



Oil Palm Use by Adjacent Communities of Chimpanzees at Bossou and Nimba Mountains, West Africa

Tatyana Humle^{1,3} and Tetsuro Matsuzawa²

Received May 8, 2003; Revision September 2, 2003; accepted October 6, 2003

*We investigated oil palm (*Elaeis guineensis*) use for feeding in 3 chimpanzee communities: Bossou and Seringbara in Guinea and Yealé in Côte d'Ivoire. Bossou was used as the benchmark for comparison. Bossou chimpanzees (*Pan troglodytes verus*) exhibit a wide range of oil palm targeted behaviors. We used direct observations of their two tool use, i.e., nut-cracking and pestle pounding, to establish strict and reliable criteria to ascertain the presence of comparable behaviors at the two adjacent Nimba sites. Based on monthly surveys of oil palms across the three sites, significant differences in patterns of use emerged. Bossou chimpanzees demonstrated the greatest frequency of oil palm use, while Seringbara chimpanzees, 6 km away, failed to exhibit any use and Yealé chimpanzees, 12 km away, showed all uses comparable to Bossou chimpanzees except pestle pounding and mature leaf pith-feeding. We examined the density and distribution of oil palms, tool availability for nut-cracking and pestle pounding, fruit, flower and nut availability, competition with sympatric species for fruit and nuts and the diversity of fruit species in the diet across the 3 sites. We found no clear difference in proximate environmental variables underlying observed variations in oil palm use among the 3 sites, yielding the conclusion that the differences are cultural. Assuming individual interchange between communities and the involvement of social learning in the intracommunity transmission and maintenance of oil palm uses, the result*

¹Department of Psychology, University of Stirling, Stirling, FK9 4LA, Scotland, UK.

²Primate Research Institute, University of Kyoto, Japan.

³To whom correspondence should be addressed; e-mail: tatyana.humle@stir.ac.uk.

raises interesting questions about diffusion of behavior between neighboring chimpanzee communities.

KEY WORDS: *Elaeis guineensis*; *Pan troglodytes verus*; culture; elementary technology; feeding ecology.

INTRODUCTION

Culture and the Environment

In the 1950's, Japanese primatologists described the social transmission of sweet-potato washing in a population of Japanese macaques (*Macaca fuscata*) on Koshima Island (Kawai, 1965; Matsuzawa, 2003). Their observations played a key role in raising scientists' attention to the issue of culture in nonhuman animals. Culture is a set of dynamic behavioral traditions socially transmitted within and between generations in groups and populations of the same species (adapted from Laland and Hoppitt, 2003; Parker and Russon, 1996). The concept of culture in chimpanzees and other animals has since been a source of much debate and controversy. Skeptics challenge the attribution of culture to non-human animals by postulating instead environmental explanations for observed variations in behavior (Galef, 1992; Tomasello, 1994, 1999; Tomasello *et al.*, 1993). Nonetheless, 4 decades of field studies of wild chimpanzees in Africa have revealed substantial differences in behavioral repertoires among subspecies, populations and communities (Whiten *et al.*, 1999, 2001; Yamakoshi, 2001). The list of differences is extensive and comprises a multitude of behaviors encompassing tool use, feeding, and the social and communication domains (McGrew, 1985, 1992, 1998; McGrew *et al.*, 1979; Nishida, 1987; Nishida *et al.*, 1983; Sugiyama, 1993, 1997). Whiten *et al.* (1999, 2001) identified 39 candidate behavioral patterns as potential cultural variants on the grounds that they occur sufficiently frequently at ≥ 1 site(s) to be consistent with social transmission, yet absent at ≥ 1 other(s), where environmental explanations can be rejected.

Several studies on wild chimpanzees focusing on nut-cracking and aimed at testing environmental hypotheses versus a by default cultural hypothesis have provided strong evidence of culture. Nut-cracking in chimpanzees is a socially learnt, (Inoue-Nakamura and Matsuzawa, 1997; Biro and Matsuzawa, in press) conspicuous and complex tool use activity, whose presence within a community can be assessed fairly reliably, even during short-term studies, due to the presence of leftover artifacts. McGrew *et al.* (1997) examined several hypotheses, exploring environmental and cognitive parameters, as to why chimpanzees at Lopé do not crack nuts, including oil palm nuts. They concluded that the best current explanation for the absence

of this tool use behavior at Lopé is neither environmental nor cognitive but rather cultural, and that chimpanzees at this site simply appear to lack the knowledge that nuts can be consumed with the aid of tools, though nuts are a potentially valuable and plentiful resource in their habitat. During a nation-wide survey of chimpanzees in Côte d'Ivoire, Boesch *et al.* (1994) also found no obvious environmental difference that might explain the lack of evidence of nut-cracking east of N'Zo-Sassandra River. They concluded that nut-cracking is confined to a very small area within the evergreen forest perimeter of West Africa, more precisely west of the N'Zo-Sassandra River. They argued that the river has acted as a major geographical barrier to the diffusion of nut-cracking via social transmission processes from far western Africa to the east.

Origins of the Oil Palm Tree and Its Distribution Across Africa

Oil palm (*Elaeis guineensis*) remains occur in early Tertiary deposits in West Africa and there is little doubt that the species originated there (Adebisi Sowunmi, 1999; Hartley, 1988; Zeven, 1972). The palynological record suggests that the occurrence of oil palms in West Central Africa is much more recent than in West Africa (Adebisi Sowunmi, 1999). The introduction and the spread of the species in West-Central Africa were probably greatly influenced by humans during the late Holocene. The Arab slave trade (700-1911 AD) was also most certainly responsible for its wider dispersion further east, where the oil palm occurs in the wetter areas along the Great Rift (Hartley, 1988). Therefore, in general, the oil palm is widespread across Africa and its presence in forest habitats is often a good indicator of recent or past human presence.

Oil palms grow in a variety of habitats such as secondary, riverine and open and dry forests, gallery forests in savanna areas, fresh water swamp forests and on the margin of rainforests and savanna (Hartley, 1988; Letouzey, 1986). They require a relatively open area to grow and to reproduce, and they thrive best when soil moisture is maintained (Hartley, 1988). Therefore, due to their growth requirements, they are usually absent from primeval rainforest.

Oil Palm Use in Chimpanzees

McGrew (1985) pointed out that patterns of use of oil palms in chimpanzees might also reflect variations in culture. Chimpanzees at many different study sites across Africa use oil palms for nesting and also for feeding on fruit mesocarp, leaf petiole and pith, heart (apical meristem), inflorescences,

nut (endosperm) and resin, and palm wine produced by humans (Table I). With the exception of Mahale, all long-term field sites report chimpanzee use of the oil palm. However, the extent of oil palm use and the number of parts consumed vary remarkably.

Only Bossou and Gombe chimpanzees rely heavily on oil palms for food, especially during periods of fruit scarcity (Wrangham, 1975; Yamakoshi, 1998). At other sites, oil palms are used for feeding to a lesser extent. As illustrated by Sapo and Tai, oil palm nut-cracking is not consistent across all sites where chimpanzees crack nuts and where oil palms are present (Table I). In addition, at sites where oil palms are peripheral, i.e. Kasakati and Mt Assirik, or found only in groves, i.e. Mahale, or where chimpanzees have not been studied extensively, i.e. Sapo, there is no evidence of oil palm use (Table I).

Aims of Study

Considering that the presence of oil palms outside West Africa is an evolutionarily recent development, the use of the oil palm by chimpanzees, especially the eastern subspecies, can be assumed to be a relatively recent behavioral innovation. In addition, there is strong evidence (Table I) of traditional variation in the use of the oil palm between geographically separated chimpanzee communities across Africa (McGrew, 1985, 1992; McGrew *et al.*, 1997). We aimed to conduct the first detailed study of the differential use of oil palms between adjacent communities.

McGrew (1992) hypothesized that some behaviors are transferred by individuals migrating from one community to another, so that a cultural region larger than the original communities is formed. Cultural regions that coincide with the limits of the 4 subspecies of chimpanzees have been proposed by Nishida (1987), Struhsaker and Hunkeler (1971) and Sugiyama (1985) who contrasted nut-crackers of West Africa versus the termite-fishers of Central and eastern Africa, and by Teleki (1974) and McGrew *et al.* (1979) who noted termite-fishers of eastern Africa versus termite-diggers or termite-probers of Central Africa. However, according to distribution maps of behaviors proposed to be cultural, cultural regions are such not clearly identifiable (Whiten *et al.*, 2001). Nevertheless, the narrow distribution of nut-cracking and its specificity to chimpanzee communities west of the Nzo-Sassandra River supports the cultural region hypothesis (Boesch *et al.*, 1994).

Bossou chimpanzees rely extensively on oil palms for feeding (Yamakoshi, 1998) and nesting (Humble and Matsuzawa, 2001). Because oil palms are also available at Seringbara and Yealé in the Nimba Mountains

Table 1. Summary of the use of oil palms as a food resource across 8 long-term and 3 short-term (*) chimpanzee field sites (excluding oil palm wine drinking at Bossou)

Site	Country	Availability	Fruit	Nut	Leaf		Flower	Resin	Heart	Fibers of dead wood		References
					Petiole	Pith				Heart	dead wood	
Bossou	Guinea	Present	✓	✓	✓	✓	✓	✓	✓	✓		Sugiyama and Koman, 1979, 1992; Sugiyama, 1981; Yamakoshi and Sugiyama, 1995
Taï	Côte d'Ivoire	Present; Patchy	✓(rare)	○	✓	○	○	○	✓	○		Boesch and Boesch, 1983; Boesch, pers. comm.
Sapo*	Liberia	Present	○	○	○	○	○	○	○	○		Anderson <i>et al.</i> , 1983; McGrew, 1992
Mt. Assirik	Senegal	Peripheral; Patchy	○	○	○	○	○	○	○	○		McGrew <i>et al.</i> , 1981; McGrew, 1992
Okorobiko*	Equ. Guinea	Absent	×	×	×	×	×	×	×	×		Jones and Sabater, 1971; Sabater, 1979; McGrew, 1992
Lopé	Gabon	Present; Patchy	✓	○	✓	○	○	○	○	○		Tutin and Fernandez, 1993; Tutin, pers. comm.
Gombe	Tanzania	Abundant	✓	○	✓	✓	✓	○	○	✓		Goodall, 1968, 1973; Wrangham, 1975; Clutton-Brock and Gillett, 1979; Wrangham, pers. comm.
Kasakati*	Tanzania	Rare; Peripheral	○	○	○	○	○	○	○	○		Reynolds and Reynolds, 1965; Izawa and Itani, 1966; Sugiyama, 1968; Suzuki, 1969; Kano, 1972
Mahale-K	Tanzania	Abundant (Groves)	○	○	○	○	○	○	○	○		Nishida <i>et al.</i> , 1983; Nishida and Uehara, 1983
Budongo	Uganda	Absent	×	×	×	×	×	×	×	×		Egging, 1947
Kibale	Uganda	Absent	×	×	×	×	×	×	×	×		Struhsaker, 1975; Ghiglieri, 1984

Note: ✓ : Used; × : Not available; ○ : No reported use, although oil palm available.

only 6 km from Bossou, we explored:

- (1) the chimpanzee pattern of oil palm use for feeding across the 3 sites; and,
- (2) environmental variables across the 3 sites that may explain differential emerging patterns of use, including:
 - a) The density and distribution of oil palms within the home ranges of the 3 chimpanzee communities. Significant differences in oil palm density and availability may explain variation in frequency and occurrence of oil palm uses among the 3 sites.
 - b) Tool availability for nut-cracking and pestle-pounding. Inadequate tool availability for either nut-cracking or pestle-pounding may justify their absence from either of the 2 Nimba sites.
 - c) Fruit, flower and nut availability. Oil palm fruit, flower and nut availability may differ significantly among the 3 sites, thus explaining observed variations in their use.
 - d) Competition with sympatric species for oil palm fruit and nuts. If competition for fruit and nut kernels is intense, chimpanzees may be left with little opportunity to exploit these resources.
 - e) The diversity of fruit species in the diet. Chimpanzees may ignore oil palms because higher-quality items, such as fruit, are available.

METHOD

Study Sites

Bossou

The village of Bossou ($7^{\circ}38'71.7''$ N and $8^{\circ}29'38.9''$ W) is situated in southeastern Guinea, West Africa. A small community of chimpanzees (*Pan troglodytes verus*) inhabits the forest surrounding the village. Since 1976, community size has ranged between 16 and 23 individuals and currently numbers 19 members (Sugiyama, 1999). The village of Bossou is surrounded by small hills 70–150 m high that are covered in primary and secondary forest constituting the core area of the Bossou community. At the foot of the hills, cultivated or abandoned fields and secondary, riverine and scrub forests form a patchy mosaic for *ca.* 6 km in all directions.

Nimba Sites

Bossou is *ca.* 6 km away from the foot of the Nimba Mountains. The massif of Nimba forms a natural boundary between Guinea, Côte d'Ivoire,

and Liberia. The Nimba Mountains were established as nature reserve in 1943 in Côte d'Ivoire and in 1944 in Guinea. The reserve on the Guinean side extends over 13,000 ha and 5,000 ha on the Côte d'Ivoire side. The Guinea portion of the massif was classed as a Biosphere Reserve in 1980, with a 21,780 ha core area, comprising the classified forest of Déré, near the border with Côte d'Ivoire, and the Bossou Hills. Both the Guinean and the Ivorian portions of the massif are a World Heritage Site, gazetted in 1981 for Guinea and in 1982 for Côte d'Ivoire. The World Heritage Site extends over 220 km² and its highest peak - le Mont Richard Molard - is at 1752 m (Fig. 1).

The Nimba Mountains are cut up by deep, richly forested valleys and are endowed with great topographical diversity, with valleys, plateaus, rounded hilltops, rocky peaks, abrupt cliffs and bare granite blocks. The area constitutes a vast water catchment (WCMC, 1992). The mountains are characterized by evergreen forest of medium altitude (Guillaumet and Adjanohou, 1971). The region <800 m is entirely covered by primary tropical forest and, >800 m, where the mountain becomes steeper, the vegetation is interspersed with montane forest and high altitude grasslands. The grasslands and some areas of the forest experience bush fires during the dry season, promoting swards of Poaceae growth on the upper slopes and of Marantaceae and Zingiberaceae species in forest areas. Chimpanzees at both study sites remain unhabituated to human observers. Accordingly, direct behavioral observations are infrequent.

Seringbara, Republic of Guinea

The village of Seringbara (7°37'50.0"N and 8°27'44.7"W) is situated at the foot of the Nimba Mountains on the Guinean side, only 6 km to the southeast of Bossou (Fig. 1). Intermittent chimpanzee research has been ongoing there since 1999 (Humle and Matsuzawa, 2001; Shimada, 2000).

Yealé, Republic of Côte d'Ivoire

The village of Yealé (7°31'21.8"N and 8°25'29.1"W) is located 12 km southeast of Bossou, on the Côte d'Ivoire side of the Nimba Mountains (Fig. 1). Boesch *et al.* (1994) conducted a short-term study of chimpanzees in the region as part of a nationwide survey of the distribution of nut-cracking in Côte d'Ivoire. Research has since been conducted in the region over several study periods (Matsuzawa and Yamakoshi (1996); Humle and Matsuzawa (2001)).

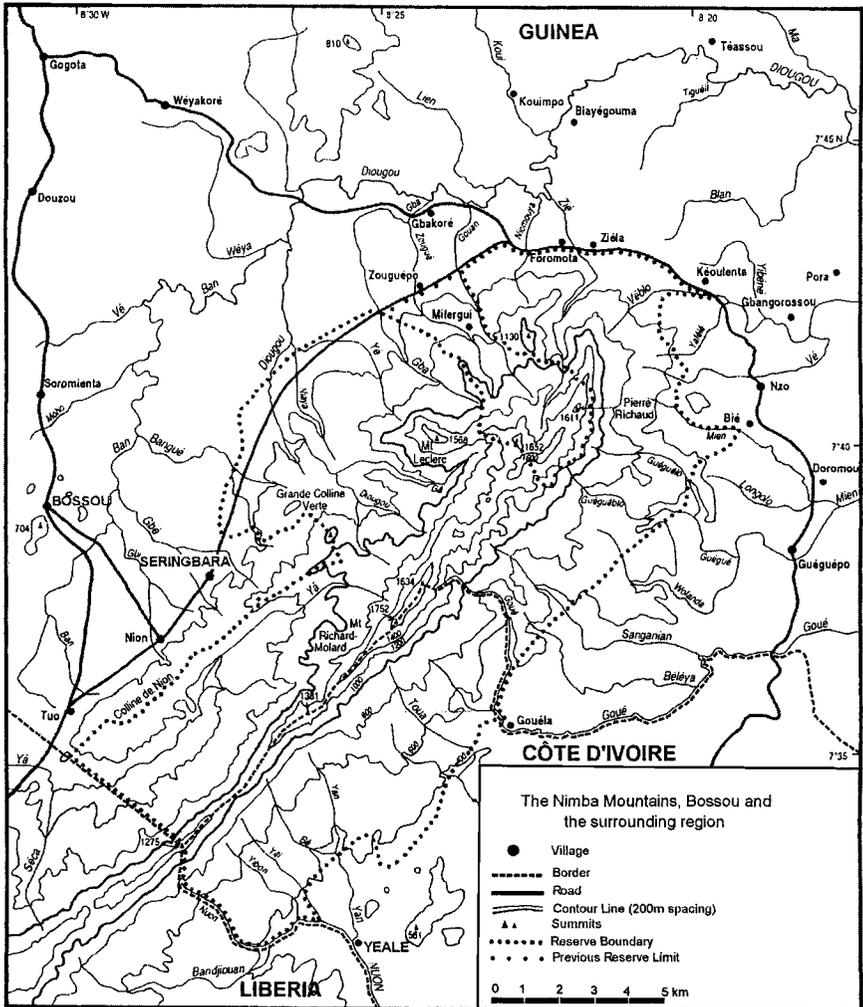


Fig. 1. Map of the Bossou and Nimba region, West Africa.

Oil Palm Survey

We intermittently tagged oil palms at Bossou, Seringbara and Yealé during forest exploration of different areas of the chimpanzee home ranges ($N = 127$ for Bossou; $N = 68$ for Seringbara; $N = 127$ for Yealé). We surveyed these oil palms on a monthly basis during 2 rainy seasons between June

and September 2000, and June and September 2001. However, there was no survey at Yealé in September 2000 due to political unrest in the region.

Oil Palm use by Chimpanzees, Humans or Other Animals

We checked each tagged oil palm monthly for use by chimpanzees, humans or other animals. For humans, if the oil palm had been used between survey dates, 3 types of uses were distinguished: 1) cutting down of a fruit bunch (for palm oil extraction); 2) cutting off palm fronds or leaves (for use in construction); 3) cracking nuts using a hammer and anvil stone. By default if none of the criteria used to ascribe nut-cracking to chimpanzees were met, we assumed the nut-cracking to have been performed by humans if, in addition, indications of human activity in the vicinity were noticeable and/or use of the site by humans could be confirmed through local knowledge.

Segmented worms (annelids), insects, and mammals—rodents, bush-pigs or hedgehogs—also consume nut kernels. Although we occasionally saw the latter consume kernels, most often only traces of footprints and foraging activity and the state of nutshells provided evidence of their feeding. We also saw several species of monkeys—sooty mangabeys (*Cercocebus atys*), lesser spot-nosed guenons (*Cercopithecus petaurista*) and Diana monkeys (*Cercopithecus diana diana*)—and squirrels in oil palms, consuming the reddish oily mesocarp of the fruit. These usually dropped the nut and some mesocarp to the ground whilst feeding. These often carried distinctive toothmarks that helped to confirm the presence of these primates since the last survey date. We recorded indications of recent fruit and kernel feeding by insects, annelids or mammals monthly to test for differences in interspecific competition for oil palm resources across the different sites.

For chimpanzees, we noted details on part eaten—kernel, fruit, petiole, palm heart, flower and tool use, pestle-pounding, (Yamakoshi and Sugiyama, 1995) and nut-cracking. Although Bossou chimpanzees most often swallow oil palm fruit intact along with the nut after sucking on the mesocarp, they also occasionally spit out the seed and/or a wadge of oil palm fruit fibers. We usually further confirmed fruit consumption via fecal analysis because nuts and fibers appear in the feces. We inferred kernel, petiole, palm heart, and flower consumption from monthly surveys of foraging evidence in and around each tagged oil palm. We also regularly checked other untagged oil palms within the habitat of the chimpanzees for use when encountered during daily tracking of the chimpanzees.

Previous direct observations of oil palm use by Bossou chimpanzees enabled us to establish criteria to assess feeding details, especially to distinguish between simple petiole feeding and pestle-pounding from fallen

fronds. Based on 48 direct observations at Bossou, a palm frond to be used as a pestle was usually modified by chimpanzees, either 1) via shortening towards the distal end, so a clear breaking point could be discerned (14.6%), or 2) by stripping away leaves towards its base (60.4%). Both modifications were applied to the same tool in 25% of recorded observations of pestle tool manufacturing. In addition, the basal tip of the frond is a good indicator for pestle-pounding since it was not only frequently chewed, indicating petiole feeding, but, also distinctly frazzled and crushed as a consequence of the pounding action.

We also employed a set of criteria to assess evidence of nut-cracking. Used hammers were stones or wooden clubs that demonstrated wear due to nut-cracking (*sensu* McGrew *et al.*, 1997). Used anvils were emergent tree roots or loose or embedded stones that showed traces of wear due to nut-cracking and/or upon or around which lay nutshell remains whose presence could not be attributed to any other animal but the chimpanzee. In order to exclude the possibility that nuts might have been cracked by humans rather than chimpanzees, at all sites, we ascribed nut-cracking to chimpanzees only if ≥ 1 of the following conditions was met: 1) the chimpanzees had previously been heard or seen cracking at the site, 2) fresh traces of chimpanzees, such as knuckle or foot prints, were found ≤ 5 m of a recently used nut-cracking site, 3) the nut-cracking tools and/or atelier were practically inaccessible to humans, even children, e.g. under dense bush.

Monthly intervals between surveys of the tagged oil palms were appropriate for monitoring the frequency of use of a single oil palm, because at Bossou, use would very rarely be targeted more than once a month at the same oil palm. Indeed, only once was nut-cracking directly observed to take place beneath the same oil palm on more than one occasion in the span of a month during our focal study periods.

Assessing Tool Availability: Nut-cracking and Pestle-pounding

We recorded hammer and anvil availability within a 5-m radius of each tagged oil palm. Because not all stones or branches can be used as tools for cracking oil palm nuts, we used an operational definition of tools, principally based on data gathered from tools employed at Bossou and criteria used in other studies (Boesch *et al.*, 1994; McGrew *et al.*, 1997). Accordingly, from 46 nut-cracking sites at Bossou, we weighed 87 confirmed anvil stones and 109 confirmed hammer stones via a pocket-sized spring balance, calibrated to the nearest 100 g, and recorded maximum width and length to the nearest mm. A potential anvil is a loose or embedded stone or a tree root whose hardness and shape allows it to serve as a base on which to crack open oil

palm nuts. A loose anvil stone weighed >400 g, the minimum recorded from the used anvils stones at Bossou ($N = 87$; mean = 2,340.2 g; SD = 1,987.7; Range: 400–10,000 g). Shape criteria, which focused primarily on the working surface available for cracking, were ≥ 7 cm wide ($N = 87$; mean = 12.1 cm; SD = 4.8; Range: 7.0–17.4 cm) and >10 cm long ($N = 87$; mean = 16.1 cm; SD = 6.5; Range: 10.2–38.4 cm) and provided a workable flat surface for cracking. Hardness was adequate if the anvil could sustain the force of 5 drops of a 1 kg granite stone from a 0.5 m height. This criterion is based on 20 trials. A maximum of 5 falls was required to crack open the nut, with the mean number of drops being 3.2 (SD = 0.89).

Potential hammers are stones or hard wooden clubs. They should not break when banged vigorously against a hard surface and should weigh >100 g and <2.5 kg ($N = 109$; mean = 848.6 g; SD = 363.4; Range: 100–2,200 g). Hammers that are too heavy may not be easily manipulated by the chimpanzees and may also result in crushing the kernel. Potential hammers should have a width of >5 cm ($N = 109$; mean = 9.9 cm; SD = 2.3; Range: 5.1–10.6 cm) and a length of more than 10 cm ($N = 109$; mean = 12.4 cm; SD = 2.8; Range: 10.3–17.6 cm). Some stones both operational definitions and were consequently classed as potentially serving both functions. The criteria for hammers and anvils facilitated differentiation between stones and wooden materials available on the forest floor that might or might not be used by the chimpanzees for cracking oil palm nuts.

Of 85 pestle pounding tools recorded at Bossou, 92% (78/85) were young fronds rather than mature ones. Accordingly, we monitored the presence of young leaves at the center of the palm crown monthly in the context of tool availability for pestle pounding. We recorded availability on a scale of 0–2 (0: absent; 1: present but ≤ 2 young new leaves/fronds emerging from the crown; 2: >2 young leaves/fronds present).

Fruit, Flower and Nut Availability

For each site we recorded the status of each tagged oil palm in terms of availability of fruit, flowers, young fronds and nuts. We noted fruit and flower availability on a scale of 0–2 (0: none or old; 1: young bunch; 2: mature bunch). Nut availability on the ground was noted follows: 0: none; 1: 1–25 nuts; 2: 26–50 nuts; 3: >50 nuts. We assessed nut quality as a percentage of edible nuts from a standardized sample of ≤ 20 randomly collected nuts for oil palms with a nut availability of 1, ≤ 30 for oil palms with a nut availability of 2; and ≥ 50 for oil palms with a nut availability of 3. We did not open the sample nuts so as not to affect future availability. Humle and local guides collectively judged the suitability of nuts for cracking. Since local people also crack oil

palm nuts, they usually know which nuts provide an edible kernel and which ones are rotten. We also recorded the availability of young fronds or petioles as previously detailed.

Oil Palm Density

In order to assess oil palm density at the 3 sites, we set up random north-south and east-west vegetation transects (50 m long and 10 m wide) within the core area of each study group in approximate proportion to the different habitat types available at each site (Chapman and Wrangham, 1994). We used random number tables to yield GPS points within the home range of the chimpanzees, which marked the beginning of each transect line. Thus, we set up 50 transect lines at Bossou, 48 at Yealé and 40 at Seringbara. We recorded all trees with a DBH > 5 cm.

Data Analysis

In order to control for monthly variations in fruit, flower and nut availability and interspecific competition for some of the resources, we only included months that were surveyed across all 3 sites in our data analysis. We checked the data for normality and used parametric or non-parametric tests accordingly. All statistical tests performed on the data are two-tailed, and the significance threshold is $p < 0.05$.

RESULTS

Oil Palm Use across Three Sites

Bossou

During the 2 rainy season oil palm surveys, we also collected focal animal data: 581 h of systematic behavioral data based on 20-min focal samples, averaging 5.3 h/day (SD = 1.6; range = 2.0–9.7 h). Bossou chimpanzees spent 23.9% of their feeding time consuming, oil palm parts; viz., 8.3% the heart, 7.8% the petiole, 4.1% the fruit, 2.9% the nut and 0.8% the pith of mature leaves. This confirmed their substantial reliance upon the oil palm during the rainy season, when fruit is scarce (Takemoto, 2002; Yamakoshi, 1998). The frequency of consumption of the different oil palm parts correlates significantly with data gathered from continuous focal animal sampling (Pearson Rank Correlation: $N = 6$; $R = 0.971$; $p < 0.001$). This result suggests that the

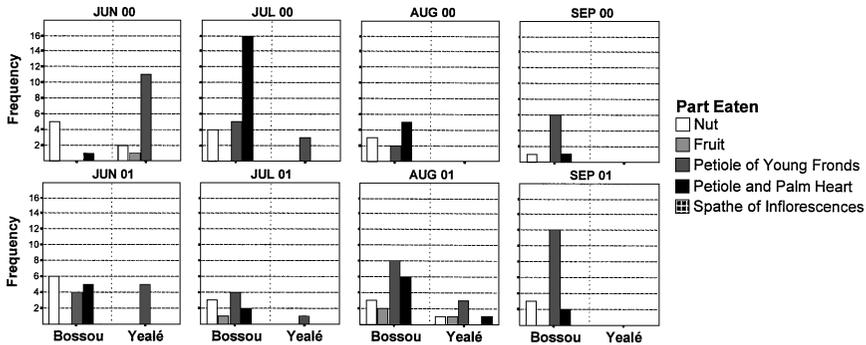


Fig. 2. Monthly frequency of oil palm plant part consumption by chimpanzees at Bossou and Yealé (Bossou: N = 127 during both study periods; Yealé: N = 127 in June 2000, 126 in July 2000 and 123 between August 2000 and September 2001 due to oil palm death. The Yealé site was not surveyed in September 2000).

oil palm surveying method adequately reflects the relative amount of time that Bossou chimpanzees spent on oil palm feeding activities.

In accordance with the focal sampling data from Bossou, the oil palm surveys indicated that pestle-pounding and petiole feeding were the 2 most frequent behaviors aimed at oil palms between June and September 2000 and 2001 (Fig. 2). Consumption of fruit mesocarp and nut-cracking were less common, but nevertheless regularly occurred (Fig. 2). Daily observations of the Bossou chimpanzees also confirmed that they fed on the stem of the oil palm flower and the pith of mature leaves, as indicated by the presence of wedges of pith at the foot of the oil palm (Table II). However, neither of them emerged as being consumed from the survey data. Though we noted feeding on the pith of mature leaves during focal animal sampling, flower consumption was not noted and was only observed *ad libitum* on 2 occasions (Table II).

Nimba Sites

The chimpanzees near Seringbara in the Nimba Reserve never used oil palms for feeding or nesting (Table II). Indeed, none of the 68 oil palms surveyed on a monthly basis, or any of the other oil palms checked for use during daily tracking of the chimpanzees, or the fecal analysis, gave any indication that they employ oil palms as a food resource (Table II).

Conversely, at Yealé chimpanzees consumed oil palm fruit, the petiole of young fronds and the stems and spathes (bracts protecting and enclosing immature inflorescences) of new flowers (Table II). Bossou chimpanzees ate

Table II. Oil palm parts confirmed to be consumed by chimpanzees at 3 sites and basis for supporting evidence

Item consumed	BOSSOU			SERINGBARA			YEALÉ		
	Surveyed oil palms	Feces* oil palms	Other oil palms	Surveyed oil palms	Feces* oil palms	Other oil palms	Surveyed oil palms	Feces* oil palms	Other oil palms
<i>Kernel of nut</i>	+	-	+	-	-	-	+	-	+
<i>Mesocarp of fruit</i>	+	+	+	-	-	-	+	+	+
<i>Petiole of young fronds</i>	+	-	+	-	-	-	+	-	+
<i>Oil Palm heart</i>	+	-	+	-	-	-	-	-	-
<i>Flower stem</i>	-	-	+	-	-	-	+	-	+
<i>Spathes of flower</i>	-	-	+	-	-	-	+	-	+
<i>Pith of mature leaf</i>	-	-	+	-	-	-	-	-	-

Note. '+' = Evidence; '-' = No evidence; 'Direct obs.' = Direct observation; *Fecal samples; Bossou: N = 220; Seringbara: N = 28; Yealé: N = 45.

spathes only once based on our records. Yealé chimpanzees also occasionally crack open palm nuts via stone tools.

There was no evidence of pestle pounding or feeding on the pith of mature leaves at Yealé (Table II). Finally, Yealé chimpanzees employed oil palms as a food resource to a lesser extent than Bossou chimpanzees (Fig. 2). Nevertheless, if the relative frequency of use determined via the monthly oil palm surveys indeed reflects the amount of time spent feeding on the different plant parts as previously established for Bossou, then Yealé chimpanzees spent more time consuming petioles of young fronds than palm fruit (Fig. 2). They also spent even less time nut-cracking and feeding on palm flowers.

The relative frequencies of nut-cracking and petiole feeding, which are common to both Bossou and Yealé, did not differ significantly (Chi-square test with continuity correction: $\chi^2 = 2.78$; $df = 1$; $N = 115$; *n.s.*). However, evidence of the activities was less frequently encountered at Yealé.

Oil Palm Density and Distribution

A possible explanation for the differential use of oil palms among the 3 sites is that there are significant differences in their availability. Based on vegetation transects, oil palm density at Bossou was 7.2 oil palms/km² within the core area (excluding cultivated fields) used by the chimpanzees, versus 1.0 oil palm/km² at Seringbara and 4.2 oil palms/km² at Yealé. At Bossou, oil palms are very abundant in certain areas and comparatively more uniformly distributed than at Seringbara and Yealé, where their distribution is far more localized and clumped. Yealé chimpanzees employed oil palms as a food resource to a much lesser extent than Bossou chimpanzees, and the lower densities observed at Yealé may explain this difference. However, differences in availability fail to explain the differential patterns of use between the 2 communities.

Seringbara harbors the fewest oil palms; however, traces of chimpanzees—nests and feeding remains—were found near them. Thus, in spite of a lower density of oil palms and their clumped distribution within the habitat, Seringbara chimpanzees clearly have access to them.

Considering the high-energy returns gained from feeding on the kernels of oil palm nuts, the apical meristem or the mesocarp of the fruit (Hartley, 1988) and that access is not a limiting factor, why do Seringbara chimpanzees not feed on oil palms? Might this reflect cultural variation or a possible failure of knowledge transmission and diffusion, assuming 1) individual interchange between the Bossou and Seringbara communities, and between Yealé and Seringbara, and 2) social learning in the acquisition of oil palm feeding behaviors? Or are there environmental differences that could explain these divergences in behavior?

Tool Availability for Nut-cracking and Pestle-pounding

Restricted tool availability might explain why Yealé chimpanzees do not pestle pound and so rarely crack oil palm nuts, and why Seringbara chimpanzees perform neither behavior. Based on the random sample of oil palms, at Bossou, *ca.* 25% had suitable nut-cracking tools, i.e. a minimum set of one anvil stone or tree root and one hammer stone or wooden club, available within a 5-m radius, and 22.8% showed evidence of nut-cracking (Fig. 3). Therefore, at Bossou, 87.9% of oil palm sites with tools had been employed recently for cracking oil palm nuts. At Seringbara, *ca.* 33% of oil palm sites had suitable nut-cracking tools available, but there was no evidence of use (Fig. 3). At Yealé, 75% of oil palms yielded a minimum of one suitable anvil and hammer set; however, only 2.4% indicated nut-cracking (Fig. 3).

Because potential tools were available at all 3 sites within a 5-m radius of oil palms, limited availability of tools cannot explain the absence of the behavior at Seringbara and its rarity at Yealé.

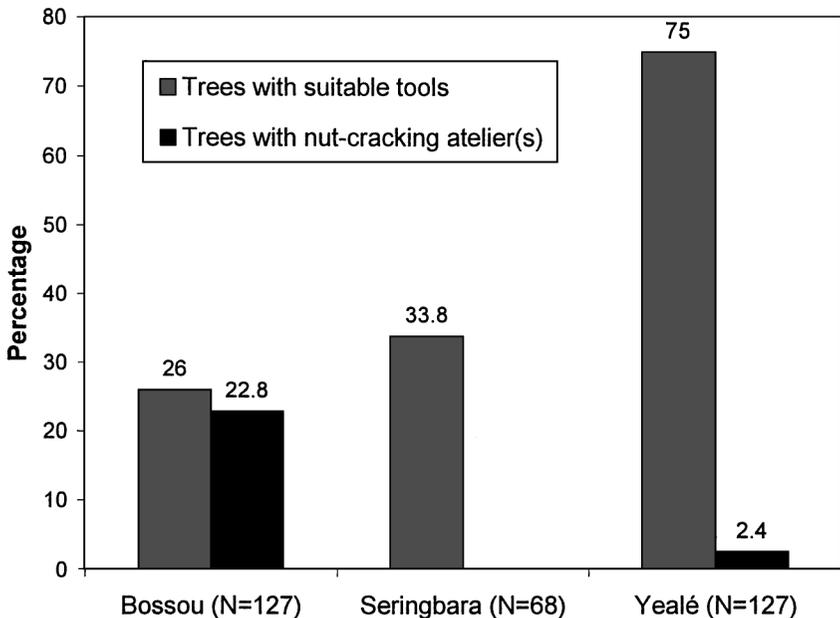


Fig. 3. Percentage of oil palms providing suitable nut-cracking tools (a minimum set of one anvil stone or tree root and one hammer stone or wooden club) and exhibiting evidence of nut-cracking across the three sites.

In addition, all oil palms from Seringbara had young fronds available for pestle pounding or petiole feeding throughout both study periods, while at Bossou and Yealé, the availability of young leaves was affected by either petiole feeding and/or pestle-pounding activities. Between June 2000 and September 2001, among the surveyed oil palms, no deaths occurred at Bossou, while 4 palms died at Yealé. However, if petiole feeding was recorded during the monthly surveys at Bossou and Yealé, 82.5% and 87.5% of oil palms respectively no longer exhibited young fronds. Average recovery time for the production of a novel set of leaves post petiole feeding was 3 mo (N = 19; SD = 0.94; r = 1–5 mo). Due to pestle-pounding, 94.4% of oil palms had all their young leaves removed, while 5.6% had <2 leaves left. Average recovery time post pestle pounding was 3.3 mo (N = 22; SD = 1.1; r = 1–5 mo). Accordingly, restricted availability of young fronds could explain neither the absence of pestle-pounding at Yealé nor petiole feeding and pestle pounding at Seringbara, where young fronds were consistently available throughout both survey periods.

Fruit, Flower and Nut Availability

There was no significant difference in the mean monthly percentage of oil palms exhibiting mature fruit across the 3 sites (One-way ANOVA: $F_{2,21} = 3.124$, n.s.); (Fig. 4). In general, some oil palms harbored a mature

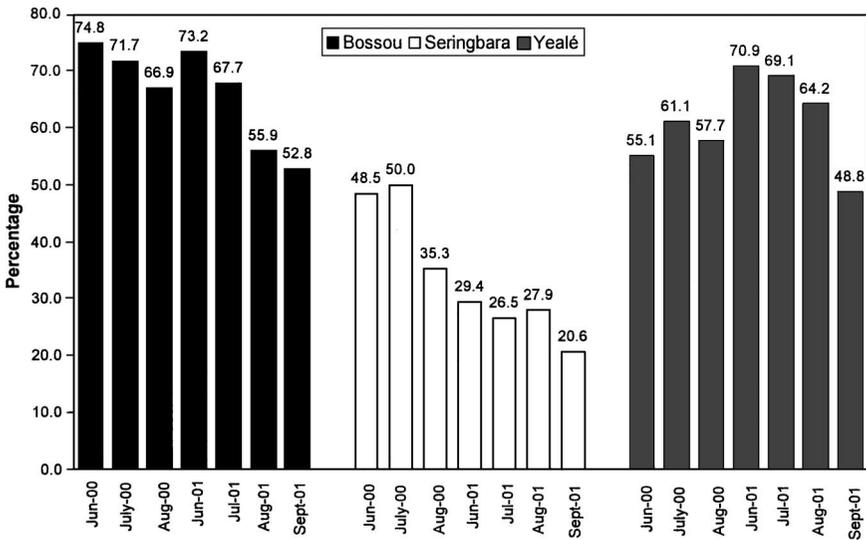


Fig. 4. Percentage of oil palms exhibiting mature fruit on a monthly basis across 3 sites.

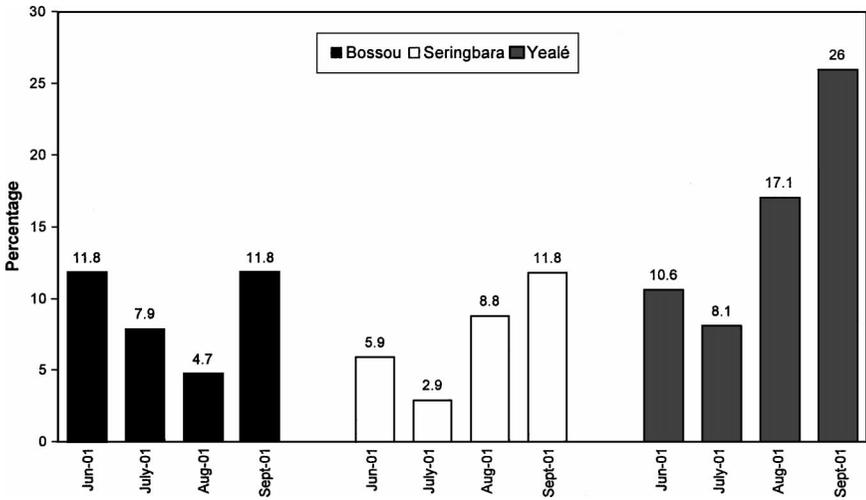


Fig. 5. Percentage of oil palms exhibiting immature and mature flowers on a monthly basis across 3 sites.

bunch of fruit every month; however, as the rainy season progressed, the monthly percentage of oil palms with available fruit decreased (Fig. 4). Further, monthly fruit availability during the 2 survey periods did not differ significantly among the 3 sites, thus we reject the hypothesis that Seringbara chimpanzees do not consume oil palm fruit due to its paucity or absence.

We recorded the availability of immature and mature flowers only during the second study period (June–September 2001). There was no significant difference in the monthly percentage of oil palms providing immature and mature flowers across the 3 sites (One-way ANOVA: $F_{2,11} = 2.426$; n.s.) (Fig. 5). Immature or mature flowers were available at the 3 sites throughout the study period, with September exhibiting the greatest percentage of available immature and mature flowers, portending greater fruit availability later in the dry season (Fig. 5).

There was a significant difference among the 3 sites in the monthly percentage of oil palms supplying edible nuts (One-way ANOVA: $F_{2,21} = 23.839$; $p < 0.0001$) (Fig. 6). Tukey's HSD *post hoc* test showed no significant difference between Bossou and Yealé in the percentage of oil palms providing edible nuts; however, significantly fewer oil palms at Seringbara offered more intact nuts than those at either Bossou ($p < 0.001$) or Yealé ($p < 0.001$) (Fig. 6).

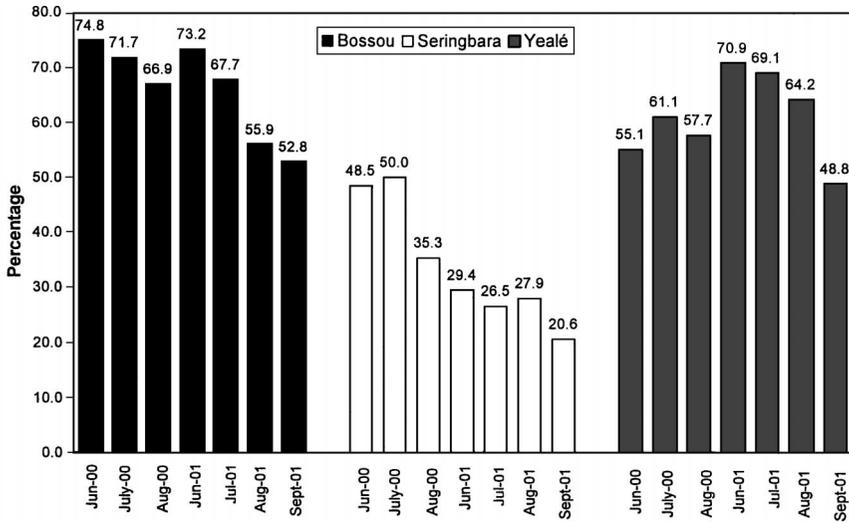


Fig. 6. Monthly percentage of oil palms providing edible nuts across 3 sites.

Competition with Sympatric Species for Oil Palm Fruit and Nuts

Squirrels were the prime consumers of oil palm fruit at all 3 sites (Table III). Although absent from Bossou, sooty mangabeys (*Cercocebus atys*), lesser spot-nosed guenons (*Cercopithecus petaurista*) and Diana monkeys (*Cercopithecus diana diana*) also consumed the mesocarp of oil palm fruit at the Nimba sites (Table III). At Bossou and Yealé, humans occasionally cut off fruit bunches from oil palms near the forest edge for palm-oil production.

There was no significant difference among the 3 sites in the monthly percentage of fruit-bearing oil palms with evidence of fruit-eating competitors

Table III. Percentage of fruit-bearing oil palms with evidence of fruit consumption by animals other than the chimpanzee between June and August 2000 and June and September 2001 across the 3 sites

Site Competitor	Bossou (n = 78)	Seringbara (n = 65)	Yealé (n = 173)
<i>Squirrel</i>	26.9	19.6	18.1
<i>Human</i>	6.4	—	2.4
<i>Sooty mangabey</i>	—	3.9	1.2
<i>Lesser spot-nosed guenon</i>	—	2.—	—
<i>Diana monkey</i>	—	—	-0.6

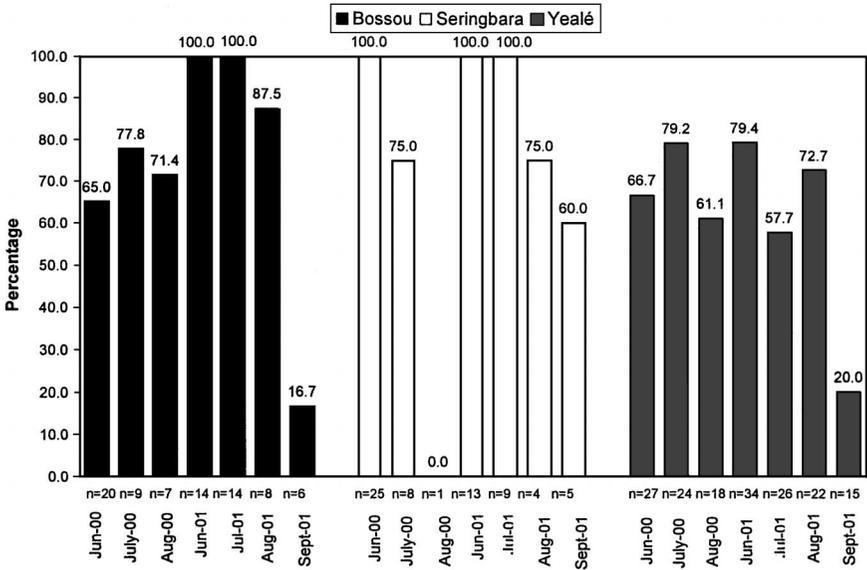


Fig. 7. Monthly percentage of surveyed fruit-bearing oil palms exhibiting evidence of a fruit-eater competitor across 3 sites.

other than chimpanzees (One-way ANOVA: $F_{2,21} = 0.342$; n.s.) (Fig. 7). Therefore, differences in the levels of competition with sympatric species for oil palm fruit failed to provide a satisfactory environmental explanation for why Seringbara chimpanzees do not consume this highly nutritious food source.

To address the issue of competition for nuts, we recorded the animal taxa responsible for nut consumption between each survey date for each oil palm. Insects and annelids, pooled together, accounted for most kernel consumption at Bossou, whereas at the Nimba sites, most nuts were consumed by various species of rodents (rat) (Table IV). At Yealé, hedgehogs and bushpigs

Table IV. Percentage of nut-bearing oil palms with evidence of nut kernel consumption by sympatric species between June and August 2000 and June and September 2001 across 3 sites

Site Competitor	Bossou (n = 588)	Seringbara (n = 162)	Yealé (n = 532)
<i>Insect/Worm</i>	34.5	1.5	7.3
<i>Rat</i>	17.3	42.9	34.5
<i>Hedgehog</i>	—	—	4.1
<i>Bushpig</i>	—	0	2.7

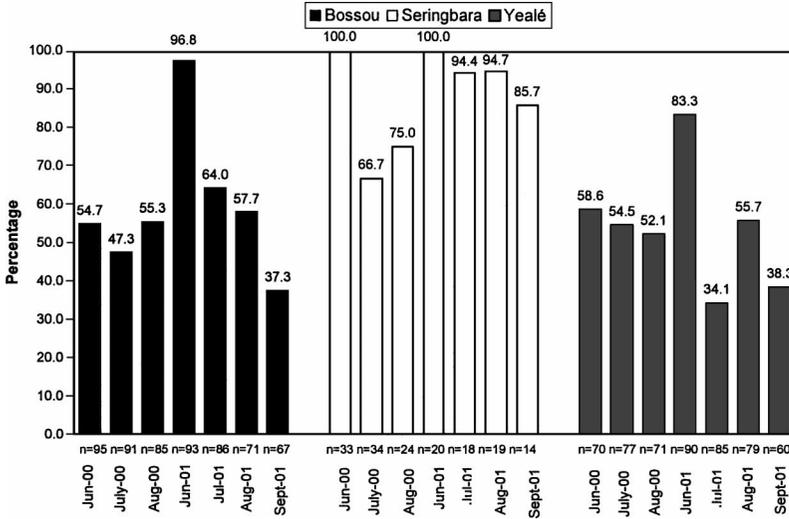


Fig. 8. Monthly percentage of nut-bearing oil palms presenting evidence of nut kernel consumption by non-chimpanzees across 3 sites.

also consumed nuts (Table IV). Bushpigs are absent from Bossou and their presence was not recorded in areas harboring oil palms at Seringbara. Although hedgehogs were confirmed at both sites, they were rare and infrequent consumers of oil palm nuts. A significant difference emerged among the 3 sites in the monthly percentage of nut-bearing trees with evidence of nut consumers other than chimpanzees (One-way ANOVA: $F_{2,21} = 9.288$; $p < 0.01$) (Fig. 8). Indeed, a Tukey HSD *post hoc* test indicated that at both the Bossou and Yealé sites significantly fewer nut-bearing oil palms were subject to nut consumption by sympatric species versus those at Seringbara ($p < 0.001$), while Bossou and Yealé did not differ significantly (Fig. 8).

The recorded estimates of nut quantity and quality provided useful additional variables allowing further exploration into differences in competition for nuts among the 3 sites. There was a significant difference in mean monthly nut quantity among sites (One-way ANOVA: $F_{2,21} = 9.288$; $p < 0.0001$) (Fig. 9). Tukey’s HSD *post hoc* test revealed that significantly more nuts across both study periods were available at Bossou than at either Yealé ($p < 0.01$) or Seringbara ($p < 0.001$), and there were more nuts at Yealé than at Seringbara ($p < 0.001$) (Fig. 9). However, at both Yealé and Seringbara, rodents, which tend to remove nuts from beneath oil palms, were the prime nut consumers for 34.5% and 42.9%, respectively, of the oil palms versus only 17.6% at Bossou (Table IV). Pooled data from the 3 sites showed that significantly fewer nuts remained when rodents were the main consumer

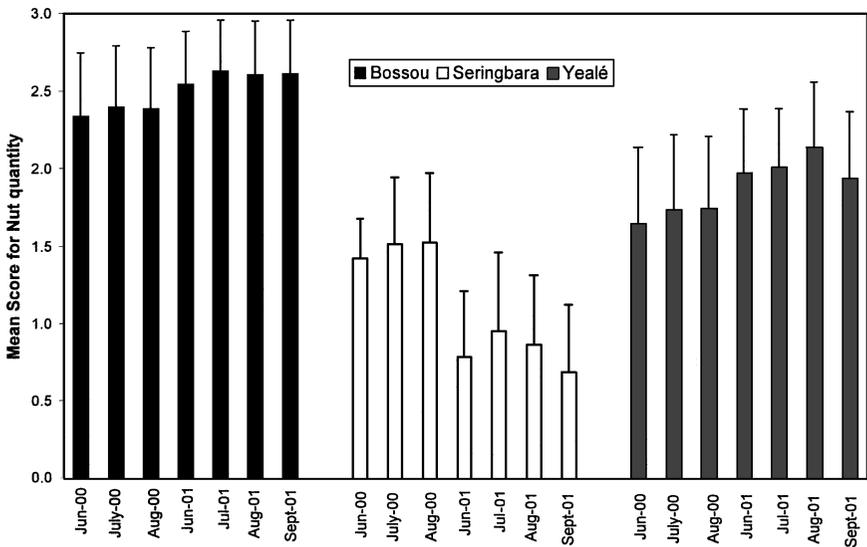


Fig. 9. Mean (SD) monthly score for nut quantity of surveyed oil palms across 3 sites.

versus insects and annelids (Mann-Whitney U-test: $N = 1181$; $z = -9.914$; $p < 0.001$).

Assuming that fruit bunches were equally productive across the 3 sites, competition for nuts by sympatric species was further revealed to be greatest at Seringbara on the basis of estimated lower nut quality and quantity. With the exception of September 2001 at Yealé, >50% of oil palms at both Yealé and Bossou provided edible nuts on a monthly basis, compared to consistently <50% at Seringbara (Fig. 6). Nevertheless, edible nuts were available in all months we surveyed oil palms (Fig. 6). Thus, Yealé chimpanzees had ample opportunities for cracking nuts, while Seringbara chimpanzees also had access to edible nuts. However, both Yealé and Bossou chimpanzees, versus Seringbara chimpanzees, benefited from both greater nut quality and availability, i.e. more conducive conditions for nut-cracking.

Diversity of Fruit Species in the Diet of the Chimpanzees

Bossou chimpanzees rely heavily upon oil palms for food during the rainy season, which corresponds to a period of fruit scarcity (Yamakoshi, 1998). The various edible plant parts provided by oil palms act as important fallback foods or keystone resources (Terborgh, 1986) for the Bossou

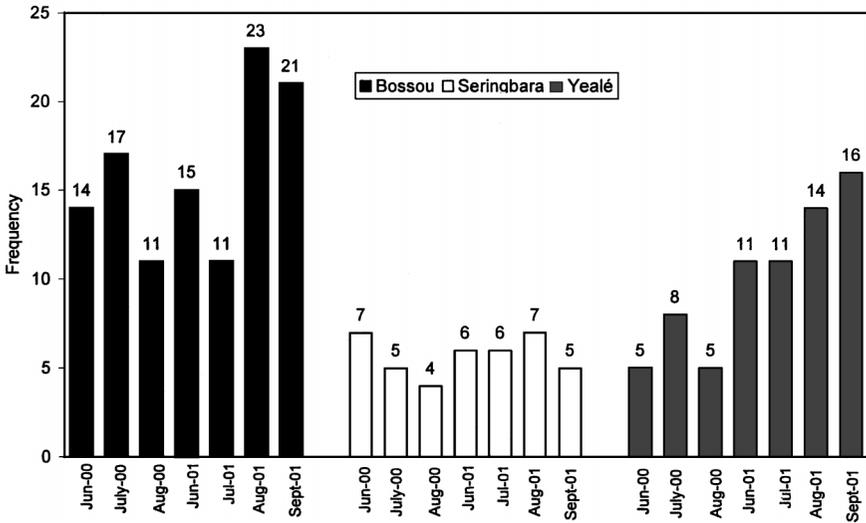


Fig. 10. Monthly frequency of fruit species in the diet of chimpanzees at Bossou, Yeaélé and Seringbara, based on feeding remains, fecal analysis and direct observations of feeding behavior.

community. We did not conduct systematic monthly phenological survey of alternative foods in parallel to the oil palm surveys. However, monthly records of feeding remains, direct observations and analysis of fecal samples provided data on the diversity of fruit species in the diet.

During the 2 survey periods, the number of fruit species consumed by chimpanzees across the 3 sites differed significantly (One-way-ANOVA: $F_{2,18} = 13.704$; $p < 0.001$) (Fig. 10). A Tukey HSD *post hoc* test indicated that the diversity of fruit species in the diet of Bossou chimpanzees was significantly greater than that of Yeaélé ($p < 0.05$) and Seringbara chimpanzees ($p < 0.001$), while there was no difference between the 2 Nimba sites. Most fruiting species at Bossou were in secondary forest, which is less common at the Nimba sites.

The pulp of fruit typically constitutes the largest portion of chimpanzees' diet. At Bossou, Yamakoshi (1998) showed a significant positive correlation between monthly fruit availability and the number of fruit species consumed. Although the monthly diversity of fruiting species in the diet of the Nimba chimpanzees may have been underestimated, it still reflects the low fruit availability at the 2 sites during the rainy season. Nimba chimpanzees certainly face a severe shortage of fruit then. Accordingly, oil palms are a potentially important fallback resource. It is therefore unclear why Seringbara chimpanzees fail to exploit oil palms, while Yeaélé chimpanzees consume some oil palm plant parts during this rainy season.

DISCUSSION

Patterns of Use of Oil Palms

Differential patterns of oil palm use are evident at Bossou, Seringbara and Yealé. Yealé chimpanzees displayed all the uses of the oil palm exhibited by Bossou chimpanzees except pestle-pounding and feeding on the pith of mature leaves. In addition, they consumed the base of the spathes of palm flowers, which is rarely consumed by Bossou chimpanzees. However, regarding the feeding behaviors they shared, Yealé chimpanzees performed them less frequently than Bossou chimpanzees did. Thus, they seldom cracked nuts via a hammer and anvil stone. Nevertheless, the relative occurrence of petiole feeding and nut-cracking was not significantly different between the 2 sites.

Seringbara chimpanzees did not show any evidence of oil palm use, but “absence of evidence is not evidence of absence” (McGrew *et al.*, 1997, p. 368). Therefore, Seringbara chimpanzees may simply 1) not have engaged in any of the behaviors during the 2 study periods or 2) may have done so, but in areas of their range that we did not explore. Considering the durability of oil palm feeding remains, excepting traces of feeding on mesocarp and flowers, if Seringbara chimpanzees had performed any of the activities in previous months, some evidence was likely to have been noticeable. The second possibility cannot be rejected with certainty. However, since 1999 we have acquired good estimates of chimpanzee ranging patterns and we also regularly monitored oil palms that were not focal in the monthly survey but that were encountered during daily tracking.

Environmental Explanations

Following the approach of Boesch *et al.* (1994) and McGrew *et al.* (1997), we explored environmentally based hypotheses to explain variation in oil palm use. Yealé chimpanzees might utilize oil palms less frequently than Bossou chimpanzees do because oil palms occur at greater densities and are more uniformly distributed at Bossou. Although oil palm density was lowest at Seringbara, where there was no evidence of oil palm use, the chimpanzees nested and fed on other fruit species and herbaceous terrestrial vegetation near areas where oil palms were available.

Furthermore, at Seringbara oil palms consistently provided young fronds for petiole consumption and tools for pestle-pounding. Moreover, fruit bunches and flowers prevailed at all 3-sites during the 2-survey periods and there was no significant difference in competition for oil palm fruit by

sympatric species. In addition, hammer and anvil sets were not a limiting resource for potential nut-cracking purposes at either Seringbara or Yealé.

Competition by sympatric species for nuts was greater at Seringbara than at either Bossou or Yealé. At Bossou, rodents less frequently consumed or removed nuts, and insects and annelids accounted for most nut consumption. At Yealé, consumption or removal of nuts by rodents had a significant impact on the quantity of nuts available. However, the impact of rodents on the availability of edible nuts was most notable at Seringbara, where on a monthly basis, $\geq 50\%$ of oil palms failed to provide edible nuts. Nevertheless, many oil palms provided nuts suitable for cracking, and Yealé chimpanzees cracked oil palm nuts, albeit infrequently. Accordingly, Seringbara chimpanzees may possess oil palm nut-cracking knowledge but might choose not to apply it because of poor nut quality and quantity. This is unlikely given that Seringbara chimpanzees failed to evince cracking of any species of nuts. Several species provoking tool-assisted nut-cracking elsewhere, e.g. *Detarium senegalensis* and *Parinari excelsa*, are available in Seringbara, whereas others are not, e.g. *Coula edulis*, which is cracked by Yealé chimpanzees (Humble and Matsuzawa, 2001).

June–September is a period of low fruit availability at Bossou and the Nimba sites, though we conducted no systematic monthly assessment of fruit availability. The low fruit diversity in the chimpanzees' diet across the 3 sites then indirectly confirmed the scarcity of fruit. Oil palm nut kernels are rich in energy, protein, calcium, phosphorous, fatty acids, and vitamin A; the oil in the mesocarp may vary between 35 and 60% (Hartley, 1988). The sap, which is exposed whilst pestle-pounding, is also a source of Vitamin B. Clearly, the energy returns and calorific and nutritional contents of some oil palm products are substantial and could be important during times of fruit scarcity. One would thus expect chimpanzees to use at least some of them if access to oil palms is not a limiting factor and appropriate knowledge is available.

Finally, proximate environmental parameters generally failed to provide a satisfactory explanation for the absence of pestle-pounding and mature pith-feeding at Yealé and of any of the oil palm targeted behaviors, generally observed at Bossou or Yealé, at Seringbara. Accordingly, we conclude that the differences are cultural. But what does this potentially tell us about diffusion of behavior in chimpanzees?

Culture and Diffusion of Behavior

Our study may provide preliminary insights into issues pertaining to culture, viz., diffusion of behavior or transfer of knowledge and transmission of behavioral patterns between communities. In addressing this issue

with respect to the 3 sites, we need to make two assumptions: 1) individual interchange between them and 2) social learning in the transmission of the oil palm targeted behaviors.

Individual interchange between Bossou and the Nimba sites and between Seringbara and Yealé has yet to be confirmed. However, Bossou chimpanzees have been sighted as far as the village of Seringbara at the foothills of the Nimba Mountains. Furthermore, Yealé and Seringbara chimpanzees share the same stretch of contiguous forest and evidence of chimpanzee trails and feeding remains on both sides of the massif occur as far as the summit, crossing between Guinea and Côte d'Ivoire. In addition, the study of Sugiyama *et al.* (1993) on paternity discrimination by GT dinucleotide repeat PCR analysis confirmed that Bossou chimpanzees were not reproductively isolated from their neighbors in the Nimba Mountains until at least 1986–1987.

Since 1976, 26 chimpanzees that have disappeared from the Bossou community might have emigrated to neighboring communities in the Nimba Mountains on the Guinean side or towards the Liberian or Ivorian portions of the massif (Table V). After 1990, researchers documented the nut-cracking and pestle-pounding ability of many of the individuals before their disappearance. Among 10 chimpanzees that disappeared between 1990 and May 2000, 3 females knew how to crack open oil palm nuts via a hammer and anvil stone, while 2 females and 3 males were experienced pestle-pounders as well as nutcrackers. Therefore, if they successfully emigrated, 80% and 50% of them, respectively, could have served as models for the transmission of nut-cracking and pestle-pounding to chimpanzees in other communities. Bossou chimpanzees have cracked oil palm nuts at least since the early 1960's. Yamakoshi and Sugiyama (1995) postulated that pestle-pounding is a recent innovation at Bossou, because it had not been documented before 1990. Since 1978, Bossou chimpanzees have been confirmed to feed on the petioles of young palm fronds, and fruit and flowers (Sugiyama, pers. comm.).

On the premise that all the above assumptions hold true, one might expect oil palm targeted behaviors to be prevalent at all 3 sites and diffusion to have taken place. But why have we seen none of the behaviors at Seringbara? And why do Yealé chimpanzees not pestle pound, and so rarely perform nut-cracking? If pestle pounding is indeed a recent innovation at Bossou, then it is possible that no Bossou chimpanzee with pestle-pounding knowledge has emigrated to Yealé. In addition, the rarity of oil palm nut-cracking at Yealé suggests that it may be habitual (versus customary), i.e. performed repeatedly by only a few members of the community, or present only in a single individual. Yealé nutcrackers may be emigrants from Bossou or may have discovered the behavior independently. The 3 oil palms at Yealé that showed evidence of nut-cracking by chimpanzees

Table V. Chimpanzees of Bossou that have disappeared since 1976 and could have potentially emigrated to the Nimba Mountains. After 1990, the pestle-pounding or nut-cracking ability or both, prior to disappearance, of many of the chimpanzees was confirmed (based on Humle, 2003; Matsuzawa *et al.*, 2001; Sugiyama, 1981; 1984; 1999; Yamakoshi and Sugiyama, 1995)

Name	Sex	Approx. date disappeared	Age	Age-class	Pestle pounding	Nut-cracking
Kubo	Female	Feb-77	5	Juvenile		
Aiwa	Male	May-77		Adult		
Bafu	Male	May-77		Adult		
Non	Male	May-77	8	Adolescent		
Fino	Female	Mar-80	9	Adolescent		
Kure	Female	Mar-80	11	Adolescent		
Jima	Male	Mar-80	6	Juvenile		
Vu	Male	Mar-80	8	Adolescent		
Yiri	Male	Mar-80	6	Juvenile		
Fon	Female	Mar-83	7	Juvenile		
Nyu	Female	Mar-83	7	Juvenile		
Vuna	Male	Mar-83	6	Juvenile		
Yana	Male	Apr-83	5	Juvenile		
Jieza	Male	Apr-88	10	Adolescent		
Vube	Female	Mar-90	8	Adolescent		Yes
Kakuru	Female	Mar-91	4	Juvenile		Yes
Kie	Female	Mar-91	16	Adult		Yes
Pru	Male	Nov-91	11	Adolescent	Yes	Yes
Ja	Female	Feb-93	10	Adolescent	Yes	Yes
Yunro	Male	Feb-93	9	Adolescent		No
Na	Male	Apr-96	11	Adolescent	Yes	Yes
Vui	Male	Jul-99	13	Adult	Yes	Yes
Pili	Female	Mar-01	14	Adult	Yes	Yes
Pokulu	Male	Mar-01	5	Juvenile		
Juru	Female	Dec-01	8	Adolescent	Yes	No
Nto	Female	Dec-01	8	Adolescent	Yes	Yes

Note. Yes: confirmed to perform behavior; No: never confirmed to perform behavior; empty cell: knowledge unknown to date.

were located at the border of the reserve. This is an area not necessarily frequented by all members of the chimpanzee community, which could limit transmission of this behavior.

Conversely, at Seringbara it appears that neither independent innovation nor transmission of oil palm targeted behaviors has occurred. Perhaps during the rainy season, Seringbara chimpanzees focus on alternative fall-back foods with high-energy returns, e.g. hunting for mammalian prey, and simply do not need to exploit oil palms. However, there is no evidence to support this hypothesis: there were no mammalian remain in the fecal samples. Alternatively, an emigrant from Bossou may have had too few chances to perform any of the behaviors because of pressure to maintain contact with other party members in an initially unfamiliar ecological and social environment. In addition, Biro and Matsuzawa (in press) showed that youngsters are

most prone to acquire behavioral innovations. Therefore the social structure and dynamics of a community may place limitations on transmission of novel behaviors.

Finally, diffusion of behavior between chimpanzee communities may not necessarily yield contiguous cultural regions. Cultural transmission may only occur if the complex interplay between adaptation to local ecological conditions and social structure and dynamics provides propitious conditions.

ACKNOWLEDGMENTS

In the Republic of Guinea, we thank the Ministère de l'Enseignement Supérieur et de la Recherche Scientifique, in particular the Direction Nationale de la Recherche Scientifique for granting us the permission to carry out the study. In the Republic of Côte d'Ivoire, we thank both the Ministère de l'Enseignement Supérieur et de la Recherche Scientifique and the Ministère de l'Environnement et des Forêts for granting us permission to work at Yealé. We also acknowledge all the trackers who have worked with us, especially P. Chérif, P. Goumi, G. Doré, B. Zogbila at Bossou, K. Doré and F. Doré at Seringbara and D. Gray, A. Gogo, F. Pahon, A. Go-pu and A. Wanseu at Yealé. We are also very grateful to W.C. McGrew, G. Yamakoshi, D. Biro and L.R. Moscovice for their critical comments on the manuscript. The study was supported in part by grants from the Ministry of Education, Science and Culture, Japan (Nos. 21COE, 12002009 and 10CE2005 to T. Matsuzawa) and a University of Stirling Postgraduate Fellowship.

REFERENCES

- Adebisi Sowunmi, M. (1999). The significance of the oil palm (*Elaeis guineensis* Jacq.) in the late Holocene environments of west and west central Africa. *Vegetation His. Archaeobotany* 8: 199–210.
- Anderson, J. R., Williamson, E. A., and Caster, J. (1983). Chimpanzees of Sapo forest, Liberia: Density, nests, tools and meat eating. *Primates* 24: 594–601.
- Biro, D., and Matsuzawa, T. (in press). Cultural innovation and transmission of tool use in wild chimpanzees: Evidence from field experiments. *Anim. Cogn.*
- Boesch, C., and Boesch, H. (1983). Optimisation of nut-cracking with natural hammers by wild chimpanzees. *Behaviour* 83: 265–286.
- Boesch, C., Marchesi, P., Marchesi, N., Fruth, B., and Joulian, F. (1994). Is nut-cracking in wild chimpanzees a cultural behaviour? *J. Hum. Evol.* 26: 325–338.
- Chapman, C. A., and Wrangham, R. W. (1994). Indices of habitat-wide fruit abundance in tropical forests. *Biotropica* 26: 160–171.
- Clutton-Brock, T. H., and Gillett, J. B. (1979). A survey of forest composition in the Gombe National Park, Tanzania. *Afr. J. Ecol.* 17: 131–158.
- Eggeling, W. J. (1947). Observations on the ecology of the Budongo rain forest, Uganda. *J. Ecol.* 34: 20–87.
- Galef, B. G., Jr. (1992). The question of animal culture. *Hum. Nat.* 3: 157–178.
- Ghiglieri, M. (1984). *The Chimpanzees of Kibale Forest*, Columbia University Press, New York.

- Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Anim. Behav. Monogr.* 1: 161–311.
- Goodall, J. V. L. (1973). Cultural elements in a chimpanzee community. In Menzel, E. W. (ed.), *Precultural Primate Behavior*, S. Karger, Basel, Switzerland, pp. 144–184.
- Guillaumet, J., and Adjanohou, E. (1971). Le Milieu Naturelle de la Côte d'Ivoire. *Mém. ORSTOM* 50: 157–264.
- Hartley, C. W. S. (1988). *The Oil Palm* (3rd edn.), Longman, London, England.
- Humle, T. (2003). *Culture and Variation in Wild Chimpanzee Behaviour: A Study of Three Communities in West Africa*, PhD Dissertation, University of Stirling, Scotland, UK.
- Humle, T., and Matsuzawa, T. (2001). Behavioural diversity among the wild chimpanzee populations of Bossou and neighbouring areas, Guinea and Côte d'Ivoire, West Africa. *Folia Primatol.* 72: 57–68.
- Inoue-Nakamura, N., and Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* 111: 159–173.
- Izawa, K., and Itani, J. (1966). Chimpanzees of the Kasakati basin, Tanganyika. (I) Ecological study in the rainy season 1963–1964. *Kyoto Univ. Afr. Stud.* 1: 73–156.
- Jones, C., and Sabater Pi, J. (1971). Comparative ecology of *Gorilla gorilla* (Savage and Wyman) and *Pan troglodytes* (Blumenbach) in Rio Muni, West Africa. *Afr. Bibl. Primatol.* 13: 1–96.
- Kano, T. (1972). Distribution and adaptation of the chimpanzee on the eastern shore of Lake Tanganyika. *Kyoto Univ. Afr. Stud.* 7: 37–129.
- Kawai, M. (1965). Newly acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima islet. *Primates* 6: 1–30.
- Laland, K. N., and Hoppitt, W. (2003). Do animals have culture? *Evol. Anthropol.* 12: 150–159.
- Letouzey, R. (1986). *Manual of Forest Botany: Tropical Africa*, Centre Technique Forestier Tropical, Nogent-sur Marne, France.
- Matsuzawa, T. (2003). Koshima monkeys and Bossou chimpanzees: Long-term research on culture in non-human primates. In de Waal, F. B. M., and Tyack, P. L. (eds.), *Animal Social Complexity*, Harvard University Press, Cambridge, MA, pp. 374–387.
- Matsuzawa, T., Biro, D., Humle, T., Inoue-Nakamura, N., Tonooka, R., and Yamakoshi, G. (2001). Emergence of culture in wild chimpanzees: Education by master apprenticeship. In Matsuzawa, T. (ed.), *Primates Origins of Human Cognition and Behavior*, Springer-Verlag, Tokyo, Japan, pp. 557–574.
- Matsuzawa, J., and Yamakoshi, G. (1996). Comparison of chimpanzee material culture between Bossou and Nimba, West Africa. In Russon, A., Bord, K., Parho, S. (eds.), *Reaching into Thought: The mind of the great apes*, Cambridge University Press, Cambridge, pp. 211–232.
- McGrew, W. C. (1985). The chimpanzee and the oil palm: Patterns of culture. *Soc. Biol. Hum. Aff.* 50: 7–23.
- McGrew, W. C. (1992). *Chimpanzee Material Culture: Implications for Human Evolution*, Cambridge University Press, Cambridge, MA.
- McGrew, W. C. (1998). Behavioural diversity in populations of free-ranging chimpanzees in Africa: Is it culture? *Hum. Evol.* 13: 209–220.
- McGrew, W. C., Baldwin, P. J., and Tutin, C. E. G. (1981). Chimpanzees in a hot, dry and open habitat: Mt. Assirik, Senegal, West Africa. *Man* 10: 227–244.
- McGrew, W. C., Ham, R. M., White, L. J. T., Tutin, C. E. G., and Fernandez, M. (1997). Why don't chimpanzees in Gabon crack nuts? *Int. J. Primatol.* 18: 353–374.
- McGrew, W. C., Tutin, C. E. G., and Baldwin, P. J. (1979). Chimpanzees, tools and termites: Cross-cultural comparisons of Senegal, Tanzania and Rio Muni. *Man* 14: 185–214.
- Nishida, T. (1987). Local traditions and cultural transmission. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate Societies*, University of Chicago Press, Chicago, pp. 462–474.
- Nishida, T., and Uehara, S. (1983). Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): Long-term record from the Mahale Mountains, Tanzania. *Afr. Stud. Monogr.* 3: 109–130.

- Nishida, T., Wrangham, R. W., Goodall, J., and Uehara, S. (1983). Local differences in plant-feeding habits of chimpanzees between the Mahale Mountains and Gombe National Park. *J. Hum. Evol.* 12: 467–480.
- Parker, S. T., and Russon, A. E. (1996). On the wild side of culture and cognition in the great apes. In Russon, A. E., Bard, K. A., and Parker, S. T., (eds.), *Reaching into Thought: The Minds of the Great Apes*, Cambridge University Press, Cambridge, UK, pp. 430–450.
- Reynolds, V., and Reynolds, F. (1965). Chimpanzees of the Budongo forest. In DeVore, I. (ed.), *Primate Behaviour*, Holt, Rinehart and Winston, New York, pp. 368–424.
- Sabater Pi, J. (1979). Feeding behaviour and diet of chimpanzees (*Pan troglodytes troglodytes*) in the Okorobiko Mountains of Rio Muni (West Africa). *Z. Tierpsychol.* 50: 265–281.
- Shimada, M. (2000). A survey of the Nimba Mountains, West Africa from three routes: Confirmed new habitat and ant catching wand use of chimpanzees. *Pan Afr. News* 7: 7–10.
- Struhsaker, T. T. (1975). *The Red Colobus Monkey*, University of Chicago Press, Chicago.
- Struhsaker, T. T., and Hunkeler, P. (1971). Evidence of tool-using by chimpanzees in the Ivory Coast. *Folia Primatol.* 15: 212–219.
- Sugiyama, Y. (1968). Social organization of chimpanzees in the Budongo forest, Uganda. *Primates* 9: 225–258.
- Sugiyama, Y. (1981). Observations on the population dynamics and behavior of wild chimpanzees at Bossou, Guinea, in 1979–1980. *Primates* 22: 435–444.
- Sugiyama, Y. (1984). Population dynamics of wild chimpanzees at Bossou, Guinea, between 1976–1983. *Primates* 25: 391–400.
- Sugiyama, Y. (1985). The brush-stick of chimpanzees found in south-western Cameroon and their cultural characteristics. *Primates* 26: 361–374.
- Sugiyama, Y. (1993). Local variation of tools and tool-use among wild chimpanzee populations. In Berthelet, A., and Chavaillon, J., (eds.), *The Use of Tool by Humans and Non-Human Primates*, Clarendon Press, Oxford, England, pp. 175–187.
- Sugiyama, Y. (1997). Social traditions and the use of tool-composites by wild chimpanzees. *Evol. Anthropol.* 6: 23–28.
- Sugiyama, Y. (1999). Socioecological factors of male chimpanzee migration at Bossou, Guinea. *Primates* 40: 61–68.
- Sugiyama, Y., Kawamoto, S., Takenaka, O., Kumazaki, K., and Miwa, N. (1993). Paternity discrimination and intergroup relationships of chimpanzees at Bossou. *Primates* 34: 545–552.
- Sugiyama, Y., and Koman, J. (1979). Tool-using and -making behavior in wild chimpanzees at Bossou, Guinea. *Primates* 20: 513–524.
- Sugiyama, Y., and Koman, J. (1992). The flora of Bossou: Its utilization by chimpanzees and humans. *Afr. Stud. Monogr.* 13: 127–169.
- Suzuki, A. (1969). An ecological study of chimpanzees in a savanna woodland. *Primates* 10: 103–148.
- Takemoto, H. (2002). *Feeding Ecology of Chimpanzees in Bossou, Guinea: Coping with the Seasonal Fluctuation of Food Supply and Micrometeorology in the Tropical Forest*, PhD Dissertation, Kyoto University, Japan.
- Teleki, G. (1974). Chimpanzee subsistence technology: Materials and skills. *J. Hum. Evol.* 3: 575–594.
- Terborgh, J. T. (1986). Keystone plant resources in the tropical forest. In Soulé, M. E. (ed.), *Conservation Biology: The Science of Scarcity and Diversity*, Sinauer Associates, Sunderland, MA, pp. 330–344.
- Tomasello, M. (1994). The question of chimpanzee culture. In Wrangham, R. W., McGrew, W. C., de Waal, F. B. M., and Heltne, P. G. (eds.), *Chimpanzee Cultures*, Harvard University Press, Cambridge, MA, pp. 301–317.
- Tomasello, M. (1999). *The Cultural Origins of Human Cognition*, Harvard University Press, Cambridge, MA.

- Tomasello, M., Kruger, A. C., and Ratner, H. H. (1993). Cultural learning. *Behav. Brain Sci.* 16: 495–552.
- Tutin, C. E. G., and Fernandez, M. (1993). Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé reserve, Gabon. *Am. J. Primatol.* 30: 195–211.
- WCMC (1992). *Guinea/Côte d'Ivoire-Réserve Naturelle Intégrale des Mont Nimba*, UNEP-WCMC (World Conservation Monitoring Centre) Infobase Report.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., and Boesch, C. (1999). Cultures in chimpanzees. *Nature* 399: 682–685.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., and Boesch, C. (2001). Charting cultural variation in chimpanzees. *Behaviour* 138: 1481–1516.
- Wrangham, R. W. (1975). *The Behavioural Ecology of Chimpanzees in Gombe National Park, Tanzania*, PhD Dissertation, University of Cambridge, England, UK.
- Yamakoshi, G. (1998). Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool-use. *Am. J. Phys. Anthropol.* 106: 283–295.
- Yamakoshi, G. (2001). Ecology of tool use in wild chimpanzees: Towards reconstruction of early hominid evolution. In Matsuzawa, T. (ed.), *Primate Origin of Human Cognition and Behavior*, Springer-Verlag, Tokyo, Japan, pp. 537–556.
- Yamakoshi, G., and Sugiyama, Y. (1995). Pestle-pounding behavior of wild chimpanzees at Bossou, Guinea: A newly observed tool-using behavior. *Primates* 36: 489–500.
- Zeven, A. C. (1972). The partial and complete domestication of the oil palm *Elaeis guineensis*. *Econ. Botany* 26: 274–279.