The Chimpanzees of the Taï Forest

Behavioural Ecology and Evolution

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This monograph synthesizes sixteen years of observations on wild common chimpanzees (*Pan troglodytes*) by a husband and wife team working in Taï National Park in the Côte d'Ivoire. Boesch and Boesch-Achermann utilize an "ethnological approach" (p. vi) in their study, and treat certain admired subjects as if they were trusted human informants. They believe that this approach is warranted because of subtle differences in individual behavior. In fact, the Taï chimpanzees show the highest known incidence of hunting and tool use among any wild chimpanzee populations. They also show evidence of symbolic behavior in auditory communication (drumming on tree buttresses) that may coordinate the pace of group movement and the direction of travel. The book is richly illustrated with photographs, and there is a reference section and a detailed index. Two appendices conclude the book, one containing a list of all identified chimpanzees and known genealogies, and one providing a list of mammals in Taï National Park and the frequency with which they were observed.

Taï yields the most detailed information about West African chimpanzees, because animals from the site of Bossou in Guinea, 300 km north of Taï, are less well studied. The rainforests of West Africa remain the major stronghold for chimpanzees, and the species reaches its greatest abundance and density within these lowland rainforest habitats. The authors argue that chimpanzee behavioral ecology within some of these rainforest habitats has been least impacted by human presence, and may therefore better reflect the original, unaltered chimpanzee behavioral repertoire. They argue for greater behavioral diversity among the chimpanzees dwelling within the dense forests of Taï than among East African chimpanzees dwelling in highly disturbed and depauperate environments. The authors constantly compare results from Taï with the two best known East African chimpanzee study sites, Gombe and Mahale, both in Tanzania, and both severely affected by human population buildup and subsequent environmental disturbance. Gombe, for example, is now an insular reserve surrounded entirely by a sea of farmland. This affects chimpanzee behavior, because animals cannot disperse naturally, and are highly restricted in their movements.

Yet, if Taï represents a more undisturbed environment than East Africa, it, too, is being reduced to a refuge area. Taï National Park is now the only undisturbed rainforest in the Côte d'Ivoire, and the forest surrounding the park has been reduced by 80 percent through agriculture and human migration. Furthermore, even the chimpanzee population at Taï has suffered a recent marked decline, which underscores the endangered status of the species as a whole. Boesch and Boesch-Achermann documented the presence of several chimpanzee communities at Taï, but collected detailed observations on only one of them. The authors identified 123 chimpanzees (77 females and 46 males) during the course of the Taï study. Most of these animals are now dead.

At first contact, there were 80 animals in the study community. There are now about 30 animals in the group. Numbers remained stable during an initial period of research, but two periods of steep decline followed. During the first decline, leopard predation accounted for 42 percent of the deaths, especially among older infants and juveniles, over the course of 5 years. A single leopard that specialized in eating chimpanzees was apparently responsible for these deaths. This degree of predation is significant, because chimpanzees were always thought to be relatively immune to sympatric carnivores. However, if a single chimpanzee ambushed by a leopard is not killed immediately, then it must be large and strong enough to fend the predator off until other chimpanzees converge on the attack site. Younger chimpanzees succumb before help arrives. The second chimpanzee population decline was caused by two outbreaks of the Ebola virus. The disease was probably transmitted to the chimpanzees through consumption of meat from infected colobus monkeys, who are immune to the disease. With a fatality rate of 100 percent, Ebola accounted for 66 percent of the deaths during the second period of decline. Ebola is thus the primary source of mortality, with leopard predation the secondary source. Human poaching with snares and guns also accounts for chimpanzee deaths, but is far less important than Ebola and leopard predation. With 40–60 percent juvenile mortality, low replacement rates, and the prospect of further Ebola outbreaks and continuing human encroachment, the Taï chimpanzee study group appears doomed to extinction.

Female chimpanzees in the community always outnumber males by about 3:1. Boesch and Boesch-Achermann detect the Trivers-Willard effect: dominant females invest 2 more years in sons, while subordinate females invest 11 months more in daughters. Sons of dominant mothers have better survivorship, and attain higher rank. Mothers contribute to their son's rise by accompanying them during challenges to higher-ranking males, and there is some evidence that mothers initiate such challenges. Demographic analysis reveals that females first give birth at 14 years, and continue to give birth every 5.75 years. Fertility does not decline with age. Menopause does not exist, unlike the situation at Mahale. The authors suggest that the impoverished environment at Mahale is responsible for the presence of menopause there. Taï females produce sexual swellings even when they are sterile, as adolescent new immigrants, or as young and subordinate mothers. The authors suggest that these sexual swellings function as a "social passport," allowing the females to defuse social stress that would otherwise be directed at them by males.

The genotypes of all chimpanzees living at Taï between 1991 to 1995 are known, and it can therefore be determined whether infants were sired by resident or stranger males. A surprising 55 percent of the infants were fathered by males from outside the community. Interactions between communities are very different from those observed in East Africa. The Taï chimpanzees are territorial, but inter-community contact is relatively benign. Territorial behavior occurs about twice a month, but a status quo is maintained among neighbors. At Taï , the core area comprises only 35 percent of the total territory, but is occupied 75 percent of the time. This core area remains very stable, shifting only 300 meters over 13 years.

No deaths were observed as the result of inter-community aggression at Taï, but chimpanzees exterminated an entire neighboring community at both Gombe and Mahale. Taï chimpanzees temporarily take stranger mothers "prisoner", and bite and harass them. These females eventually escape relatively unscathed. The infants that they carry are never harmed. Because reproduction is partly decoupled from the social group, the authors suggest that Taï chimpanzees scout out potential future mates during territorial encounters with other groups. Females are involved in territorial defense. When attacks occur, females are part of the attack party 72

percent of the time, and they comprise 35 percent of the party. Females also patrol more than half of the time, and they form nearly half of the patrol party.

There is seasonal variation in diet and ranging behavior. Taï chimpanzees hunt during the wet season, and eat fruit and nuts during the dry season. The average day range of Taï chimpanzees is 2.5-3.5 kms/day—higher than in East African chimpanzees. Animals range the most when eating fruit. They range less when hunting, and range least of all when eating nuts. The day range when nuts are consumed is less than half that of other months. Party size is large during a hunt, and is especially large when meat is consumed.

Boesch and Boesch-Achermann consider meat-eating to be the generator of social life and prolonged associations at Taï. Taï chimpanzees hunt much more frequently and collaboratively than in East Africa. In fact, the authors question whether true group hunting occurs at all at Gombe (p. 178). Hunts for vertebrate prey were observed 413 times at Taï, resulting in 267 kills. There were 274 group hunts. Hunting is concentrated in September and October, when the chimpanzees hunt every day, sometimes more than once. This hunting peak coincides with the birth season for red colobus monkeys, which constitute 80 percent of the prey. Taï chimpanzees specialize in hunting colobines. Colobines account for 93 percent of the prey taken; many potential prey species are ignored. Half of the animals killed are adults. Lone hunters rarely capture prey, because the hunt occurs in dense rainforest, and the pursuit takes place in three dimensions. There is a sexual division of labor, with males hunting 85 percent of the time. Females can receive meat regardless of whether they have hunted, and some females may dominate most males in access to meat. Hunters eat the most meat, independent of their social rank, because females support the hunters against dominant individuals. Boesch and Boesch-Achermann document that individuals contributing most to a hunt receive the most meat. Thus, "cheating" is not rewarded. Successful hunting requires a long learning period, and only males over 30 years old can perform the most complex hunting task—anticipating prey movements.

Table 9.1 contains the first published inventory of all tool behavior among Taï chimpanzees. The principal tool behavior by far is nut-cracking, with about 1,800 observations. The authors also describe for the first time how nut-cracking is learned. Animals may spend hours a day engaged in this activity, and gain a major portion of their caloric (3,450 kcal/day) and protein intake from nuts. Five species of nuts are pounded open, with *Coula* and *Panda* nuts being the most important species. Both wooden and stone hammers are used, although *Panda* nuts can only be opened with a stone hammer. Females engage in nut-cracking far more than males, possibly because it is a solitary behavior, and males prefer to socialize. Females also crack nuts in the trees, and are more efficient tool users on the ground. Nut-cracking is limited in its distribution, because chimpanzee populations 30 km away do not exhibit it. Its existence therefore depends upon learning. It takes 4 years to learn how to open *Coula* nuts—7 years for *Panda*. Mothers share both nutmeats and tools with youngsters, thus providing an incentive to learn. However, they share more nutmeats with their sons. Daughters therefore become independent earlier, and practice longer.

A major theme of the book is the great behavioral disparity between the Taï chimpanzees and those of East Africa. In fact, the Taï chimpanzees more nearly resemble bonobos in their behavior. The authors attribute this to the fact that both Taï chimpanzees and bonobos live within dense tropical rainforest, rather than within the relatively arid and disturbed habitats of Tanzania. They believe that the behavioral repertoire of bonobos and Taï chimpanzees may be primitive for the genus *Pan*, and may perhaps have characterized the first hominids, as well. Some of the similarities between bonobos and Taï chimpanzees include: a larger party size for most of the year; more association between males and females (two-thirds of the parties at Taï included both sexes); prolonged sexual swellings that conceal ovulation; no deaths from inter-community aggression; no infanticide

(there was only one possible instance of infanticide at Taï); resident females show less aggression to immigrant females; and a higher degree of female-female bonding.

The authors conclude the book by searching for traits that uniquely link chimpanzees with humans among the primates. Boesch and Boesch-Achermann argue that chimpanzees have a broader degree of behavioral diversity than other non-human animals because they have a fission-fusion social system, form coalitions, engage in territorial interactions with other chimpanzee communities, hunt vertebrate prey, and frequently exhibit tool behavior. However, these behaviors are observed in other social animals, including several primate species. In particular, Boesch and Boesch-Achermann slight the evidence for frequent tool behavior in tufted capuchin monkeys (*Cebus apella*) of the New World, much of it involving the type of habitual nut-cracking behavior that they find so remarkable in the Taï chimpanzees. The authors nevertheless introduce an interesting environmental factor into the discussion about the origins of complex sociality—the rainforest habitat. They believe that, because the Taï chimpanzees live in dense rainforest, their behavior is more complex than that of East African chimpanzees. The Taï chimpanzees hunt arboreal prey in trees, pursuing their prey in three dimensional space, and act with members of their own and other communities in an environment where vision is restricted to a maximum of about 20 meters. The authors believe movement through vertical space in a confined area where distance vision is limited is important. It selects for the ability to create accurate three dimensional maps of resources, to assess the potential movement of prey in three dimensions, and to communicate auditory information about group movement through apparently symbolic drumming on rainforest tree buttresses. Boesch and Boesch-Achermann thus invert the traditional explanation for hominization, which views increasing aridity and open-country habitats as the environmental trigger for hominid origins.

If rainforest habitat is the explanation for more complex behaviors in Taï chimpanzees than chimpanzees in Tanzania, should one expect that ancient hominids in forested habitats would exhibit more behavioral complexity than contemporary hominids in open-country? In this light, one must note the evidence for forest habitat at sites that yield the earliest fossil hominid taxa. Boesch and Boesch-Achermann believe that the earliest australopithecines, like the Taï chimpanzees, must have regularly hunted colobine monkeys and frequently used wooden and stone tools to extract social insects and to pound nuts. The australopithecines did not need tools to hunt colobine monkeys, because the Taï chimpanzees hunt and consume colobines without tools. Stone tools for processing carcasses appear only with the advent of genus *Homo*, when meat and marrow are removed from vertebrate remains. Fossil colobine species occur at many hominid sites, but did early hominids prey on colobines? Certainly, australopithecines could climb. Yet, the large canine teeth of Taï chimpanzees allow them to pierce skin, dismember carcasses, and sever meat from bone, and all australopithecines had small canine teeth. Granted, they might be able to kill colobines, but how could they butcher a carcass without stone tools?

Lastly, the authors introduce a hominization scheme based on their observations of the Taï chimpanzees. They assume that hominization occurs within a tropical rainforest setting. The existence of a fission-fusion social system within dense rainforest mandates the appearance of mechanisms allowing isolated foraging parties to rendezvous with the main group and coordinate movements, even though animals are not in constant visual contact. The mechanisms that allow such behavioral coordination pre-adapt animals for hunting arboreal prey in three dimensions. Group hunting and cooperation increase under difficult conditions. This type of hunting, in turn, leads to increased tool behavior, which influences hunting in a