

Habituation of Wild Chimpanzees (*Pan troglodytes*) of the South Group at Taï Forest, Côte d'Ivoire: Empirical Measure of Progress

Paco Bertolani^a · Christophe Boesch^b

^aDepartment of Biological Anthropology, University of Cambridge, Leverhulme Centre for Human Evolutionary Studies, Cambridge, UK;

^bDepartment of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

Key Words

Chimpanzee · *Pan troglodytes* · Habituation · Sex differences · Taï National Park

Abstract

The last part of the chimpanzee (*Pan troglodytes*) habituation process of the Taï South Group was monitored over 2 years (1994–1996), during which all males and most of the females became habituated to observation by humans. The time needed (5–7 years) to habituate the community was similar to that recorded for the Taï North Group and is comparable to other populations studied in Africa. Variation emerged in habituation rate: males were habituated earlier than females, and among females, sexually cycling individuals were habituated faster than non-cycling females. Such differences may be a function of both the methods used to find the chimpanzees and the sex of the individual. Reproductive status and individuality may also have influenced habituation rates by affecting the number of contacts required to habituate a chimpanzee to neutral humans.

Copyright © 2007 S. Karger AG, Basel

Introduction

The flight reaction shown by wild primates upon seeing humans is well known to field primatologists and is a major obstacle for observing their behaviour [Boesch and Boesch-Achermann, 2000; Williamson and Feistner, 2003]. Many studies on wild primates have dedicated preliminary periods to habituate the animals to human presence. Habituation of wild apes is generally considered an initial, obligatory step that the researchers must go through before tackling more interesting behavioural questions. The aim of this research was to systematically monitor the habituation process of individual wild chimpanzees in Taï National Park, Côte d'Ivoire.

KARGER

Fax +41 61 306 12 34
E-Mail karger@karger.ch
www.karger.com

© 2007 S. Karger AG, Basel
0015–5713/08/0793–0162\$24.50/0

Accessible online at:
www.karger.com/fpr

Paco Bertolani, Department of Biological Anthropology
University of Cambridge
Leverhulme Centre for Human Evolutionary Studies
Henry Wellcome Building, Fitzwilliam Street
Cambridge CB2 1QH (UK), Tel. +44 1223 764 719
Fax +44 1223 764 710, E-Mail mpb44@cam.ac.uk

The time needed to habituate a group of primates varies by species from days in nocturnal primates to years in apes [Williamson and Feistner, 2003]. Habituating chimpanzees can be a long and frustrating process; their large home range and fission-fusion social system make it more difficult than in other primate species. In the early studies during the 1960s, researchers used prized food (i.e. provisioning) to attract the animals, who learned with time to tolerate observers [Goodall, 1986]. Strictly speaking this is associative learning, and not habituation, because habituation occurs only with the repetition of a neutral stimulus [Thorpe, 1963]. Humans dispensing food are not neutral, and provisioning likely affects important aspects of chimpanzees' ecology and behaviour, such as diet, ranging patterns and social behaviour, by elevating aggression levels between conspecifics, baboons and toward human observers [Wrangham, 1974].

The first habituated chimpanzees at Taï were the North Group [Boesch-Acher- mann and Boesch, 1994]. Provisioning was never used at Taï, and the first years of research yielded few direct observations. The first signs of improved habituation were only recorded after 5 years, and some specific behavioural patterns (e.g. tool use to dip for driver ants) were only seen after 8 years [Boesch and Boesch, 1990]. Even after 15 years, some females were still not completely habituated [Boesch-Acher- mann and Boesch, 1994; Boesch and Boesch-Acher- mann, 2000].

Here we present data on a significant phase of the habituation process of the Taï South Group, during which all males and many females became habituated; the factors that may have affected individual habituation rates are discussed.

Methods

The Taï National Park is the largest remaining continuous block of West African forest with an area of 4,540 km², and it represents one of the most important refuges for western chimpanzees (*Pan troglodytes verus*) as well as for other primates and mammals [Herbinger et al., 2003].

Habituation of chimpanzees of the South Group began in 1989 [Boesch-Acher- mann and Boesch, 1994; Herbinger et al., 2001] by a team of students and researchers directed by Christophe Boesch. Data presented here were collected from August 1994 to July 1996. During this period, 2 researchers and 2 Ivorian assistants tried to locate the chimpanzees, often separating to search different parts of the forest in order to maximize the chances of finding a party. While in the first 3 months observations were made in 2 teams of 2, in the following months each of the 4 observers went to the forest alone. Following Boesch's methods of habituation for the North Group [Boesch and Boesch, 1981, 1983], we tried to make the observers' physical appearance and behaviour as inoffensive as possible by wearing drab clothes, moving slowly, talking softly, making few noises, not pursuing fleeing individuals and not using bush knives. Special emphasis was given to being in the forest early to listen for early morning vocalizations; such early morning calls are frequent in chimpanzees, as well as calls in the late afternoon when chimpanzees regularly reunite after scattering during the daily forays.

We used a map (based on a 250-metre grid) and compass to orientate ourselves in the forest, in addition to keeping track of the distance travelled and counting elapsed time or steps taken. Chimpanzees were found by listening for their vocalizations, drumming or nut-cracking sounds. We listened for an hour or more at scattered locations within the presumed home range of the community. If nothing was heard, we moved to another spot at least 1 km away.

When the above sounds were heard, we noted the direction and estimated distance; by compass bearing we moved slowly toward the chimpanzees' sounds. Other times we searched for the chimpanzees at places where we had recently met them or at known and previously vis-

ited food sources. The ratio of time spent with the chimpanzees and within the forest searching for the chimpanzees was calculated for the first 4 months of the study. Following habituation of the first males, individuals could be followed from nest to nest.

The degree of habituation attained by different individuals by the end of the study period (July 1996) is compared empirically by defining 4 operational classes, based on the chimpanzees' behaviour in the presence of humans: minimal = the individual always moves away when humans appear; partial = the individual stays in the party if others are present, but tends to assume a peripheral position and cannot be followed when alone; good = the individual appears fully habituated if with other chimpanzees and during certain activities (e.g. feeding in the trees), and it is possible to follow from a distance at the limits of visibility (around 20 m); full = the individual accepts humans (and apparently ignores them) at close range during all activities; they appear calm when they are alone with humans and are relatively easy to follow while travelling.

To compare the monthly habituation state by individual we simplified this classification to two categories: (1) minimal and partial habituation; (2) good or full habituation. Each identified individual was assigned a score for each month based on the predominant category. The 4 categories could not be analysed separately and were collapsed to 2 because the less habituated individuals were contacted few times per month, often by a single observer; thus, we could not reconstruct an unbiased and more detailed picture of the habituation status of all individuals. Individuals were identified by recording their physical characteristics, such as size, hair and skin colour, ear cuts, missing fingers, oestrus shape or presence of scars. An individual was considered identified and was given a name when the 4 observers agreed on its identifying signs. Some individuals had already been identified by students working with the South Group before P.B.'s arrival. Consistency in rating between all 4 observers was the operational criterion used to assess habituation at the end of the study.

We define cycling females as those females who showed cyclical sexual swelling and mated with males when maximally swollen. The 6 individuals in this condition included 4 adult females with a juvenile offspring, 1 adult female without offspring (Eva) and 1 adolescent female (Pilar). Non-cycling females (19 individuals) did not show sexual swelling, and all were with dependent infants, some of them also with another juvenile offspring.

To test for the influence of sex and reproductive state, we used 2-tailed Mann-Whitney tests to compare habituation of males versus females and cycling versus non-cycling females. The dependent variables tested are the number of months before identification occurred (number of empty cells for each individual in table 1) and the number of months spent in intermediate habituation status (category 1). All individuals were assumed to have been members of the South Group since the beginning of this study (August 1994); thus, time to reach category 1 status indicates time to be identified.

The number of individuals included in each test varies; for example, individuals who were already identified or habituated at the beginning are not considered in the tests, nor are females who never reached category 2 by the end of the study.

Results

Qualitative

The reaction of chimpanzees to humans changed over the process of habituation, from suddenly running away to apparently ignoring humans. Habituation was a dynamic process, and these changes were gradual and variable; the typical reactions described were not necessarily recorded in all individuals.

At first, unhabituated individuals fled from the observers, giving alarm calls. In a panic reaction, the chimpanzees interrupted their activities, and if they were in the trees, they quickly descended and ran away on the ground. This typical response lasted for several years, but it was highly variable. Given that habituation of the South

Table 1. Habituation status of adult and adolescent individuals of the Tai South Group from August 1994 to July 1996

Individual	Year and month																							
	1994					1995										1996								
	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J
<i>Males</i>																								
Natan	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Niro	1	1	1	1	1	2	2	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Gaston	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2
Zyon						1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Mkubwa						1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Charlie							1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2
Rafiki								1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2
Kaos												1	1	1	2	2	2	2	2	2	2	2	2	2
<i>Females</i>																								
Zora	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Wapi	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Eva</i>					1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
<i>Pilar</i>					1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2
<i>Sumatra</i>					1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Margot						1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Atra</i>							1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2
Louise							1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Coco								1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2
<i>Duna</i>									1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2
Tita										1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Olivia											1	1	1	1	1	1	1	1	1	1	1	1	1	1
Bombay												1	1	1	1	1	1	1	1	1	1	2	2	2
Fatima													1	1	1	1	1	1	1	1	2	2	2	2
<i>Kabisha</i>													1	1	2	2	2	2	2	2	2	2	2	2
Garuda														1	1	1	1	1	1	1	1	1	1	1
Haraka														1	1	1	1	1	1	1	2	2	2	2
Uganda															1	1	1	1	1	1	1	1	2	2
Yucca															1	1	1	1	1	1	2	2	2	2
Julia																1	1	1	1	1	1	1	1	1
Nubia																	1	1	1	1	1	1	1	1
Rubra																		1	1	1	1	1	1	1
Virunga																		1	1	1	1	1	1	1
Isha																			1	1	1	1	1	1
Mandy																								

Blank = Individuals not yet identified; 1 = minimal or partial habituation; 2 = good or full habituation; dash = dead. Females who were cycling when identified are italicized. Niro and Gaston disappeared during the study period. Margot was seen maximally swollen after being identified, so she is not considered a cycling female in the statistical tests.

Group had started more than 4 years before, alarm calls and flight were observed less often during these 2 years. The flight reaction gradually changed into more relaxed avoidance. The chimpanzees continued to try and avoid humans, but instead of fleeing they slowly moved out of sight, without panic or alarm. If they moved away be-

cause of the arrival of humans, we usually found them again not far from their initial position. When they were found in the trees, they normally continued eating or resting. A maximum possible distance was maintained between the observer and chimpanzees and consequently the chimpanzees were repeatedly lost and found. At a more advanced stage, the chimpanzees accepted observers at closer distances, and they appeared actively interested in humans, by repeatedly staring at them. In this phase, the apes commonly directed threats to the observer. Arm-waving, branch-shaking, head-tipping and cough-threats were all exhibited by many individuals. Only once did an adult male, Niro, make a direct charge at observers, and this was the last episode of his aggressiveness. Displays of isolated threats were common in infants and juveniles, or they were included as part of more complex play sessions. Finally, fully habituated chimpanzees showed no interest in humans; the most habituated individuals only rarely stared at observers. They approached the observer at a distance of less than 1 m, in order to collect fruit or just to pass by.

During the study period, it was common to meet parties composed of individuals with different levels of habituation. Typically in such situations, the less habituated females and their offspring tolerated us at closer distances than when they were alone.

Quantitative

Over the time spent in the forest in 1994 (484 h), the chimpanzees were located by the 2 researchers on 26 occasions and were observed for a total of 67 h; however, these included the observations of Zora (9 times for 36 h), the only fully habituated female at the beginning of our study. The duration of contact with the chimpanzees greatly increased after the first males had become habituated. The change probably reflects variation in the methods used to find and to follow the chimpanzees. With some males already habituated, continuous following of these individuals became normal, and within a few days, nest-to-nest all-day follows were the rule. The big rise in time spent with chimpanzees was probably favoured by the nut season (*Coula edulis*). In this period *Coula* nuts were the major food of chimpanzees, and the forest echoed with the chimpanzees' nut-cracking sounds [Boesch and Boesch, 1981, 1983], which made it easier for observers to find a party.

During the first 4 years of habituation of the South Group, from 1989 to 1994, one female, Zora, became fully habituated. An adult male, Natan, had a good habituation status, 2 other males, Niro and Gaston, were respectively partly and minimally habituated, and another female, Wapi, was minimally habituated. In the next 2 years, from 1994 to 1996, all the other individuals, except 1 female (Mandy), of the South Group were identified and their habituation status improved to differing degrees.

The following data are a 2-year window within the longer and more complex habituation process; however, during this period, most individuals became habituated, and their typical reaction to humans changed from avoidance to unconcern.

Table 1 gives the monthly habituation status of the 32 adult and adolescent chimpanzees of the South Group. Males were habituated earlier than females. By October 1995, all 7 adult and adolescent males of the community were habituated, while 11 out of 25 females were still unhabituated and 5 were still unidentified.

Table 2 shows the composition of the community by age, sex and habituation status at the end of the study period, July 1996. Over the final 24 months of habitu-

Table 2. Tai South Group at the end of the study period (July 1996), by sex, age and habituation status

Habituation	Adult		Adolescent		Juvenile		Infant		Total
	male	female	male	female	male	female	male	female	
Full	7	9	1	1	1		5	3	27
Good		5			1		3	3	12
Partial		3				2	1	2	8
Minimal		6			1	3	4	2	16
Total	7	23	1	1	3	5	13	10	63

Two male individuals (1 adult and 1 adolescent) who disappeared during the study period are also included.

ation (excluding individuals whose habituation status remained constant over the 2-year period), males were habituated and reached minimal habituation significantly earlier than females (6.8 vs. 11.9 months; $U_{N1:5, N2:22} = 23$; $z = -2.01$; $p < 0.05$). However, there was no significant difference between males and females in time spent in intermediate habituation status (4.6 vs. 5.9 months; $U_{N1:5, N2:15} = 27$; $z = -0.93$; $p > 0.35$). These results are summarized in figure 1a and b.

Females who resumed cycling (Eva, Sumatra, Kabisha) and those who showed irregular swellings (Duna; Atra, irregularly cycling while pregnant, and Pilar, an adolescent female) were more quickly habituated than those who were non-cycling. The differences are significant for both variables considered: time to be identified (6.8 vs. 13.8 months; $U_{N1:6, N2:16} = 10.5$; $z = -2.78$; $p < 0.01$) and time spent in intermediate habituation status (3.8 vs. 7.2 months; $U_{N1:6, N2:9} = 6.0$; $z = -2.50$; $p < 0.05$; fig. 1c, d).

The only 2 adolescents, 1 male (Gaston) and 1 female (Pilar), showed similar habituation trends as the adults, but habituation of independent juveniles sometimes differed from their mothers. Sagu from the beginning was habituated much like his mother Sumatra, but daughters Tosha and Dawa were less habituated than their mothers, Tita and Duna, respectively. Dependent infants were (by definition) equally habituated as their mothers.

An adult female, Haraka, became habituated in 1 day when her 2-year-old infant died (the sex of the infant was unknown). Haraka was scared of humans and had never approached the observers. In February 1996 she was found with her infant showing bad injuries on his head and body. The comatose infant died after 1 day, having been passively transported by the mother.

At the beginning of the study, adult female Zora was already fully habituated. In the first month she was the only individual whom it was possible to follow for hours in close proximity. It was therefore assumed that she had migrated from the habituated North Group; however, this was not in agreement with the long-term data [Boesch, unpubl. data]. On the other hand, Wapi, an easily recognizable female, represented the opposite situation, for despite regular contacts during the whole study period she never became habituated (table 1).

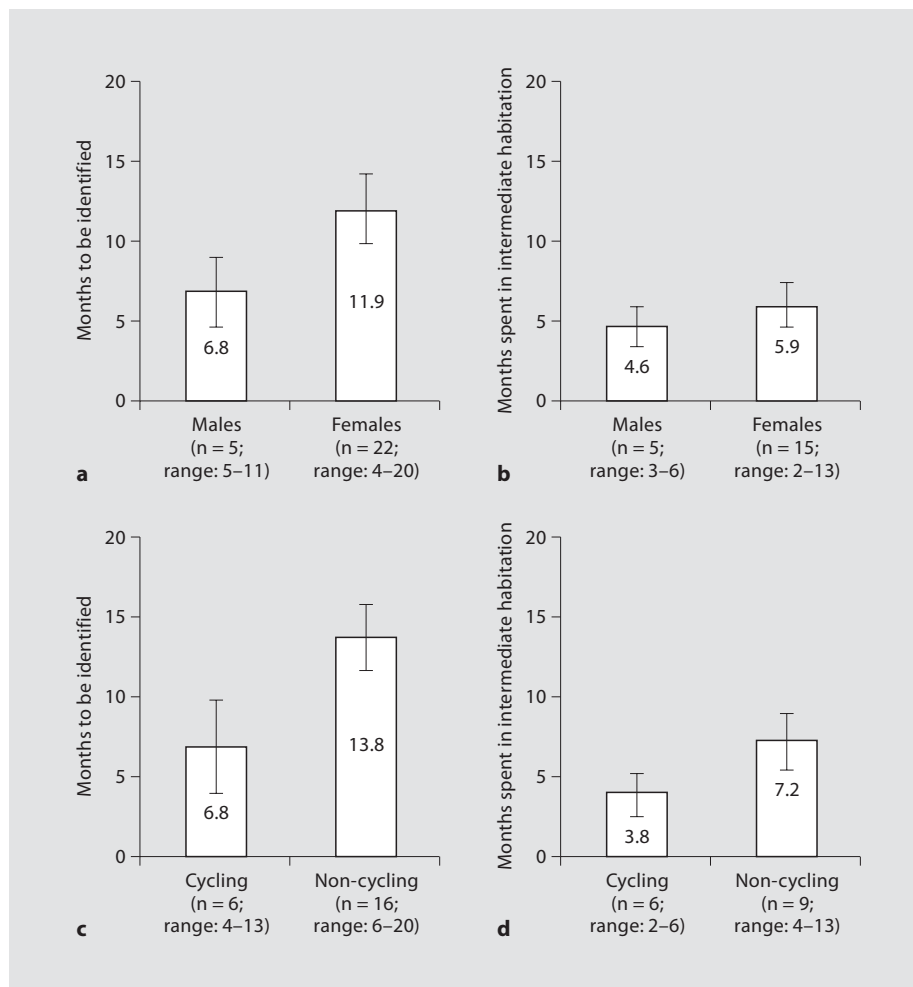


Fig. 1. Average number of months to be identified (**a, c**) and spent in intermediate habitation status (**b, d**) by males and females (**a, b**), cycling and non-cycling females (**c, d**) during the 2 years of this study. The error bars represent the standard errors of means. Only individuals not yet identified at the beginning of this study are included.

Discussion

The longer time needed for individual identification of chimpanzees without provisioning may depend on different learning mechanisms entailed in the two techniques. Human presence per se is a variable factor, because it refers to diverse human actions, and it can be considered a negative (e.g. poaching), neutral (research) or positive (provisioning) stimulus. In unprovisioned communities, the positive component is lacking and chimpanzees require more associations with humans to be-

come habituated. In provisioned communities the positive stimulus may function as reinforcement, and the learning process may resemble more positive reinforcement (associative learning) than neutral habituation. The time required for habituation may be less, but many aspects of the chimpanzees' behaviour and ecology may be affected, in addition to other factors such as disease transmission [Wrangham, 1974]. However, although at Gombe some individuals were quickly identified at the beginning of the study, it took some years to be able to follow them outside the provisioning area [Goodall, 1986], and the time needed for habituation was de facto similar to unprovisioned chimpanzees.

The flight reaction shown by unhabituated Taï chimpanzees upon seeing humans is similar to that of populations across the chimpanzees' range [McGrew et al., 1981; Tutin and Fernandez, 1991], but there are exceptions [Morgan and Sanz, 2003; Werdenich et al., 2003]. The most notable is that of a wild population in the Goualougo Triangle, Democratic Republic of Congo, where the first observed typical reaction of the chimpanzees to humans was curiosity [Morgan and Sanz, 2003]. This suggests that the panic reaction commonly seen at other sites may be not only a response to a potentially dangerous stimulus, but also to a stimulus known to be dangerous. Poachers regularly visited the home range of the South Group chimpanzees, and gunshots, fresh trails and temporary camps were encountered during the whole study period.

As suggested by Boesch-Achermann and Boesch [1994], it is likely that a critical factor affecting the rate of habituation is the frequency of contacts with humans. This is consistent with the learning process proposed for habituation to a constant stimulus [Thorpe, 1963]. The sex difference observed may simply be the outcome of the higher probability of males meeting humans, which is a consequence of the methods used to find the chimpanzees in the forest. Chimpanzee males show higher levels of vocalizations than females [Goodall, 1986]; drumming displays are almost exclusively done by males, and females generally call when males are present in their party. If a male in the community is already habituated and he is often followed by humans, he indirectly exposes his companions to human presence, and so these other males habituate faster.

More frequent contacts can also explain why cycling females habituated faster than non-cycling females with offspring. Given that males tend to associate with cycling females, especially during periods of swelling, if males are habituated and accompanied by humans, then the cycling females are forced to increase their contacts with humans and as a consequence they too become habituated.

But other factors may play a role: the simple habituation learning mechanism may be modulated by other variables, such as sex-biased differences in temperament or idiosyncrasy. Males engage in more aggressive and dangerous activities, e.g. hunting, territorial defence, incursions into neighbouring territories and conspecific killing [Boesch and Boesch-Achermann, 2000; Wilson and Wrangham, 2003]. In the Taï population, the vast majority of females are with dependant infants and often with a juvenile as well. In such a situation, females may be much more wary than males towards intruders, predators and unknown human observers. Males have been seen to defend group members from leopards and even attack them, while females retreat to safety [Boesch, 1991; Boesch and Boesch-Achermann, 2000]. We suggest that this difference may explain the different levels of tolerance towards humans. The different temperaments of males and females influence many behavioural patterns, which

can include interactions with humans. Males may need fewer contacts with humans than females because of their generally bolder temperament. Similarly, cycling females may need fewer contacts as a consequence of their sexual condition. Hormone fluctuation may affect their boldness in a general way that extends its effects to habituation to humans. The case of Haraka, the female who became habituated overnight with the death of her infant, suggests another modulating influence, perhaps mediated by stress. If she was so deeply focused on the death of her infant that the threshold to the avoidance reaction to humans was temporarily diminished, this distraction might explain her sudden lack of avoidance.

However, we should not stress the sex factor too strongly, as Zora, one of the oldest females of the group, was habituated quickly to the presence of humans and was willing to stay for many consecutive days alone with observers. As we knew that she did not come from a habituated group, it may be that her personality explains much of what we observed. In contrast to Zora, Mandy, another adult female of the group, was so intolerant towards observers that she was not identified during our observational period; she illustrates the other extreme of the spectrum of what can be seen in wild chimpanzees.

Several factors can explain the variation in the rate of habituation shown by members of the community, but it is likely based on different individuals' experiences with humans. Certain individuals may have met poachers, or even witnessed the killing of a conspecific; traces of the poachers that frequent the chimpanzees' home range suggest that this is likely. But many factors affect behaviour, including age, sex, reproductive status, social rank, kinship and experiences, which interact in complex ways and give each individual a unique profile. Only further, detailed study can elucidate this.

Acknowledgments

We are grateful to: Hedwige Boesch, co-director of the Taï Chimpanzee Project, for manifold assistance; Elisabetta Visalberghi for constant encouragement over years; the Ministère des Eaux et Forêts and the Ministère de la Recherche Scientifique en Côte d'Ivoire for support and facilities in the Taï National Park; Jacob Zinsstag, director of Centre Suisse de Recherche Scientifique en Côte d'Ivoire, for assistance in Abidjan; the director and staff of IET station for assistance in Taï. Special thanks go to Chloé Cipolletta, Valentin Yagnon and Benjamin Gouclaon for their field work during this study, and Gerard Radl, Susane Pierel and Franca Donati for their previous work in the habituation of the South Group. Finally we thank William McGrew and three anonymous reviewers for their critique of the manuscript.

References

- Boesch C (1991). The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour* 117: 220–242.
- Boesch C, Boesch H (1981). Sex differences in the use of natural hammers by wild chimpanzees: a preliminary report. *Journal of Human Evolution* 10: 585–593.
- Boesch C, Boesch H (1983). Optimisation of nut-cracking with natural hammers by wild chimpanzees. *Behaviour* 83: 265–286.
- Boesch C, Boesch H (1990). Tool use and tool making in wild chimpanzees. *Folia Primatologica* 54: 86–99.

- Boesch C, Boesch-Achermann H (2000). *The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution*. New York, Oxford University Press.
- Boesch-Achermann H, Boesch C (1994). The Taï chimpanzee project in Côte d'Ivoire, West Africa. *Pan Africa News* 1: 5–7.
- Goodall J (1986). *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, Harvard University Press.
- Herbinger I, Boesch C, Rothe H (2001). Territory characteristics among three neighboring chimpanzee communities in the Taï National Park, Côte d'Ivoire. *International Journal of Primatology* 22: 143–167.
- Herbinger I, Boesch C, Tondossama A (2003). Cote d'Ivoire. In *West African Chimpanzees: Status Survey and Conservation Action Plan* (Kormos R, Boesch C, Bakarr MI, Butinski TM, eds.), pp 99–109. Gland, IUCN/SSC Primate Specialist Group.
- McGrew WC, Baldwin PJ, Tutin CEG (1981). Chimpanzees in a hot, dry and open habitat: Mt. Assirik, Senegal, West Africa. *Journal of Human Evolution* 10: 227–244.
- Morgan D, Sanz C (2003). Naive encounters with chimpanzees in the Goulougou Triangle, Republic of Congo. *International Journal of Primatology* 24: 369–381.
- Thorpe WH (1963). *Learning and Instinct in Animals*. London, Methuen.
- Tutin CEG, Fernandez M (1991). Responses of wild chimpanzees and gorillas to the arrival of primatologists: behaviour observed during habituation. In *Primate Responses to Environmental Change* (Box HO, ed.), pp 187–197. London, Chapman & Hall.
- Werdenich D, Dupain J, Arnheim E, Julve C, Deblauwe I, Van Elsacker L (2003). Reactions of chimpanzees and gorillas to human observers in a non-protected area in south-eastern Cameroon. *Folia Primatologica* 74: 97–100.
- Williamson EA, Feistner ATC (2003). Habituating primates: processes, techniques, variables and ethics. In *Field and Laboratory Methods in Primatology: A Practical Guide* (Setchell JM, Curtis DJ, eds.), pp 25–39. Cambridge, Cambridge University Press.
- Wilson ML, Wrangham RW (2003). Intergroup relations in chimpanzees. *Annual Review of Anthropology* 32: 363–392.
- Wrangham RW (1974). Artificial feeding of chimpanzees and baboons in their natural habitat. *Animal Behaviour* 22: 83–93.