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Edited by Christophe Boesch, Gottfried Hohmann and Linda F. Marchant
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Behavioural Diversity in *Pan*

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A BRIEF HISTORY

In the late 1950s, the great anthropologist Louis Leakey searched for a student to study wild chimpanzees in their natural habitat; he was convinced that this kind of investigation would provide important information about the behaviour of our early ancestors. His quest eventually ended with Jane Goodall, who began her research on chimpanzees in Gombe in the early 1960s, near the shore of Lake Tanganyika in Tanzania, East Africa.

During the course of the following years, our knowledge of wild chimpanzees relied almost exclusively on observations collected from two communities – Goodall's work at Gombe, and the work of Toshisada Nishida and his colleagues, conducted in Mahale Mountains National Park, some 200 km south of Gombe. Both populations, located on the eastern side of Lake Tanganyika, live in relatively similar environments, characterised by a mosaic of savanna, woodland and dense shrub habitats. The last three decades of the 20th century saw the success of these two studies turn the Tanzanian chimpanzee into something of a prototype for 'The Wild Chimpanzee', and behavioural diversity was restricted to the differences between these two populations. Anthropological and psychological literature and textbooks are still strongly biased in assuming that Tanzanian chimpanzee behaviour represents all chimpanzees.

The chimpanzee: variations revealed

Meanwhile, new populations of chimpanzees have been studied in different types of environments throughout their distribution in Africa. West African chimpanzees have been the focus of two studies that began in the late 1970s, one in Guinea in the small Bossou forest and the second one in the Taï National Park, Côte d'Ivoire. It quickly became apparent that our knowledge about Tanzanian chimpanzees could not simply be assumed to apply to all chimpanzee populations. For example, the tool use repertoire was discovered to differ markedly for each of the studied populations (Sugiyama & Koman 1979; Boesch & Boesch 1990; McGrew 1992), and the hunting behaviour seemed to be more organised in West Africa (Boesch & Boesch 1989). Rapidly, new studies of other chimpanzee populations in East Africa started as well, for example in the Budongo and Kibale forests (Ghiglieri 1984; Newton-Fisher, Chapter 9). The picture emerging from all these studies was that each wild population presents many different behaviours, not only in the domain of tools and hunting, but in core, basic social interactions as well. A recent review of nine chimpanzee populations revealed that cultural differences are systematic, and that it is more precise to talk about the 'Gombe chimpanzee', the 'Mahale chimpanzee' or the 'Taï chimpanzee' than 'chimpanzees' in general. The current volume extends this approach by presenting new and important aspects of chimpanzee behaviour from known populations, and also by providing data on new populations about which little has been known.

The 'pygmy chimpanzees': bonobos coming into their own

Looking to the chimpanzees' 'sister species', studies of bonobos, originally called pygmy chimpanzees, started much later than was the case for chimpanzees. Consequently, we know relatively less about them. The questions we address are can we speak of a 'prototype bonobo', or are we also dealing with population-specific behaviour patterns here? These questions remain more difficult to answer, and the contributors to this collection can help us only up to a point. This is primarily because we have detailed observations from fewer populations of bonobos, so it is simply too early to answer such a question fully and properly. Bonobos at Lomako and Wamba have been studied for many years, but the two populations live near each other and within very similar forest types (Hohmann & Fruth, Chapter 10; Furuichi & Hashimoto, Chapter 11). These populations represent only a small proportion of the habitat inhabited by this species. The new observations of the Lukuru bonobos,

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situated in a drier forest further south than the sites at which earlier research on bonobos was conducted, are therefore of special interest (Myers-Thompson, Chapter 4).

WHEN SHOULD WE EXPECT BEHAVIOURAL DIVERSITY?

Chimpanzees

Modern evolutionary thinking predicts that populations of the same species living in different habitats will need to adopt different strategies in order to survive and reproduce because of the different challenges they face daily (Ridley 1995; Futuyma 1998). In animal species, the response to environmental conditions can have a genetic base, or be behaviourally based on extended learning abilities. Learning is expected to be more flexible than genetics, and species that learn how to respond flexibly are expected to exhibit high levels of behavioural diversity. Primates, in general, possess more learning abilities than other mammals (Byrne 1995; Tomasello & Call 1997). Chimpanzees and bonobos in particular have demonstrated extended learning abilities under different conditions, whether in captivity or in their natural habitat (Goodall 1986; Byrne 1995; Boesch & Boesch-Achermann 2000). In addition, it has been known for a long time that chimpanzees and bonobos live in diverse environments, ranging from tropical rainforest to very dry savanna regions that contain some gallery forests (Suzuki 1969; Kano 1971; McGrew *et al.* 1979; Kortlandt 1983; Moore 1996). Therefore, we should expect chimpanzee populations to show greater behavioural diversity than species living under more similar conditions.

The main problem we face in expanding our knowledge about these populations is the need for more detailed behavioural observations in order to answer questions about behavioural diversity in this species. More informed answers can come only if more scientists go into the field and study more wild chimpanzee populations living under different ecological conditions. What might we expect to be the outcome of such research? The more divergent the habitats, the more diverse the behavioural strategies adopted by chimpanzees. New research projects currently under way that are investigating as yet little-known populations will eventually advance our knowledge and convincingly demonstrate that this knowledge is refined and increased with the number of populations examined. For example, a new study of chimpanzees in the Kalinzu Forest, Uganda, revealed the first instances in this region of the use of tools to dip for driver ants (Hashimoto *et al.* 2000). Some observations of the Tenkere chimpanzees in Sierra Leone, revealed the use of small branches as 'stepping-sticks' and 'seat-sticks' (Alp 1997). These observations remain unique for all known chimpanzee populations. Similarly, new observations of tool use in the Lossi chimpanzees in Congo revealed the existence of a tool-set consisting of three components, which they use in sequence – a stout chisel, a bodkin, and a dip-stick – to extract honey from melipone bee nests (Bermejo & Illera 1999). Lossi chimpanzees are the first known wild populations using such a complex tool-set. Finally, Ndakan chimpanzees in the Dzanga-Sangha region in Congo are the only ones known to pound nests of Melipone bees with large pieces of wood to gain access to the honey (Fay & Carroll 1994).

This collection of articles presents detailed data on some new populations of chimpanzees, some of which live in especially dry conditions compared to the classical image of the chimpanzee as living in a humid forest. The Tongo chimpanzees in the Democratic Republic of Congo and the Semliki chimpanzees of Uganda nicely illustrate the extent to which we still might be underestimating behavioural diversity in this species. Both populations live in areas where, at certain times of the year, water is an important limiting factor, and both populations have invented unique ways to obtain access to water during these periods. Tongo chimpanzees live in a forest that grows on volcanic soil and where water rapidly infiltrates the ground. When water is limited, Tongo chimpanzees dig rather deep holes into the soil to reach large tubers that contain plenty of water; they then suck the tubers, extracting as much of the moisture as possible (Lanjouw, Chapter 3). Semliki chimpanzees live in a much more open habitat, cut by the gallery forest and following small rivulets. When the rivulet beds are dry, Semliki chimpanzees were seen digging holes in the dry beds to reach the underground water. These holes functioned like wells, providing the chimpanzees with clear water (Hunt & McGrew, Chapter 2). Never before had chimpanzees been seen digging wells in order to access underground water sources! It has been suggested that exploitation of underground resources was a niche that our human ancestors discovered, and we see here that chimpanzees in dry environments also seem to use such resources. These two examples show just how inventive chimpanzees can be and how much more we might learn about chimpanzee behaviour if more populations are studied.

Bonobos

To date, bonobos have only been studied in the deep forest of the Congo basin, and they were thought to be restricted to such tropical rainforests. However, their precise distribution within the Congo Basin remains unclear and questions have been raised about how far south they occur and in what kinds of environments they can survive. New observations presented in this volume about the bonobos of the Lukuru region in the south of the Democratic Republic of Congo, show that they can live in a mosaic forest with large savanna areas. They have been observed entering deep into the savanna to feed on grass, as well as venturing into swamp areas, walking bipedally into waist-deep water of streams or pools (Myers Thompson, Chapter 4). This behaviour demonstrates unexpected flexibility in bonobos, seeming to indicate greater behavioural diversity than previously assumed. Here as well, the type of habitat inhabited seems crucial in explaining behavioural diversity. Thus, part of the information presented here points out that, if we want to know the real spectrum of behavioural diversity in bonobos, then we need to be patient – more data on new populations are required. Hopefully, both chimpanzees and bonobos will survive long enough in Africa, despite the present threats to their well-being, so that we can more fully address and answer questions about the behavioural diversity that exists in these species.

HOW DO ENVIRONMENTAL DIFFERENCES AFFECT BEHAVIOUR?

Dating from the time of the great trophy hunters, long before researchers appeared on the scene, we have known about the differences in geographic distribution of the two *Pan* species: chimpanzees occur in many different parts of tropical Africa, while bonobos were restricted to the Democratic Republic of Congo (formerly Zaïre). And these observations later came to be supported by scientific data. Chimpanzees have always lived in diverse environments (Suzuki 1969; Kano 1971; McGrew *et al.* 1979). The distribution of bonobos is still a matter of debate, but it seems clear that the tropical rainforest of Central Africa is their main habitat.

Traditionally, socio-ecological models have placed heavy emphasis on the importance of food resources in influencing social structure and grouping patterns (Wrangham 1980; Dunbar 1988; Begon *et al.* 1990), although others have suggested predation to be the most important in explaining grouping patterns (van Schaik & van Hooff 1983; Dunbar 1988). The large body size of the great apes and the relatively weak evidence of predation against them was taken as confirmation that, as an explanation of the differences in social behavior between chimpanzees and bonobos, food is a more important influence on social structure and grouping patterns (Wrangham 1986; White & Wrangham 1988; Stanford *et al.* 1994; Doran 1997; but see Boesch 1991). More precisely, chimpanzees' greater dependence on large fruit patches and bonobos' more extensive reliance on terrestrial herbal vegetation (TVP) were suggested as an explanation of the supposed important differences in social domain between the two species (White & Wrangham 1988). Alternatively, proposals positing that additional factors, for example the presence of estrous females, were important in explaining social grouping in chimpanzees (Goodall 1986; Boesch 1996; Boesch & Boesch-Achermann 2000) have also been put forth. This debate between an unifactorial explanation of social grouping patterns versus a multifactorial one has been limited by the quality of data available on food distribution and production in the different populations compared.

Food availability, sexual opportunity and party size

A number of researchers in this book present precise quantifications of food production and distribution in different populations, allowing us for the first time to test the influences these different factors may exert on social grouping patterns in chimpanzees (Anderson *et al.*, Chapter 6; Mitani *et al.*, Chapter 7). Based on painstaking monitoring of fruit production of many trees of the most important food species over the whole year and estimation of the density of these species, a precise quantification of fruit availability was obtained, making a test of the relative importance of food versus sexual opportunities possible. The results are fascinating. In Ngogo chimpanzees, both food availability and number of estrous females present in the party explain the largest part of the variation seen in party sizes (Mitani *et al.*, Chapter 7), and the influence of each of these factors seems to be independent of the other. In the Taï forest, the number of estrous females present in a party was shown to be the only factor affecting party size – the more estrous females present, the larger the party. Food availability played a clear role only if no estrous female was present in the party

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(Anderson *et al.*, Chapter 6). In this case, the more food available, the larger the party size. Thus, the only two studies that have been able to test the respective roles of food availability and sexual opportunities on party size in chimpanzees concur in granting sexual opportunity at least as much importance as food availability.

Although direct comparisons between the sites are still difficult, greater food availability in Taï might explain the differences between the two sites, in the sense that the presence of estrous females may be a more important factor than food availability in explaining group size in chimpanzees. If food is generally less abundant in the habitat, then it will play a more important role, as it does in the Ngogo chimpanzee population. Food might be even more limited in Gombe, as suggested by their smaller body size, and food competition might dominate, as suggested by the results presented and discussed in Chapter 14 (Williams *et al.*). An analysis of rainfall, often proposed as a good indicator of an area's food productivity, shows that in both Budongo and Gombe, the number of estrous females and party size have a very high correlation. However, in Gombe party size decreases before the dry season, while in Budongo party size decreases after the dry season (Wallis, Chapter 13). Since a precise quantification of food production is still missing for both sites, these results are difficult to interpret, but they do at least show that party size fluctuates more directly with the number of estrous females than with the amount of rainfall. We might, therefore, be witnessing a general pattern in chimpanzees, where party size is driven much more by sexual opportunity than food.

Hunting behaviour

Hunting behaviour in chimpanzees is another domain where the role of the environment has been proposed as an important one (Boesch 1994; Boesch & Boesch-Achermann 2000): forest structure has been suggested as a key agent since it directly affects the ways in which hunters can achieve a capture. Alternatively, it has been proposed that the number of hunters or the number of males in the party is the key factor in explaining the occurrence of hunting and its success (Stanford *et al.* 1994; Mitani & Watts 1999). A direct test of these hypotheses shows that, independent of party size, when Ngogo chimpanzees hunt for red colobus in a continuous forest, their success is much lower than when they hunt them in an interrupted forest (Watts & Mitani, Chapter 18). Interestingly, if the hunting takes place in continuous forest, then success of the Ngogo chimpanzees is the same as that of the Taï chimpanzees, although the former have three times more males in the community. Thus, forest structure seems to be the key factor affecting hunting success in chimpanzees, and demographic parameters, for example number of males, may play a more limited role in hunters' compensating for a lower organisation during the hunt. Ngogo chimpanzees reach surprising success with lower level of organisation (Watts & Mitani, Chapter 18). Similarly, a comparison of the interactions between hunters and red colobus prey across the Mahale, Gombe and Taï sites revealed that the structure of the forest where the hunt takes place plays a crucial role (Boesch *et al.*, Chapter 16).

BONOBOS AND CHIMPANZEES: DIFFERENCES AND SIMILARITIES

Morphological differences between bonobos and chimpanzees were first thought to be rather clear, and led to the name 'pygmy chimpanzee' for *Pan paniscus,* thought to be smaller than the chimpanzee (*Pan troglodytes*). However, measurements made in the late 1970s using a larger sample of individuals showed that, while bonobos were not smaller than chimpanzees (most anatomical measurements overlapped between the two species), body proportions were distinct: the bonobo has shorter upper limbs and longer lower limbs (Zihlmann 1996). Molecular analysis of both nuclear and mitochondrial DNA confirms that bonobos and chimpanzees are very closely related (Bradley & Vigilant, Chapter 19). These results suggest a separation between the two species somewhere between 1.2 and 2.7 million years ago, while the divergence between chimpanzee and human is proposed to have occurred 5–8 million years ago (Kaessmann *et al.* 1999). However, despite these similarities in morphology and genetics, many aspects of bonobo and chimpanzee sexual and social behaviour are quite different. The bonobo has been portrayed as overly sexual, with regular homosexual interactions between the females, and as exhibiting very cohesive social grouping patterns, with females dominant over males (Kano 1992). Chimpanzees, in contrast, have been presented as generally less cohesive, with smaller social groups where males are more social, and clearly dominant over females (Wrangham 1986; Nishida & Hiraiwa-Hasegawa 1987). Initially, these differences were considered to be interspecies differences (Wrangham & Peterson 1996; de Waal & Lanting 1997). However, new data from forest chimpanzees emphasise the intraspecies variability, attributed to living under different ecological conditions: the differences between chimpanzees and bonobos

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could be related more to the ecological conditions prevailing in the populations under consideration than to interspecies differences (Boesch 1996; Boesch & Boesch-Achermann 2000). Recently, it has also been suggested that the differences between the two species are more apparent than real, simply because there are fewer data available on bonobos (Stanford 1998).

Many contributions to this current collection add important information to this debate over interspecies differences. Furthermore, they confirm that given that behavioural diversity is a function of the different types of environments a species inhabits, we need to take ecological differences into consideration when comparing the two species. For example, sexual behaviour differs less between the two species than initially thought (Takahata *et al.* 1996; Furuichi & Hashimoto, Chapter 11), to the point that both species could be directly included in the same framework, showing that strategies used by female bonobos and by females of some chimpanzee populations (Taï) are very similar and could be explained by the higher cohesiveness in the social grouping typical for both populations (Wrangham, Chapter 15). Similarly, when looking at social dynamics from the point of view of feeding competition, the pattern that emerges is that females react in the same way in the two species, and if conditions permit, bonobo and chimpanzee females may adopt very similar social grouping patterns (Hohmann & Fruth, Chapter 10; Matsumoto-Oda, Chapter 12; Williams *et al.*, Chapter 14). The image emerging is that both species, due to their long and common phylogenetic history, are likely to respond very similarly to changes in local conditions. In a multivariate analysis of differences between the bonobo and chimpanzee, it has been shown that the analysed differences correlated most powerfully with the number of dry months per year, with rainforest chimpanzees occupying a position most similar to rainforest bonobos (Doran *et al.*, Chapter 1).

The answer (or answers) to questions of how different and how similar bonobos and chimpanzees are from and to each other will affect the way we understand the evolutionary forces located at the origin of the divergence between the two species of *Pan*. Based only on the distribution of the two species, many scenarios have been proposed to explain how different the two species *should* be. In this sense, the information about the Lukuru bonobos is very important because it indicates that both species could survive outside the dense forest during the more dry periods in the past, and that differences in this respect are not enough to explain the divergence that led to the two species. Similarly, the fact that both species seem to make similar adaptations to the tropical rainforest environment indicates that it is not only the shift from open to closed forest that led to the divergence between the two species.

Our models for the evolution of both species need to be refined by including some of the evidence presented here. The classical proposition is that an important change in the ecological conditions in East Africa produced a split, one leading to chimpanzees and one leading to modern humans. This savanna model argued that climatic changes East of the Rift Valley changed the forest environment into a savanna, and that the ancestors trapped there had to adapt in order to survive (Dart 1925; Leakey 1980; Johanson & Edey 1981). However, after comparing forest and savanna chimpanzees, it has been suggested that the ancestors common to chimpanzees, bonobos and humans were living in a more forested environment than normally proposed by anthropologists (Boesch & Boesch 1989). Recent discoveries of three possible early ancestors of the human evolutionary lineage seem to support this possibility completely: the environment in which *Ardipithecus* sp. and *Orrorin tugenensis* lived between 6 and 3.5 million years ago seems to have been predominantly a woodland and not a drier savanna habitat (WoldeGabriel *et al.* 2001; Leakey *et al.* 2001; Pickford & Senut 2001), a habitat that is still inhabited today by a few bonobo populations and a number of chimpanzee populations. This, combined with further evidence that more recent ancestors, for example the *Australopithecus* (Rayner *et al.* 1993; Brunet *et al.* 1995), occupied a wooded habitat suggests that it was a woodland habitat where the common ancestors of humans, chimpanzees and bonobos could be found, and that it was also the habitat in which the split occurred. *Orrorin tugenensis* lived some 6 million years ago, a time that is within the range of the last common ancestor between humans and chimpanzees (Senut *et al.* 2001). If the dating of *Orrorin tugenensis* is accurate, then, contrary to the savanna model, which suggests that an important shift in ecological conditions is responsible for the divergence between human and chimpanzee ancestors, the recent discoveries of fossils, as well as new evidence included in the chapters that follow on the distribution and behaviour of chimpanzees and bonobos living in relatively dry habitats, suggest that a woodland habitat was part of the living environment for much of the line from the last common ancestor to contemporary populations of chimpanzees and bonobos. The cause of the divergence in those lines may either be found in subtle ecological differences within the ‘woodland’ framework, or in changes in life-history traits due to the selection pressure that comes from increasing predation.

ARE ALL BEHAVIOURAL DIFFERENCES RELATED TO ECOLOGICAL DIFFERENCES?

This question has been the centre of a lively debate because it is directly related to the question of culture in animals. When the behavioural repertoire differs between two populations of the same species, but the environmental conditions are the same, then the differences might be cultural, that is learned from other group members (Kummer 1971; Bonner 1980; Boesch 1996). Excluding environmental factors is more easily said than done, however, since the influence might be more subtle than expected (Tomasello 1990). Nevertheless, consensus is growing that chimpanzees have cultural abilities, and that many of the differences we observe between populations cannot all simply be explained by ecological differences (Boesch & Boesch 1990; McGrew 1992; Boesch *et al.* 1994; Boesch 1996; Whiten *et al.* 1999; Whiten & Boesch 2001). Yet this is, by no means, the last word on the breadth of cultural abilities in chimpanzees. For example, as demonstrated by Nakamura (Chapter 5), cultural variation might develop in the social domain through interactions between individuals, and an analysis of social grooming patterns has revealed differences between Mahale and other populations that are apart from any ecological explanations.

In addition to chimpanzees, the possession of cultural abilities has also been suggested in whales, dolphins and killer whales, as well as in orangutans and in some birds (Bonner 1980; van Schaik & Knott 2001; Rendell & Whitehead 2001). The conservative expectation is that we will find similar abilities in bonobos but, to test whether or not this expectation will be fulfilled, we need more data on more bonobo populations. If bonobos do have similar cultural abilities, then it seems safe to assume that such abilities were common within the chimpanzee–bonobo–human clade, and this assumption will require using new eyes when studying the human cultural abilities (e.g. Boesch & Tomasello 1998).

The extent to which behavioural diversity exists has been one of the important lessons learned from the growing number of observations of more and more wild populations of chimpanzees and bonobos. The contributions made to this area of primatology by this volume indicate that we have still more to learn about the full degree of diversity in both species. Yet even at this point in time, we can already say that it is larger than we ever suspected.

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Part I
Behavioural flexibility

Introduction

TETSURO MATSUZAWA

Chimpanzees and bonobos are our closest living relatives. However, many aspects of their lives in the natural environment – which ranges from the moist primary forest to dry open habitat – still elude us. This book, particularly the section on behavioural flexibility, outlines some of the most recent advances in our knowledge of the two species. People inhabiting the tropical forests of Africa have long coexisted with the two extant species of *Pan*, chimpanzees and bonobos, while sharing partly overlapping niches. Take, for example, the 20 or so chimpanzees living at Bossou, Guinea, West Africa, who have been studied continuously for more than two decades. More than 600 plant species (664, to be precise) have been identified as comprising the flora of Bossou (Sugiyama & Koman 1992). Chimpanzees utilise 200 of these for food and at least two species for medicinal use, while humans use 76 species for food and 81 as traditional medicine, in addition to those utilised in the construction of houses, furniture and for other purposes.

There are only a handful of tribes whose totem beliefs prohibit the hunting of chimpanzees. In others, hunters have been killing chimpanzees for meat and using parts of the body such as the skull for medicinal and animistic religious practices. This kind of coexistence may have been common practice throughout Africa for thousands of years.

The first chimpanzees known to have been brought to Europe came from Angola and were presented to the Prince of Orange in 1640 (Yerkes & Yerkes 1929). Over the next three centuries, white people continued to shoot chimpanzees, not for meat, but as specimens to be transported back to Europe and studied for their anatomy and morphology, all in the name of 'natural history'. Large numbers of chimpanzee skulls and bones are still kept in museums and universities. Demand for individual chimpanzees to be trapped and shipped to the West also came from various zoological gardens.

With the opportunity to observe them in captivity, people began to realise that chimpanzees were in many respects much like us: they could use tools, and even build tools to obtain food out of reach by joining sticks together. However, realising the necessity for studying the behavior of chimpanzees in their natural habitat is relatively recent. After some earlier attempts by others, Jane Goodall, a young British woman, working under the auspices of the visionary palaeontologist Louis Leakey (1903–72), arrived in Gombe, Tanzania, on 14 July 1960. At about the same time, Adriaan Kortlandt of the Netherlands was setting up a short field study in Congo, Kinji Imanishi (1902–92) and Junichiro Itani (1925–2001) and their students from Japan had just begun field surveys in Tanzania, and Vernon and Frances Reynolds arrived in Uganda for a 9-month study in the Budongo Forest.

Knowledge about wild chimpanzees' behavioural diversity has accumulated chiefly through research carried out at the six main sites where long-term projects have continued for more than two decades: Gombe, Mahale, Budongo, and Kibale for Eastern (*P. troglodytes schweinfurthii*) chimpanzees, and Bossou and Taï for Western (*P. t. verus*) chimpanzees. For an overview of the behavioural diversity of chimpanzees, three original books are especially useful: for Gombe see Goodall (1986), for Mahale see Nishida (1990), and for Taï see Boesch & Boesch-Achermann (2000).

Until recently, in contrast to chimpanzees, our knowledge of wild bonobos was scarce. Takayoshi Kano, one of Imanishi's last students, carried out an extensive survey in the Congo Basin in 1973. He rode his bicycle from village to village, questioning locals. He compiled information from 103 villages, and confirmed traces of bonobo feeding and nesting in 30. He finally settled at Wamba, in what was then Zaïre, to begin his direct observation of the last unkown ape in the wild (Kano 1992).

The last two decades of the 20th century saw a great deal of effort devoted to learning more about chimpanzees and bonobos in their natural habitat. Many people struggled with binoculars and field notes in the humid forests and dry, hot savannas of Africa. Guns were replaced, first by still cameras, then by video equipment. A genuine coexistence between humans and their evolutionary neighbours started to take shape.