewhere.

Intriguingly, pygmy chimpanzees have been observed to use only a few kinds of tools.[11,17] Younger bonobos do use small branches as toys during play sessions, and during rain pygmy chimpanzees often cover their heads with a leafy branch.[17] This repertoire is not as extensive as that observed in Taï chimpanzees. Pygmy chimpanzees, however, do not provide an adequate population for testing the savanna model. There is no pygmy chimpanzee population that lives in a relatively open environment, as is the case of *Pan troglodytes*. Moreover, studies comparing the two species suggest that their predispositions for tool use are not the same (Savage-Rumbagh, personal communication).[18]

For paleoanthropologists, the nut-cracking behavior has special significance: it is the animal tool use that most regularly involves lithic tools resembling those seen in the excavation of sites of Oldowan technology. In addition, the artifacts the chimpanzees produce while pounding are astonishingly like hominid artifacts.

Figure 2. Fritz, an adolescent male, holds his wooden hammer while collecting *Coula* nuts. Unlike *Panda* nuts, *Coula* nuts are soft enough to be cracked with relatively abundant wooden hammers, which the chimpanzees transport from one nut-cracking site to another.

Figure 3. A young chimpanzee watches his mother fish for the honey of wood-boring bees (A). A moment later (B) she gave the tool and honey to her son, an example of sharing tool-obtained food that has not been observed in other chimpanzee populations.

Given the importance of this similarity, we will detail the main feature of this activity.[9,15]

Nut Cracking

The chimpanzees of Taï forest pound five species of nuts. Two of them, *Coula edulis* and *Panda oleosa*, occur regularly and seasonally every year, *Coula* from November to March and *Panda* from February to May. The other three species (*Parinari excelsa*, *Detarium senegalense*, and *Sacoglottis gabonensis*) are less regular, being abundant one year and absent the next. In general, the Taï chimpanzees pound nuts with the help of tools throughout the year, with a regular season from November to April. Tool use in this community is done by all individuals except the youngest, who start to learn it when they are three years old. The anvil is usually a horizontal surface root or, if one is available, a rock. Traces of wear on the anvil depend on the nature of its material and the quantity of nuts pounded. These traces vary from a neat hole exactly the size of the pounded nut to a large number of depressions clustered on the anvil surface over more than a meter. The majority of tools are fallen branches of convenient size and weight (Fig. 2). Seventy-seven percent of the branches weigh less than 2 kg; 15.5% weigh 2 to 4 kg. The branches range from 20 to 80 cm in length and have diameters of 4 to 10 cm. Granite, laterite, or quartz stones weighing 1 to 24 kg constitute 18% of all hammers used, but 90% of those used to crack the hard *Panda* nuts.[9] The wooden hammers are made as needed; that is, they are purposefully broken to a certain length, an action we have often witnessed.[15] Intent in the manufacture of stone hammers cannot be ascertained. A stone may accidently break in two when it is being used for pounding nuts; both pieces are then used as hammers. However, hammers are chosen optimally: for the hardest nuts, the chimpanzees use the hardest and heaviest hammers.[9] Measurements of hardness have revealed that *Panda oleosa* is not only the hardest nut cracked, but that it is harder than any food processed by the hunter-gatherers in eastern and southern Africa.[16]

...at Taï, we became aware of an intriguing sex difference: females are more efficient in cracking nuts than males.

Transport of Tools and Cognition

To open *Panda* nuts, a stone is required but stones are rare in the Taï forest. Thus, the chimpanzees regularly carry tools and nuts between cracking sites. They carry heavier stones, and over longer distances, for *Panda* than for *Coula* nuts. Obviously, simplicity is not the rule in nut crack-

Figure 4. An adult male, Kendo, eats the meat of an adult red colobus monkey. Colobus monkeys account for almost all of chimpanzee prey, even though the Taï forest is rich in medium-sized mammals. Such a specialization is not accidental, but rather, indicates planned hunting tactics.

ing. Transporting a tool to a nut-producing tree requires at least a simple association process. To crack *Coula* nuts directly on a tree branch at the beginning of the nut season, the chimpanzees anticipate their action, choosing a hammer before climbing the tree. In the case of *Panda* trees, which, in contrast to the abundant *Coula* trees, grow at distances from each other that exceed the range of visibility (about 20 m), hammer transport is surprisingly complex.

We undertook a detailed analysis of hammer transport for cracking *Panda* nuts within a region of about 5 sq km. We measured the distance between all *Panda* trees and weighed and marked all the available stones. Within a range of 300 m of a goal tree, four or five stones of various weights were usually available. We found that hammers were chosen to be optimal with regard to their material, that is, they were always stone. (We never saw chimpanzees transport wooden hammers for cracking *Panda* nuts.) Furthermore, the weight of a hammer and the distance it had to be carried were considered. The chimpanzees consistently selected the stone nearest to a goal tree, even though only the stone and the tree were too far apart to be seen at the same time. In 65% of all cases, distance and weight were simultaneously optimal. Such selection requires mental operations: measurement and conservation of distance, comparison of several distances, permutation of objects in a given map, and permutation of the point of reference.[17] The simultaneous performance of these four operations requires a sophisticated spatial representation based on a mental map. Using the criteria of Piaget, these four operations belong to the concrete operations period of childhood development. Thus, in their hammer transport, the Taï chimpanzees demonstrate a Euclidian mental map comparable to that of a nine year old child.[19]

Why should Taï chimpanzees develop such high faculties in spatial representation? Why have similar faculties not been observed in other populations? In human cross-cultural comparisons it has been shown that nomadic hunting-and-gathering people such as Eskimos or aborigines develop spatial skills to a higher degree than do sedentary agricultural people.[20] We propose that the pressure to make optimal use of patchy but rich food sources within a habitat of poor visibility, as exists in the case of the

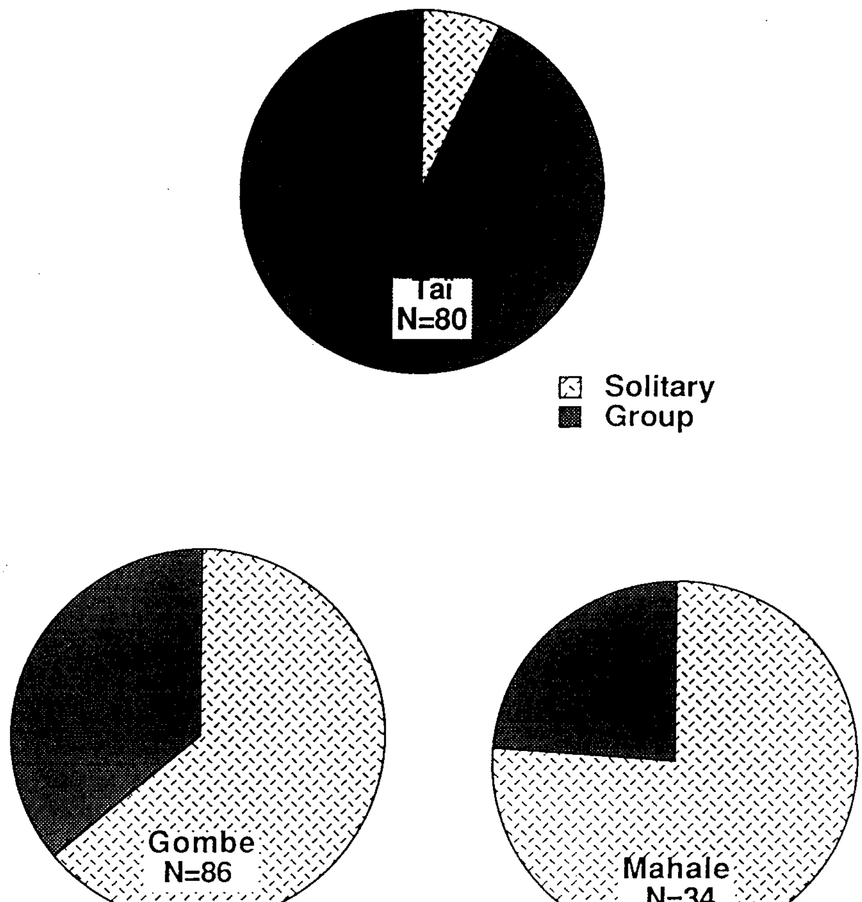

Figure 5. Group-hunting tendencies in three chimpanzee populations.

chimpanzees with *Panda* nuts, contributes to the high development of spatial capacities, which may be less critical for a population living in a habitat such as a savanna, which allows a greater range of visibility.

IS NUT-CRACKING A CULTURAL BEHAVIOR?

It seems logical that the Taï chimpanzees have developed such an elaborate tool activity, given the high nutritional value of the nuts available to them. However, it is surprising that not all chimpanzee populations have developed similar activities. Why do not all chimpanzee populations living in forests of nut-producing trees crack the nuts? In a recent analysis, we found that the eastern limit of the nut-cracking behavior is within the Côte d'Ivoire.[21] Chimpanzees west of the Sassandra River crack nuts; those east of the Sassandra River do not. None of the ecological parameters we controlled for explained this difference. Nut-producing trees, tools, and anvils were available on both sides of the river. Moreover, the densities of the chimpanzee populations were similar in both regions. This was the case for sites no more than 30 to 50 km apart, with flora belonging to exactly the same botanical categories, at the same altitude.[21]

The clear-cut limit in the distribution of nut-cracking behavior argues in favor of a cultural difference.[22] The fact that the chimpanzees west of the river crack nuts and that the ones east of the river do not might be explained by the history of the forests in the region, which suffered a severe drought about 18,000 years ago. Apparently, the area west of the Sassandra River was the only forest refuge at that time.[21]

Another line of evidence supports a cultural explanation of nut cracking, in that this behavior is transmitted between individuals partly by imitation and teaching. We saw mothers intervene in their offspring's nut-cracking attempts either by providing them with tools and nuts, or by actively correcting their errors and demonstrating the correct technique (Fig. 3).[23] Many authors relate culture in humans to a social learning process. Our observations of nut cracking show that the most sustained explanation for it is cultural.

SEX DIFFERENCE IN TOOL USE

Theories of human evolution disagree about the relative contributions of the sexes. The theories that give great importance to hunting tend to emphasize men as playing the driving role in the evolution of our ancestors.[1,9] Theories centered around gathering take the opposite view, emphasizing the contribution of women to human evolution.[3] The antagonistic aspect of such scenarios sometimes makes them difficult to reconcile. An independent test with chimpanzees may contribute to this debate. It is a rather straightforward finding that in all chimpanzee populations for which there are enough reliable data, the males are responsible for most hunts.[14,24,25] But what is the situation with regard to gathering activities?

In addition to the various technical skills we observed in the nut-cracking behavior at Taï, we became aware of an intriguing sex difference: females are more efficient in cracking nuts than males. Specifically, they crack more nuts per minute and need fewer hits to open a nut. Females are also the majority of those who pound nuts directly in trees. On the ground, females = 336, males = 255; in trees females = 68, males = 6; $p<0.001$.[26] Pounding nuts in a tree not only requires the anticipatory transport of a hammer, but also great dexterity in collecting, cracking, and holding the nuts, up to ten pieces, while also holding the hammer. When females undertake this task, they must also satisfy one or two babies that are keen on nuts too, all at a height of 25 m. Females also crack *Panda* nuts much more often than do males (females = 89, males = 19, $p< 0.05$).[26] Thus, females are the sophisticated users and transporters of stone tools between *Panda* trees. In general, we noted that females transport tools more often than males and, unlike males, do not start to carry a tool and then suddenly leave it on the ground without having used it.[26]

We believe that sociality could explain this sex difference. As a rule, whenever any sort of social activity started within the group of nut-pounding chimpanzees, the males would readily leave the nut cracking and deal with whatever was happening. The females, generally, would favor their cracking activity and stay behind if the males rushed away. We also noted that, even while pounding nuts, males would regularly glance around, turning their heads to the left and right. Thus, males seem to control for the presence of other group members and interrupt their activity whenever they lose sight of them. We interpret this behavior of the adult males as indicating a need for them to remain in tight groups. This can explain why, as a rule, only females crack nuts directly in the trees, for visibility from a tree crown to the ground is limited. Only twice did we see adult males crack nuts in the tree and both times there seemed to be an understandable reason, namely an interesting female in estrus. In addition, both males maintained auditory contact with another male on the ground, constantly emitting soft grunts that were answered from below. Other kinds of tool use, such as ant dipping and termite fishing (Fig. 3), are also predominantly female activities in Taï.[15] In Gombe as well, females were observed to be the prime termite fishers and, based on feces analysis, it seems that they are also the main ant dippers.[24]

Females are thus the prime tool users in chimpanzees' gathering activities. This supports the "female gatherer" point of view. However, because male chimpanzees are the main hunters, we also have to deal with a "hunter-gatherer" image involving both sexes, with their respective, but not exclusive, specialties. Sharing patterns could pave the way for a true division of labor. Among chimpanzees, sharing is abundant. For example, males share meat with females. However, reciprocity between adults is the exception in gathering activity. These observations give some support to the hypothesis that in early hominids women were the inventors and users of tools. We noted that female chimpanzees produced flaked stones by pounding the hard *Panda* nuts, three times when using granite, once with a quartzite. These chimpanzee-made artifacts suggest that early hominids could have accidently produced such tools when they used stones as hammers in a gathering activity. We may

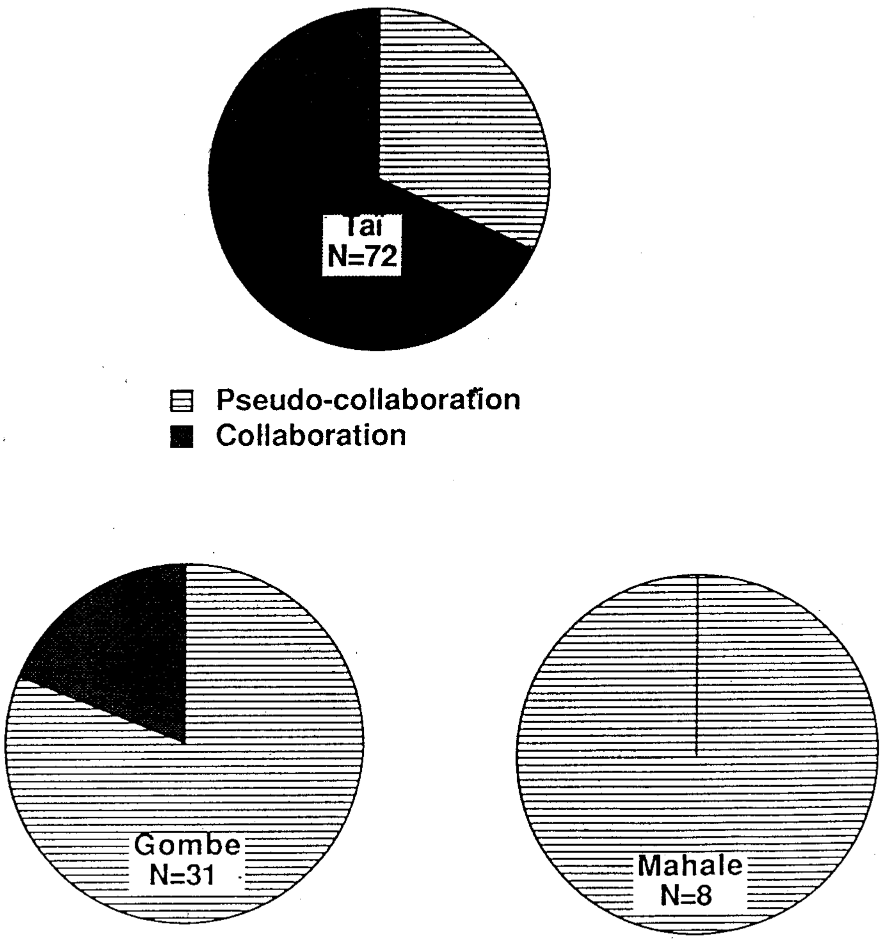

Figure 6. Collaboration in three chimpanzee populations (group hunt without collaboration is called pseudo-collaboration).

speculate that, as among chimpanzees, the individuals who did so were females, who tend to concentrate more strongly on isolated foraging activities than do males.

HUNTING AND COOPERATION IN WILD CHIMPANZEES

The savanna model predicts that individuals in an open environment will be forced to hunt for meat more frequently if they are to survive and, in doing so, will hunt as a team, leading to the emergence of elaborate cooperative and sharing behaviors. New evidence contradicts this simple approach to the emergence of hunting by humans. First, field observations show that hunting by chimpanzees is much more regular than was previously thought,[14,24] being performed an average of once every three to five days. This suggests that hunting is part of the heritage of both chimpanzees and humans.

Early data on hunting behavior in wild chimpanzees from savanna-woodland sites (Gombe and Mahale in Tanzania) provided support for the savanna model of human evolution. The observations from the Taï forest community of chimpanzees contradict this hypothesis, as we have shown with regard to tool use. When exactly the same method is used to evaluate the frequency of hunting by Gombe and Taï chimpanzees, it appears that the forest population hunted colobus monkeys (Fig. 4) about twice as frequently as did their counterparts in a more open environment (Gombe, 66 colobus per year, Taï, 125 colobus per year).[27] Correcting for the fact that colobus monkeys constitute a smaller portion of the diet of Gombe chimpanzees (65% of prey)[24] than that of Taï chimpanzees (86% of prey),[14] the Gombe hunting rate is still a third less than that of Taï chimpanzees. In addition, Taï chimpanzees hunt more often in groups (Fig. 5) and, when in groups, collaborate more often (Fig. 6) than do Gombe chimpanzees.

Why do some chimpanzees cooperate less than others when they hunt? What factors favor cooperation and group hunting? Gombe chimpanzees sometimes hunt in the same elaborately collaborative way that Taï chimpanzees do. Thus, the difference between their customary hunting behavior and that of the Taï chimpanzees is not a matter of difference in abilities.[27] Why is it, then, that Gombe chimpanzees do not cooperate more frequently? Simply stated, they do not because they do not need to: Single Gombe hunters are highly successful when hunting colobus monkeys, achieving a capture about five times more quickly than do single Taï hunters.[28] Consequently, there is no need for them to use more demanding ways of hunting. In contrast, Taï chimpanzees hunt monkeys in a high-density forest, which gives the monkeys many ways to keep a large distance between themselves and the hunter. Single hunters in Taï have a low success rate when hunting colobus monkeys. To overcome these difficulties, Taï chimpanzees have to elaborate their techniques by hunting in groups and by attacking the monkeys from different angles as well as by capturing larger individual prey.[27,28] This adoption of different and complementary roles while hunting constitutes our definition of collaboration.[14]

Among chimpanzees, it appears that an ecological factor, the distance between prey and hunter imposed by the forest structure, directly affects hunting behavior by influencing the time needed to achieve a capture. In forests, this distance is generally larger than in woodlands. Thus, forest chimpanzees need to hunt more often in groups and cooperate in order to be successful. This is in opposition to what is commonly expected under the savanna model.

CONCLUSION

All the aspects of tool use and hunting we have analyzed in chimpanzees show that forest chimpanzees have been forced to rely on more demanding means of adapting. Chimpanzees are not human, and we have to be careful in making inferences from one species to another. However, biologists agree that some general rules affect species that have similar needs. Chimpanzees and humans share many common features as a result of their close relatedness. The two have diverged only recently, and 98% of their genetic material is the same.[29] New evidence in paleoecology[8,13] tends to indicate that our ancestors may have lived in environments like the forested habitat in which most modern chimpanzees live. The environment does play an important role, but some paleontologists certainly have been much too simplistic in interpreting it as favoring a savanna model. This interpretation underestimates the difficulty that confronts a large social primate living in the forest. The constraint on visibility presents a major challenge in everyday life. In hunting, the difficulties of detecting and capturing prey are important parameters for the evolution of group hunting and cooperation. At Taï, where visual detection of prey is very difficult, chimpanzees intentionally search for arboreal monkeys, their main prey.[14,27] This behavior has never been observed in other chimpanzee populations. Once detected, the monkeys can easily escape into the high trees. Indeed, preying on such an agile primate is demanding.[27,28] Thus, the forest pressure favors behaviors such as cooperation, just as it would if the prey were large and powerful.[14] Similarly, the presence of large quantities of a highly valued but hard-embedded food favors acquisition of a tool culture to facilitate gathering.

Studying chimpanzees has proved that specific aspects of the environment can have a great impact on the behavior of different populations. A clearer knowledge of the environment in which our ancestors lived would be necessary to gain insight in their behavior. Nevertheless, we can already say that some sets of behavior that are currently considered as part of the hominization process are actually, or also, part of the "chimpanzination" process. Indeed, Diamond[30] has proposed man as the third chimpanzee. Thus, chimpanzee studies directly contribute to the knowledge of what may be typically human.

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