Culture and Variation in Wild Chimpanzee Behaviour: a Study of Three Communities in West Africa

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ABSTRACT

The concept of culture has recently been used to explain behavioural variation and trans-generational continuity of behaviour in non-human animals and in chimpanzees in particular. However, few studies in the wild have systematically investigated how the environment and behavioural adaptation might influence behavioural diversity. In this context, one habituated community of wild chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea, and two neighbouring non-habituated communities in the Nimba Mountains region of Guinea and Côte d'Ivoire were the subject of a detailed study of behavioural variation at the intra- and inter-community level. An ecologically-based approach was adopted to investigate variation in nest building, in the use of the oil-palm tree (*Elaeis guineensis*), in ant-dipping and in tool-choice and -manufacturing. A significant influence of environmental variables on nesting parameters emerged explaining much of the variation observed between the three sites. However, some differences that arose are more likely to reflect differences in social structure and organisation. The comparative study of the utilisation of the oil-palm tree failed to reveal proximate environmental parameters that might explain significant observed variations in use. These findings raise interesting and important questions pertaining to diffusion of behaviour between neighbouring chimpanzee communities. Dipping for driver ants, *Dorylus* spp., is often cited as one of the best examples of culture in chimpanzees. A detailed analysis of this behaviour at Bossou suggests that risk exposure affects frequency of performance in the developing chimpanzee and reveals a strong influence of prey characteristics, including aggressiveness and/or gregariousness, on tool length and technique employed. Variations in tool-choice and tool-manufacturing within and between three tool-use behaviours at Bossou involving the use of a stick or a stalk were found to be significantly associated with the nature of the task and its predictability, emphasising the importance of environmental affordance and constraints on these processes. In addition, efficiency in behaviour across another set of three tool-use behaviours was explored focusing chiefly on age-class differences. An analysis of individual and community-level patterns of laterality in hand-use between these three tool-use behaviours is also provided. The data supply some evidence to support the selective advantages of lateralization in hand-use with respect to behavioural efficiency. The findings also suggest that haptic tasks have played an important evolutionary role in driving population-level handedness, and reveal that although complex tool-uses exhibited high levels of lateralization, these failed to show task specialisation across individuals. Finally, this thesis presents a comprehensive review analysis of individual and community-wide variation across a range of behaviours observed in chimpanzees and identifies paths and hypotheses that warrant further exploration and testing with the aim to gain further insight into cultural processes in non-human animals.

LIST OF COLOUR PLATES

Chapter 1

Introduction

1.1 The Chimpanzee: taxonomy and distribution

There exist two species of chimpanzees: the common or robust chimpanzee (*Pan troglodytes*) and the bonobo, also known as the pygmy chimpanzee (*P. paniscus*). Both species are only found in Africa. Most chimpanzees inhabit evergreen forests, but some populations have been shown to exist in deciduous woodland and grassland biotopes interspersed with gallery forest. Most wild chimpanzees live between 13°N and 7°S of the equator.

Taxonomists generally agree that *Pan troglodytes* can be further divided into four subspecies that exhibit mutually exclusive geographical ranges: 1) the eastern chimpanzee (*P. t. schweinfurthii*) living in Sudan, Burundi, Rwanda, Tanzania, Uganda and the Democratic Republic of Congo; 2) the central chimpanzees (*P. t. troglodytes*), living in Angola, Central African Republic, Equatorial Guinea, Cameroon, Democratic Republic of Congo, Gabon; 3) the Nigerian chimpanzee (*P. t. vellerosus*) in eastern Nigeria and western Cameroon; and 4) the western chimpanzee (*P. t. verus*), close to extinction in Burkina Faso, Ghana, Guinea Bissau, Senegal, Togo (Butynski, 2001, Lee *et al.,* 1988. IUCN, 2002), but still found in Mali, Guinea, Côte d'Ivoire, Sierra Leone, and Liberia. The Nigerian subspecies has only recently been recognised as a separate subspecies (Gonder *et al.*, 1997) and very little is known about its behaviour and ecology.

It has been suggested that the western subspecies (*P. t. verus*) separated from the central and east African subspecies (*P. t. troglodytes* and *P. t. schweinfurthii*) about a million years ago (Morin *et al.*, 1994). Morin *et al.* (2001) have argued that it warrants classification as a separate species altogether (*P. verus*); however, this is still being debated. Regardless, the genus *Pan* comprises the closest living relatives of humans (*Homo sapiens*), both having shared a common ancestor about 5-6 million years ago (Goodman *et al.*, 1998).

1.2 Defining culture

The ascription of culture to chimpanzees and other non-human animals has been controversial and a source of much debate. Much of this debate hinges on the definition of culture that is employed. In 1952, Kroeber and Kluckhohn produced a review of concepts and definitions of culture, compiling 168 definitions, all implying a human prerogative. However, as scientists began to recognise some forms of culture in non-human animals, a divide between anthropologists and biologists with regards to the definition of culture became apparent. Indeed, it is still commonly assumed by anthropologists that culture is a unique human characteristic. Some definitions, therefore, refer specifically to the human nature of culture centred on language, symbols, teaching and imitation, and consequently exclude non-human animals, including early hominids such as *Australopithecus* sp. and *Homo habilis* (McGrew, 1992). One biological definition of culture is the transfer of information by behavioural means, particularly by the process of teaching (Bonner, 1980). Such a definition is not very different from that given by anthropologists, which proposes that culture encompasses the learned behaviours and attitudes that are characteristic of a particular society (Ember and Ember, 1985).

Primatologists have proposed another, broader definition, in which cultures are seen as behavioural variants induced by social modifications that create individuals who will in turn modify the behaviour of others in the same way

(Kummer, 1971). Under this definition, the behaviour of two groups with the same gene pool and with the same type of habitat can only differ in their culture (Kummer, 1971, McGrew, 1992). Therefore, to grant culture to an animal species under this definition, the criteria are stringent. Simply showing a patchy distribution of a given behaviour is not acceptable as evidence, although it may be strongly suggestive if it is shown to be independent of environmental and genetic factors.

In their formulation of criteria for culture in non-human animals, McGrew and Tutin (1978) proposed an operational definition based upon eight criteria - innovation, dissemination, durability, standardisation, diffusion, tradition, non-subsistence and naturalness (cf. McGrew, 1992). Their exclusion of subsistence activities from cultural behaviours, because they "are directly involved in energy budgeting" and are likely "to be correlated with the distribution of resources in the environment" (McGrew and Tutin, 1978, p.247) has since been reconsidered. Nishida *et al.* (1983) postulated that differences in food-processing techniques between Gombe and Mahale chimpanzees in Tanzania can be defined as cultural, and indeed many behaviours now recognised as cultural in chimpanzees involve subsistence activities (e.g. Boesch *et al.*, 1994; McGrew *et al.*, 1997; Whiten *et al.*, 1999, 2001).

According to McGrew (1992), behavioural differences between populations or groups of chimpanzees should not be termed cultural if they can be accounted for by ecological factors involving individual, rather than social, transaction between the organism and the environment. Nishida *et al.* (1983) had previously suggested nevertheless that if differences in behaviour across populations are maintained from generation to generation through social learning, one can refer to them as cultural differences, regardless of how they originated. A sensible and operational definition of culture, which I shall adhere to in this thesis, is that cultures are dynamic behavioural traditions socially transmitted within and between generations in groups and populations within a species that may aid them in adapting to local conditions, i.e. ecological, demographic, or social (Parker and Russon, 1996, Laland and Hoppitt, in press).

1.3 Culture and social learning processes

Once social learning or transmission of behaviour was recognised as an essential component of culture, psychologists focused much attention on determining and defining the particular social learning processes characterising cultural transmission (Galef, 1990; Tomasello, 1990, Tomasello *et al.*, 1993, Whiten and Ham, 1992).

Many have proposed that culture, as we recognise it in humans, requires social learning through imitation, teaching or collaborative learning, i.e. cultural learning (Cavalli-Sforza *et al.*, 1982; Galef, 1990; Heyes, 1993; Tomasello *et al.*, 1993). Based upon these criteria, Tomasello *et al.* (1993) isolated three essential characteristics of culture unique to humans: (1) a cultural behaviour should be performed by all group members, (2) its form should be a faithful reproduction of that of the model and (3) an accumulation of modifications should exist.

The first statement has been contested by cultural anthropologists, such as Ingold (1993), who pointed out that variations in culture in humans, according to age, sex and social status of the individual, are frequent. The third characteristic, also referred to as the ratchet effect, which implies an increase in complexity or efficiency over time, has also been doubted as uniquely human. For example, Japanese macaques (*Macaca fuscata*) on Koshima Island in Japan have been known to modify their sweet-potato-washing technique from freshwater to seawater (Watanabe, 1994) and they also have adapted their wheat sluicing technique to reduce pilfering by dominant individuals (Kawai *et al.*, 1992). Whether these behaviours represent valid examples of the ratchet effect in non-human animals or not is under debate (Laland and Hoppitt, in press). However, as pointed out by de Waal (2001), it seems unlikely that complex sequences of co-ordinated actions observed in some animal species arose at once and were not the result of a long and steady perfection of skills.

Tomasello *et al*'s (1993) second statement has also been criticised. Wynn (1993) has clearly demonstrated that quite simple forms of social learning have a role in the cultural transmission process in humans. Indeed, in some human populations, learning through imitation or teaching is rare or even absent, as in for example the Kung Bushmen (Olson and Astington, 1993; Rogoff *et al.*, 1993) and the Aka pygmies (Hewlett and Cavalli-Sforza, 1986). Studies of human children have also revealed that imitation is more complex and variable than is generally realised. Far from being a perfect replication of entire sequences of actions, children's imitation shows wide variability in completeness and fidelity to the model's actions, with various insertions and recombinations with other actions (Speidel and Nelson, 1989). Why be so restrictive when non-human animals are concerned when it is clear that social learning processes other than imitation, teaching and collaborative learning, can be involved in the transmission of cultural behaviours? If we are to accept that cultural patterns of behaviour exist among chimpanzees, then we must concur that some form of cultural transmission exists as well.

1.4 Culture in chimpanzees

In the 1950's, Japanese primatologists began to describe the social transmission of novel behaviours in Japanese macaques as "cultural" (Itani, 1974; Itani and Nishimura, 1973; Kawai, 1965; Kawamura, 1959; Menzel, 1973). Kawamura (1959) used the term "sub-culture" and later used the term "preculture" (Kawamura, 1972) in his descriptions of the potato-washing behaviour of Japanese macaques. Kawamura introduced this terminology controversially to the Anthropological Society of Nippon and the Japanese Society of Ethnology in 1955 to describe invention and social transmission of local food habits within troops of Japanese macaques through "imitation" (Itani and Nishimura, 1973). Since then, the terminology used has been a mixture of the term "protoculture" (Menzel *et al.*, 1972) and "culture", first used in relation to non-human primates by Kummer (1971), although Kroeber, already in 1928, had contemplated the possibility of an "ape culture" (Kroeber, 1928, p.331).

Field studies of chimpanzees have revealed distinctive differences in behavioural repertoires suggesting cultural variation between populations and communities (McGrew, 1992). A systematic synthesis of these cultural variants has recently been published, based primarily on information acquired from long-term field studies of chimpanzees across Africa (Whiten *et al.*, 1999, 2000). The emerging differences in patterns of behaviour can be classified into three broad categories: social traditions, personal hygiene, food-processing techniques that can be broadly subdivided into non-subsistence and subsistence activities.

Non-subsistence activities

Some authors have argued against culture in chimpanzees. They suggest rather that what is observed is a similar response in animals of all populations to similar ecological conditions, i.e. if only one way of solving the task is possible given the sensorimotor capacities of the animal, then individual learning leads to standardisation (Galef, 1990; Tomasello, 1990, 1999; Tomasello *et al.*, 1993; Visalberghi and Fragaszy, 1990). However, examples of different social traditions across chimpanzee communities cannot be explained in those terms, since they exclude ecological conditions.

Handclasp grooming and leaf grooming

McGrew and Tutin (1978) were the first to describe hand-clasp grooming, which they defined as simultaneous and reciprocal grooming performed by two individuals while extending an arm overhead, bracing or clasping the other's wrist or hand. This particular grooming technique is widespread at the community level among chimpanzees at Mahale (Tanzania) and Kibale (Uganda) and has commonly been observed in some individuals at Lopé (Gabon) and Taï (Côte d'Ivoire), but has never been recorded at other long-term study sites such as Gombe (Tanzania) or Budongo (Uganda) (Whiten *et al.*, 1999). So far, one single observation of this behaviour has been made at Bossou (Guinea) (Yamakoshi, pers. obs.). It is evident that ecological differences cannot explain the distribution of this behaviour and its variants, and thus it is a good example of culture in chimpanzees.

More recently, Nakamura *et al.* (2000) described another social behavioural pattern customarily shown by members of the M-group of Mahale chimpanzees. This behaviour, termed "social scratch", occurs during grooming episodes and literally involves one individual scratching the other's back. A variant of this behaviour has also been observed among the chimpanzees of the Ngogo community in Kibale (McGrew, pers. comm.) and has to date not been reported from any other long-term chimpanzee field site. This behaviour has been proposed to represent a social cultural behavioural variant in wild chimpanzees.

Leaf-grooming, whereby a chimpanzee collects one or more leaves, and, while peering at them intently, grooms them carefully and sometimes lip-smacks at the same time (Goodall, 1986), has also been recognised as a cultural behaviour, only observed at long-term field sites of the eastern subspecies (*P. t. schweinfurthii*) (Whiten *et al.*, 1999, 2001). It appears to have a communicatory function, since after initiation of this behaviour, which usually attracts the attention of one or several group members, some other interaction such as grooming or playing often ensues. At Gombe, a variant to leaf-grooming, i.e. leaf-squashing, is also observed and involves squashing of ectoparasites on leaves whilst grooming (Boesch, 1995). Similarly to handclasp grooming or social scratching, leaf-grooming and leaf-squashing do not seem to have any ecological explanation, but rather represent examples of socially transmitted behavioural patterns that are reinforced by members of the community.

Leaf clipping and its communicatory function

During leaf-clipping, the chimpanzee generally noisily pulls to bits one or more leaves using the fingers or the mouth, often leaving only a stripped petiole behind (Nishida, 1980). The frequency of mouth to finger leaf-clipping varies between chimpanzee communities (Boesch, 1996). In addition, leaf-clipping has been recorded at all other long-term study sites across Africa, except for Gombe (Whiten *et al.*, 1999). At Bossou and Mahale (K-group), exclusive use of the mouth for leaf-clipping occurs, whereas at other sites both mouth and finger use in leaf-clipping have been noted, with varying frequencies (Whiten *et al.*, 1999, 2001). In addition, Mahale chimpanzees tend to repeatedly bite small pieces away, while at Taï, using their lips, the chimpanzees rather rip the leaf blades in a single movement (Nishida, 1987; Boesch, 1996a).

This behaviour is clearly ritualised and has a communicatory function, which is usually context-dependent. Indeed, the signalling function of leaf-clipping varies across communities. For example, at Mahale, most cases of leaf-clipping occur during courtship, directed from a male to a female in oestrus (Nishida, 1987). But there have been a few recorded instances when the leaf-clipper acted in apparent frustration, usually in response to lack of access to a tempting incentive, such as food possessed by others. At Bossou, on the other hand, most examples of leaf-clipping reflect frustration; only a few occur in a courtship context (Sugiyama, 1981). Leaf clipping at Bossou is also observed in youngsters at play. At Taï, leaf-clipping is mainly part of the tree drumming sequence of adult males, but it also occasionally occurs during resting episodes or more seldom during situations when chimpanzees exhibit anxiety or frustration (Boesch, 1995). Similar contexts and communicatory functions were identified at Kibale in the Ngogo chimpanzee community.

Although differences in the function of this behaviour are apparent across sites, in all cases it seems to be a ritualised displacement activity. Again, it appears difficult to propose ecological reasons for the fact that chimpanzee communities use leaf-clipping in different contexts and employ different techniques. The arbitrariness in the contexts observed suggests that leaf-clipping is a cultural behaviour whose context of use is locally determined by a social norm reinforced by group members (Boesch, 1996a).

Personal hygiene

Other examples of cultural behaviours concern personal hygiene. At both Gombe and Mahale, body cleaning by chimpanzees is commonly observed. For example, males at both those sites regularly wipe semen from their penis after copulation (Goodall, 1986), a behaviour never observed at Taï (Boesch and Boesch, 1990) or Bossou (Sugiyama, per. comm.; Humle, pers. obs.).

Subsistence activities

Ecological differences underlie some differences in subsistence-related behaviours between chimpanzee communities (c.f. Whiten *et al.*, 1999). However, several studies aimed at carefully investigating possible environmental influences on subsistence activities between chimpanzee populations have often concluded that variations are cultural or not necessarily environmentally dictated (e.g. McGrew and Tutin, 1978; McGrew *et al.*, 1979; McGrew *et al.*, 1997; Boesch *et al.*, 1994).

Diet and food processing

The plant-feeding habits of chimpanzee populations (*Pan troglodytes schweinfurthii*) were compared between the Gombe National Park and the Mahale Mountains, Tanzania (Nishida *et al.*, 1983). Comparison of food lists revealed fifteen clear differences in the frequency of species consumed that occur commonly at both sites, and four differences in the processing of similar food species. This study was based on major dietary differences, thus excluding any local differences in species that are rare or eaten only occasionally. However, the relative and absolute availability and quality of these plant species and inter-specific competition for them may differ between Gombe and Mahale, and these could provide alternative hypotheses to local differences in feeding behaviour. These variables were unfortunately not investigated.

An example of a traditional difference in food processing in chimpanzees concerns leaf eating. Leaf-stripping involves encircling the stem generally with thumb and fingers, and then swiftly sweeping it length-wise, thus tearing away several leaves all at once and then ingesting the gathered bunch. This behaviour which has been observed at Mahale (group-M), Gombe, Bossou and Kibale, has never been observed at Taï or Budongo (Whiten *et al.*, 1999). It has, therefore, been described as cultural.

Tool-use

Cultural differences in tool-use behaviour in chimpanzees can be viewed at three different levels. Firstly, differences in the target item are apparent across some sites and some of these do not seem to be explained by environmental differences. Secondly, variations in tool-choice and tool-making have been described. Thirdly, divergences in technique employed have also been reported.

Target item

At least thirteen populations of the west African subspecies of chimpanzee (*P. t. verus*) use a "hammer", defined as an object that can be manipulated and is hard enough to cause a nut to crack open as a result of pounding, and an "anvil", defined as a fixed object, usually in the substrate, that is hard enough to resist the impact of a target object smashed against it (McGrew *et al.*, 1999), to crack open nuts to consume the kernel within. Nut-cracking has never been reported in the central, east African or Nigerian subspecies.

Boesch *et al.* (1994) examined the distribution of nut-cracking in Côte d'Ivoire. They showed that the eastern boundary of the behaviour is the N'Zo-Sassandra River. Their detailed and extensive study revealed no obvious environmental differences between one side of the river and the other. They therefore concluded that the environment could not explain the presence or absence of nut-cracking at the local level. By exclusion, they hypothesised that the best explanation was cultural, with the river acting as a zoogeographical barrier to diffusion of this tool-use pattern from west to east. Similarly, in their study at Lopé, Gabon, McGrew *et al.* (1997) examined several hypotheses (mainly exploring environmental parameters) as to why chimpanzees at Lopé do not crack nuts. They concluded that the best current explanation for the absence of this tool-use behaviour at this site is not environmental but cultural, and that chimpanzees in the Lopé Reserve never learned to utilise hammer and anvil tools to crack open nuts, although nuts are a potentially valuable and plentiful resource in their habitat.

Seven species of nut-bearing trees have been identified as targets of nut-cracking by chimpanzees, but not all these species are cracked at sites where nut-cracking is present and these species available (see Table 1.1). In addition, within most of these habitats, there exist other species of nut-bearing trees, such as *Klainedoxa gabonensis* or *Ongokea gore,* whose edible nuts have never been reported to be cracked by chimpanzees or consumed by chimpanzees.

Differences in target item selection have also commonly been described for ant-dipping and termite-fishing by chimpanzees. For example, Mahale chimpanzees have never been observed to dip for commonly found driver ants (*Dorylus* spp.), although chimpanzees at Gombe, 170 km to the north, regularly do so (McGrew, 1974; Nishida, 1987). Moreover, at Bossou, where termite mounds of the species *Macrotermes bellicosus* are very common, only one single case of termite-fishing has been recorded (Humle, 1999), while at Gombe this species is frequently fished and consumed (Goodall, 1986).

In addition, algae-scooping for *Spirogyra* sp. using a wand has only so far been reported for Bossou although this species of algae also occurs elsewhere, for example, at Mahale (Nishida, pers. comm.).

Tool-choice and tool-making

Differences in tool-choice are most notable in the nut-cracking behaviour of chimpanzees. In Guinea, Bossou chimpanzees have only been observed using stone tools to crack oil-palm nuts, although potential anvil roots and wooden clubs are also available in the habitat. However, in an outdoor laboratory experiment, Sakura and Matsuzawa (1991) demonstrated that when the experimenter limited the availability of stone tools, Bossou chimpanzees could use a tree trunk as an anvil. Nut-cracking stone tools from Bossou are significantly smaller than the stone tools employed by Taï chimpanzees (c.f. Sakura and Matsuzawa, 1991; Boesch and Boesch, 1983). As well as using stone hammers and anvils, Taï chimpanzee most often use anvil roots or hammer clubs (Boesch and Boesch, 1983).

However, Boesch and Boesch (1983) showed that Taï chimpanzees select their nut-cracking tools according to the hardness of the nut species being cracked. Thus, since chimpanzees at Taï do not crack oil-palm nuts, the difference in tool-choice between Bossou and Taï chimpanzees could conceivably be explained by differences in optimal tool selectivity, since oil-palm nuts differ in shape and hardness to those species of nuts cracked at Taï. A comparison of tools used between sites where the same species of nuts is being cracked would be more useful for exploring potential traditional differences in tool-choice for nut-cracking.

Differences in tool-choice and tool-making have also been extensively analysed in studies of termite-fishing. McGrew *et al.* (1979) reported population differences that could not solely be explained by ecological differences among the

Table 1.1 Nut species selected by chimpanzees at study sites where chimpanzees have been confirmed nut-cracking.

Country	SITE	*Panda oleosa*	*Coula edulis*	*Parinari excelsa*	*Saccoglottis gabonensis*	*Detarium senegalensis*	*Elaeis guineensis*
Guinea	Diécké	✓	✓	?	?	?	⊙
	Bossou	✖	✖	⊙	✖	✖	✓
	Seringbara	✖	✖	⊙	✖	⊙	⊙
Côte d'Ivoire	Taï	✓	✓	✓	✓	✓	⊙
	Mt Betro	✓	?	⊙	?	⊙	⊙
	Scio (Mt Zoa)	✓	?	⊙	?	?	?
	Monogaga	✓	?	⊙	?	?	?
	Banco	?	✓	?	?	?	?
	Yealé	⊙	✓	⊙	✖	⊙	✓
Liberia	Cape Palmas	?	✓	⊙	?	?	⊙
	Sapo	✓	✓	?	✓	?	⊙
	Mt Kanton	?	✓	?	?	?	?
Sierra Leone	Tiwai	✖	⊙	⊙	?	✓	✖
Senegal	Mt Assirik	✖	✖	⊙	✖	✖	✖

References: *Diécké*: Matsuzawa *et al.*, 1999; Humle and Matsuzawa, 2001; *Bossou*: Sugiyama and Koman, 1979b, 1987, 1992; Sugiyama, 1981, 1994b; Sakura and Matsuzawa, 1991; Fushimi *et al.*, 1991; *Yealé*: Boesch *et al.*, 1994; Joulian, 1994; Matsuzawa and Yamakoshi, 1996; Humle and Matsuzawa, 2001; *Taï*: Boesch and Boesch, 1981, 1983, 1984, 1990; Boesch, 1978; *Côte d'Ivoire sites*: Boesch *et al.*, 1994; Joulian, 1994; *Cape Palmas*: Savage and Wyman, 1843/44; *Sapo*: Anderson *et al.*, 1983; *Mt Kanton*: Kortlandt and Holzhaus, 1987; *Tiwai*: Whitesides, 1985; *Mt Assirik*: McGrew, pers. comm.

Legend: ✓: Species cracked; ✖: Species not cracked since unavailable; ⊙: Species not cracked, although available; ?: Availability not reported.

groups studied. They compared termite-fishing techniques in three populations – Gombe (Tanzania), Mt Assirik (Senegal) and Okorobiko (Rio Muni) – and concluded that the fishing technique of the Gombe and Mt Assirik groups, and the perforating technique (refer to *p.18* for more details) of the Okorobiko group, could be seen as local adaptations to the differing demands of the three environments (see Section on *technique employed*). However, they could find no ecological reasons for differences between Gombe and Mt Assirik in the choice of tool materials, for the way the tools were fashioned with respect to bark-peeling, or for whether the group used one or both ends of the probe. At Gombe more than half of the tools were made of grass blades or stems, while at Mt Assirik almost half of the tools were woody twigs, with leaf-stalks or petioles accounting for nearly another third (McGrew *et al.*, 1979; McGrew, 1992). Gombe chimpanzees never used leaves as tools, nor did Assirik's ever use bark or palm fronds, which were used at Gombe (McGrew, 1992). However, McBeath and McGrew (1982) demonstrated that tool selection for fishing probes at Mt Assirik mirrored the availability of the best raw materials within a 5-metre radius of the termite mounds. Such a study was unfortunately not done at the Gombe site.

Aspects of tool modification and use were, nevertheless, proposed to represent potential cultural variants. For example, vines or twig tools were never stripped of their bark at Gombe, but a significant majority of such tools were stripped of bark, either entirely or partially, at both Mt Assirik and Okorobiko. In addition, the use of one or both ends of the tool varied across the three sites. At Mt Assirik, most tools were used only at one end, while at Gombe and Okorobiko, no significant difference in the use of both ends or a single end was detected, regardless of the class of raw material used. It should be noted that the data from the latter two sites is rather incomplete and that the sample sizes for all three groups are relatively small for this particular analysis. Tomasello (1990) suggested that some subtle difference in the behaviour of the particular termites (*Macrotermes* spp.) between the sites might explain these variations in tool-choice and -manufacture. This possibility has not yet been fully investigated. Certainly, more data on termite-fishing tools and their respective availability across those sites and others are required to clarify possible cultural differences in tool-choice and -manufacturing in chimpanzees in relation to termite-fishing.

With regards to tool-choice, Bossou chimpanzees have been found to show a high degree of selectivity for the leaves they use for water-drinking. The social interactions leading to convergence in selectivity for *Hypselodelphis pogeana* leaves were analysed by Tonooka *et al.* (1994). Unfortunately, no comparable data are available from other sites where water-drinking behaviour using tools occurs. However, anecdotal reports suggest that water-drinking may be more variable than originally reported and variations in tool-choice may be prevalent. Thus, chimpanzees in Tongo, Democratic Republic of Congo, apparently sponge water using moss (Lanjouw pers. comm. cited in Wrangham *et al.*, 1994) and chimpanzees in the Kibale forest, Uganda, employ stem sponges (Wrangham pers. obs. cited in Wrangham *et al.*, 1994).

Technique employed

Two different techniques for ant-dipping have been reported at sites where this tool-use behaviour has been observed (e.g. Boesch and Boesch, 1990; Goodall, 1986) (see *Chapter 6* for more details). Both Gombe and Taï chimpanzees use sticks or wands that they dip into the nest entrance or migrating columns of driver ants (*Dorylus* spp.) in order to gather the ants before ingesting them. At Gombe, the chimpanzee uses one hand to hold the stick among the attacking ants and, once they have swarmed about half way up the tool, it usually withdraws the stick and sweeps it through the closed fingers of the free hand, a technique known as "pull-through". The mass of ants is then rapidly transferred to the mouth and chewed (McGrew, 1974). At Taï, on the other hand, the chimpanzee holds the stick among the soldier ants with one hand until they have swarmed about 10 cm up the tool (Boesch, 1996a). On withdrawal of the tool, the chimpanzee then twists the hand holding the wand and always directly picks off the ants with the lips, a technique referred to as "direct mouthing".

Boesch (1996a) explored ecological factors at both sites that might favour the use of either technique, but could not find any. This difference in ant-dipping technique between Gombe and Taï probably originates through social learning, which limits variation in its performance within each one of these communities.

Of the many kinds of tool-making and tool-using behaviours performed by chimpanzees, termite-fishing is one of the most widely distributed, and it involves in most cases *Macrotermes* spp. as the target prey. At Gombe, Mahale (B-group) and Mt Assirik, chimpanzees open a hole on the bare surface of the termites' earthen mound by gouging, or they use tunnels formed by the swarming termites during the early or mid-rainy season, and then proceed to extract the termites using a long flexible, slender probe, which is inserted into the mound and attacked by the termites within. The chimpanzees gently withdraw the tool and nibble the termites from the probe using their lips (Goodall, 1964, 1968; Uehara, 1982, McGrew, 1992). Chimpanzees at those sites display a seasonal pattern of termite-fishing which coincides with the swarming period of the termites.

However, a very different picture has emerged for the central African subspecies of chimpanzees (*P. t. troglodytes*). Most observations of termite-fishing in central Africa involve the use of a tool-set, i.e. a perforating stick (whose function is not always clear and which has been suggested to act either 1) as a stopper for reuse of hole later, 2) a tool to dig a hole to facilitate the insertion of a slender probe or 3) a brush-stick to actually fish for termites (Suzuki *et al.*, 1995; Bermejo and Illera, 1999)) and a fishing probe, similar to that found at Gombe, Mahale or Mt Assirik. Chimpanzees at Campo, Cameroon (Sugiyama, 1985), at Belinga, Gabon (McGrew and Rogers, 1983), at Ndoki (Suzuki *et al.*, 1995) and in the Lossi forest, Congo (Bermejo and Illera, 1999), at Ndakan and at Bai Hokou, Central African Republic (Fay and Carroll, 1994) all appear to use sticks and probes to obtain termites. Finally, no apparent ecological difference in mound formation or structure, or in prey behaviour, can explain this difference in termite-fishing technique between the central African subspecies of chimpanzee and its two neighbours, the eastern and the western subspecies. No information is as yet available on the Nigerian subspecies. However, unlike the eastern and western subspecies, the central subspecies appears to fish for termites all year round, and the perforating stick may then be helpful for gaining access to the termites deep inside the mound outside the termite swarming season when natural tunnels are unavailable (Suzuki *et al.*, 1995). More data on termite-fishing at those sites are required to clarify the importance of seasonality or non-seasonality in this behaviour across these different sites. Regardless, these differences in termite-fishing techniques remain often cited examples of cultural variation in chimpanzees.

Two water-drinking techniques employed by chimpanzees have now been identified. The most widespread technique is leaf-sponging which involves the use of a chewed-up wad of leaves or vegetation to soak up water, usually from a tree hole. However, another technique, thus far only observed at Bossou, has now been recognised. Instead of leaf-sponging, Bossou chimpanzees usually fold a leaf in their mouth and place it by hand into the water hole using it as a receptacle from which they then drink or lick off the drops (Matsuzawa, 1999b; Tonooka, 2001). The leaf-folding and leaf-sponge techniques employed by chimpanzees for water-drinking also appear to be cultural behaviours that are socially transmitted across members of the same community. Nevertheless, this difference could also be attributed to the type of leaves used, a hypothesis which remains unexplored.

Finally, differences in behavioural repertoire in chimpanzees have so far been reported between subspecies, within subspecies, and even between neighbouring communities. Although some of this variation can be explained ecologically, much convincingly points towards culture in chimpanzees. The marked differences between communities, along with the apparent low within-community variance in tool-choice, tool-manufacture and technique employed clearly suggest that some social learning process is at work.

1.5 Social and cultural transmission of behaviour in chimpanzees

Lefebvre and Palameta (1988) reviewed one hundred studies on socially transmitted patterns of foraging behaviour amongst natural populations of animals. These include the spread of novel food-related behaviours among Japanese macaques (Kawai, 1965; Tsumori, 1967), termite-fishing (Goodall, 1964, 1968) and nut-cracking in chimpanzees (Boesch, 1991; Matsuzawa, 1994, 1999; Inoue-Nakamura and Matsuzawa, 1997) the opening of milk bottles by British tits (Fisher and Hinde, 1949; Sherry and Galef, 1984, 1990), and the opening of mussels by oystercatchers (Norton-Griffiths, 1967, 1969). Other examples of cited animal traditions include the use of migratory routes and the return to specific breeding grounds (Bonner, 1980); the transmission of territories (Galef, 1976) and of bird song (Marler and Tamura, 1964; Nottebohm, 1972; Lynch *et al.*, 1989). These studies suggest that many animal populations may possess socially transmitted patterns of behaviour that are relatively stable over many generations. However, since often these examples cannot exclude the involvement of individual learning and/or genetic transmission in the establishment of these traits, these cannot confidently be termed cultural. Unfortunately, systematic examination of the mechanisms of behavioural transmission is difficult in the field (McGrew and Tutin, 1978) and unless social learning can be established, sceptics of culture in non-human animals will remain critical and unconvinced.

Finally, despite the multitude of studies of social transmission of behaviour in wild and captive animal populations, very few have convincingly demonstrated social learning or elucidated the transmission mechanisms taking place. If based on hard experimental evidence, some of the most convincing examples of culture and studies of social transmission of behaviour in non-human animals are, according to Laland and Hoppitt (2003, in press), in some species of birds, whales and two species of fish. So what about chimpanzees? Have studies both in the field and in captivity really failed to demonstrate ability for social transmission of behaviour and to clarify the mechanisms at work in chimpanzees?

In captivity

Attempted simulations of social transmission of tool-use behaviours in captive subjects have often failed to yield conclusive results and, if successful, have ever partially elucidated the mechanisms of propagation at work. Nevertheless, diffusion studies of complex tasks in chimpanzees have provided useful insights into the apes' social learning abilities. Tonooka *et al.* (1997) studied the emergence and the propagation of the use of a drinking tool in a group of nine captive chimpanzees based at the Kyoto University Primate Research Institute, Inuyama, Japan. The experimental apparatus, placed in the chimpanzees' outdoor enclosure, consisted of an acrylic cylinder filled with orange juice and with an oval opening at the side, just large enough for a chimpanzee to insert its hand and reach the liquid using its fingers. The chimpanzees had free access to leaves, twigs, branches, straw and other materials available in their compound. Although the chimpanzees could use their hand to reach the juice, eight of the nine subjects used tools. Two chimpanzees began using twigs of a shrub, *Thuja occidentalis*, which they successfully inserted, to obtain some of the juice. Although 28 different species of trees and several kinds of grasses were available in the compound and 15 kinds of materials were reported to be used overall, this species clearly became the favoured tool for this task among four of the eight individuals observed performing the task. Indeed, as the experimental sessions went on, the variety of tools used by these chimpanzees decreased and convergence in the use of *Thuja occidentalis* leaves increased.

This study of juice drinking behaviour in a group of captive chimpanzees showed that convergence in tool-choice by members of the group could have potentially been socially transmitted. Indeed, convergence in the use of *Thuja occidentalis* leaves reflected the pattern of social interactions taking place at the vicinity of the apparatus. .As described above, studies in the wild have revealed that tool materials, tool-manufacture and tool-using techniques may differ greatly between communities. Tonooka *et al.* (1997)'s experiment suggests that such differences are likely to be passed on socially, so that a standardisation of behaviour emerges across most members of a social group. However, the authors also raise the possibility that convergence may have also been influenced by some individual optimisation in behavioural efficiency and by the close proximity of *Thuja occidentalis* leaves from the apparatus, when compared to available species similar in shape and structure.

Hirata and Morimura (2000) tested the influence of observation of experienced conspecifics on naïve chimpanzees' performance in a simulated honey feeding task in the same captive group of chimpanzees used in Tonooka's experiment. Inside an experimental room, two sets of panels providing honey in a small polythene bottle with a small hole on one side and artificial materials, not all appropriate to the task, were available to the chimpanzees. Six pairs of naïve and experienced chimpanzees were tested. Naive chimpanzees never observed their experienced partners after their own success but did so after their own failure or before their first attempts. Hirata and Morimura (2000) proposed that spontaneous observation of an appropriate behavioural sequence, enhanced by environmental cues provided by skilled individuals, plays an important role in the transmission of tool-use in chimpanzees.

Sumita *et al.* (1985) trained three chimpanzees to use stone tools to crack walnuts (*Juglans ailanthifolia*) at the Tama Zoological Park, Tokyo, Japan. They then proceeded to place these three individuals together with 11 others, in a setting with one single embedded anvil stone and an attached hammer stone and walnuts, to see if the technique would spread. Of these naive individuals, only one subject (a 3-year old female) subsequently acquired the new behaviour. Moreover, only the infants of the group showed interest in the behaviour. Therefore, this experiment failed to demonstrate social transmission of nut-cracking behaviour within a group of chimpanzees. However, the fact that during the group experiment tool availability was limited to a single nut-cracking "atelier" could have limited the transmission of this new behaviour. Thus, the experimental design was not entirely appropriate for the purpose of the study.

Hannah and McGrew (1987) found more substantial evidence for social transmission of behaviour and observational learning in chimpanzees in relation to nut-cracking. This study was not a controlled laboratory study, but it will be discussed here since it involved captive chimpanzees rather than wild subjects. Sixteen chimpanzees, between 5-20 years of age, were released from captivity to a natural island setting on Bassa Island, Liberia, where oil-palm nuts (*Elaeis guineensis*) are naturally available. On the day of her release, one 9 year-old individual, who had been in captivity since she was 1 year old, began cracking oil-palm nuts with a concrete block on a concrete slab. On that same day, two other chimpanzees attempted to crack nuts in a similar manner, but not as successfully or skilfully as the "inventor". Within two months though, 13 of the 16 chimpanzees were cracking nuts. None had been observed performing this behaviour while in captivity, and none of the ten chimpanzees, released onto the island prior to the "inventor", had been observed cracking nuts before. Moreover, styles of nut-cracking varied little within the group, except for slight idiosyncratic differences in, for example, preference for root anvils.

In summary, these captive studies point to the existence of some form of social transmission of behaviour in the chimpanzee. These diffusion studies may help to integrate and interpret the findings of other laboratory and field research, as well as providing novel insights into the dynamics of social transmission. However, there are problems with studies using captive chimpanzees, such as the differential level of enculturation of individual chimpanzees and the frequent lack of knowledge of the subjects' experiential and developmental history. These can seriously affect the outcome of diffusion studies and compromise the interpretation of results. As proposed by Laland *et al.* (1993, p.255), many questions remain to be answered, and diffusion studies and field work will both help elucidate some of these, such as for example: "Will cultural information be lost in transmission? [...]What is the relationship between the social learning mechanism and the rate and pattern of diffusion of the behaviour through a population? How do patterns of social interaction affect the dynamics of transmission?" And how are cultural differences among groups maintained? Studies of chimpanzees in their natural habitat will continue to help us explore the dynamics of transmission within and between chimpanzee communities and contribute hypotheses, testable in controlled captive conditions or even potentially back in the wild.

In the field

Few studies have been carried out in the field to investigate in any detail social transmission of behaviour in chimpanzees. However, in recent years, Matsuzawa and colleagues have undertaken field experiments on cultural transmission, to indirectly address differences in traditions between neighbouring communities of chimpanzees (*P. t. verus*), and to elucidate the possible dynamics of this process (Matsuzawa, 1994; 1999). In an outdoor laboratory, situated within the core area of the Bossou chimpanzees, in Guinea, nuts of *Coula edulis*, normally unavailable in the Bossou range, were provided to observe the reaction of the chimpanzees. Bossou chimpanzees are known to crack oil-palm nuts and are, therefore, highly familiar with nut-cracking, but only one adult female, Yo, spontaneously cracked the new nuts using stones; most of the other chimpanzees only examined the fruits and tried to bite them. During the next two days, only two juveniles, Vui, aged 6, and Pili, aged 5, cracked nuts, even though they seemed averse to the taste. Although *Coula* nuts were made available for another two weeks, no other member of the community attempted to crack them, although Yo continued to crack and eat them.

A year later, another experiment was conducted in which the chimpanzees were given wooden balls similar in size and shape to the *Coula* nuts. Yo ignored these fake nuts, while the two juveniles - Vui, Pili - and an adolescent male - Na, 8 years old - tried to crack them immediately. This supplementary experiment indicated that Yo recognised the *Coula* nut as a source of food, whereas the juvenile chimpanzees were prepared to crack a nut-like object without having prior knowledge as to whether it was edible or not. Their behaviour could have been prompted by Yo's cracking of *Coula* nuts the year before. Subsequent experiments with *Coula* nuts revealed that the behaviour has spread to six other chimpanzees, who now readily crack and eat *Coula* nuts when given the opportunity (Matsuzawa *et al.*, 2001).

Similarly to the *Coula* experiment in the outdoor laboratory, nuts of *Panda oleosa*, which are also not available in the home range of the Bossou chimpanzees, were introduced to the chimpanzees alongside oil-palm nuts and later also alongside *Coula* fruits and nuts (January, 2000, unpub. data). However, this time, not a single member of the community responded in a fashion that suggested familiarity with *Panda* nuts and no spontaneous attempt was made to crack open the fruit to gain access to the fatty seeds within (Matsuzawa *et al.*, 2001). Of the 13 nut-cracking individuals, only four eventually attempted to crack the unfamiliar *Panda* nut. Two were adult females (Yo, Jiré) and two were adolescents (Yolo, Vuavua), but none actually ingested the cracked nuts, which were instantly spat out once tasted. The video analysis of the *Coula* and *Panda* experiments is still in progress and will reveal more about observational learning within this community, the social context of transmission and finer details of the adoption of a new behaviour by members of the community. These experiments have allowed field researchers to tap indirectly into the dynamics of social transmission between groups of chimpanzees, as well as into the knowledge of the chimpanzees present within the community, where the migratory history of most individuals is unknown and could only possibly be revealed with difficulty, employing genetic techniques.

Finally, the combination of field and captive research seems be a successful new, complementary approach to elucidating the dynamics of social transmission in animals, and particularly the concept of cultural transmission in the chimpanzee.

1.6 Adaptive value of cultural traits

Lefebvre and Palameta (1988, p.147) pointed out that "in the field, an innovation will only spread if it provides some advantage with respect to behavioural alternatives already present in the population".

However, it has been suggested that some sets of behaviours defined as cultural in chimpanzees are not necessarily the best solution to a given task within a particular environment (e.g. Boesch *et al.*, 1994). For example, the mean tool length used in ant-dipping at Taï is significantly shorter than that found at Gombe (Boesch and Boesch, 1990). Moreover, the ant-dipping techniques of chimpanzees at these sites differ significantly with Gombe chimpanzees exhibiting predominantly the "pull-through" technique and Taï chimpanzees only displaying the "direct mouthing" technique (see Section on *Culture in Chimpanzees*, p.16-17 for more details). It has been estimated that the length of the sticks used by Taï chimpanzees to dip for ants and their different feeding technique makes them four times less efficient at capturing ants than Gombe chimpanzees (Boesch and Boesch, 1990; Boesch, 1996a).

However, so far there has not been any other reported evidence for poorly adaptive behavioural cultural variants in chimpanzees. In addition, it is unclear whether ant-dipping as performed by Taï chimpanzees is truly not the most effective technique to gather driver ants at this site since environmental variables, such as the behaviour of the ants, may differ significantly between Taï and Gombe (see *Chapter* 6). Nevertheless, evidence of the existence of poorly adaptive cultural behavioural variants in chimpanzees would help establish their relative independence from environmental factors and the predominance of social influences (Boesch and Boesch, 1990; Boesch *et al.*, 1994).

1.7 Hypotheses of cultural transmission in chimpanzees

McGrew (1992) hypothesised that some behaviours 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 four subspecies of chimpanzees, have been proposed in the past by several authors, i.e. the nut-crackers of west Africa versus the termite-fishers of central and east Africa (Nishida, 1987; Struhsaker and Hunkeller, 1971, Sugiyama, 1985), and the termite-fishers of east Africa versus the termite-diggers or termite-probers of Central Africa (Teleki, 1974; McGrew *et al.*, 1979). However, according to distribution maps of behaviours proposed to be cultural, such cultural regions are mostly not clearly identifiable (Whiten *et al.*, 2001). Nevertheless, there is still some supportive evidence for diffusion of behaviour within regional populations of chimpanzees. For example, nut-cracking behaviour has still only ever been observed in communities of the west African subspecies of chimpanzee situated west of the N'zo-Sassandra River in Côte d'Ivoire (Boesch *et al.*, 1994). Whiten *et al.* (2001) consequently concluded that much of the variation observed between chimpanzee communities is most consistent with a model of diffusion that incorporates differentiation in concert with diffusion. Matsuzawa and Yamakoshi (1996) had previously suggested that behavioural differences between communities are formed and maintained by balancing adjustments to local environments with dynamic cultural interchange, and that these traditional behaviours must be maintained or modified across generations through social transmission.

The diffusion of information between groups implies dispersal of adults or sub-adult members of at least one sex (Kummer, 1971). It also entails that the local traditions have arisen through social transmission of novel behaviours invented by members of the group or through importation of novel behaviours into a group by immigrants from other groups. To the extent that female primates play a privileged role in the transfer of information to their offspring, their dispersal out of one group has greater potential for disseminating new behaviours to other groups through their progeny. So where there is directed social learning, if one sex is more effective at transmitting or receiving information than the other, it may make a big difference to the diffusion process if the species concerned is patrilocal or matrilocal (Laland and Kendal, in press). This process may also, however, be affected by the social structure and organisation of the community, population or species studied.

1.8 Aims

The following chapters focus on one habituated community of wild chimpanzees (*P. t. verus*) at Bossou in Guinea and two neighbouring non-habituated communities in the Nimba Mountains region in Guinea and Côte d'Ivoire and aim to address behavioural variation at the intra- and inter-community level.

The first two chapters adopt an ecologically based approach to looking at inter-community variation in behaviour. Bed or nest-building in chimpanzees, which has recently been acknowledged as not having received enough attention (Whiten *et al.*, 2001), is addressed in *Chapter 4*. Indeed, there exist few examples of detailed published studies of nesting in chimpanzees, particularly in the West African subspecies (*P. t. verus*). Nesting behaviour is a material skill pervasive across all chimpanzee communities and the other species of great apes. This chapter is mainly concerned with assessing the impact of habitat variables on nesting parameters in order to gain some measure of flexibility and selectivity in nesting behaviour, with the aim to discern differences and similarities across the three sites and speculate on the cultural dimension of this behaviour.

Chapter 5 deals with intra- and inter-community variation in oil-palm (*Elaeis guineensis*) use at Bossou and the two Nimba sites. The uses of the oil-palm tree by chimpanzees across Africa and at Bossou in particular, are remarkably diverse, encompassing nesting and feeding activities, and requiring varying level of processing; some involving simple reaching, while others the use of a tool. Such a comparative study of the utilisation of the oil-palm across neighbouring chimpanzee communities is conducive to investigating underlying environmental factors that might explain variations in use and to test predictions about diffusion of socially learnt behavioural patterns.

Chapter 6 focuses on ant-dipping behaviour at Bossou. Dipping for driver ants, *Dorylus* spp., is often cited as one of the best examples of culture in chimpanzees with reported inter-community variations in tool length and technique employed (Boesch and Boesch, 1990, McGrew, 1992). This tool-use behaviour is explored at a micro-ecological level and from an ontogenetic perspective.

Chapter 7 presents an analysis of tool-choice and tool-manufacturing within and between three stick- or stalk-use behaviours observed at Bossou, relating emerging features and characteristics to tool function. Furthermore, a comparison of ant-dipping tools between Bossou, Seringbara and Yealé is provided, with an examination of possible cultural variations in aspects of tool-choice and -manufacturing.

Lastly, in *Chapter 8*, efficiency in behaviour across three tool-use behaviours at Bossou is explored focusing chiefly on age-class differences. An analysis of individual and community-level patterns of laterality in hand-use between these three tool-use behaviours is also provided, leading finally to an attempt to address the selective advantages of lateralisation in hand-use with respect to behavioural efficiency.

Chapter 2

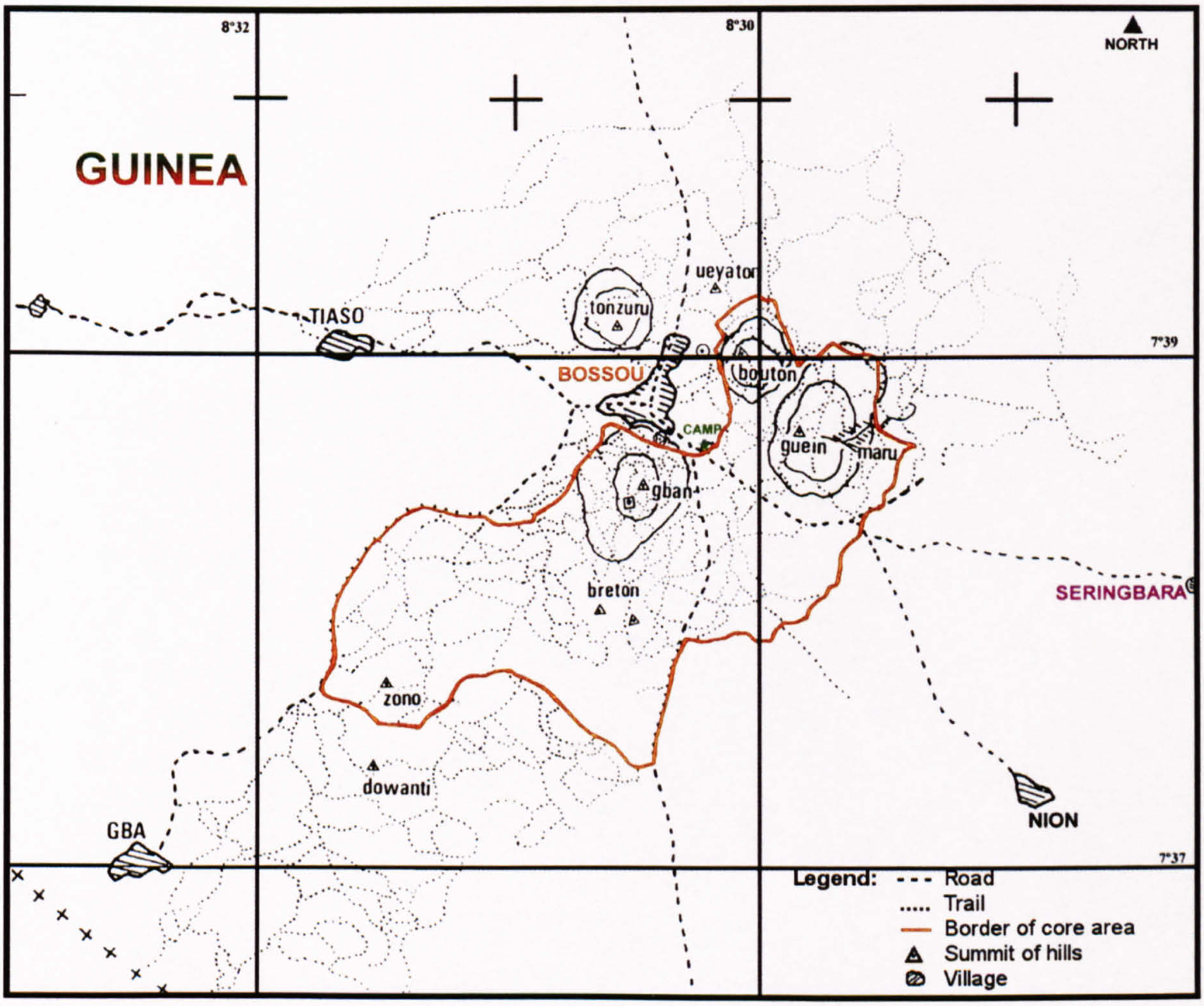
Study sites and the Bossou chimpanzee community

2.1 Locations

Bossou, Republic of Guinea

A community comprised of 19 habituated chimpanzees lives in the forest surrounding the village of Bossou (latitude 7° 38’71.7’’ N and longitude 8° 29’38.9’’ W) in the south-eastern part of Guinea, located about 6 km from the foothills of the Nimba Mountains, which span the border with Côte d’Ivoire and Liberia (see Fig 2.1).

Fig 2.1 Map of Bossou and surrounding hills indicating the core area utilized by the chimpanzees.



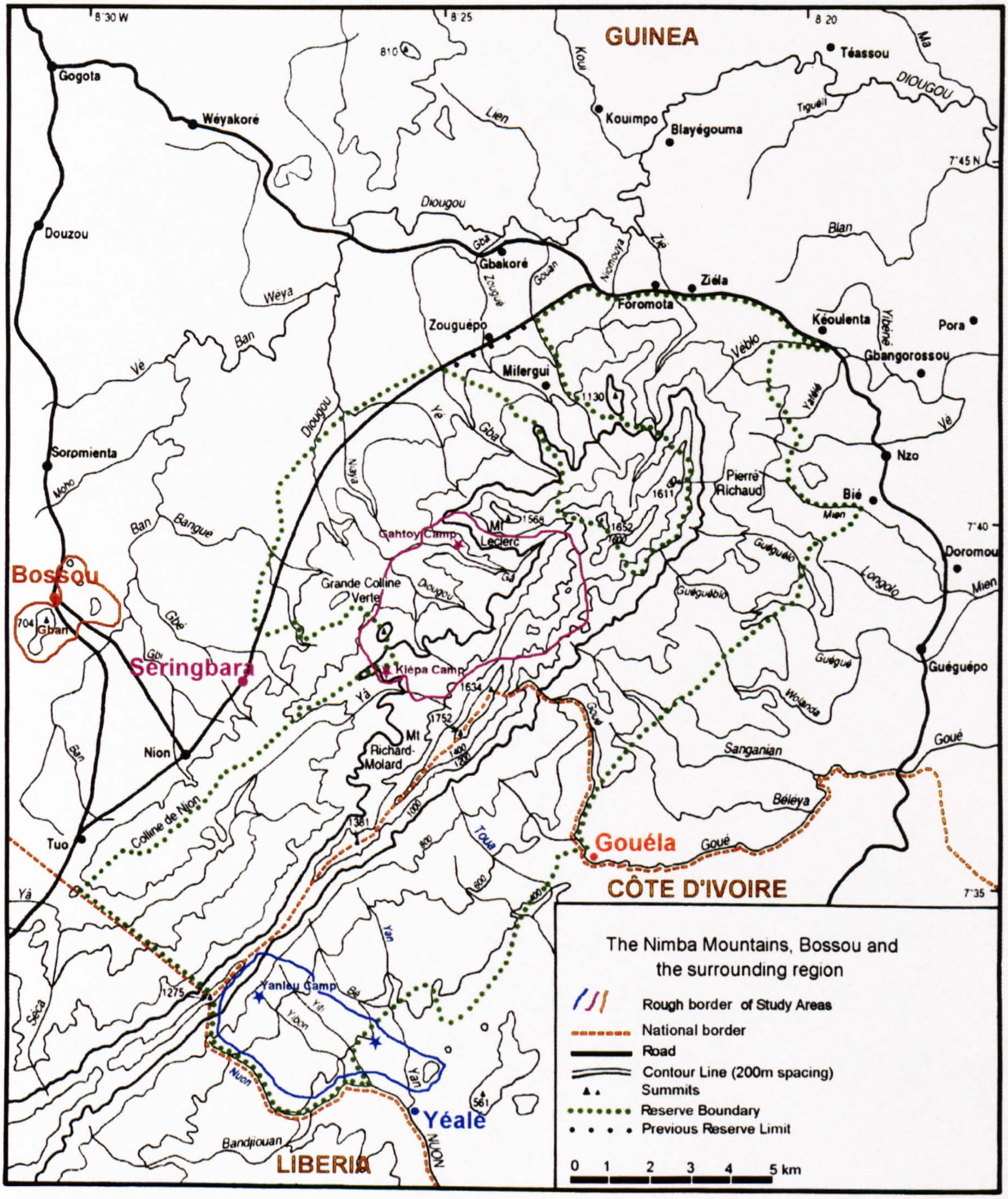
The village of Bossou is 550 m above sea level. It is surrounded by small hills 70-150 m high that are covered in primary and secondary forest (Sugiyama and Koman, 1979a, Yamakoshi, 1998). At the foot of those hills, cultivated or abandoned fields and secondary, riverine and scrub forests form a patchy mosaic for about 6 km in all directions. This habitat constitutes the core area of the Bossou community (see Fig. 2.1). The Bossou chimpanzees mostly confine their daily activity within a core area of about 6 km², though they sometimes travel to adjacent forests using the few remaining gallery forest corridors that extend their home range to around 15 km². The nearest currently known chimpanzee populations have their ranges in the Nimba Mountains, about 6 km to the southeast of Bossou.

The Nimba Mountains

The Nimba Mountains are located directly to the southeast of Bossou (see Fig. 2.2). The massif of Nimba is situated on the border between Guinea, Côte d'Ivoire, and Liberia and forms a natural boundary between the three countries. Nimba is situated 230 km northwest of the Taï Forest, where a community of chimpanzees has been intensively studied since 1976 (Boesch, 1978). The Nimba Mountains were established as a nature reserve - the Réserve Naturelle Intégrale du Mont Nimba - in 1943 in Côte d'Ivoire and in 1944 in Guinea. The Guinea portion of the massif was classed as a Biosphere Reserve in 1980, consisting of 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 have also been recognised as a World Heritage Site, gazetted in 1981 for Guinea and in 1982 for Côte d'Ivoire. However, the Liberian portion still lacks any formal legal status as a protected area.

The World Heritage Site extends over 220 km² and its highest peak - le Mont Richard Molard - is at 1752 m (see Fig 2.2.). The reserve on the Guinean side extends over 13,000 ha and 5,000 ha on the Côte d'Ivoire side. The Nimba Mountains are cut up by deep, richly forested valleys and are endowed with great topographical diversity, with valleys, plateaux, rounded hilltops, rocky peaks, abrupt cliffs and bare granite blocks, and the whole area constitutes a vast water catchment (WCMC, 1982).

Fig 2.2 Location of Bossou and the Nimba sites, including Seringbara, Guinea and Yealé, Côte d'Ivoire.



Seringbara, Republic of Guinea

The village of Seringbara (latitude 7° 37'50.0"N and longitude 8° 27'44.7"W) is located at the foot of the Nimba Mountains on the Guinean side, only 6 km to the southeast of Bossou (see Fig 2.2). For research purposes, two basic camp sites (the Gahtoy camp (latitude 7° 39'43.8"N and longitude 8° 25'10.3" W) and the Kiépa camp (latitude 7° 37'78.8"N and longitude 8° 26'08.0" W)) were established within the reserve in 2000 (see Fig 2.2). Both consist of two huts built from *Raphia* palm fronds and an outdoor cooking area.

Yealé, Côte d'Ivoire

The village of Yealé (latitude 7° 31'21.8"N and longitude 8° 25'29.1"W) is located 12 km southeast of Bossou, on the Côte d'Ivoire side of the Nimba Mountains (see Fig. 2.2). One camp site (the Yanleu camp: latitude 7° 32'50.09"N and longitude 8° 28'03.01"W), similar to those built at Seringbara, was established approximately 5.18 km from the village of Yealé within the reserve towards the upper slopes of the mountain in 2000 (see Fig. 2.2). A second camp was established beside the village (the Danton camp) at the foothills of the mountains and at the border of the reserve (see Fig 2.2).

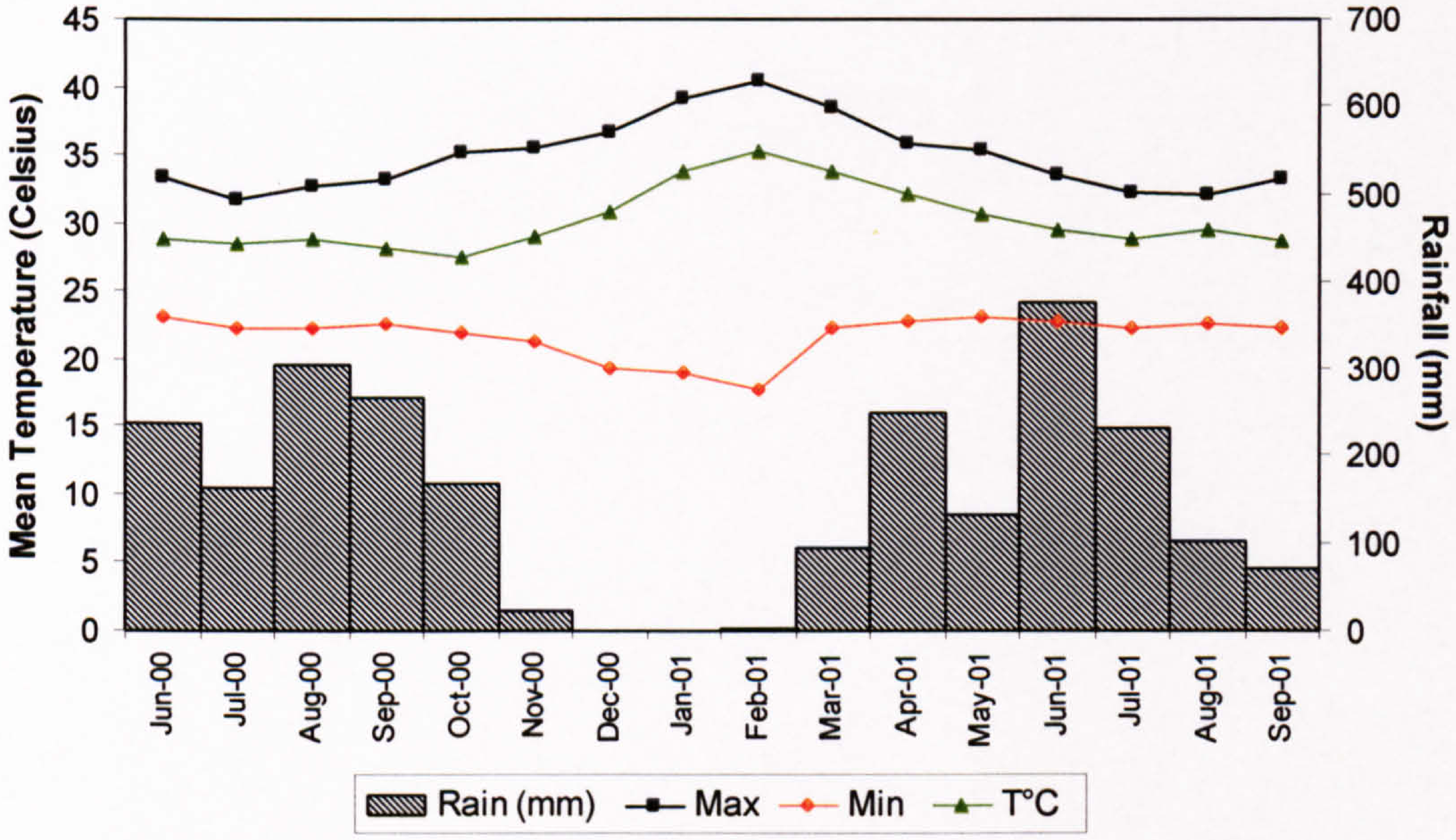
2.2 Climatic variables

Weather stations were set up on the forest edge beside the villages of Bossou, Yealé and Seringbara. Rainfall was measured on a daily basis using a standard rain gauge, placed in an open area approximately 20 m from the forest edge. Minimum and maximum temperatures, as well as the temperature at 5:30 p.m., were recorded on a daily basis at all three sites using a standard dual scale maximum-minimum thermometer nailed to a tree trunk and protected from direct sunlight exposure. The resulting climatic profiles indicate differences in rainfall and temperature between Bossou and the two Nimba sites.

Bossou, Republic of Guinea

The climate at Bossou is characterised by a distinct rainy season (March-October) and a dry season (November-February) (see Fig. 2.3). Total rainfall between July 2000 and July 2001 was 1779.4 mm and average annual temperature was 30.6° (range: 12.0°-43.0°).

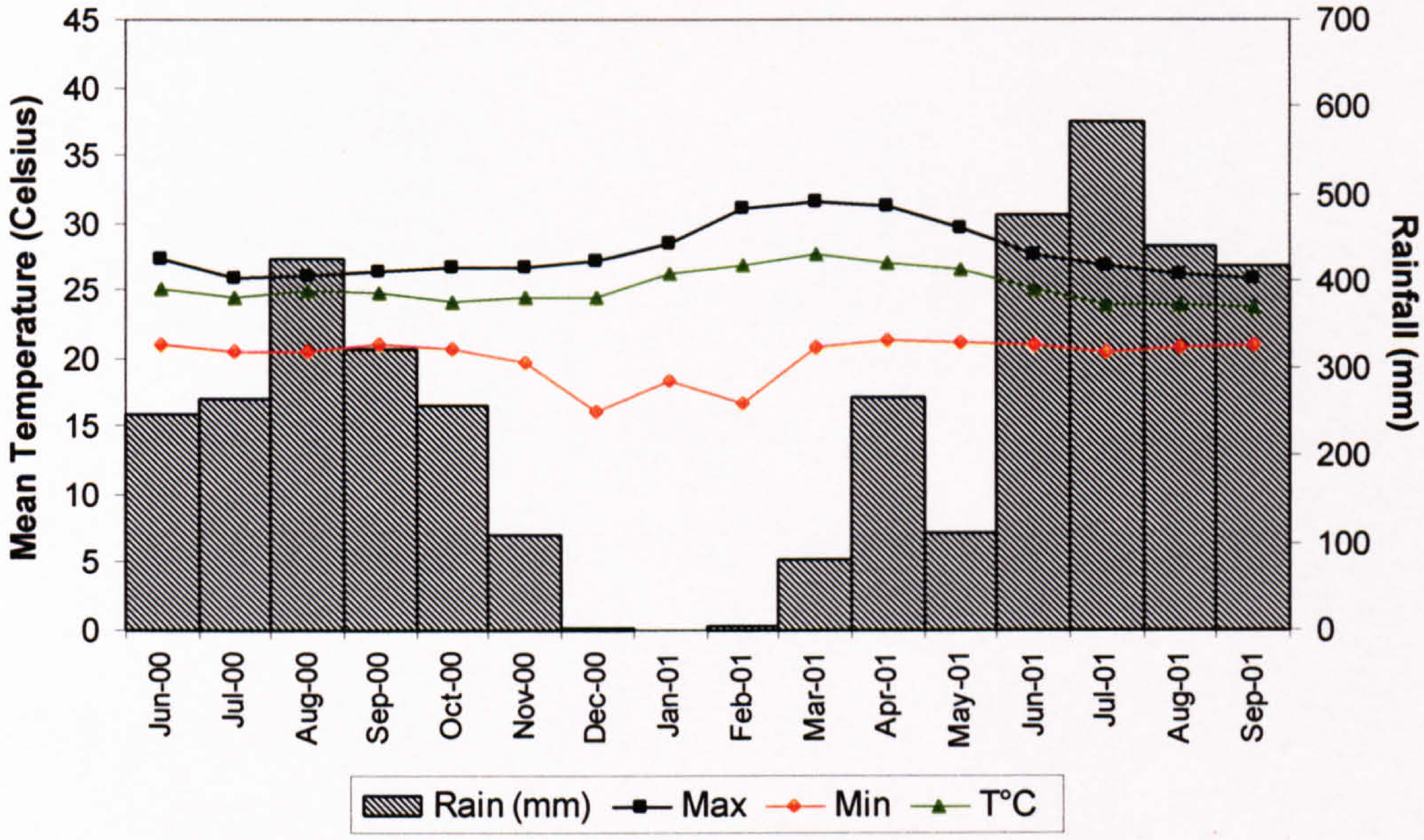
Fig. 2.3. Rainfall and temperature data from Bossou, Guinea, between June 2000 and September 2001 (T°C: Temperature at 5:30 pm).



Seringbara, Republic of Guinea

The climate at the foothills of the Nimba Mountains on the Guinean side is also characterised by a rainy season (March-November), which is slightly longer than observed at Bossou, and a dry season (December-February), which spans only 3 months (see Fig. 2.4). Total annual rainfall between July 2000 and June 2001 was 2,428.4 mm and average annual temperature was 25.4° (range: 11.5°-41.0°), nearly 5° lower than at Bossou.

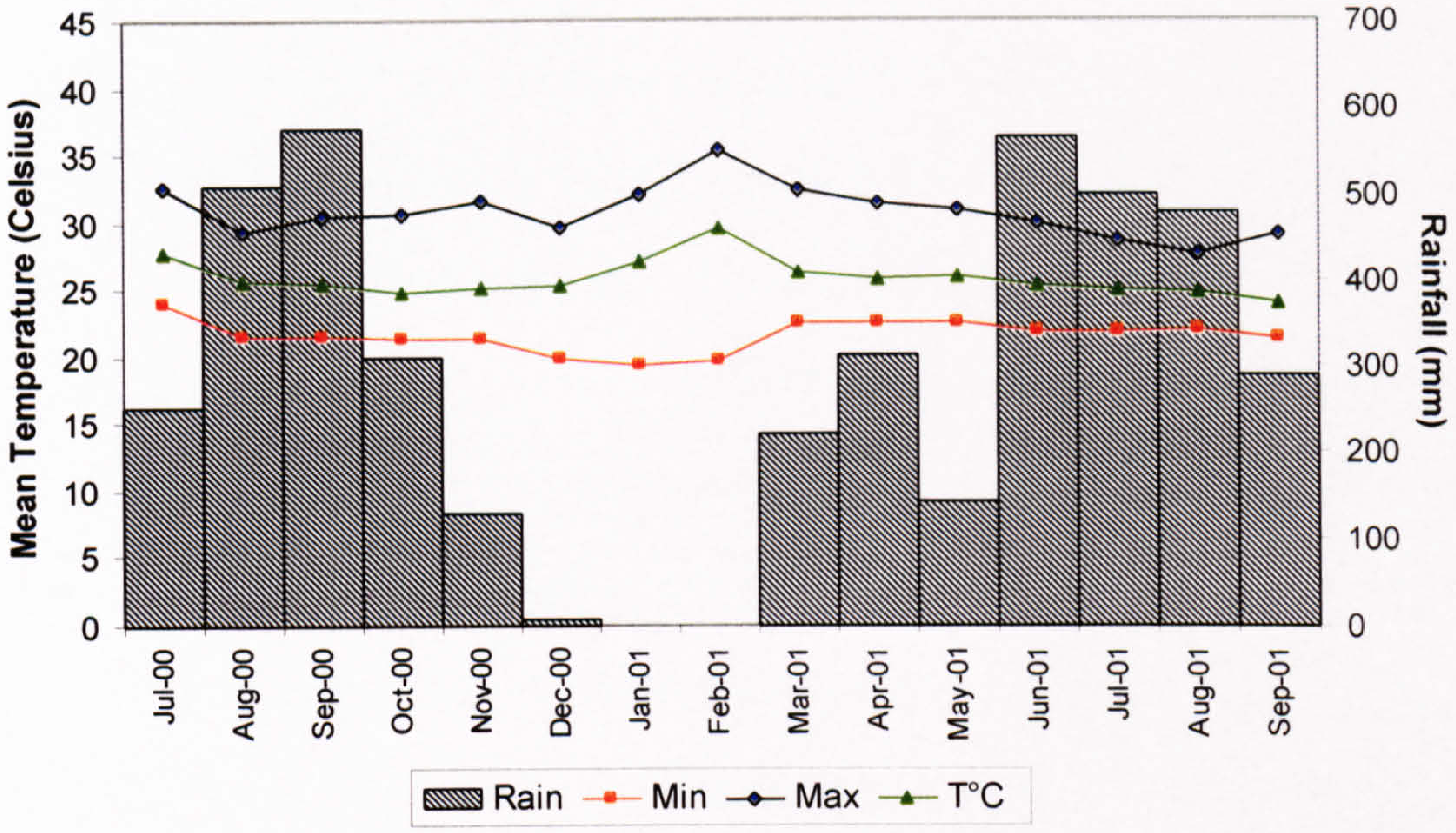
Fig. 2.4. Rainfall and temperature data from Seringbara, Guinea, between June 2000 and September 2001 (T°C: Temperature at 5:30 pm).



Yealé, Côte d'Ivoire

The climate at the foothills of the Nimba Mountains on the Ivorian side is also characterised by a long rainy season (March-November) and a brief dry season (December-February) (see Fig. 2.5). Rainfall between July 2000 and June 2001 was greater than at either Bossou or Seringbara with a recorded total annual rainfall of 3,027.6 mm. This period was characterised by an average temperature of 26.1° (range: 13.0°-43.3°).

Fig. 2.5. Rainfall and temperature data from Yealé, Côte d'Ivoire, between July 2000 and September 2001 (T°C: Temperature at 5:30 pm).



2.3 Forest types and vegetation

Bossou, Republic of Guinea

The home range of the Bossou chimpanzees is dominated by secondary and scrub forest, which has resulted from the abandonment of agricultural fields on the lower slopes of the hills. The secondary forest is exemplified by species such as *Elaeis guineensis, Musanga cecropioides, Carapa procera, Albezia zygia*. Primary forest only covers about 1 km² and is mostly located at the summit of one of the hills (Gban) (see Fig 2.1). Five areas dominated by riverine forest are available and regularly frequented by the chimpanzees. The small hills that constitute the home range of the Bossou community and one of the core areas of the Biosphere Reserve of the Nimba Mountains are also surrounded by rice paddies and agricultural fields, which are raided by the chimpanzees, especially during periods of natural fruit scarcity (Yamakoshi, 1998). Finally, the Bossou hills are practically enclosed by savanna vegetation interspersed, with gallery forests, beyond which lie, on the southeastern side, the Nimba Mountains.

The Nimba Mountains

The Nimba Mountains are characterized by evergreen forest of medium altitude (Guillaumet and Adjanohoun, 1971). The region below 800 m is entirely covered by primary tropical forest and, above 800 m, where the mountain becomes steeper, the vegetation is interspersed with montane forest and high altitude grasslands.

There are principally two vegetation types, which dominate the Nimba massif (WCMC, 1992; Humle, pers. obs.): 1) High altitude grassland near the summit and woody plants on the slopes, which are absent from the ridges. These areas are interspersed with patches of montane forest, dominated by Myrtaceae species, and Marantaceae and Zingiberaceae growths. The grassland, which regularly succumbs to natural fires in the dry season, is broken by gallery forests between 1,000m and 1,600m. *Parinari excelsa* and *Afrosersalisia cerasifera* are dominant tree species above 1,000m, where there is also an abundance of epiphytes. 2) Predominantly primary forest, located mainly on the foothills and in the valleys, with dominant species including *Triplochiton scleroxelon, Chlorophora regia, Morus mesozygia, Terminalia ivorensis, Lophira alata, Heritiera utilis, Gambeya perpulchrum, Rinorea* spp., *Octoknema borealis, Microdesmis keayana* and *Trichilia pleuriana.* Drier mid-altitude forests with trees such as *Carapa procera, Chidlowia sanguinea, Mareya micrantha, Ituridendron bequaertii, Canarium schweinfurthii, Piptadeniastrum africanum* and *Parkia bicolor* are found most commonly on the steeper slopes of the massif, especially on the Côte d'Ivoire side. More than 2,000 plant species have been described from the Nimba region, and about 16 are thought to be endemic (Adam, 1971-1983). The area has, as a result, been identified as a centre of plant diversity under the IUCN-WWF Plants Conservation Program (IUCN/WWF, 1988).

2.4 The fauna of Bossou and the Nimba Mountains

Bossou, Republic of Guinea

Bossou is home to the Manon people, an ethnic group now dispersed among several villages in that south-eastern region of Guinea, the north of the Côte d'Ivoire and Liberia. Bossou provides a rare example of a site where wild chimpanzees and local people have been living harmoniously, sharing the resources of the same forest. This peaceful coexistence stems from the beliefs of the Manon people, who consider the chimpanzee as one of their totems and the reincarnation of their ancestors (Kortlandt, 1986). However, in recent years, environmental conditions for the chimpanzees have become less favourable due to an increase in cultivation and deforestation of unprotected areas within their home range since 1990, resulting in part from an influx of over a thousand Liberian refugees into the area (Hirata *et al.,* 1998). Still, the totemisation of the chimpanzee by the villagers explains why this species of great ape has survived so close to the village for so many generations.

However, few large mammals other than the chimpanzee (*P. t. verus*) inhabit this forest. Indeed, many mammalian species that may have roamed these forests in the past must have succumbed to hunting and poaching activities and remaining ones are extremely shy of humans. Nevertheless, there have been occasional sightings of red-flanked duikers (*Cephalophus rufilatus*), Demidoff's bushbabies (*Galagoides demidoff*), squirrels (*Funisciurus sp.*), cane rats (*Thryonomys swinderianus*), several species of mongooses and the tree pangolin (*Phataginus tricuspis*) (Kingdon, 1997).

The Nimba Mountains

More than 500 new species of fauna have been discovered in the Nimba Mountain Reserve and there are more than 200 endemic species (WCMC, 1992). Species diversity is exceptionally high due to the presence of a variety of ecotones created by the presence of grasslands laced with forest. Some of the mammals found in the Nimba Mountains are listed in Table 2.1.

Table 2.1. List of the main mammal species present in the Nimba mountains (scientific name based on Kingdon, 1997).

Common Name	**Scientific name**
Bushbuck	*Tragelaphus scriptus*
Maxwell's duiker	*Cephalophus maxwelli*
Black duiker	*Cephalophus niger*
Bay duiker	*C. dorsalis*
Forest buffalo	*Syncerus caffer nanus*
Bushpig	*Potamochoerus larvatus*
Warthog	*Phacochoerus aethiopicus*
Scaly anteaters, e.g. the white-bellied pangolin	*Phataginus tricuspis*
Pygmy hippopotamus	*Hexaprotodon liberiensis*
Leopard	*Panthera pardus*
Golden cat	*Felis aurata*
Two-spotted palm civet	*Nandinia binotata*
African civet	*Civettictis civetta*
Forest genet	*Genetta maculata*
Servaline genet	*Genetta servalina*
Johnston's genet	*Genetta johnstoni*
Cane rat	*Thryonomys swinderianus*
African clawless otter	*Aonyx capensis*
Lesser otter shrew	*Micropotamogale lamottei*
Potto	*Perodicticus potto*
Lesser bushbaby	*Galago senegalensis*
Sooty mangabey	*Cercocebus atys*
Lesser spot-nosed guenon	*Cercopithecus petaurista*
Western black and white colobus	*Colobus polykomos*
Red colobus	*Procolobus badius*
Diana monkey	*Cercopithecus diana diana*
Chimpanzee	*Pan troglodytes verus*

There also exists a great diversity of amphibians, including *Nectophrynoides occidentalis* and *N. liberiensis*, two of the few species of tailless amphibians in the world that are totally viviparous (Lamotte, 1959). The Nimba massif is also home to a great diversity of birds, many of which are rare and endemic to this area (Colston and Curry-Lindahl, 1986).

2.5 History of research at Bossou and the Nimba Mountains

Bossou, Republic of Guinea

Bossou was originally discovered as an important chimpanzee field site by the French Zoologist M. Lamotte in 1942 (Kortlandt, 1986). Kortlandt visited Bossou briefly several times during the early 60's and was the first primatologist to conduct research on this chimpanzee community (Kortland, 1962). However, it was not until 1976 that Bossou was established as a long-term field site for the study of chimpanzees by Sugiyama from the Kyoto University Primate Research Institute, Japan (Sugiyama and Koman, 1979a, 1979b; Sugiyama, 1981).

Research at Bossou has since focused primarily on the life history, population dynamics, tool-use, and only more recently on the feeding ecology of this community. Published papers include information on conservation activities (Hirata *et al.*, 1998), the flora of Bossou (Sugiyama and Koman, 1992), folklore about chimpanzees (Holas, 1954), population dynamics (Matsuzawa, 1997a; Matsuzawa *et al.,* 1990; Sakura, 1991, 1994; Sugiyama and Koman, 1979a, Sugiyama, 1981, 1984, 1989a, 1994a, 1999), social structure (Sakura *et al.,* 1991; Sugiyama, 1981, 1984, 1989a, 1991; Sugiyama and Koman, 1979a), feeding behaviour (Sugiyama and Koman, 1987; Yamakoshi, 1998), grooming behaviour (Muroyama and Sugiyama, 1994; Sugiyama, 1988), genetics (Sugiyama *et al.*, 1993a), and tool-use with particular emphasis on the ontogeny and social transmission of behaviour and material culture (Fushimi *et al.,* 1991; Hirata *et al.,* 1998; Humle, 1999; Humle and Matsuzawa, 2001; Humle and Matsuzawa, 2002; Inoue-Nakamura and Matsuzawa, 1997; Kortlandt, 1986, 1989; Kortlandt and Holzhaus, 1987;

Matsuzawa, 1991, 1994, 1996, 1997b, 1998, 1999a,1999b; Matsuzawa and Yamakoshi, 1996; Matsuzawa *et al.*, 2001; Sakura and Matsuzawa, 1991; Sugiyama, 1989b, 1993; 1994b, 1995a, 1995b, 1997; Sugiyama *et al.*, 1993b; Sugiyama and Koman, 1979b; Sugiyama *et al.*, 1988; Tonooka, 2001; Yamakoshi and Sugiyama, 1995).

The Nimba Mountains

The Nimba Mountains have attracted the interest of scientists, including geographers, geologists, soil experts, botanists, zoologists and other specialists ever since the late 1930's (Kortlandt, 1986). Botanical, zoological and geological inventories that were carried out under the auspices of the Institut Fondamental d'Afrique Noire (IFAN) represent the greatest scientific effort ever conducted in the region, mainly focusing on the Guinean and Côte d'Ivoire portions of the massif. These projects resulted in an extensive taxonomical bibliography on Nimba. The single most important work, a comprehensive and extensive record of the flora of the Nimba Mountains, was produced by Adam (1971-1983). The Guinea and Côte d'Ivoire parts of Nimba are also well known through a number of other publications. The major works include Schnell (1952), Angel *et al.* (1954 a, b), Leclerc *et al.* (1955), Heim de Balsac (1958), Heim de Balsac and Lamotte (1958), Guibé and Lamotte (1958,1963), Laurent (1958), Lamotte (1959), Aellen (1963) and Lamotte and Xavier (1972). Although, less information was gathered concerning the Liberian portion of the range, the most comprehensive study of avifauna ever carried out in the region took place in Liberia (Coston and Curry-Lindahl, 1986). This study includes a detailed investigation of avian biology, ecology, vertical distribution and zonation, and migratory movements.

Since 1982, the governments of both Guinea and Côte d'Ivoire have also organised various missions and training conferences together with UNESCO in order to redefine the problems of ecosystem protection in the Nimba Mountain region (Pascual *et* *al.*, 1988; Pascual *et al.*, 1989). All these publications and missions have additionally contributed to the scientific knowledge of various species of fauna (Lamotte, 1982) and flora (Fournier, 1987; Schnell, 1987) of the Nimba Massif.

2.6 Review of chimpanzee research at Bossou and in the Nimba Mountains

Bossou, Republic of Guinea

Tool-use: studies in the field and in an outdoor laboratory

The Bossou chimpanzees display a large repertoire of tool-using behaviours, some of which are unique to this community (see Table 2.1). Two of those behaviours, so far exclusively observed at Bossou – algae-scooping and pestle pounding –, are customary behaviours, meaning that they occur in all or most able-bodied members of at least one age-sex class (Whiten *et al.*, 1999).

Although the chimpanzees of Bossou have been studied intensively since 1976, many tool-use behaviours performed by this community have only recently been discovered (see Table 2.1). The possibility that these behaviours are recent innovations cannot be excluded; however, it is also possible that these behaviours were not observed earlier due to: 1) the poor level of habituation of the chimpanzees before 1990, 2) the rarity of some of these behaviours and, 3) their seasonal occurrence. Indeed, algae-scooping was observed for the first time in 1995 during the rainy season and, before 1995, no research had ever been carried out at Bossou during this time of year.

The Bossou chimpanzees display use of five types of tool-composites, while no use of tool-composites has been recorded in *P. t. schweinfurthii*, the eastern subspecies of chimpanzee (Sugiyama, 1997) (see Table 2.2). A tool-composite consists of "two or more tools having different functions that are used sequentially and in association to achieve a single goal" (Sugiyama, 1997, p.23).

Since most research at Bossou has focused on tool-use, I shall proceed to describe some of those behaviours, some of which are unique to this community.

Chimpanzees at Bossou customarily dip for driver or safari ants (*Dorylus* spp.) using wands (Sugiyama *et al.*, 1988; Sugiyama, 1995a). Before proceeding to dip, ants' nests are usually dug up by hand, but on one occasion a digging stick may have been used to excavate the topsoil covering the nest (Sugiyama *et al.*, 1988) (see Table 2.2). Chimpanzees at Bossou have also been observed to feed on columns of ants. When dipping, the chimpanzees typically hold the wand between their index and middle finger and perform a back and forth movement of the wand so as to stimulate the ants to attack the object. Ants that climb up the wand are then ingested and chewed vigorously (see *Chapter 6* for more detail).

Other insect feeding behaviours involving the use of a tool include the use of a prizing stick to remove bee larvae encased in a dead branch and a single observation of termite fishing (see Table 2.1). The first ever case of termite fishing by wild chimpanzees for *Macrotermes* with twigs was reported at Gombe, Tanzania (Goodall, 1964). Up until 1997, no cases of termite fishing had ever been reported from Bossou, although *Macrotermes* mounds are common within the home range of the chimpanzees. In 1997, during the end of the rainy season, an adult female, Yo, and her juvenile offspring, Yolo, aged six, were observed using a short flexible stalk to fish for *Macrotermes* termites (Humle, 1999). As at Gombe, termites inside the newly formed mound attacked the intruding object and on withdrawal of the tool or probe, the chimpanzees brought the tip to their lips to ingest the termites. This example constitutes the first and so far only record of termite fishing with tools for ground-dwelling termites by Bossou chimpanzees.

Table 2.1 Tool-use behaviours observed at Bossou (note: **Date**: represents the year the behaviour was first observed, *: The behaviour has not been reported elsewhere, so far exclusively observed among Bossou chimpanzees; Behavioural pattern in *Italics*: Anecdotal) (adapted from Sugiyama, 1997).

Behavioural Pattern	**Date**	**Customary**	**Function**	**Reference**
Nut-crack	-	Yes	Use anvil and hammer stone to crack oil-palm nuts	Sugiyama & Koman, 1979b; Matsuzawa, 1994
Ant-dip	-	Yes	Use of stalk or stick to dip for driver ants	Sugiyama et al., 1988; Sugiyama, 1995a
Aimed throw	-	Yes	Throwing a branch or stone at specific target (e.g. human)	Sugiyama, 1997
Play start	-	No	Break off or pick up branch or leafy twig to initiate play	Sugiyama, 1997
Branch drag	-	No	Dragging a leafy branch in display, observed in males	Sugiyama, 1997
Flailing stick or club	-	Yes	Flailing a stick or branch and strike an object or conspecific	Sugiyama, 1997
Leaf clip	-	Yes	Strip leaf blade from petiole of one to several leaves with mouth	Sugiyama, 1981
Leaf-sponge	-	Yes	Use chewed up leaves for drinking water from tree hole	Tonooka et al., 1994; Tonooka, 2001
*Branch haul stick**	1977	No	Use long stick to haul another branch closer	Sugiyama & Koman, 1979b
*Gum-collect**	1980	No	Use probing stick to collect gum	Sugiyama, 1997
*Push-pull**	1988	No	Secondary tool used for water drinking (see Table 2.2)	Sugiyama, 1995b
Pestle pound*	1990	Yes	Palm frond used to pestle palm heart	Sugiyama, 1994b; Yamakoshi & Sugiyama, 1995
*Anvil-prop**	1991	No	Metatool used in nut-cracking, used to wedge anvil	Matsuzawa, 1991
Leaf-fold*	1994	Yes	Use folded leaf to collect water from tree hole	Tonooka et al., 1994; Tonooka, 2001
Algae scoop*	1995	Yes	Stalk or stick used to fish algae from pond surface	Matsuzawa et al., 1996
Leaf cushion	1997	No	Leaves used to sit on wet ground	Hirata et al., 1998
Termite fish	1997	No	Stalk used to fish for termites	Humle, 1999
Larvae prize	2000	No	Stick used to reach bee larvae in dead branch	Matsuzawa, pers.obs.
Expel	2000	Yes	Stout stick used to expel animal prey from tree hole	Humle, pers. obs.

Table 2.2 Tool-composites observed at Bossou (*: Anecdotal) (adapted from Sugiyama, 1997).

Behavioural Pattern	**Tool-composite**	**Customary**	**Reference**
Ant-nest digging and ant-dipping	Digging stick/Dipping wand	No*	Sugiyama et al., 1988
Water drinking	Leaf sponge or receptacle/Push-pull stick	No*	Sugiyama, 1995; Tonooka et al.,1994
Palm-sap collecting	Pestle pounding/Fibre sponge	No*	Sugiyama, 1994b
Nut-cracking	Stone Hammer/Anvil	Yes	Sugiyama & Koman, 1979b
Nut-cracking /Anvil propping	Stone Hammer/Anvil/Wedge	No	Matsuzawa, 1991

Chimpanzees at Bossou are mostly renowned for their use of a pair of stones as a hammer and an anvil to crack open oil-palm nuts (*Elaeis guineensis*) (Sugiyama and Koman, 1979b). Nut-cracking has only been reported among chimpanzees of a limited area of West Africa (Kortlandt, 1986; McGrew, 1992; Sugiyama, 1993; Boesch *et al.*, 1994), although oil-palm nuts, other nut-bearing tree species, stones, wooden clubs and tree roots are also available at many sites across central and east Africa (e.g. McGrew *et al.*, 1997). Among all the tool-use behaviours observed in the wild, nut-cracking is, probably, the most sophisticated performed by chimpanzees.

As previously discussed in *Chapter 1*, Matsuzawa and colleagues started field experiments to gain more insight into nut-cracking behaviour, by placing stones and nuts at the top of a hill in the core range of the chimpanzees (Sakura and Matsuzawa, 1991; Matsuzawa, 1991, 1994; Fushimi *et al.*, 1991; Sugiyama *et al.*, 1993b). These experiments revealed that the chimpanzees optimized their inter-individual spacing during cracking bouts, showed selectivity in their choice of nuts, i.e. a strong preference for moderately aged ones, and a consistent hand preference when using a hammer stone (Sakura and Matsuzawa, 1991; Fushimi *et al.*, 1991; Sugiyama *et al.*, 1993b). Indeed, the adults all displayed exclusive use of one hand for holding the hammer stone (Matsuzawa, 1994), while no adult or immature member of this community showed a significant hand preference while food picking or carrying (Sugiyama *et al.*, 1993b).

During these nut-cracking experiments, it also emerged that each chimpanzee had his or her favourite stone tools at the experimental site and transported them around this outdoor laboratory (Matsuzawa, 1999). Furthermore, three chimpanzees were observed using a third stone as a wedge to keep the surface of the anvil stone flat and stable. The wedge was classified as a metatool, i.e. a tool that was used to improve the function of another tool (Matsuzawa, 1991) (see Table 2.1 and 2.2).

These experiments also yielded useful insights into the acquisition of nut-cracking by young chimpanzees (Inoue-Nakamura and Matsuzawa, 1997). These longitudinal experimental field studies revealed the ontogenetic development of stone tool-use and suggested the existence of a critical learning period for acquisition, spanning the ages of 3 to 5 years old. Three developmental stages were distinguished (Inoue-Nakamura and Matsuzawa, 1997). The first stage is the action of manipulating a single object, such as a nut or a stone, typically observed among infants of one year of age. The second stage is the action of relating two objects - a nut and a stone or a stone and a nut. This action can generally be seen in 2-year-old infants. The third stage is co-ordinating the multiple actions to manipulate the object appropriately for their specific tasks. This behaviour is typically first observed at around 3 years of age.

Inoue-Nakamura and Matsuzawa's (1997) study also suggests that as infants get older they spend more time manipulating stones and nuts while not in physical contact with other chimpanzees and that they still observe adults' performances even after succeeding in performing nut-cracking. In addition, infants still occasionally take kernels from their mothers, even after being successful at cracking nuts. Finally, older infants tend to observe other members of the community more often than their own mother during nut-cracking bouts. The overall learning mechanism involved in the acquisition of this behaviour was concluded to be observational learning from other community members and direct experience. Indeed, as well as paying attention to the tool (stimulus enhancement), infants also learned something about the general functioning of the task and the results obtained by the model, indicating the involvement of emulation learning as defined by Tomasello (1996). Only infants have the opportunity to freely access stones and nuts from other individuals, thus gaining ample opportunity for individual experience with manipulating stones and nuts, whereas adults are usually less tolerant of juveniles behaving in the same fashion.

As well as looking at the social transmission of nut-cracking behaviour at Bossou, Matsuzawa and colleagues have been carrying out field experiments on social transmission of behaviour as an indirect approach to investigate social transmission of traditions between neighbouring communities of chimpanzees (Matsuzawa, 1994, 1996; Matsuzawa *et al.*, 2001). In the outdoor nut-cracking laboratory, nuts of *Coula edulis* and *Panda oleosa*, normally unavailable in the Bossou range, were provided and the reaction of the chimpanzees observed (see *Chapter 1* for details).

The series of experiments using *Coula* nuts led to the hypothesis that Yo is an immigrant individual to the Bossou community, possibly from a community where *Coula* nut-cracking is a habitual or customary tool-use behaviour, such as at Yealé in the Nimba mountains, only 10 km away (Matsuzawa and Yamakoshi, 1996; Humle and Matsuzawa, 2001). Yo and her offspring, Yolo, have so far been the only members of the Bossou community observed termite-fishing. In addition, Yo is the only adult who has never been seen pestle pounding (Yamakoshi and Humle, pers. obs.). Interestingly, Yolo, now an adolescent, is also inept at performing this tool-use behaviour. All these elements strongly support the hypothesis that she is not native to the Bossou community and comes from an adjacent community where such behaviours either persist or are lacking (refer to *Chapter 5* for more details). Finally, the results from the *Coula* and *Panda* nut experiments provide some insight into the possible mechanisms of cultural transmission both within and between communities. These experiments also indicate that youngsters are the most susceptible candidates for acquiring new behaviours.

The chimpanzees of Bossou also use leaves as a sponge or as a recipient for drinking water (Sugiyama, 1995b; Tonooka, 2001). In order to obtain more details about this behaviour, another outdoor laboratory for observing and video recording the behaviour was set up (Tonooka *et al.*, 1994). Through this experiment, a new technique of leaf tool-use for drinking was observed, whereby the chimpanzee would fold a leaf in its mouth and then place it by hand into the water hole using it as a receptacle. Moreover, on one occasion, a four-year old female was observed using a tool-set to collect water (see Table 2.1 and 2.2). She was seen drinking water from a tree hole with a narrow opening. As the water level decreased after repeated drinking, the leaf could no longer reach the source of moisture, so she resorted to using a small branch, which she inserted into the opening to push the leaf further down the hole. She then used the stick to retrieve the leaf from which she drank, before repeating the sequence of actions. All water drinking episodes thus far recorded at Bossou whether under experimental or natural conditions, revealed a convergence in tool choice for the leaf of *Hypselodelphis pogeana*, which is wide, soft and hairless (Tonooka *et al.*, 1994; Tonooka, 2001).

The Bossou community is currently the only community of chimpanzees where pestle pounding has been observed (see Table 2.1). Sugiyama first observed this tool-use behaviour in 1990 (Sugiyama, 1994). It consists of several discrete sequential behavioural components that have been described by Yamakoshi and Sugiyama (1995). A pestle pounding sequence usually comprises the following steps:

1. A chimpanzee climbs to the centre of the crown of an oil-palm (*Elaeis guineensis*).
2. It usually proceeds to spread out the radiating mature leaves using its hands and feet in order to expose the base of the central young shoots.
3. These young fronds and shoots are removed by tugging to gain access to the apical meristem.
4. The petiole of these spear leaves is then usually consumed.

5. A palm frond is subsequently used as a pestle to pound at and to excavate the centre of the palm crown, resulting in a softening of the palm heart.
6. The palm heart is extracted by hand and eaten.

In the summer of 1995, a new tool-use behaviour was observed (Matsuzawa *et al.*, 1996). The chimpanzees were observed using a wand to scoop up floating algae (*Spirogyra* sp.) from the surface of ponds, a behaviour, which was later described as algae scooping (see Table 2.1) (refer to *Chapter 7* for description of this behaviour). These ponds are non-existent during the dry season (Matsuzawa, pers. comm.), and therefore this tool-use behaviour is seasonal in its occurrence.

Bossou chimpanzees also display tool-use behaviours that are unrelated to subsistence. These include the use of leaf cushions, exploratory probing, leaf-clipping (for description of this behaviour refer to *Chapter 1*), play starting, branch dragging, branch hauling, stick or club flailing and aimed throwing (see Table 2.1). Bossou chimpanzees have indeed been observed to arrange large leaves on the ground as cushions to sit on in order to avoid contact with the moist or wet ground beneath, a behaviour first described by Hirata *et al.* (1998) as 'leaf cushion'. Two occurrences of this behaviour have been recorded, the first involving leaves of the parasol tree (*Musanga cecropioides*) and the second using leaves of a *Carapa procera* tree. Bossou chimpanzees also occasionally insert sticks or twigs, usually less than 20-30 cm long, into tree-holes or into the ground and then sniff the tip upon removal as a form of play or exploratory behaviour (Sugiyama, 1997). Finally, chimpanzees at Bossou, as well as at many other study sites across Africa, have been observed throwing a branch at a conspecific in display or in an aggressive context or at human observers. Stones are similarly occasionally used and targeted at humans.

Feeding and ranging behaviour

At Bossou more than 200 plant species, representing approximately 30% of available species in the habitat, are consumed by the chimpanzees, comprising more than 246 plant parts (Sugiyama and Koman 1992). Yamakoshi (1998) showed that Bossou chimpanzees spend approximately 60.7% of their feeding time consuming fruit. Leaves and woody pith are the next two most important foods for the chimpanzees at this site. Indeed, Bossou chimpanzees spend about 10.8% and 10.1% respectively feeding on these two food items. Seeds and the pith of herbaceous plants also comprise a non-negligible portion of their diet. Takemoto (2002) also noted that cultivars comprise 6.4% of the annual diet of Bossou chimpanzees and are thus fully integrated in their dietary repertoire, although their seasonal proportion in the diet can fluctuate quite significantly (Yamakoshi, 1998). Bossou chimpanzees also eat flowers, bark, roots and tubers, tree gum and insects; e.g. adult termites (Isoptera) and ants (*Dorylus* spp. and *Oecophylla longinoda*) and the eggs and larvae of ants, bees and several species of beetle such as the Raphia coleopteran (*Rhynchophorus quadrangulus*). Other food items consumed more infrequently include algae, mushrooms, honey, bird eggs and mammals such as the tree pangolin (*Phataginus tricuspis*). Hunting for animal prey at this site is relatively rare compared to other sites where chimpanzees have been studied, probably due to the paucity of other mammalian species in the habitat.

Some species of plants are important for the chimpanzees, especially in times of fruit scarcity, which at Bossou, corresponds to the rainy season. Yamakoshi (1998) showed that Bossou chimpanzees heavily rely upon the parasol tree (*Musanga cecropioides*) and the oil-palm (*Elaeis guineensis*) during such times. The oil-palm provides them with year round food resources, including the rich mesocarp of the fruit, the oily nut kernel, the petiole of young palm fronds, the base of immature flowers, the pith of mature leaves and the sugary and nutritious palm heart (see *Chapter 5* for more details). Yamakoshi (1998) showed that, when fruits are scarce, Bossou chimpanzees effectively increase their tool-use activities, especially nut-cracking and pestle pounding, in order to gain access to otherwise inaccessible food resources and to boost their energy intake. In addition, during such times of fruit scarcity, when food resources may be patchily distributed and rarer, Takemoto (2000) demonstrated that Bossou chimpanzees spend less time feeding and moving and decrease their dietary diversity.

Demography and social organisation

Factors affecting party size and composition at Bossou have also been investigated (Sakura, 1991, 1994). Party size was found to be negatively correlated with feeding ratio, i.e. ratio of the total number of scanned feeding individuals in a focal party over the total number of scanned individuals in the party. Larger parties were observed in more dangerous situations, i.e. crossing roads. When parties included oestrous females, juvenile and adolescent males tended to forage with them, separately from their mothers. In addition, lactating females with infants tended to spend more time alone, but not as much as observed at Gombe (Wrangham and Smuts, 1980). Sakura (1994) concluded that the pattern of party formation of the Bossou chimpanzees is very similar to that observed in other populations where influential factors influencing party size and composition include food supply, presence of danger or predators, oestrous females and infants.

However, Bossou chimpanzees differ from other communities in that they tend to form more cohesive groups (Sugiyama and Koman, 1979a) and inter-female relationships are highly affiliative when compared with those of the Gombe and Mahale communities in Tanzania (Sugiyama, 1988). Furthermore, male-male grooming frequency was found to be lower than that recorded in the east African subspecies (*P. t.*

schweinfurthii). The community size at Bossou is not large and since 1976 the number of adult males has been small. Infanticide has never been observed at Bossou. Females with infants may, therefore, have no need to avoid adult males. Moreover, the low frequency of female dispersal in this community and the semi-isolation of the group (Sugiyama, 1981, 1984, 1989a) might have increased relatedness among females, which might in turn explain the high degree of affiliation between them.

Sugiyama (1994a) found the mean interbirth interval for Bossou female chimpanzees to be 4.6 years, or 5.1 years if cases in which the previous infant had died within its first 3 years were excluded. This mean interbirth interval is relatively short when compared with those of Mahale (6 years overall) (Hirawai-Hasegawa *et al.*, 1984; Nishida *et al.*, 1990), Gombe (5.5 years, excluding cases of infants dying before the age of 3) (Teleki *et al.*, 1976; Goodall, 1983, 1986) and Taï (5.9 years overall) (Boesch & Boesch-Achermann 2000). The probability of infant survival to the age of 5 at Bossou is 0.71 (Sugiyama 1989, 1994), which, with the exception of Kibale, is much greater than that reported from other long-term field sites (*cf.* Boesch and Boesch-Achermann, 2000, p.40). In addition, female age at first parturition can be as young as 9.6, which is much younger than that reported at other sites (*cf.* Boesch and Boesch-Achermann, 2000, p.49).

Finally, the Bossou community has atypical demographic features and population dynamics, which can possibly be explained by its semi-isolation from adjacent communities in the Nimba Mountains and its access to high energy foods such as crops and oil-palms during periods of fruit scarcity.

The Nimba Mountains

Before 1999, little information was available about the population of chimpanzees in the Nimba Mountains region (Sugiyama, 1981, 1995a; Boesch *et al.*, 1994; Matsuzawa and Yamakoshi, 1996). Sugiyama visited Seringbara several times since 1976. He interviewed the villagers, and conducted two surveys of the forest surrounding the village in order to determine the presence of chimpanzees in the area. He concluded that the chimpanzees were only seasonally transient to the region (Sugiyama, 1981). However, over 70 nests and numerous feeding remains of chimpanzees were discovered in 1999 in the forest beside the village, while vocalisations of chimpanzees were regularly heard (Shimada, 2000). These findings suggested rather the presence of a resident group near Seringbara.

In early April, 1991, Sugiyama (1995a) briefly explored the eastern area of the Nimba Mountains at Gouéla (Goera), on the Guinean side of the massif near the border with Côte d'Ivoire, only 13 km from Bossou (see Fig 2.2). This region of the Nimba Reserve is covered in both dense rainforest and drier undisturbed open forest. Sugiyama (1995a) confirmed the presence of chimpanzees at this site, as well as the existence of ant-dipping for *Dorylus* spp. ants. The evidence for this behaviour was in the form of a destroyed ants' nest, nearby which lay two freshly used ant-dipping wands (Sugiyama, 1995a).

Primatologists also explored the Côte d'Ivoire side of the Nimba Mountains. Joulian, as a member of a survey team investigating the distribution of nut-cracking behaviour in Côte d'Ivoire (Boesch *et al.,* 1994), conducted a preliminary study beside Yealé near the Nuon River (see Fig. 2.2). Boesch *et al.* (1994) found two *Coula*-cracking sites in the area, but were cautious to attribute these findings to chimpanzees since human presence had been confirmed, and the local people (Yacouba and Manon) are also known to crack this species of nut. Joulian also confirmed the presence of *Panda oleosa, Parinari excelsa* and *Detarium senegalensis* trees on this side of the massif (Joulian, 1994).

In January 1994, Matsuzawa and Yamakoshi (1996) carried out two brief surveys of Nimba chimpanzees in the area of the Nuon River. Table 2.3 summarises their preliminary findings. Matsuzawa established the Yealé study site in 1994. Since then, attempts to habituate the chimpanzees in the area have been intermittent, co-ordinated by a local agent of the "Centre des Eaux et Forêts" of Danané. Preliminary surveys and information from local people suggest that three groups of chimpanzees may reside in the region, each one adjacent to one of three major rivers found in the Reserve: the Nuon, the Yan and the Toua (see Fig. 2.2). I carried out a pilot study in the region in September 1999, focusing on the Nuon and the Yan ranges, which have since been the focus of research at this site (Humle and Matsuzawa, 2001).

Table 2.3 Summary of behaviours possibly displayed by Nimba chimpanzees beside Yealé, Côte d'Ivoire (*: behaviour has not been reconfirmed since these original surveys) (after Matsuzawa and Yamakoshi, 1996).

Behaviour
1. Building nests on the ground (possibly used as night nests)
2. Medicinal Use of Leaves
Polycephalium capitatum
3. Eating Snails*
4. Nut-cracking using stones
Coula edulis
*Carapa procera**
5. Cracking *Strychnos* with stone*
6. Ant-dipping for *Dorylus spp.*

2.7 The Bossou Community

Typically in chimpanzees, females emigrate by around the age of puberty (9-13 years old) and males are philopatric, remaining within their natal community (Goodall 1983, Hiraiwa-Hasegawa *et al.*, 1984, Boesch and Boesch-Achermann, 2000). Consequently, chimpanzees have been considered to represent an exception among non-human primates, for most species form female-bonded groups (Greenwood, 1980).

However, accumulated demographic data on the Bossou community strongly suggest that males as well as females emigrate (Sugiyama, 1999) (see Fig. 2.6). Since 1976, group size has remained stable (range: 16-23) (Sugiyama, 1981, 1984, 1999). In October 2002, the group consisted of 2 adult males, 7 adult females, 3 adolescents, 4 juveniles and 3 infants (age-class categories based on Sugiyama (1999): infant: 0-3; juvenile: 4-7; adolescent: 8-11; adult: >11) (see Table 2.4).

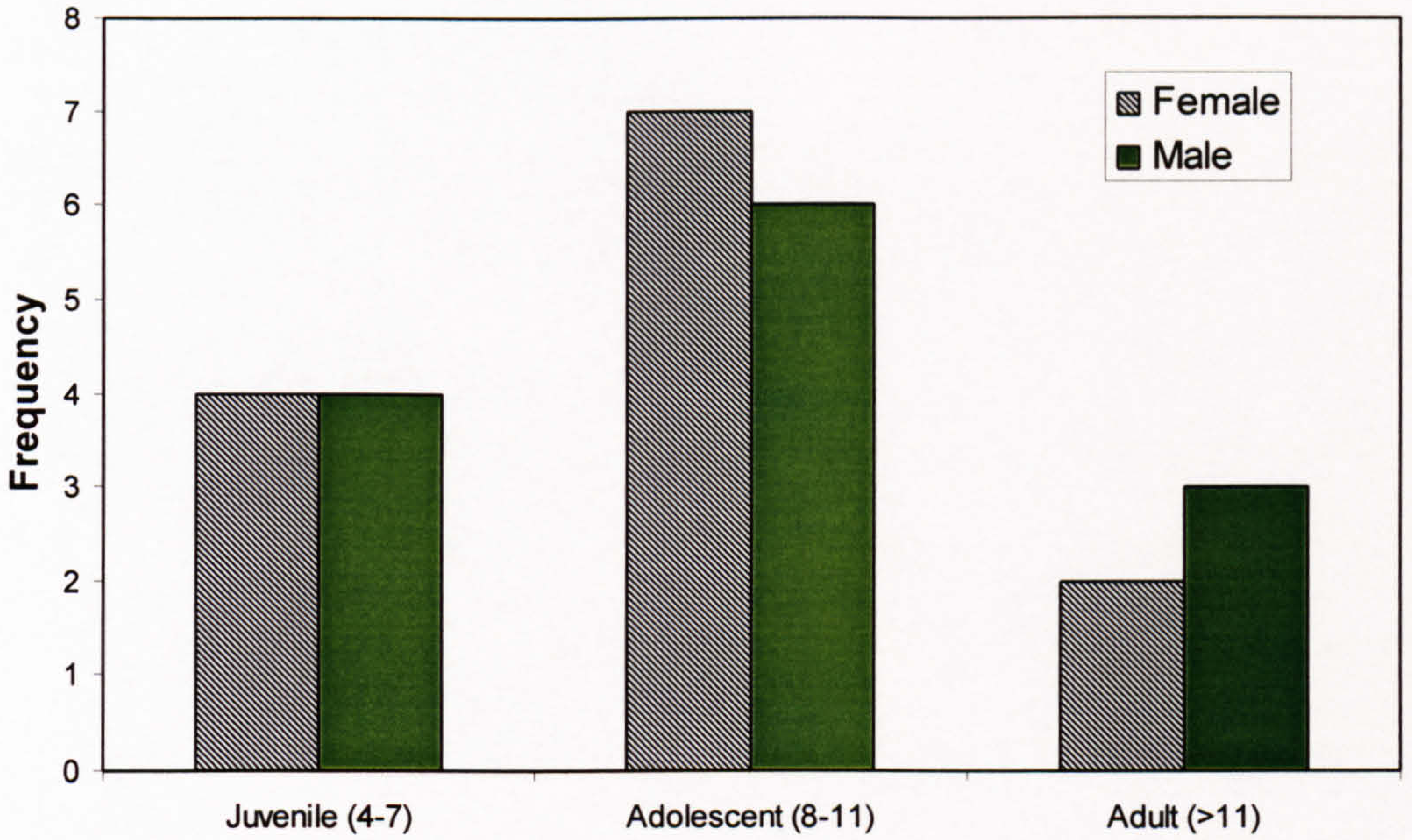
Out of 17 females born at Bossou since 1976, 5 remain in the community (2 adolescents, 2 juveniles and 1 infant) and 3 probably died in infancy (see Table 2.4). Nine others have presumably emigrated from Bossou, 4 as juveniles and 5 as adolescents, as no traces of their remains were ever found. Out of 16 males born in the community since 1976, 2 may have died during infancy, and one was found dead as a juvenile (see Table 2.4). Only 6 of these males remain in the community (2 infants, 1 juvenile, 2 adolescents and 1 adult). The latter adult male, Foaf, became the new alpha-male of the group in 1997. Three males disappeared as juveniles, 3 as adolescents and 1 as an adult (see Table 2.4). These 7 individuals were all healthy males and neither sickness nor weakness could easily account for their disappearance. It is therefore very likely that both males and females at Bossou emigrate from their natal community; however, this still requires confirmation, e.g. via the observation of ex-Bossou members in neighbouring communities or matching of genetic samples from disappeared individuals with samples collected from Nimba.

Sugiyama (1999) hypothesised that male dispersal at Bossou is influenced by intra-group male-male competition and the habitat ecology and structure of Bossou. The absence of immediate adjacent groups and of predators may mean that males are not so much required for territorial defence as observed at other field sites such as Gombe, Tanzania (Goodall, 1986) or Taï, Côte d'Ivoire (Boesch and Boesch-Achermann, 2000).

Table 2.4 The Bossou Community since 1976 in October 2002.

Name	Abbr.	Sex	Birth: Day/Month/Year	Status
BAFU	BF	m	Unknown (adult in 1976)	Disappeared: 05/77
TUA	TA	m	Unknown (adult in 1976)	**Present**
AIWA	AW	m	Unknown (adult in 1976)	Disappeared: 05/77
SAFI	SF	m	Immigrated (21/01/77)	Disappeared: 09/02/77
SAKAI	SK	m	Immigrated (04/80-11/82)	Disappeared: 04/83
KAI	Ka	f	Unknown (adult in 1976)	**Present**
KIE	Ki	f	1975 (estimated)	Disappeared: 05/03/91
KAKURU	Kk	f	Late 1986	Disappeared: 05/03/91
KUBO	Kb	f	1972 (estimated)	Disappeared: 22/02/77
KURE	Kr	f	1969 (estimated)	Disappeared: 03/80
NINA	Nn	f	Unknown (adult in 1976)	**Present**
NTO	Nt	f	Early 1993	Disappeared 12/01
NYELE	Ne	f	27/03/91	Disappeared: 05-08/91
NA	NA	m	1985	Disappeared: 03-05/96
NPEI	NP	m	Early 1981	Died: 01/01/88
NYU	Ny	f	1976 (estimated)	Disappeared: 03/83
NON	NO	m	1969 (estimated)	Disappeared: 05/77
FANA	Fn	f	Unknown (adult in 1976)	**Present**
FANLE	Fl	f	8-18/10/97	**Present**
FOTAYU	Ft	f	Middle 1991	**Present**
FOKAYE	Fk	m	5-18/07/01	**Present**
FOAF	FF	m	Late 1980	**Present**
FON	Fo	f	1976 (estimated)	Disappeared: 03/83
FINO	Fi	f	1971 (estimated)	Disappeared: 03/80
JIRE	Jr	f	Unknown (adult in 1976)	**Present**
JIMATO	?	m	5-12/10/02	**Present**
JEJE	JJ	m	12/97	**Present**
JURU	Ju	f	19/11/93	Disappeared 12/01
JOKORO	Jk	f	Early 1989	Disappeared: 25/01/92
JA	Ja	f	Late 1983	Disappeared: 02/93
JIEZA	JZ	m	1978	Disappeared: 04/88
JI	JI	m	1975 (estimated)	Disappeared: 05/77
JIMA	JM	m	1972 (estimated)	Disappeared: 03/80
VELU	VL	f	Unknown (adult in 1976)	**Present**
VUAVUA	Vv	f	Middle 1991	**Present**
VEVE	VE	f	18-23/05/01	**Present**
VUI	VI	m	Late 1986	Disappeared: 07/99
VUBE	Vb	f	1982	Disappeared:03/90
VUNA	VN	m	1977	Disappeared: 03/83
VU	VU	m	1972 (estimated)	Disappeared: 03/80
YO	YO	f	Unknown (adult in 1976)	**Present**
YOLO	YL	m	Middle 1991	**Present**
YERA	YE	m	Middle 1989	Disappeared: 03/90
YUNRO	Yu	f	Late 1984	Disappeared: 02/93
YAKA	Yk	f	Early 1982	Disappeared: 05/03/83
YANA	YN	m	1978	Disappeared: 04/83
YIRI	YR	m	1974 (estimated)	Disappeared: 03-/80
PAMA	Pm	f	Unknown (adult in 1976)	**Present**
PELEY	Pe	f	04/98	**Present**
PONI	PO	m	04/02/93	**Present**
PILI	PL	f	Early 1987	Disappeared 01/01-05/01
POKURU	PK	m	08/96	Disappeared 01/01-05/01
PIRE	PI	m	Early 1985	Disappeared: 10/01/86
PRU	PR	m	Late 1980	Disappeared: 11/91

Fig 2.6 Number of weaned chimpanzees born at Bossou that have disappeared since 1976, according to age-sex class (as of October 2002).



In addition, competition for oestrous females may incite alpha males to expel young males from the community. No immigration of females has ever been recorded at Bossou, although there is suggestive evidence that one female, Yo, might be an immigrant (Matsuzawa, 1994; Humle, 1999). Three male immigrations into the community have nevertheless been recorded (Sugiyama, 1981, 1984, 1999) (see Table 2.4). One old male and an adolescent male were transient visitors into the group. They arrived together and stayed, respectively for approximately 3 weeks, while another male stayed for an undetermined period of at least 3 months. This latter male could not be proven to have sired any offspring while at Bossou, although one male offspring in the community, Vui, could not be genetically linked to any of the resident males of the group through PCR (Polymerase Chain Reaction) paternal analysis (Sugiyama *et al.*, 1993a). Sugiyama *et al.* (1993)'s study of paternity discrimination by GT dinucleotide repeat PCR analysis confirmed that Bossou chimpanzees were not reproductively isolated from their neighbours in the Nimba Mountains until at least 1986-1987.

2.8 The Nimba communities of chimpanzees

In the region beside the Nuon River, Yealé, Côte d'Ivoire, the chimpanzee population was estimated to be about 50 individuals, with a density of 0.5 chimpanzees/km^2 (Boesch *et al.*, 1994; Hoppe-Dominik, 1991). In Guinea, based on the maximum nesting group size recorded (see *Chapter 4*), one chimpanzee community near Seringbara may harbour as many as 30 chimpanzees and maybe more, ranging over at least 16 km^2. However, overall, still little remains known of 1) the precise number of chimpanzees in the region, 2) of the number of communities prevailing in the entire massif, and 3) of their precise ranging patterns. Continuous research presence in the region is necessary if these questions are to be answered with more certainty.

Chapter 3

General methods

3.1 General overview

Since each following result's chapter offers a detailed description of the methodologies and analyses employed, this current chapter aims to provide a simple overview of the data collection methods and data analyses applied, as well as information on observation conditions and tracking methods used. Field data were collected continuously between June-September 2000 and June-September 2001, a total of 8 months.

Direct observational data of the chimpanzees' behaviour were chiefly collected from Bossou, the only site where chimpanzees were habituated and tolerated the presence of observers. At Bossou, a total of 581 hours of systematic behavioural data were collected by myself with the assistance of two guides. At the Nimba sites, I usually worked with three guides who helped me with the oil-palm surveys, the vegetation transects, the collection of nesting and tool-use data and with tracking the chimpanzees.

I had previously visited Bossou twice as a volunteer between June-September 1995 and August-November 1997 during which time I became acquainted with the individual chimpanzees, their behavioural repertoire, and the plant species present in their habitat, as well as the ones specifically comprising their diet. I also carried out a pilot study at both Bossou and Yealé between August-September 1999 to establish the feasibility of exploring the questions addressed in this thesis and to design or refine the methodologies to be employed.

3.2 Time allocation between sites

On a monthly basis, time was allocated between the three sites, Bossou and Seringbara, Republic of Guinea, and Yealé, Côte d'Ivoire, as described in Table 3.1 below. A total 101 working days were spent at Bossou, 48 at Seringbara and 61 at Yealé in Côte d'Ivoire.

Table 3.1. Time allocation between study sites between June-September 2000 and June-September 2001.

Location	Date	Working Days
Bossou	26/05/00-07/06/00	12
	13/06/00-21/06/00	8
	01/07/00-06/07/00	5
	13/07/00-20/07/00	7
	30/07/00-05/08/00	6
	01/09/00-06/09/00	5
	13/09/00-19/09/00	6
	01/06/01-13/06/01	12
	30/06/01-11/07/01	11
	28/07/01-15/08/01	18
	22/08/01-24/09/01	2
	04/09/01-13/09/01	9
	Sub-Total	**101**
Seringbara	08/06/00-12/06/00	5
	07/07/00-12/07/00	6
	06/08/00-11/08/00	6
	07/09/00-12/09/00	6
	14/06/01-19/06/01	6
	12/07/01-17/07/01	6
	16/08/01-21/08/01	6
	14/09/01-20/09/01	7
	Sub-Total	**48**
Yealé	22/06/00-30/06/00	9
	21/07/00-29/07/00	9
	12/08/00-20/08/00	9
	None (Evacuated)	
	21/06/01-29/06/01	9
	19/07/01-27/07/01	9
	25/08/01-03/09/01	10
	22/09/01-27/09/01	6
	Sub-Total	**61**
	Total	**210**

Originally a 13 months study had been planned between June 2000 and July 2001. However, border conflicts in the region between September 2000 and March 2001, compelled me to discontinue my fieldwork, which resumed in June 2001 for another 4 months. During the time spent at each site, a monthly oil-palm survey was conducted; and faecal samples and data on nesting, diet and tool-use were gathered. In addition, the chimpanzees were tracked or followed varying on the habituation conditions of the site. Direct and indirect behavioural data were thus collected at the three sites during each visit. Between June-September 200 and June-September 2001, the local guides also collected faecal samples and tool-use data while I was absent from the site.

3.3 Oil-palm surveys

A sample of oil palm trees encountered during exploration of the chimpanzees' habitat were tagged on a random basis at the three sites (N=127 for Bossou; N=68 for Seringbara; N=127 for Yealé). These tagged palms were then routinely surveyed on a monthly basis.

The aim of these surveys was to track and quantify any differences in phenology of the oil-palm tree, as well as tool availability, nut quantity, quality, fruit and petiole availability, and competition for oil-palm resources across the three study sites. In addition, these surveys served to indirectly examine patterns of oil-palm use at each site.

3.4 Tree species density

In order to assess tree species availability for nesting purposes and oil-palm density at the three sites, north-south and east-west vegetation transects (50 m long and 10 m wide) were set up randomly within the core area of each study group in approximate proportion to the different habitat types available at each site (Chapman and Wrangham, 1994). Random number tables were used to yield GPS points, within the home range of the chimpanzees, which marked the beginning of each transect line. All trees with a diameter at breast height (DBH), i.e.1.5 m, above 5 cm were identified at the species or genus level or by their vernacular name when taxonomically not identifiable.

3.5 Habituation and visibility levels

Bossou, Republic of Guinea

Although Bossou chimpanzees have been studied since 1976 (Sugiyama and Koman, 1979a, b), the group has only recently been suitably habituated to the presence of observers without the use of provisioning. Indeed, since 1990, habituation has progressed considerably since more fieldwork was then conducted on a more continuous basis by various researchers and PhD students. Nevertheless, observation conditions are occasionally rendered difficult by the nature of the environment, which consists in places of dense secondary or scrub forest. Indeed, visibility levels are especially poor in areas of abandoned fields with forest regrowth, characterised by extremely dense vegetation. In addition, the density of the vegetation in some parts of the home range made it difficult for the observers to move quietly behind a party at a distance that is close enough to maintain visual contact. I never attempted to approach closer than 5 m to the chimpanzees, in order to minimise interference and minimise the possibility of disease transfer, and observation distance currently typically varies between 5 and 15 m.

There is no systematic trail system at Bossou. Instead, observers follow well-established chimpanzee trails that are regularly cut back for easy movement within the home range and for rapid access from one area to another.

The Nimba Mountains: Seringbara and Yealé

Some trails had been set up by local guides at both sites in the Nimba Mountains, since 1994 for Yealé and 1999 for Seringbara. During this study, new trails were cut during follows of the chimpanzees to facilitate easy access to different areas of the forest, i.e. across valleys. Already established chimpanzee trails were also incorporated into the prevailing trail system. However, as at Bossou, no systematic trail system was established. The trails were cut using machetes or secateurs, depending on the density of the surrounding vegetation. The chimpanzees at the two sites eventually started using these new trails to move through the forest, which facilitated tracking.

Visibility conditions at these two sites were variable. In most cases, these were better than that at Bossou, with more open woodland areas available, especially in the middle altitude range between 400m and 700m. However, the prevalence of a greater abundance of Marantaceae type forest and extensive lower vegetation growth, especially on the upper slopes and in areas affected by natural forest fires, hampered visibility.

Direct sightings of the chimpanzees at these two sites were few during the study periods concerned and are recorded in Table 3.2. Based on the number of tracking days, at Seringbara, chimpanzees were thus sighted on average every 4.7 days and at Yealé, every 4.5 days. However, chimpanzee encounter rate would have certainly been greater had research presence been more continuous. Indeed, auditory contact was made every 2.8 days at Seringbara and every 2 days at Yealé. Therefore, these figures do not reflect accurately the habituation potential of those sites. Both study periods spanned the rainy season, during which time fruit availability is known to be low (Kassié and David, pers. comm.) and working and visibility conditions not ideal. Most of the data collected from these two sites were consequently in the form of indirect behavioural observation.

3.6 Tracking of the chimpanzees

At all three sites, the chimpanzees were located using one or a combination of four techniques:

- Visiting known fruiting trees and waiting for the chimpanzees to arrive at the feeding site.
- Following the direction of origin of chimpanzee vocalisations.
- Chance location of individuals.
- Returning to the area where the chimpanzees had nested the previous night or where they had last been observed during the previous afternoon.

The methods used varied depending on the level of habituation and knowledge of the home range of each of these chimpanzee communities. In practice, each method was used at all sites. Where the chimpanzees were not habituated the difficulty of locating them or their approximate whereabouts was especially difficult during the rainy season, which was characterised by fruit scarcity and during which the chimpanzees appear to travel in smaller parties and to vocalise less frequently. At the Nimba sites, when a party of chimpanzees was located, we tried to remain with it as long as possible. However, most of the time, as soon as one or several chimpanzees would spot us; they would leave and disappear in the undergrowth where it was usually difficult to follow them.

Table 3.2. Record of direct sightings of chimpanzees at Seringbara and Yealé between June-September, 2000 and June and September, 2001 (Juv.: Juveniles; Adol.: Adolescents; Ad.: Adults).

Site	**Date**	**Individuals observed**							**Total**	**Activity**	**Time Obs. (min.)**
		Male			Female			Infants			
		Juv..	Adol.	Ad.	Juv.	Adol.	Ad.				
Seringbara	07/09/00	1		1			2	1	5	Feed	3
	09/09/00			1					1	Travel	1
	13/07/01			1	1		1		3	Travel	1
	18/08/01	1					1	1	3	Feed	7
	20/08/01				1				1	Travel	1
	15/09/01	1	2	2	4	3	3	4	19	Feed	6
	16/09/01		1	1			1	1	4	Rest	25
Yealé	25/06/00			1					1	Feed	5
	29/06/00	3	2	2	2	3	5	4	21	Feed	18
	27/07/00			1			1		2	Rest	2
	12/08/00			2			2	2	6	Travel	1
	24/06/01		1	3					4	Feed	6
	27/06/01		2	3		2	2	2	11	Feed	30
	21/07/01			1					1	Travel	1
	26/07/01					1	1	1	3	Feed	12

We always travelled as silently as possible through the forest in case we came across chimpanzees by chance. Our searching parties usually never exceeded three people, with an optimum of two, so as to keep noise to a minimum. As a rule, randomly searching for the chimpanzees was not productive, which explains the few sightings of chimpanzees in the early months of the study at the two Nimba sites (see Table 3.1). As we gained knowledge of the habitat and the diet of the chimpanzees, we were able to predict more successfully their whereabouts. When we had absolutely no idea as to the locations of the chimpanzees, we would visit particular areas in the forest which offered good auditory conditions, i.e. slightly elevated or a small clearing away from rivers, and quietly sit and wait for the chimpanzees to vocalise. However, we also spent a lot of the time exploring different areas so as to accumulate knowledge of the habitat and indirect evidence of feeding remains and other behavioural patterns of the chimpanzees, such as nesting and tool-use.

At Bossou, the same methods were employed and once a party of chimpanzees was located, the decision to stay with it or to look for another party was dictated by the presence of certain individuals and the perceived likelihood of finding another party. Also, at Bossou radios (Motorola GP340) were regularly used when more than one group of field assistants and/or researchers were in the field. This was useful in helping us rapidly locate the whereabouts of individual chimpanzees and different parties. We attempted to use radios at the Nimba sites, however, these proved ineffective due to the particularly mountainous topography of the area.

3.7 Comparable data on diet

Feeding remains and direct observations of feeding behaviour

All feeding remains left behind by chimpanzees and judged to be less than a month old were identified and recorded during the monthly visits to the Nimba sites and data on their feeding behaviour based on direct observations were also gathered. The diet of Bossou chimpanzees was noted on a daily basis while following the chimpanzees. All foods observed being eaten and fresh feeding remains come across were recorded during each chimpanzee follow. These data were used to identify fruit species diversity in the diet and any potential site differences in the consumption of alternative foods, particularly high energy foods during the two study periods over which oil-palm tree surveys were conducted.

Faecal collection

The above data were supplemented by faecal analysis. Faecal samples were collected from all three study sites and preserved in 70% alcohol until analysis (Bossou: N=220; Seringbara: N=28; Yealé: N=45). Three to four times a month, the accumulated faecal samples were analysed and placed in metal sieves with a 1 mm mesh and washed in running water. Once the soluble portion disappeared, the remaining seeds were sorted. Most fruit foods were identified to the species level from the seeds, and classed by genus for those fruiting species that had seeds that were difficult to distinguish (e.g. *Ficus* sp.). Insects that had been consumed (e.g. *Dorylus* spp.) could usually be identified from their chitinous body parts (e.g. heads) that had not been digested. No mammalian matter was recovered from any of the faecal samples collected.

3.8 Behavioural sampling at Bossou

Overview of behavioural sampling methods

The recording of behavioural data is based on two systematic rules (Martin and Bateson, 1993). The first, *sampling rules*, specifies which subject to watch and when. This rule comprises various means of sampling, which includes focal sampling, scan sampling, behavioural sampling and *ad libitum* sampling. The second, *recording rules*, specifies when and how the behaviour is to be recorded. This rule distinguishes between continuous recording and time sampling. During this study, all direct observations of the chimpanzees at Bossou, were collected using a combination of continuous focal sampling and *ad libitum* recording of behaviour (Martin and Bateson, 1993).

All behavioural data were collected using a notebook and a pencil. At least one of my guides and me were equipped with Nikkon 10 x 42 binoculars and I also used a TIMEX (ironman) watch to record time.

Focal animal sampling data

Focal animal sampling means observing one individual for a specified amount of time and recording classes of behaviour. Ideally, the choice of focal animal is determined prior to the observation session. This behavioural sampling method is generally the most satisfactory approach to studying behaviour (Martin and Bateson, 1993). In this study, data on activity budget were collected by performing 20-minute focal samples on all individuals over 3 years of age (Altmann, 1974). If I ever lost sight of the focal individual, I would usually call "time out" before resuming my recording until a full 20-minute focal was completed. On contact with a group of chimpanzees, the order of sampling was usually decided according to which individual had the least number of completed focal samples during that particular month.

The categories of behaviour recorded during focal sampling included:

-*Forage*: the individual is processing one or several food items and consumes it or them. The target item eaten was noted and any tool-use behaviour involved in the foraging episode was identified.

-*Rest*: the individual is sitting or lying on the ground without engaging in any particular activity or the individual is lying inactive in a nest.

-*Play*: the individual is engaged alone or with several other individuals in a playful activity, e.g. chase, jump up and down branches, slap, swing, or decorate itself with leaves or branches or other items.

-*Travel*: the individual is walking on the ground or moving in the canopy for a distance exceeding 10 m.

-*Groom*: the individual is engaged in a "co-ordinated fine manipulation, sometimes linked with the use of lips or tongue, and close inspection of the body surface of the self or of another individual' (McGrew, 1998, p.210).

-*Other:* includes behaviours such as *display* whereby the individual, usually with hair erect and loudly pant hooting, runs energetically along the ground and/or branches of a tree, occasionally shaking and grabbing items in its passage; *mate* whereby the individual is copulating with another individual; *nest* whereby the individual is engaged in the construction of a sleeping or resting structure by bending small twigs or herbs in a circular fashion around the rim on the ground or in a tree or *vocalise*.

This data were used to evaluate percentage time spent engaged in oil-palm feeding activities at the community level in proportion to the total time spent feeding.

Ad libitum data collection

During *ad lib* data collection, no systematic constraints are placed on what is recorded or when. The observer simply notes down whatever is visible and seems relevant at the time (Martin and Bateson, 1993). During daily follows of the Bossou chimpanzees, the identity of any chimpanzee in sight involved in an oil-palm tree directed activity was noted on an *ad lib* basis. Details of the precise activity and sequence of activities (e.g. petiole feeding followed by pestle pounding and then nesting) and of tool-manufacturing performed by individuals were also noted.

3.9 Video recordings and analysis

All tool-use activities performed by Bossou chimpanzees during the two main study periods were filmed using a digital SONY hand-held video camera (Digital Handycam; 120 x Digital Zoom). Some tool-use sessions, focusing particularly on ant-dipping, nut-cracking and pestle pounding, had also been video recorded during previous visits to Bossou in 1997 and 1999, as well as by other members of the Kyoto University Primate Research team. Most of the filming was done, using a tripod, either by myself or by one of the guides, when I was engaged in continuous focal sampling or absent from Bossou. As well as contributing to a video archive of tool-use behaviours observed at Bossou, these video recordings allowed for detailed analyses of tool-use behaviours. The data extracted from these video footages depended on the questions being addressed. Although between-observer reliability in the scoring of the video data was not measured by either calculating the index of concordance for nominal measures or by performing a correlation test for other scales of measurement, all the video analyses were repeated at least twice until divergences in recording were eliminated. Many ant-dipping sessions were also analysed by a second person blind to the hypotheses being tested and again these recording sessions were repeated until agreement in the scoring was established.

3.10 Data analysis

Each result's chapter that is to follow describes in detail the statistical procedures and tests carried out in dealing with the data. When relevant, careful attention was always made to the issue of independence of data points particularly in the analysis of tool-use behaviours. Thus bouts and sessions were always clearly defined. A variety of statistical tests were employed during the course of the analyses of the data depending on the question being addressed and the scale of measurements obtained. The data were systematically checked for normality using a normality probability plot and a Kolmogorov-Smirnov test. If the data deviated significantly from normality, non-parametric two-tailed tests were used; otherwise by default two-tailed parametric tests were employed.

All analyses were performed using SPSS version 10/11 and Minitab version 13. Both Microsoft Excel '97 and the SPSS package were employed in the graphical presentation of the data. Throughout the thesis, the significance threshold was set at 0.05. Although exact ρ-values are not provided, distinctions were made between $\rho<0.05$, $\rho<0.01$ and $\rho<0.001$.

Chapter 4

Nesting behaviour among the chimpanzees of Bossou and Nimba

4.1 Introduction

Nest building or bed making is a behaviour shared by all great ape species. According to McGrew (1992), it reflects the general ability of great apes for environmental problem solving. The classification of nest building in the great apes as a form of tool-use has been controversial (Goodall, 1968; Alcock, 1972; Beck, 1980, Galdikas, 1982); however, Fruth and Hohmann (1996, p.226) proposed that "nest building (in great apes) is not only properly placed within the realm of tool use, but it is also the original tool that led to the mental and physical ability to use tools we see today". Nest building remains the most pervasive form of material skill in great apes.

Nest building in chimpanzees

Chimpanzees (*Pan troglodytes*) have the broadest geographical distribution among all of the great apes and inhabit the widest range of habitats. Many long term and short term studies of chimpanzees with detailed investigations of nest building have been published (e.g. for *Pan t. schweinfurthii*: Goodall, 1962; 1968; Suzuki, 1969; Reynolds and Reynolds, 1965; Ghiglieri, 1984; Brownlow *et al.*, 2001; Basabose and Yamagiwa, 2002; for *Pan t. troglodytes*: Jones and Sabater Pi, 1971; Tutin and Fernandez, 1983, 1984; Wrogemann, 1992; for *Pan t. verus*: Nissen, 1931; De Bournonville, 1967; Boesch, 1978; Baldwin *et al.*, 1981, 1982; Tutin *et al.*, 1983). Fruth and Hohmann (1996) have also presented a detailed review of nesting in chimpanzees and other species of great apes.

Generally, weaned and healthy chimpanzees build an arboreal nest every night. Chimpanzees, like other great ape species, build their arboreal nests by preparing a foundation of solid side branches or forks, bending, breaking and inter-weaving side branches crosswise (Fruth and Hohmann, 1996). They complete this arboreal construction by bending most of the smaller twigs in a circular fashion around the rim. Detached twigs are added for lining (Davenport, 1967; Goodall, 1968; Horn, 1980). Chimpanzees also construct nests during the day for resting. Day nests are generally arboreal, but day nests on the ground have also been reported at Taï (Boesch, 1995) and in the Nimba mountains (Matsuzawa and Yamakoshi, 1996), Côte d'Ivoire and at Bossou, Guinea (pers. obs.; Sugiyama and Koman, 1979b, Sugiyama, 1981). Ground nests have been observed in other parts of Guinea (Ham, pers. comm.; Fleury-Brugière, 2001), at Gombe, Tanzania, Budongo (Whiten *et al.*, 1999), Kalinzu (Furuichi and Hashimoto, 2000) and Bwindi National Park, Uganda (Maughan and Stanford, 2001). Matsuzawa and Yamakoshi (1996) suggested that some of the ground nests found in Yealé in the Nimba Mountains region might actually serve as night nests. However, this proposition remains to be confirmed via direct observation of the chimpanzees' nesting behaviour. In addition, 3 ground nests discovered in the Kalinzu forest in Uganda were proposed to be night nests due to their association with elaborately constructed arboreal nests of the same age presumed to be used at night (Furuichi and Hashimoto, 2000). Moreover these 3 nests contrasted remarkably in structure to terrestrial nests used by day that were described to be more like 'cushions' (Furuichi and Hashimoto, 2000). Height of chimpanzee nests varies between 0 and 45 m, with most nests being constructed between 10-20 m (Fruth and Hohmann, 1996).

Chimpanzees are selective in their choice of nesting site. Most studies of nesting in chimpanzees have revealed that nests accumulate in specific areas depending on forest type and on proximity to water and food resources (Baldwin *et al.*, 1982; Groves and Sabater Pi, 1985; Sept, 1992, Kortlandt, 1992; Pruetz *et al.*, 2002). With respect to the material for nest construction, Goodall (1968) claimed that almost any type of tree might be used for nesting; however, she did not compare availability and choice of nest material. Wrogemann (1992) provided one of the first detailed studies on availability and choice of nest material in chimpanzees, based on data collected at Lopé, Gabon. She demonstrated that chimpanzees at Lopé are selective for tree height and that they use 56 species of trees for nest construction. Brownlow *et al.*'s (2001) study of the Sonso chimpanzee community at Budongo, Uganda, so far represents the most comprehensive study of nesting behaviour in chimpanzees, and provides strong evidence for tree species preference for nesting while controlling for availability. Basabose and Yamagiwa (2002) also showed that chimpanzees at Tshibati, Kahuzi-Biega National Park in the Democratic Republic of Congo demonstrate a strong preference for night-time nesting tree species.

Detailed descriptions of nest building and types of nest constructions in chimpanzees are provided by Bolwig (1959) and Goodall (1962, 1968). They observed that nests range from very rough and superficial structures, usually day nests, to carefully and elaborately built nests. Brownlow *et al.* (2001) showed that day nests were indeed structurally simpler than night nests. In general, chimpanzees do not hesitate to integrate trees when these interface (resulting in the construction of an integrated nest), but more commonly they only use one tree. The maximal number of trees integrated in a single nest is 4 at Mt. Assirik, Senegal (cf. Fruth, 1995), and the largest number of nests found in a single tree that has ever been reported is 10, observed by Goodall (1962) at Gombe, Tanzania.

Re-use of nests, about which little has been published, seems more frequent the drier the habitat, nest sites being limited in such habitats (Hiraiwa-Hasegawa, 1989). Regarding sex differences, Hiraiwa-Hasegawa (1989) reported that male chimpanzees less often constructed day nests than females at Mahale, Tanzania. A similar result was obtained by Brownlow *et al.* (2001) in their study of the Sonso chimpanzee community at Budongo, Uganda. Brownlow *et al.* (2001) also found that males from this community nested lower than females.

Although individual chimpanzees may occasionally nest solitarily, nest building is often a social event. Indeed, several members of a community will converge at dusk, climb neighbouring trees and undertake nest construction, thus forming a nest group or nest party. Bernstein's (1962) study on the response to nesting materials of wild-born and captive-born chimpanzees at the Yerkes Regional Primate Research Centre, revealed that nesting was observed in all the wild-born animals and in only a few of the captive-born chimpanzees. Two follow-up studies (Bernstein, 1967, 1969) revealed that the laboratory-born adult chimpanzees failed to build nests when provided with suitable materials even after being paired with animals that constructed nests every night. These studies clearly suggest that nest building is not independent of early experience and some form of individual and/or social learning is involved in the acquisition of this skill. In the wild, infants benefit from a great deal of exposure to nest construction and opportunities for observation and practice. Infants between 2 and 3 years of age will often practice bed making, although they may continue to sleep with their mother for up to five and a half years (Clark, 1977, cited in Anderson, 1984). Indeed, Hiraiwa-Hasegawa (1989) noted that chimpanzee infants at Mahale made day nests ten times more frequently than did adults. Goodall (1968) also noted that infants as young as 8 months old begin to build rudimentary nests in play. Finally, Bernstein (1962) proposed that if nesting is a learned behavioural pattern in the wild chimpanzee, then it could probably be considered a "tradition". He then predicted that nests constructed by separate and isolated groups of chimpanzees in the wild would vary in specific detail.

Culture in nest building?

Baldwin *et al.* (1981) compared nests made by two different populations of chimpanzees, one in Rio Muni, Equatorial Guinea and the other at Mt. Assirik, Senegal. Their study currently represents the only direct comparative study of nesting behaviour of two chimpanzee populations. They concluded that there were real differences in the nests built by the two populations, e.g. concerning nest height, cover, girth of tree used for nesting, and that these differences could all be attributed directly or indirectly to environmental factors in the habitat. Thus, a cultural element to nest building behaviour in chimpanzees was not demonstrated by this comparative study. Further comparative studies of this kind are, however, clearly lacking and needed.

It appears though that chimpanzees and other great apes readily adapt their nest building behaviour to environmental conditions and that no real evidence of cultural elements emerges from any studies to date. Indeed, as indicated by the above-mentioned studies, the techniques employed in nest building in chimpanzees depend on the site and on the availability of materials. However, several studies of nest building in chimpanzees also clearly demonstrate that they are highly selective toward specific tree species.

Females construct single nests for themselves and their dependent offspring and weaned individuals build and use their own nest. The learning mechanisms involved in the acquisition of nest-making behaviour are likely to involve some combination of stimulus enhancement, trial and error learning and imitation as suggested by Baldwin *et al.* (1981). Indeed, there exist several lines of evidence suggesting that great apes learn to build their night nests through social learning (Bernstein, 1962, 1967, Anderson, 1984). In spite of the fact that learning is involved in the development of successful nest building, studies of nesting behaviour still have not shown convincing evidence of cultural variation.

However, all species of great apes show some inter-populational differences in nest building behaviour (for review c.f. Fruth and Hohmann, 1996). Tree species preference for nest building is a good example, as exemplified by chimpanzee nesting in oil-palms (*Elaeis guineensis*). Nesting in oil-palms is not common to all sites where chimpanzees have been studied and oil-palms are present. It has been reported in a recent primate survey of Guinea-Bissau (Gippoliti and Dell'Omo, 1996) and some areas of western Guinea (De Bournonville, 1967; Albrecht and Dunnett, 1971; Ham, pers. comm.) and is commonly observed at Bossou, south-eastern Guinea, although Nissen (1931) in his early account of nesting habits of Guinean chimpanzees had noted that palms were not used for nesting. Goodall (1968) reported nesting in oil-palms by chimpanzees in the Semliki forest, Queen Elizabeth National Park, Uganda. She also described nesting in oil-palms at Gombe, Tanzania, as a short-lived fashion adopted by this community of chimpanzees.

Given the wide distribution of chimpanzees across equatorial Africa, with many of them now living in isolated populations, one might expect inter-population variation in nesting behaviour. However, if variation exists, it is important to examine how much of it is environmentally influenced, e.g. type of vegetation available and used. Some of this variation may not exhibit any clear environmental determinant. Such variation may represent socially transmitted patterns of behaviour passed on from one generation to the next within and even perhaps across communities, thus constituting social customs, that might be termed cultural (Baldwin *et al.*, 1981). However, up to now studies of nest building in chimpanzees and great apes in general have failed to convincingly demonstrate cultural variation in nesting behaviour.

4.2 Aims

-Nesting behaviour of the chimpanzees of Bossou will be explored in detail to assess whether these apes express a nesting preference for certain habitat types or particular plant species. In addition, I will attempt to discern community-wide patterns in nesting variables and environmental influences on nesting behaviour within this community of chimpanzees.

-Age and sex class differences in nesting behaviour will also be investigated.

-Nest height, nesting tree DBH, tree integration, plant species preference and habitat preference for nesting will be explored for the two Nimba sites – Seringbara and Yealé.

-Differences in nesting behaviour among the three sites will be addressed, with reference to the community-wide patterns uncovered above. The comparison will address environmental influences on plant and habitat choice, and I will speculate on cultural aspects of nesting behaviour in chimpanzees.

4.3 Methods

Seven hundred and seventy one nests were recorded from Bossou, and 281 and 377 nests were encountered respectively at the Seringbara and the Yealé sites (see Table 4.1). Nesting data were collected over three rainy season periods: July-September, 1999; June-September, 2000; June-September, 2001. None of the Nimba sites' nests were seen to be constructed, whereas 27.9% (n=215) of the nests recorded at Bossou were reliably assigned to the individual chimpanzee who was responsible for the construction.

Table 4.1. Summary of nesting data gathered from Bossou and the two Nimba sites.

Site	No. Nests Recorded	No. Nest Groups	Single nests	No. Day Nests	No. Night Nests	No. Nests (Type Unknown)	No. Individually Identified Nests	No. Nests Identified at the Species Level
Bossou	771	132	50	142	256	373	215	745
Seringbara	281	45	28	23	169	89	0	246
Yealé	378	72	68	21	222	135	0	332

Table 4.2. Summary of the number of 50 m transects carried out at all three sites where nests were recorded, in relative proportion to habitats available.

Site	No. Transects	Surface Area (m^2)	Habitat Type (No. of 50 m transects)				
			Primary	Secondary	Riverine	Old Field	Marantaceae
Bossou	50	25,000	20	22	6	2	0
Seringbara	40	20,000	22	4	10	0	4
Yealé	48	24,000	34	2	12	0	4

The following variables were recorded, measured or estimated for each nest:

1.Plant species used in nest building: Most tree or plant species employed in nest construction were identified at the species level or at the family taxon level. Species were determined by the morphological features of the trunk, bark, sap, leaves and fruit (Letouzey, 1986; Adam, 1971-83). Some plant species could not be identified taxonomically. However, some of these were identified by their vernacular name by the local guides or villagers. For integrated nests (comprised of more than one tree or liana), all plant species used in nest construction were noted whenever possible.

2.Diameter at Breast Height (DBH): The circumference (C) of each tree used in nest building was measured at breast height (=1.5 m) using a tape measure. The stem diameter (DBH) was calculated, thereafter, by using the formula $C=2\pi r$, whereby $DBH=2r=C/\pi$. Note: No liana species at any of the three sites provided the main frame for nest construction.

3.Nest type: For each nest encountered, I noted, whenever possible, whether it was a day nest or a night nest. Night nests were nests in which the chimpanzee remained after sunset, usually through the night until sunrise. Day nests were nests made or used solely during daylight hours. In their study of nesting behaviour among the chimpanzees of Budongo, Uganda, Brownlow *et al.* (2001) showed that night and day nests were distinct structurally; with night nests more strongly built than day nests. Therefore, new nests that were elaborate in their construction and were associated with the presence of faeces below the nest and characterised by a strong smell, indicating that the chimpanzee had lain in it for a long period of time, were classed as night nests, while nests that were simple in construction and thought structurally too weak to support a chimpanzee overnight, were classed as day nests. Many nests encountered during this study were not classed as either night or day nests. Direct observations of nesting behaviour at Bossou during the rainy season revealed that some day nest constructions could be as elaborate as that of night nests, thus unless the above criteria were all met then nest type was conservatively recorded as unknown.

4.Height of the nest: Nest height was estimated from ground level. Nest height data were always recorded based on a consensus between myself and a minimum of two guides. These data were subsequently classed into height classes of 5 m intervals.

5.Age of nest: Four age classes for nests were used (*sensu* Tutin and Fernandez, 1983): 1) New: leaves still green and healthy: nest probably less than a couple of days old; 2) Recent: leaves still green but the state of the leaves and branches indicate that this nest is more than a few days old and most likely less than a week old; 3) Old: nest is mainly made up of dead leaves, but is still intact, nest most probably less than a month old; 4) Very old: nest structure still visible, although leaves are absent, having dried up and fallen off. Only nests that were classed as either new or recent were retained for analysis, since I wanted to concentrate on nesting behaviour during the rainy season period only.

6.Number of nests of the same age per tree.

7.Nest integration: Number of trees employed in a nest contruction.

8.Number of nests in a nest group. A nest group was defined as 2 or more nests of the same age constructed and used within a maximum of 30 m from each other. This 30-m criterion for classifying nests as belonging to the same nest group was established on the basis of the maximum distance observed between two nests at Bossou where parties of chimpanzees were regularly seen making day or night nests together.

9.Habitat type: Five different habitat types were recognised: 1) Primary forest (excluding Riverine areas); 2) Secondary forest; 3) Riverine forest; 4) Recently abandoned fields; 5) Marantaceae forest, dominated by herbaceous plants belonging to the Marantaceae and Zingiberaceae family.

10.Nest re-use: Nest re-use was established on the basis of direct observations of nesting behaviour, whereby a chimpanzee would construct a "new" nest by folding new branches or leaves over an old nest. Nest re-use was also occasionally established on an indirect basis when two distinct layers of vegetation at different stages of decay (the newest and fresher layer being the one above) could clearly be discerned, since when an old nest is being re-used, the chimpanzee will supplement it with fresher material.

11.Altitude category: At the Yealé site in the Nimba Reserve, the mountain slopes progressively at first and then more steeply up to the summit. Nests were ascribed to one of three altitude categories on the basis of location along the mountain face: 1) Lower altitude (<500 m); 2) Mid altitude (500-800 m); 3) Upper altitude (>800 m).

At Bossou, whenever possible, nest builder identity, age and sex were recorded in order to examine age and sex class differences in nesting behaviour. Age-class categories followed those employed by Sugiyama (1999): 1) Infant (1-3 years old); 2) Juvenile (4-7 years old); 3) Adolescent (8-11 years old) and 4) Adults (>11 years old).

Chimpanzee selectivity for nesting plant species was assessed by examining the relationship between availability of potential nesting tree species in the habitat and choice by the chimpanzees. Systematic analysis of tree species availability at each site was based on randomly set up north-south and east-west vegetation transects (50 m x 10

m) in approximate proportion to the availability of different habitat types available to the chimpanzees (see Table 4.2). All trees with a DBH above 5 cm were identified and their circumference measured using a tape measure.

4.4. Data analysis

Sample sizes for the different variables recorded were not necessarily constant, reflecting missing values for certain nest records. For purposes of statistical testing, nest heights were grouped in 5 m intervals and height was recorded as the mid-point of the interval (c.f. Brownlow *et al.*, 2001). To obtain mean heights, interval midpoints were summed and the result was divided by the total number of nests.

For nests incorporating more than one tree species, as in integrated nests, a data point for preference was attributed to the principal tree in the nest, i.e. the tree providing the main support for the nest frame. In addition, when looking at the DBH data, only the DBH of the principal tree was considered.

The data were checked for normality using a normality probability plot and a Kolmogorov-Smirnov test. Non-parametric or parametric tests were employed as appropriate in the analysis of the data.

To determine preference in tree species used, Manly's alpha was calculated for each tree species used for nesting overall and for day and night nests separately at each site. This index of preference takes into account the prevalence of each tree species within the chimpanzees' habitat and was calculated using the following formula (see Krebs, 1999):

$$\alpha_i = \frac{r_i}{n_i} * \frac{1}{\Sigma(r_j/n_j)}$$

where α_i = Manly's α (preference index) for tree species i

r_i, r_j = Proportion of tree species i or j used for nesting (i and $j = 1, 2, 3, ..., m$)

n_i, n_j = Proportion of tree species i or j available in the environment

m = Number of tree species available for nesting, established on the basis of the transect data and nesting data.

Preference was rejected for Manly's alpha values less than $1/m$ and accepted for values greater than $1/m$, i.e. 0.007692 at Bossou, 0.005714 at Seringbara and 0.005181 at Yealé.

4.5. Results

Nesting behaviour, nest features and characteristics at Bossou

Nest height, number of nests per tree and nesting tree DBH

Mean overall nest height was 13.7 m, 13.9 m for day nests and 13.0 m for night nests (see Table 4.3). Approximately 40% of nests, whether overall, day or night nests, were built between 10 and 15 m above ground (see Table 4.4). Very few nests overall or for night-time were built above 30 m, while no day nests were built higher than 30 m (see Table 4.4). Only one day ground nest, constructed by an adolescent male, Yolo, by bending over small tree saplings onto the ground, was recorded. Finally, no difference in nest height was uncovered between day and night nests (Mann Whitney U-test: N=382; z=-1.515; *n.s.*) (see Table 4.3).

Table 4.3. Summary statistics of nest height overall and for night and day nests at Bossou.

	No.	Mean (m)	Median (m)	SD	Range (m)
Overall	755	13.7	12.5	5.7	2.5-37.5
Day Nests	137	13.9	12.5	5.5	2.5-27.5
Night Nests	245	13.0	12.5	5.0	2.5-32.5

Table 4.4. Nest height frequency and percentage for each 5 m height class interval at Bossou.

Height Interval (m)	Overall		Day		Night	
	Frequency	%	Frequency	%	Frequency	%
0-5	12	1.6	4	2.9	4	1.6
5-10	190	25.2	27	19.7	65	26.5
10-15	293	38.8	59	43.1	105	42.9
15-20	168	22.3	27	19.7	53	21.6
20-25	50	6.6	15	10.9	11	4.5
25-30	36	4.8	5	3.6	6	2.4
30-35	5	0.7	0	0	1	0.4
35-40	1	0.1	0	0	0	0
TOTAL	**755**	**100**	**137**	**100**	**245**	**100**

Mean tree DBH was 32.5 cm overall (N=715; SD=19.5 cm; range: 5.1-131.8 cm), 40.2 cm for day nests (N=125; SD=19.3 cm; range: 5.7-116.9 cm) and 32.1 cm for night nests (N=218; SD=20.5 cm; range: 5.1-114.6 cm). An analysis of tree DBH and nest height revealed a significant positive correlation between these two variables, overall and for both day and night nests (overall: R_s=0.583; N=711; ρ<0.001; day nests: R_s=0.476; N=121; ρ<0.001; night nests: R_s=0.637; N=218; ρ<0.001). Tree DBH (i.e. excluding lianas and oil-palms) is generally accepted to reflect tree height up to the first branches (Letouzey, 1986). This correlation indicates that nest height is influenced by the height of the tree in which the chimpanzee chooses to nest.

Trees bearing night nests most often accommodated single nests and the maximum number of night nests belonging to the same nest group recorded in a single tree was 5 (see Table 4.5). For day nests, slightly more than 30% of trees supported single nests, while nearly 40% had two and the maximum number of day nests within a single tree was 8 (see Table 4.5). The number of nests per tree was significantly positively correlated with the DBH of the tree, overall and for trees supporting day or night nests analysed separately (overall: $R_s=0.345$; $N=429$; $\rho<0.001$; day: $R_s=0.387$; $N=63$; $\rho<0.01$; night: $R_s=0.271$; $N=167$; $\rho<0.001$). This result supports the idea that the larger the DBH, the more nests the tree can accommodate, and that the chimpanzees are behaving consequently.

Table 4.5. Percentage and frequency of trees supporting different numbers of nests belonging to the same age group, overall, and for day and night nests for nest groups.

	No.	**Percentage (Freq.)**							
No. of nests/tree		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Overall	473	67.7 (320)	22 (104)	5.7 (27)	2.7 (13)	1.1 (5)	0.6 (3)	0 (0)	0.2 (1)
Day Nests	72	34.7 (25)	38.9 (28)	12.5 (9)	8.3 (6)	1.4 (1)	2.8 (2)	0 (0)	1.4 (1)
Night Nests	201	77.6 (156)	15.4 (31)	3.5 (7)	2.5 (5)	1 (2)	0 (0)	0 (0)	0 (0)

Nest integration and re-use

Just over 90% of overall, day and night nests were constructed in a single tree (see Table 4.6). The maximum number of integrated trees recorded for a nest construction was 4. No day nests were constructed using more than two trees, while nearly 2% of night nests were built with a combination of three to four trees (see Table 4.6). No significant difference emerged though in the proportion of the observed and expected number of integrated nests between day and night nests ($\chi^2(1, N=297)=0.425$; *n.s.*).

A significant negative correlation emerged between the DBH of the principal tree and the number of integrated trees employed in the construction of the nest, overall and for day and night nests analysed separately (overall: $R_s=-0.153$; $N=715$; $\rho<0.001$; day nests: $R_s=-0.181$; $N=125$; $\rho<0.05$; night nests: $R_s=-0.251$; $N=218$; $\rho<0.001$).

Moreover, there was a significant difference in median tree DBH between nests built in a single tree and nests constructed by tree integration, overall and for day and night nests analysed separately (overall: Mann Whitney U-test: N=715; z=-4.075; ρ<0.001; day nests: Mann Whitney U-test: N=125; z=-2.018; ρ<0.05; night nests: Mann Whitney U-test: N=218; z=-3.672; ρ<0.001) (see Table 4.7). In addition, nests built in a single tree were constructed significantly higher than nests constructed by tree integration (overall: Mann Whitney U-test: N=755; z=-2.078; ρ<0.05) (see Table 4.7). This result suggests that nest integration is influenced by the DBH of the principal tree providing the main frame for nest construction. Considering that tree DBH is correlated with tree crown size (Chapman *et al.*, 1992), this would indicate that trees exhibiting a small DBH are likely to provide either inadequate support or insufficient foliage for nest building. When constructing nests in trees with a small DBH, chimpanzees tend to resort to employing branches and leaves from neighbouring trees to successfully complete a nest able to sustain their weight.

Table 4.6. Percentage and frequency of nests constructed in a single tree or resulting from the combination of several trees.

	No.	**Percentage (Freq.)**			
Number of trees used		**1**	**2**	**3**	**4**
Overall	770	94.8 (730)	4.7 (36)	0.4 (3)	0.1 (1)
Day Nests	141	92.2 (130)	7.8 (11)	0 (0)	0 (0)
Night Nests	256	90.2 (231)	8.2 (21)	1.2 (3)	0.4 (1)

Table 4.7. Summary statistics of nesting tree DBH (cm) overall, for day and night nests, and overall nest height (m) of single tree nests and integrated nests at Bossou.

Variable	Nest Type	No. of Trees	No.	Mean	Median	SD	Range
DBH (cm)	**Overall**	**Single**	**678**	**33.1**	**30.6**	**19.7**	**5.4-131.8**
		Integrated	**37**	**22.0**	**19.8**	**13.2**	**5.1-73.2**
	Day Nests	**Single**	**117**	**41**	**35.6**	**19.6**	**5.7-116.9**
		Integrated	**8**	**27.7**	**26.2**	**6.8**	**19.8-36.9**
	Night Nests	Single	193	33.6	30.9	20.8	6.4-114.6
		Integrated	25	21.2	17.8	14.9	5.1-73.2
Height (m)	**Overall**	Single	715	13.8	12.5	5.8	2.5-37.5
		Integrated	40	11.7	12.5	3.8	2.5-22.5

Nest re-use was rarely observed at Bossou, occurring at nearly equal frequency whether by day or night. Sub-adults tended to re-use nests more often than adults. Only 1.9% of all nests recorded (15/770), 2.8% (4/141) of day nests and 3.5% (9/256) of night nests constructed in trees were re-used. Most records of nest re-use occurred in riverine forest (40%), with 33.3% in abandoned fields, 20% in secondary forest and 6.7% in primary forest. Of the instances of nest re-use for which the identity of the individual could be established (N=8), 75% were carried out by sub-adults (3 adolescents: 2 females: Fotayu ($N_{\text{day nest}}=2$; $N_{\text{night nest}}=1$), Nto ($N_{\text{night nest}}=1$), 1 male: Yolo ($N_{\text{day nest}}=1$), and 1 juvenile female: Juru ($N_{\text{night nest}}=1$)), while only 25% ($N_{\text{day nest}}=1$; $N_{\text{night nest}}=1$) were carried out by one adult female, Pama. Of the 4 instances of nest re-use for night-time nesting for which individual identification was possible, 3 were observed in oil-palms in abandoned fields and were performed by sub-adults, i.e. Fotayu, Nto, Juru. However, since the sample size for observed instances of nest re-use is small, no pattern in age-class differences can be statistically confirmed based on the data presented above, and only trends are noted. Over 90% of all instances of nest re-use (14/15) occurred in trees that bore some consumable item for the chimpanzees in the form of either fruit, leaves, petiole, apical meristem or gum at the time of nesting.

The only exception was the re-use of a nest in a *Carapa procera* tree, which was used for night-time nesting.

Habitat preference

The most preferred nesting habitat for the Bossou chimpanzees, overall and by day, was secondary forest, with abandoned fields being the second preferred choice. Together, these habitats accounted for 75.8% and 87.7% of all nest groups or single nests recorded encountered respectively overall and by day (see Table 4.8).

For night nests, nest groups were separated from single nests, i.e. those constructed by a solitary male or female with or without dependent offspring and not associated with any other nests within a 30 m radius, in order to assess any differences in habitat use in nesting behaviour between singletons and groups. No such distinction was made for day nests or overall, since although some day nests occurred singly, the presence of other chimpanzees in the vicinity could not be excluded. Indeed, some chimpanzees may rest by day without constructing a nest.

At night, nest groups occurred predominantly in both secondary forest areas and abandoned fields (see Table 4.8). In contrast to daytime nesting, at night, Bossou chimpanzees tended to nest less frequently in groups in secondary forest and more often sought riverine forest areas, rarely used by day, or abandoned fields (see Table 4.8). Almost all single night nests recorded were located in secondary forest, while riverine forest and abandoned fields were not observed to be used by 'solitary' individuals.

Table 4.8. Frequency and percentage of nest groups and/or single nests in each habitat type at Bossou overall and during day- and night-time.

	Overall		**Day Time**		**Night Time**			
					Nest group		***Single Nest***	
Habitat Type	**Freq.**	**%**	**Freq.**	**%**	**Freq.**	**%**	**Freq.**	**%**
Primary	20	11.0	5	8.8	2	4.5	3	25
Secondary	99	54.4	36	63.2	18	40.9	9	75
Riverine	24	13.2	2	3.5	6	13.6	0	0
Abandoned field	39	21.4	14	24.5	18	40.9	0	0
TOTAL	182	100	57	100	44	100	12	100

Table 4.9. Percentage of nests in the 10 (11 for night nests) most commonly used tree species overall (N=770) and for day (N=141) and night nests (N=256) (in **bold**: tree species appearing in all three columns; Pref.: Preference; α: Manly's Alpha).

Tree Species	**All Nests (%)**	α	**Pref.**	**Tree Species**	**Day Nests (%)**	α	**Pref.**	**Tree Species**	**Night Nests (%)**	α	**Pref.**
Elaeis guineensis	18.44	0.1098	Yes	***A. adianthifolia***	30.5	0.2414	Yes	***E. guineensis***	29.69	0.2090	Yes
Musanga cecropioides	12.60	0.0321	Yes	***M. cecropioides***	21.99	0.0912	Yes	***M. cecropioides***	7.81	0.0236	Yes
Carapa procera	9.74	0.0149	Yes	***A. zygia***	10.64	0.0309	Yes	***T. heudelotii***	5.47	0.0346	Yes
Albizia adianthifolia	6.75	0.0329	Yes	***P. bicolor***	6.38	0.0309	Yes	*P. angolensis*	5.08	0.0357	Yes
Trichilia heudelotii	4.16	0.0223	Yes	***E. guineensis***	4.96	0.0480	Yes	***P. bicolor***	4.69	0.0165	Yes
Pseudospondias microcarpa	4.03	0.0065	Not	***T. heudelotii***	4.96	0.0432	Yes	*C. procera*	4.3	0.0078	Yes
Albizia zygia	3.90	0.0070	Not	*Tetrapleura tetraptera*	3.55	0.3088	Yes	*Terminalia ivorensis*	3.91	0.0354	Yes
Parkia bicolor	3.51	0.0104	Yes	***S. tragacantha***	2.84	0.0023	Not	*P. microcarpa*	3.52	0.0067	Not
Sterculia tragacantha	2.86	0.0014	Not	*Samanea dinklagei*	2.84	0.1235	Yes	***A. adianthifolia***	2.73	0.0157	Yes
Pycnanthus angolensis	2.08	0.0124	Yes	*Spondias mombin*	2.84	0.0137	Yes	***A. zygia***	2.73	0.0058	Not
								S. tragacantha	2.73	0.0016	Not
Total Percentage	**68.1**				**91.5**				**72.7**		

Tree species preference

Although 130 tree species were recorded during vegetation transects and were thus available to the chimpanzees for nesting, only 67 species were used for nest construction (see Table 4.9). Overall, 68.1% and 52.7% of all nests were built respectively in 10 and 5 tree species. When considering Manly's alpha index of preference, the 5 most used tree species for nesting overall were significantly preferred by the chimpanzees, while among the 10 most used species, 3 were not preferred. These 3 species happened to provide fruit, i.e. *Pseudospondias microcarpa* and *Sterculia tragacantha* or gum, i.e. *Albizia zygia*, during the rainy season, the period over which nests were recorded (see Table 4.9).

For day nests, the 10 and 5 most frequently used tree species provided the substrate for respectively 91.5% and 74.5% of all nests recorded, and a total of 19 tree species were used (see Table 4.9). Only one of the 10 most commonly used species, i.e. *Sterculia tragacantha*, proved not to be a preferred species according to Manly's alpha preference index (see Table 4.9). Of these 10 species, 7 were important food resources for the chimpanzees during the study periods: 4 provided fruit (*Musanga cecropioides, Trichilia heudelotti, Spondias mombin, Sterculia tragacantha*), 2 gum (*Albizia zygia* and *A. adianthifolia*) and 1 (*Elaeis guineensis*: the oil-palm) several different consumable plant parts. The other 3 species, i.e. *Parkia bicolor*, *Tetrapleura tetraptera* and *Samanea dinklagei*, all belong to the Mimosaceae family, to which the 2 *Albizia* species also belong. The Mimosaceae family exhibits small, bipinnate leaves, which seem to be preferred by the chimpanzees for nesting purposes.

Seven of the tree species used for nest building by day were also among the 11 most frequently employed by night, but these were used at differing frequencies (see Table 4.9). During night-time nesting, the most frequently used tree species was the oil-palm (see Plate 4.1). Chimpanzees would often feed on the petiole of young fronds, and pestle pound or feed on palm fruit, before nesting in oil-palms. Of 47 direct observations of night-time nesting in oil-palms, chimpanzees were recorded to have consumed some part of the tree in 52.1% (N=25) of cases before initiating nest construction.

Plate 4.1. Oil-palm nest at Bossou.

For night nests, 72.7% and 51.7% of nests were respectively constructed in 11 and 5 different tree species. A total of 42 tree species were recorded as being used for night nest construction. Out of the 11 most frequently used tree species, 3 were not preferred and were the same as those noted for the overall nesting data; however, the 5 most frequently employed tree species were all preferred by the chimpanzees (see Table 4.9). Seven of the 11 species provided food for the chimpanzees during the study periods over which nests were recorded, while 4 (*Carapa procera, Parkia bicolor, Pycnanthus angolensis* and *Terminalia ivorensis*) were only used for nesting (see Table 4.9). Based on Table 4.9, 6 of the 7 food-providing tree species used for nesting by night were the same as those employed by day. *Spondias mombin*, which was commonly used by day, was not commonly employed or even preferred by night, however, *Pseudospondias microcarpa* was not a preferred nesting tree species either by day or by night, but was more commonly used for night-time nesting.

Age and sex class differences

Nesting data on 20 individuals (10 adults: 8 females and 2 males; 6 adolescents: 4 females and 2 males; 2 juvenile females and 2 infants: 1 male and 1 female) were gathered. However, since only two infant nests were recorded, this age-class was excluded from the analysis. Integrated nests were considered separately in order to avoid confounding the analysis.

There was no difference in either nest height or DBH of nesting tree between adults, adolescents and juveniles whether overall or for day nests (see Table 4.10). For night nests, due to insufficient data for juveniles, juveniles and adolescents were regrouped into a sub-adult class of their own. For night nests, no significant difference in nest height or tree DBH emerged between sub-adults and adults. Finally, overall, there was no significant difference between the three age classes in the number of integrated nests produced, although juveniles were never observed to integrate trees during nest construction ($\chi^2(2, N=213)=5.083$; *n.s.*). Tree integration was observed in 8.3% (11/133) of adult nests and 16.6% (11/66) of adolescent nests.

Since no age-class differences emerged above, all females and males, excepting infants, were included in the sex-class comparison. No sex differences emerged in nest height or DBH of nesting tree whether overall or for day and night nests analysed separately (see Table 4.11). Moreover, overall, there was no difference between females and males in the proportion of integrated nests produced ($\chi^2(1, N=213)=0.169$; *n.s.*). Tree integration was observed in 10.8% (18/167) of nests constructed by females and 8.7% (4/46) of nests built by males.

Table 4.10. Summary data and statistical comparison of nest height and DBH of nesting trees, excluding integrated nests, between age-classes at Bossou.

Nest Type	Nesting Variable	Age-Class	No.	Mean	Median	SD	Range	Statistical Test
Overall	Height (m)	Adult	111	13.4	12.5	5.4	2.5-27.5	Kruskal-Wallis test:
		Adolescent	52	14.3	12.5	5.5	2.5-27.5	$\chi^2(2, N=176)=2.443$; *n.s.*
		Juvenile	13	15.1	12.5	4.8	7.5-22.5	
	Tree DBH (cm)	Adult	96	38.2	32.8	18.2	9.2-93.0	Kruskal-Wallis test:
		Adolescent	46	38.6	34.1	21.7	8.9-116.9	$\chi^2(2, N=152)=0.148$; *n.s.*
		Juvenile	10	41.7	33.9	21.5	20.6-76.1	
Day Nests	Height (m)	Adult	56	14.0	12.5	5.7	2.5-27.5	Kruskal-Wallis test:
		Adolescent	37	15.3	12.5	5.9	2.5-27.5	$\chi^2(2, N=103)=2.029$; *n.s.*
		Juvenile	10	16.0	12.5	5.3	7.5-22.5	
	Tree DBH (cm)	Adult	54	41.3	35.6	18.5	14.0-76.4	Kruskal-Wallis test:
		Adolescent	35	42.0	34.8	20.8	131-116.9	$\chi^2(2, N=97)=0.006$; *n.s.*
		Juvenile	8	44.0	33.9	23.1	20.6-76.1	
Night Nests	Height (m)	Adult	55	12.8	12.5	5.1	2.5-27.5	Mann Whitney-U test:
		Sub-adult	18	11.9	12.5	2.9	7.5-17.5	$z=-0.293$; *n.s.*
	Tree DBH (cm)	Adult	42	34.3	29.3	17.2	9.2-93.0	Mann Whitney-U test:
		Sub-adult	13	28.4	22.9	20.7	8.9-90.1	$z=-1.616$; *n.s.*

Table 4.11. Summary data and statistical comparison of nest height and DBH of nesting tree between females and males at Bossou.

Nest Type	Nesting Variable	Sex	No.	Mean	Median	SD	Range	Mann Whitney U-test
Overall	**Height (m)**	Female	137	13.9	12.5	5.6	2.5-27.5	z=-0.077; *n.s.*
		Male	39	13.4	12.5	4.6	2.5-22.5	
	Tree DBH (cm)	Female	124	39.0	34.0	19.8	9.2-116.9	z=-0.223; *n.s.*
		Male	28	36.8	32.6	18.1	8.9-90.1	
Day Nests	**Height (m)**	Female	83	14.9	12.5	5.8	2.5-27.5	z=-0.880; *n.s.*
		Male	20	13.5	12.5	5.5	2.5-22.5	
	Tree DBH (cm)	Female	81	42.2	35.6	20.1	13.1-116.9	z=-0.447; *n.s.*
		Male	16	39.6	34.2	16.8	19.8-76.1	
Night Nests	**Height (m)**	Female	54	12.3	12.5	5.0	2.5-27.5	z=-1.455; *n.s.*
		Male	19	13.2	12.5	3.4	7.5-17.5	
	Tree DBH (cm)	Female	43	32.8	28.7	17.8	9.2-93.0	z=-0.510; *n.s.*
		Male	12	32.9	31.1	19.6	8.9-90.1	

Nest features and characteristics at Seringbara, Nimba

Nesting height, number of nests per tree and DBH

Mean overall nest height was 11.9 m, 7.5 m for day nests and 12.5 m for night nests (see Table 4.12). Overall and for night nests, the height class that comprised the most nests, i.e. between 5-10 m, contained just over 30% of nests, while nearly 40% of day nests were built between 0-5 m (see Table 4.13). Thus, whether overall, or for day or night nests, at least 50% at Seringbara were constructed between 5-15 m (see Table 4.13).

Nearly 9% (25/281) of all nests recorded and 34.8% (8/23) of day nests found were ground nests. Among the 25 ground nests encountered, 18 were made from saplings, while 7 were lined using THV material (Terrestrial Herbaceous Vegetation), mainly plants belonging to the Marantaceae and Zingiberaceae family. Nine ground nests were single nests, not associated with any other nests, while the other ground nests were in close proximity to others of the same age category (see Table 4.14). Four nest groups were comprised of only ground nests and two of a combination of terrestrial and arboreal nests (see Table 4.14). Based on the elaborate structure of these ground nests and the associated nests, it seems possible that some of these ground nests may have been used at night rather than by day; however, only direct observation of nest building behaviour at this site will reveal whether ground nests are used for night-time nesting or not.

Table 4.12. Summary statistics of nest height overall and for night and day nests at Seringbara.

	No.	Mean (m)	Median (m)	SD	Range (m)
Overall	277	11.9	12.5	7.6	2.5-37.5
Day Nests	23	7.5	7.5	5.0	2.5-17.5
Day Nests (Excluding ground nests)	15	10.2	7.5	4.2	2.5-17.5
Night Nests	169	12.5	12.5	7.9	2.5-37.5

Table 4.13. Nest height frequency and percentage for each 5 m height class interval at Seringbara.

Height Interval (m)	**Overall**		Day		Night	
	Frequency	**%**	**Frequency**	**%**	**Frequency**	**%**
0-5	44	15.9	9	39.1	15	8.9
5-10	89	32.1	7	30.4	56	33.1
10-15	69	24.9	5	21.7	43	25.4
15-20	41	14.8	2	8.7	29	17.2
20-25	11	4.0	0	0	7	4.1
25-30	13	4.7	0	0	10	5.9
30-35	8	2.9	0	0	7	4.1
35-40	2	0.7	0	0	2	1.2
TOTAL	**277**	**100**	**23**	**100**	**169**	**100**

Table 4.14. Frequency of ground nests associated with a nest group and percentage of ground nests within each nest group.

Nest Type	Group No.	Frequency	Nest group size	% of ground nests
Day Nest	1	2	2	100
	2	3	3	100
Unknown	1	2	9	22.2
	2	1	6	16.7
	3	4	4	100
	4	4	4	100

A significant difference in nest height between day and night nests emerged: day nests were built at lower heights than night nests (Mann Whitney U-test: N=192; z=-3.524; p<0.001) (see Table 4.12). Indeed, 91.2% of day nests were constructed below 15 m and none were above 20 m, while 32.5% of night nests were found at heights greater than 15 m (see Table 4.13). However, when excluding ground nests from the data set and analysing only tree nests, there was no difference in nest height between day and night nests (Mann Whitney U-test: $N=184$; $z=-1.252$; *n.s.*) (see Table 4.12).

Mean tree DBH was 26.1 cm overall ($N= 243$; $SD=24.3$ cm; range: 4.1-135.0 cm), 16.5 cm for day nests ($N=15$; $SD=6.1$ cm; range: 6.2-26.1 cm) and 28.7 cm for night nests ($N=157$; $SD=28.4$ cm; range: 4.7-135.0 cm). An analysis of tree DBH and nest height revealed a significant positive correlation between these two variables both overall and for day and night nests (overall: $R_s=0.766$; $N=242$; $\rho<0.001$; day nests: $R_s=0.561$; $N=15$; $\rho<0.05$; night nests: $R_s=0.753$; $N=157$; $\rho<0.001$). This correlation indicates that, as at Bossou, nest height is influenced by the DBH and the height of the tree in which the chimpanzee chooses to nest.

Whether overall or for day or night nests examined separately, nearly 90% of trees contained only a single nest, while the maximum number of nests encountered in a single tree belonging to the same nest group was 8 (see Table 4.15). Overall and for night nests, the number of nests per tree was positively correlated with the DBH of the tree used (overall: $R_s=0.258$; $N=199$; $\rho<0.001$; night: $R_s=0.234$; $N=125$; $\rho<0.01$). No such correlation emerged for day nests (day: $R_s=0.034$; $N=14$; *n.s.*); the maximum number of day nests of the same age observed in any one tree was 2. Thus, in general, trees with a large DBH were able to support a greater number of nests and, with the exception of day nests, the chimpanzees' nesting behaviour reflects this relationship.

Table 4.15. Percentage and frequency of trees with different numbers of nests belonging to the same age group overall and for day and night nests.

	No.	**Percentage (Freq.)**							
No. Nests/Tree		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Overall	211	87.7 (185)	7.6 (16)	3.3 (7)	0.5 (1)	0.5 (1)	0 (0)	0 (0)	0.5 (1)
Day Nests	14	92.9 (13)	7.1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Night Nests	137	87.6 (120)	6.6 (9)	4.4 (6)	0 (0)	0.7 (1)	0 (0)	0 (0)	0.7 (1)

Nest integration and re-use

The majority of nests, around 80%, whether overall, by day or night, were made in a single tree (see Table 4.16). The maximum number of integrated trees used was 7. None of the day nests were built by integrating more than two trees, while 8.5% of night nests resulted from a combination of more than two trees (see Table 4.16). No difference emerged in the proportion of integrated nests observed between day and night nests (Fisher's Exact test: *n.s.*).

Table 4.16. Percentage and frequency of nests constructed in a single tree or resulting from the combination of several trees.

	No.	**Percentage (Freq.)**						
No. trees used		**1**	**2**	**3**	**4**	**5**	**6**	**7**
Overall	254	79.9 (203)	15.4 (39)	3.1 (8)	0.8 (2)	0.4 (1)	0 (0)	0.4 (1)
Day Nests	15	86.7 (16)	13.3 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Night Nests	169	82.6 (140)	8.7 (16)	4.3 (7)	1.4 (2)	1.4 (2)	0 (0)	1.4 (2)

A significant negative correlation was uncovered between the DBH of the principal tree and the number of integrated trees employed in nest construction overall and for night nests (overall: R_s=-0.490; N=242; ρ<0.001; night: R_s=-0.480; N=157; ρ<0.001). No correlation emerged though when analysing the data for day nests; however the sample size for integrated daytime nests was most likely too small to reveal a significant correlational trend (day: R_s=-0.409; N=15; *n.s.*). Nevertheless, as at Bossou, this result suggests that nest integration at Seringbara is influenced by the DBH of the principal tree used for nest construction.

In addition, overall and for night nests, median nest height for nests constructed in a single tree was significantly greater than for those built by tree integration (overall: Mann Whitney U-test: N=254; z=-7.484; ρ<0.001; night nests: Mann Whitney U-test: N=169; z=-4.402; ρ<0.001) (see Table 4.17).

Table 4.17. Summary statistics of nest height (m) of single tree nests and integrated nests, overall and for night nests at Seringbara.

	Number of Trees	No.	Mean	Median	SD	Range
Overall	Single	203	14.1	12.5	7.3	2.5-37.5
	Integrated	51	6.7	7.5	3.1	2.5-12.5
Night Nests	Single	132	14.9	12.5	7.9	2.5-37.5
	Integrated	37	7.1	7.5	3.2	2.5-12.5

Only one nest was noticed to have been re-used. This nest was a night nest, which resulted from the integration of two trees.

Habitat preference

Overall, primary forest was the most commonly used habitat for nesting, with riverine forest being the second habitat of choice (see Table 4.18). Secondary and marantaceae forest areas were also used for nesting, although more rarely (see Table 4.18). By day, although the sample size is small (N=6), half of the recorded nest groups or single nests were found in primary forest habitat (see Table 4.18). The second habitat of choice was marantaceae forest, while not a single day nest was observed in secondary forest areas (see Table 4.18).

Nearly 90% of night-time nest groups were found in primary or riverine forest, but the other two habitats also contained nest groups, although in much lower frequencies (see Table 4.18). As for single night nests, primary and marantaceae forest habitats were the most frequently used, accounting for together 85.8% of all single night nests (see Table 4.18). One single night nest was encountered in secondary forest, while none were found in riverine forest (see Table 4.18). Thus, although the sample set of single nests was comparatively small, differences in nesting habitat choice emerged between nest groups and single nests at this site.

Tree species preference

Overall, 60.2% and 42.2% of all tree nests recorded were made respectively in 11 and 5 tree species, and 58 tree species were used in nest construction, although a minimum of 175 tree species were available to the chimpanzees (see Table 4.19). The 5 most used tree species were significantly preferred by the chimpanzees, while among the 11 most commonly used tree species, only 3 were not preferred based on the Manly's alpha index (see Table 4.19). These 3 species, i.e. *Rinorea* sp., *Trichilia pleuriana*, *Carapa procera*, did not provide food to the chimpanzees over the rainy season period when nests were recorded. However, 3 other tree species among the 11 most commonly used for nesting bore fruit consumed by chimpanzees during the rainy season; these included *Octoknema borealis*, *Afrosersalisia cerasifera* and *Ituridendron bequaertii*.

For day nests, a total of 9 tree species were identified as being used by the chimpanzees. The 9 and 5 most commonly used tree species accounted for respectively 93.3% (6.7% of day nests were built in unidentified tree species) and 66.7% of all day nests recorded (see Table 4.19). All 9 tree species used were preferred by the chimpanzees and two, i.e. *Octoknema borealis* and *Cola cordifolia*, provided fruit for the chimpanzees over the study periods during which nests were recorded (see Table 4.19).

Table 4.18. Frequency and percentage of nest groups and/or single nests in each habitat type available at Seringbara overall and for day- and night-time nesting.

	Overall		Day Time		Night Time			
					Nest group		*Single Nest*	
Habitat Type	**Freq.**	**%**	**Freq.**	**%**	**Freq.**	**%**	**Freq.**	**%**
Primary	30	41.1	3	50.0	15	55.6	3	42.9
Secondary	12	16.4	0	0	2	7.4	1	14.2
Riverine	22	30.1	1	16.7	9	33.3	0	0
Marantaceae	9	12.4	2	33.3	1	3.7	3	42.9
TOTAL	73	100	6	100	27	100	7	100

Table 4.19. Percentage of nests in the 10 most commonly (11 species for all nests and only 9 for day nests) used nesting tree species overall (N=256) and for day (N=15) and night nests (N=169) (in bold: tree species appearing in all three columns; Pref.: Preference; α: Manly's Alpha).

Tree Species	All Nests (%)	α	Pref.	Tree Species	Day Nests (%)	α	Pref.	Tree Species	Night Nests (%)	α	Pref.
Chidlowia sanguinea	13.67	0.0467	Yes	***G. perpulchrum***	20.00	0.0495	Yes	***C. sanguinea***	18.93	0.0744	Yes
Gambeya perpulchrum	10.16	0.0254	Yes	*Beilschmiedia mannii*	13.33	0.4514	Yes	***G. perpulchrum***	10.06	0.0289	Yes
Ituridendron bequaertii	7.42	0.0331	Yes	*Carapa procera*	13.33	0.0315	Yes	*I. bequaertii*	8.28	0.0425	Yes
Afrosersalisia cerasifera	5.86	0.0668	Yes	*Cola cordifolia*	13.33	0.2257	Yes	*A. cerasifera*	8.28	0.1085	Yes
Plagiostyles africana	5.08	0.1042	Yes	***C. sanguinea***	6.67	0.0226	Yes	*Piptadenia africana*	5.92	0.1395	Yes
Piptadenia africana	3.91	0.0801	Yes	***P. africana***	6.67	0.1354	Yes	***P. africana***	3.55	0.0837	Yes
Octoknema borealis	3.91	0.0103	Yes	***O. borealis***	6.67	0.0174	Yes	*Trichilia pleuriana*	2.96	0.0079	Yes
Rinorea sp.	3.91	0.0025	Not	*Microdesmis keayana*	6.67	0.0133	Yes	*Anthonotha macrophylla*	2.37	0.0215	Yes
Trichilia pleuriana	2.34	0.0055	Not	*Xylopia aethiopica*	6.67	0.0271	Yes	*Nauclea diderrichii*	1.78	0.0697	Yes
Anthonotha macrophylla	1.95	0.0154	Yes					***O. borealis***	1.78	0.0054	Not
Carapa procera	1.95	0.0047	Not								
Total Percentage	**60.2**				**93.3**				**63.9**		

Concerning night-time nesting, 49 tree species were used. Four of the 10 most commonly used tree species were also among the 9 species recorded as being used for daytime nesting (see Table 4.19). The 10 and 5 most frequently used tree species accounted for respectively 63.9% and 51.5% of all night nests (see Table 4.19). Nine of these 10 species were significantly preferred species; *Octoknema borealis*, although preferred overall and for daytime nesting, was used to a lesser extent for night nest construction (see Table 4.19). Four of the 10 most commonly used tree species, i.e. *Octoknema borealis*, *Ituridendron bequaertii*, *Afrosersalisia cerasifera* and *Nauclea diderrichii*, supplied food, namely fruit, for the chimpanzees over the rainy season period.

Nest features and characteristics at Yealé, Nimba

Nesting height, number of nests per tree and DBH

Mean overall nest height was 16.1 m, 13.9 m for day nests and 18.7 for night nests (see Table 4.20). Overall and for night nests, the height class category comprising the highest percentage of nests was 10-15 m and the greatest proportion of nests were constructed at heights ranging between 5-15 m (see Table 4.21). The data on day nests provide a wider spread in nest height preference, with most nests built either between 0-5 m or 15-20 m. Over 80% of all day nests were constructed below 20 m. However, the data set available for day nests at this site is comparatively small relative to the sample for night nests and may not accurately reflect day nest height.

Ground nests were also recorded at this site, comprising 3.7% (14/378) of the total number of nests encountered and 14.3% (3/21) of all day nests (see Plate 4.2). Nine of the 14 ground nests were constructed using small tree saplings, while the other 5 were lined with THV material, mainly plants belonging to the Marantaceae and Zingiberaceae family. Seven ground nests were singletons, i.e. not associated with any other nests. One group of two nests was made up of only ground nests; the remaining 5 ground nests all belonged to groups mainly comprised of arboreal nests (see Table 4.22). Similarly to Seringbara, several ground nests were found in close proximity to nests of the same age, thought to be night nests. No significant difference in nest height emerged between day and night nests, whether ground nests were excluded or not from the analysis (including ground nests: Mann Whitney U-test: N=243; z=-1.875; *n.s.*; excluding ground nests: Mann Whitney U-test: N=240; z=-0.877; *n.s.*) (see Table 7.20).

Table 4.20. Summary statistics of nest height overall and for night and day nests at Yealé.

	No.	Mean (m)	Median (m)	SD	Range (m)
Overall	378	16.1	12.5	10.2	2.5-42.5
Day Nests	21	13.9	12.5	9.8	2.5-32.5
Day Nests (Excluding ground nests)	18	15.8	15.0	9.2	2.5-32.5
Night Nests	222	18.7	17.5	10.7	2.5-42.5

Table 4.21. Nest height frequency and percentage for each 5 m height class interval at Yealé.

Height Interval (m)	**Overall**		**Day**		**Night**	
	Frequency	**%**	**Frequency**	**%**	**Frequency**	**%**
0-5	33	8.7	5	23.8	6	2.7
5-10	86	22.8	3	14.3	44	19.8
10-15	98	25.9	4	19.8	55	24.8
15-20	60	15.9	5	23.8	39	17.6
20-25	24	6.3	0	0	19	8.6
25-30	32	8.5	2	9.5	20	9.0
30-35	25	6.6	2	9.5	19	8.6
35-40	3	0.8	0	0	3	1.4
40-45	17	4.5	0	0	17	7.7
TOTAL	**378**	**100**	**21**	**100**	**222**	**100**

Table 4.22. Frequency of ground nests associated with a nest group and percentage of ground nests within each nest group at Yealé.

Nest Type	Group No.	Frequency	Nest group size	% of ground nests
Day Nest	1	2	2	100
	2	1	12	8.3
Unknown	1	1	5	20.0
	2	1	6	16.7
	3	1	4	25.0
	4	1	2	50.0

Plate 4.2. Example of a ground nest from Yealé.

Mean tree DBH was 33.9 cm overall (N=334; SD=29.8 cm; range: 1.9-150.0 cm), 25.1 cm for day nests (N=18; SD=14.0 cm; range: 6.5-48.0 cm) and 42.4 cm for night nests (N=192; SD=34.8 cm; range: 1.9-150.0 cm). A significant positive correlation between nest height and tree DBH emerged overall and for day and night nests analysed separately (overall: R_s=0.772; N=334; ρ<0.001; day: R_s=0.792; N=18; ρ<0.001; night: R_s=0.782; N=192; ρ<0.001). Thus, similarly to Bossou and Seringbara, nest height at Yealé was also influenced by the DBH of the tree in which the chimpanzee chose to nest.

Over 70% of trees employed in nesting, whether overall, by day or night, contained only one nest (see Table 4.23). Although for night nests and overall, respectively 85.2% and 91.0% of trees supported either only one or two nests, some trees contained up to 6 nests, while for day nests, no tree ever had more than 2 nests (see Table 4.23). The number of nests per tree was significantly positively correlated with DBH, overall and for trees supporting day or night nests analysed separately (overall: R_s=0.351; N=261; ρ<0.001; day: R_s=0.560; N=15; ρ<0.001; night: R_s=0.467; N=136; ρ<0.001). Thus, the larger the DBH of the tree, the more nests chimpanzees were able to construct within the crown of the tree, while the smaller the tree DBH, the smaller number of nests were built.

Table 4.23. Percentage and frequency of trees containing different numbers of nests belonging to the same age group overall and for day and night nests at Yealé.

	No.	**Percentage (Freq.)**					
No. Nest/Tree		**1**	**2**	**3**	**4**	**5**	**6**
Overall	288	78.5 (226)	12.5 (36)	6.9 (20)	0.7 (2)	0.7 (2)	0.7 (2)
Day Nests	16	81.3 (13)	18.8 (30	0 (0)	0 (0)	0 (0)	0 (0)
Night Nests	155	71.0 (110)	14.2 (22)	11.0 (17)	1.3 (2)	1.3 (2)	1.3 (2)

Nest integration and re-use

The great majority of nests, about 90%, whether overall, for day or night nests, were constructed in a single tree (see Table 4.24). The maximum number of integrated trees was 4. Although most day nests were built employing material from a single tree, one was the result of the integration of four trees. However, no difference emerged in the proportion of integrated nests observed between day and night nests (Fisher's Exact test: *n.s.*).

Table 4.24. Percentage and frequency of nests constructed in a single tree or resulting from the combination of several trees at Yealé.

	No.	**Percentage (Freq.)**			
Number of trees used		**1**	**2**	**3**	**4**
Overall	364	86.8 (316)	10.4 (38)	2.2 (8)	0.6 (2)
Day Nests	18	94.4 (17)	0 (0)	0 (0)	5.6 (1)
Night Nests	222	87.4 (194)	10.3 (23)	1.8 (4)	0.5 (1)

A significant negative correlation emerged between the DBH of the principle tree and the number of integrated trees used in nest construction, overall and for day and night nests analysed separately (overall: R_s=-0.218; N=333; ρ<0.001; day: R_s=-0.352; N=18; ρ<0.001; night: R_s=-0.248; N=192; ρ<0.001). Overall and for night nests, median height for nests constructed in a single tree was significantly greater than for those built by integration (overall: Mann Whitney U-test: N=364; z=-6.513; ρ<0.001; night nests: Mann Whitney U-test: N=126; z=-5.699; ρ<0.001) (see Table 4.25). This analysis was not carried out for day nests since the sample of integrated nests was too small (N=1). Finally, none of the nests encountered at Yealé showed any indication of re-use.

Table 4.25. Summary statistics of nest height (m) of single tree nests and integrated nests, overall and for night nests at Yealé.

	Number of Trees	No.	Mean	Median	SD	Range
Overall	Single	316	17.7	15.0	10.1	2.5-42.5
	Integrated	48	8.7	7.5	3.8	2.5-17.5
Night Nests	Single	194	13.6	12.5	7.7	2.5-32.5
	Integrated	28	9.3	7.5	3.4	2.5-17.5

Habitat preference and altitude

Table 4.26 presents the frequency and percentage of use for nesting purposes of all four habitat types recorded at Yealé. Overall, during the study periods over which nests were recorded, the habitats of choice for nesting were primary and riverine forest, accounting together for 74.9% of all nest groups or singleton nests encountered.

For daytime nesting, the majority of nest groups or single nests were located in Marantaceae forest, while a few were also observed in the other three habitat types. However, the sample set is too small to confidently infer any general trend in habitat choice for nesting by day at this site.

For night-time nesting, the habitat of choice for nesting was primary forest, especially for single nests. Nest groups were also encountered at nearly equal frequency in the other three habitat types identified, although riverine forest was used by nest groups slightly more frequently than either marantaceae or secondary forest areas. Secondary forest was generally the least employed habitat for nesting.

At Yealé, nest location was also described on the basis of its position relative to the mountainside, considering that in this region of the Nimba Mountains, categories such as lower, mid and higher altitude could clearly be distinguished. These were used to subsequently help tease out varying hypotheses pertaining to influences on ground nesting behaviour at this site (see *Discussion* for further details). About 50% of all nest groups or single nests, overall or for night-use, and 67% used by day were situated on the mid-altitude region of the massif (see Table 4.27). During the rainy season period, no day nest groups or single day nests were encountered in the upper altitude regions (see Table 4.27). Overall, the lower altitudes were also used more frequently than the upper altitudes; however, for night-time nesting, both lower and upper altitude regions were employed in roughly equal frequency (see Table 4.27).

Table 4.26. Frequency and percentage of nest groups or single nests in each habitat type available at Yealé overall and during day- and night-time nesting.

	Overall		**Day Time**		**Night Time**			
					Nest group		***Single Nest***	
Habitat Type	**Freq.**	**%**	**Freq.**	**%**	**Freq.**	**%**	**Freq.**	**%**
Primary	59	42.1	2	22.2	15	38.5	19	67.8
Secondary	12	8.7	1	11.1	7	17.9	1	3.6
Riverine	46	32.8	2	22.2	9	23.1	4	14.3
Marantaceae	23	16.4	4	44.5	8	20.5	4	14.3
TOTAL	72	100	9	100	39	100	28	100

Table 4.27. Frequency and percentage of nest groups and single nests encountered on the lower, mid or upper altitudes of the Nimba massif in the region of Yealé.

		Lower Altitudes	**Mid Altitudes**	**Upper Altitudes**
Overall (N=131)	**Frequency**	41	62	28
	Percentage	31.3	47.3	21.4
Daytime (N=9)	**Frequency**	3	6	0
	Percentage	33.3	66.7	0
Night-time (N=58)	**Frequency**	14	27	17
	Percentage	24.1	46.6	29.3

Table 4.28. Percentage of nests in the 10 most commonly used nesting tree species overall (N=364) and for day (N=18) and night nests (N=222) (in bold: tree species appearing in all three columns; Pref.: Preference; α: Manly's Alpha).

Tree Species	All Nests (%)	α	Pref.	Tree Species	Day Nests (%)	α	Pref.	Tree Species	Night Nests (%)	α	Pref.
Chidlowia sanguinea	12.65	0.0190	Yes	***G. perpulchrum***	11.11	0.0212	Yes	*C. sanguinea*	15.15	0.0207	Yes
Gambeya perpulchrum	8.82	0.0184	Yes	*Blighia welwitschii*	11.11	0.0412	Yes	***G. perpulchrum***	9.60	0.0183	Yes
Rinorea sp.	8.24	0.0086	Yes	*Mareya micrantha*	11.11	0.0334	Yes	***P. africana***	6.06	0.0423	Yes
Dacryodes sp.	6.76	0.2333	Yes	*Lophira alata*	11.11	0.0389	Yes	***Rinorea sp.***	4.55	0.0043	Not
Plagiostyles africana	4.12	0.0316	Yes	*Albizia lebeck*	11.11	0.7009	Yes	*H. utilis*	4.55	0.0357	Yes
Carapa procera	3.53	0.0057	Yes	***Rinorea sp.***	5.56	0.0053	Yes	*P. microcarpa*	4.55	0.0168	Yes
Heritiera utilis	2.94	0.0254	Yes	***P. africana***	5.56	0.0389	Yes	*C. procera*	4.04	0.0059	Yes
Musanga cecropiodes	2.94	0.0085	Yes	*Octoknema borealis*	5.56	0.0032	Not	*P. macrophylla*	4.04	0.2536	Yes
Pseudospondias microcarpa	2.94	0.0119	Yes	*Ituridendron bequaertii*	5.56	0.0097	Yes	*M. cecropiodes*	3.54	0.0092	Yes
Pentaclethra macrophylla	2.35	0.1623	Yes	*Myrianthus arboreus*	5.56	0.0875	Yes	*Parkia bicolor*	3.03	0.0634	Yes
Total Percentage	**55.3**				**83.4**				**59.1**		

Tree species preference

Overall, the 10 and 5 most used tree species supported 55.3% and 40.6% respectively of all nests encountered (see Table 4.28). A total of 64 tree species were employed for nesting purposes of a total 193 tree species identified in the transects and thus available to the chimpanzees. In addition, based on Manly's alpha index, all 10 most frequently used tree species were preferred by chimpanzees at this site (see Table 4.28). Among the 10 most commonly used tree species, two, i.e. *Musanga cecropioides* and *Pseudospondias microcarpa*, were confirmed to provide food in the form of fruit to the chimpanzees during the study periods over which nests were recorded (see Table 4.28).

For day nests, the 10 and 5 most frequently used tree species provided support respectively for 83.4% and 55.5% of all nests recorded, and a total of 11 tree species were used for nest construction (see Table 4.28). Nine of the 10 most commonly used tree species were preferred by the chimpanzees. *Octoknema borealis* was the only tree species, which was not a preferred tree species for daytime nesting (see Table 4.28). Three of the 10 tree species listed in Table 4.28, i.e. *Octoknema borealis, Ituridendron bequaertii* and *Myrianthus arboreus,* bore fruit that were consumed by the chimpanzees during the rainy season. Only 3 of the 10 most commonly used tree species by day were also among the 10 most frequently employed species by night (see Table 4.28).

Forty-nine tree species were used for night-time nesting and 59.1% and 39.9% of all night nests recorded were found respectively in the 10 and 5 most commonly used tree species (see Table 4.28). Only 2 of the 10 most commonly used tree species provided food for the chimpanzees, the same species as listed for the pooled nesting data set. From the list provided in Table 4.28, *Rinorea* sp. was the only tree species not preferred by the chimpanzees during night-time nesting based on Manly's alpha index, although it was a preferred species both overall and for daytime nesting.

Comparison between Bossou and the Nimba sites

Nest height, tree DBH and nest height-to-tree DBH ratio

For the comparison of nesting variables across all three sites, only arboreal nests constructed in single trees were considered. Nest height and tree DBH were compared. Also, given that across all three sites a significant positive correlation was obtained between nest height and the DBH of the tree used for nesting, the ratio between these two variables was compared to check for variations in nest height while controlling for DBH. Oil palm trees, only used for nesting at Bossou, although available in Nimba, were excluded from the ratio calculations. This comparative analysis was carried out for night nests only, for each habitat type separately in order to minimise the influence of differences in habitat choice and structure between the three sites. Day nests were excluded from the analysis due to the small sample sizes obtained from the two Nimba sites.

No difference emerged in nest height, tree DBH or their ratio across the three sites in secondary forest or between the two Nimba sites in marancateae forest (see Table 4.29). Although there was no significant difference in tree DBH between the three sites in primary forest habitat, a significant difference in nest height and ratio was revealed (see Table 4.29). A *post hoc* analysis indicated that Bossou chimpanzees nested lower ($\rho<0.05$) than chimpanzees at Yealé and exhibited a smaller nest height-to-tree DBH ratio ($\rho<0.05$) than chimpanzees at Seringbara. In riverine forest habitat, a significant difference in nest height and tree DBH between the three sites was revealed (see Table 4.29). A *post hoc* analysis revealed no difference between Bossou and Seringbara. The difference lay with Yealé chimpanzees nesting higher than either

Bossou or Seringbara chimpanzees ($\rho<0.05$) and nesting in trees of greater DBH compared to Seringbara and Bossou ($\rho<0.05$) in riverine forest habitat. No difference in nest height-to-tree DBH ratio in riverine forest emerged between the three sites, indicating that the above differences were mainly due to differences in tree DBH (see Table 4.29).

Ground nests

Ground nests were found significantly more frequently at both Seringbara (25/281) and Yealé (14/378) than at Bossou (1/771) ($\chi^2(2, N=1430)=59.77$; $\rho<0.001$). Bossou chimpanzees have never been observed to construct night nests on the ground, while the data emerging from the two Nimba sites suggest that ground nests are commonly made by chimpanzees by day and that some may also serve as night nests, based on their association with more elaborately constructed arboreal nests likely to have been used for resting at night.

Tree integration and nest re-use

At Bossou, only 5.2% (40/770) of all nests resulted from the integration of several trees, with a maximum of 4 trees being used for any one nest. Forty-five percent and 42.5% of these nests were respectively located in abandoned fields and secondary forest areas. However, tree integration in nest building occurred at higher frequency at both Nimba sites and, relative to Bossou, was more frequent than expected ($\chi^2(2, N=1388)=52.463$; $\rho<0.001$). Indeed, at Yealé, 13.2% (48/364) of nests encountered combined 2 to a maximum of 4 trees. These were predominantly located in riverine (39.6%) and secondary forest (31.3%) regions. At Seringbara, 20.1% (51/254) of nests were integrated with a maximum of 7 trees being used. These nests were mostly encountered in riverine and primary forest areas, each containing respectively 58.8% and 37.3% of the total number of integrated nests recorded at this site.

Table 4.29. Summary statistics of nest height, nesting tree DBH and the ratio of nest height-to-tree DBH (m/cm) across all three sites for each habitat types discerned, for arboreal night nests built in a single tree, and related test statistic.

Habitat type	Variable	Site	No.	Mean	Median	SD	Range	Test statistic
Primary	Height (m)	Bossou	8	11.3	7.5	7.4	7.5-22.5	Kruskal-Wallis test: χ^2(2, N=158)=7.926; ρ<0.05
		Seringbara	85	16.4	17.5	8.7	2.5-37.5	
		Yealé	65	20.4	17.5	11.8	2.5-42.5	
	DBH (cm)	Bossou	8	36.0	26.8	32.7	13.0-115.0	Kruskal-Wallis test: χ^2(2, N=158)=4.592; *n.s.*
		Seringbara	85	37.5	23.9	35.1	6.0-135.0	
		Yealé	65	49.2	40.1	43.5	8.0-150.0	
	Ratio (m/cm)	Bossou	7	0.35	0.28	0.13	0.24-0.56	Kruskal-Wallis test: χ^2(2, N=157)=6.398; ρ<0.05
		Seringbara	85	0.59	0.56	0.31	0.08-2.12	
		Yealé	65	0.54	0.48	0.27	0.12-1.36	
Secondary	Height (m)	Bossou	89	11.9	12.5	5.0	2.5-27.5	Kruskal-Wallis test: χ^2(2, N=109)=0.554; *n.s.*
		Seringbara	6	10.0	10.0	2.9	7.5-12.5	
		Yealé	14	11.4	12.5	4.0	7.5-17.5	
	DBH (cm)	Bossou	89	29.7	28.7	15.8	6.0-69.0	Kruskal-Wallis test: χ^2(2, N=109)=0.086; *n.s.*
		Seringbara	6	28.9	26.2	6.5	25.0-39.0	
		Yealé	14	26.9	29.2	7.2	12.0-38.0	
	Ratio (m/cm)	Bossou	81	0.47	0.41	0.21	0.16-1.19	Kruskal-Wallis test: χ^2(2, N=101)=1.318; *n.s.*
		Seringbara	6	0.35	0.31	0.09	0.28-0.49	
		Yealé	14	0.44	0.41	0.14	0.24-0.64	
Riverine	Height (m)	Bossou	34	12.2	10.0	5.6	7.5-27.5	Kruskal-Wallis test: χ^2(2, N=118)=38.110; ρ<0.001
		Seringbara	21	10.8	12.5	3.7	7.5-17.5	
		Yealé	63	24.1	22.5	11.3	7.5-42.5	
	DBH (cm)	Bossou	34	32.7	31.2	18.8	7.0-90.0	Kruskal-Wallis test: χ^2(2, N=118)=18.189; ρ<0.001
		Seringbara	21	19.6	18.3	8.1	8.0-39.0	
		Yealé	63	52.2	35.0	34.8	9.0-121.0	
	Ratio (m/cm)	Bossou	31	0.48	0.49	0.25	0.13-1.08	Kruskal-Wallis test: χ^2(2, N=115)=3.209; *n.s.*
		Seringbara	21	0.61	0.53	0.26	0.32-1.49	
		Yealé	63	0.58	0.51	0.26	0.19-1.26	
Marantaceae	Height (m)	Seringbara	12	12.5	12.5	6.4	2.5-27.5	Mann Whitney U-test: z=-1.856; *n.s.*
		Yealé	28	16.4	17.5	6.7	2.5-32.5	
	DBH (cm)	Seringbara	12	27.9	27.6	15.2	8.0-64.0	Mann Whitney U-test: z=-0.591; *n.s.*
		Yealé	28	30.0	30.7	12.7	9.0-76.0	
	Ratio (m/cm)	Seringbara	12	0.54	0.42	0.40	0.19-1.67	Mann Whitney U-test: z=-1.299; *n.s.*
		Yealé	28	0.58	0.57	0.25	0.24-1.12	

No difference in the number of integrated nests observed across all three sites emerged between day and night nests. However, both at Bossou and Seringbara, integrated day nests were never observed to combine more than two trees. The only integrated day nest encountered at Yealé incorporated four trees and was located 2 m above ground.

Finally, variation between the three sites was observed in the habitat types in which integrated nests occurred, thus ruling out to some extent the possibility that differences in their frequency of occurrence could be habitat dependent. However, a more detailed exploration of tree availability and DBH at locations where integrated nests are constructed would be required to exclude with more certainty the influence of environmental factors on the frequency of this behaviour.

More records of nest re-use were made at Bossou (N=15) than at either Seringbara (N=1) or Yealé, where in fact no nests showed any obvious indications of re-use. However, it is likely that re-use at both Nimba sites may have been underestimated due to a layer of fresh vegetation sometimes obscuring an older nest beneath.

Habitat choice

Based on a single data point for each nest group or 'solitary' nest encountered, Bossou chimpanzees distinctly preferred to nest during the rainy season in secondary forest, with abandoned fields being the second preferred habitat (see Table 4.8). In contrast, at Seringbara and Yealé, primary forest was the most preferred habitat for nesting, with riverine forest areas coming second (see Table 4.18 and 4.26). No significant difference in habitat preference emerged between the two Nimba sites whether analysing the overall nesting data ($\chi^2(3; N=213)=3.296$; *n.s.*) or the data for night nests only ($\chi^2(3; N=101)=1.277$; *n.s.*). Such an analysis was not conducted on day nests since the sample size was too small at both sites.

Tree species preference

In terms of tree species preference, it is worth noting that *Carapa procera*, a non-food species for the chimpanzees, appears in the top 11 most commonly used species at all three sites, although, based on Manly's alpha, it is not a preferred species at Bossou, while it is at the two Nimba sites (see Table 4.9; 4.18 and 4.28). In addition, whether by day or night, Bossou chimpanzees more commonly nested in food bearing tree species when compared with Nimba chimpanzees. The oil-palm was a preferred nesting tree species at Bossou, while it was recorded as being used only once at Yealé and never at Seringbara.

One cannot easily directly compare the tree species used for nesting at Bossou with Seringbara and Yealé since composition and availability across these habitats is very different; however, the two Nimba sites may be more comparable, exhibiting similar habitat types in relatively similar proportions. Among the 11 most commonly used species at both these sites, 5, i.e. *Chidlowia sanguinea*, *Gambeya perpulchrum*, *Rinorea* sp., *Plagiostyles africana* and *Carapa procera*, were the same for the two sites, comprising respectively 34.8% and 37.4% of all nests recorded from Seringbara and Yealé (see Table 4.18 and 4.28). All 5 of these tree species were preferred for nesting at Yealé while *Rinorea* sp. and *Carapa procera* were not preferred at Seringbara.

4.6 Discussion

This study of nesting behaviour at Bossou and Nimba was mainly concerned with assessing the impact of habitat variables on nesting parameters, with the aim to discern differences and similarities across the three sites.

Patterns of similarity

When considering arboreal nests only, no significant difference in nest height emerged between day and night nests at Bossou, Seringbara or Yealé. This result contrasts with that observed at other sites where day and night nests have been distinguished and compared. Brownlow *et al.* (2001) noted that at Budongo, Uganda, day nests were constructed higher than night nests and were made at feeding height. Chimpanzees from the Kanyawara community at Kibale, Uganda, also nested higher by day than by night (Llorente, pers. comm.). Additionally, Fruth (1995) noted that day nests of bonobos at Lomako were higher than night nests. Thus the pattern of nest height of day and night nests emerging from this study differs from that reported at other study sites.

At both Nimba sites, most trees contained only a single nest. At Bossou, although the great majority of trees used for night nest construction supported a single nest, most trees used by day tended to support more than one nest. However, at all three sites, whether overall, for day or night nests, a significant positive correlation was revealed between tree DBH and the number of nests within a single tree.

Across all three sites, nest height was significantly positively correlated with the DBH of the principal nest-bearing tree. Such a correlation has not systematically been reported in other publications on nesting. Fleury-Brugière (2001), however, reported a similar correlation in her unpublished survey of chimpanzees in the National Park of Haut Niger in Guinea.

Moreover, at all three sites, whether overall, for day or night nests, a significant negative correlation between the DBH of the principal tree and the number of trees in integrated nests was found. This indicates that tree integration is associated with the use of trees of small DBH and that in order to construct an adequate supportive structure in a tree of small DBH chimpanzees will incorporate branches and leaves from neighbouring trees. However, trees with smaller DBHs may also lend themselves better to integration since they may be more densely distributed so easier to reach, or have branches that are easier to bend than trees with larger DBHs. In addition, although no difference emerged between day and night nests in the frequency of nest integration, with the exception of one nest at Yealé, integrated day nests never exceeded two trees, while night nests sometimes incorporated more than two. Day nests are usually less elaborate in construction than night nests and the difference in nest integration emerging from this study supports this observation. In addition, integrated nests at all three sites were generally built lower than nests constructed using a single tree.

Patterns of difference

Nest integration was more common at the Nimba sites than at Bossou. Considering that integrated nests at all three sites were lower than single-tree nests, it may be that at the Nimba sites social factors lead to a greater frequency of nest integration if some individuals prefer to nest lower than others, while still nesting arboreally. Ecological constraints may also apply, but there appears to be no shortage of large single trees for nesting at the Nimba sites even in areas where integrated nests were encountered. At Bossou, no age or sex differences emerged in nest height construction, tree DBH or in frequency of nest integration, although juveniles were never observed to make integrated nests. Brownlow *et al.* (2001) also found that among Budongo chimpanzees in Uganda young chimpanzees had difficulties in integrating nests simply because they were not strong enough to keep the nest together. However, at Budongo, male chimpanzees tended to nest lower than females (Brownlow *et al.*, 2001). Fruth and Hohmann (1993) also reported that male bonobos nested lower than females. In addition, male chimpanzees from the Kanyawara community at Kibale, Uganda, nested lower and more commonly integrated nests than did females; nest integration at this site appears unusually common with approximately 30% of night nests being integrated (Llorente, pers. comm.).

Four alternative explanations for sex differences in nest height have been proposed. 1) Male chimpanzees will nest lower to protect females and sub-adults from predators such as leopards (Baldwin *et al.*, 1981). 2) Since adult males are heavier than adult females, they will nest lower to the ground to minimise the risk of injury from falling (Reynolds, 1967). 3) Females commence nesting first, occupying the prime nesting sites in the foliage of the upper and middle layers and leaving the males to occupy the lower branches; 4) Lower-ranking males or males with a female in oestrous may nest lower to reduce mating competition (Maughan and Stanford, 2001).

Bossou chimpanzees are free from predation, therefore males may not be constrained or required to nest lower than females at this site. However, Nimba chimpanzees may still be subject to predation by leopards (although this still needs to be confirmed, since there have been no recent sightings of leopards in the region) and have also been a target prey for human hunters in the recent past. Males at Nimba may be motivated to nest lower due to greater predation pressure and may thus need to resort to nest integration to do so.

If male weight is a determining factor in nest height as proposed by the second hypothesis listed above, why do male chimpanzees at Bossou not nest lower than females? The greater weight of males' hypothesis may not, indeed, be a satisfactory explanation for sex differences in nest height.

It is possible that nest site choice by females may affect nesting by males, if females begin nesting prior to males. Data relevant to this hypothesis are required. Brownlow *et al.* (2001) found that at Budongo, Uganda, females and males both initiated nesting at dusk. In addition, Brownlow *et al.* (2001) failed to find any effect of the presence of oestrous females on male nest height; however, such an effect may depend on the sex ratio of the community and the level of mating competition in each community. At Bossou, during the study periods, the number of adult males was two, with the alpha male, Foaf, spending most of his time with a core group of females, while the older male, Tua, rarely associated with Foaf's main party. Thus mating competition within this community may not be as high as in other communities where males associate more frequently and are more likely to compete for mating opportunities. If mating competition ever proves to be a valid hypothesis for explaining sex differences in nest height at any other site, it may thus explain why no sex differences emerged at Bossou.

Further studies of nesting behaviour and social organisation of the Seringbara and Yealé chimpanzee communities could elucidate the possible influences of predation and mating competition on nesting behaviour, and possibly the differences in nest integration observed, considering that nest integration enables individuals to nest arboreally at lower heights.

Fruth and Hohmann (1996, p. 230) proposed that "nest re-use by chimpanzees is mostly a question of habitat and availability of suitable nest material". Nest re-use, although mentioned in the literature on nesting behaviour in chimpanzees, has never been quantitatively analysed. It was found to be more common at Bossou than at the two Nimba sites, but the sample sizes were very small. In addition, as previously mentioned, nest re-use at those sites may have been underestimated. At Bossou, sub-adults tended to re-use nests more often than adults and for night-time nesting, this behaviour mainly concerned oil palm trees (*Elaeis guineensis*), which was the most preferred tree species for nesting at this site. Bending an oil palm leaf requires much strength. It is therefore likely that sub-adults unable to perform this behaviour for lack of strength will occasionally re-use such nests, particularly in areas such as abandoned fields where access to alternative nesting trees is limited. However, nest re-use also occurred in other habitat types where accessibility to trees was not obviously a limiting factor, thus not fully providing support for Fruth and Hohmann's (1996) hypothesis. At Bossou, nest re-use was also significantly associated with food providing tree species, but more data are required before making any inferences about such a pattern. Direct observations of nest re-use will be required from Bossou and other study sites to shed further light on this behaviour and its true extent within any one habitat.

Night nest height, nesting tree DBH and nest height-to-tree DBH ratio were compared between the three sites for each habitat type. No differences emerged in these variables in secondary, primary and marantaceae forest between the two Nimba sites or in secondary forest between the three sites. In addition, there was no difference in nest height-to-tree DBH ratio for any habitat type between the two Nimba sites. However, in primary forest, Bossou chimpanzees tended to nest at lower heights compared to Yealé chimpanzees, and lower relative to tree DBH compared to Seringbara chimpanzees. In riverine forest, Yealé chimpanzees nested higher, but chose larger trees than either Bossou or Seringbara chimpanzees. Finally, with the exception of nests in riverine forest, night nests at the two Nimba sites were more similar to each other in terms of height, tree DBH and their ratio, than night nests at Bossou.

The two Nimba sites also showed similarities in habitat choice and in tree species employed for nesting, with the same 5 tree species being amongst the 11 most commonly used tree species at both sites. Although only 3 were preferred species at Seringbara, all 5 were preferred species at Yealé, indicating that this convergence in choice is predominantly independent of species availability within the habitat. One species, *Carapa procera*, was among the 11 most commonly used species at all three sites, preferred at the Nimba sites, but not at Bossou. Bossou chimpanzees tended to nest more commonly in food-bearing trees than Nimba chimpanzees. This difference may be explained by a higher frequency of disturbance by diurnal or nocturnal foragers at the Nimba sites compared to Bossou, where fewer birds and mammals occur.

In this study single night nests were distinguished from night nest groups. The frequency of occurrence of single night nests was generally small across all three sites and no consistent differences in habitat choice emerged between nest groups and single nests, although it appeared that single nests were less frequently encountered in riverine forest or disturbed habitats such as abandoned fields at Bossou or secondary forest at Nimba. Such a distinction may be useful for indirectly assessing the influence of predation on habitat choice for nesting, since one would expect nest groups to be less vulnerable to predation than singletons.

The habitat at Bossou is more varied than at the two Nimba sites and is therefore less suitable for direct comparison. However, Seringbara and Yealé differ greatly in their topography and in the density and availability of different tree species and, therefore, the similarities observed between the two sites cannot be entirely explained on environmental grounds. While Seringbara is characterised by a succession of hills and valleys of forest, at Yealé, the mountain face gradually increases in elevation up to the summit where the slope becomes steeper without the deep-forested valleys observed at Seringbara.

At Yealé, differences in nesting emerged depending on elevation. These could be explained on the basis of food availability at different altitudes, with most fruit-bearing trees during the rainy season available in the mid-altitude region and then in the lower-altitude region, with the upper altitudes exhibiting the least fruit during this period of the year. Nesting patterns at Yealé are therefore likely to vary seasonally, reflecting fruiting patterns and availability at different altitudes.

More ground nests were encountered at the two Nimba sites than at Bossou. Some of the ground nests encountered at Nimba may also have served as night nests, although this requires confirmation via direct observation of nesting behaviour. Matsuzawa and Yamakoshi (1996) previously reported that 35.4% of 464 nests recorded at Yealé during the dry season were ground nests. Thus, ground nest making may vary seasonally at Nimba.

Matsuzawa and Yamakoshi (1996) advanced three hypotheses to explain the high frequency of ground nests at Yealé. 1) The high and steep altitudes of the Nimba Mountains may not provide good material for tree nests. 2) The predation pressure by carnivores or human hunters may be low at high altitudes. However, during this study half of the ground nests encountered were either located in the lower or mid altitude region of the massif. Moreover, human hunting of chimpanzees around Yealé has been reported in the recent past, and leopards are still thought to occur in the area, meaning that predation pressure cannot be ruled out. 3) High winds at high altitudes, especially in the dry season, may drive the chimpanzees to nest on the ground. This may explain the higher rate of ground nests during the dry season, which could also simply be explained on the basis that the chimpanzees may be more reluctant to nest on wet ground during the rainy season. Still, ground nests do occur in the rainy season.

The environmental factors underlying the presence of terrestrial nest building in some communities but not others and the possibility of ground nest use at night-time are still unclear and require more systematic investigation. In those communities that make ground nests, it also remains unclear whether the behaviour is performed only by certain individuals of the community or if it can be considered a community wide pattern. Genetic studies would be useful in elucidating this issue.

Summary and culture in nesting behaviour

This study has revealed important environmental correlates of nesting behaviour that are consistent across all three sites explored, especially concerning DBH of the principal tree employed in nesting (see Table 4.30).

Table 4.30. Significant environmental correlates of nesting consistent across Bossou, Seringbara and Yealé.

Independent variable	Dependent variable	Correlation
Tree DBH	Nest Height	Positive
Tree DBH	Number of trees employed in nest integration	Negative
Tree DBH	Number of nests/tree	Positive

In addition, patterns of similarity in nesting have also been demonstrated across the three sites (see Table 4.31).

Table 4.31. Variables pertaining to nesting consistent across Bossou, Seringbara and Yealé (≈: no significant difference; >:significantly greater; ≥: greater).

Variable			
Nest Height (excl. ground nests)	Day nest	≈	Night nest
Nest Height	Non-integrated nests	>	Integrated nest
Frequency of integration	Day	≈	Night
Number of integrated trees used (exception Yealé)	Night	≥	Day

Contrary to findings emerging from other field sites, at Bossou no sex differences emerged during the rainy season in nest height, nesting tree DBH chosen and frequency of integrated nests (see Table 4.32). Release from predation pressure and mating competition may explain this lack of differences between the sexes. Also, no significant difference in nest height, tree DBH or nest integration emerged between adults and sub-adults (adolescents and juveniles) (see Table 4.32). However, juveniles were never observed to make integrated nests. In addition, although based on a small sample, sub-adults were observed re-using nests more often than adults (see Table 4.32).

Table 4.32. Age- and sex-class patterns in nesting at Bossou overall, and for day and night nests analysed separately, sample size permitting (≈: no significant difference; ≥: greater).

	Variable			
Sex	Nest height	Male	≈	Female
	Tree DBH	Male	≈	Female
	Nest integration	Male	≈	Female
Age	Nest height	Adult	≈	Sub-adult
	Tree DBH	Adult	≈	Sub-adult
	Nest integration	Adult	≈	Adolescent
	Nest integration	Adult/Adolescent	≥	Juvenile
	Nest Re-use	Sub-adult	≥	Adult*

* Note: this result is based on a too small sample size to confirm trend with certainty.

Although some differences in nesting behaviour emerged between the three sites, the two Nimba sites proved to be remarkably similar to each other and contrasted significantly more with nests observed at Bossou (see Table 4.33). Population comparisons in nesting behaviour are definitely fraught with difficulties, especially between sites exhibiting wide divergence in habitat types, past and current levels of predation pressure, and climatic conditions.

However, although they differ in topography and in the density and distribution of common tree species, Seringbara and Yealé may share enough similar habitat to account for the similarities in nesting behaviour observed at these two sites. An alternative explanation may be convergence in certain aspects of nesting behaviour of the two communities through social transmission. Similarities may thus be due to more individual interchange between these two chimpanzee communities, both in the past and currently, than with Bossou. This is plausible in view of the relative proximity of Seringbara and Yealé and the presence of a continuous undisturbed forest expanse between them.

One potential cultural variant linked to nesting behaviour that has emerged so far relates to the discovery of pillows, detached foliage employed by chimpanzees for comfort purposes, observed at Kibale, Uganda in the Kanyawara chimpanzee community (Llorente, pers. comm.). This behaviour appears to differ from the nest lining behaviour that is observed during nest construction, since it aims specifically at providing a headrest for the resting chimpanzee (Llorente, pers. comm.). Although it emerges that environmental factors may explain much of the variation observed in nesting behaviour between chimpanzee communities, influences of social structure and organisation on nesting patterns require more detailed investigation. By applying similar methodologies across sites and controlling for environmental as well as social determinants to nesting, we may then be able to clarify what aspects of nesting are likely to be socially transmitted and reinforced, thereby constituting possible cultural variants in behaviour.

Table 4.32. Patterns of similarities and differences in nesting behaviour across the three sites (≈: no significant difference; ≥: greater than; ≤ less than; ≠: different; <: significantly smaller than).

Forest type	Variable					
	Nest integration	Bossou	<	(Seringbara	≈	Yealé)
	Nest re-use (maybe underestimated though!)	Bossou	≥	(Seringbara	≈	Yealé)
	Ground nests	Bossou	<	(Seringbara	≈	Yealé)
	Food-bearing tree species used (among the 10 most commonly used species)	Bossou	≥	(Seringbara	≈	Yealé)
	Habitat choice	Bossou	≠	(Seringbara	≈	Yealé)
Primary	Height	Bossou	(≈	Seringbara)	<	Yealé
	Tree DBH	Bossou	≈	Seringbara	≈	Yealé
	Ratio	Bossou	<	Seringbara	(≈	Yealé)
Secondary	Height	Bossou	≈	Seringbara	≈	Yealé
	Tree DBH	Bossou	≈	Seringbara	≈	Yealé
	Ratio	Bossou	≈	Seringbara	≈	Yealé
Riverine	Height	(Bossou	≈	Seringbara)	<	Yealé
	Tree DBH	(Bossou	≈	Seringbara)	<	Yealé
	Ratio	Bossou	≈	Seringbara	≈	Yealé
Marantaceae	Height	Unavailable		Seringbara	≈	Yealé
	Tree DBH	Unavailable		Seringbara	≈	Yealé
	Ratio	Unavailable		Seringbara	≈	Yealé

Chapter 5

The oil-palm and its use by chimpanzees at Bossou and Nimba

5.1 Introduction

The origins of the oil-palm and its distribution across Africa

The palm (family: Palmae) is found throughout tropical and temperate warm regions of the world. In tropical Africa, it is represented mainly by arborescent species, such as the oil-palm (*Elaeis guineensis*) and the raphia (*Raphia sp.*) (Letouzey, 1986) (see Plate 5.1).

Plate 5.1. Close-up of the crown of an oil-palm (*Elaeis guineensis*).

The oil-palm is known from early Tertiary deposits in West Africa and there is little doubt that this species originated in the region (Zeven, 1972; Hartley, 1988; Adebisi Sowunmi, 1999). The palynological record suggests that the occurrence of the oil-palm in West-Central Africa is much more recent than in West Africa (Adebisi Sowunmi, 1999). The introduction and the spread of this species in West-Central Africa were most probably greatly influenced by humans during the late Holocene period.

According to Adebisi Sowunmi (1999), the real palm belt runs from the Fouta Djallon region of Guinea, through the southern latitudes of Sierra Leone, across the southern countries of West Africa, through to the equatorial regions of Congo-Brazzaville and the Democratic Republic of Congo. The oil-palm spread more recently from the Congo into East Africa and can now be found in the wetter areas along the Great Rift. The Arab slave trade was responsible for its wider dispersion further east (c.f. Hartley, 1988). Therefore, in general, the presence of the oil-palm in forest habitats is often a good indicator of recent or past human presence.

Growth of the oil-palm

The oil-palm is the highest yielding oil-bearing plant (Hartley, 1988). The oil-palm is monoecious and has only one terminal growing point. The reproductive cycle is short, lasting only two to eight months and fruiting occurs by the fourth or fifth year from seed. The apical meristem lies in a depression at the apex of the stem. In mature palms, this depression is 10-12 cm in diameter and 2.5-4cm deep. The apex is conical and is buried in the crown of the palm within a soft mass of young leaves and leaf bases commonly known as the 'cabbage' (Hartley, 1988).

The oil-palm today can be found in a variety of habitats such as secondary, riverine and open/dry forests, gallery forests in savanna areas, fresh water swamp forests and on the margin of rainforests and savanna (Letouzey, 1986; Hartley, 1988). The oil-palm requires a relatively open area to grow and reproduce; and it thrives best when soil moisture is maintained (Hartley, 1988). Therefore, due to its growth requirements, it is not usually found in primeval rainforest.

Use by humans and chimpanzees

Palms are often widely used for feeding purposes and may also act as a keystone resource, by definition available when main foods are scarce (Terborgh, 1986). For different species of apes, including the orang-utan (*Pongo pygmaeus*), the lowland gorilla (*Gorilla gorilla gorilla),* humans (*Homo sapiens*) and the chimpanzee (*Pan troglodytes*) (e.g. orang-utan: Leighton and Leighton, 1983, gorilla: Blake *et al.*, 1995; Nishihara, 1995, human: Adebisi Sowunmi, 1999; chimpanzee: McGrew, 1985, 1992; Yamakoshi, 1998). More specifically, the oil-palm constitutes an important resource for both humans and chimpanzees across many regions of Africa.

Use by humans

The oil-palm is a very important crop in tropical West and West-Central African economies; its numerous products are of immense commercial and domestic value. Its products include oils and fats, edible nuts, alcoholic beverage, fuel, medicine and animal feed. After minimal processing, the fibrous reddish-orange mesocarp of the fruit is a very good source of oil used for cooking and sold commercially (see Plate 5.2). The oil extracted from the kernel (see Plate 5.2) is also used to make soap in certain parts of Africa. In addition, the oil-palm is used for various household and building materials, as well as for rituals and divination in certain traditional religions (Adebisi Sowunmi, 1999).

Plate 5.2. Oil-palm fruit bunch and nuts (photo courtesy of T. Matsuzawa).

Use by chimpanzees

Chimpanzees at many different study sites across Africa have been observed to use the oil-palm as a resource. Some of these uses include nesting, as previously mentioned in *Chapter 4*, feeding on the mesocarp of the fruit, the petiole and pith of leaves, the heart or the apical meristem, the flower, the resin or the kernel of the nuts and even drinking of palm wine produced by humans.

Long-term and short-term field sites

Table 5.1 summarises the use by chimpanzees of the oil-palm as a food resource across eight long-term and three short-term field sites. At Budongo and Kibale in Uganda, oil-palms are absent from the habitat of the chimpanzees. Moreover, there exists no report of the presence of these palms at Okorobiko in Equatorial Guinea.

Table 5.1. Summary of the use of the oil-palm as a food resource across eight long-term and three short-term chimpanzee field sites in Africa (excluding oil-palm wine drinking observed at Bossou).

Site	Country	Status in home range	Fruit	Nut	Leaf Petiole/Pith	Flower	Resin	Heart	Fibres of dead wood	References
Bossou	Guinea	Present	✓	✓	✓	✓	✓	✓	✓	Sugiyama and Koman, 1979b, 1992; Sugiyama, 1981 Yamakoshi and Sugiyama, 1995
Taï	Côte d'Ivoire	Present; Patchy	✓(rare)	⊙	✓	⊙	⊙	✓	⊙	Boesch and Boesch,, 1983; Boesch, pers. comm.
Sapo (short-term)	Liberia	Present	⊙	⊙	⊙	⊙	⊙	⊙	⊙	Anderson *et al.*, 1983; McGrew, 1992
Mt. Assirik	Senegal	Peripheral; Patchy	⊙	⊙	⊙	⊙	⊙	⊙	⊙	McGrew *et al.*, 1981; McGrew, 1992
Okorobiko (short-term)	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 (short-term)	Tanzania	Rare; Peripheral	⊙	⊙	⊙	⊙	⊙	⊙	⊙	Reynolds and Reynolds, 1965; Izawa and Itani, 1966; Sugiyama, 1968; Suzuki, 1969; Kano, 1972
Mahale-K	Tanzania	Abundant; (Groves)	⊙	⊙	⊙	⊙	⊙	⊙	⊙	Nishida *et al.*, 1983; Nishida and Uehara, 1983
Budongo	Uganda	Absent	✖	✖	✖	✖	✖	✖	✖	Eggelings, 1947
Kibale	Uganda	Absent	✖	✖	✖	✖	✖	✖	✖	Struhsaker, 1975; Ghiglieri, 1984; McGrew, 1992

Table legends: ✓: Used; ✖: Not available; ⊙: No reported use, although oil-palm available.

At Kasakati in Tanzania and Mt Assirik in Senegal, no evidence of use has been recorded, possibly since oil-palms are only present on the periphery of the home range of the chimpanzees. Indeed, at Mt. Assirik, oil-palms are absent from the core study area of 50 square kilometres that was explored in the 1970's (McGrew 1992). Although elsewhere in the park oil-palms are available in gallery forests that are accessible to the chimpanzees by riverine routes, there is as yet no indication that chimpanzees use these oil-palms either for nesting or for consumption (McGrew 1992).

In Sapo, eastern Liberia, although the chimpanzees were observed cracking four species of nuts and oil-palms were present in the home range of the chimpanzees, no use of the oil-palm was recorded during a 3-month study carried out at this site by Anderson *et al.* (1983).

Oil-palms were fairly recently introduced to Gombe and Mahale, Tanzania. At Mahale, with the exception of two conspicuous groves, the oil-palm grows close to human settlements that are not easily accessible to the chimpanzees. As a result, chimpanzees at Mahale have never been observed using the oil-palm as a resource (Nishida *et al.*, 1983; Nishida and Uehara, 1983). In contrast, the chimpanzees of Gombe have had free access to oil-palms since at least 1947, when the area was declared a reserve (Nishida *et al.*, 1983). Oil-palms are abundant in the home range of the Gombe chimpanzees (Clutton-Brock and Gillett, 1979), who frequently consume the mesocarp of the fruit and depend on this species of palm for survival during periods of fruit scarcity (McGrew, 1992; McGrew, pers. comm.). Goodall (1968) recorded that bark or wood of dead oil-palms was also occasionally eaten, a behaviour also observed at Bossou. Moreover, Wrangham (1975) noted that Gombe chimpanzees also ate the flower, the pith and the petiole of young leaves and the resin of the oil-palm.

At Lopé, Gabon, Tutin and Fernandez (1993) reported that chimpanzees consumed oil-palm fruit and the pith of leaves, but no other parts of the oil-palm. After exploring alternative hypotheses, McGrew *et al.* (1997) concluded that chimpanzees at Lopé do not crack oil-palm nuts, simply because this behaviour is not part of their set of traditions.

At Tai, Côte d'Ivoire, oil-palms are available to the chimpanzees; however, they are quite rare and limited to swampy areas (Boesch, pers. comm.). Nevertheless, chimpanzees at this site eat the pith of young leaves of mature oil-palms and feed quite regularly on the palm cabbage. According to Boesch (pers. comm.), this feeding behaviour greatly affects the fruiting of the palms, so only a few get to produce fruit. No direct observation of feeding on the mesocarp of the fruit has ever been made. Only once has an oil-palm seed been recovered from a faecal sample at this site (Boesch, pers. comm.), indicating that these chimpanzees very rarely feed on the mesocarp of the fruit.

At Bossou, Guinea, the oil-palm is the dominant species of palm in the habitat of the chimpanzees. It is commonly found in secondary forest and in abandoned fields. Bossou chimpanzees consume many parts of the oil-palm and the extent of its use by this community does not appear to be paralleled at any other site. The Bossou chimpanzees feed on the fleshy and fibrous mesocarp of the fruit, on the kernel of the nut, on the petiole of the young fronds, on the pith of mature leaves, on the inflorescence, on the palm heart and cabbage and also occasionally the woody fibres of dead palms (see Plate 5.3). Bossou chimpanzees employ tools to gain access to two of these resources: they crack open the nut using a stone hammer and anvil to gain access to the kernel inside, and they pound the centre of the crown to soften the heart using a palm frond as a pestle. Using the leaf-folding technique observed when drinking water from tree holes, Bossou chimpanzees also occasionally indulge in oil-palm wine being fermented in plastic containers attached below the crown of the palm.

Plate 5.3. Juvenile chimpanzee from Bossou pulling out a young frond of an oil-palm to feed on the petiole or basal tip of the leaf.

Other reports of use by chimpanzees

There have been reports of the use of the oil-palm in other regions of Africa. Savage and Wyman (1843/44) mentioned that oil-palms are abundant and freely eaten by the chimpanzees of the Cape Palmas area of Liberia, near the border with Côte d'Ivoire. However, they failed to mention what part of the oil-palm was consumed. Also from Liberia, Beatty (1951) made one of the earliest reports of the use of stones to crack open oil-palm nuts, in the south-east of the country.

Other reports come from short-term studies carried out in Guinea. Nissen (1931, p.57), who conducted the first scientific study of wild chimpanzees in Guinea, near Kindia, found that chimpanzees consumed oil-palm nuts. Later, De Bournonville (1967, Table VIII) found in a survey of western Guinea lasting four months that chimpanzees often fed on oil-palm nuts and the petiole of young leaves. However, these two studies did not make any reference to the use of tools to gain access to the kernel within the nut.

The earliest report of cracking of oil-palm nuts and oil-palm use by wild chimpanzees comes from Sierra Leone. Sept and Brookes (1994) report a quote by a Portuguese Jesuit priest, Manuel Alvares, dating back to 1615: "A *dari* (chimpanzee) takes a small quantity of *chaveo* (palm nuts) and with a stone in its hand breaks the nuts and eats them". Alvares also observed that "(the chimpanzee) is such a well-built and strong animal that it can tear out the palm cabbage from a palm tree, hence they ruin the trees in those parts of the forest where they alone feed." However, no details are provided as to how this behaviour was performed, but it is strongly reminiscent of the petiole and palm cabbage feeding behaviour observed at both Bossou and Taï.

Harding (1984) noted that in the Kilimi area of Sierra Leone, on the border with Guinea, oil-palm fruits are eaten by mangabeys (*Cercocebus torquatus*) and Guinea baboons (*Papio papio*), but not by sympatric chimpanzees. These chimpanzees were probably too shy to approach the village in the vicinity of which the oil-palms grew.

Other reports referring to the use of the oil-palm in chimpanzees concern rehabilitated or captive chimpanzees. Hannah and McGrew (1987) made observations of sixteen wild-born chimpanzees being rehabilitated from a laboratory back to a natural island setting in Liberia; the apes readily took to cracking oil-palm nuts using a hammer and anvil tool. The behaviour was initiated by one adult female and it then spread to twelve others over periods varying from a few seconds to several weeks. The chimpanzees were eventually observed to transport both hammers and nuts to new sites in the forest and to make use of tree branches, fallen logs and mangrove roots as anvils (Hannah and McGrew, 1987). It remained unclear whether the behaviour spread to the other group members through observational learning or not. McGrew (1992) suggested that the performance by the initiating female prompted long-dormant memories in the others, retained from when they still were in the wild.

De Bournonville (1967) reported that two captive adult male chimpanzees in Guinea refused to eat oil-palm fruit, although they accepted other fruits. He speculated that they came from an area of Guinea where oil-palms were absent and that they were showing dietary conservatism. From a cultural viewpoint, an alternative explanation would be that, even if oil-palms were available in the home range of the community where they originated from, feeding on oil-palm fruit may simply not have been a tradition of their natal community.

It is noteworthy that, with the exception of Mahale, at all long term field sites where oil-palms are present in the home range of the chimpanzees some part of the palm is consumed by the chimpanzees. However, the extent of oil-palm use and the number of parts consumed vary remarkably between sites. Boesch *et al.* (1994) argued that diffusion of nut-cracking via social transmission from far-western Africa to the east has probably been prevented by the major geographical barrier represented by the N'Zo-Sassandra River. However, as illustrated by Sapo and Taï, oil-palm nut-cracking is not necessarily consistent across all sites where chimpanzees are known to crack nuts and where oil-palms are present. In addition, so far at sites where oil-palms are peripheral, i.e. Kasakati and Mt Assirik, found only in groves, i.e. Mahale, or where chimpanzees have not been studied extensively, i.e. Sapo, no evidence of oil-palm use by chimpanzees has emerged.

The oil-palm and culture

Considering that the presence of feral oil-palms across 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 behavioural innovation. In addition, as discussed above, there is strong evidence of cross-cultural variation in the use of the oil-palm across several geographically separated chimpanzee communities across Africa (McGrew, 1985, 1992; McGrew *et al.*, 1997). Chimpanzees may consume many different parts of the oil-palm, and in some communities may rely on tool-use to gain access to some of these resources. A study of the differential use of the oil-palm across neighbouring communities and of the modes of transmission of these uses within a community may thus be useful in shedding light on the mechanisms and the dynamics of cultural transmission in the chimpanzee.

5.2 Methods and data analysis

A random sample of oil-palms at three sites - Bossou, Seringbara and Yealé - were tagged when encountered during forest exploration of the chimpanzees' habitat (N=127 for Bossou; N=68 for Seringbara; N=127 for Yealé). These tagged oil-palms were surveyed on a monthly basis during two rainy season periods between June and September 2000, and June and September 2001. However, no survey was conducted at Yealé in September 2000 due to political unrest in the region during that period.

Oil-palm use by chimpanzees, humans or other animals

Each tagged oil-palm was routinely checked for use by chimpanzees, humans or other animals. For humans, if the oil-palm had been used between survey dates, three types of uses were distinguished: 1) cutting down of fruit bunch (for palm oil extraction); 2) cutting off palm fronds/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 (as described below), nut-cracking was then assumed to have been performed by humans if, in addition, indications of human activity in the vicinity were noticeable and/or use of this site by humans could be confirmed through local knowledge.

Some nuts had distinctly been fed on by annelids, insects or mammals, e.g. rodent, bush-pig or hedgehog. Occasionally direct sightings of these mammals consuming oil-palm nuts were made, but most often only traces of mammalian footprints and foraging activity, and the state of nutshell remains provided evidence of their feeding on the nuts. Several species of monkeys; e.g. the sooty mangabey (*Cercocebus atys*), the lesser spot-nosed guenon (*Cercopithecus petaurista*) and the Diana monkey (*Cercopithecus diana diana)*, and squirrels were also sighted in oil-palms, consuming the mesocarp of the fruit. These usually would drop the nut and some fibres to the ground whilst feeding. These fruit remains often carried distinctive tooth-marks that helped indirectly confirm their presence since the last survey date. Indications of recent fruit and nut feeding by insects, annelids or mammals were thus logged on a monthly basis to test for differences in inter-specific competition for these resources across the different sites.

Concerning use by chimpanzees, details such as part eaten (i.e.; nut; fruit; petiole; palm heart and flower), tool use involved (i.e.; pestle pounding, nut cracking), presence or absence of nest (i.e. nest less than a month old, nest over a month old or nest reuse) were noted. Although chimpanzees at Bossou most often swallow the 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 fibres onto the ground. Fruit consumption was usually further confirmed via faecal analysis, since nuts and fibres appeared in the faeces (see Plate 5.4). As for nut, petiole, palm heart and flower consumption, all these could be established during the monthly surveys by looking out for evidence at the foot or in the crown of each tagged oil-palm (see Plate 5.5). Other untagged oil-palms within the habitat of the chimpanzees were also regularly checked for use when encountered during daily tracking of the chimpanzees.

Plate 5.4. Seed and fibres of the oil-palm fruit in the faeces of a chimpanzee.

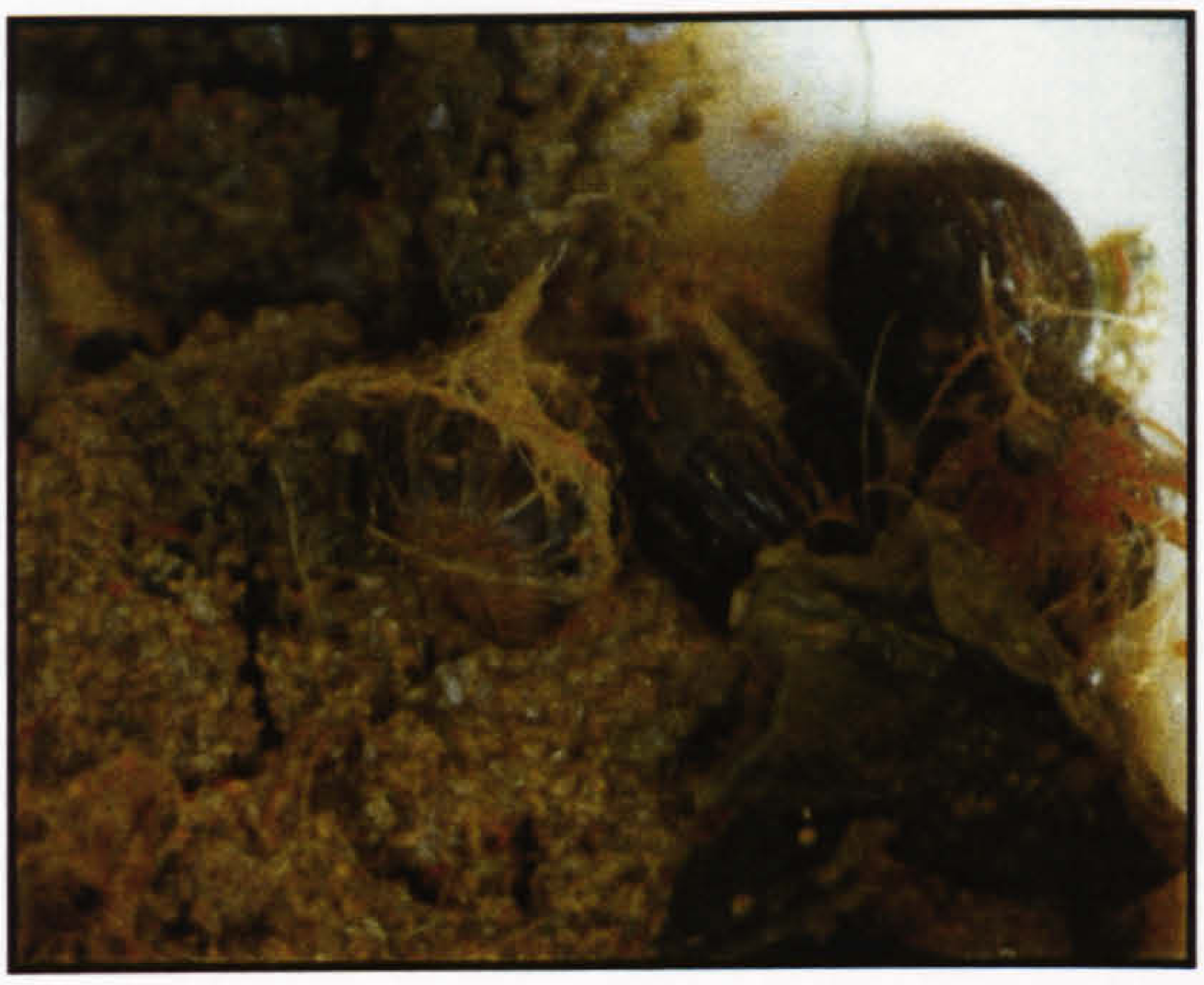


Plate 5.5. Remains of oil-palm fronds dropped to the ground beneath an oil-palm after a chimpanzee consumed the petiole and pestle pounded.

Previous direct observations of use of the oil-palm by chimpanzees at Bossou had enabled the establishment of criteria for assessing the above details - especially for distinguishing between simple petiole feeding and pestle pounding from fallen fronds on the ground. Based on 48 direct observations from Bossou, a palm frond used as a pestle was usually modified in two ways, either 1) it was shortened towards the distal end, so a clear breaking point could be discerned (14.6%), or 2) leaves towards its base were stripped away (60.4%). Both modifications were applied to the same tool in 25% of recorded observations of pestle tool manufacturing. In addition, observation of the basal tip of the frond was used as a good indicator for pestle pounding since not only was it frequently chewed (indication of petiole feeding), but in all cases it was also distinctly frazzled and crushed as a consequence of the pounding action.

A set of criteria was also employed to assess evidence of nut-cracking. Used hammers were defined as stones or wooden clubs that showed evidence of wear due to nut cracking. Used anvils were emergent tree roots or stones (loose or embedded) which 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, nut cracking was ascribed to chimpanzees only if at least one of the following conditions was met: 1) the chimpanzees had previously been heard or seen cracking at the site (see Plate 5.6), 2) fresh traces of chimpanzees, such as knuckle or foot prints, were found within five meters 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.

Details of behaviour were thus inferred according to the observable evidence gathered. Monthly intervals between surveys of the tagged oil-palms were appropriate for monitoring the frequency of use of a single oil-palm, since at Bossou, any of the above mentioned uses would very rarely ever be targeted more than once a month at the same oil-palm. Indeed, only once was nut-cracking observed to take place beneath the same oil-palm on two separate occasions in the span of a month.

Plate 5.6. Chimpanzees cracking oil-palm nuts at Bossou using a hammer and anvil stone (photo courtesy of T. Matsuzawa).

Assessing tool availability

For nut cracking

Hammer and anvil availability were recorded within a 5-metre radius of each tagged oil-palm (see Plate 5.7). As not all stones or branches can be used as tools for cracking oil-palm nuts, an operational definition of tools was used, principally based on data gathered from tools employed at Bossou and criteria used in other studies (cf. Boesch *et al.*, 1994; McGrew *et al.*, 1997). Thus, from 46 nut-cracking sites present at Bossou, 87 confirmed anvil stones and 109 confirmed hammer stones were weighed using a pocket-sized spring balance, calibrated to the nearest 100 g, and their dimensions – maximum width and length - measured to the nearest millimetre. A potential anvil was thus defined as a stone (loose or embedded) 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 weighs more than 400 g, the minimum recorded from the set of 87 used anvils stones weighed 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 more than or equal to 7 cm wide (N=87; mean=12.1 cm; SD=4.8; Range: 7.0-17.4 cm) and more than 10 cm long (N=87; mean=16.1 cm; SD=6.5; Range: 10.2-38.4 cm) and providing a workable flat surface for cracking. Hardness was estimated as 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 was based on 20 trials performed by dropping a 1 kg granite stone from 0.5 m onto an oil-palm nut placed on suitable anvil. A maximum of 5 falls was required to crack open the nut, with the mean number of falls recorded being 3.2 (SD=0.89).

Plate 5.7. Example of a stone hammer/anvil set from Bossou (photo courtesy of T. Matsuzawa).

Potential hammers were stones or wooden clubs hard enough to open oil-palm nuts. These should not break when banged vigorously against a hard surface and weigh more than 100 g and no more than 2.5 kg (N=109; mean=848.6 g; SD=363.4; Range: 100-2,200 g). An upper weight limit was used since stones that are too heavy may not be easily manipulated by the chimpanzees and may also result in crushing the kernel to pieces. Potential hammers should have a width of more than 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 fitted both operational definitions and were consequently classed as potentially serving both functions. These criteria for hammers and anvils facilitated the differentiation between stones and branches lying on the forest floor that might or might not be used by the chimpanzees for cracking oil-palm nuts.

For pestle pounding

Of 85 pestle pounding tools recorded at Bossou, 92% (78/85) were young fronds rather than mature ones. The presence of young leaves at the centre of the palm crown was thus monitored during the monthly surveys in the context of tool availability for the purpose of pestle pounding. Their availability was recorded on a scale of 0-2 (0: absent; 1: present but no more than two young new leaves/fronds emerging from the crown; 2: more than two young leaves/fronds present).

Oil-palm phenology

For each site, the status of each tagged oil-palm in terms of availability of fruit, flowers, young fronds and nuts was recorded on a monthly basis. Fruit and flower availability was noted on a scale of 0-3 (0:none; 1: young bunch; 2: mature bunch; 3: old bunch). Nut availability on the ground was noted as follows: 0: none; 1: 1-25 nuts; 2: 26-50 nuts; 3: >50 nuts. Nut quality was assessed as a percentage of edible nuts from a standardised sample of 20 randomly collected nuts or fewer for oil-palms with a nut availability of 1, of 30 or less for oil-palms with a nut availability of 2 and of 50 or more for oil-palms with a nut availability of 3. These collected nuts were not cracked so as not to affect future availability. Agreement was reached between myself and the guides as to which nuts were suitable for cracking or not. Since local people also crack oil-palm nuts, they usually know which nuts are good and which ones are rotten. The availability of young fronds or petioles was also recorded as detailed above. This monthly phenology of the tagged oil-palms was useful for comparing availability of the different edible plant parts between the three sites, and it facilitated an assessment of the impact of competitors on availability of fruit and nuts.

Data analysis

In order to control for monthly variations in fruit, flower and nut availability and inter-specific competition for some of these resources, only months that were surveyed across all three sites were included in the data analysis. All statistical tests were non-parametric and two-tailed.

5.3 Aims

Bossou chimpanzees are known for their extensive reliance on the oil-palm for feeding (Yamakoshi, 1998) and nesting (refer to *Chapter 4*). Since oil-palms are also available at both Seringbara and Yealé in the Nimba mountains, the main aim of this study was to assess:

(1) whether the chimpanzees at these two sites make use of this resource or not;

(2) if so, what edible plant part(s) of the oil-palm is (are) consumed and is tool-use involved or not;

(3) the existence of any environmental differences between these sites and Bossou that may explain why chimpanzees at any one of these two sites exhibit a differential pattern of use of the oil-palm. In this respect, five alternative hypotheses were tested:

(1) The density of oil-palms within the home range of the chimpanzees is too low and the chimpanzees do not frequent the areas where these oil-palms are located.

(2) There is inadequate tool availability for either nut-cracking or pestle pounding.

(3) Oil-palm fruit, flower and leaf productivity is too low for use by chimpanzees.

(4) Competition with sympatric species is intense, presenting chimpanzees with little opportunity to exploit oil-palm resources.

(5) Chimpanzees ignore oil-palm food resources because higher-quality items are available at the same net cost of acquisition and processing (Günther and Boesch, 1993).

5.4 Results

Oil-palm use across the three sites

Bossou

During the two rainy season periods over which the oil-palm surveys were conducted and focal animal data collected, Bossou chimpanzees were observed to spend 23.9% of their feeding time consuming some part of the oil-palm (see Fig. 5.1). This result confirmed their substantial reliance upon the oil-palm during the rainy season, which corresponds to the period of fruit scarcity at this site (Yamakoshi, 1998; Takemoto, 2001). The frequency of consumption of the different oil-palm parts based on the monthly surveys correlates significantly with the data gathered from continuous animal focal sampling ($N=6$; $R=0.971$; $\rho<0.001$). This result suggests that the oil-palm surveying method adequately reflects the relative amount of time that Bossou chimpanzees spent on these various oil-palm feeding activities.

In accordance with the focal sampling data, the oil-palm surveys at Bossou indicate that pestle pounding and petiole feeding were the two most frequent behaviours aimed at oil-palms between June and September 2000 and 2001 (see Fig. 5.2). Consumption of the fruit mesocarp and nut-cracking were less common, but were nevertheless regularly noted (see Fig. 5.2). Daily observations of the Bossou chimpanzees also confirmed that they feed on the oil-palm flower and the pith of mature leaves, as confirmed by the presence of wadges of pith at the foot of the oil-palm (see Plate 5.8 and 5.9). However, neither of these edible items emerged as being consumed from the survey data and, although feeding on the pith of mature leaves was noted during focal animal sampling, flower consumption was not and was indeed only observed *ad lib* on two occasions (see Table 5.2).

Fig. 5.1. Time spent consuming different oil-palm plant parts as a percentage of total feeding time by Bossou chimpanzees over two rainy season periods (June-September 2000 and June and September 2001).

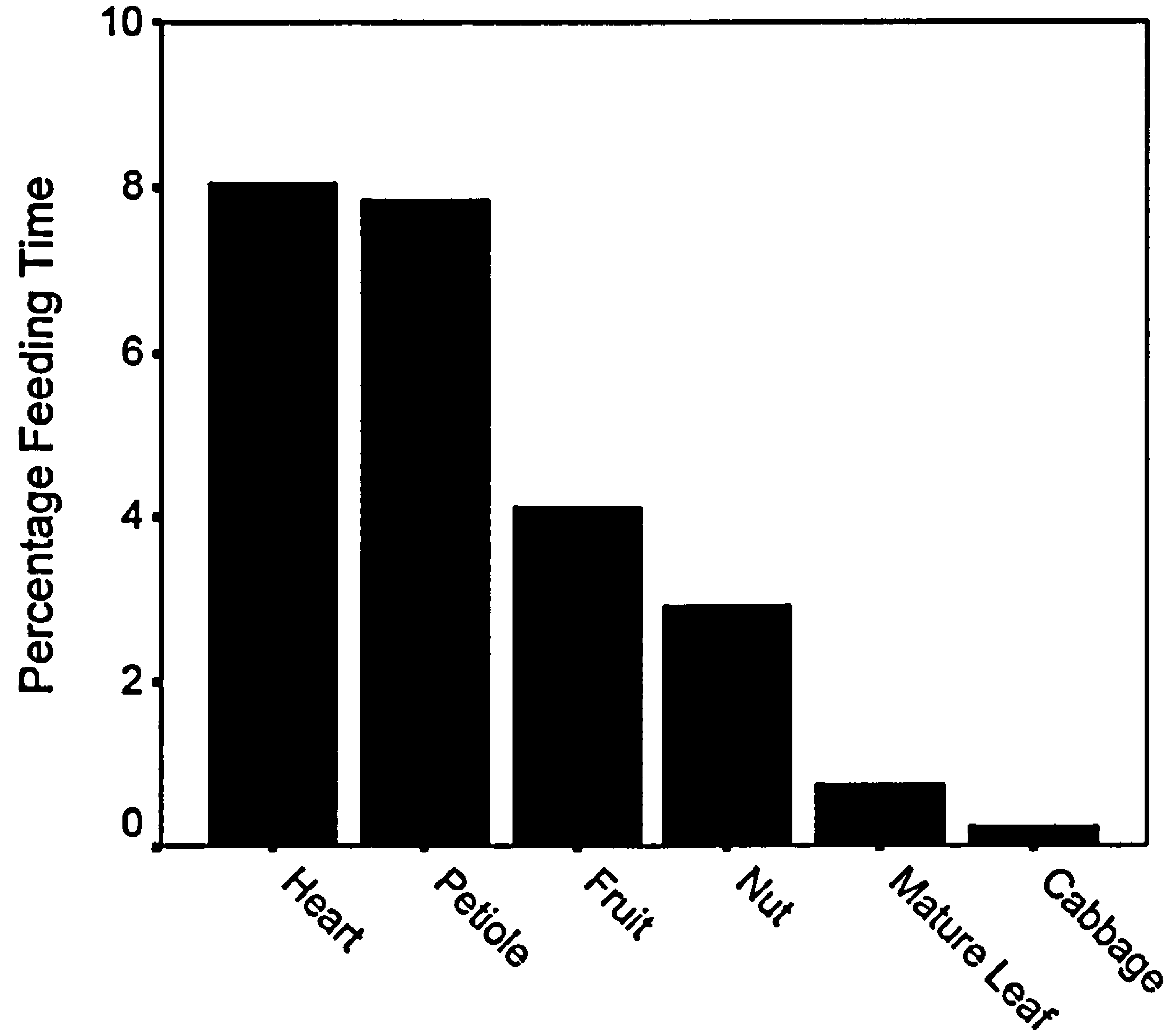


Plate 5.8. Wadges of oil-palm leaf pith and feeding remains left behind by Bossou chimpanzees on the forest floor.

Plate 5.9. Remains of an oil-palm flower after a Bossou chimpanzee was observed consuming the base of the stem.

The Nimba Sites

Six kilometres to the east of Bossou, the chimpanzees near Seringbara in the Nimba Reserve were never observed to use the oil-palm either for feeding (see Fig. 5.2) or nesting (for nesting refer to *Chapter 4*). 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 faecal analysis, gave any indication that these chimpanzees employ the oil-palm as a food resource (see Table 5.2).

On the other hand, almost 14 kilometres to the south-east of Bossou, at Yealé in the same Reserve of Nimba, chimpanzees consume the oil-palm fruit, the petiole of young fronds and the stem and the perianth of new flowers (see Fig. 5.2 and 5.3) (see Plate 5.10). The perianth has never been recorded as being consumed at Bossou. In addition, they also occasionally crack open the nuts employing stone tools (see Fig. 5.2 and 5.3). At Yealé, only 2.4% of surveyed oil-palms (3/127) provided evidence of nut-cracking, which is few compared to Bossou, where 22.8% (29/127) of all surveyed oil-palms presented nut-cracking ateliers.

No evidence of pestle pounding or feeding on the pith of mature leaves emerged from Yealé (see Fig. 5.2 and 5.3). Finally, Yealé chimpanzees employ the oil-palm as a food resource to a lesser extent than Bossou chimpanzees (see Fig. 5.2). Nevertheless, if the relative frequency of use determined via the monthly oil-palm surveys holds up as at Bossou, then Yealé chimpanzees spent more time consuming the petiole of young fronds than the fruit (see Fig. 5.2). They also spent an even lesser amount of time nut-cracking and feeding on the flower (see Fig. 5.2).

Plate 5.10. Appearance of the crown of an oil-palm at Yealé after a chimpanzee removed its young leaves to feed on the petiole and the new young leaf shoots.

During the first month of both survey periods, past use, assumed to be greater than a month old and less than 9 months old on the basis of the state of the remains, was also recorded. This information indicated that chimpanzees at both Bossou and Yealé also used the oil-palm for food outside the peak months of the rainy season period (June-September). In addition, if one compares the overall total frequency of records of oil-palms supplying evidence of nut-cracking and petiole feeding, two activities common to both sites, no significant difference emerged between the two sites in their observed and expected frequencies (Chi-square test with continuity correction: χ^2=3.660; *n.s.*) (see Fig. 5.3). Thus in relative terms, the proportion of oil-palms targeted for nut-cracking and petiole feeding did not differ significantly between Bossou and Yealé. Nevertheless, evidence of these activities was less frequently encountered at Yealé.

Fig. 5.2. Monthly percentage (not to scale) use of surveyed oil-palms by chimpanzees across the three sites (Past: refers to traces that were judged to be more than a month and less than 9 months old; PP: petiole and palm heart consumed; Pet: Petiole; Frt: Fruit; * and **:Total number of oil-palms inconsistent due to death).

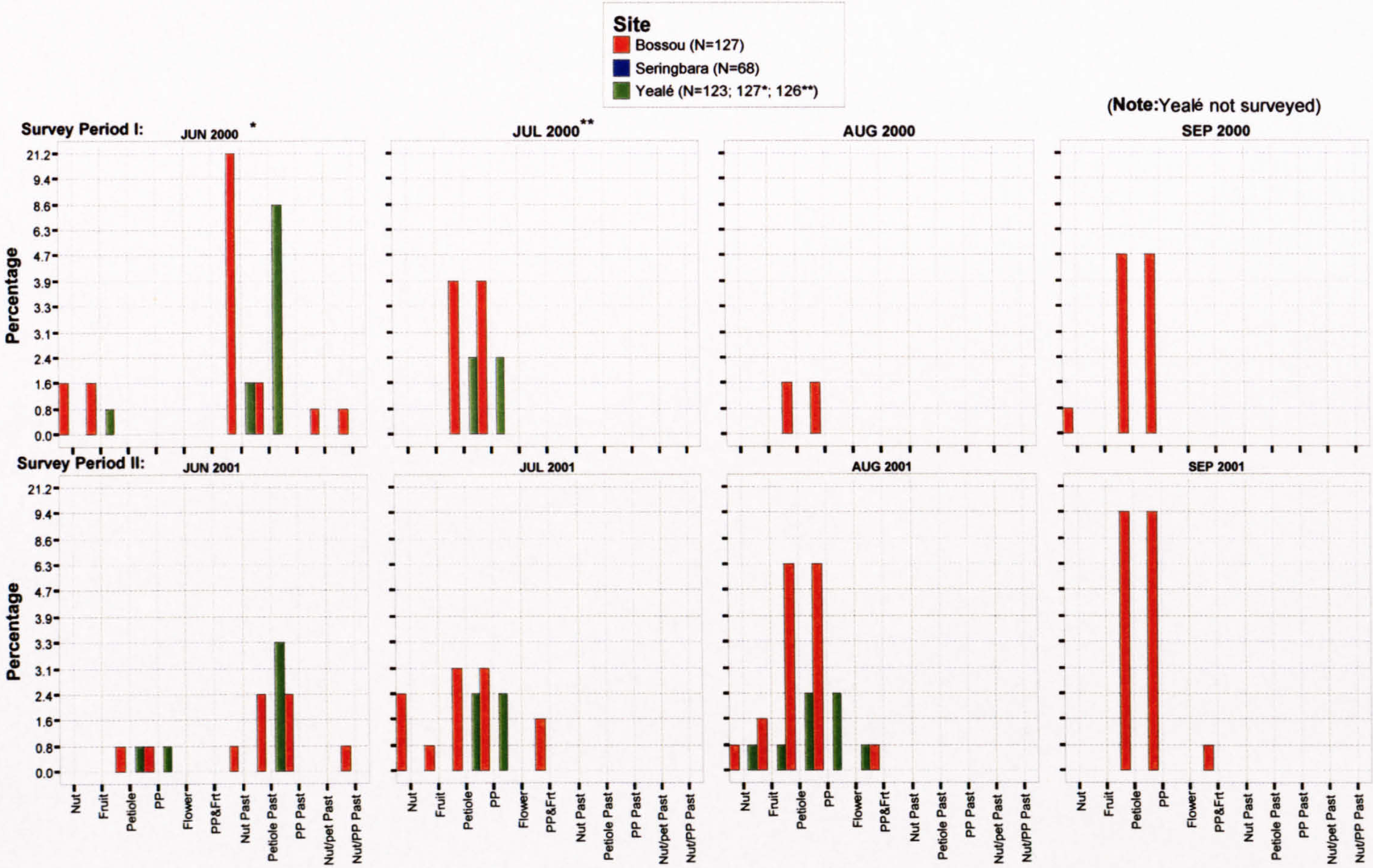
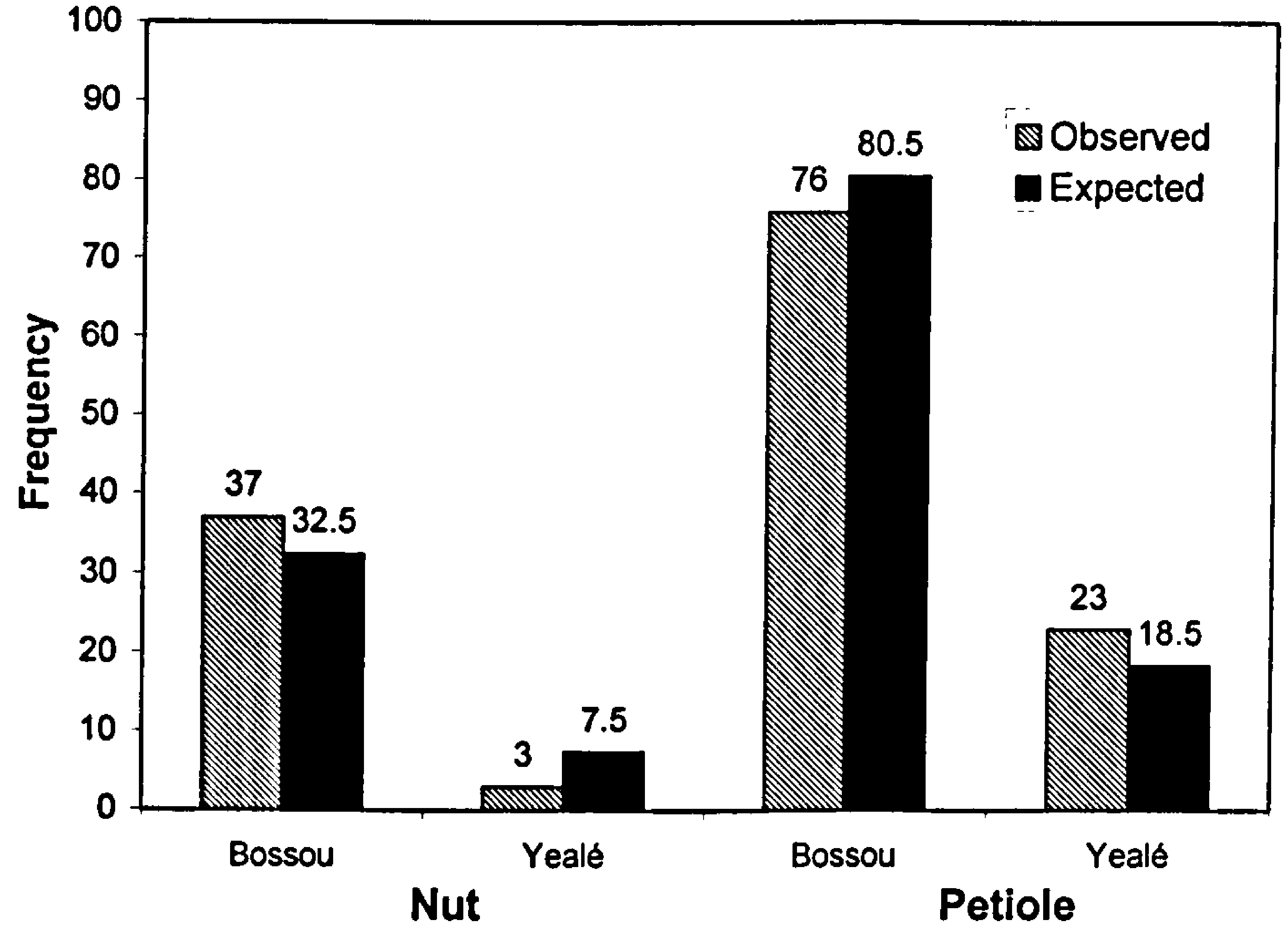


Table 5.2 Oil-palm parts confirmed to be consumed by chimpanzees at the three study sites and basis for supporting evidence.

	Site	*Type of evidence*			
Item consumed		***Surveyed palms***	***Faeces***	***Other oil-palms***	***Direct Observation***
Nut	Bossou	✓	✗	✓	✓
	Seringbara	✗	✗	✗	✗
	Yealé	✓	✗	✓	✗
Fruit	Bossou	✓	✓	✓	✓
	Seringbara	✗	✗	✗	✗
	Yealé	✓	✓	✗	✓
Petiole	Bossou	✓	✗	✓	✓
	Seringbara	✗	✗	✗	✗
	Yealé	✓	✗	✓	✓
Heart	Bossou	✓	✗	✓	✓
	Seringbara	✗	✗	✗	✗
	Yealé	✗	✗	✗	✗
Flower	Bossou	✗	✗	✓	✓
	Seringbara	✗	✗	✗	✗
	Yealé	✓	✗	✓	✗
Pith of Mature Leaf	Bossou	✗	✗	✓	✓
	Seringbara	✗	✗	✗	✗
	Yealé	✗	✗	✗	✗

Legend: ✓ =Evidence found; ✗ =No evidence found

Fig. 5.3 Overall observed and expected frequencies of surveyed oil-palms exhibiting evidence of nut-cracking or petiole feeding at Bossou and Yealé (excluding September 2000 for Bossou, since Yealé was not surveyed that month).



Oil-palm density and distribution

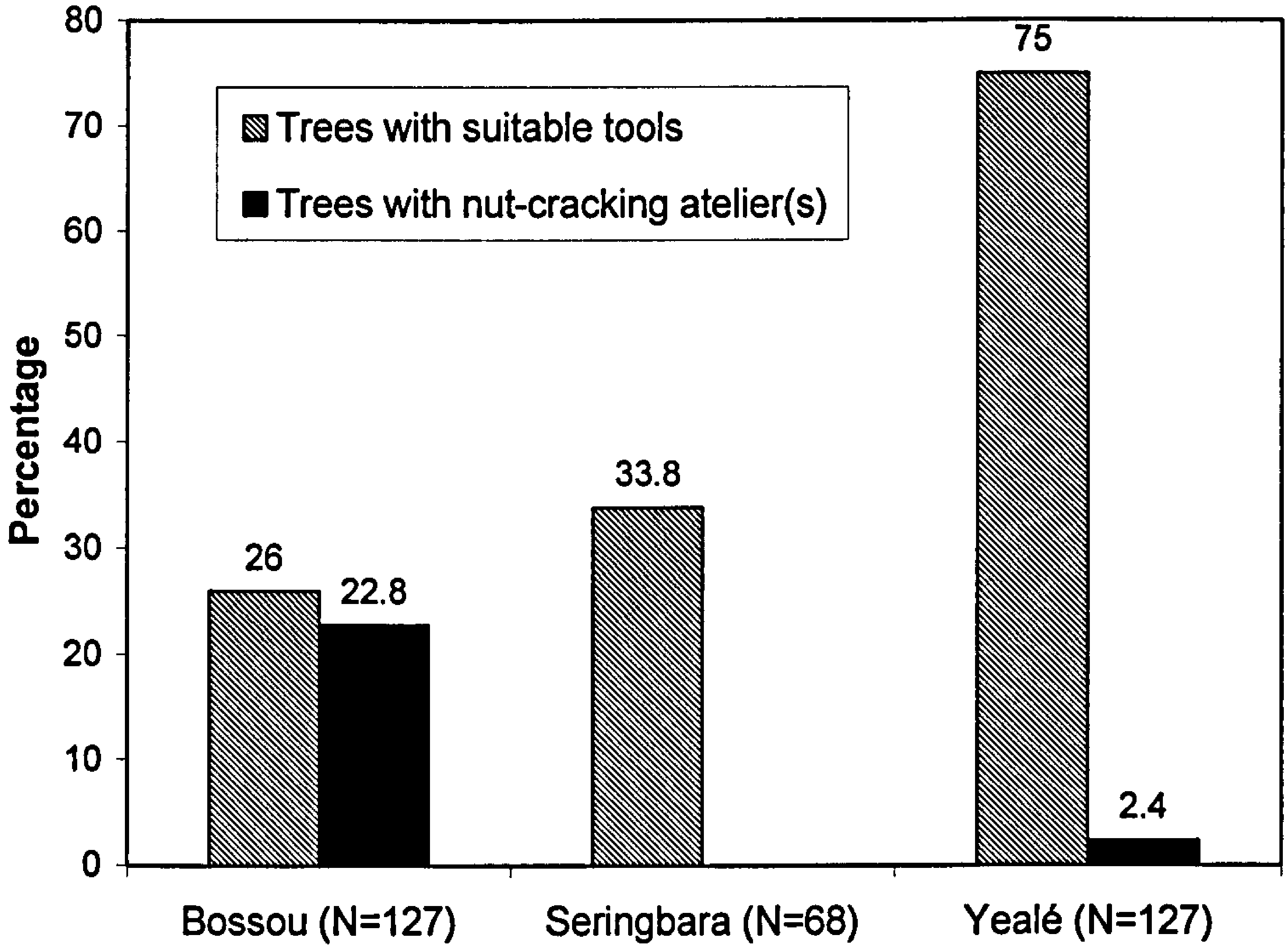
One possible reason for the differential use of the oil-palm between these three sites is that there are significant differences in oil-palm availability. Based on vegetation transects (refer to Chapter 4), oil-palm density at Bossou was 7.2 oil-palms/km^2 within the core area used by the chimpanzees, compared to 1.02 oil-palms/km^2 at Seringbara and 4.15 oil-palms/km^2 at Yealé. At Bossou, oil-palms are very abundant in certain areas and comparatively more uniformly distributed than at either Seringbara or Yealé, where their distribution is far more localised and clumped. Chimpanzees at Yealé employed the oil-palm 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 why we observe differential patterns of uses between these two communities.

It is also clear that Seringbara harbours the fewest oil-palms; however, traces of chimpanzees, i.e. nests and feeding remains, were found near areas where oil-palms were available. Thus in spite of a lower density of oil-palms and their clumped distribution within the habitat, Seringbara chimpanzees clearly have access to these oil-palms. Considering the high energy returns gained from feeding on the kernel of the oil-palm nut, on the apical meristem or the mesocarp of the fruit (Hartley, 1988) and that access is not a limiting factor, why do Seringbara chimpanzees not show any indications of feeding on the oil-palm? Might this reflect cultural variation or a possible failure of knowledge transmission and diffusion, assuming 1) individual interchange between the Bossou and the Seringbara communities, as well as between Yealé and Seringbara, and 2) social learning in the acquisition of these behaviours? Or are there environmental differences that could explain these divergences in behaviour? Several environmentally based hypotheses will thus be explored.

Tool availability for nut-cracking or pestle pounding

It is conceivable that restricted tool availability explains why Yealé chimpanzees do not pestle pound and so rarely crack oil-palm nuts, and why Seringbara chimpanzees perform neither. Based on the random sample of surveyed oil-palms, at Bossou, just over a quarter provided suitable nut-cracking tools, i.e. a minimum set of one anvil stone or tree root and one hammer stone or wooden club, and 22.8% showed evidence of nut-cracking (see Fig. 5.4). Therefore, at Bossou, 87.9% of oil-palms providing tools had been employed at some point in their recent history for cracking oil-palm nuts. At Seringbara, just over one third of the oil-palms surveyed supplied suitable nut-cracking tools, but no evidence of this tool-use activity was found (see Fig. 5.4). At Yealé, three quarters of the surveyed oil-palms provided a minimum of one suitable anvil and hammer set; however, only 2.4% revealed indications of nut-cracking (see Fig. 5.4).

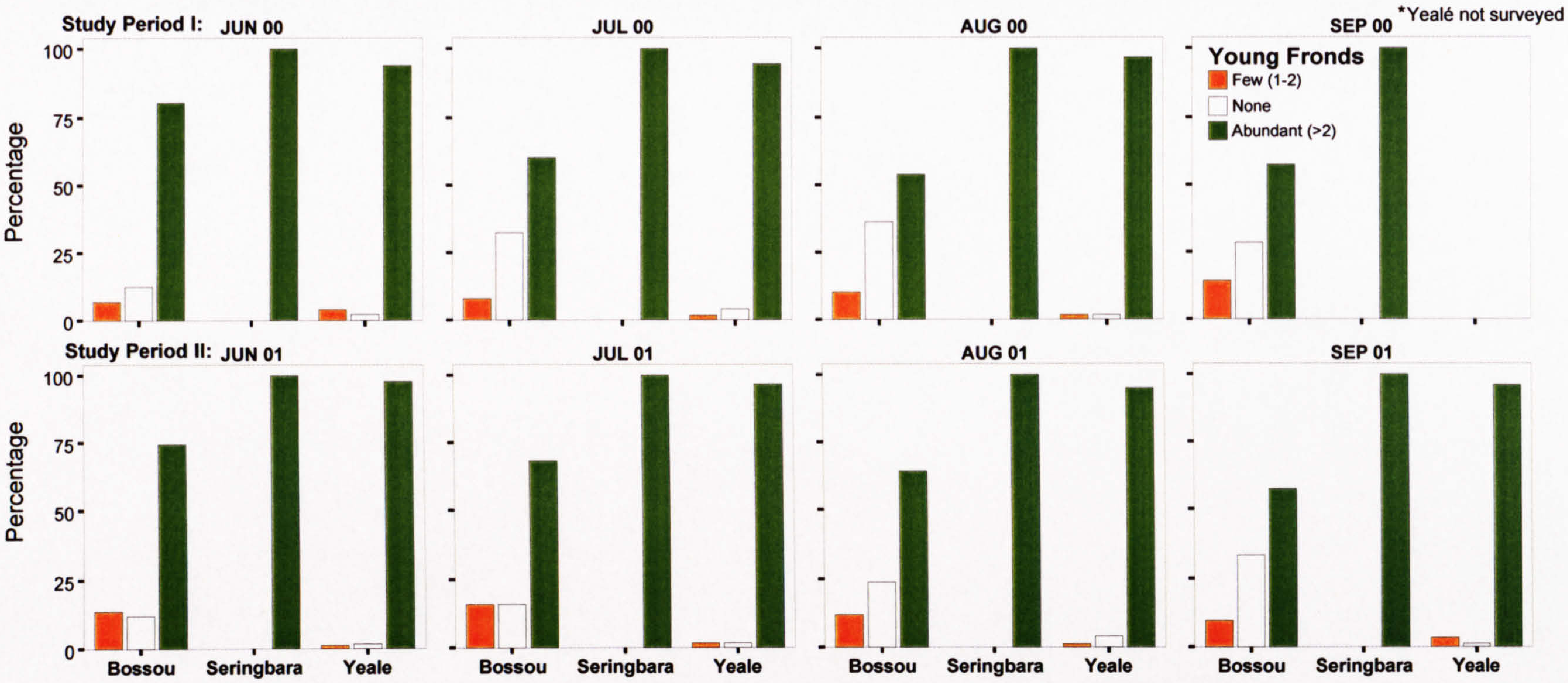
Fig. 5.4. Percentage of oil-palms surveyed providing suitable nut-cracking tools (a minimum set of one anvil stone or tree root and one hammer stone or wooden club) and exhibiting evidence of nut-cracking across the three sites.



It is apparent that potential tools suitable for cracking oil-palm nuts were available at all 3 sites within a 5-m radius of a number of oil-palms surveyed. Therefore, limited availability of nut-cracking tools cannot explain the absence of this behaviour at Seringbara and its rarity at Yealé, a site where most oil-palms presented potential tools.

In addition, all surveyed 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 (see Fig. 5.5). Between June 2000 and September 2001, among the surveyed oil-palms, no deaths were recorded at Bossou, while only 3 were noted at the Yealé site. However, if petiole feeding was recorded during the monthly surveys at Bossou and Yealé, respectively 82.5% (33/40) and 87.5% (7/8) of oil-palms

Fig. 5.5 Monthly percentage availability of young fronds based on monthly surveys of oil-palms across the three sites.



no longer exhibited young fronds and the rest only 1 to 2. Average recovery time for the production of a novel set of leaves post petiole feeding was 3 months (N=19; SD= 0.94; Range: 1-5 months). As for pestle pounding, of 36 records, 94.4% indicated that all young leaves had been removed, while 5.6% had less than 2 leaves left. Average recovery time post pestle pounding was 3.3 months (N=22; SD=1.1; Range: 1-5 months). So, 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 available throughout both survey periods.

Fruit, flower and nut availability

A significant difference emerged in the overall fruit availability across the three sites (Chi-square test: $\chi^2(2)=41.059$; $\rho<0.001$) (see Fig. 5.6). At Yealé, the observed frequency of fruiting oil-palms available exceeded the expected frequency; while at Bossou, far fewer oil-palms than expected exhibited mature fruit (see Fig. 5.6). Regarding the percentage of surveyed palms providing fruit on a monthly basis, Yealé always presented a greater percentage than either Bossou or Seringbara, with the exception of June 2000 when Seringbara had more than a third of its oil-palms harbouring a mature bunch of fruit (see Fig. 5.7). In addition, with the exception of the month of August, a greater percentage of oil-palms provided mature fruit at the Seringbara site than at Bossou (see Fig. 5.7). In general, at all three sites, some surveyed oil-palms harboured mature fruit every months; however, as the rainy season progressed, the monthly percentage of oil-palms with available fruit decreased (see Fig. 5.7). Finally, overall and monthly fruit availability during the two survey periods was greater at the Nimba sites than at Bossou, thus falsifying the hypothesis that Seringbara chimpanzees do not consume oil-palm fruit since these are absent or rarely available.

Fig. 5.6. Observed and expected frequencies of surveyed oil-palms exhibiting mature fruit or not across all months for which all three sites were surveyed.

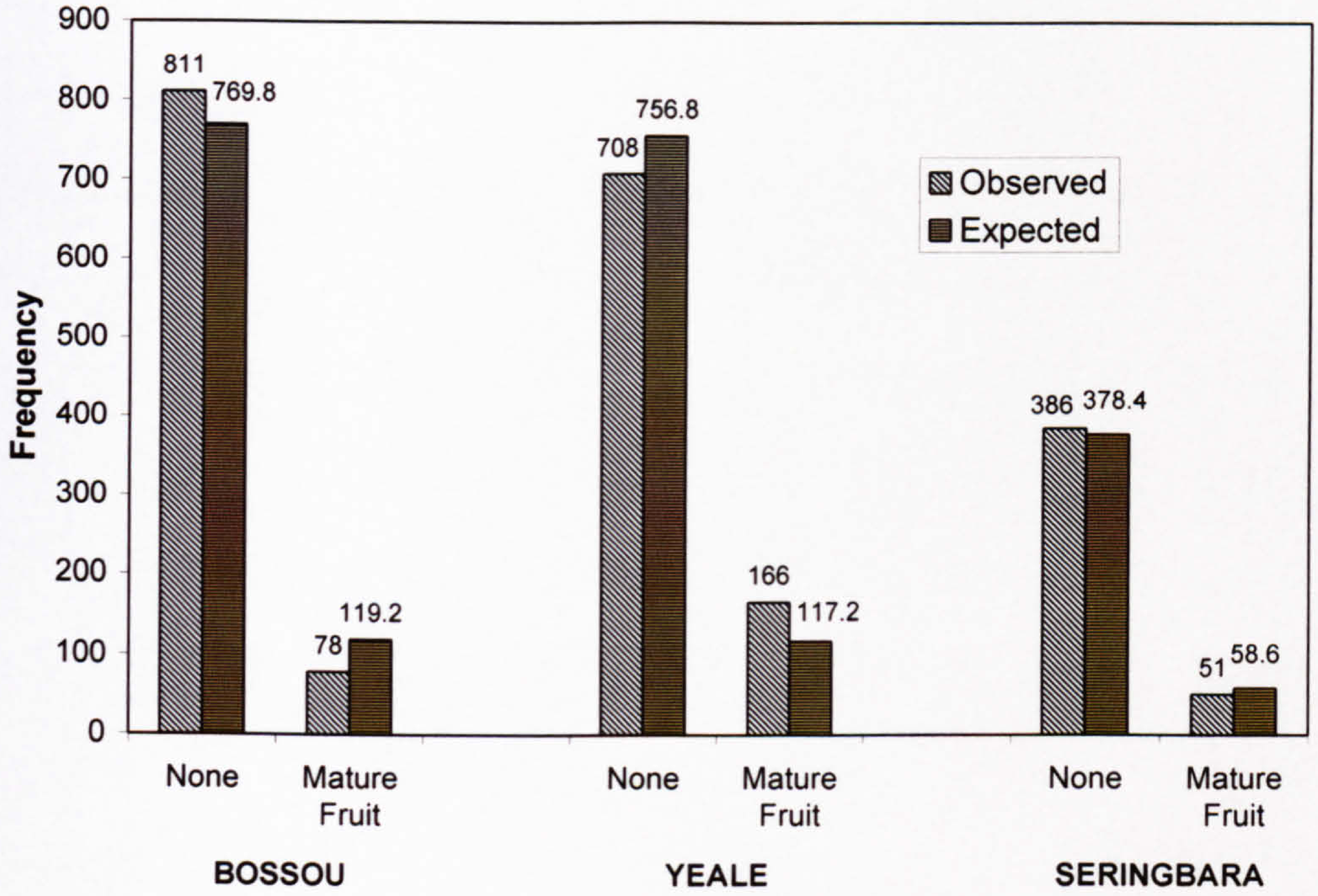
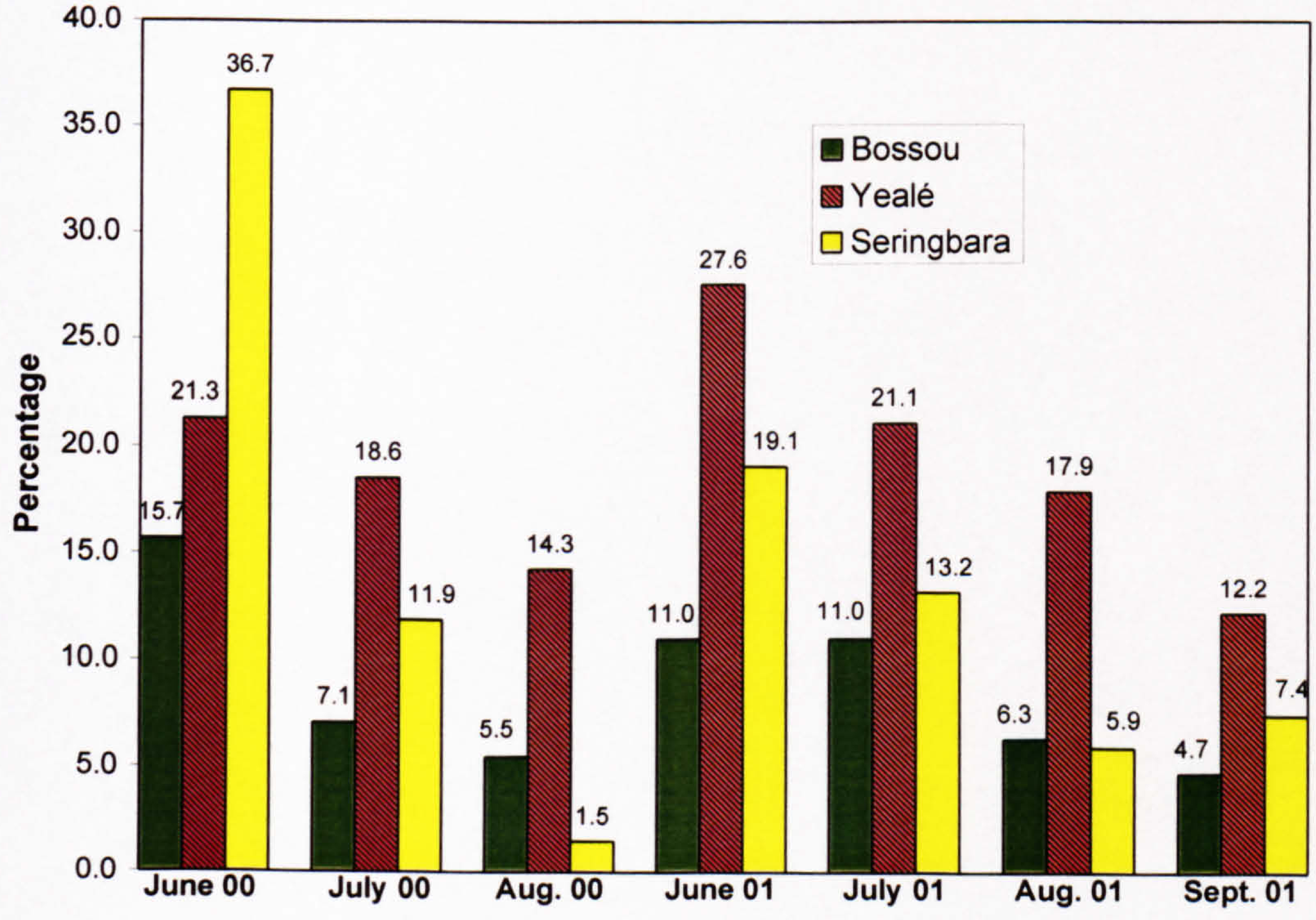


Fig. 5.7. Percentage of surveyed oil-palms exhibiting mature fruit on a monthly basis across all three sites.



The availability of immature and mature flowers was recorded only during the second study period (June-September 2001). Once again a significant difference emerged in the observed and expected frequencies of oil-palms providing immature and mature flowers across the three sites (Chi-square test: $\chi^2(2)=15.363$; $\rho<0.001$) (see Fig. 5.8). As indicated in Figure 5.8, oil-palms at Yealé provided more immature and mature flowers than expected, while at Bossou and Seringbara the trend was reversed. Immature or mature flowers were nevertheless available at all three 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 (see Fig. 5.9).

Competition with sympatric species for oil-palm fruit and nuts

Squirrels were the prime consumers of oil-palm fruit at all three sites (see Fig. 5.10). Although absent from Bossou, sooty mangabeys (*Cercocebus atys*), lesser spot-nosed guenons (*Cercopithecus petaurista*) and Diana monkeys (*Cercopithecus diana diana*) consumed the mesocarp of the oil-palm fruit at the Nimba sites (see Fig. 5.10). Humans both at Bossou and Yealé would also occasionally cut off the fruit bunch from oil-palms available near the forest edge for palm-oil production (see Fig. 5.10). Overall, if one compares the frequency of fruit-bearing oil-palms exhibiting no evidence of competitors and those displaying evidence of their presence between the three sites, no significant difference emerges (Chi-square test: $\chi^2(2)=3.387$; *n.s.*) (see Fig 5.11). Therefore, differences in the levels of competition with sympatric species for oil-palm fruit fail to provide a satisfactory environmental explanation of why Seringbara chimpanzees do not consume this potentially highly nutritious food resource.

Fig. 5.8. Observed and expected frequencies of surveyed oil-palms exhibiting mature and immature flowers or not across all months for which all three sites were surveyed.

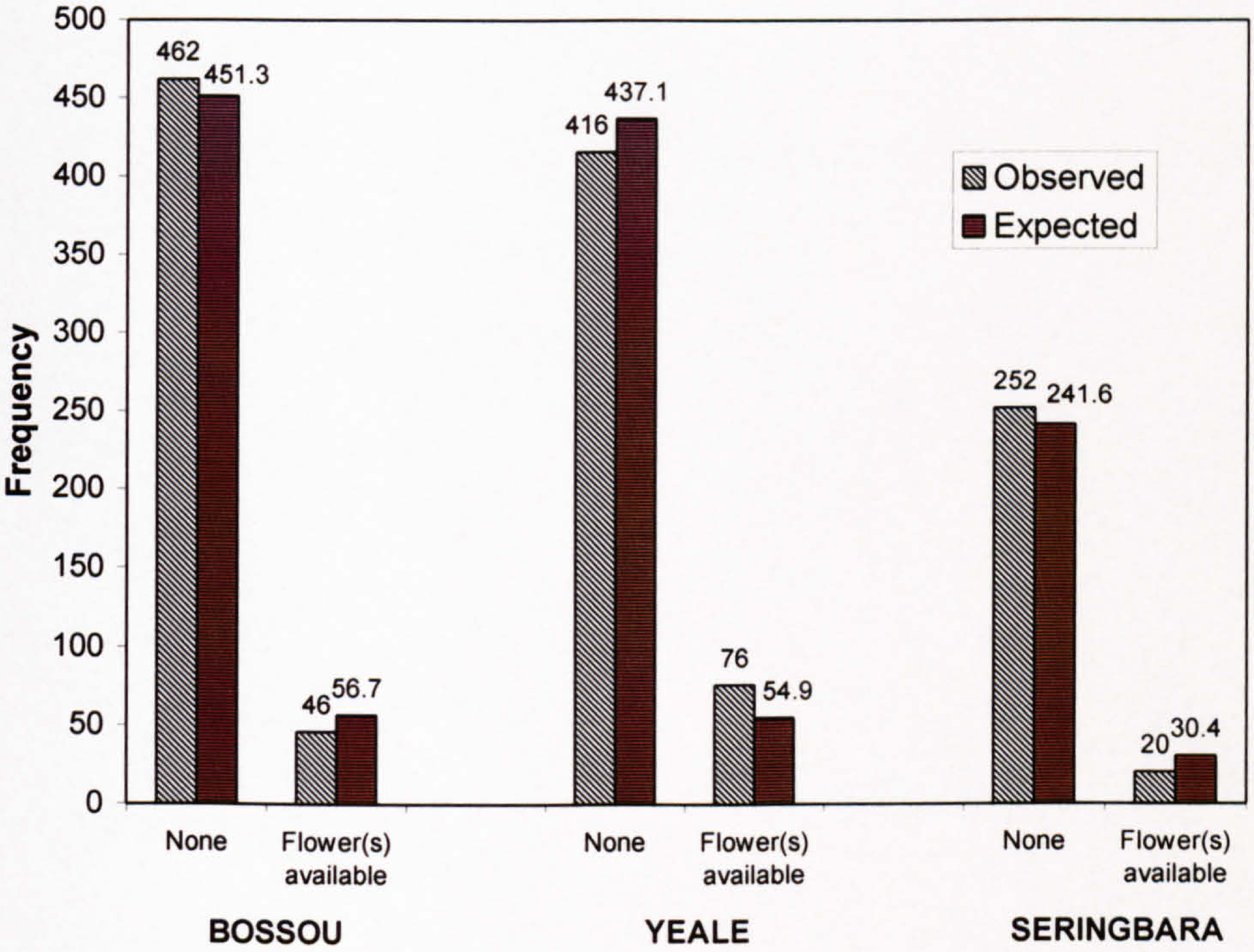
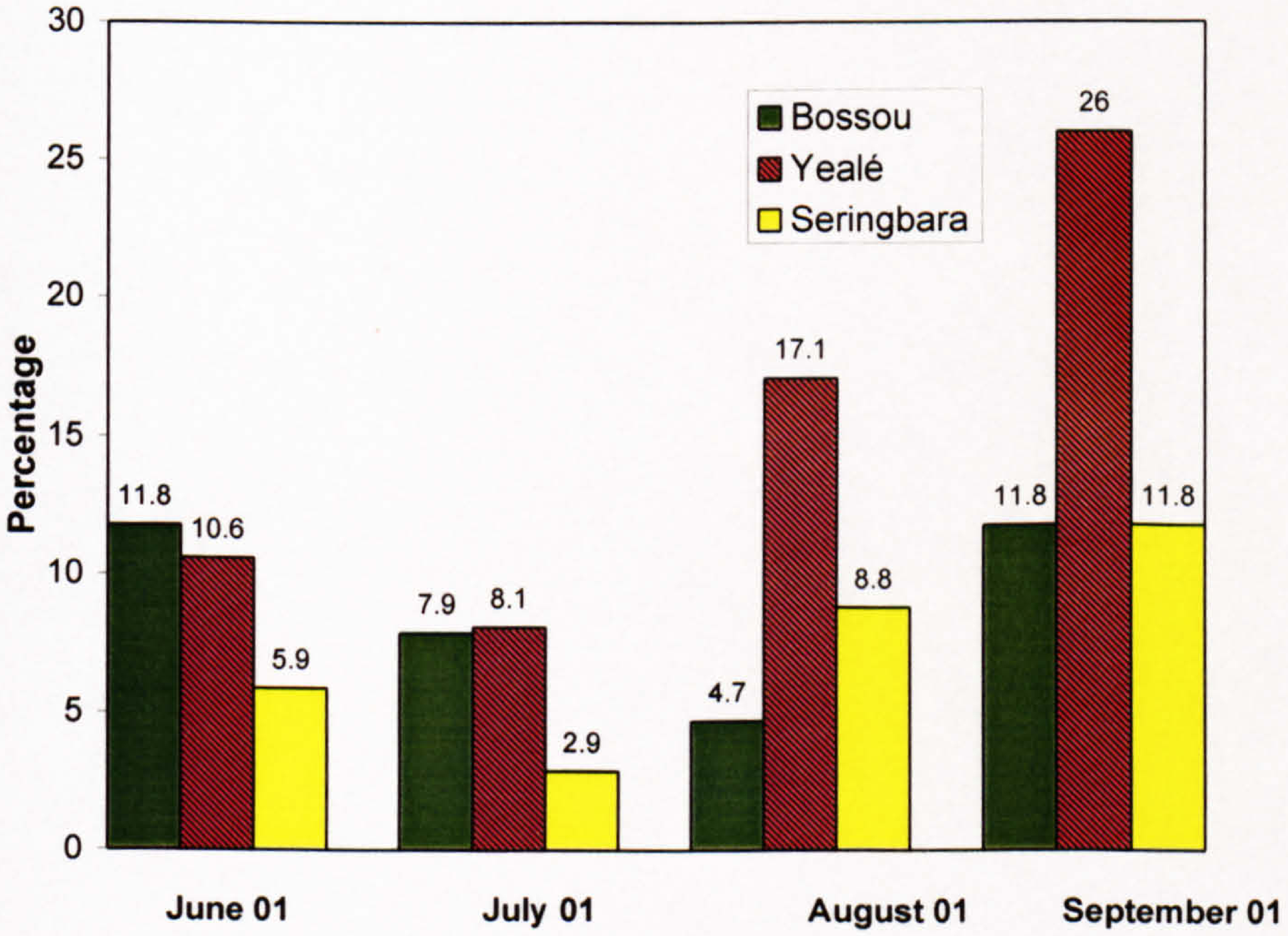


Fig. 5.9. Percentage of surveyed oil-palms exhibiting immature and mature flowers on a monthly basis across all three sites.



To address the issue of competition for nuts, the animal taxon responsible for most evidence of nut consumption between each survey date was recorded for each oil-palm. Insects and annelids, pooled together, accounted for most kernel consumption at Bossou, whereas at the two Nimba sites most nuts were consumed by various species of rodent ('rat') (see Fig. 5.12 and 5.13). This difference in competitor pattern was significant (Chi-square test: $\chi^2(6)=359.14$; $\rho<0.001$) (see Fig. 5.13). At Yealé, the hedgehog and the bush-pig were also noted to consume nuts (see Fig. 5.12). Bush-pigs were absent from Bossou and Seringbara, and although hedgehogs were confirmed at both these sites, they were rare and infrequent predators of oil-palm nuts.

The recorded estimates of nut quantity and quality provided useful additional measures for further indirect exploration of differences in competition for nuts between the three sites. A significant difference in nut quantity emerged across sites (Kruskal-Wallis test: $\chi^2(2, N=2233)=573.676$; $\rho<0.001$) (see Table 5.3 and Fig. 5.14). Dunn's *post hoc* test revealed that significantly more nuts across both study periods were available at Bossou than at either Yealé ($\rho<0.01$) or Seringbara ($\rho<0.001$), and at Yealé than at Seringbara ($\rho<0.01$) (see Table 5.3 and Fig. 5.14). However, at both Yealé and Seringbara, rodents, which tend to remove nuts from beneath oil-palms to conceal them for future consumption, were the prime nut consumers respectively for 34.5% and 42.9% of all oil-palms surveyed, compared to only 17.6% at Bossou (see Fig. 5.12). Pooling the data from the three sites, if one compares nut quantity between oil-palms targeted by insects and annelids and those by rodents, significantly less nuts remained when rodents were the main consumer (Mann-Whitney U-test: $N=1181$; $z=-9.914$; $\rho<0.001$).

Fig. 5.10. Percentage of fruit-bearing oil-palms with evidence of fruit consumption by non-chimpanzees during the monthly surveys at the three sites.

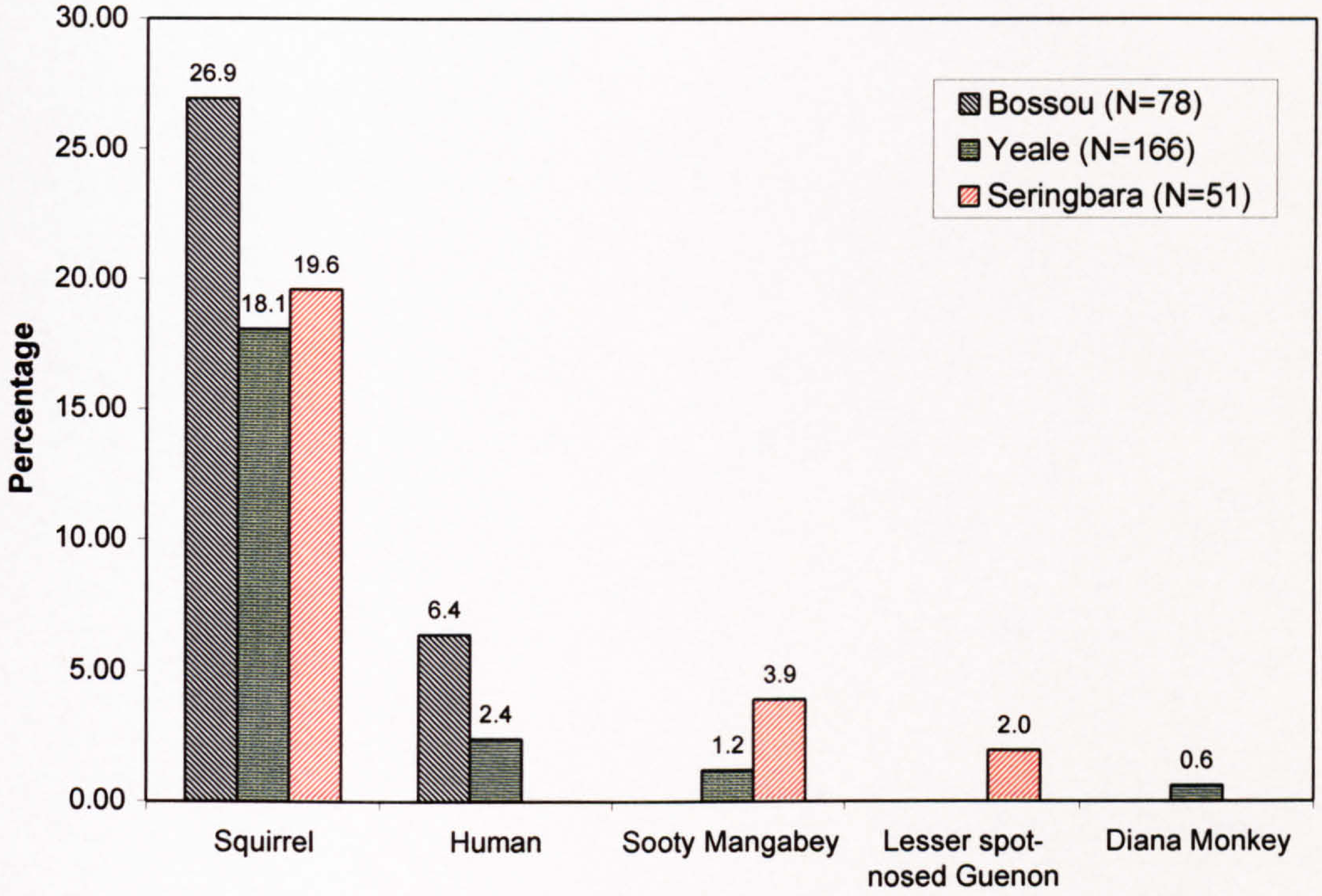


Fig. 5.11. Observed and expected frequency of fruit-bearing oil-palms surveyed with evidence of fruit-eating "competitors" (Yes) and those exhibiting none (No) across the three sites.

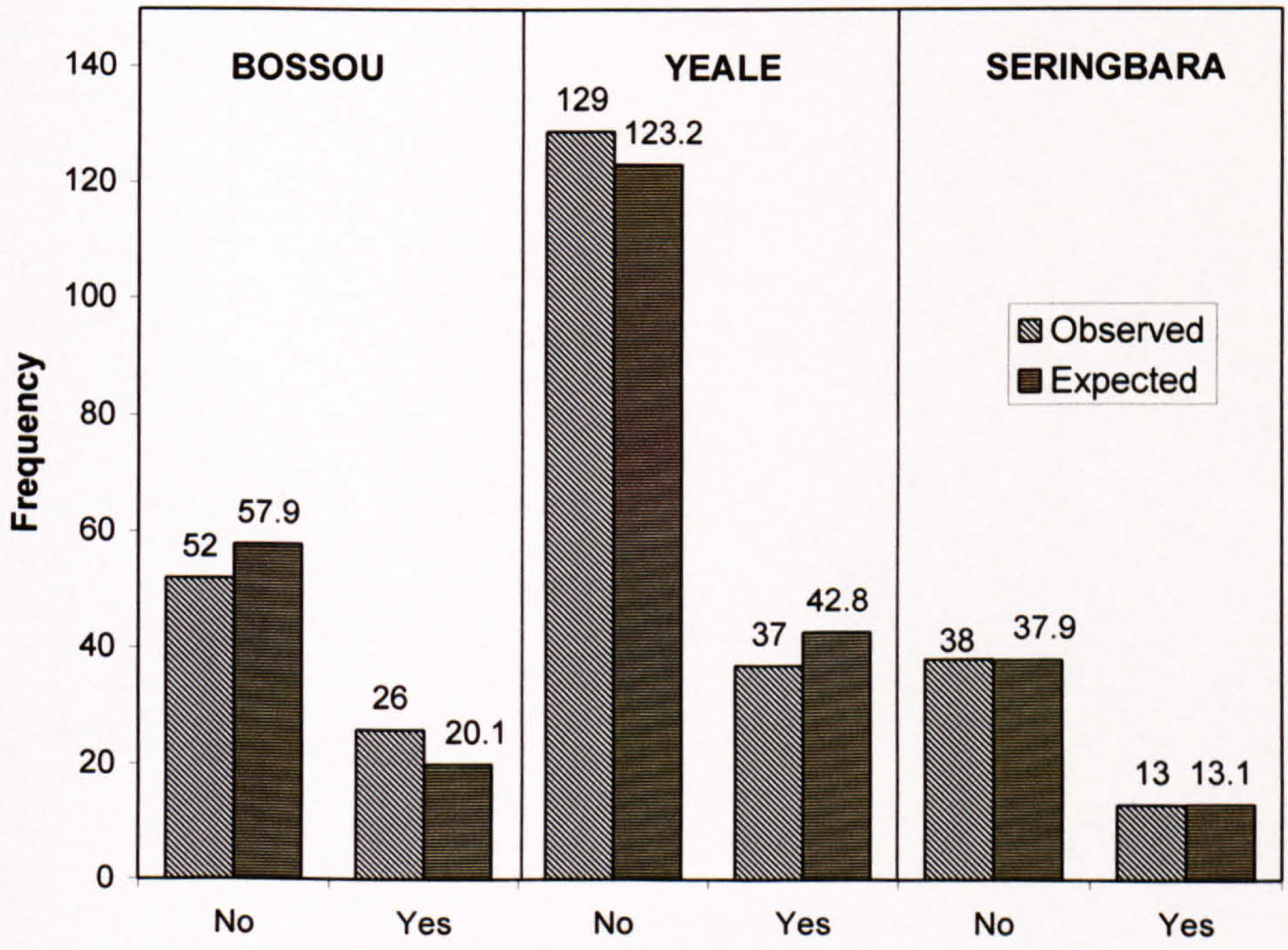


Fig. 5.12. Percentage of nut-bearing oil-palms with evidence of nut consumption by non-chimpanzees during the monthly surveys at the three sites.

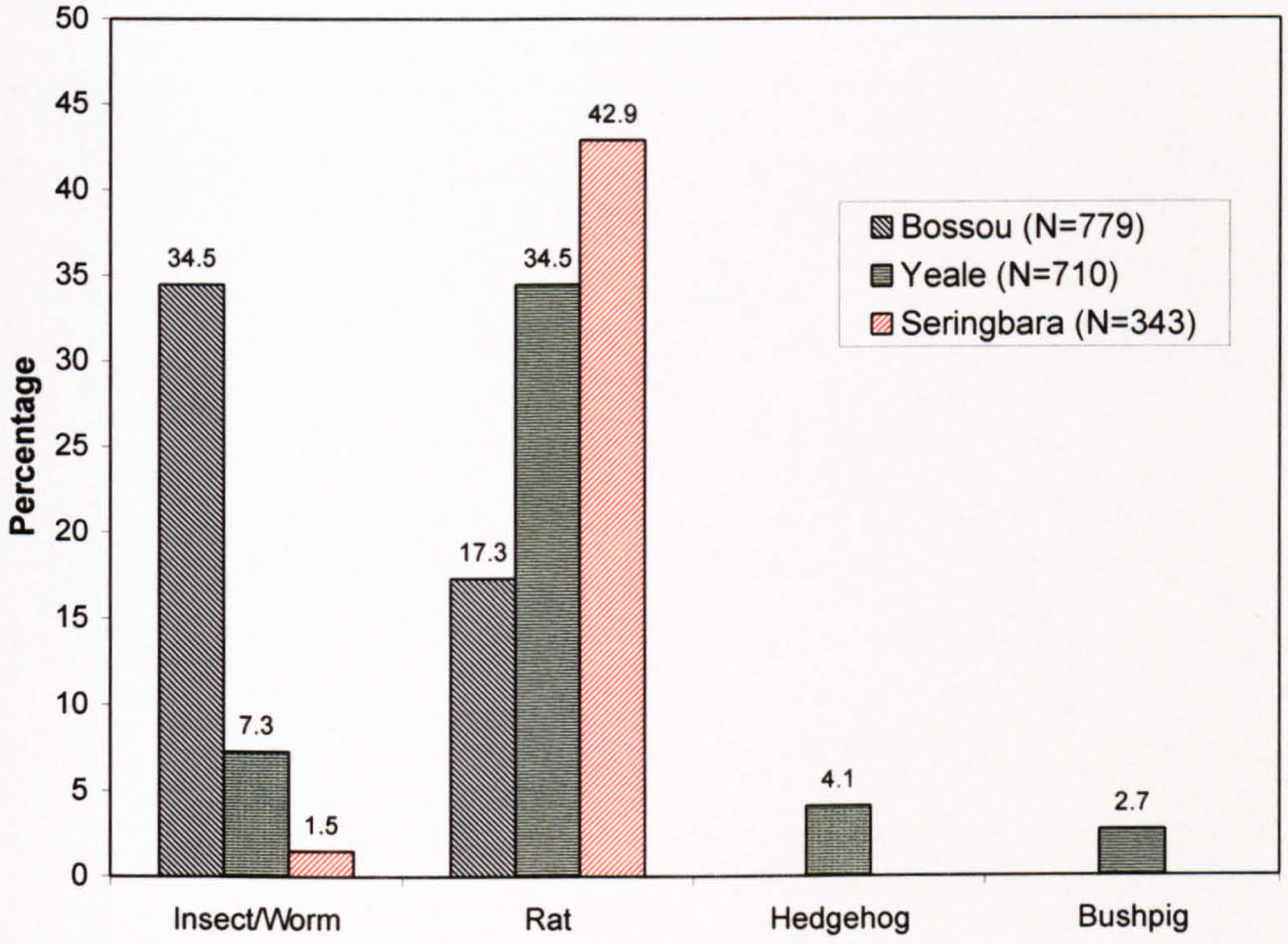
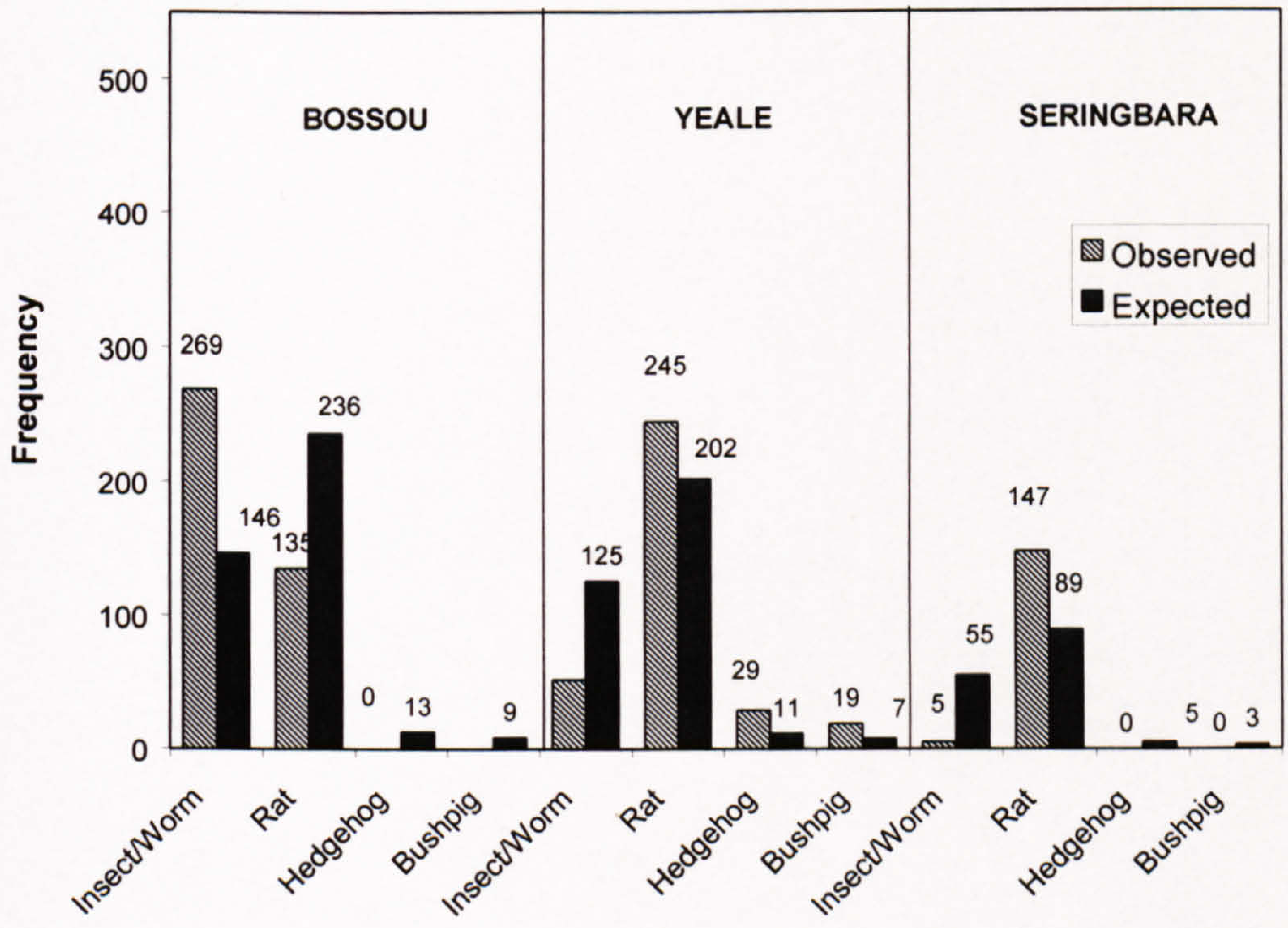


Fig. 5.13. Observed and expected frequency of surveyed oil-palms presenting evidence of nut-consumers across the three sites.

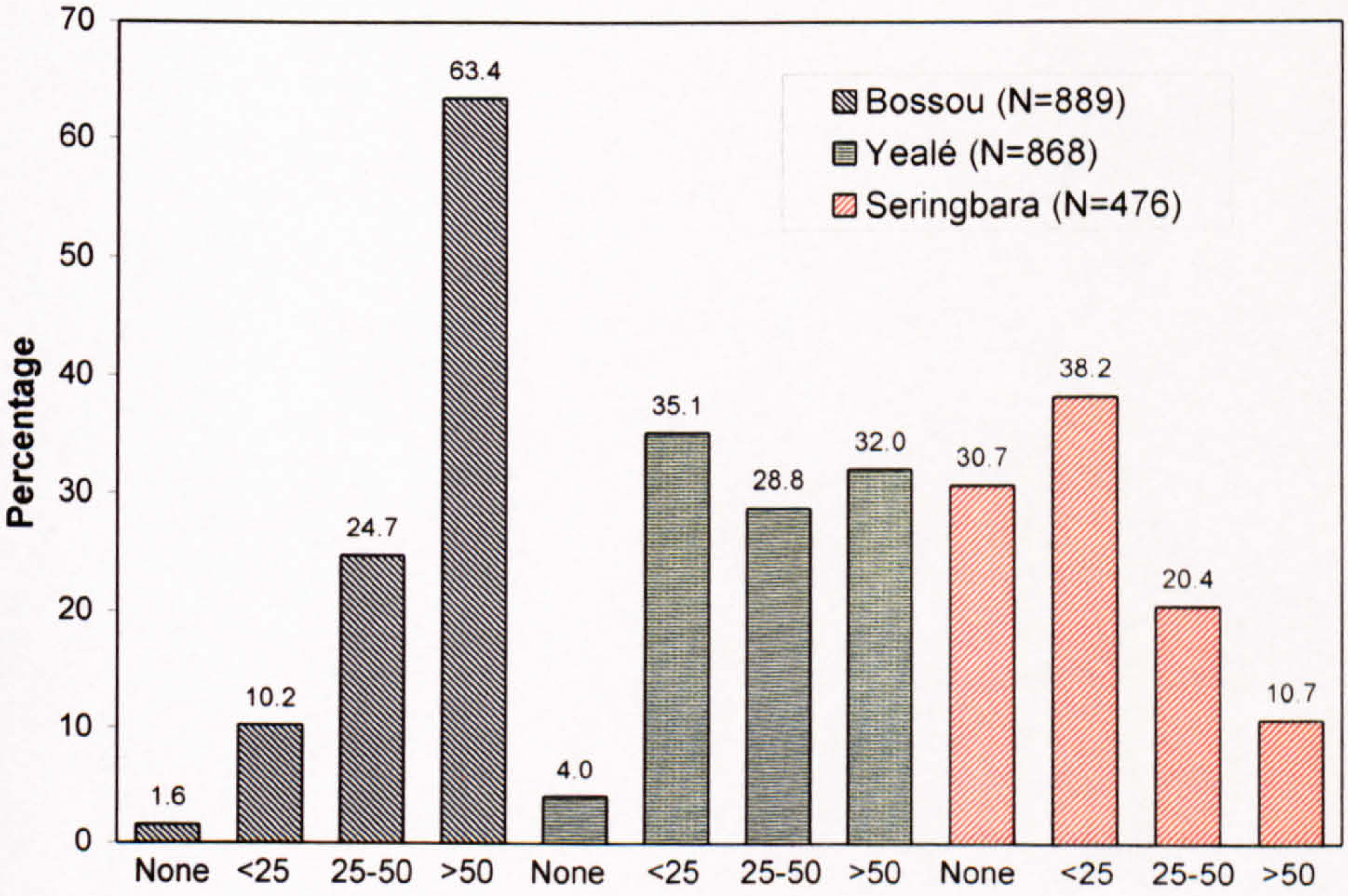


There was also a significant difference between the three sites in the percentage of edible nuts available (Kruskal-Wallis test: $\chi^2(2, N=2011)=13.934$; $\rho<0.001$) (see Table 5.3). Dunn's *post hoc* test showed no significant difference between Bossou and Yealé in the percentage of edible nuts available; however, the oil-palms from Seringbara presented overall significantly fewer good and intact nuts than those from either Bossou ($\rho<0.05$) or Yealé ($\rho<0.01$) (see Table 5.3).

Table 5.3. Descriptive summary of nut quantity (categorical) and nut quality (percentage of edible nuts) across both study periods for all oil-palms surveyed at Bossou, Yealé and Seringbara.

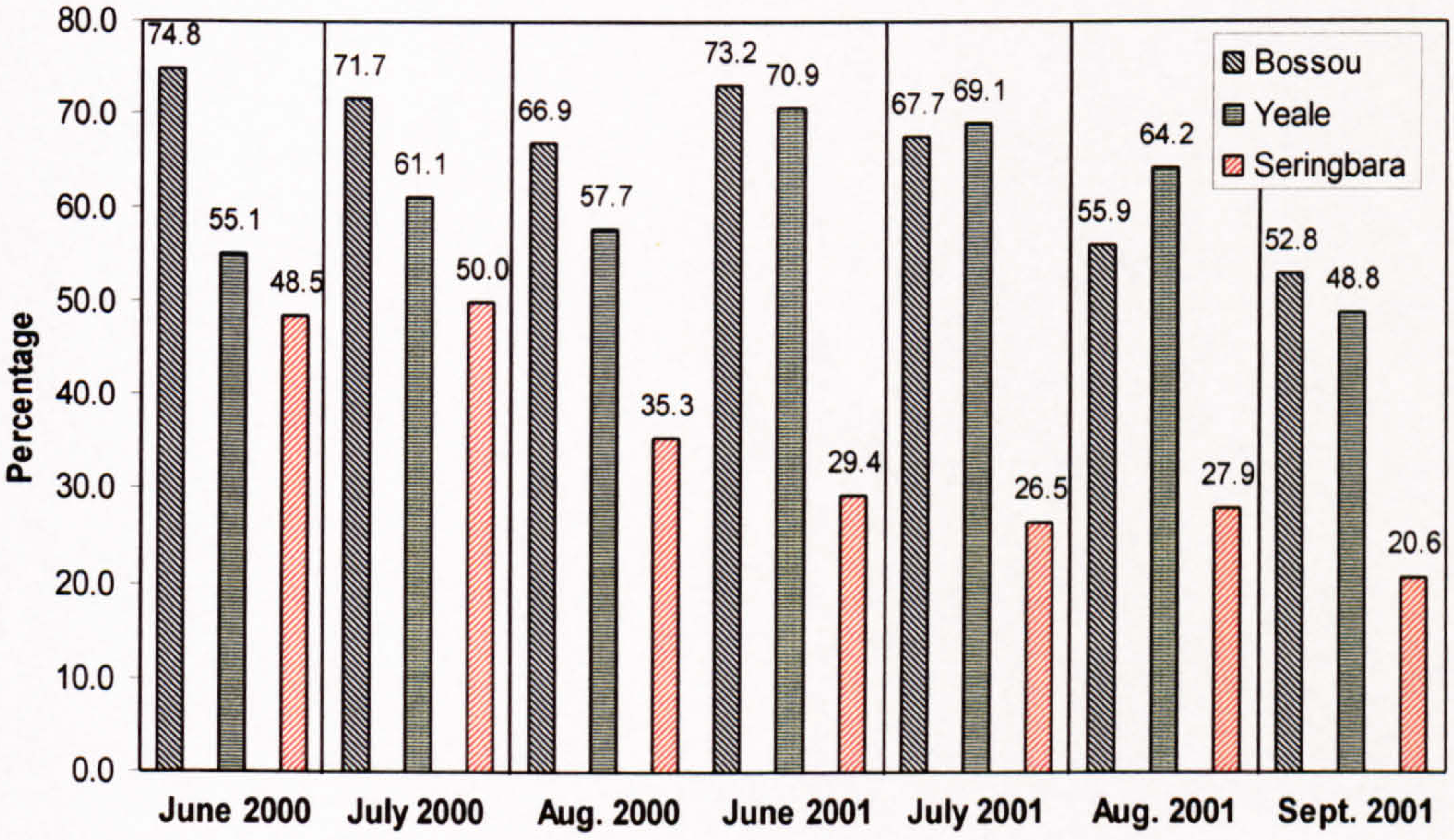
		No.	**Mean**	**SD**	**Median**	**Range**
Nut Quantity	***Bossou***	889	2.5	0.74	3	0-3
	Yealé	868	1.89	0.91	2	0-3
	Seringbara	476	1.08	0.95	1	0-3
Nut Quality	***Bossou***	876	17.1	23.1	6.7	0-100
	Yealé	838	22.5	29.0	8.0	0-100
	Seringbara	335	17.9	26.6	0	0-100

Fig. 5.14. Percentage of surveyed oil-palms providing different number of nuts sorted by categories.



Thus, assuming that fruit bunches were equally productive across the three sites, competition for nuts by sympatric species was further revealed to be greatest at Seringbara on the basis of lower nut quality and quantity estimates. With the exception of September 2001 at Yealé, more than half of the oil-palms surveyed at both Yealé and Bossou provided edible nuts on a monthly basis, compared to consistently fewer than half at Seringbara (see Fig. 5.15). Nevertheless, edible nuts were available across all months that oil-palms were surveyed (see Fig. 5.15). Thus, Yealé chimpanzees had ample opportunities for cracking nuts, while Seringbara chimpanzees also had the possibility to do so. Bossou chimpanzees, compared to Seringbara, benefited from greater nut quality and availability, i.e. more conducive conditions for nut-cracking.

Fig. 5.15. Monthly percentage of surveyed oil-palms providing edible nuts.

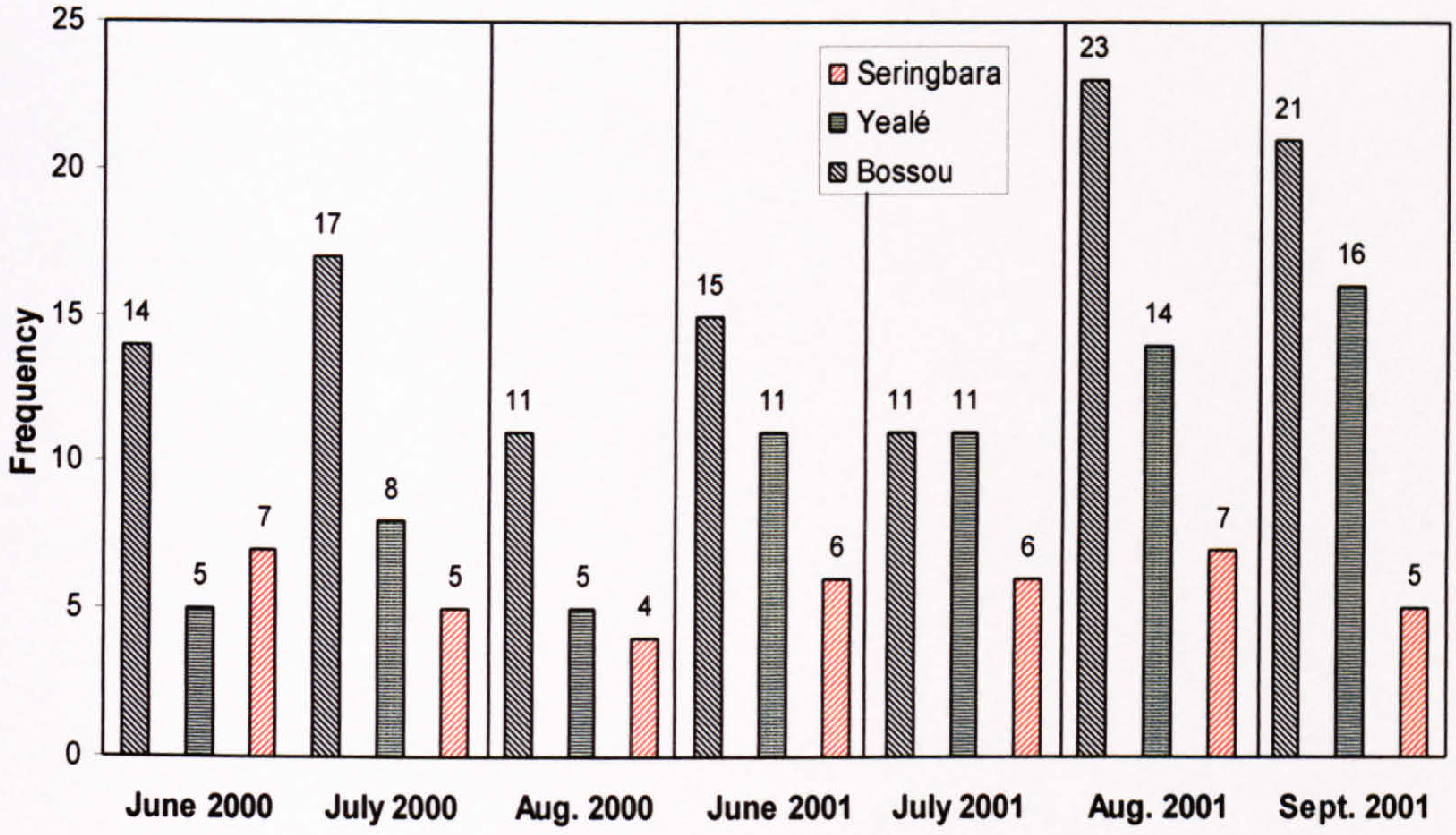


Alternative food resources

As observed during this study and previous studies at Bossou (c.f. Yamakoshi, 1998), Bossou chimpanzees heavily rely upon the oil-palm as a food resource during the rainy season, which, at this site, corresponds to a period of fruit scarcity. The various edible plant parts provided by the oil-palm act as important "fallback foods" or "keystone resources" (c.f. Terborgh, 1986) for the Bossou community. No systematic monthly phenological surveys of alternative foods were conducted in parallel to the oil-palm surveys. However, monthly records of feeding remains left by chimpanzees, of foods directly observed being consumed and analysis of faecal samples provided data on the diversity of fruit species in the diet of the chimpanzees across the three sites.

During the two survey periods the number of fruit species consumed by chimpanzees across the three sites differed significantly (One-way-ANOVA: $F_{2,18}=13.704$; $p<0.001$) (see Fig. 5.16). A *post hoc* test indicated that, over the two study periods concerned, Bossou chimpanzees Yealé and Seringbara was consistently equal to or less than that recorded at Bossou. Most fruiting species available at Bossou were in secondary forest. Although the diversity of fruiting species comprising the diet of the Nimba chimpanzees may be underestimated, it reflects the low fruit availability in the two sites during the rainy season. Nimba chimpanzees appear to face a severe food shortage during that period of the year. Therefore, the oil-palm should represent a potentially important fallback resource for the chimpanzees at both sites. Thus, it remains unclear why Seringbara chimpanzees fail to exploit the resources provided by the oil-palm, while Yealé chimpanzees do incorporate some oil-palm plant parts into their diet during that same time of year.

Fig. 5.16. Monthly frequency of fruit species in the diet of chimpanzees at Bossou, Yealé and Seringbara, based on feeding remains, faecal analysis and direct observations of feeding behaviour.



5.5 Discussion

The oil-palm as a focus of study

As a result of McGrew's publication of "Chimpanzee Material Culture" in 1992, the issue of culture in chimpanzees received renewed attention and vivid criticism by sceptics who challenged the attribution of culture to non-human animals postulating instead environmental explanations for observed variations in behaviour. Several recent studies on wild chimpanzees aimed to test environmental hypotheses versus a 'by default' cultural hypothesis. Nut-cracking in chimpanzees, a socially learnt, salient 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 left over artefacts proved to be a highly suitable subject for such an analysis.

McGrew *et al.* (1997) examined several hypotheses, exploring environmental and cognitive parameters, about 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 behaviour at this site is neither environmental nor cognitive but rather cultural, and that chimpanzees at Lopé simply appear to lack the knowledge that nuts can be consumed with the aid of tools, although nuts are a potentially valuable and plentiful resource in their habitat. Furthermore, during a nation-wide survey of chimpanzees in Côte d'Ivoire, Boesch *et al.* (1994) found no obvious environmental differences that might explain the lack of evidence of nut-cracking east of N'Zo-Sassandra River[1]. 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 this 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.

As reviewed in the *Introduction* to this chapter (section 5.1), the uses of the oil-palm by chimpanzees across Africa and at Bossou in particular, are remarkably diverse, ranging from feeding activities requiring varying level of processing, from simple reaching and detaching to the use of one or several tools, to nesting. A comparative study of the utilisation of the oil-palm by different chimpanzee communities is conducive to testing out underlying environmental parameters that might explain variations in use. In this study, Bossou was used as the bench-mark for comparison, since chimpanzees at this site exhibit the widest diversity of oil-palm targeted behaviours recorded at any site. Direct observations of Bossou chimpanzees performing

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[1] Note: F. Joulian recently discovered evidence for nut-cracking in a very small area east of the Sassandra river (McGrew, pers. comm.).

these oil-palm activities were useful in setting up criteria for ascertaining the presence of any of these behaviours at the two Nimba sites, especially nut-cracking and pestle pounding. At Nimba, where chimpanzees remain unhabituated to observers, the survey method was supplemented by direct behavioural observations, faecal analysis and *ad lib* controls of untagged oil-palms. A monthly survey of tagged palms also proved useful for measuring the actual relative time spent in these activities by the community at large.

Pattern of use of the oil-palm

Differential patterns of use of the oil-palm emerged from the comparative study of Bossou, Seringbara and Yealé. Yealé chimpanzees displayed all the uses of the oil-palm observed at Bossou with the exception of pestle pounding. In addition, they consumed the base of the perianth of the flower, a plant part not consumed by chimpanzees at Bossou. However, regarding the behaviours they shared, Yealé chimpanzees performed these feeding activities less frequently than Bossou chimpanzees. Thus, they seldom cracked nuts using a hammer and anvil stone. Nevertheless, the relative occurrence of these activities was not significantly different between the two sites.

Chimpanzees at Seringbara, only 6 km from Bossou, did not show any evidence of oil-palm-use. Of course, as pointed out by McGrew *et al.* (1997, p.368), "absence of evidence is not evidence of absence". Therefore, Seringbara chimpanzees may simply 1) not have engaged in any of these behaviours during the two study periods or 2) may have, but in areas of their range which we did not explore. But considering the durability of oil-palm feeding remains, excepting traces of feeding on the mesocarp and the flower, if Seringbara chimpanzees had performed any of these activities in previous months, some evidence was likely to have been noticed. The second possibility cannot be rejected with certainty; however, since 1999 we have been able to acquire a good estimate of the range of the chimpanzees in the region. Also, oil-palms that were not covered by the monthly survey but that were encountered during daily tracking were regularly checked for use, but still showed no indications of use.

Environmental explanations

Following a similar methodological approach to that adopted by Boesch *et al.* (1994) and McGrew *et al.* (1997), several environmentally-based hypotheses apt to explain this variation in oil-palm use between the three sites were explored. Differences in density and distribution of oil-palms could potentially explain why Yealé chimpanzees utilise the oil-palm less frequently than at Bossou, where oil-palms are found at greater densities and are more uniformly distributed. Although oil-palm density was lowest at Seringbara, where no evidence of oil-palm use emerged, chimpanzees at this site nested and spent time feeding on other fruit species and herbaceous terrestrial vegetation near areas where oil-palms were available.

Furthermore, surveyed oil-palms at Seringbara consistently provided healthy young fronds for petiole consumption or for use as tools for pestle pounding during both survey periods. Moreover, fruit bunches and flowers prevailed at all three sites during the two surveys periods and no significant difference in competition for oil-palm fruit by sympatric species emerged between the three sites. In addition, hammer and anvil sets were not a limiting resource for potential nut-cracking purposes at either Seringbara or Yealé.

However, competition by sympatric species for nuts was greater at Nimba than at Bossou, where rodent species less frequently consumed or removed nuts, and insects and annelidss accounted for most nut degradation. At Yealé, consumption or removal of nuts by rodent species had a significant impact on the quantity of nuts available, and this was notably more so at Seringbara, where on a monthly basis, 50% or more of oil-palms failed to provide edible nuts. Nevertheless, many oil-palms still provided nuts suitable for cracking and Yealé chimpanzees cracked oil-palm nuts, although on an infrequent basis. However, since nut quantity and quality at Seringbara was significantly inferior to those at Bossou and Yealé, chimpanzees at this site may not seek to crack nuts, even if they know how to do so. But Seringbara chimpanzees have so far not shown any evidence of cracking of other nut species available in their habitat such as *Detarium senegalensis* and *Parinari excelsa,* whereas Yealé chimpanzees also crack *Coula edulis* nuts, which are absent from Seringbara.

June to September represents a period of low fruit availability at Bossou as at the two Nimba sites, although no systematic monthly assessment of fruit availability was carried out. Low fruit diversity within the chimpanzees' diet across the three sites during that time indirectly confirmed the scarcity of fruit availability. The oil-palm nut kernel is rich in energy, protein, calcium and phosphorous and fatty acids as well as vitamin A; the oil percentage contained in the mesocarp may vary between 35-60 percent (Hartley, 1988). The sap, which is exposed whilst pestle pounding, is also a good source of Vitamin B. Clearly, the energy returns and calorific contents of some of these oil-palm products are not negligible, particularly potentially important at times of fruit scarcity. One would thus expect chimpanzees to make use of at least some of these resources, 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 at Yealé and of any of the oil-palm targeted behaviours, generally observed at Bossou or Yealé, at Seringbara. The conclusion emerges, therefore, that these differences in behaviour are cultural; however what does this potentially tell us about cultural transmission in chimpanzees?

Culture and diffusion of behaviour

This study may provide us with preliminary insight into another issue pertaining to culture, that of diffusion of behaviour or transfer of knowledge and transmission of behavioural patterns between communities. In addressing this issue with respect to the three populations considered here, we need to make two assumptions: 1) individual interchange between these three communities and 2) social learning in the transmission of these oil-palm targeted behaviours.

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 foot hills of the Nimba Mountains. Furthermore, Yealé and Seringbara chimpanzees share the same stretch of contiguous forest and evidence for chimpanzees' trails and feeding remains on both sides of the massif have been uncovered as far as the summit, crossing over between Guinea and Côte d'Ivoire.

Since 1976, 26 chimpanzees that have disappeared from the Bossou community could have potentially emigrated to neighbouring communities in the Nimba mountains on the Guinean side or towards the Liberian or Ivorian portions of the massif (see Table 5.4). After 1990, the nut-cracking and pestle pounding ability of many of these individuals was recorded prior to their disappearance. Among 10 chimpanzees that disappeared between 1990 and May 2000, 3 females knew how to crack open oil-palm nuts using a hammer and anvil stone, while 2 females and 3 males were both experienced pestle pounders as well as nut-crackers. Therefore, if these individuals successfully emigrated, respectively 80% and 50% of them could potentially have served as models for the transmission of nut-cracking and pestle pounding to chimpanzees from other communities. Bossou chimpanzees have been known to crack oil-palm nuts ever since the early 1960's. Yamakoshi (1998) postulated that pestle pounding is a recent innovation at Bossou, as this conspicuous tool-use behaviour had never been observed before 1990. Ever since 1978, Bossou chimpanzees have been confirmed to nest in oil-palms, to feed on the petiole of young fronds and to consume the fruit and the flower (Sugiyama, pers. comm.).

Table 5.4. Chimpanzees of Bossou who have disappeared since 1976 and who could have potentially emigrated to the Nimba mountains. After 1990, the pestle pounding and/or nut-cracking ability, prior to disappearance, of many of these chimpanzees was confirmed.

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		✓
Kakuru	Female	Mar-91	4	Juvenile		✓
Kie	Female	Mar-91	16	Adult		✓
Pru	Male	Nov-91	11	Adolescent	✓	✓
Ja	Female	Feb-93	10	Adolescent	✓	✓
Yunro	Male	Feb-93	9	Adolescent		
Na	Male	Apr-96	11	Adolescent	✓	✓
Vui	Male	Jul-99	13	Adult	✓	✓
Pili	Female	Mar-01	14	Adult	✓	✓
Pokulu	Male	Mar-01	5	Juvenile		
Juru	Female	Dec-01	8	Adolescent	✓	
Nto	Female	Dec-01	8	Adolescent	✓	✓

On the premise that all the above assumptions hold true, one might expect oil-palm targeted behaviours to be prevalent at all three sites and diffusion to have taken place. But why have none of these behaviours so far been observed 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 yet emigrated to Yealé and provided an opportunity for this behaviour to be transmitted. In addition, the rarity of oil-palm nut-cracking at Yealé suggests that this tool-use behaviour 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 nut-crackers may be emigrants from Bossou or have discovered the behaviour independently. The three oil-palms at Yealé that showed evidence of nut-cracking by chimpanzees, were located at the border of the reserve, not far from the village, an area not necessarily frequented by all members of the community; this could limit transmission of this behaviour. Only further habituation of the chimpanzees in the region will help shed further light on this issue.

At Seringbara, in contrast, it appears that neither independent innovation nor transmission of oil-palm targeted behaviours has occurred. It remains a possibility that, during the rainy season, Seringbara chimpanzees focus on alternative fallback foods with high energy returns, e.g. hunting for mammalian prey, and simply do not need to exploit oil-palms as a resource. However, no evidence emerged from this study to support this hypothesis. Alternatively, an emigrant from Bossou may have had too few chances to perform any of those behaviours because of pressure to maintain contact with other party members in an initially unfamiliar ecological and social environment.

Finally, diffusion of behaviour between chimpanzee communities may not necessarily yield contiguous cultural regions. Cultural transmission may only take place if the complex interplay between adaptation to local ecological conditions and social structure and dynamics provides propitious conditions. These sets of conditions require further investigation and their relative roles in influencing the process of diffusion of behaviour need to be assessed.

Chapter 6

Ant-dipping at Bossou and some comparisons with other sites

6.1 Introduction

Dipping for driver ants or safari ants, *Dorylus* spp., is often cited as one of the best examples of culture in chimpanzees (Boesch and Boesch, 1990; McGrew, 1992). In most cases of tool-use to obtain social insects, a tool is used to gain access to the target food item within a protected structure, i.e. the nest, as in termite fishing, ant fishing or honey dipping. Dipping for driver ants, which was first recorded in 1963 by Goodall at Gombe, Tanzania (Goodall, 1963), slightly differs from the above in that the chimpanzees focus their behaviour towards columns of migrating ants or the usually structurally unprotected nest, which the ants use as a temporary bivouac.

The prey

Ants

As shown in Table 6.1, many ant species are eaten by chimpanzees across different field sites in Africa. The table is incomplete, because of lack of data on the insect fauna present at all the different field sites. Nevertheless, all three sub-species of chimpanzees listed (lacking information on the Nigerian subspecies of chimpanzee: *P.t.vellerosus*) feed on ants and tools are used in the consumption of some or all ant species present in the habitat of the chimpanzees at the field sites listed (see Table 6.1). However, not all ant species available in each habitat are consumed by chimpanzees, as is the case for driver or safari ants, *Dorylus nigricans*, which are widespread but have never been recorded as being eaten by chimpanzees at Lopé (Gabon), Mahale and Kasakati (Tanzania) or Budongo (Uganda). In addition, for a given prey species, the use of a tool is not consistent across all sites. For example, the weaver ant, *Oecophylla* *longinoda*, is reportedly consumed at five field sites, but only at Bossou do chimpanzees use tools to obtain these ants. Moreover, *Camponotus vividus*, a species of wood-boring ant, is eaten at Mahale with the aid of a tool, while it is consumed directly by hand without a tool at Lopé.

Driver ants

Driver or safari ants, which occur in all sites where chimpanzees have been studied, often travel on the ground or amongst low terrestrial herbaceous vegetation in great numbers, up to several million individuals, often hunting for prey or simply emigrating to a new nesting site (Gotwald, 1972). These columns of ants are of multi-caste composition. These ants construct tunnel-nests underground, which can reach up to 1 m in diameter and half a metre in depth. The entrance of the nest is often covered by a layer of fallen leaves and vegetation and is therefore well camouflaged. Safari ants are usually very aggressive and soldier ants can cause painful bites to chimpanzees. The use of a tool for ant-dipping allows more efficient and less painful harvesting of these biting ants than taking them directly by hand or mouth (McGrew, 1974). So far three species of *Dorylus* ants preyed on by chimpanzees have been distinguished: *D. (Anomma) gerstaeckeri* (Emery), *D. (Anomma) molestus* (Gerstaecker), *D. (Anomma) nigricans* (Illiger) (see Table 6.1). Whereas *D. gerstaeckeri* is smaller than the other two, the latter are very difficult to distinguish.

Table 6.1 Ant species eaten across different chimpanzees study sites.

Study Site	Bossou	Taï	Mt Assirik	Tenkere	Lopé	Gombe	Mahale	Kasakati	Budongo
Country	Guinea	Côte d'Ivoire	Senegal	Sierra Leone	Gabon	Tanzania	Tanzania	Tanzania	Uganda
Subspecies	*P. t. verus*				*P. t. troglodytes*	*P. t. schweinfurthii*			
References Ants Species	Sugiyama, 1995a	Boesch & Boesch, 1990	Baldwin, 1979; McGrew, 1983	Alp, 1993	Tutin *et al.*, 1995	Goodall, 1963; McGrew, 1974; Goodall, 1986	Nishida, 1973; McGrew, 1992; Goodall, 1986	Suzuki, 1966	Reynolds & Reynolds, 1965
Dorylus nigricans		●	●	●	✓	●	✓	✓	✓
D. molestus	●	✖							
D. gerstaeckeri	✖	●							
Oecophylla longinoda	●		○		○	○	○	●?	
Camponotus sp.						✓		●?	
C. brutus					●				
C. vividus					○		●		
C. maculatus							●		
C. myromotrema							●		
Crematogaster sp.						●			
C. clariventris							○		
C. stadelmanni					○				
C. depressa					○				
Megaponera foetens			○						
Paltothyreus tarsatus					●				
Monamorium sp.						✓	○		
Tetramorium sp.							○		
Unidentified arboreal ant								●?	○

Legend: ●: Species mainly eaten with the aid of a tool; ●?: Species possibly eaten using tools, but not known with certainty ○: Species eaten without the aid of a tool; ✓: Species available, but not consumed; ✖: Species absent from the habitat; Empty cell: No data on consumption or presence of ant species at the site

Length of ant-dipping tools

Table 6.2 summarises available data on ant-dipping tools or wands at several chimpanzee study sites across Africa. So far ant-dipping has only been observed directly at three long-term study sites: Gombe (Tanzania), Taï (Côte d'Ivoire) and Bossou (Guinea). When comparing data from Sugiyama *et al.* (1988) and Sugiyama (1995a), it is clear that a sufficiently large sample size is required before making generalisations about tool length at the community level (see Table 6.2). Therefore, at other field sites, where indirect evidence of this behaviour has been found, e.g. abandoned tools, sample size is generally too small to infer any general trends in tool length. Thus, although comparisons at this stage are only preliminary, a small tool sample size can provide useful insights into potential similarities and divergences in length of tools across chimpanzee communities.

Interesting differences in wand length are nevertheless emerging (see Table 6.2). Wands at Gombe are significantly longer than at Taï. Mean tool length at Bossou is intermediate between those recorded from Gombe and Taï. Yealé tools appear similar in length to those found at Gombe, but the sample size from Yealé is too small to infer a general trend from this pattern. Moreover, although also based on a small data set, mean tool lengths thus far recorded from Mt Assirik, Tenkere, Kalinzu and Gouéla (Goera), Mt Nimba, are even longer than that recorded at Gombe.

Table 6.2 Summary of published information about ant-dipping tools or wands and technique employed across different chimpanzee field sites.

	Taï	**Bossou**	**Bossou**	**Gouéla, Mt Nimba**	**Yealé, Mt Nimba**	**Mt Assirik**	**Tenkere**	**Gombe**	**Kalinzu**	**Ntale**
Country	Côte d'Ivoire	Guinea	Guinea	Guinea	Côte d'Ivoire	Senegal	Sierra Leone	Tanzania	Uganda	Cameroon
Chimpanzee subspecies	*P. t. verus*							*P. t. schweinfurthii*		*P.t.troglodytes*
Reference	Boesch & Boesch, 1990	Sugiyama, 1995a	Sugiyama et al., 1988	Sugiyama, 1995a	Shimada, 2000	Baldwin, 1979	Alp, 1993	McGrew, 1974; Goodall, 1986	Hashimoto et al., 2000	Ingmanson, 1997*
Dorylus species	Mainly D. gerstaeckeri, occasionally D. nigricans	D.molestus	D.molestus	D. nigricans/ molestus	D.nigrican/ molestus	D.nigricans	D.nigricans	D. nigricans	D. nigricans	Dorylus sp.
N. of obs.	20	7	1	1	1	1		17	2	1
N. of tools used	35	60	5	2	3	9	7	13	14	7
Tool length in cm (range)	23.9 cm (11-50)	46.7 cm (SD=15.9)	66.2 cm (52.6-89.3)	72.5 cm (60-85)	63.3 cm (51-81)	71.6 cm (36-161)	79.8 cm (65-95.4)	66 cm (15-113)	79 cm (60-90)	41-80 cm
Technique employed	Only direct mouthing, with nibbling of ants off the tool		Direct mouthing, with wiping of tool through teeth or lips					Mainly pull-through with rare obs. Of direct mouthing		
Feeding on larvae, pupae and/or eggs	Frequent (N=70)	None (N=0)						Rare (N=3)		

*** Note: Last 2-3 cm of each stick had a brush end**

Techniques used to gain access to social insects or honey

As discussed in Chapter 1, striking differences in ant-dipping technique exist between Gombe and Taï (Boesch and Boesch, 1990; McGrew, 1992) (see Table 6.2). Gombe chimpanzees characteristically display the *pull-through* technique (McGrew, 1974), while *direct mouthing* of the safari ants by nibbling them off the tool is the only technique that has ever been recorded at Taï. However, some Gombe chimpanzees also occasionally take ants directly from the tool by mouth, either by nibbling or by pulling the tool sideways through the lips, as in termite fishing (McGrew, 1974). Although Boesch (1996b) explored ecological factors at both sites that might favour the use of either technique, he could not find any. Boesch (1996b), however, did not describe the ecological variables that he investigated or how he came to invalidate their influence.

It has been suggested that the differences in ant-dipping technique between Gombe and Taï are based on social learning, and reflect cultural variation among chimpanzees (Boesch and Boesch, 1990; McGrew, 1992). Sugiyama (1995a) reported that Bossou chimpanzees also employ a *direct mouthing* technique when dipping for ants, similar to that observed at Taï. The mouthing technique at Bossou appears though to differ slightly from that seen at Taï, in that the chimpanzees nearly exclusively pull the tool sideways through the lips to remove the ants, rather than nibble them off as at Taï. As will be discussed in this chapter, recent observations of ant-dipping from Bossou indicate that some members of the Bossou community sometimes employ another technique, i.e. the *pull-through* technique observed at Gombe. The *pull-through* technique was first noticed at Bossou in 1997 by Humle in a juvenile individual named Fotayu, aged six years.

Several hypotheses have been put forward regarding differences in tool length and technique between Gombe and Taï. Sugiyama (1995a, p.203) proposed that differences in ant-dipping techniques, tool length, dipping posture and material selection may depend on variations in prey characteristics, most particularly the aggressiveness of the prey, *Dorylus* spp., across these different study sites, and "may [also] to some extent reflect a tradition in the chimpanzee community". Hashimoto *et al.* (2000) further suggested that differences in the length of wands might reflect the difference in techniques used for catching ants.

Examples of the effect of differences in aggressiveness of insect species on techniques employed and tool length can be found in the literature concerning honey feeding in chimpanzees. Tutin *et al.* (1995) reported that chimpanzees at the Lopé Reserve, Gabon, use stick tools to obtain honey from the hives of African honey bees (*Apis mellifera*). Direct observations of this behaviour indicated that the chimpanzees were rarely stung and *Apis* bees at Lopé did not readily leave the hive to deter intruders. This contrasts with observations at Gombe, Tanzania, and Mt Assirik, Senegal, where this same species of bees is more aggressive (Tutin *et al.*, 1995). Indeed, it appears that the behaviour of this species of bees varies across Africa from highly aggressive to docile. At Mt Assirik, bees may chase and sting chimpanzees and humans who pass within 25 m of nests, while at Gombe, bees sting chimpanzees that raid their hives and pursue them for short distances, but they are not as aggressive as at Mt Assirik, while at Lopé, these bees are far more docile. Given the differences in aggressiveness of honey bees across these different sites, one would expect honey-fishing tools to be longer at Mt Assirik than at Lopé and those of Gombe to be intermediate, assuming that longer tools reduce the risk of getting stung. Based on Bermejo *et al.*'s (1989) study, mean tool length employed in fishing for honey of *Apis* bees at Mt Assirik is 93.25 cm (N=4 and range: 60-170 cm). This mean is much greater to that observed at Lopé where mean length is 78.5 cm (N=95, range=23-149.5 cm) (Tutin *et al.*, 1995). This observation supports the predicted relationship between the aggressiveness of the honey bees and tool length to obtain honey across different chimpanzee habitats. However, the Mt Assirik sample size is very small. In addition, no published data are available to date on tool length for honey fishing at Gombe.

In their study of chimpanzees in Bwindi-Impenetrable National Park, Uganda, Stanford *et al.* (2000) compared lengths of tools to obtain honey of stinging *Apis* bees and the stingless *Meliponula* bees. Tools used to gain access to *Apis* honey (N=9; mean length=60 cm, range: 25-85 cm) were significantly longer than those used for honey of *Meliponula* sp. (N=12, mean length=27 cm, range: 14-70.5 cm). This finding further supports the hypothesis that the risk posed by the bee species whose honey is targeted influences the length of tools employed by the chimpanzees. However, alternatively, longer tools may be employed to obtain the honey of *Apis* bees since these construct much larger hives than *Meliponula* bees, a hypothesis which remains to be tested (McGrew, pers. comm.).

However, at Kibale, chimpanzees have been observed raiding the nests of honey bees (*Apis millifera*) by hand, and only occasionally using sticks to gain access to the honey within the hive (Wrangham, pers. comm. cited in Stanford, 2000). So are honey bees at Kibale very docile? Wrangham (pers. comm. cited in Stanford, 2000) suggested that aggressiveness of the bees could in fact discourage the use of honey-foraging tools. Indeed, at Taï, chimpanzees usually extract honey combs from undisturbed hives with their hands and then run away from the bees before feeding on the honey and other products thus obtained (Boesch and Boesch, 1990). By contrast, honey-fishing tools at Taï are usually only used when hives have already been disturbed, either through the tree falling or because of activity by other predators, and when the threat of being stung may be reduced (Boesch and Boesch, 1990). These examples reveal that different techniques employed across different study sites and even within a same community depend on the belligerence of the prey and the potential discomfort incurred by the chimpanzees.

Some subtle differences in ant-dipping have also emerged between the Gombe and the Taï sites that may be related to differences in aggressiveness of safari ants at those sites (see Table 6.2). Although chimpanzees from both sites eat driver or safari ants with the help of sticks, at Taï, they dip for two species of ants (*Dorylus nigricans* and *D. gerstaeckeri*), while at Gombe, *D. nigricans* is the only species of driver ants so far thought to be available and dipped for by chimpanzees at this site (Boesch and Boesch, 1990; Goodall, 1986). These two species of safari ants behave very similarly to each other, by making a nest in the ground and usually hiding the entrance with loose soil and vegetation (Boesch and Boesch, 1990). Tai chimpanzees regularly eat the ants' eggs, larvae and pupae by directly extracting them from the nest by hand (Boesch and Boesch, 1990). This behaviour has, however, only rarely been reported at Gombe (Goodall, 1986; McGrew, 1974). Taï chimpanzees open the nest entrance by rapidly and vigorously raking out handfuls of loose soil until they excavate a hole large enough to insert an arm up to the shoulder (Boesch and Boesch, 1990). They then withdraw one or two handfuls of larvae and pupae from the bottom, which they proceed to eat in combination with leaves collected afterwards.

However, a difference in prey emphasis has been noted at Taï. The larvae and pupae of the larger species of ants (*D. nigricans*) are more frequently eaten than those of the smaller and more aggressive species (*D. gerstaeckeri*) (Boesch and Boesch, 1990). Compared to *D. nigricans*, *D. gerstaeckeri* have more painful bites, but move less rapidly up the stick (Boesch and Boesch, 1990).

Although tools employed for ant-dipping at Taï are especially used for the more aggressive prey, this does not explain why Taï ant-dipping tools are shorter than those found at Gombe and why a different technique should be observed at this site. Are differences in technique used and tool lengths for ant-dipping at different study sites socially learnt or are they the result of a combination of individual learning processes driven by environmental constraints?

Ontogeny of ant-dipping and other related tool-use behaviours

At Gombe, the ontogeny of ant-dipping is somewhat delayed relative to termite fishing (Goodall, 1986). At 5-6 years old, juveniles begin to dip, but they are not very skilled, and it is only a few years later that they attain adult competence (McGrew, 1977). Infant and juvenile chimpanzees at Gombe avoid aggressive safari ants, and ant-dipping is the only tool-use behaviour in which an adult level of proficiency is not achieved before the age of 7 (McGrew, 1977).

With regards to termite-fishing at Gombe, Goodall (1970) found that (i) the use of tools was not observed in infants under two years of age, although infants between the ages of 1 and 2 were often observed manipulating and preparing tools as a form of play; (ii) infants between the age of 2-3 used tools in the correct contexts, but they often used inappropriate materials, i.e. too short and/or too thick, and clumsy techniques; (iii) 3-4 year-old infants still used tools ineffectively; (iv) 4-year-olds showed a more elaborate adult technique, and spent more time fishing than infants, but their tools were usually shorter than those of adults. Their fishing movements, their sequential integration and their choice of raw material rapidly improved thereafter. By the time they reach the age of 5-6, juveniles have become proficient termite fishers.

Ant-fishing differs from ant-dipping in that it involves the use of a probe to extract arboreal ants from tunnels, usually holes in tree trunks. Ant-fishing is customarily observed at Mahale. At this site, no infant under the age of 2 was ever observed using tools for ant-fishing (Nishida and Hiraiwa, 1982). The earliest age at which the behaviour was recorded was 32 months. Young chimpanzees fished for ants using tools at around the age of 55 months and acquired the efficacy of adults only by the age of 6 or 7.

Thus, when comparing the ontogeny of termite-fishing at Gombe with that of ant-fishing at Mahale, ant-fishing skills appear to mature slightly later than termite-fishing skills while the development of ant-dipping at Gombe seems to lag behind. Indeed, in contrast to termite- and ant-fishing, during ant-dipping sessions at Gombe, infants and juveniles keep their distance during the 2-5-year age period, most probably for fear of the painful bites of driver ants (McGrew, 1977). Therefore, they have less opportunity to observe and practice.

Nishida and Hiraiwa (1982) proposed the following characteristic stages in the development of ant-fishing and other related stalk-using behaviours in young chimpanzees: (i) manipulatory play, (ii) tool-manufacture, (iii) motor-skill of tool-use, (iv) knowledge of the quality of the tool and efficiency of its use, (v) motor-skill in response to the anti-predator behaviour of the insect-prey. As observed above, these stages may appear at different ages depending on the specific tool-use behaviour in question and the defensive tactics of the insect-prey. According to Nishida and Hiraiwa (1982), the final determinants of chimpanzees' ability to exploit insects are probably not the preparation or making of the tools, but the motor skills involved in tool-use, associated with knowledge of the relationship between the quality of the tools, e.g. shape, length, thickness and flexibility, and the efficiency of prey-procurement. Moreover, McGrew (pers. comm.) believes that less practised youngsters have a more varied set of techniques than adults, who generally adopt more stereotyped patterns of behaviour.

According to Nishida (1987), fishing for termites and ants and dipping for ants provide examples of true imitation. He argued that the ability is gradually acquired by young chimpanzees through observing and imitating their mothers. For the wild chimpanzee, the primary socialising agent is the mother. Indeed, for at least the first five years of life, the vast majority of the infant's social interactions are with her (McGrew, 1977). This period of prolonged dependency ensures that the infant is exposed to all of her activities at close range, including those that are community traditions, such as ant-dipping. Therefore, one would expect that the mother would be the prime model for the infant, providing the latter with exposure and opportunities for practising a given behaviour. Trial-and-error learning has, however, also been acknowledged to be involved in the selection and preparation of tools, in perfecting the techniques, and in dealing with the insects' antipredator responses (van Lawick-Gooodall, 1973; McGrew, 1977).

6.2 Aims

Considering that Bossou chimpanzees display two ant-dipping techniques and a wide range of tool lengths, this site thus presents a good opportunity to explore variables that may influence tool length and technique used.

-Ant-dipping will be analysed in detail by looking at the characteristics of this behaviour among the chimpanzees of Bossou. The issue of cultural differences in techniques employed and in tool length in ant-dipping will be re-addressed on the basis of the Bossou data. Variables such as tool length, ant condition (migrating or at the nest site), technique employed, dipping position and age of tool-user will be considered. Emphasis will be given to inter-relationships between these variables and their variability in relation to prey species' identity, prey characteristics, such as aggressiveness and gregariousness, and behavioural efficiency.

-The ontogeny of ant-dipping behaviour at Bossou will also be reviewed based on cross-sectional data and contrasted with developmental data from other field sites and from other stalk-using behaviours.

6.3 Methods

Direct observations of ant-dipping were made on an opportunistic basis in August to October, 1997 and July to September, 1999 (see Table 6.3). A *session* is defined as a period during which at least one chimpanzee is engaged in tool behaviour; the session is terminated when the last remaining chimpanzee of the subgroup ends tool-use. A *bout* is "a period during which an individual is engaged in tool-using behaviour", represented by elements of the tool-task being performed, separated by intervals when no tool is held or the chimpanzee changes position (McGrew and Marchant, 1992, p.115).

An individual in good view was chosen and data were gathered when possible on the location, ant species, time starting dipping, time of removal of tool, hand used to hold tool, technique used to feed on the harvested ants, i.e. *direct mouthing* or *pull-through*, and position while dipping. Individuals for which no or little data had previously been collected were generally favoured over individuals for which data had already been acquired. For five of these sessions, ant species and ant condition were recorded.

Table 6.3 Summary of observational data recorded on ant-dipping in 1997 and 1999.

Individual	**Date**	**Sex**	**Age**	**Session No.**	**No. of Bouts**	**No. of Dips**	**Time (sec.) (No. dips based on)**
Yo	22/08/97	F	Adult	1	1	14	205 (14)
Yo	30/09/97	F	Adult	2	1	2	13 (2)
Yo	04/10/97	F	Adult	3	3	48	1365 (48)
Yolo	22/08/97	M	Juvenile	1	3	80	1450 (80)
Yolo	30/09/97	M	Juvenile	2	1	3	47 (3)
Yolo	04/10/97	M	Juvenile	3	2	3	159 (3)
Vui	01/09/97	M	Adolescent	4	1	11	122 (5)
Vui	06/10/97	M	Adolescent	5	1	2	78 (2)
Vuavua	01/09/97	F	Juvenile	4	1	14	395 (14)
Vuavua	29/09/97	F	Juvenile	6	1	7	223 (7)
Vuavua	07/10/97	F	Juvenile	7	1	4	192 (4)
Kai	01/09/97	F	Adult	4	1	4	No record
Kai	04/10/97	F	Adult	3	1	7	321 (7)
Kai	07/10/97	F	Adult	7	1	2	41 (1)
Juru	07/09/99	F	Juvenile	8	3	69	1952 (69)
Fotayu	01/09/97	F	Juvenile	4	3	39	1676 (39)
Fotayu	08/09/97	F	Juvenile	9	1	9	297 (9)
Fotayu	30/10/97	F	Juvenile	10	1	10	377 (10)
Fotayu	07/09/99	F	Juvenile	8	1	8	1499 (8)
TOTAL				**10**	**28**	**336**	**10412 (325), 2h53min32sec**

Between June and September 2000 and June and September 2001, video records were made using a Sony DCR-TRV20 digital camera, and in October 1997, some ant-dipping sessions were filmed using a Sony Hi8 video camera (see Table 6.4). Some video data were donated by G. Yamakoshi, which were collected between August and October 1999 using a Sony DCR-TRV9 digital camera. G. Ohashi recorded one session in August 2001. In total, over ten hours of video data were thus accumulated, encompassing 24 ant-dipping sessions, 291 bouts and 1041 dips.

Table 6.4 Summary of video data recorded at Bossou 1997-2001.

Individual	Date	Sex	Age	Session N.	N. of Bouts	N. of Dips	Time (sec.) (N. dips based on)
Foaf	29/10/97	M	Adult	1	1	5	141
Vui	29/10/97	M	Adolescent	1	5	8	415
Yo	29/10/97	F	Adult	1	2	11	293
Fotayu	24/08/99	F	Adolescent	2	1	8	217
Yo	24/08/99	F	Adult	2	6	10	499
Tua	13/09/99	M	Adult	3	2	24	569
Velu	13/09/99	F	Adult	3	7	43	961
Vuavua	13/09/99	F	Adolescent	3	6	7	465
Jire	14/09/99	F	Adult	4	1	11	389
Juru	14/09/99	F	Juvenile	4	9	30	763
Foaf	26/09/99	M	Adult	5	1	4	162
Foaf	26/09/99	M	Adult	6	2	10	275
Juru	26/09/99	F	Juvenile	6	5	19	599
Kai	26/09/99	F	Adult	6	4	29	673
Yo	26/09/99	F	Adult	6	5	33	773
Yolo	26/09/99	M	Adolescent	6	11	28	1242
Nto	27/09/99	F	Juvenile	7	1	5	132
Yolo	27/09/99	M	Adolescent	7	1	1	63
Fotayu	03/10/99	F	Adolescent	8	1	7	276
Yo	17/06/00	F	Adult	9	6	8	361
Foaf	17/07/00	M	Adult	10	2	3	95
Juru	17/07/00	F	Juvenile	10	1	3	175
Yo	17/07/00	F	Adult	10	3	3	56
Foaf	04/08/00	M	Adult	11	2	3	143
Jeje	04/08/00	M	Infant	11	6	22	614
Jire	04/08/00	F	Adult	11	1	17	649
Juru	04/08/00	F	Juvenile	11	9	21	804
Kai	04/08/00	F	Adult	11	1	2	51
Velu	04/08/00	F	Adult	11	1	6	207
Vuavua	04/08/00	F	Adolescent	11	3	11	368
Yo	04/08/00	F	Adult	11	3	22	690
Fotayu	07/09/00	F	Adolescent	12	3	8	1747
Juru	07/09/00	F	Juvenile	12	16	74	2294
Foaf	17/09/00	M	Adult	13	2	4	204
Kai	17/09/00	F	Adult	13	1	3	140
Velu	17/09/00	F	Adult	13	1	4	95
Vuavua	17/09/00	F	Adolescent	13	7	27	2081
Yo	17/09/00	F	Adult	13	3	24	742
Yolo	17/09/00	M	Adolescent	13	7	41	1425
Juru	03/07/01	F	Juvenile	14	11	11	1188
Velu	03/07/01	F	Adult	14	1	1	48
Vuavua	03/07/01	F	Adolescent	14	2	8	392
Yo	03/07/01	F	Adult	14	18	101	3194
Tua	12/07/01	M	Adult	15	1	2	62

Table 6.4. Summary of video data recorded at Bossou 1997-2001 (continued).

Individual	**Date**	**Sex**	**Age**	**Session N.**	**N. of Bouts**	**N. of Dips**	**Time (sec.) (N. dips based on)**
Jire	14/07/01	F	Adult	16	4	6	160
Juru	14/07/01	F	Juvenile	16	1	1	33
Nto	14/07/01	F	Adolescent	16	1	2	44
Tua	14/07/01	M	Adult	16	3	15	416
Vuavua	14/07/01	F	Adolescent	16	1	9	208
Yo	03/08/01	F	Adult	17	29	57	1534
Yolo	03/08/01	M	Adolescent	17	4	15	759
Juru	11/08/01	F	Juvenile	18	1	2	No Record
Tua	11/08/01	M	Adult	18	1	1	No Record
Yolo	11/08/01	M	Adolescent	19	2	4	No Record
Juru	11/08/01	F	Juvenile	20	1	2	41
Foaf	06/09/01	M	Adult	21	2	6	228
Nto	06/09/01	F	Adolescent	21	1	1	62
Foaf	08/09/01	M	Adult	22	1	2	81
Juru	08/09/01	F	Juvenile	22	6	27	1514
Nina	08/09/01	F	Adult	22	4	27	941
Nto	08/09/01	F	Adolescent	22	21	62	3538 (58)
Yo	08/09/01	F	Adult	22	2	18	328
Yolo	08/09/01	M	Adolescent	22	20	36	1407
Yolo	24/09/01	M	Adolescent	23	1	3	112
Juru	22/08/00	F	Juvenile	24	1	1	33
TOTAL				**24**	**291**	**1041**	**38590 (1030); 10h43min43sec**

All of the video data were analysed twice by myself and 14 sessions once by a second observer blind to the hypotheses being tested. Any divergences in scoring were reviewed by both observers until a consensus was reached and deviations in scoring were eliminated. After each filming session, the ant species dipped for was collected for taxonomical identification and the condition of the ants (nest or migrating) was noted. In addition, tool length was recorded for each individual as either less than, or greater than or equal to 50 cm. This 50 cm demarcation was based on the average between mean tool length reported by Sugiyama (1995a) (46.7 cm) and that found in the present tool sample set (53.7 cm). Ascription to these two categories was based on either precise tool length data when available (48.5% of tools) or simply comparing the length of the wand with objects of known length in the environment. Tools were assigned to one of five categories depending on the technique employed during the use of that tool: 1) Mouth only; 2) *Pull-through* only; 3) Mouth dominant (i.e. more than 50% *direct mouthing* observed during the use of that tool); 4) *Pull-through* dominant 5) Both techniques equal (i.e. technique ratio for that tool was 50:50). These categories were used for the sole purpose of graphical presentation of individual patterns of tool and technique use and of discerning tools which exhibited during use only one or the other dipping technique. Therefore, these uneven categories were never employed as variables in any statistical analyses undertaken in this study. Position of the tool-user was noted as: hanging from above, sitting above ground, e.g. on a bent over-sapling, standing tripedally, or sitting at ground level. These categories were subsequently collapsed into two, i.e. above ground and at ground level, for the purpose of analysis.

Tools were collected over four study periods: July-October, 1997; July-September, 1999, June-September, 2000 and June-September, 2001, on departure of the chimpanzees and, whenever possible, only with absolute certainty, tools were assigned to specific users. Occasionally, ant-dipping tools were also found during daily tracking of the chimpanzees or after arriving at a site where chimpanzees had previously been heard. These artefacts could always confidently be attributed to the chimpanzees based on other indicators of chimpanzees' presence, i.e. faeces, nests, foot, and/or knuckle prints (McGrew *et al.*, 1979). Although Bossou chimpanzees feed on columns of migrating ants, all the ant-dipping tools found "indirectly" were associated with ants' nests. The nests had been partially excavated. At these sites, the ants were sometimes still moving around on the ground beside the nest entrance, or they had already deserted their temporary bivouac, thus preventing recording of ant species dipped for. Some tools collected in the 1997 study period were assigned to ant type, but recording of ant condition was not systematically recorded. However, from all the recovered tools, data on length (cm) were recorded.

The following ant dipping experiment was conducted in September 2001 using measures. A human (a tracker not aware of the hypotheses being tested) dipped for ants using wands of three different lengths based on measures obtained from 89 wands that I had collected from Bossou prior to June 2001: 1) mean lower quartile length (28.1 cm), 2) mean length (55.3 cm) and 3) mean upper quartile length (101.7 cm). Each tool was made from *Maranthacloa* sp., the commonest plant species used for wand-making at Bossou (refer to *Chapter 7*). Since several species of driver ants were consumed by chimpanzees at Bossou (see *Section 6.5*), dipping sessions were done on *Dorylus lamottei* (Bernard) and *Dorylus militaris* (Santschi), classed as the Red type and *Dorylus nigricans* (Illiger), classed as the Black type, in both nesting and migrating conditions, thus creating four conditions (see Table 6.5). *D. kohli* (Wasmann), the third species classed as Red, was not included in the experiment, since when the experiment was carried out, we were still unaware of the presence of a third species of the Red type. Indeed, identification of the ant species dipped for during the experiment was only confirmed after returning from the field. For each tool used and on a random basis over a total of 8 sessions (2 sessions for Black/Migrating, 2 for Black/Nest, 2 for Red/Migrating and 2 for Red/Nest), we dipped for ants using different predetermined bout durations (range=2-120 sec.) also presented on a random basis. An average of 18 dips (range=16-22) per tool for each session were thus performed. The ants harvested from each "mimic dip" were placed in a sealable polythene bag and counted. A bout duration corresponded to the time the wand made contact with the ants to when the wand was just being inserted into the sealable bag. One person was timing, while another, the same throughout the experiment, dipped for the ants in a fashion similar to that observed among Bossou chimpanzees, making slight regular back and forth movements of the tool to stimulate swarming of the ants. A new tool was made for each session. The time taken for the ants to swarm up the length of the tool was also recorded over several trials interspersed within the original experiment.

The purpose of the experiment was to assess differences in prey density and belligerence across ant condition and the two types of *Dorylus* ants. In addition, I was able to acquire an estimate of ant speed and a measure of the number of ants harvested across tools of different length under these four conditions.

6.4 Data analysis

The continuous data on tool length were checked for normality using a normality probability plot and a Kolmogorov-Smirnov test. The data deviated significantly from normality, so non-parametric two-tailed tests were used for the data analysis. All detailed analysis pertaining to technique used, tool-length category at the individual level, dipping position, bout length, dipping-time, were based on the video data. The latter data were most often either ordinal or nominal and therefore non-parametric tests were conducted. For 2 x 2 contingency tables with expected values of less than 5, the Fisher's Exact test was used instead. When data on more than 6 subjects were available across conditions, a Wilcoxon Signed Ranks test was employed for analysis of data gathered on a interval scale and a two-tailed Sign test was used when ratios were concerned. Otherwise, a one tailed Z-test was employed to compare two proportions[1]. When a significant result was obtained using a Kruskal-Wallis test, Dunn's *post hoc* test was utilised.

The issue of independence of data points was tackled by avoiding the 'pooling fallacy' (Martin and Bateson, 1993). For tool length, classed by categories, a single data point was given each time a new tool was used and each time the tool was modified in

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[1] It should be noted that this kind of analysis should be interpreted with caution since with dealing with a small sample size, a few individuals may contribute disproportionately to some of the results.

length during use. For technique used, i.e. *direct mouthing* or *pull-through*, a single data point was given each time there was a switch in technique employed or in tool used. Therefore if a chimpanzee dipped with a same tool 20 consecutive times and each time was observed directly mouthing, this was scored as a single mouthing data point. Postural data during ant-dipping were scored each time the chimpanzee changed position from above ground to ground level or *vice versa.*

To analyse differences between age-classes in ant-dipping behaviour and explore the ontogeny of this behaviour, a cross-sectional approach was adopted. An individual longitudinal approach would have been preferable; however, insufficient data were available for this. Observational and video data were combined for frequency analyses pertaining to this section.

6.5 Results

Driver ant species available at Bossou

Samples of driver ants were assigned to species by ant specialist, Dr. B. Taylor (http://www.antbase.org). This taxonomic evaluation revealed that Bossou chimpanzees consume several species of *Dorylus* ants. These have been classed into two categories, i.e. Red, including *D. kohli, D. lamottei* and *D. militaris,* and Black, corresponding to *D. nigricans*. During the ant-dipping experiment, there was no difference in the quantity of ants harvested between the two Red species either overall or in the two conditions, which justified pooling them (see Table 6.5). Moreover, the Red species have morphological similarities, such as size and colour of the soldier ants that distinguish them from *Dorylus nigricans*, which is predominantly black and whose soldier ants are generally larger.

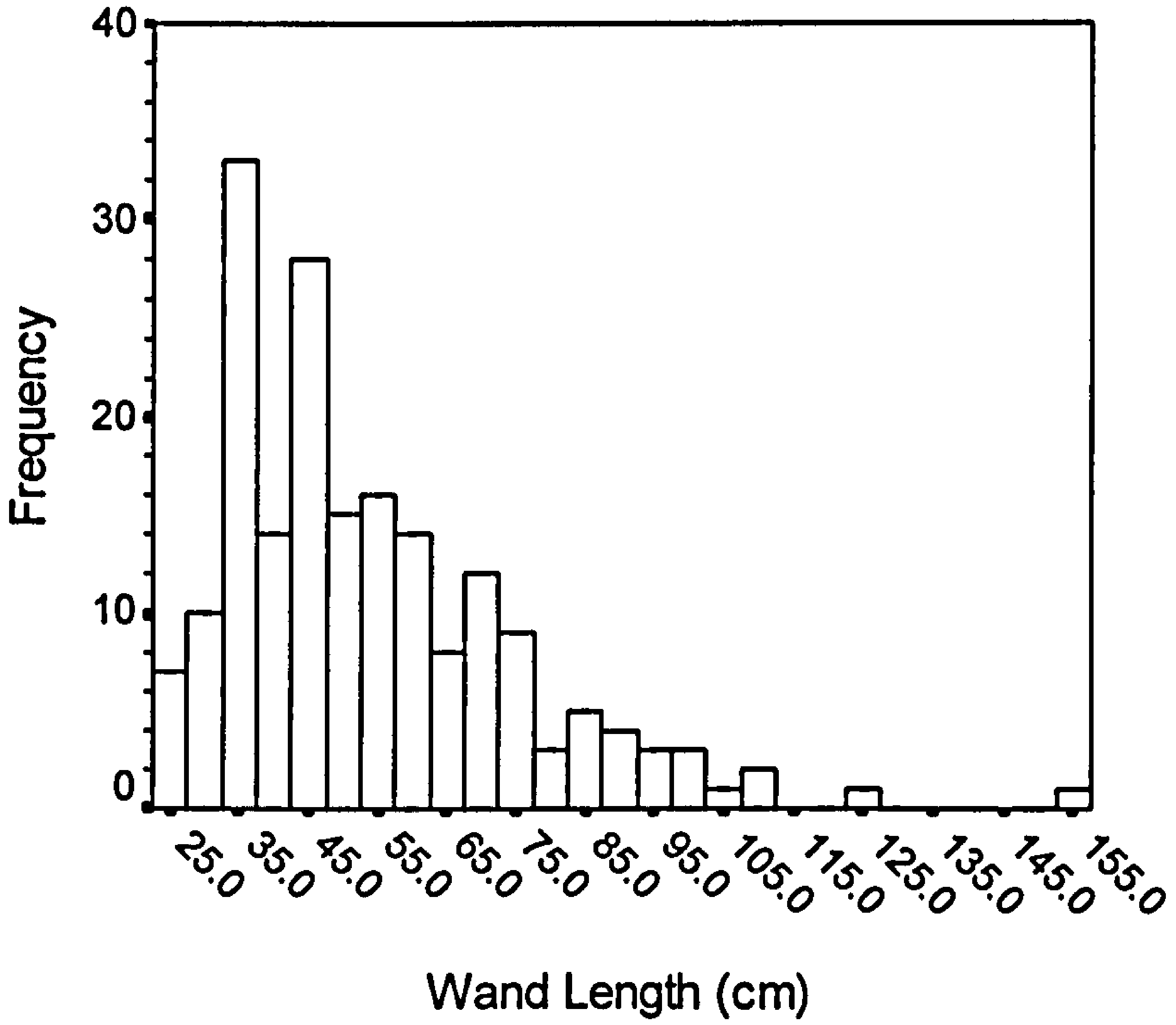
Table 6.5. Number of *Dorylus* ants harvested during the ant dipping experiment compared within two species of the Red type.

Condition	**Groups compared**	**N dips**	**Mean/ Dip**	**SD**	**Median/ Dip**	**Range**	**Mann-Whitney: z value and ρ-value**
Overall	*D. lamottei*	124	36.6	29.7	31	5-266	**z =-0.132; *n.s.***
	D. militaris	115	44.8	66.5	30	4-599	
Nest	*D. lamottei*	64	42.6	36.9	40.5	5-266	**z =-0.933; *n.s.***
	D. militaris	49	42.6	20.7	43	4-93	
Migrating	*D. lamottei*	60	30.2	17.6	25.5	6-76	**z =-0.995; *n.s.***
	D. militaris	66	46.4	86.2	21	4-599	

Length of ant-dipping tools

Based on 189 recovered tools, mean wand length was 53.7 cm (range: 23-154 cm; SD=21.01; Median=48.2 cm), intermediate between those found at Gombe and Taï (see Fig. 6.1). This mean does not differ significantly from the more recently published results on ant-dipping tools from Bossou (Sugiyama, 1995a) (see Table 6.2). The sample of wands from this study is, however, much larger, and thus may better reflect mean tool length at the community level.

Fig. 6.1. Distribution of wand lengths (N=189) for ant-dipping at Bossou.



Aggressiveness and gregariousness of Red and Black Dorylus

During the ant-dipping experiment, under each condition and overall, significantly more Black than Red ants were harvested (see Table 6.6). Moreover, Bossou chimpanzees sometimes reached manually for eggs, larvae and pupae at the nest site. During this study, egg or grub feeding directly by hand was recorded in 66.7% of the ant dipping sessions taking place at the nest site (N=9) and seven of ten individuals observed dipping at a nest engaged in this behaviour. However, it was exclusively targeted at Red *Dorylus* ants' nests.

Observations of the chimpanzees' behaviour at Bossou and across other sites support their sensitivity to these biting ants, regardless of the species involved (McGrew, 1974; Boesch and Boesch, 1990). The chimpanzees will vigorously brush off the ants from their fur and bare skin, i.e. feet and face, when exposed to driver ants. Our own experiences with these ants though indicate that Black *Dorylus* soldier ants inflict more painful bites than Red soldier ants, which are slightly smaller in size. Therefore, whether based on their higher level of aggressiveness or gregariousness, Black *Dorylus* clearly appear to pose greater discomfort to the ant dipping chimpanzee than the Red type.

Table 6.6. Number of *Dorylus* ants harvested during the ant-dipping experiment, compared across ant types and ant condition.

Condition	**Groups compared**	**N dips**	**Mean/ Dip**	**SD**	**Median /Dip**	**Range**	**Mann-Whitney: z value and ρ-value**
Overall	Red	239	38.9	51.2	29	2-599	**$z = -4.783$;**
	Black	205	63.5	72.5	39	3-544	**$\rho < 0.001$**
Nest	Red	113	42.6	30.8	42	4-266	**$z = -5.85$;**
	Black	99	93.9	88.0	66	19-544	**$\rho < 0.001$**
Migrating	Red	126	35.6	64.2	21	2-599	**$z = -2.312$;**
	Black	106	35.0	36.2	27	3-243	**$\rho < 0.05$**
Overall	Nest	212	66.6	69.0	47	4-544	**$z = -9.137$;**
	Migrating	232	35.3	53.1	24	2-599	**$\rho < 0.001$**
Red	Nest	113	42.6	30.8	42	4-266	**$z = -5.17$;**
	Migrating	126	35.6	64.2	21	2-599	**$\rho < 0.001$**
Black	Nest	99	93.9	88.0	66	19-544	**$z = -7.976$;**
	Migrating	106	35.0	36.2	27	3-243	**$\rho < 0.001$**

Tool length in relation to Dorylus species dipped for

Given the more aggressive nature and the possible greater gregariousness of the Black species, I predicted that longer tools would be used on Black ants, to allow the tool-user to better keep its distance from the ants while dipping. Overall, and at the nest site, Bossou chimpanzees used significantly longer tools while dipping for Black *Dorylus* ants compared to Red ones (see Table 6.7).

Although the trend was in the same direction, this difference was not significant for ants dipped while migrating on the ground (see Table 6.7), but the sample size for Black ants was relatively small. Thus, in a second analysis based on the categorical data from the video analysis, yielding a larger and more equal sample size, a Sign test, comparing, on an individual basis, the ratio of use of tools greater than 50 cm long to the total number of tools used under each condition between dipping on migrating Black and migrating Red driver ants, revealed that the chimpanzees were significantly more likely to use tools greater than 50 cm long for the Black driver ants than the Red (two-tailed Sign test: N=9; $\rho<0.05$) (see Table 6.8). This result supports the prey aggressiveness/gregariousness hypothesis.

Table 6.7. Length of ant-dipping tools compared across *Dorylus* species and ant condition based on retrieved tools.

Condition	**Groups compared**	**N**	**Mean (cm)**	**SD**	**Median (cm)**	**Range (cm)**	**Mann-Whitney: z value and ρ-value**
Overall	Red	117	50.8	18.6	46.4	23-126	**z =-2.802;**
	Black	52	62.4	26.0	59.65	24-154	**ρ<0.01**
Nest	Red	54	58.4	20.6	55.1	26-126	**z =-2.563;**
	Black	30	72.5	26.0	70.65	33-154	**ρ<0.01**
Migrating	Red	55	44.3	13.2	43.6	23-89	**z =-0.389; *n.s.***
	Black	7	46.7	13.7	42	31-69	
Overall	Nest	86	63.1	23.3	58	26-154	**z =-5.383;**
	Migrating	62	44.6	13.2	43.55	23-89	**ρ<0.001**
Red	Nest	54	58.4	20.6	55.1	26-126	**z =-3.918;**
	Migrating	55	44.3	13.2	43.6	23-89	**ρ<0.001**
Black	Nest	30	72.5	26.0	70.65	33-154	**z =-2.715;**
	Migrating	7	46.7	13.7	42	31-69	**ρ<0.01**

Table 6.8. Frequency of tools ≥ 50 cm and < 50 cm long used by individual chimpanzees respectively on Black and Red migrating driver ants.

Individual	Black *Dorylus*		Red *Dorylus*	
	< 50 cm	≥ 50 cm	< 50 cm	≥ 50 cm
Foaf	2	2	1	0
Jiré	1	0	2	0
Juru	0	7	11	2
Kai	0	1	1	0
Tua	1	0	1	0
Velu	1	0	1	0
Vuavua	2	0	2	0
Yo	2	2	4	0
Yolo	0	1	3	0
Total	**9**	**13**	**26**	**2**

Dorylus density/aggressiveness at the nest versus migrating

During the ant-dipping experiment, more ants were harvested at the nest site than in migrating or foraging columns whether pooling the data for both *Dorylus* species or analysing them separately (see Table 6.6). This result clearly indicates that driver ants are found at greater density and/or are more belligerent at the nest than while on the move.

Tool length in relation to the condition of the ants

Having established that the density of safari ants and/or their aggressiveness is greater at the nest than while migrating, I predicted that longer tools would be used for dipping at the nest site than when the ants were migrating. The data showed that wand length was significantly greater for ant-dipping at the nest, both overall and for each driver ant type analysed separately (see Table 6.7). This result supports the hypothesis that the chimpanzees use longer tools at the nest site to reduce the risk of being bitten. However, it is also conceivable that extra tool length may be required at the nest because the wand is inserted into the nest rather than just placed against the ground, as when dipping on migrating ants. But close observations of dipping at the nest site indicate that the chimpanzees most often dip near the nest entrance where swarming soldier ants gather, rather than inserting their tools into the nest cavity.

Dipping Technique and Ant Condition

The *direct mouthing* technique is more frequently observed at Bossou than the *pull-through* technique (see Fig. 6.2). A two-tailed Sign test, comparing, on an individual basis, the ratios of instance of independent instances of *pull-through* to the total number of independent technique data points for that condition between nesting and migrating ants, clearly indicated that an individual chimpanzee is significantly more likely to employ the *pull-through* technique at the nest site than on migrating ants (two-tailed Sign test: $N=9$; $\rho<0.05$) (see Fig. 6.2). A single young individual, Juru, was responsible for the rare instances of pulling through observed on migrating ants (see Fig. 6.2).

Although *pull-through* was more frequently observed with dipping at the nest site, individual variation among chimpanzees was observed (see Fig. 6.2). For example, three adult females, Kai, Nina and Velu, were never seen using the *pull-through* technique while dipping on ants at the nest. However, the latter technique was observed in seven other individuals and these included adults (Foaf, Tua and Yo), as well as adolescents (Yolo, Vuavua and Nto) and juveniles (Juru, Nto) of both sexes (see Fig. 6.2).

Frequency of dipping on the different Dorylus spps and of technique employed

Based on a single data point for each ant-dipping session, no deviation from expected values was found in the frequency of dipping on the different *Dorylus* types whether at the nest or while migrating (Fisher's Exact test: $N_{nest/black}=3$; $N_{nest/red}=6$; $N_{migrating/black}=7$; $N_{migrating/red}=13$; *n.s.*). Nevertheless, overall, the chimpanzees tended to dip more often on migrating ants then on ants at the nest; however, this trend just fell short of significance (Binomial test: $N_{nest}=9$; $N_{migrating}=20$; $\rho=0.063$).

Technique and tool length

The video data revealed that the *pull-through* technique was significantly more likely to occur when a chimpanzee employed a tool greater than or equal to 50 cm long than a wand less than 50 cm in length (see Fig. 6.3). This tendency was significant overall (two-tailed Sign test: $N=7$; $\rho<0.05$) and at the nest site (with tools ≥ 50 cm: 23/65; with tools < 50 cm: 0/14; one-tailed Z-test comparing two proportions: $z=5.97$; $\rho<0.001$). Even when restricting the analysis to "*pull-through* only" versus "*mouthing* only" tools, the association was still highly significant (overall: two-tailed Sign test: $N=6$; $\rho<0.05$; nest: with tools ≥ 50 cm: 17/35; with tools < 50 cm: 0/14; one-tailed Z-test comparing two proportions: $z=5.75$; $\rho<0.001$). Indeed, all cases of use of tools less than 50 cm long were associated with *direct mouthing*, while the *pull-through* technique was only observed with tools greater than or equal to 50 cm long (see Fig. 6.3).

However, the associations between pulling-through and tools ≥ 50cm long and pulling-through and ant dipping at the nest, call for a re-examination of the previously detected positive relationship between longer tools and dipping at the nest. This analysis was carried out on "mouthing only" tools. Wands ≥ 50 cm long were significantly more likely to be used when dipping on ants at the nest than on migrating ants (two-tailed Sign test: $N=9$; $\rho<0.05$).

Ant-dipping Position

Regardless of ant condition, above ground and at ground level position was independent of tool length (overall: $\chi^2(1, N=238)=0.107$; n.s; nest: $\chi^2(1, N=135)=0.083$; n.s; migrating: $\chi^2(1, N=103)=2.979$; n.s), technique used (overall: $\chi^2(1, N=238)=1.433$; n.s; nest: $\chi^2(1, N=130)=0.413$; n.s; migrating: Fisher's Exact test: $N=101$; n.s) and type of *Dorylus* ant dipped for (overall: $\chi^2(1, N=238)=0.210$; n.s; nest: Fisher's Exact test: $N=135$; n.s; migrating: $\chi^2(1, N=103)=0.114$; n.s) (see Table 6.9).

Table 6.9. Frequency of position scores overall and when dipping on nesting and migrating ants depending on tool length, ant type and technique used.

	Position	**Tool Length**		**Ant Type**		**Technique Used**	
Condition		**< 50 cm**	**≥ 50 cm**	**Black**	**Red**	**Mouth**	**Pull**
Overall	**Above Ground**	56	77	23	117	111	28
	Ground Level	42	64	15	90	85	14
Nest	**Above Ground**	23	63	4	82	59	23
	Ground Level	12	37	0	49	37	11
Migrating	**Above Ground**	33	14	14	33	47	3
	Ground Level	30	26	15	41	48	3

Chimpanzees dipping at the nest site were significantly more likely to be above ground than chimpanzees dipping on migrating ants (two-tailed Sign test: $N=9$; $\rho<0.05$). (see Fig. 6.4). This result again suggests that the chimpanzees respond to the greater risk of being bitten by ants at the nest. Dipping from a position above ground probably provides more protection from biting ants.

Technique, Dipping Time and Efficiency

Dipping time in seconds was assessed from the video records. Dipping time refers to the time elapsed between the chimpanzee placing its wand into the mass of ants and starting to ingest the ants. The question was: What is the relationship between dipping time and technique used? A Wilcoxon Signed Ranks test indicated that dipping times were significantly longer for pulling-through than mouthing ($N=8$, $z=-2.100$, $\rho<0.05$) (see Table 6.10).

Table 6.10. Summary statistics of median dipping time (sec.) depending on technique used, ant type dipped for and ant condition across all individual subjects employed in the Wilcoxon Signed Ranks tests conducted.

Variable		No.	Mean (sec.)	Median (sec.)	SD	Range (sec.)
Technique	Pull	8	**31.5**	**28.0**	**10.9**	**19.5-50.0**
	Mouth	8	**24.6**	**25.5**	**6.9**	**14.5-35.0**
Ant Type	Black	8	**28.8**	**28.0**	**5.4**	**23.0-39.0**
	Red	8	**20.7**	**22.0**	**5.4**	**13.0-28.0**
Ant Condition	Nest	9	**23.3**	**21.0**	**9.4**	**13.0-38.0**
	Migrating	9	**23.5**	**24.0**	**7.7**	**7.0-33.0**

Fig. 6.2. Ant-dipping at the nest site and on migrating ants and associated technique (based on independent data points) for each individual chimpanzee.

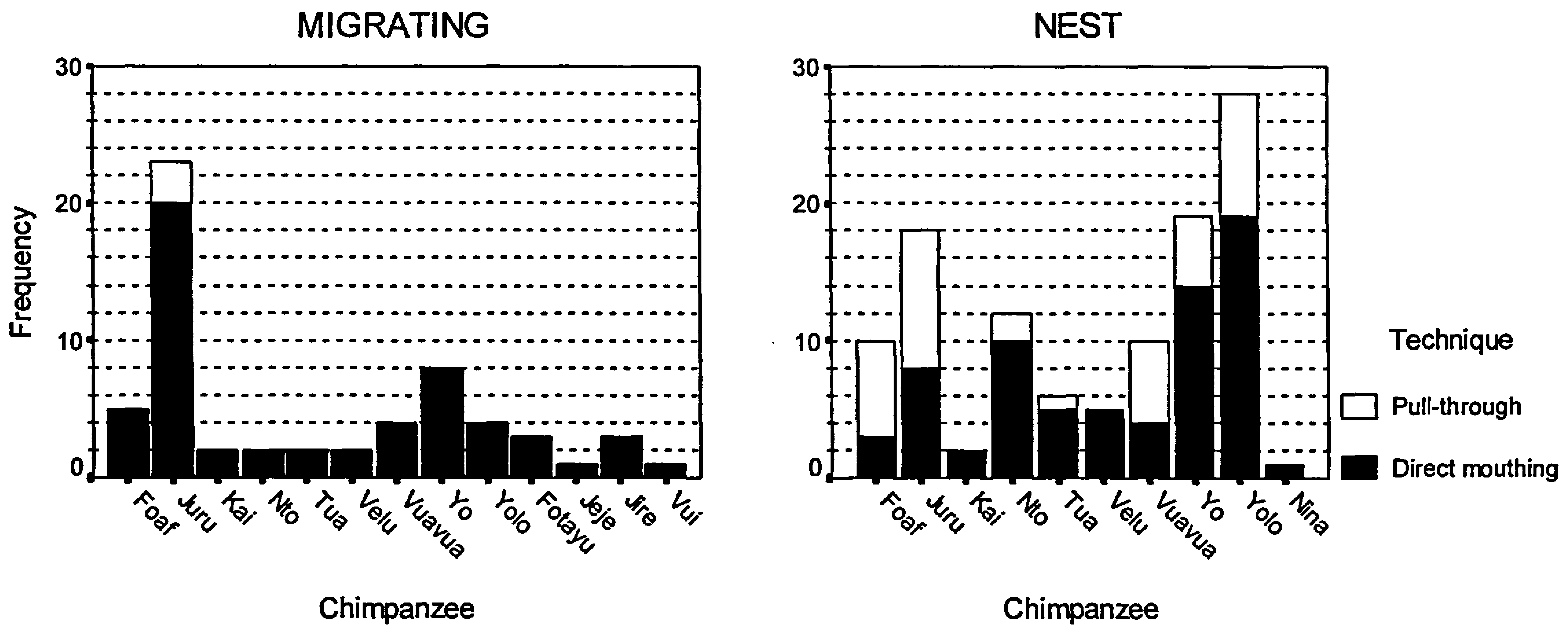
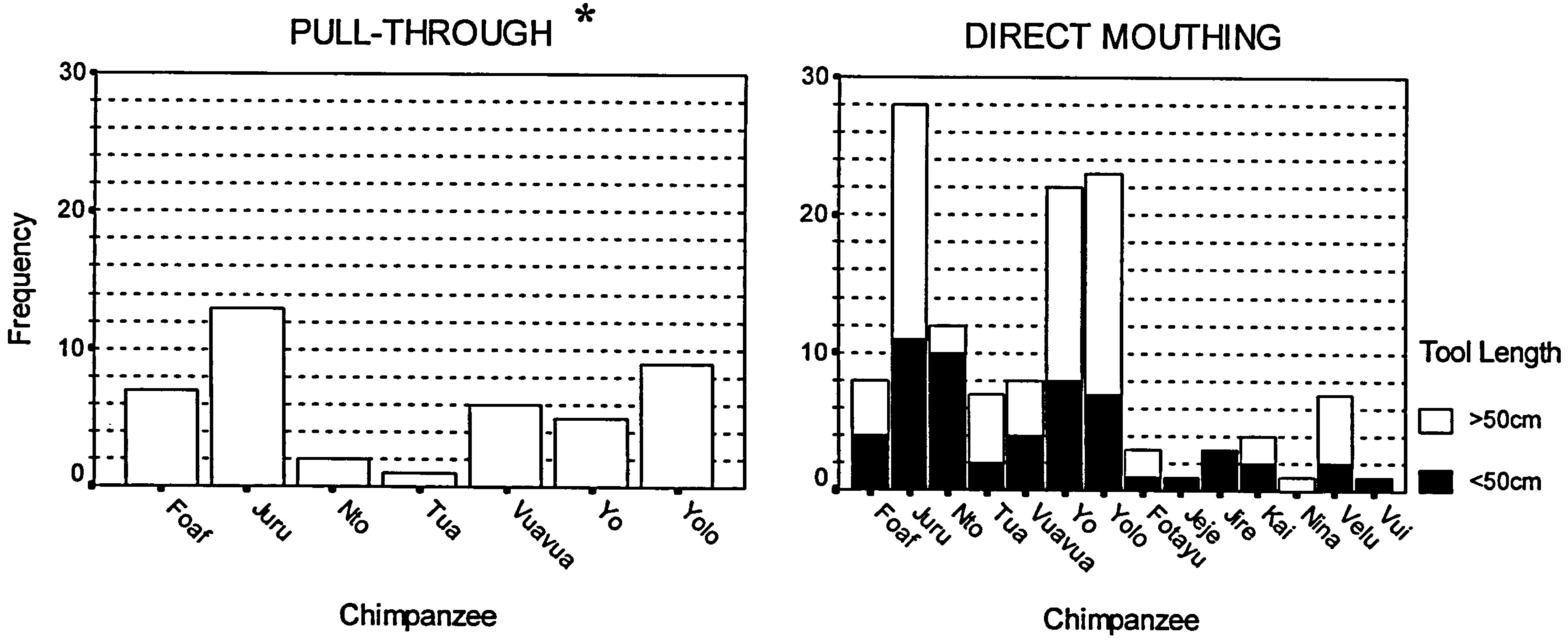
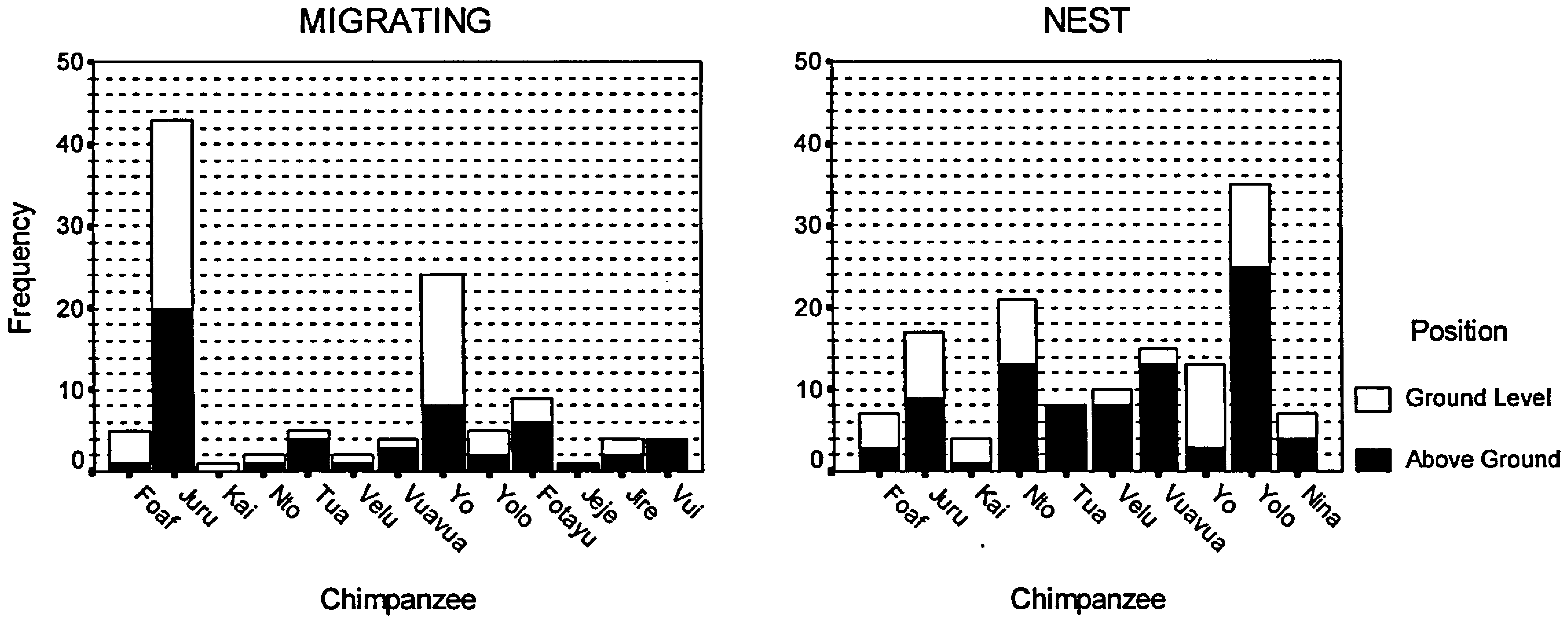


Fig. 6.3. Frequency of independent ant dipping technique data points and associated tool length for individual Bossou chimpanzees.



*Note: Pull-through was never observed for tools <50cm long.

Fig. 6.4. Frequency of independent position scores (above ground or ground level) as a function of ant condition across individual members of the Bossou Community.



Overall, dipping time was also significantly longer when dipping for Black *Dorylus* than for the Red type (Wilcoxon Signed Ranks test: N=8, z=-2.521; ρ<0.05) (see Table 6.10). However, the Red species (N_{Red}=63; Mean=3.9 cm/sec.; SD=1.4; Median=4.02 cm/sec.; Range: 0.73-8.25 cm/sec.) were faster at climbing up the wand than *Dorylus nigricans* (N_{Black}=53; Mean=3.4 cm/sec.; SD=1.5; Median=2.98 cm/sec.; Range: 1.12-9.16 cm/sec.) (Mann-Whitney U-test: z=-2.696; ρ=0.007).

Another question posed was whether dipping time varied with whether the ants were at the nest site or moving on the ground. However, no significant difference in dipping time emerged between the two ant conditions (Wilcoxon Signed Ranks test: N=9, z=-0.415; *n.s.*) (see Table 6.10).

In the ant-dipping experiment, there was no correlation between dipping time and quantity of ants harvested either overall (R_s=0.041; N=444; *n.s.*) or on migrating ants (R_s=-0.102; N=232; *n.s.*). In contrast, there was a significant positive correlation between dipping time and the number of ants collected when ants were dipped for at the nest (R_s=0.316; N=212; ρ<0.001) (see Fig. 6.5). Thus, longer dipping times at the nest were related to enhanced ant harvesting.

During the ant-dipping experiment a significant difference in the amount of ants gathered at the nest site was found across the three different tool lengths employed (Kruskal-Wallis test: χ^2=8.521 df=2; ρ<0.05) (see Table 6.11). Dunn's *post hoc* test indicated that the long tool yielded more ants than either the short tool or the medium length tool; however, there was no difference between the latter two (see Table 6.11). No difference across the three tools occurred for migrating ants (Kruskal-Wallis test: χ^2=1.747; df=2; *n.s.*) (see Table 6.11). Therefore, the use of longer tools at the nest site is probably not simply a response to the greater biting risk, but also an adaptation for greater efficiency.

Fig.6.5. Graph of dipping time (log. scale) against numbers of ants harvested, including all castes, at the nest site.

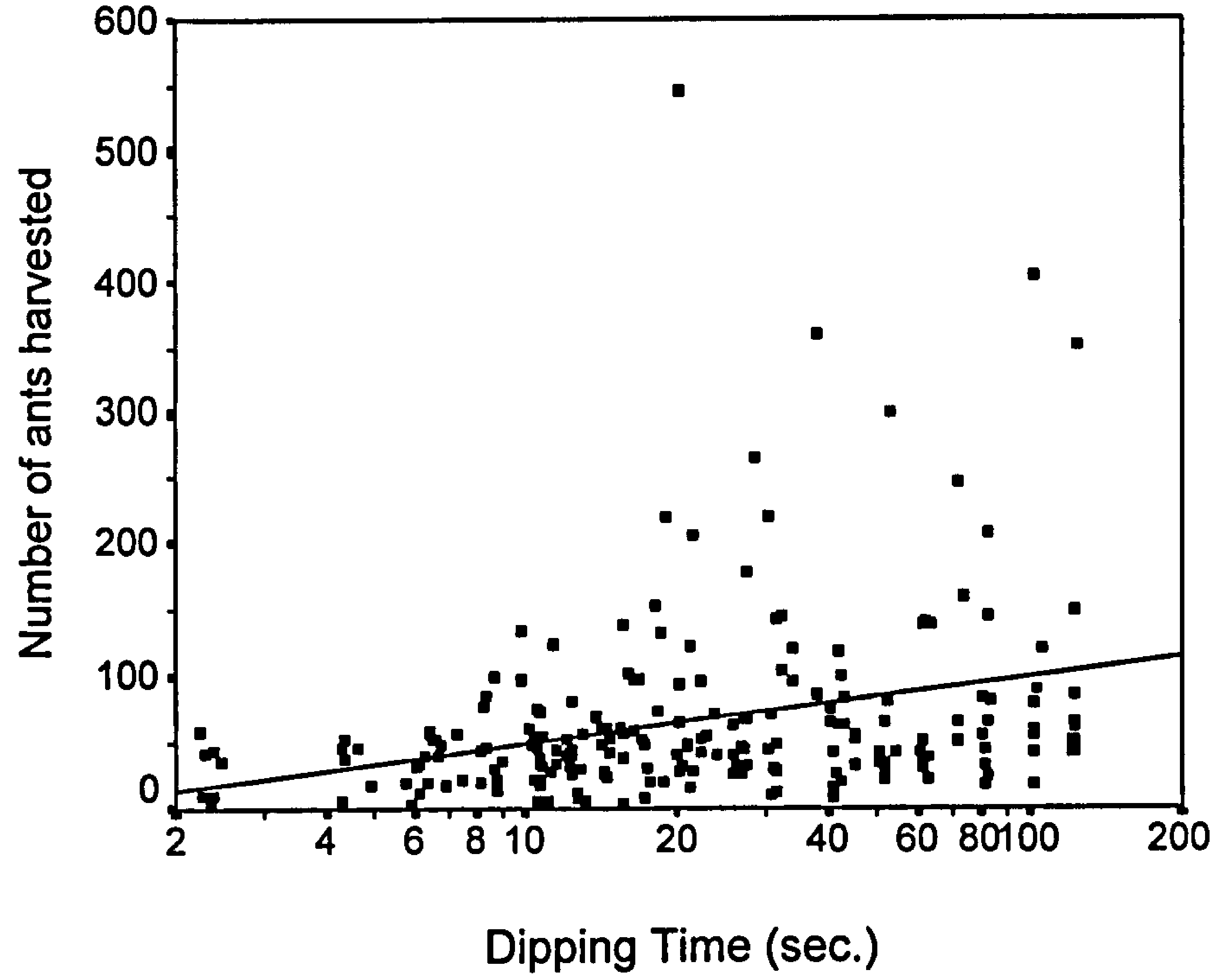


Table 6.11. Summary statistics of numbers of ants gathered during the ant-dipping experiment according to ant condition and depending on tool length employed.

Ant Condition	Tool Length	No.	Mean	Median	SD	Range
	Short (28.1 cm)	70	67.3	45.0	81.5	4-404
Nest	Medium (55.3 cm)	68	54.2	43.0	42.1	5-220
	Long (101.7 cm)	74	77.2	59.5	74.7	13-544
	Short (28.1 cm)	82	35.9	21.0	69.6	2-599
Migrating	Medium (55.3 cm)	78	35.8	26.0	41.5	4-243
	Long (101.7 cm)	72	34.1	24.0	42.2	3-263

Based upon 1104 successful dips, chimpanzees at Bossou performed the dipping movement on average 2.37 times per minute (SD=2.7). Adult chimpanzees (12 years old and over) performed dipping acts 2.6 times per minute (SD=2.3), based upon 610 successful dips. Based on 444 dips across both types of *Dorylus* and under both ant conditions, the overall mean number of ants harvested during the ant dipping experiment was 50.24 per dip (SD=63.1). Based on these figures, chimpanzees at Bossou gathered on average 119 ants per minute (SD=105.1) during an average dipping session, and adults gathered an average of 131 ants per minute (SD=77.6).

Age differences in ant-dipping and ontogeny of ant-dipping at Bossou

Age-class differences in dipping depending on ant condition and type of Dorylus ant dipped for

Differences were explored in the frequency of dipping across age-classes, i.e. juvenile (4-7); adolescent (8-11) and adult (>11), between the two ant conditions, based on a single data point for each individual for each ant-dipping session observed. A significant association between ant-dipping condition and age-class emerged ($\chi^2(2, N=56)=4.912$; $\rho<0.05$). In this instance, juveniles dipped significantly more often on migrating columns (15/18) than adults (20/38) (see Table 6.12) (two-tailed Z-test comparing two proportions: $z=2.57$; $\rho<0.01$). No significant difference though emerged in the proportions of dipping on migrating ants between adults (20/38) and adolescents (13/21) (two-tailed Z-test comparing two proportions: $z=-0.70$; *n.s.*) or adolescents (13/21) and juveniles (15/18) (two-tailed Z-test comparing two proportions: $z=-1.56$;*.n.s.*) (see Table 6.12).

Concerning frequency of dipping on the two different types of *Dorylus*, an association with age-class just failed to reach statistical significance ($\chi^2(2, N=77)=5.845$; $\rho=0.054$) (see Table 6.12). Adolescent individuals tended, however, to dip significantly more often on Red *Dorylus* ants than did juveniles (adolescent/Red: 18/21; juvenile/Red: 9/18; two-tailed Z-test comparing two proportions: $z=2.54$; $\rho<0.05$).

Table 6.12. Ant-dipping frequency depending on ant condition and type of *Dorylus* dipped for across age-classes (one data point ascribed to each chimpanzee for each session observed).

Age Class	Ant Condition	Dorylus Type	Frequency
Adult (>11 years old)	Nest	Black	2
		Red	16
	Migrating	Black	12
		Red	8
Adolescent (8-11 Yrs.)	Nest	Red	8
	Migrating	Black	3
		Red	10
Juvenile (4-7 Yrs.)	Nest	Black	1
		Red	2
	Migrating	Black	8
		Red	7

Comparisons of wand length and technique employed

There was no significant difference between the different age-classes in the length of tools employed, both overall and for both ant conditions (see Table 6.13).

Moreover, based on the video data and on independent sample points for technique used, no significant association between technique used and age-class emerged, whether overall or at the nest (see Table 6.14). For dipping on migrating ants, adults were never observed pulling-through. The only rare examples of this technique in this context were performed by one single individual, Juru, once as a juvenile and twice as an adolescent (see Table 6.14).

Table 6.13. Age-class differences in wand lengths based upon tool data overall, at the nest or on migrating columns of ants.

Condition	N			Mean (cm)			Std. Deviation			Median (cm)			Range (cm)			Statistic
	Adult	Adol.	Juv.	Adult	Adol.	Juv.	Adult	Adol.	Juv.	Adult	Adol.	Juv.	Adult	Adol.	Juv.	Kruskal-Wallis Test
Overall	29	28	14	52.11	53.63	60.79	21.89	26.79	23.07	46.7	44.75	61.8	31-126	25-154	23-108	χ^2=2.482; df=2; *n.s.*
Nest	8	8	6	76.29	73.36	74.68	25.96	41.65	19.93	72.15	70.5	70.8	48-126	26-154	53-108	χ^2=0.228; df=2; *n.s.*
Migrating	12	18	7	43.92	45.19	46.36	9.9	12.51	18.27	44.45	44.2	46.1	33-64	25-73	23-69	χ^2=0.053; df=2; *n.s.*

Table 6.14. Observed frequencies of technique used (independent data points) depending on age-class based upon video data overall, at the nest or on migrating ants and associated Chi-square test.

Condition	**Observed Frequencies**						**Chi-Square Test**
	Adult		Adolescent		Juvenile		
	Mouth	*Pull-through*	*Mouth*	*Pull-through*	*Mouth*	*Pull-through*	
Overall	51	13	54	25	21	5	χ^2=3.019; df=2; *n.s.*
Nest	30	13	37	23	4	4	χ^2=1.442; df=2; *n.s.*
Migrating	21	0	17	2	17	1	-

Age-class comparisons of ant-dipping position

A significant association between ant-dipping position, whether above ground or at ground level, and age-class emerged overall and at the nest, while there was none on migrating ants (see Table 6.15). A *post hoc* analysis revealed that, overall and at the nest, adolescents positioned themselves significantly more often above ground than adults (overall: adolescent/above ground: 72/113; adult/above ground: 40/87; two-tailed Z-test: *z*=2.53; ρ<0.05; nest: adolescent/above ground: 58/80; adult/above ground: 25/47; two-tailed Z-test: *z*=2.19; ρ<0.05).

Table 6.15. Statistical summary of analysis of ant-dipping position (independent data points) across different age-classes and different ant conditions.

Condition	Age-class	Above Ground		Ground Level		Statistic
		Observed	Expected	Observed	Expected	
	Adult	40	48.6	47	38.4	**χ^2=6.282;**
Overall	Adolescent	72	63.1	41	49.9	**df=2;**
	Juvenile	21	21.2	17	16.8	**ρ<0.050**
	Adult	25	30.1	22	16.9	**χ^2=6.383;**
Nest	Adolescent	58	51.2	22	28.8	**df=2;**
	Juvenile	4	5.8	5	3.2	**ρ<0.050.**
	Adult	15	18.0	25	22.0	**χ^2=3.170;**
Migrating	Adolescent	14	14.9	19	18.1	**df=2;**
	Juvenile	17	13.1	12	15.9	***n.s.***

Ontogeny of ant-dipping

The youngest member of the Bossou community observed ant-dipping during this study was a 32-month old male infant (Jéjé), who dipped for migrating ants with a short tool, while hanging from a vine and sitting on the back of his mother. The latter was also engaged in dipping, standing tripedally on the ground. The behavioural sequence performed by Jéjé was similar to that of adults, although it was apparent that the gain was small and the competence level relatively poor.

During the study, three 6-year old juveniles (Fotayu, Juru and Nto) were avid ant-dippers, however they were only observed dipping on migrating columns of ants.

Thus at Bossou, by the age of six, young chimpanzees appear to be fairly accomplished ant-dippers, although they avoided this activity when the risk of getting bitten was high, as at the nest site. Indeed, out of five juveniles observed ant-dipping, Juru, was the only one ever observed dipping at the nest, which she did by the age of seven. Juru, was also responsible for the three instances of *pull-through* observed on migrating ants (see Fig. 6.3).

Based on a single data point for each individual for each session, juveniles preferred to dip on migrating ants than on ants at their temporary bivouac ($N_{Nest}=3$; $N_{Migrating}=15$; Binomial test; $\rho<0.01$). Among juveniles, no difference in dipping for the two *Dorylus* types was found ($N_{Red}=9$; $N_{Black}=9$; Binomial test; *n.s.*). In addition, there was no indication of preferential dipping for ant types depending on ant condition (Fisher's Exact test, *n.s.*) (see Table 6.12).

Adolescent chimpanzees showed no preference for dipping at either the nest or on migrating columns of ants ($N_{Nest}=8$; $N_{Migrating}=13$; Binomial test, *n.s.*), although they preferentially dipped for Red *Dorylus* than Black ones ($N_{Red}=18$; $N_{Black}=3$; Binomial test; $\rho<0.01$). No significant divergence between observed and expected frequencies was found among adolescents in dipping for the two ant types depending on their condition (Fisher's Exact test, *n.s.*) (see Table 6.12).

Finally, adults dipped on nesting and migrating *Dorylus* indiscriminately ($N_{Nest}=18$; $N_{Migrating}=20$; Binomial test, *n.s.*) and expressed no significant preference for either ant type, although they tended to dip more frequently for the Red type ($N_{Red}=24$; $N_{Black}=14$; Binomial test; *n.s.*). However, at the nest, adults dipped significantly more often on the Red species (16/18) than on the Black (2/18) (two-tailed Z-test comparing two proportions: $z=7.42$; $\rho<0.001$) (see Table 6.12).

At last, there was no apparent association between mother and offspring in technique employed. Two mother-infant pairs did not match in the repertoire of techniques they displayed, i.e. Nina/Nto and Velu/Vuavua, while one exception was Yo/Yolo (see Fig. 6.2). Both Nto and Vuavua were observed occasionally pulling through while dipping on ants at the nest site, but neither mother did so.

6.6 Discussion and summary

Prey influence on tool length

A clear influence of prey condition and behaviour on the length of ant-dipping wands used by Bossou chimpanzees during ant-dipping emerged. As discussed in *Section 6.1*, an influence of insect behaviour on tool attributes and employment has previously been reported for honey feeding (cf. Tutin *et al.*, 1995; Bermejo *et al.*, 1989; Stanford, 2000; Boesch and Boesch, 1990), as well as ant-dipping at Taï (Boesch and Boesch, 1990). This study revealed that Bossou chimpanzees employed significantly longer tools when dipping for ants at their nest than on migrating ants, where ants were at lower densities and/or were more belligerent. This trend was independent of the technique employed or type of ants examined and suggests that the chimpanzees were responding to the risk of being bitten by the ants.

Bossou chimpanzees dip for several species of driver ants. The Black type, *D. nigricans*, was found to be more gregarious and/or more belligerent than the Red *Dorylus*. Analysis of tools and video records indicated that the chimpanzees tended to use significantly longer tools at the nest and were more likely to employ tools greater than or equal to 50 cm long on migrating columns when dipping for the Black type than the Red. The ant-dipping experiment failed though to distinguish between gregariousness and aggressiveness of the two *Dorylus* types. These two variables were inevitably confounded, as the number of ants biting or attacking the intruding object, i.e.

the wand, is dependent upon both the density and belligerence of the ants.

Regardless, some form of discomfort assessment appeared to influence tool-selection or tool-making and therefore tool length among the chimpanzees of Bossou. The finding that tool length was influenced by the condition of the prey supports Sugiyama's (1995a) hypothesis that the length of the wand must be determined by characteristics of the prey. However, other variables, such as technique employed, were also influenced by prey condition and closely associated with tool length.

Prey, technique and tool-making

Two ant-dipping techniques were observed at Bossou: 1) *direct mouthing* of the tool, removing the ants with the teeth or lips and 2) swiping the length of the tool to gather the ants in the hand before rapid transfer to the mouth, also known as the *pull-through* technique. There were individual differences in the relative employment of the techniques, which were age independent and not necessarily matched between mother and offspring.

At Bossou, the technique employed was related to the condition of the ants and tool length. The *pull-through* technique was only observed with the use of tools greater than or equal to 50 cm long and almost solely associated with dipping at the nest. In addition, although *direct mouthing* took place under both ant conditions, it was more likely to occur on migrating ants than on ants at the nest, and tools less than 50 cm in length were exclusively associated with this technique.

Implications in relation to ant-dipping at Gombe and Taï

Differences in prey aggressiveness and behaviour may lead to differences in tool length within and between communities of chimpanzees. However, as suggested by Hashimoto *et al.* (2000), differences in tool length may also reflect the different techniques used for catching ants. These two hypotheses are supported by the findings of this study, but to what extent can these results be applied to what is observed at Taï and Gombe? Extrapolating from the present study, Gombe chimpanzees would be expected to exhibit the *pull-through* technique since they more often employ tools greater than 50 cm long (McGrew, 1974: N=13; Mean=66 cm; Range: 15-113 cm) than at Taï (Boesch and Boesch, 1990: N=35; Mean=23.9 cm; Range: 11-50 cm). Finally, Taï chimpanzees should only perform *direct mouthing*, since they use wands shorter than 50cm. Observations of ant dipping technique at those sites support these predictions (McGrew, 1974; Boesch and Boesch, 1990).

Considering that longer tools at Bossou were associated with greater prey aggressiveness/gregariousness, one may predict that the *Dorylus* species dipped for at Gombe is more aggressive or better at deterring intruders than the species dipped for at either Taï or Bossou. As yet, no data contrasting prey aggressiveness or density across these three sites are available to test this prediction.

However, there may exist indirect measures available to compare differences in prey aggressiveness. McGrew (1974) pointed out that Gombe chimpanzees stayed off the ground in 74% of ant dipping episodes, while Bossou chimpanzees in this study ant dipped from above ground only 55.9% of the time (No. of independent "above ground" data points/Total No. independent position data points). Although position was independent of tool length, technique used and type of *Dorylus* spp. dipped for, Bossou chimpanzees were significantly more likely to be positioned above ground when dipping on nesting ants than on migrating ones. This result suggests an influence of prey density or aggressiveness on chimpanzee position during ant dipping, thus supporting the argument that the species of *Dorylus* ant found at Gombe may pose greater discomfort to the chimpanzees than at Bossou. To date no such data have been published for chimpanzees at Taï.

The extent of feeding on ants' eggs, larvae and pupae, food items that are more nutritious than adult ants (Wu Leung, 1968 cited in Boesch and Boesch, 1990), could also be one good indicator of prey aggressiveness. Boesch and Boesch (1990) noted a difference in prey emphasis among the chimpanzees of Taï, where two species of *Dorylus* ants are dipped for. The larvae and pupae of the larger species, *D. nigricans*, are more frequently eaten than those of the smaller and more aggressive species, *D. gerstaeckeri*, for which tools are most frequently used to capture adults (Boesch and Boesch, 1990).

Consumption by chimpanzees of *Dorylus* eggs, larvae and pupae has rarely been observed at Gombe (Goodall, 1986; McGrew, 1974), but is quite common at Taï (Boesch and Boesch, 1990) (see Table 6.2). At Bossou, chimpanzees also fed on eggs, larvae and pupae, but solely targeted the Red species of *Dorylus*. If the frequency of this behaviour is indeed influenced by prey belligerence or density, this would suggest that *D. nigricans* at Gombe is fiercer or more gregarious than those species of *Dorylus* found at either Bossou or Taï. Gombe chimpanzees would thus be more likely to use longer tools to avoid being bitten.

It is also possible that *pull-through* may be the most effective method of gathering ants off a long tool, which would then explain the predominance of this technique at Gombe. During *pull-through*, the gathered mass of ants is crumpled and jumbled so that few can bite the chimpanzee before they are consumed, whereas they pose a greater biting risk to the chimpanzee if the long tool is mouthed.

Technique, dipping time and efficiency

It has been suggested that the *pull-through* technique is generally a more efficient technique than *direct mouthing* (Boesch and Boesch, 1990). At Bossou, *pull-through* was associated with longer dipping times and, at the nest site only, with better ant harvesting. Also, the longer tools used during the ant-dipping experiment yielded more ants, but again at the nest site only. Significantly longer dipping times were also observed while dipping on the Black type; however, the Red type was found to climb the length of the wand more rapidly than the Black type.

Nevertheless, Bossou chimpanzees gathered on average only 119 ants per minute (131 ants per minute for adults) during an average dipping session, which is lower than at either Taï (Boesch and Boesch, 1990:180 ants/min.) or Gombe (McGrew, 1974: 760 ants/min). Boesch (1996b) suggested that Taï chimpanzees could gain more ants if they employed the Gombe *pull-through* technique, and that their current technique is not optimal. But why then, do chimpanzees at Bossou, who exhibit the *pull-through* technique, appear to have such a low level of efficiency compared to Gombe and Taï? Replication of these efficiency measures based on more "dipping mimics" or simulations and on a larger set of chimpanzee dips (dips/min.) are required from both Gombe and Taï.

Moreover, a taxonomic re-examination of *Dorylus* species found at the sites where chimpanzees have been shown to dip may be required, since field workers, lacking an entomological background, may have misidentified some species and hence the number of species available in each habitat. Not only may the species of *Dorylus* differ, but there may be important differences in behaviour of these ant species, whether the same or not, across sites.

Age-class differences in ant-dipping and ontogeny of this behaviour

The pattern of development of ant-dipping at Bossou is similar to that observed for Gombe (McGrew, 1977). However, youngsters at Bossou begin dipping at an earlier age than at Gombe, where chimpanzees only start at around 5 years of age (McGrew, 1977).

McGrew (1977) pointed out that infants at Gombe never tried to dip for driver ants, but performed some elements of this tool behaviour in isolation, whereas a 32-month old male infant at Bossou was observed correctly producing the ant-dipping sequence on migrating ants, although not very effectively. The youngest Gombe chimpanzee observed dipping was a 46-month old female. Given that infants and juveniles are clearly vulnerable to getting bitten by driver ants, the difference in the onset of ant-dipping between the two sites may be due to *Dorylus* ants at Bossou being less aggressive than those found at Gombe. However, due to lack of data on other infants from Bossou, the early development of this tool-use behaviour could not be explored in detail.

By the age of six, Bossou chimpanzees are able ant-dippers. When engaged in tool-use behaviour, young chimpanzees often behave in a less stereotyped fashion than adults (McGrew, 1977; Inoue-Nakamura and Matsuzawa, 1997). Juru's occasional pulling-through on migrating ants could well reflect a lack of stereotypy in behaviour or represent a different threshold to exposure to discomfort when compared to adults, who were never observed pulling-through while dipping on migrating ants.

The influence of exposure to discomfort on the ant-dipping habits of young Bossou chimpanzees was reflected by juveniles' preferential dipping for migrating ants rather than for ants at the nest. No such preference was observed in adolescents, although they dipped significantly more frequently on Red *Dorylus* than on the more gregarious/aggressive *Dorylus nigricans*. During adolescence, young chimpanzees practised ant-dipping in both ant conditions, thus increasing their understanding of the relationship between tool length, the effectiveness and suitability of a technique, the biting risk posed by the ants and the overall efficiency of their behaviour. Nevertheless, compared to adults, adolescent chimpanzees dipped significantly more often from above ground both overall and at the nest, indicating a cautious approach to dipping, particularly on nesting ants. Finally, adults, overall, showed no marked preferences between nesting and migrating ants or between the two types of driver ants. However, at the nest, they dipped significantly more often on the Red species than on the Black.

There were no age-class differences in tool length or in the proportion of techniques used. Nevertheless, adults never pulled-through on migrating ants while one sub-adult, Juru, occasionally did so. Moreover, there was no obvious link between mother and offspring in the repertoire of techniques each displayed. Considering that the mother plays a vital role in the transmission of behaviour to her offspring (McGrew, 1977), this observation suggests that technique employed is likely to be acquired via individual learning rather than social learning, unless the post-weaning environment offers the youngster exposure to alternative influential models.

Social learning and culture in the context of ant-dipping

This study could not distinguish between the different learning mechanism(s), whether social or individual, involved in the acquisition of ant-dipping. Only further detailed studies will be able to elucidate these. Ant-dipping at Bossou is, however, commonly displayed by all able-bodied members of the community and is perpetuated from one generation to the next. Moreover, some chimpanzee communities, such as Mahale, Lopé and Budongo (see Table 6.1), do not exhibit this behaviour, although driver ants are available. Finally, ant-dipping still appears to remain a good example of culture in chimpanzees.

However, although environmentally influenced, might the more intricate details of ant-dipping behaviour, such as tool length and technique employed, be socially learnt? In their study of factors influencing imitation of manipulatory actions in captive chimpanzees, Myowa-Yamakoshi and Matsuzawa (1999) demonstrated that chimpanzees can "imitate" others' actions by reproducing the final state of target objects, or movement of tools and/or target objects, but not action itself. Moreover, other studies indicate that chimpanzees do not readily copy manipulatory actions modelled by human subjects (Nagell *et al.*, 1993; Custance *et al.*, 1995). The only two studies showing that chimpanzees are able to do so were conducted on "enculturated" chimpanzees, i.e. reared by humans in a relatively enriched and stimulating environment (Hayes and Hayes, 1952; Tomasello *et al.*, 1993). This enculturation of chimpanzees at an early age may influence social learning abilities to an extent that is not observed among wild chimpanzees. However, although the results of most studies in captivity suggest that the precise techniques and tool lengths employed by wild chimpanzees during ant-dipping are unlikely to be socially learnt; the general sequence of the behaviour almost certainly involves social learning (Byrne and Russon, 1998).

Conclusion

This study clearly shows the potential usefulness of detailed investigations of ant-dipping across various field sites, particularly Taï and Gombe, so that the influence of prey characteristics, such as aggressiveness and gregariousness, at the nest and while migrating, can further be assessed. Other long-term longitudinal studies are required aimed at dissociating between individual and social learning mechanisms involved in the acquisition of this behaviour and the level at which these may intervene, and at clarifying the individual variations observed. Such investigations would contribute to a re-evaluation of the inter-relationships between the environment, social learning, cognitive abilities and culture in chimpanzees.

Chapter 7

Stick- or stalk-tools at Bossou and the Nimba mountains: Tool-choice, tool-making and function

7.1 Introduction

Stick- or stalk-using behaviours in wild chimpanzees

Stick- or stalk-using behaviour, which features the use of a number of different woody and non-woody raw materials, including stems, shoots, vines and barks, is one of the most prominent and diversified forms of tool-use in chimpanzees in their natural habitat and is a common feature of chimpanzees throughout their range (c.f. McGrew, 1992; Whiten *et al.*, 1999). The majority of these behaviours are aimed at gaining foods otherwise either not easily accessible to the chimpanzee, e.g. termites or bone marrow, or obtainable at a cost, e.g. honey or driver ants (*Dorylus spp.*), while a few are observed in non-feeding contexts (see Table 7.1 and 7.2). The prevalence of each type of behaviour differs by locality (Whiten *et al.*, 1999) (see Table 7.1 and 7.2). The ubiquity of stick- or stalk-using behaviours has been linked to the ready availability of diverse potential materials for tool-making, and when aimed at food sources, to the presence of potential target prey or foods, in all habitats in which chimpanzees live (McGrew and Collins, 1985; Collins and McGrew, 1987).

Table 7.1 Stalk- and Stick using behaviours displayed by chimpanzees in a feeding context across nine long-term field sites (adapted from Tutin *et al.*, 1995b; Whiten *et al.*, 1999, 2001; Humle and Matsuzawa, 2002).

Behaviour	**Bossou**	**Tai**	**Mt Assirik**	**Lopé**	**Gombe**	**Mahale M**	**Mahale K**	**Kibale**	**Budongo**
	Guinea	Côte d'Ivoire	Senegal	Gabon	Tanzania	Tanzania	Tanzania	Uganda	Uganda
Insect-pound (probe used to mash insects)	+	-	?	?	-	-	-	-	-
Perforate (stout stick perforates termite nest)	-	E	?	-	-	-	-	E	?
Dig (stick used as spade to dig termite nest)	+	E	?	-	-	-	-	E	?
Brush-stick (probing stick with brush-end)	-	-	?	H	-	-	-	-	-
Algae-scoop (scoop algae using wand)	C	E	?	?	E	E	E	E	E
Termite-fishing using non-leaf material	-	E	C	?	C	-	C	E	?
Ant-fish (probe used to extract ants)	+	-	?	C	+	C	C	-	-
Ant-dip-wipe (manually wipe ants off wand)	H	-	H	?	C	-	-	-	-
Ant-dip-single (mouth ants off stick)	C	C	?	?	+	-	-	-	-
Fluid dip (use of probe to extract honey or water)	-	C	?	C	C	H	H	H	-
Bee-probe (disable bees, flick with probe)	-	C	?	?	-	-	+	-	-
Marrow, brain, eye pick	-	C	?	?	-	-	-	-	-
Nut emptying (stick used to dislodge kernel from nut)	-	C	?	-	-	-	-	-	-
Bee-probe (used to disable bees at entrance of hive)	-	C	?	?	-	-	+	-	-
Gum collecting (probe used to obtain gum)	+	-	?	?	-	?	?	-	-
Lever open (stick used to enlarge entrance)	-	H	?	C	C	-	-	-	-
Expel/Stir (stick expels or stirs insects)	-	C	?	?	H	H	H	-	-
Pestle-pound (palm petiole used to mash palm heart)	C	-	E	?	-	?	?	?	?

Legend: C: customary, i.e. the behaviour is displayed by all or most able-bodied members of at least one age-sex-class; H: habitual, i.e. the behaviour has occurred repeatedly in several individuals; +: Present, i.e. the behaviour is neither customary nor habitual but is clearly identifiable; -: Absent, i.e. the behaviour has not been recorded and no ecological explanation is apparent; E: the absence of the behaviour can be explained on ecological grounds; ?:: Presence or absence still under query.

Table 7.2 Stalk- and Stick using behaviours displayed by chimpanzees in a non-feeding context across nine long-term field sites in Africa (adapted from Whiten *et al.*, 1999, 2001).

Behaviour	**Bossou**	**Tai**	**Mt Assirik**	**Lopé**	**Gombe**	**Mahale M**	**Mahale K**	**Kibale**	**Budongo**
	Guinea	Côte d'Ivoire	Senegal	Gabon	Tanzania	Tanzania	Tanzania	Uganda	Uganda
Sponge push-pull (stick and sponge tool)	+	+	?	?	+	+	E	E	-
Investigatory probe (probe and sniff)	H	C	?	?	C	H	H	+	-
Branch-hook (branch used to hook branch)	+	-	?	?	-	-	-	-	-
Stepping stick (walking on sticks over thorns)	-	-	?	?	E	?	?	E	E
Nasal probe (clear nasal passage with stick)	-	-	?	?	-	-	+	-	-
Comb (a stem is used to comb through body hair)	-	-	?	?	-	-	-	-	+
Play start (invite play holding stem in mouth)	+	H	?	?	C	C	H	C	H
Drag Branch (drag large branch in display)	H	C	?	?	C	C	C	H	H
Club (strike forcefully with stick)	+	H	?	?	H	+	-	+	-
Fly-whisk (leafy stick used to fan flies)	-	H	?	?	+	-	-	-	H
Self-tickle (tickle self with object)	-	-	?	?	H	-	-	-	-
Aimed-throw (throw object directionally)	C	C	?	?	C	C	-	+	+
Seat Stick (branch from tree used to sit on)	-	-	?	?	E	?	?	E	E

Legend: C: customary, i.e. the behaviour is displayed by all or most able-bodied members of at least one age-sex-class; H: habitual, i.e. the behaviour has occurred repeatedly in several individuals; +: Present, i.e. the behaviour is neither customary nor habitual but is clearly identifiable; -: Absent, i.e. the behaviour has not been recorded and no ecological explanation is apparent; E: the absence of the behaviour can be explained on ecological grounds; ?: Presence or absence still under query.

Three stick- or stalk tool-use behaviours observed at Bossou

Ant-dipping for driver or safari ants (Dorylus spp.)

As described in *Chapter 6*, the chimpanzees use a stick- or stalk-tool, also termed in this context a wand, to obtain *Dorylus* ants, found at a nest site or in migrating columns. When engaging in this tool-use behaviour, the chimpanzee first makes a tool typically by detaching raw material, i.e. vine, tree/shrub or herb, using its teeth and then by stripping any protruding leaves and finally occasionally stripping it off partially or completely of its bark or epidermis. When the wand is inserted into the nest or along the path taken by the ants, the driver ants stream up the tool in attack. The chimpanzee then removes the wand and swiftly ingests the ants gathered on the tool.

Algae-scooping

Spirogyra sp. is a widespread free-floating species of filamentous algae belonging to the division of eukaryotic algae termed the Chlorophyta, i.e. the green algae. Also known as water-silk, mermaids' tresses or pond scum, *Spirogyra* grows to such great numbers that it forms a thick scum on the surface of ponds, as well as streams and lakes (van den Hoek *et al.*, 1995).

Generally, during algae-scooping, the chimpanzee selects a stalk or stick, which it breaks off using its teeth. Then it half-cups one hand at the stem base and strips the leaves off the tool with a swift, upward motion of the hand. A tool more or less devoid of protruding leaves is thus obtained and used for scooping up the algae from the surface of a pond (see Plate 7.1). The tool is most frequently held between the index and the middle finger, the type of fine grip also often observed in cases of ant dipping (see Plate 7.1). The stalk is then inserted, distal end first, into the water, and a gentle swivelling action of the wrist usually follows, scooping up the surface algae (see Plate 7.1). Previous observations of algae-scooping have distinguished between two tool types, i.e. 'smooth' and 'hooked' (Matsuzawa *et al.*, 1996). 'Hooked' tools, that were described as being more pliable than 'smooth' tools, were also distinguished by having small 'hooks' projecting along their sides, i.e. remnants of petiole ends after the leaves had been stripped from the whole length of the tool.

Plate 7.1. Algae-scooping performed by a Bossou chimpanzee (Photos: T. Matsuzawa).

The stalk or stick is then brought up to the mouth. Two techniques may be used to remove the algae from the stick for consumption. Most often the proximal end of the stick is first held in the mouth and the algae are licked off over the length of the tool. More rarely, the chimpanzee gathers the algae off the stick using its free hand and then licks the algae off its hand. Occasionally, the chimpanzee bypasses the use of a tool and collects the algae from the pond surface directly by hand. Since the algae are very filamentous and slimy, these latter two techniques appear less efficient than the former.

It occurs that a tool may be discarded after several dips and a new one is subsequently fashioned or an old one lying nearby is re-used. After use, all the tools are left at the site, and these are sometimes re-used by newcomers. Bossou is the only site where this tool-use behaviour has ever been recorded, although algae was reported to have been eaten by a young adult female, migrant into the Mahale M group, Tanzania (Sakamaki, 1998).

Tool-assisted predation of mammalian prey

Chimpanzees at Bossou were observed on two occasions, once in July 2001 and another time in August 2001, employing stick tools, although unsuccessfully, to expel animal prey, thought to be a tree pangolin (*Phataginus tricuspis*), from a tree hole. The tree pangolin is a small scaly anteater, which is predominantly nocturnal with females being highly sedentary (Kingdon, 1997). They rest during the day in excavated sleeping-holes, which can also include tree hollows. In comparison with other field sites, predatory behaviour of chimpanzees at Bossou has rarely been observed. In fact, few large mammals other than the chimpanzee inhabit the home range of the Bossou chimpanzees. Nevertheless, nine examples of predatory behaviour have been recorded at Bossou since 1976. The prey species involved were mainly tree pangolins (*Phataginus tricuspis*), with one example of feeding on a West African barn owl (*Ciccaba woodfordii*) (Sugiyama, 1981; Humle, pers. obs.).

Examples of tool-assisted predation have been reported or observed elsewhere. However, cases of tool-use during predation or consumption of mammalian prey are rare and limited to inducing prey movement, self-defence, opening skulls to reveal brain, or extracting bone marrow (Plooji, 1978; Goodall, 1986; Boesch and Boesch, 1989). One Mahale chimpanzee was observed using a tool to extract a young bird nestling from a hole of a tree (Takesati, unpubl. data). At this same site, Huffman and Kalunde (1993) reported a young adult female of the M-group using a stick (73 cm long, 29 mm in width and weighing 155 g. and less than 10% stripped) to rouse and capture a squirrel hiding in the narrow hole of a tree. Other instances of chimpanzees poking a stick into the hole of a tree have been observed at Mahale and Mt Assirik, Senegal; however, it was not determined what exactly they were searching for (cf. Huffman and Kalunde, 1993). Huffman and Kalunde (1993) suggested that the inaccessibility of the prey within a tree hole and the likelihood of being bitten while attempting to extract the prey directly by hand may explain why chimpanzees have developed the use of expelling or rousing tools.

Tool-making and tool-choice among wild chimpanzees

Several studies of tool-making and tool-choice in chimpanzees have indicated that they choose and/or adapt their tools to specific tasks. A tool will be herein defined as "a detached, inanimate object used to facilitate acquisition of a goal" (McGrew *et al.*, 1979) and tool-making as the modification of the shape and size of an object to produce a tool (Boesch and Boesch, 1990).

Boesch and Boesch (1983) showed that Taï chimpanzees in Côte d'Ivoire selected the type and weight of tools for cracking nuts in accordance with the physical features of the species of nuts being opened. In another study, Boesch and Boesch (1990) compared the sizes of sticks fashioned for four types of tool-use to test whether chimpanzees fashioned tools specifically for particular tasks. They found that sticks for extracting bone marrow and emptying nuts were significantly shorter than sticks made for ant-dipping and honey fishing, and that tools used for ant-dipping and honey fishing also differed significantly in length and diameter. In addition, 93.5% of these tools were fashioned before initiating the tool task, suggesting that the chimpanzees were adapting their tool-making to the task to be undertaken, with an understanding of the relations between objects and what the task entailed (Boesch and Boesch, 1990).

This conclusion is further supported by findings from Lopé, Gabon. In their study of tool-use, Tutin *et al.* (1995b) recovered 144 tools used upon three different species of bees and two different species of ants. Comparing the tools used for ant fishing with those used to extract honey from the hives of African honey bees (*Apis millefera*) and the large stingless bees of the species *Meliponula nebulata*, they found that all three differed significantly in length. However, there was no difference in proximal or distal diameters of the tools. The differences in length were proposed to reflect variations in hive size and/or in the target prey species' aggressiveness. They noted that 142 of the 144 tools recovered were woody tools, one third were partially or completely devoid of bark, and most were frayed at one or both ends, creating a brush end (Sugiyama, 1985). However, partial or complete bark stripping was argued to be a by-product of the removal of leaves and small side branches or even of the wear of the tool against the entrance of the nest. Thus, bark stripping was not considered to be an intentional modification of the tool. Moreover, no direct benefit of such tool modification could be discerned. Brush manufacture, although not directly observed, was thought, on the other hand, to be the result of deliberate chewing. Tested by humans, these 'brush tools' were effective for fishing *Camponotus brutus* ants and were suggested to facilitate the soaking up of honey. Tutin *et al.* (1995b) concluded that overall the stick tools used at Lopé differed little between prey species in terms of the raw materials used and the degree of bark stripping and fraying at the end(s). Tool-length was adapted to the specific tool-task in which the chimpanzees were involved.

Mahale chimpanzees fish for arboreal wood-boring ants (three species of *Camponotus spp.*) with tools (Nishida, 1973; Nishida and Hiraiwa, 1982). During ant-fishing at Mahale, 76% of the raw materials were modified twice and 5.8% three times before being used as a tool (Nishida and Hiraiwa, 1982). In Taï, the proportions were reversed, 5.1% of the raw materials were modified twice and 93.4% three times for sticks used in extracting bone marrow, emptying nut shells, ant-dipping or honey-fishing (Boesch and Boesch, 1990). Clearly, these tool modifications cannot be directly compared since the tools were not made for exactly the same purposes at the two sites. However, with the exception of ant-dipping at Taï, all of the stick- or stalk-tools at Taï and Mahale were made to be inserted into holes. These tools had to conform to similar physical requirements of straightness, limited length, and thickness, depending on the tool task undertaken (Boesch and Boesch, 1990).

Descriptions of the raw materials for tools used in fishing for wood-boring ants (Nishida and Hiraiwa, 1982) indicate that Mahale chimpanzees are more selective than Taï chimpanzees, who rarely sought twigs beyond arm's reach for ant-dipping (Boesch and Boesch, 1990). At Mahale, a strong selectivity for vine species was shown for ant-fishing (Nishida and Hiraiwa, 1982). Similarly, Lopé chimpanzees almost exclusively used woody materials as tools to feed on ants or honey, thereby showing high selectivity at the plant type level, i.e. vine, tree/shrub or herb (Tutin *et al.*, 1995b). However, none of the above mentioned studies have investigated in detail the relationship between plant species availability and tool-selection. The only study to date which has focused on this issue is that of McBeath and McGrew (1982) which demonstrated that tool selection for termite fishing probes at Mt Assirik, Senegal, mirrored the availability of the best raw materials within a 5-metre radius of the termite mounds.

To explain the differences in tool-selectivity and tool-making between Mahale and Taï, Boesch and Boesch (1990) hypothesised that an increase in the sophistication of tool-making may permit less selectivity for the raw material, making individuals less dependent on the environment. However, these differences could also possibly reflect variation in the predictability of the required attributes of the tool for the task to be performed. Indeed, Nishida (1973) pointed out that the difference in the types of tools used for ant fishing at Mahale, which differ in raw material used and degree of manufacture, is conditioned by the size of the nest's entrance of the arboreal ants fished for. In addition in contrast with Taï, where only 6.5% of tools were modified further during tool-use (Boesch and Boesch, 1990), at Mahale the chimpanzees continued to modify the tool progressively during ant-fishing, i.e. testing it after each modification, until it became adequate (Nishida and Hiraiwa, 1982). This difference suggests that chimpanzees at Mahale were less able to foresee the tool requirements before initiating ant-fishing than chimpanzees enacting the stick- or stalk-use behaviours observed at

Taï. However, Boesch and Boesch (1990) failed to report if there were any intra-site differences in frequency of tool modification after first use between these tool-use behaviours.

Tool-making in ant-dipping behaviour

In the context of ant-dipping, at Bossou and at Tenkere, Sierra Leone, bark was removed from at least two thirds, and usually the whole length of the wands used (Sugiyama, 1995a; Alp, 1993). In contrast, although not quantified, at Taï and Gombe bark-stripping of tools was only occasionally seen (McGrew, 1974; Boesch and Boesch, 1990). Moreover, at Tenkere, 80% (N=4) of the tools recovered were frayed at one end by at least 10 mm (Alp, 1993) and 60% (N=3) also exhibited such fraying at Bossou (Sugiyama *et al.*, 1988). However, the sample size at these two sites was very small and these results should therefore be interpreted with caution.

At Mt Assirik, Senegal, most of the ant-dipping tools found came from a *Garcinia ovalifolia* tree growing only 3m from the dipping site (Baldwin, 1979). One tool, the longest, was made of a vine, and one was a dead stick, which could not be identified (Baldwin, 1979). Although selection of raw material for use as wands has not systematically been detailed for each site where ant-dipping has been observed, some differences have emerged. At Taï, chimpanzees used predominantly twigs as tools (Boesch and Boesch, 1990), while at least half of the tools found at Bossou and at Kalinzu, Uganda, were made from terrestrial herbaceous vegetation (THV) (Sugiyama, 1995a; Hashimoto *et al.*, 2000).

Tool-choice and -manufacture in a cultural context

Considering that chimpanzees in the wild adapt their tool-selection and -manufacturing to the task they are performing, the question then arises as to why we see differences in these processes and their outcome across different chimpanzee communities engaged in the same tool-task involving the same target food or species, e.g. ant-dipping or termite fishing. Several authors have proposed that these differences reflect cultural trends within communities (McGrew *et al.*, 1979; Boesch and Boesch, 1990; McGrew, 1992; Boesch, 1996b, Hashimoto *et al.*, 2000). The extent to which social learning is involved in tool-choice and tool-making in wild chimpanzees remains unclear and relatively unexplored due to the difficulties in identifying social transmission mechanisms in uncontrolled observational settings.

However, it appears that the tool-making process is closely associated with the predictability of the required attributes of the tool for the specific task to be performed. This aspect will be reflected in further modifications of the tool during the course of its use as observed at Mahale for ant-fishing (Nishida and Hiraiwa, 1982). Moreover, as proposed by Boesch and Boesch (1990), it seems that some trade-off between tool-making and tool-choice may occur. On the one hand, chimpanzees might spend time carefully selecting the most appropriate material to produce a tool, which then requires little further modification before initiating the task. On the other hand, material selection may be relatively indiscriminate and more adjustments to the raw material are then required for the resulting tool to be made useful before embarking on the tool task. Might such tool-producing strategies be socially transmitted and represent community-wide patterns, or do they simply rather reflect individual learning processes generating convergence due to environmental constraints acting upon item selection and the tool manufacturing process?

7.2 Aims

-Tool-selectivity and manufacture for ant-dipping at Bossou will be analysed and discussed on the basis of findings from other chimpanzee field sites.

-Stick- or stalk-tools employed in algae-scooping and in prising animal prey from tree holes will also be explored, looking at material-selection as well as tool-manufacture.

-These three stick- or stalk-tool behaviours will be compared on the basis of plant material selectivity and the observed tool manufacturing patterns characteristic of each of those tasks.

-This section will compare the tools employed during feeding on driver ants (*Dorylus* spp.) between Bossou and the two Nimba sites and speculate on the differences observed and their cultural implications.

7.3 Methods

Most ant-dipping and algae-scooping tools, and all expelling/prising tools from Bossou were collected immediately after these behaviours were observed and after departure of the chimpanzees, while all driver ant feeding tools from the Nimba sites were discovered after the occurrence of the behaviour. Occasionally, algae-scooping and ant-dipping tools at Bossou were found during daily tracking of the chimpanzees or after arriving at a site where chimpanzees had previously been heard.

Both ant-dipping and algae scooping tools were collected over four study periods: July-October 1997; July-September 1999, June-September 2000 and June-September 2001; whereas prising/expelling tools were only gathered during the latter study period.

At the Nimba sites, ant-dipping tools were most often found in association with deserted driver ants' nests during daily tracking of the chimpanzees. These tools were retrieved between June-September 2000 and June and September 2001. Traces of driver ants were discovered in chimpanzee faeces at both these sites, confirming that the chimpanzees consumed the ants, although no direct observations of this behaviour were ever made. The artefacts retrieved were attributed to the chimpanzees based on indicators of chimpanzees' presence, i.e. presence of faeces, nests, foot, and/or knuckle prints (McGrew *et al.*, 1979). Prominently bent-over saplings were also used as markers of chimpanzees' presence in the driver ant feeding context (see Plate 7.2). As at Bossou, these would most likely be used by chimpanzees to position themselves above ground in order to minimise exposure to the biting ants (refer to *Chapter 6*).

Plate 7.2. Photo of typically bent-over sapling found beside driver ants' nests after chimpanzees have been ant-dipping at the site.

For ant feeding, only tools that bore traces of use and modification were collected. They all protruded from the ants' nest or were lying within 2m of the nest site. The traces of use included: 1) indication of earth and wear, e.g. fraying, at the tip(s) of the stalk or stick; 2) indications of biting at both or one end of the stick or stalk; 3) stick or stalk usually stripped of leaves and possibly also bark or epidermis (*sensu* McGrew *et al.*, 1979). Any sticks or stalks for which use as a tool could not be ascertained were ignored. Sticks or stalks were only accepted as being used as tools based on a consensus between myself and a minimum of two guides.

For algae-scooping at Bossou, all tools retrieved 'indirectly' were found in small ponds or within 2 m from the edge of the water surface where *Spirogyra* algae were found.

From the recovered tools, data on length (cm), width at mid-point (mm), the species of plant used (whenever possible), the plant type, i.e. tree, vine or herb, the percentage of bark removal, the presence of fraying of the ends of the tool (at least 10 mm long) and notes on whether the tool was broken or not, were recorded. For ant-dipping tools, the use of one or both ends was also noted. This was indicated by traces of earth and wear at the end(s) or confirmed via direct observation. Additionally, data on weight (g.) and shape were recorded for the expelling/prising tools. Prior to 1999, data on tool width and end use for ant-dipping and tool width for algae-scooping were not systematically collected.

Ad Lib. video and observational recordings of the three tool-use behaviours allowed accurate observations of tool-making. Thus data on 24 ant-dipping, 6 algae-scooping and 2 tool-assisted predation sessions were gathered. Four separate components to tool-making were discerned: 1) detach from substrate with teeth or hands; 2) cutting to a specific length; 3) removing leaves and/or bark stripping and 4) chewing the end of the tool with teeth (fraying) (cf. Boesch and Boesch, 1990).

7.4 Data Analysis

The data were checked for normality using a normality probability plot and a Kolmogorov-Smirnov test. Non-parametric or parametric tests were employed as appropriate in the analysis of the data.

For analysis of aspects of tool manufacture, i.e. bark stripping, brush-end and end use, depending on plant material used, a chi-square test was used. For algae-scooping tools, analysis was also performed separately for tool type, i.e. 'smooth' and 'hooked', as previously distinguished in observations of algae-scooping (Matsuzawa *et al.*, 1996).

7.5 Results

Within community comparison of stick- or stalk-tools across three tool-use behaviours

Ant-dipping tools

Regarding choice of material for ant-dipping, Bossou chimpanzees used 189 tools from 34 known species of plants belonging to 19 different families (see Table 7.3). Fourteen tools could not be identified. Only five species of plants accounted for 52.9% of all the tools used (see Table 7.3), and tools made from terrestrial herbaceous vegetation (THV) comprised 49.5% of the total sample.

It is not known whether the chimpanzees are selective regarding materials for ant-dipping, since no quantitative assessment of the relative availability of the plant species used was carried out where the tools were retrieved. However, the five most represented species among the tools recorded are some of the commonest plant species available in the habitat, suggesting that there may be little or no selectivity at the species level.

With regards to tool manufacture, excluding cases where tools were re-used, 98.8% of the tools (N=87) were modified prior to ant-dipping. Indeed, all tools were removed of any leaves and were reduced in length either from one or both end(s) before engaging in ant-dipping. In addition, 38.1% of all the tools collected were partially stripped and 18.1% were completely stripped of their outer coating, i.e. bark or epidermis. Of all the tools partially or entirely stripped, 86.2% were made from woody materials. Therefore stripping tended to occur with species that possessed bark. Moreover, no herbaceous tools were stripped completely of their epidermis; instead they were only ever partially stripped. Indeed, half of these stripped herbaceous tools (N=4) were peeled of less than 20% of their epidermis, and two were stripped of half of their outer coating, while two were no more than 90% stripped. Of all the direct observations of bark stripping (N=52), 32.7% took place after the first basic modifications were made (i.e. detaching the raw material from substrate, removing any leaves and reducing tool length), and ant-dipping was in progress. Therefore, bark stripping was not necessarily an artefact of leaf removal, but also purposely performed to modify the tool.

Just over 5% of the tools were found to have a brush-end. All of these tools were made from herbaceous material, which is the weakest material used in ant-dipping. Only one observation of intentional tool fraying was observed in 106 instances of tool-making. This behaviour was performed by an adolescent male, who interrupted a dipping bout to nibble the end of the tool with his teeth, which resulted in fraying the raw material over 6 cm, thus generating a brush-end as defined by Sugiyama (1985). Therefore, the possibility that brush-ends could have resulted from tear and friction caused by the repeated backward and forward movement of the tool during dipping cannot completely be discounted.

Just over 40% of the tools recovered were used at both ends. End use was not independent of plant type material used (Chi-square test: $\chi^2(2, N=189)=6.079$; $p<0.05$). Indeed, only 30.4% of herbaceous wands were used at both ends, while 40.9% of vine-based tools and 51.6% of tree-based tools were employed at both ends. This difference in end use could be attributed to greater variability in width between the distal and the proximal ends of the tool, especially among THV tools, which make them less suitable for use at both ends. Due to lack of quantitative data on proximal and distal widths, this point cannot be investigated further. However, the thicker end of the tool was commonly the end held, while the thinner one was inserted into the mass or column of ants.

Table 7.3 Plant species used as ant-dipping tools at Bossou (In ***italic bold***: the five most used species).

Species used	**Family**	**Plant type**	**Freq.**	**%**
Maranthacloa sp.	Marantaceae	Herb	28	**14.8**
Aframomum sp.	Zingiberaceae	Herb	24	**12.7**
Hippocratea paniculata	Celastraceae	Vine	17	**9**
Alchornea cordifolia	Euphorbiaceae	Tree	16	**8.5**
Eupatorium sp.	Compositeae	Herb	15	**7.9**
Thaumatococus daniellii	Marantaceae	Herb	8	4.2
Premna hispida	Verbenaceae	Tree	7	3.7
Vismia guineensis	Hypericaceae	Tree	6	3.2
Spondias citera	Anacardiaceae	Tree	5	2.6
Aurilia latifolia	Zingiberaceae	Vine	5	2.6
Hypselodelphys poggeana	Marantaceae	Herb	4	2.1
Megaphrynium macrostachyum	Marantaceae	Herb	4	2.1
Rhaphiostylis beninensis	Icacinaceae	Tree	4	2.1
Museanda erithrophylla	Rubiaceae	Vine	4	2.1
Aningueria altissima	Sapotaceae	Tree	3	1.6
Glyphae brevis	Tiliaceae	Tree	3	1.6
Albizia zygia	Mimosaceae	Tree	2	1.1
Blighia unijugata	Sapindaceae	Tree	2	1.1
Harungana madagascariensis	Hypericaceae	Tree	2	1.1
Landolphia dulcis	Apocynaceae	Vine	2	1.1
Manihot sp.	Euphorbiaceae	Herb	1	0.5
Polycephalium aureum	Icacinaceae	Herb	1	0.5
Bridelia ferruginea	Euphorbiaceae	Tree	1	0.5
Carapa procera	Meliaceae	Tree	1	0.5
Elaeis guineensis	Palmeae	Tree	1	0.5
Ficus exasperata	Moraceae	Tree	1	0.5
Khaya ivorensis	Meliaceae	Tree	1	0.5
Monodora tenuifolia	Annonaceae	Tree	1	0.5
Piptadeniastrum africanum	Mimosaceae	Tree	1	0.5
Allophylus africanus	Sapindaceae	Tree	1	0.5
Myrianthus libericus	Moraceae	Tree	1	0.5
Myrianthus serratus	Moraceae	Tree	1	0.5
Phyllanthus sp.	Euphorbiaceae	Vine	1	0.5
Uvaria afzelii	Annonaceae	Vine	1	0.5
Unknown			14	7.4
TOTAL			**189**	**100**

The mean length of ant-dipping tools was 53.7 cm (N=189; SD=21.01; range: 23-154 cm) and the mean width was 5.2 mm (N=152; SD=2.23; range: 2-15 mm). There was a significant positive correlation between tool length and tool width across all three plant types used (Herb: $R_s=0.513$; N=69; $p<0.001$; Vine: $R_s=0.467$; N=22; $p<0.05$; Tree: $R_s=0.749$; N=60; $p<0.001$).

Tool length and width generally differed significantly between plant types used for making wands (Kruskal-Wallis test: Length: $\chi^2(2, N=188)=12.407$; $\rho<0.01$; Width: $\chi^2(2, N=151)=33.427$; $\rho<0.001$). Dunn's *post hoc* test suggested though that there was no significant difference in tool length between herbaceous and woody tools. In *Chapter 6*, I showed that ant condition, i.e. at the nest or migrating, strongly influenced tool length during ant-dipping. Therefore, differences in tool length and width across plant types were analysed for each of these two conditions separately. No significant difference in tool length emerged across plant types used under either condition (Kruskal-Wallis test: Nest: $\chi^2(2, N=85)=2.543$; *n.s.*; Migrating: $\chi^2(2, N=62)=2.804$; *n.s.*) (see Table 7.4 and Fig. 7.1). Although no difference in tool width emerged while dipping on migrating ants (Kruskal-Wallis test: $\chi^2(2, N=47)=1.139$; *n.s.*), there were significant differences in tool width between the three plant types used at the nest (Kruskal-Wallis test: $\chi^2(2, N=81)=13.380$; $\rho<0.01$) (see Fig. 7.2). Dunn's *post hoc* test confirmed differences in tool width between herb and vine tools and between herb and tree/shrub tools at the nest site. Median width for herb tools was significantly greater (see Table 7.4).

Table 7.4. Summary statistics of length (cm) and width (mm) for ant-dipping wands at Bossou overall and under both ant conditions and of tool width to length ratio (mm/cm) for the three plant types used.

Variable	Plant Type	Condition	N.	Mean	SD	Median	Range
Length (cm)	**Herb**	Overall	93	56.0	19.7	51.9	23-126
		Nest	49	64.4	20.0	62.0	31-126
		Migrating	20	42.2	13.5	37.3	23-69
	Vine	Overall	26	41.4	10.2	39.45	24-65
		Nest	4	45.9	10.1	45.1	37-57
		Migrating	14	41.9	8.3	39.9	30-64
	Tree	Overall	69	55.2	24.3	47.5	23-154
		Nest	32	63.8	28.5	58.0	26-154
		Migrating	28	47.7	14.6	46.3	23-89
Width (mm)	**Herb**	Overall	69	6.0	1.6	6.0	3-9
		Nest	49	6.5	1.4	7.0	4-9
		Migrating	12	4.3	1.3	4.0	3-7
	Vine	Overall	22	3.6	1.6	3.0	2-9
		Nest	4	3.5	0.6	3.5	3-4
		Migrating	10	3.9	2.3	3.5	2-9
	Tree	Overall	60	4.9	2.6	4.0	2-15
		Nest	28	5.9	3.1	5.0	2-15
		Migrating	25	4.1	1.3	4.0	2-7
Width/Length (mm/cm)	**Herb**	Overall	69	0.106	0.036	0.103	0.04-0.24
	Vine		22	0.089	0.029	0.086	0.05-0.14
	Tree		60	0.090	0.031	0.087	0.05-0.23

Possible tool-making adaptations to the respective properties of each plant material used were explored by looking at the width to length ratio of the tools. There was a significant difference across the three plant types in width to length ratio (Kruskal-Wallis test: $\chi^2(2, N=151)=9.765$; $\rho<0.01$) (see Fig. 7.3). Dunn's *post hoc* test indicated that tools made from tree/shrub substrates had a significantly smaller width to length ratio than tools made of herbaceous material ($\rho<0.05$); no significant difference between the means of the other plant types was found (see Fig. 7.3). Considering that woody materials, such as trees or shrubs, are more rigid and stronger than herbaceous ones, this result suggests that the chimpanzees making a tool from THV tend to choose thicker materials. As for vine materials, their flexibility and flimsiness is more variable, depending on the plant species. Indeed, some species of vines may be more similar to rigid tree materials since they are characterised by stiff woody stems, while some vines more closely resemble flimsier THV plants and possess more slender and flexible stems. Therefore, no significant difference in width to length ratio was uncovered between either tree- or herb-based tools and vine ones, due to the greater variance among these latter materials in their physical characteristics (see Fig. 7.3).

As for the number of modifications made to each new tool, 4.6% were modified twice, i.e. detached from substrate with teeth or hands and cut to a specific length, and 95.4% three times, where additionally leaves and/or bark were stripped off the tool, before initiating the behaviour. After a new tool was fashioned, 3.7% of the tools were subsequently further modified length-wise, while 7.4% underwent some reduction in width via bark stripping after use, and 0.7% were deliberately frayed at the tip. Just over 17% of tools were re-used by other members of the community and only one of these underwent further modification, i.e. shortening.

Finally, only 3.7% of the ant-dipping tools retrieved were broken (n_{Herb}=4; n_{Tree}=2 and n_{Vine}=1). These broken tools did not diverge significantly in terms of length, width or width to length ratio from unbroken ones (Length: Mann-Whitney U-test: z=-0.595; *n.s.*; Width: Mann-Whitney U-test z=-0.338; *n.s.*; Width/Length: Mann-Whitney U-test z=-0.524; *n.s.*).

Fig. 7.1. Boxplot (thick horizontal line: median; normal horizontal lines: mark quartiles 1 (below) and 3 (above); short horizontal lines: maximum and minimum) of tool length (cm) under the two ant conditions for each of the three plant materials used.

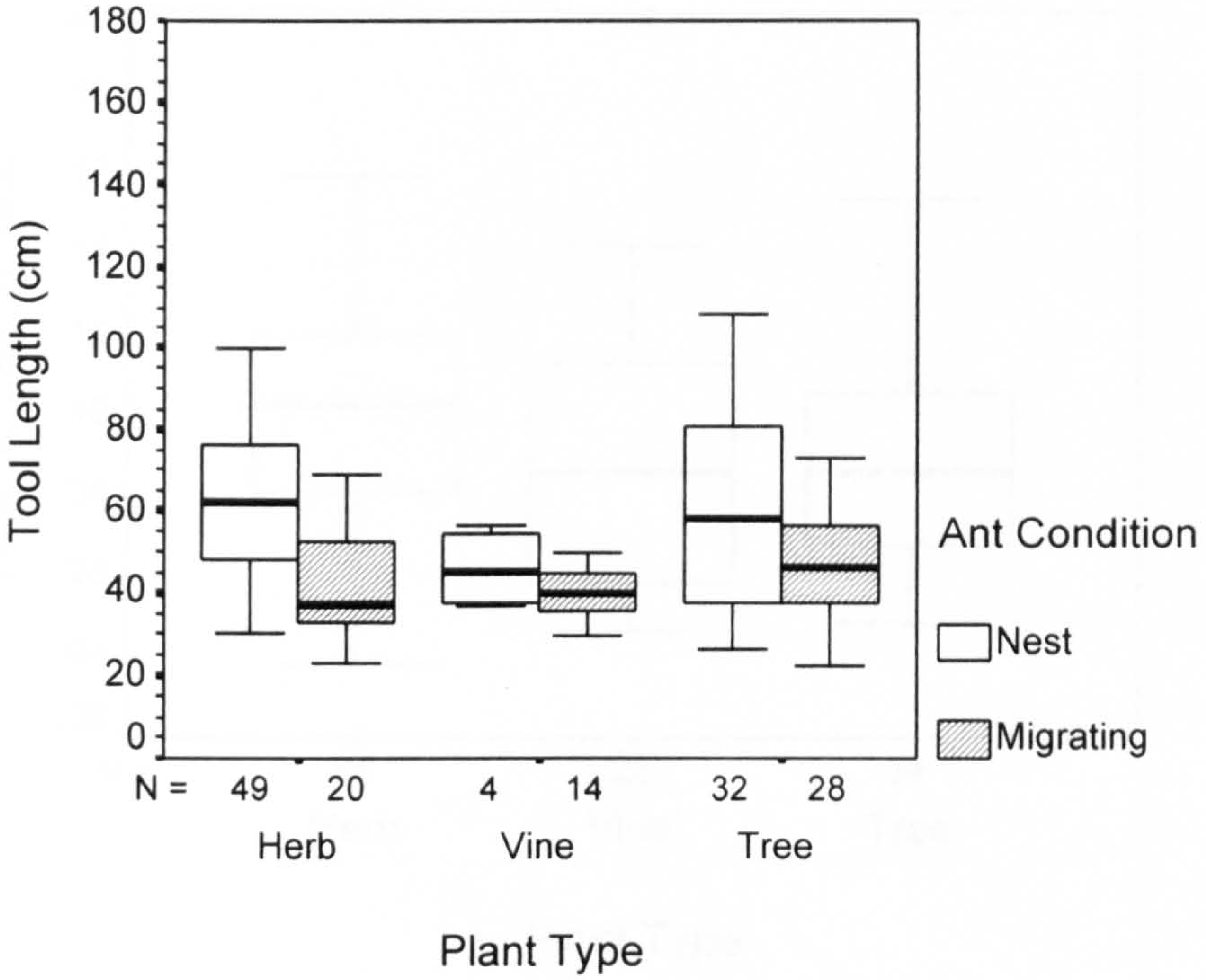


Fig. 7.2. Boxplot of tool width (mm) under the two ant conditions for each of the three plant materials used.

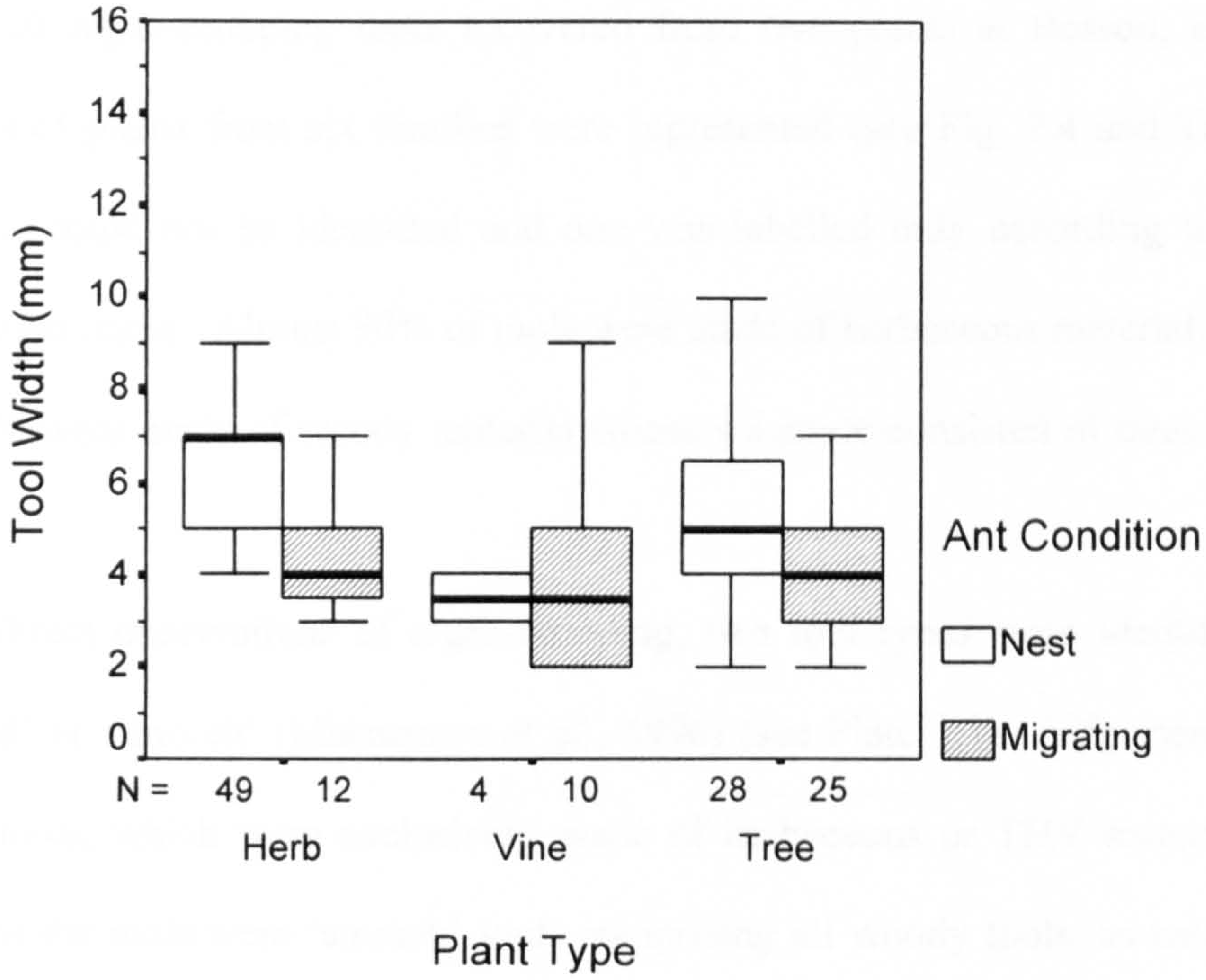
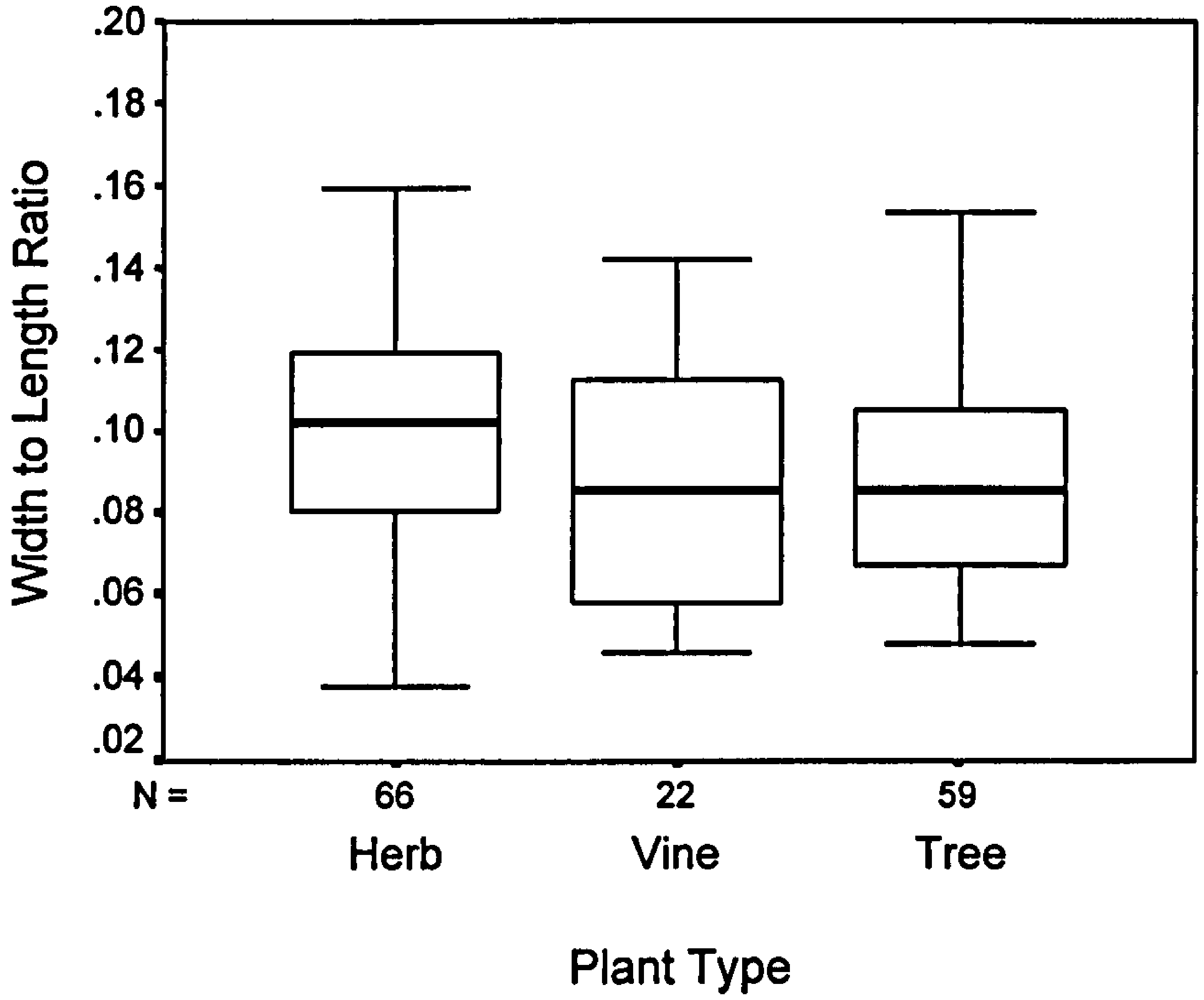


Fig. 7.3. Boxplot of tool width to length ratio (mm/cm) for each of the three plant materials used.



Algae-scooping tools

In the 108 algae-scooping tools recovered from five ponds at Bossou, eight different species of plants from six families were represented (see Fig. 7.4 and Table 7.5). Four tools could not be identified and one was labelled only according to its 'Manon' vernacular name. Almost 90% of tools were made of herbaceous material; the remaining 10.2% were made of woody material whose substrate consisted of trees and shrubs.

During direct observations of algae-scooping, two tool types were identified, labelled 'hooked' or 'smooth' (Matsuzawa *et al.*, 1996) (see Plate 7.3). Fifty percent were 'hooked' tools, which were exclusively made of herbaceous or THV materials. The other half of the tools were 'smooth' tools comprising all woody tools, as well as herbaceous ones, but including different species to those used as 'hooked' tools (see Table 7.5).

Fig. 7.4. Map of Bossou area with sites where algae-scooping has been observed and evidence recorded.

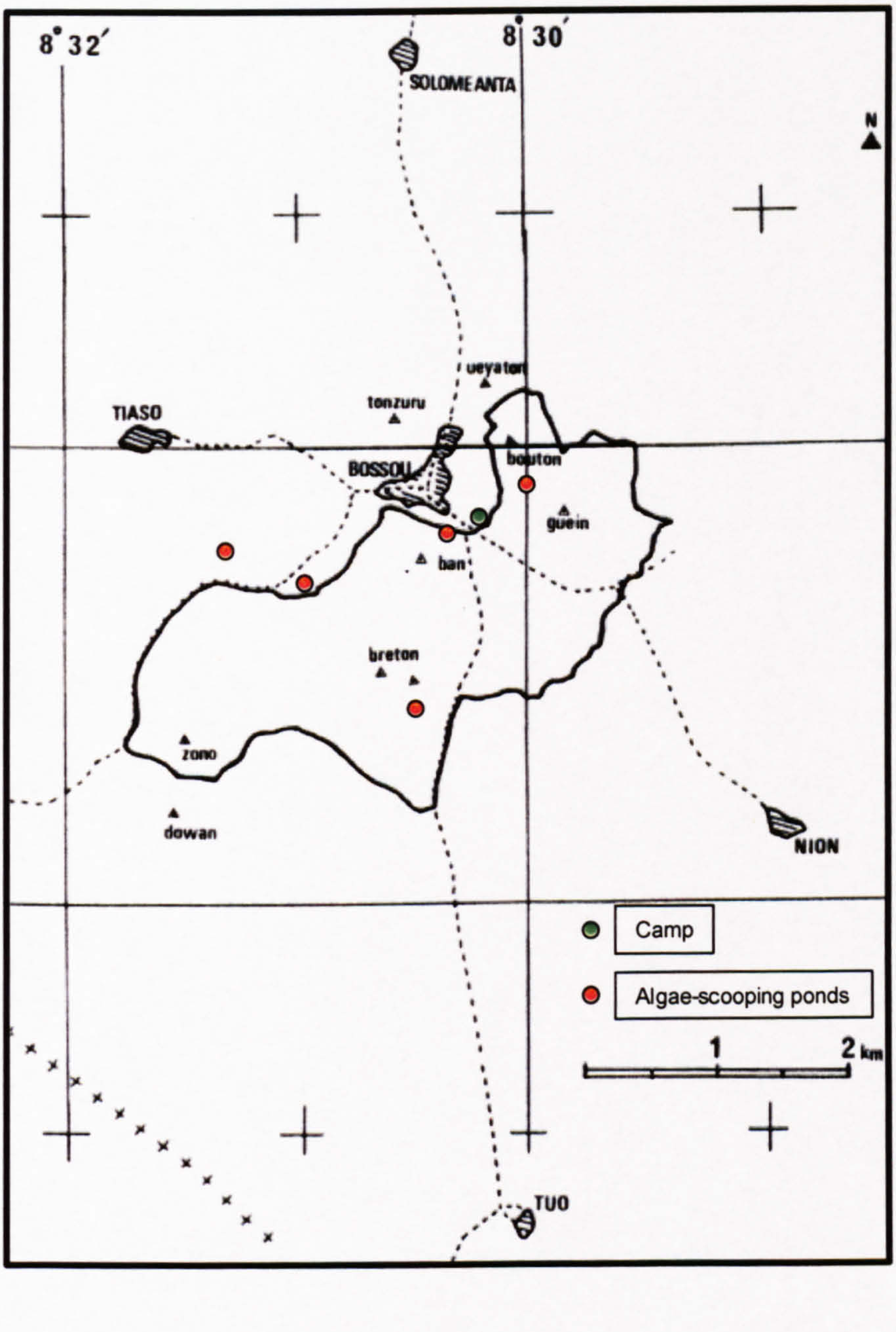
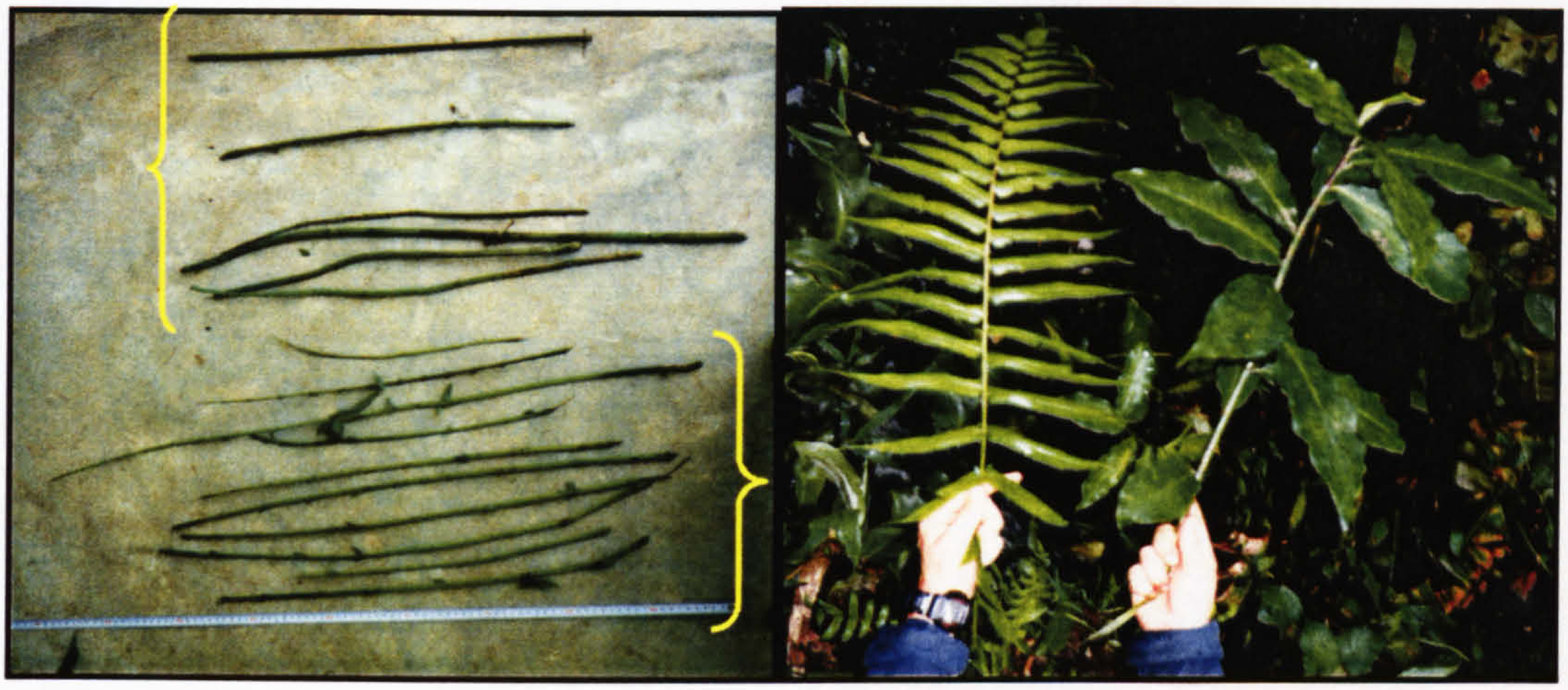


Plate 7.3. Algae-scooping tools from Bossou, illustrating the two tool types uncovered (Above: 'Smooth'; Below: 'Hooked') and the two commonest plant species employed (Left: *Tectaria aureum*; Right: *Costus afer)*.



Two species of herbaceous plants (*Costus afer* and *Tectaria aureum*) accounted for 76.8% of all the tools found (see Table 7.5 and Plate 7.3). The limited number of plant species used for algae-scooping may suggest that the Bossou chimpanzees are extremely selective in terms of the species and the type of material used. However, herbaceous plants are particularly abundant beside the ponds where algae-scooping occurs, and these plants are usually more readily accessible than woody materials, which are often absent. Moreover, the diversity of plants around these ponds is usually low and uniform. This might explain why so few plant species were used, why an overwhelming majority of the tools were produced from herbaceous materials and why the two most abundant species were dominant in the sample.

Table 7.5 Plant species used as algae-scooping tools (In ***italic bold***: the two most employed species).

Species used	Family	Plant type	Tool type	Frequency	%
Tectaria aureum	Icacinaceae	Herb	'Hooked'	50	**46.3**
Costus afer	Zingiberaceae	Herb	'Smooth'	33	**30.5**
Alchornea cordifolia	Euphorbiaceae	Tree	'Smooth'	7	6.5
Eupatarium sp.	Compositeae	Herb	'Hooked'	6	5.6
Triumfetta cordifolia	Tiliaceae	Tree	'Smooth'	4	3.7
Polypodium aureun	Polypodiaceae	Herb	'Smooth'	2	1.8
Sida sp.	Malvaceae	Herb	'Hooked'	1	0.9
Siolongolo (vernicular Manon)		Herb	'Smooth'	1	0.9
Unknown		Tree	'Smooth'	4	3.8
TOTAL				**108**	**100**

The mean length of algae-scooping tools was 55.6 cm and the mean width was 6.9 mm (see Table 7.6). As with ant-dipping tools, there was a significant correlation between length and width of tools used for algae-scooping ($R_s = 0.324$; N=87; $p<0.01$) (see Fig 7.5 and Fig. 7.6). However, looking separately at the two types of tools observed, i.e. 'hooked' and 'smooth', neither analysis yielded a significant correlation between width and length ('Hooked': $R_s=0.205$; N=39; *n.s*; 'Smooth': $R_s=0.290$; N=46; *n.s.*) (see Fig. 7.5). With regards to plant type used, THV tools showed a significant positive correlation between length and width ($R_s=0.335$; N=76; $p<0.01$), whereas no such correlation emerged for woody tools ($R_s=0.315$; N=11; *n.s.*) (see Fig. 7.6).

No significant difference was found in the length (Mann-Whitney U-test: z=-0.803, *n.s.*) or width (Mann-Whitney U-test: z=-0.116, *n.s*) of herbaceous versus woody tools. Similarly, there was no difference in width to length ratio between tools made from these two plant materials (Mann-Whitney U-test: z=-0.211, *n.s.*) (see Table 7.6). Thus, overall, no significant difference between length and width was found between tools of different plant types. Moreover, no apparent compensatory modifications were seen for flimsier, herbaceous algae-scooping tools, although a significant positive correlation between length and width was observed for tools based on such plant material.

Table 7.6 Descriptive summary of tool length (cm) and width (mm) variables overall, for the two tool types and the two plant types used in algae-scooping.

Tool/Plant type		**Length (cm)**	**Width (mm)**
	N	108	87
	Mean	55.64	6.87
Overall	SD	14.34	4.55
	Median	53.5	6
	Range	25-105	3-32
	N	53	39
	Mean	52.78	6.31
'Hooked' Tools	SD	14.94	6.03
	Median	50	5
	Range	25-94	3-32
	N	53	46
	Mean	58.53	7.48
'Smooth' Tools	SD	13.5	2.78
	Median	55	7
	Range	41-105	3-21
	N	11	11
	Mean	58.37	6.18
Tree-based	SD	13.19	1.6
	Median	54.1	6
	Range	42-80	3-8
	N	97	76
	Mean	55.32	6.97
THV-based	SD	14.5	4.82
	Median	53	6
	Range	25-105	3-32

Fig. 7.5. Scatterplot of tool length versus tool width depending on tool type.

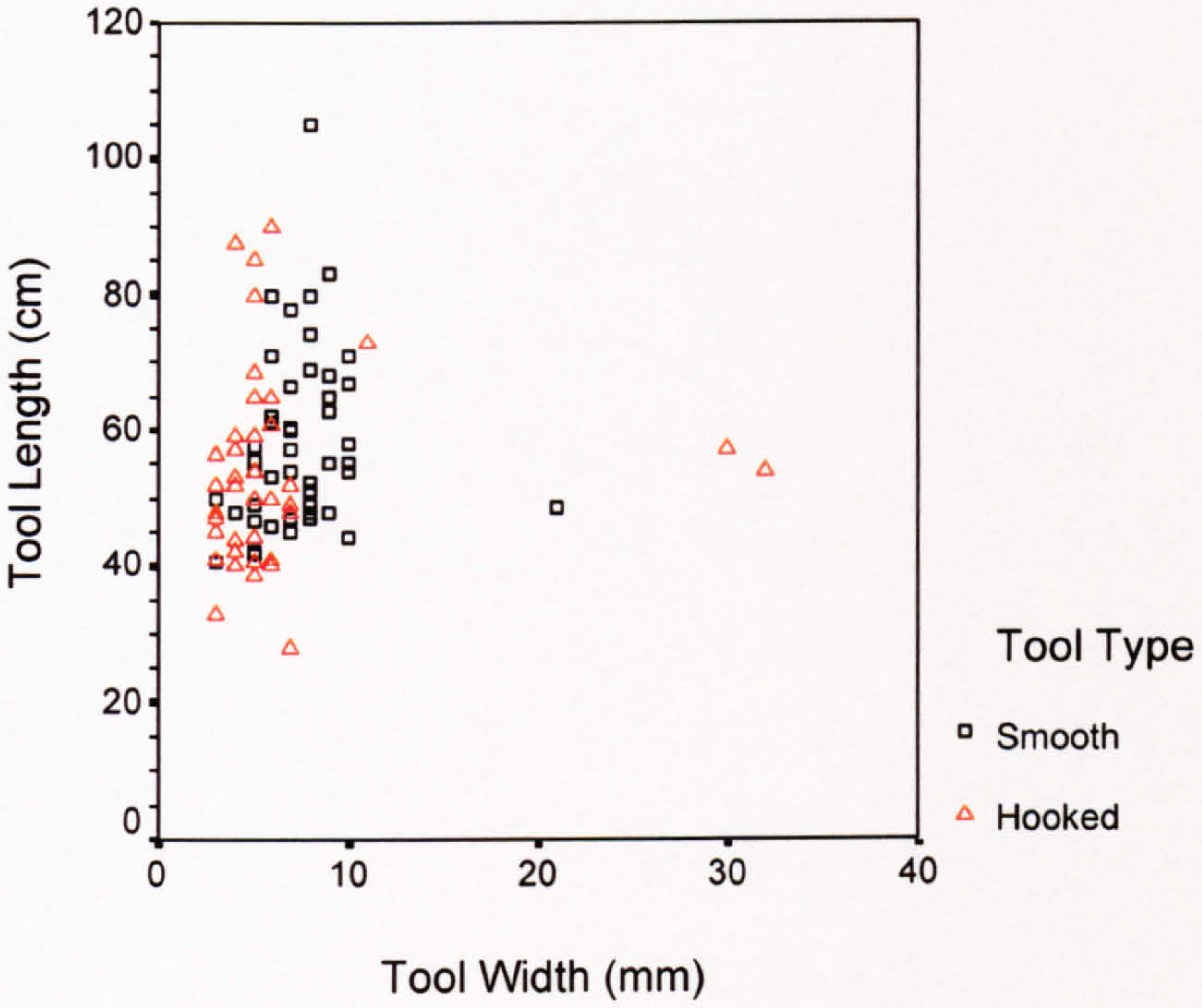
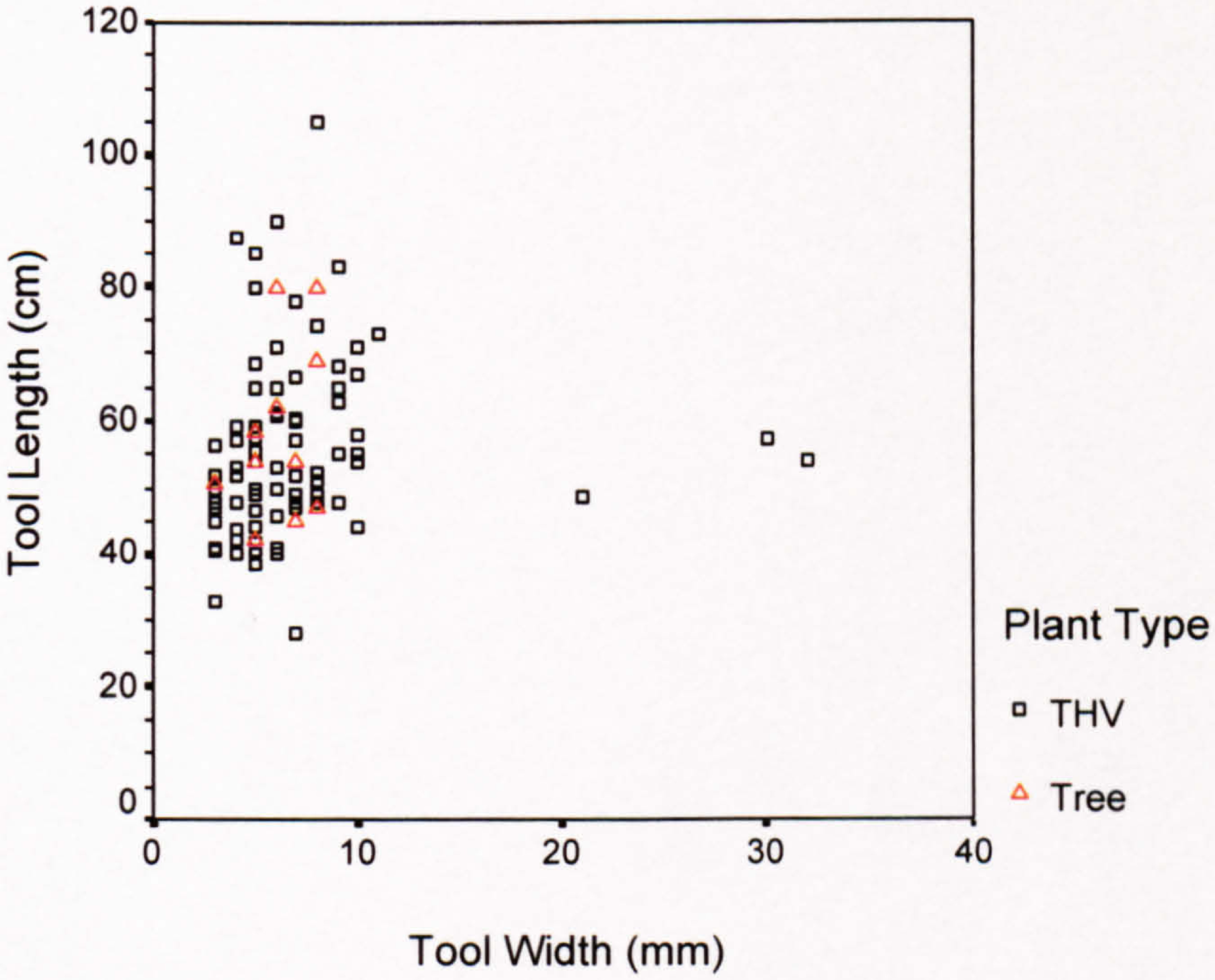


Fig. 7.6. Scatterplot of tool length versus tool width depending on plant type.



'Smooth' tools differed from 'hooked' tools, by their significantly greater length and width (Length: Mann-Whitney U-test: z=-2.494; p<0.05; Width: Mann-Whitney U-test: z=-4.424, p<0.001) (see Table 7.6). In addition, there was a significant difference in the width to length ratio between 'hooked' and 'smooth' tools (Mann-Whitney U-test: z=-3.193, p=0.001): 'hooked' tools had a smaller width to length ratio than the 'smooth' tools. Finally, although there were no differences across tools based on different raw materials, the two types of algae-scooping tools were clearly different in several respects, including stiffness and relative smoothness.

Only woody tools were stripped of bark before use, thus exposing a 'smooth' undersurface, whereas the *Costus* tools, which possess a 'smooth' stalk, were not stripped of their outer coating. These latter tools comprised 93.6% of all the 'smooth' tools (see Table 7.5). 'Hooked' tools were only made from herbaceous material and particularly the fern-like species, *Tectaria aureun*, representing 87.7% of specimens of this tool type (see Table 7.5).

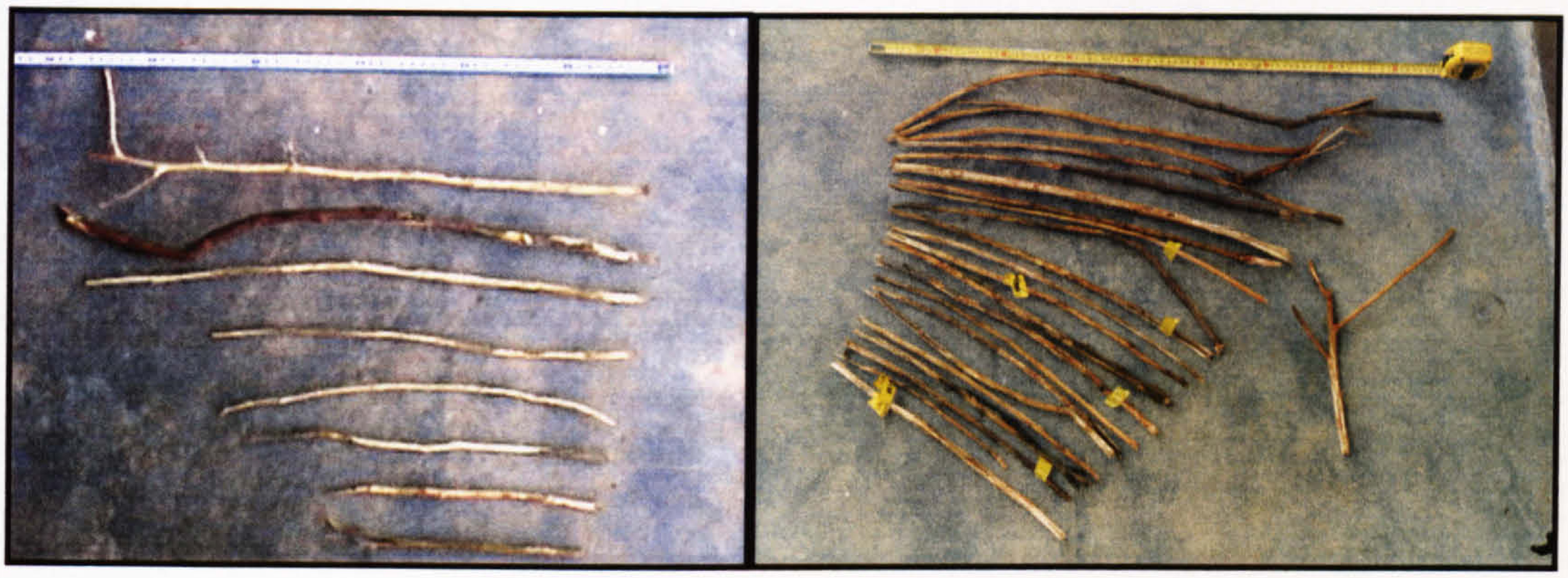
Although not quantified, during the few direct observations of algae-scooping, these two tool types appeared to be used in different contexts. The 'smooth' type was used when algae were abundant on the surface of the pond, whereas the 'hooked' type was used more frequently when algae were scarcer. The greater flexibility of 'hooked' tools could be a disadvantage when *Spirogyra* was plentiful since they were more susceptible to fracture under the weight of the algae. However, the protruding hooks were very useful when finer scooping was required and when smoother, thicker tools were less appropriate. No difference in lengths or widths of tools, though, was detected between broken and unbroken tools (Length: $N_{unbroken}$=97, N_{broken}=11; Mann-Whitney U-test: Z=-0.091, *n.s.*; Width: $N_{unbroken}$=76, N_{broken}=11; Mann-Whitney U-test: Z=-1.012, *n.s.*). In addition, there was no significant difference in the frequency of broken tools across the two tool types (Chi-square test: χ^2=0.913; *df*=1; *n.s.*). However, this result is to be expected if tools are used appropriately. Interestingly, no recovered tools made from woody material were ever found to be fractured. All direct observations of algae-scooping indicated that tools were not modified further after they were fashioned in the first place.

Finally, in terms of structure and properties, chimpanzees' choice of algae-scooping tools seems to reflect an assessment of and adaptation to the condition of the goal, i.e. density of the algae. More direct observations of this tool-use behaviour are required for a quantitative assessment of the exact context of use of the two tool types employed during algae-scooping.

'Hunting' tools

All 31 prising tools, recovered, were made from a single tree species (*Trichilia heudelotii*) (see Plate 7.4). This tree species was within arms' reach from where the chimpanzees on two separate occasions attempted unsuccessfully to expel what was presumed to be a tree pangolin from its nesting place in a tree hole. For this tool-use behaviour, the chimpanzees clearly reached out for the closest appropriate tool material available. Vines were also accessible within arms' reach, but these were ignored. The prising tool was forcefully inserted into the hole and twirled and scooped with the aim of expelling the prey within. Such movements require a robust tool that would not break when manipulated, and a woody tool is usually more solid than one based on other plant materials.

Plate 7.4. Prising/expelling tools employed in tool-assisted predation.

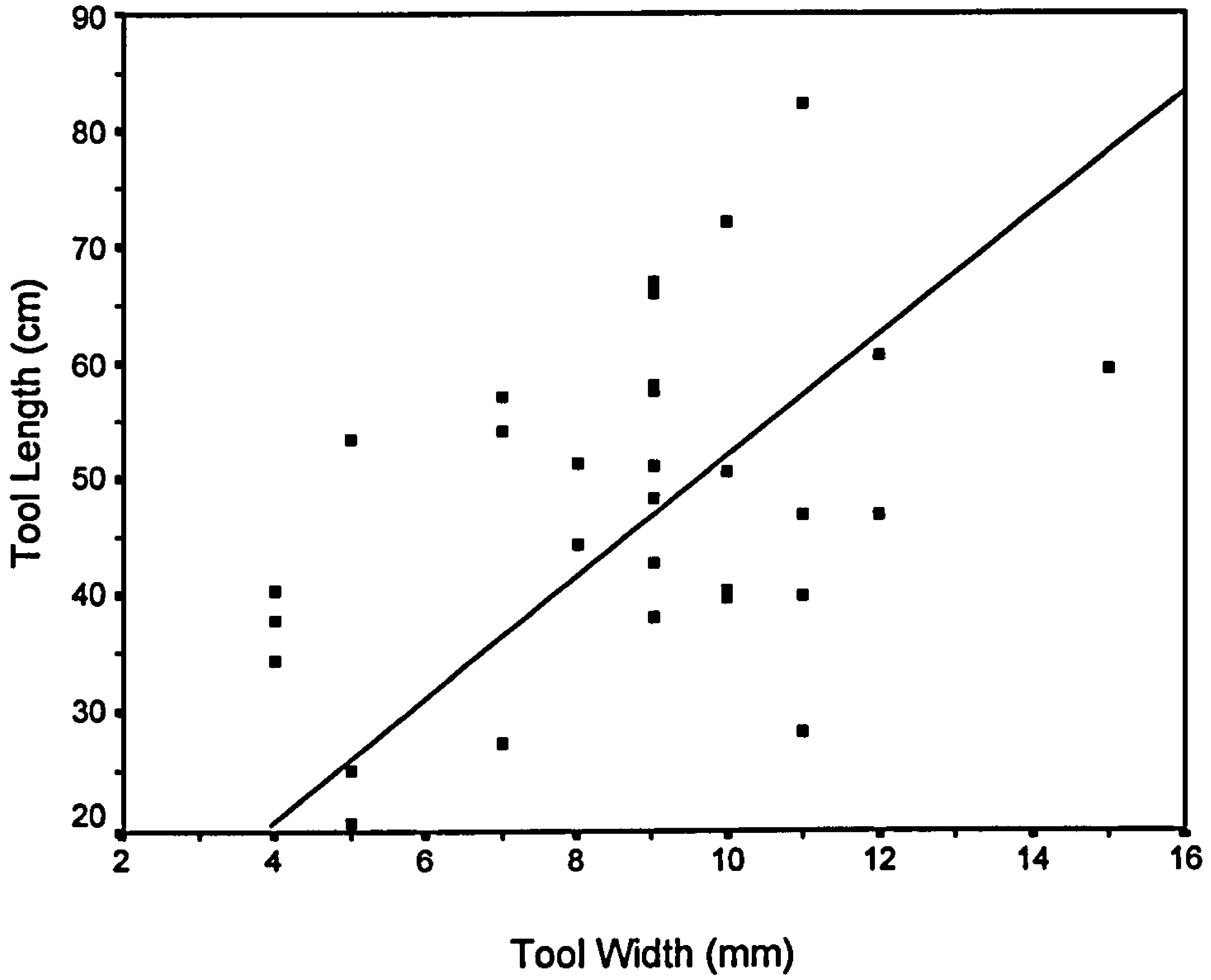


Mean tool length was 47.8 cm and mean tool width was 8.7 mm (see Table 7.7). Mean tool weight was 22.4g (see Table 7.7). There was a significant positive correlation between length and width ($R=0.405$; $N=31$; $\rho<0.05$) (see Fig. 7.7). Moreover, both length and width of the tools were strongly positively correlated with weight (Length: $R=0.689$; $N=31$; $\rho<0.001$; Width: $R=0.793$; $N=31$; $\rho<0.001$). Considering that all these tools were made from the same species of plant, these relationships are to be expected.

Table 7.7. Descriptive summary for length (cm), width (mm) and weight (g) variables of prising tools.

	Length (cm)	**Width (mm)**	**Weight (g)**
N	31	31	31
Mean	47.8	8.7	22.4
SD	14.0	2.7	16.4
Range	20.7-82.2	4-15	3-66

Fig. 7.7. Scatterplot of length (cm) versus width (mm) of prising tools.



All prising tools were stripped of bark to some extent. Seventy one percent were stripped of at least 90% of their bark. In terms of tool shape, 67.7% of the tools were straight, 25.8% were curved and 6.5% were branched. The two branched tools retrieved were made by an adolescent chimpanzee. The branched end of the tool was always inserted into the tree hole, while the other end was used as a ‘handle’. Only 6.4% of the recovered tools were distinctly fractured.

During the two episodes of tool-assisted predation recorded, a total of 31 direct observations of tool making were made. All six chimpanzees observed performing this behaviour detached a branch of the *Trichilia heudelotii* tree from within arms’ reach. They then usually removed the protruding leaves, before biting the branch to an appropriate length. Removal of the bark with the teeth was always observed before the tool was inserted into the tree hole. Thus, the raw materials were always modified three times before use: 1) detachment from substrate, 2) cutting to a specific length, and 3) leaf-stripping and/or bark-stripping. However, the chimpanzees sometimes continued to strip the bark off during tool-use. Indeed, nearly half of the tools (N=14) were subsequently modified during use. Sixty percent of these were further stripped of their bark, 20% further adjusted in terms of length or shape, by shortening it at the curvature making the tool straighter or breaking off side branches, and 20% underwent both types of alterations.

Stick- and stalk-tools at Bossou compared

The tools of the three stalk- or stick-using behaviours investigated above, indicated significant differences in their attributes, i.e. length, width and width to length ratio, raw materials used, and in the degree of manufacturing, particularly of bark stripping of woody tools. Median length of algae-scooping tools was significantly greater than for ant-dipping and prising tools (see Table 7.8 and Fig. 7.8). However, no such difference emerged between ant-dipping and prising tools (see Table 7.8). Moreover, all three categories of tools differed significantly in their width (see Table 7.8). Prising tools were significantly wider than the other types of tools, while algae-scooping tools were wider than ant-dipping ones (see Fig. 7.9). In terms of their width to length ratio, all again varied significantly (see Table 7.8), with prising tools being much larger and algae-scooping tools having a greater ratio than ant-dipping wands (see Fig. 7.10).

Moreover, a clear difference emerged in plant material employed in obtaining the three types of tools (Chi-square test: $\chi^2(4, N=327)=116.569$; $\rho<0.001$). All prising/expelling tools were based upon tree substrates, only tree- and herb-based tools were used during algae-scooping, whereas all three classes of plant materials were employed during ant-dipping (see Fig. 7.11).

With regards to bark stripping of woody tools, i.e. tree/shrub or vine, all tools employed in algae-scooping or in prising/expelling prey out of a tree hole were removed entirely or partially of their bark, compared to slightly more than half of the ant-dipping tools (see Fig. 7.12).

Table 7.8. Length, width and width to length ratio differences across tools across the three stick- or stalk-use behaviours observed.

Variable	**Tool-Uses compared**	**Mann-Whitney U-test: z-value**	**ρ -value (two-tailed)**
Length (cm)	Ant-dipping(N=189) Algae scooping(N=108)	-2.191	*
	Ant-dipping(N=189) Prising tools(N=31)	-0.927	*n.s.*
	Algae-scooping(N=108) Prising tools(N=31)	-2.535	*
Width (mm)	Ant-dipping(N=152) Algae scooping(N=87)	-3.687	***
	Ant-dipping(N=152) Prising tools(N=31)	-6.073	***
	Algae-scooping(N=87) Prising tools (N=31)	-4.073	***
Width/Length Ratio	Ant-dipping(N=152) Algae scooping(N=87)	-3.097	**
	Ant-dipping(N=152) Prising tools(N=31)	-7.355	***
	Algae-scooping(N=87) Prising tools(N=31)	-5.360	***

Levels of Significance: *: $\rho<0.05$; **: $\rho<0.01$; ***: $\rho<0.001$

Fig. 7.8. Boxplot of length (cm) of tools across the three tool-use behaviours observed.

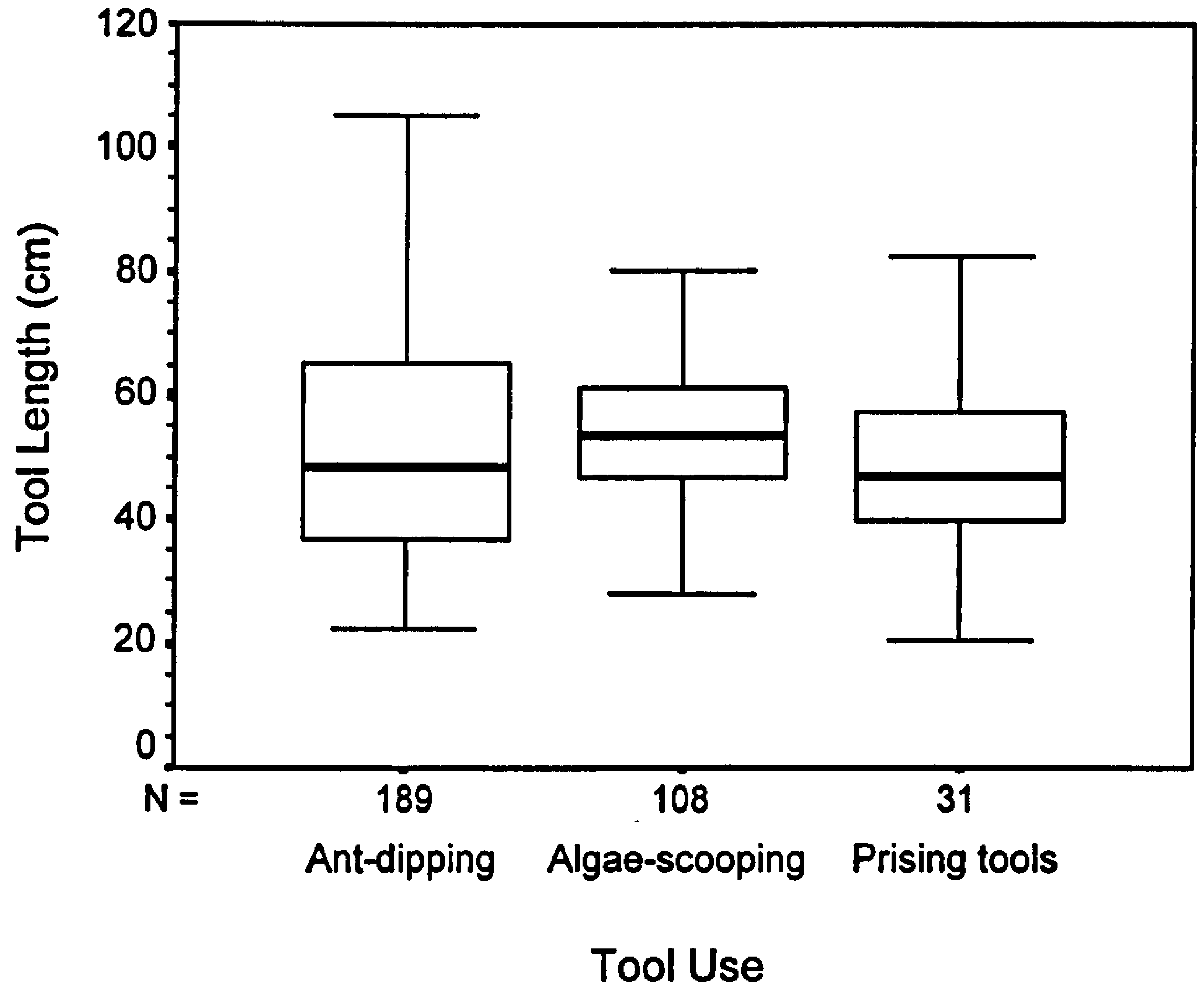


Fig. 7.9. Boxplot of width (mm) of tools across the three tool-use behaviours observed.

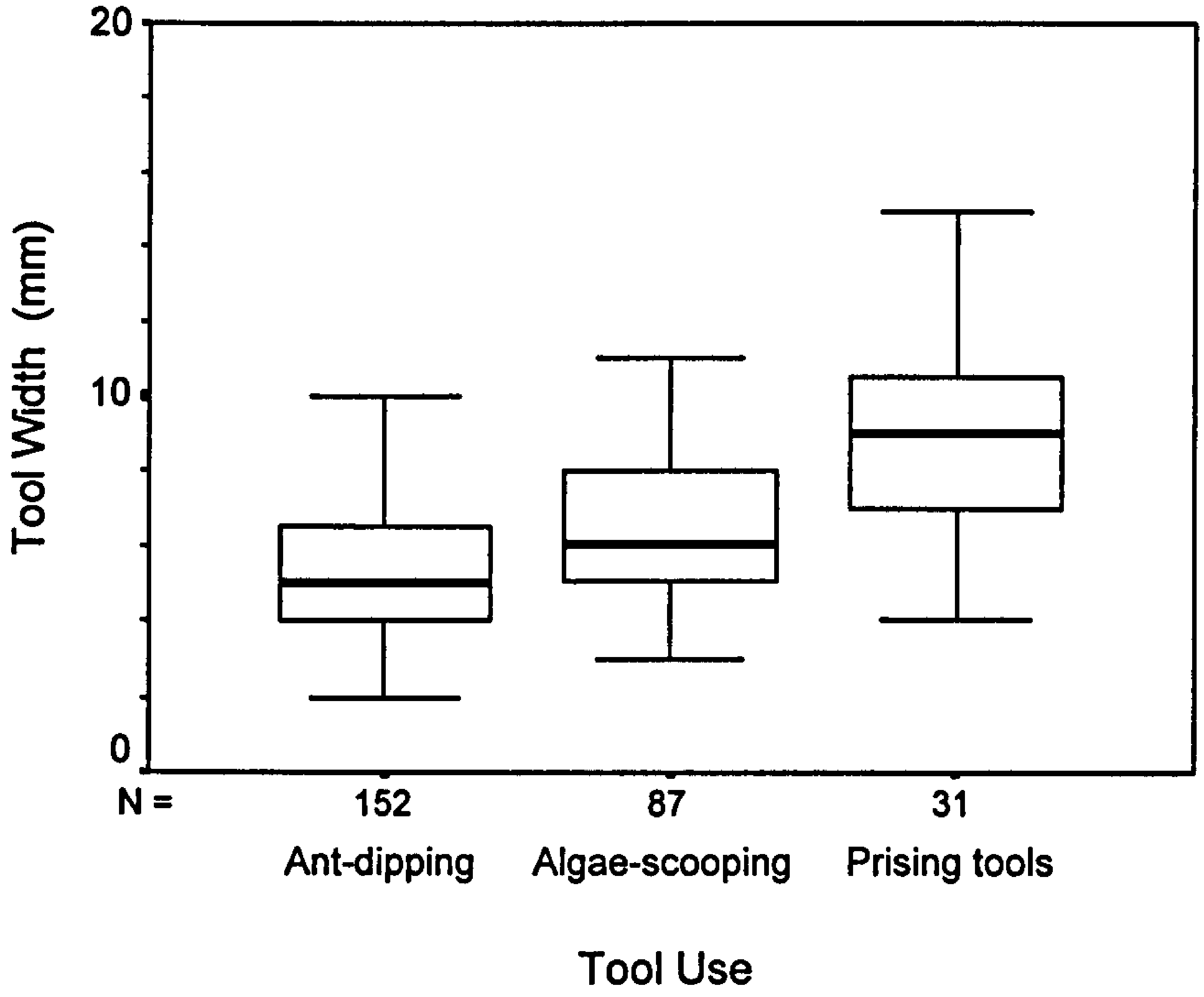


Fig. 7.10. Boxplot of width to length ratio of tools across the three tool-use behaviours observed.

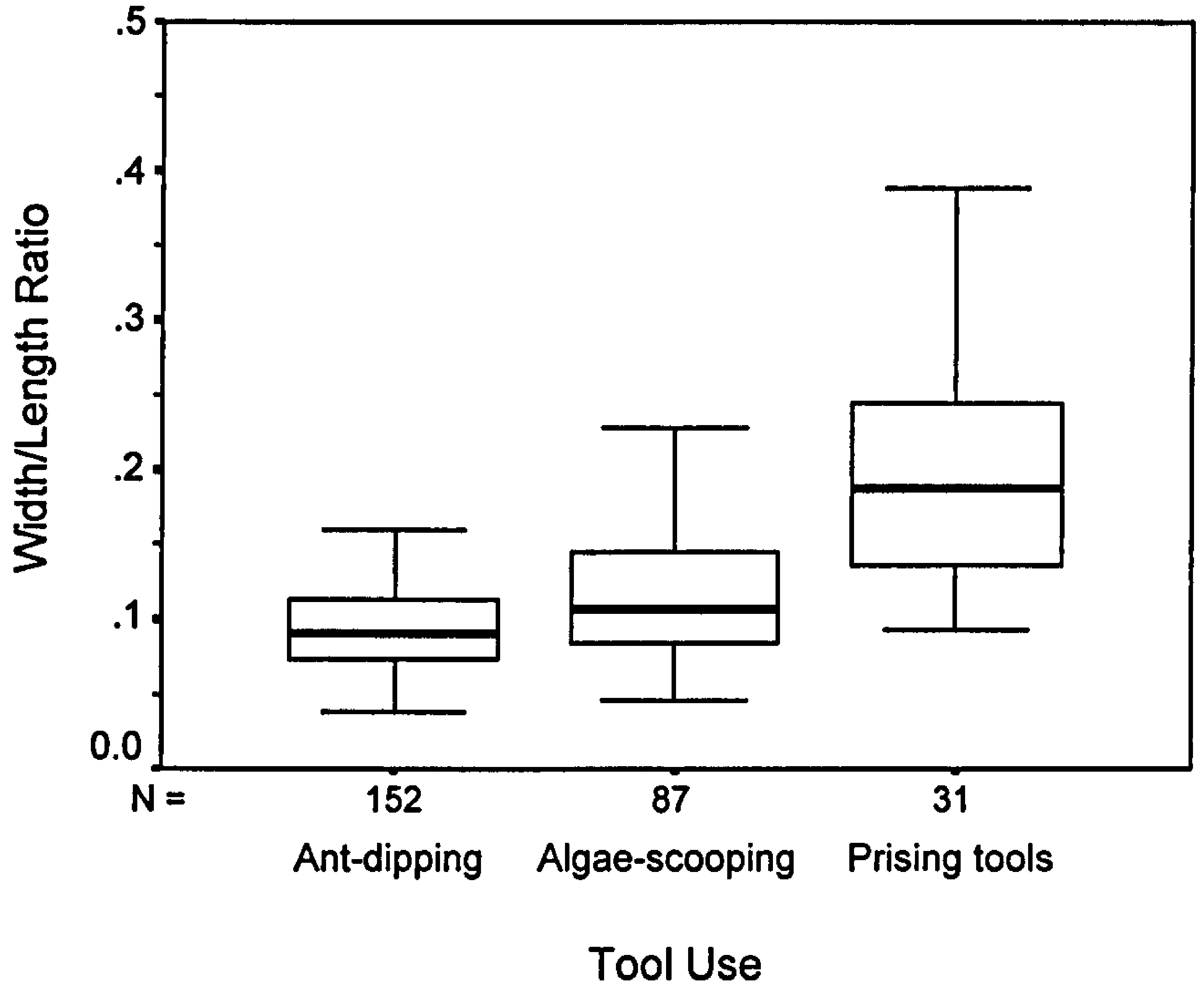


Fig. 7.11. Percentage of tools produced from the three plant substrates distinguished across the three tool-use behaviours observed.

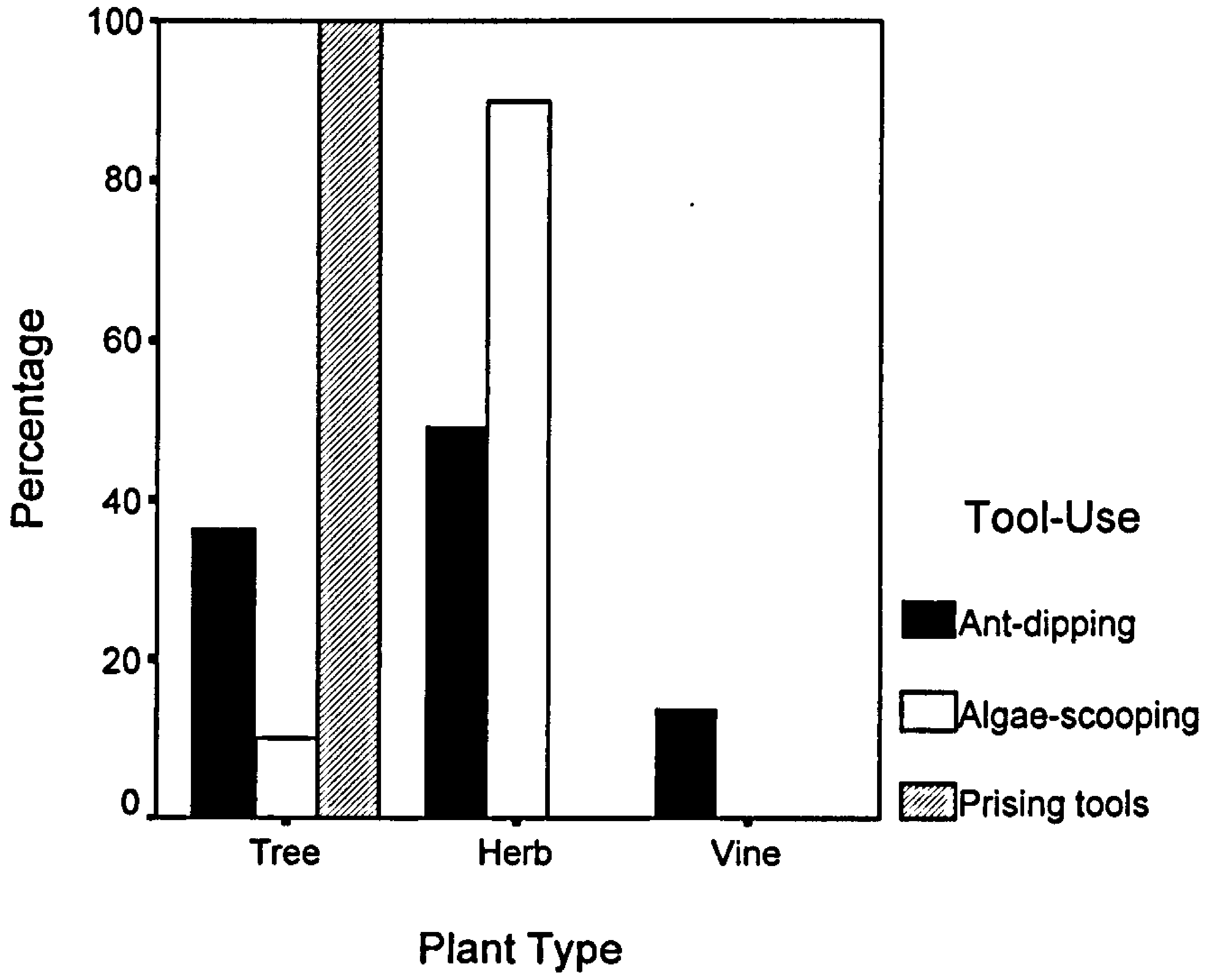
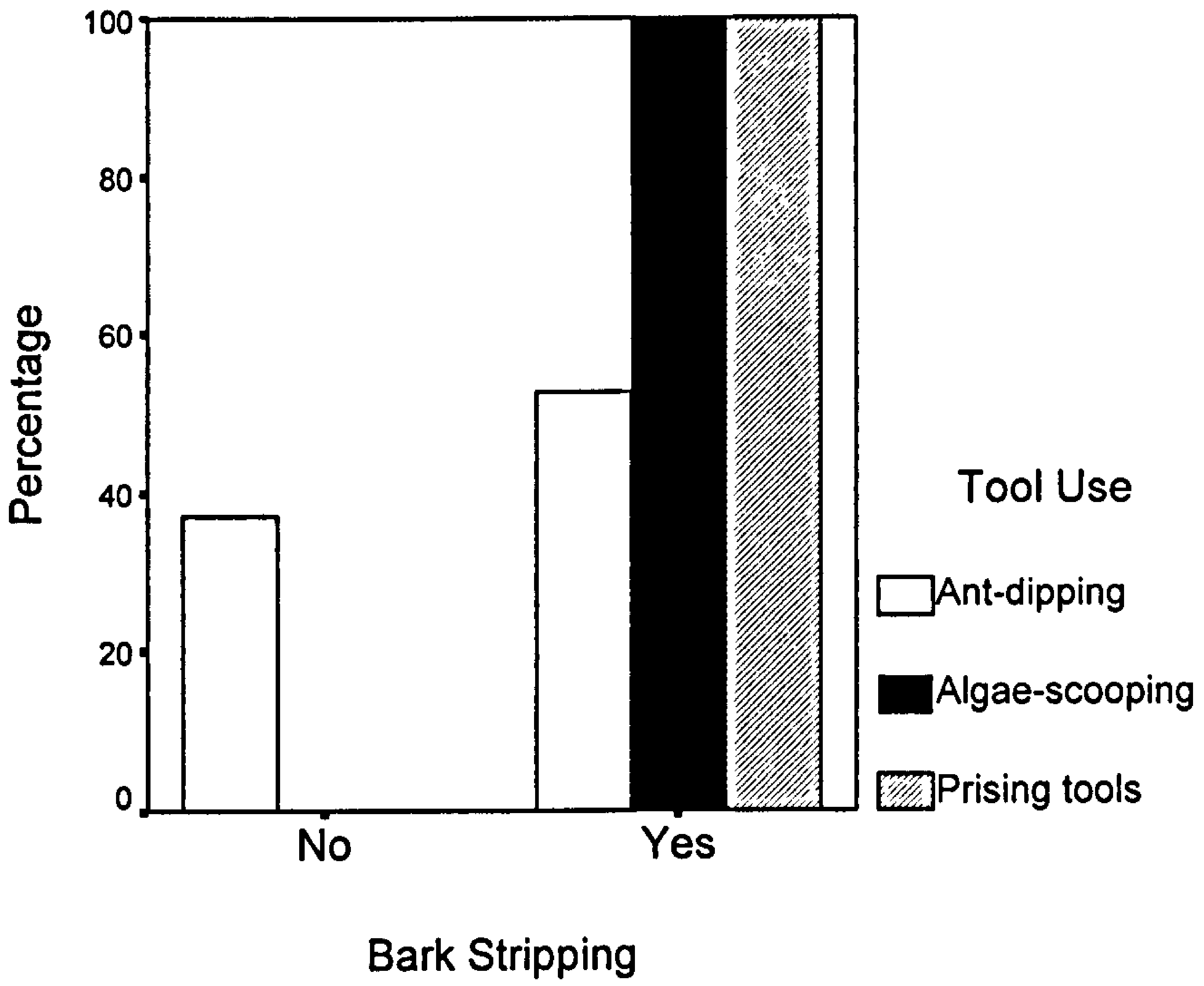


Fig. 7.12. Percentage of woody tools with some degree of bark-stripping, for the three tool-use behaviours explored.



Tools used for feeding upon driver ants at Nimba: Seringbara and Yealé

Yealé

Nine tools employed in ant feeding were collected from three old driver ant nests at the Yealé site. All came from woody substrates and only three were identifiable at the species level (see Table 7.9 and Plate 7.5).

Eight of these nine tools, i.e. 88.9%, were stripped of their bark and 55.5% were more than fifty percent stripped along their whole length. None of the tools recovered had a brush-end. Use of both ends was established for 44.4% of the tools. Only one tool showed evidence of fracture during use.

Mean tool length for ant-dipping wands at Yealé was 66.5 cm (N=9; SD=19.52; range: 38-96 cm) and mean tool width was 6.3 mm (N=9; SD=2; range: 3-9 mm).

Plate 7.5. Photo of a sample of ant-dipping tools retrieved at the Yealé site.

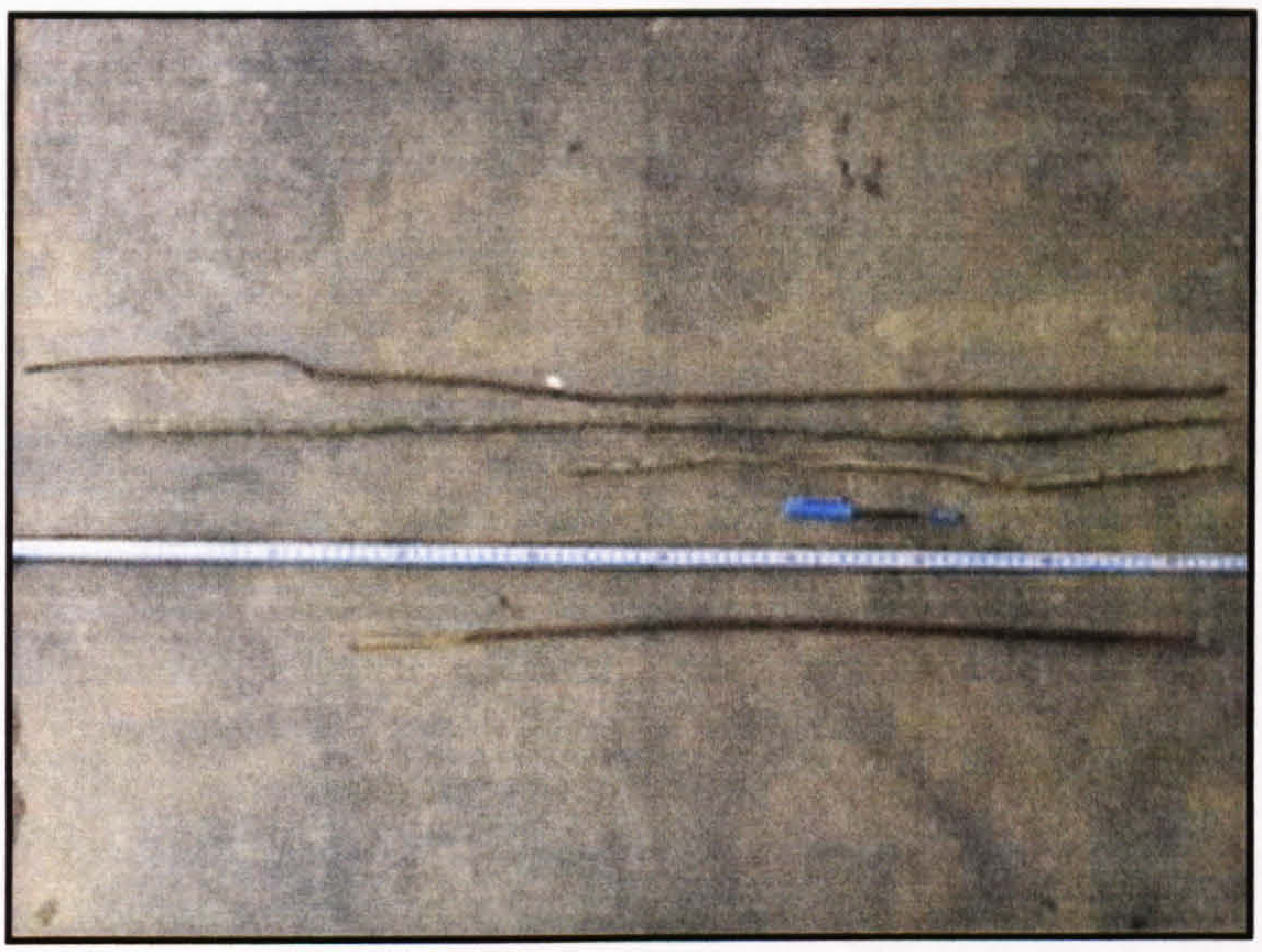


Table 7.9. Plant species used for ant-dipping at the Yealé site.

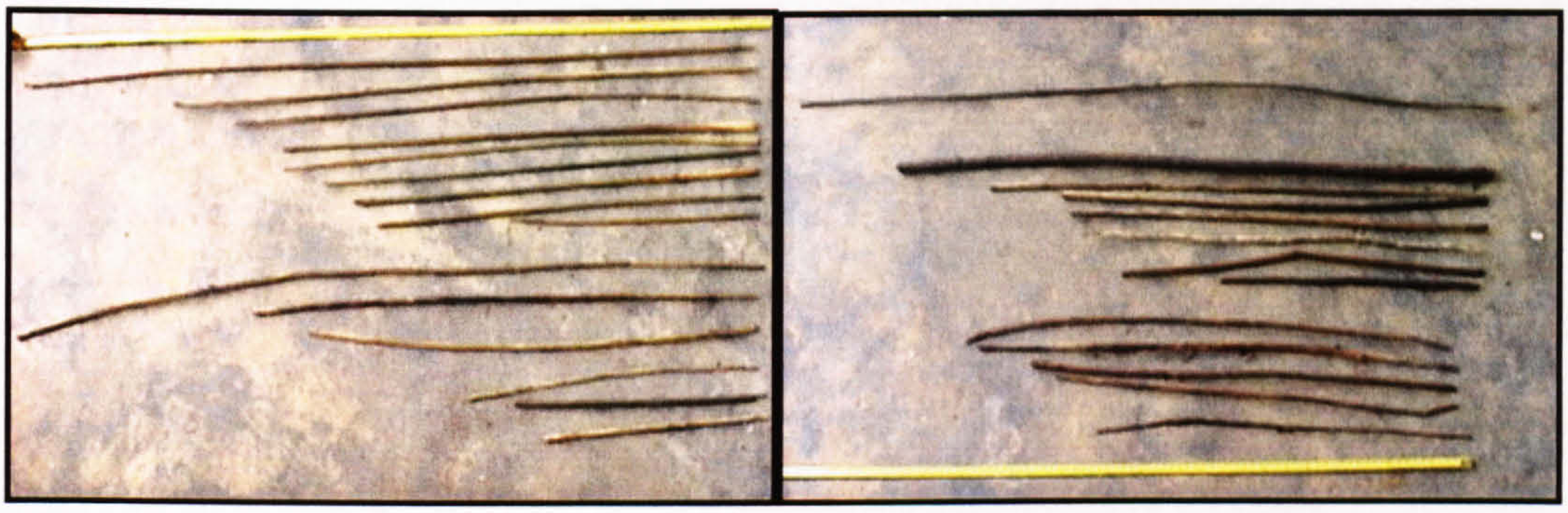
Species	Family	Plant Type	Frequency	Percent
Funtumia elastica	Apocynaceae	Tree	1	11.1
Sterculia tragacantha	Sterculiaceae	Tree	1	11.1
Drypetes ivorensis	Euphorbiaceae	Tree	1	11.1
Unknown		Tree	6	66.7
TOTAL			**9**	**100**

Seringbara

At Seringbara, 45 tools employed in ant-feeding were recovered from eight old *Dorylus* nest sites. These included tools made from 10 taxonomically determined plant species spanning 10 families, while eight tools remained unidentified (see Table 7.10).

Two types of tools though were discerned. Some tools were clearly used as wands for ant-dipping, while others were likely to have been used for 'digging' the top soil of the underground nests of the driver ants (see Table 7.10 and Plate 7.6). These tools were more heavily coated in mud particularly at the end(s) than the other tools. In addition, although 'digging ' tools did not differ in length from their associated ant-dipping wands (Mann-Whitney U-test: $z=-1.228$; *n.s.*), they were significantly thicker (Mann-Whitney U-test: $z=-4.305$; $\rho<0.001$) (see Table 7.11 and Plate 7.6). Moreover, the width to length ratio of 'digging' tools was significantly greater than for the wands used (Mann-Whitney U-test: $z=-3.323$; $\rho<0.001$) (see Fig. 7.13). Since 'digging' tools distinctly differed from the recognised dipping wands, these were analysed separately during subsequent analysis. Dipping tools were retrieved from all nest sites, whereas 'digging' tools were recovered from only four, potentially five nest sites.

Plate 7.6. Sample of tools employed in driver ant feeding at Seringbara.
1. Ant-dipping tools



2. 'Digging' tools from Seringbara.

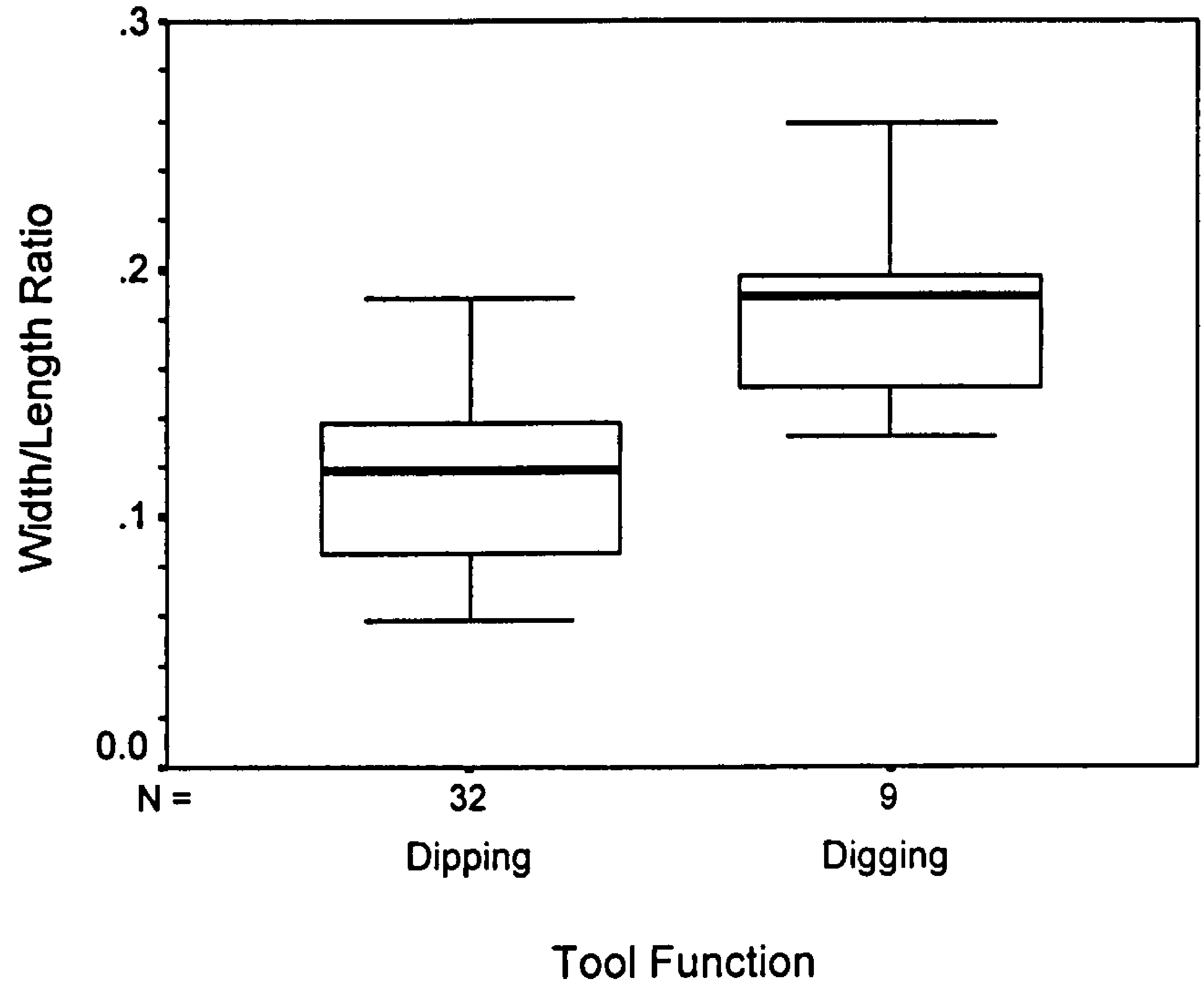
Table 7.10. Plant species used in fashioning ant-feeding tools at Seringbara.

Function	Species	Family	Plant Type	Freq.	%
Dipping	***Rhaphiostylis beninensis***	Icacinacea	Tree	9	28.1
	Megaphrynium macrostachyum	Marantaceae	Herb	6	18.8
	Unknown		Tree	6	18.7
	Rinorea sp.	Violaceae	Tree	3	9.4
	Solanum verbascifolium	Solanaceae	Tree	2	6.3
	Carapa procera	Meliaceae	Tree	2	6.3
	Memecylon angleriaenum	Melastomataceae	Tree	2	6.3
	Afromonum exscapum	Zingiberaceae	Herb	1	3.1
	Hippocratea sp.	Celastraceae	Tree	1	3.1
	TOTAL			**32**	**100**
'Digging'	***Rinorea sp.***	Violaceae	Tree	5	55.6
	Megaphrynium macrostachyum	Marantaceae	Herb	1	11.1
	Solanum verbascifolium	Solanaceae	Tree	1	11.1
	Uapaca sp.	Euphorbiaceae	Tree	1	11.1
	Memecylon angleriaenum	Melastomataceae	Tree	1	11.1
	TOTAL			**9**	**100**
Unknown	***Unknown***			2	50
	Megaphrynium macrostachyum	Marantaceae	Herb	1	25
	Lecaniodiscus cupanoides	Sapindaceae	Tree	1	25
	TOTAL			**4**	**100**

Table 7.11. Summary statistics of length (cm) and width (mm) for dipping and 'digging' tools at Seringbara.

Tool Function	Variable	N.	Mean	SD	Range
Dipping	Length (cm)	32	57.6	24.0	21-120
	Width (mm)	32	6.3	1.8	4-10
'Digging'	Length (cm)	9	65.1	17.9	39-89
	Width (mm)	9	11.3	2.5	8-17

Fig. 7.13. Boxplot of width to length ratio of the two types of tools used in ant feeding at Seringbara.



Of all the tools recovered at Seringbara, 80% were made from woody materials, the rest coming from herbaceous plants. Bark stripping was evident in 73.3% of cases. Significantly more woody tools were stripped of their bark than THV ones (Fisher's Exact test: p<0.001). Indeed, only one herb tool was found to be stripped; 5% of its epidermis was removed. However, there was no difference in bark stripping across the two tool types (Fisher's Exact test: *n.s.*). Only one tool showed any indications of a brush end. This tool was made from a tree-based material. Two tree-based tools were fractured and these appeared to have been used to dip for driver ants. Fifty eight percent of all the tools were used at both ends. There was, however, no significant difference between the two plant types used or tool function in end use (Fisher's Exact test: *n.s.*).

Comparison of ant feeding tools between Nimba and Bossou

One major difference between the sites concerning feeding upon driver ants was the potential presence of 'digging' tools (N=9) at the Seringbara site, although their precise function still needs to be ascertained through direct observation of ant-feeding at this site. These were significantly longer, wider and had a greater width to length ratio than dipping tools from Bossou (Mann-Whitney U-test: Length: z=-1.974; ρ<0.05; Width: z=-4.825; ρ<0.001; Ratio: z=-4.606; ρ<0.001) (see Fig. 7.14; 7.15; 7.16). Although they did not differ in length from wands retrieved from Yealé, they exhibited a significantly greater width and width to length ratio (Mann-Whitney U-test: Length: z=-0.044; *n.s.*; Width: z=-3.423; ρ<0.01; Ratio: z=-3.576; ρ<0.001) (see Fig. 7.14; 7.15; 7.16).

When comparing ant-dipping tools, i.e. excluding 'digging' tools from Seringbara, across the three study sites, no differences in length, width or width to length emerged between Seringbara and Yealé (see Table 7.12). However, there were differences in wand length between Bossou and Yealé (see Table 7.12 and Fig. 7.14) and in wand width and width to length ratio between Bossou and Seringbara (see Table 7.12; Fig. 7.15 and 7.16).

Table 7.12. Summary of statistical comparison of wand length, width and width to length ratio between Bossou, Seringbara and Yealé.

Study Sites (1/2)	**Variable**	**N_1**	**N_2**	**Mann-Whitney U: Z-value**	**ρ-value (2-tailed)**
Bossou/Seringbara	Length	189	32	-0.863	*n.s.*
	Width	152	32	-2.922	**
	Ratio	152	32	-2.995	**
Bossou/ Yealé	Length	189	9	-2.045	*
	Width	152	9	-1.737	*n.s.*
	Ratio	152	9	-0.184	*n.s.*
Seringbara/ Yealé	Length	32	9	-1.181	*n.s.*
	Width	32	9	-0.144	*n.s.*
	Ratio	32	9	-1.654	*n.s.*

Fig. 7.14. Boxplot of tool length (cm) for driver ant feeding at the three study sites, including both dipping and 'digging' tools.

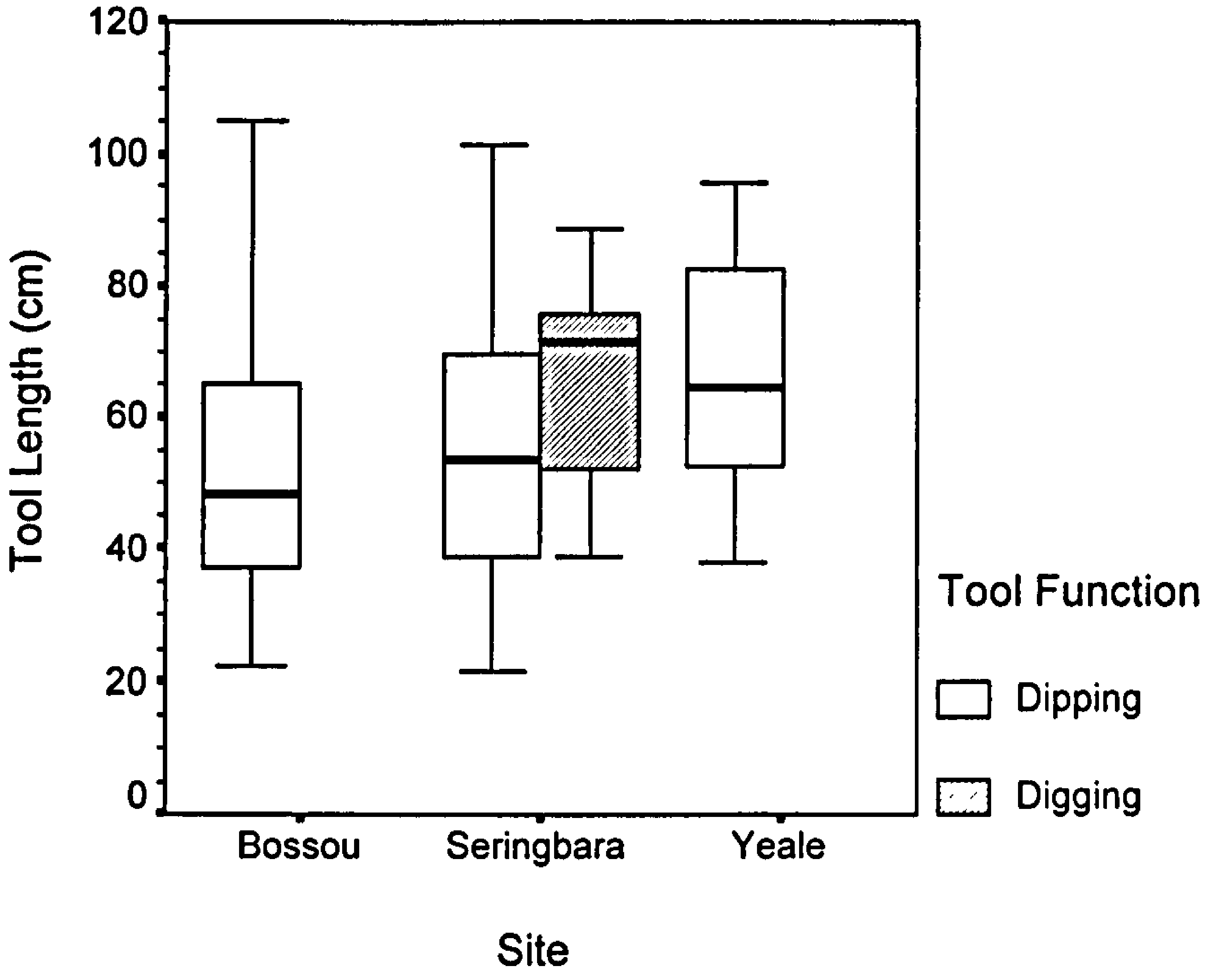


Fig. 7.15. Boxplot of tool width (mm) for driver ant feeding at the three study sites, including both dipping and 'digging' tools.

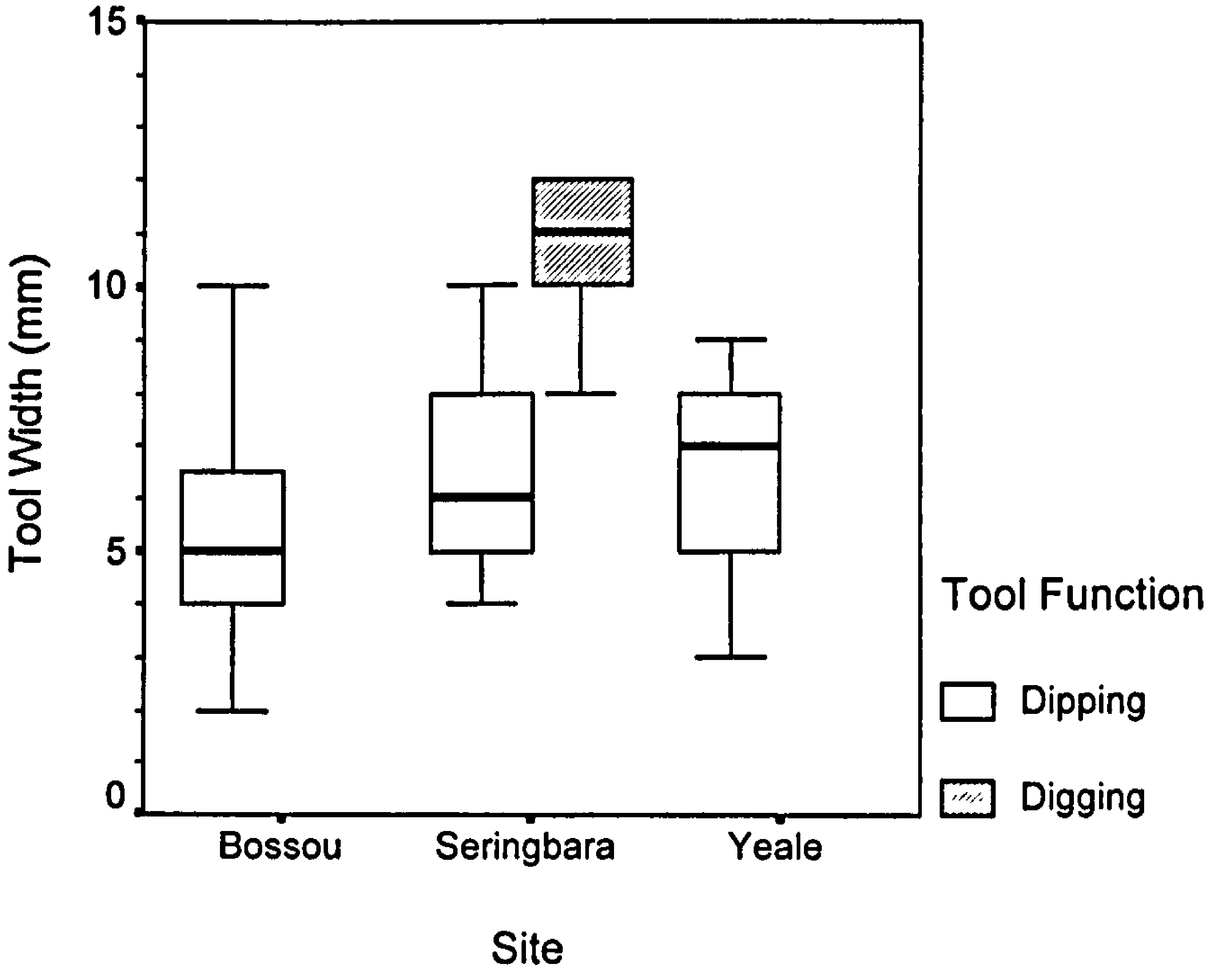
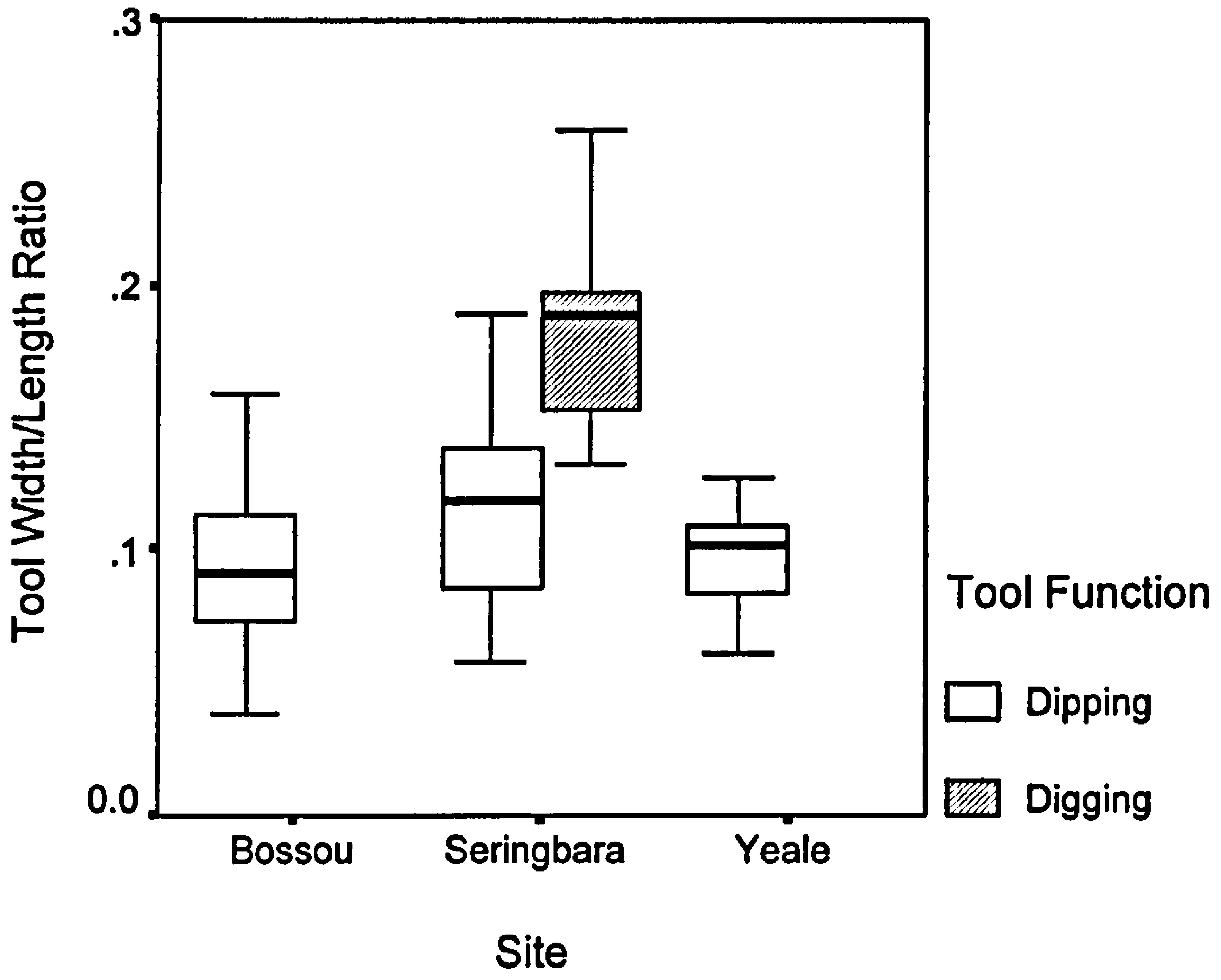
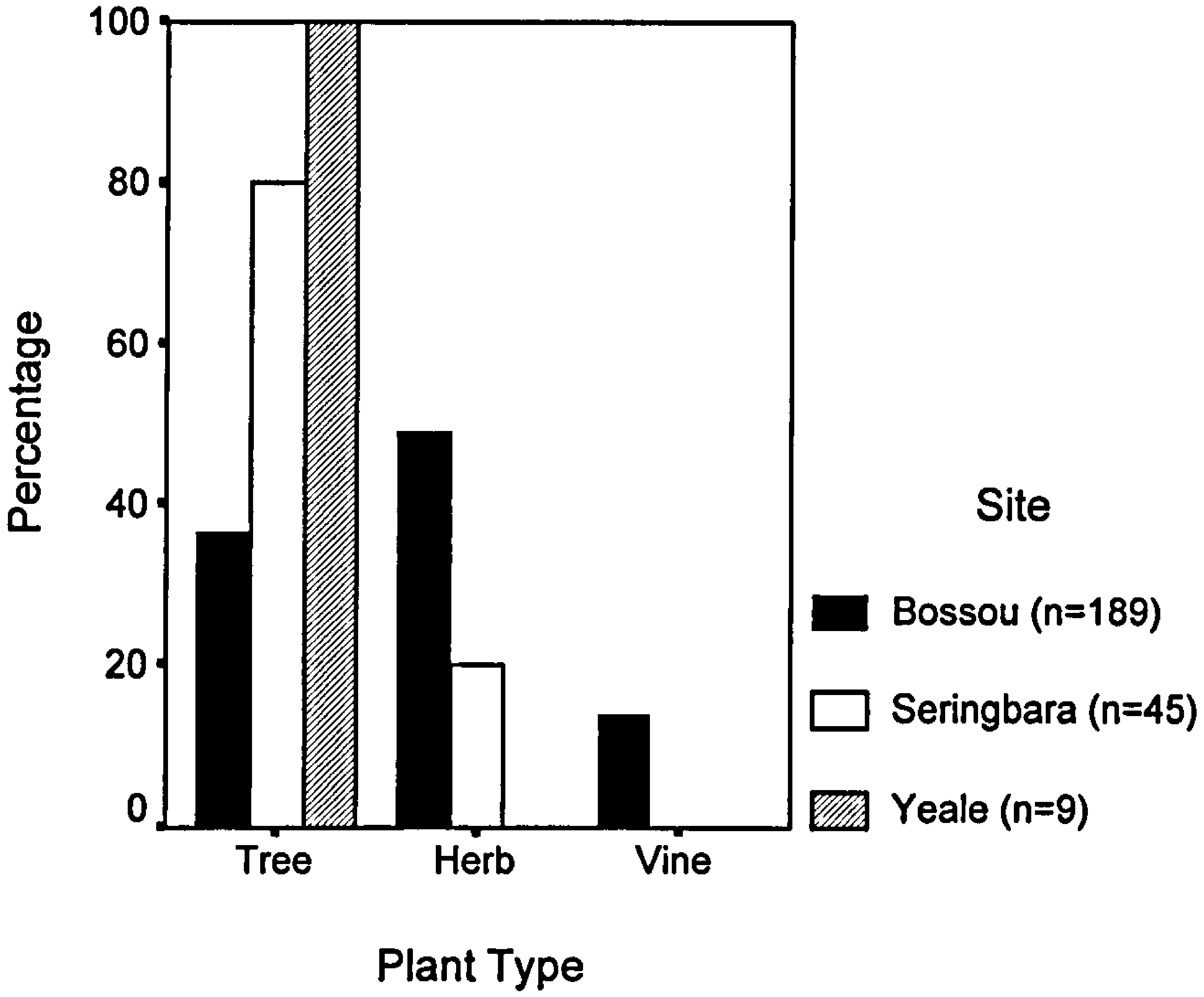


Fig. 7.16. Boxplot of tool width (mm) for driver ant feeding at the three study sites including both dipping and 'digging' tools.



Differences in plant type used for making tools across the three sites were also apparent. At the Yealé site, only tree-based tools were found, whereas at Bossou all three types were used and at Seringbara no vine tools were used for ant feeding (see Fig. 7.17). In addition, there was no significant difference across the sites in the proportion of tools used at both ends (Chi-square test: $\chi^2(2, N=201)=3.564$; *n.s.*). As bark stripping was associated with tools made of woody materials, a comparative analysis between sites was carried out excluding herbaceous tools. Tools from Seringbara and Yealé had more tools stripped of bark than expected in comparison to Bossou (Chi-square test: $\chi^2(2, N=196)=19.897$; $p<0.001$), but there was no notable difference between Seringbara and Yealé in the proportion of tools stripped (Fisher's Exact test: *n.s.*).

Fig. 7.17. Percentage of ant-feeding tools made from the three plant type materials across the three study sites.

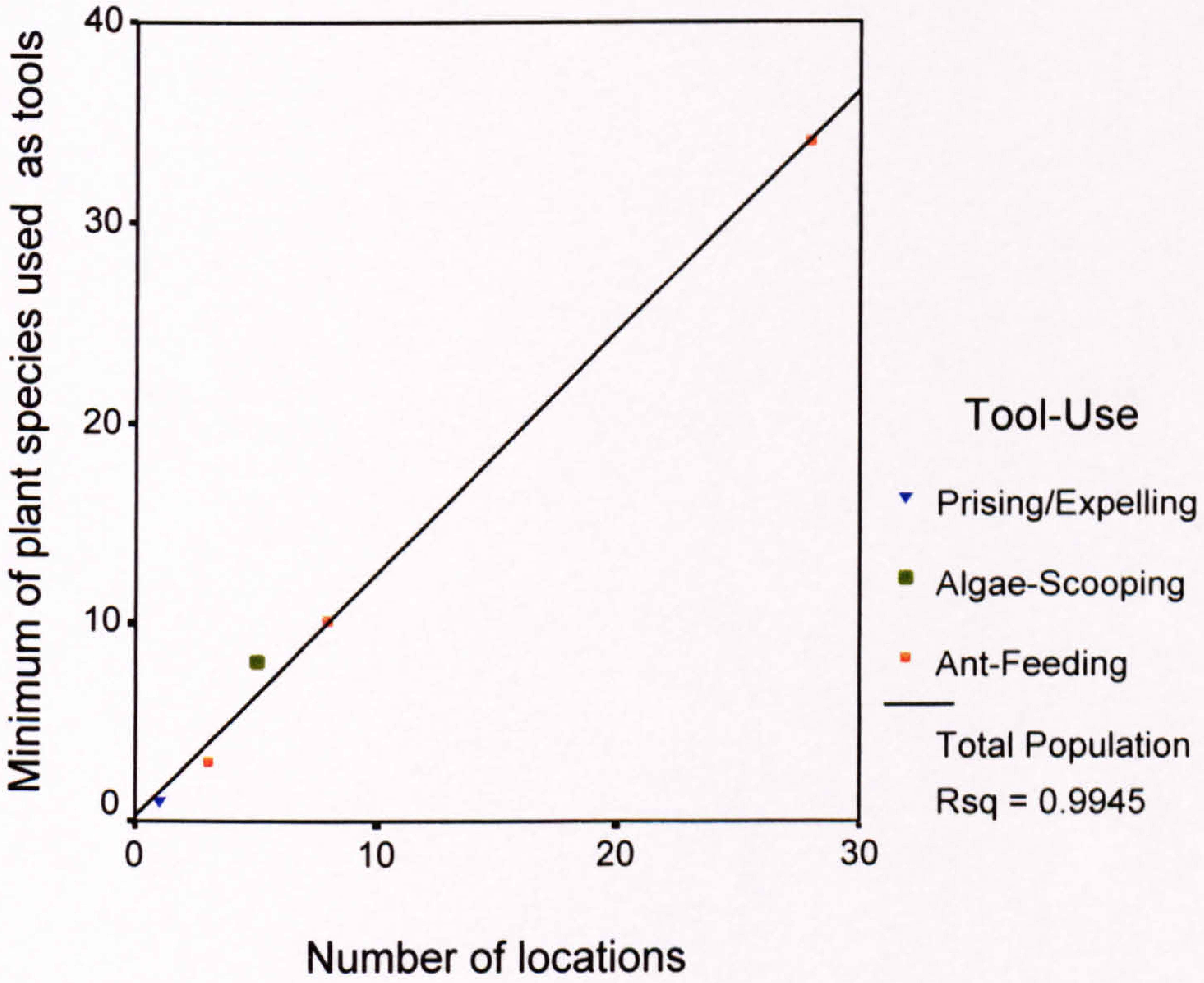


7.6 Discussion

Raw material selection

Although no quantitative assessment of plant species availability was carried out during this study, Bossou chimpanzees did not appear to be selective in their choice of plant species for fashioning stick- or stalk-tools for the three tool-use behaviours analysed. If all three stick- and stalk-use behaviours observed at Bossou are analysed together, along with the ant-feeding records from Nimba, a significant positive correlation is evident between the minimum number of plant species used as tools and the number of locations where these tool tasks occurred (two-tailed Pearson Correlation: R=0.997; N=5; $p<0.001$) (see Fig. 7.18). This correlation suggests that the chimpanzees overall are not selective at the plant species level. Moreover, at Bossou, for ant-dipping and algae-scooping, the chimpanzees tended to employ the commonest species available in the surrounding habitat and for prising or expelling an animal prey out of a tree hole, they used a raw material which was within arms' reach. Nevertheless, detailed studies assessing the relationship between availability of plant species and raw material selection for tool-manufacturing by chimpanzees are urgently needed for stick- or stalk-use behaviours across different sites to shed further light on the interaction between tool-selection and the tool-making process.

Fig. 7.18. Scatterplot of the number of locations where stick- or stalk-use behaviours were recorded against the minimum number of plant species (excluding unidentified tools) used as tools at Bossou and Nimba.



However, there were differences in plant types used, i.e. tree, herb, vine, across the three tool-use behaviours recorded at Bossou. These differences may reflect plant type availability in the immediate environment, but may also represent plant type selection in accordance with the requirements of the task at hand. Indeed, depending on the tool-task to be performed, the width to length ratio of the tools reflected specific requirements for that tool, restricting plant type choice to some extent.

The width to length ratio for prising/expelling tools, which were all made from tree material, was significantly greater than for either ant-dipping or algae-scooping tools. Algae-scooping tools in turn had a greater ratio than ant-dipping wands. Prising tools were manipulated such that they had to be thick and solid; therefore woody, as in tree-based, material was probably best suited. Algae-scooping demanded a sturdier tool than ant-dipping, especially when algae density was high, since the weight gathered surpasses that of amassed ants on a wand. However, these two behaviours did not have the same requirements for tool robustness as tool-assisted predation, thus plant type selection for algae-scooping and ant-dipping was less constrained. Overall, these results suggest that Bossou chimpanzees selected plant types appropriately for the task at hand, within restrictions imposed by the task being performed.

Finally, the majority of the tools employed were all fashioned before embarking on the tool task, suggesting that the chimpanzees had some form of mental image of what the tool should be like to be useful (Boesch and Boesch, 1990).

Tool-manufacturing process

At Bossou, the great majority of raw materials used for ant-dipping, algae-scooping and tool-assisted predation were modified three times before being employed as tools. This result is similar to the pattern at Taï, where tool-making processes appear more elaborate than at Mahale and selectivity for raw materials is relatively indiscriminate (Boesch and Boesch, 1990; Nishida and Hiraiwa, 1982). Thus, Bossou chimpanzees appear to match the Taï pattern, whereby an increase in the sophistication of tool-making appears to relax selectivity for the raw material.

Nevertheless, at Bossou, some selectivity occurred at the plant type level in relation to the required robustness of the raw material and to efficiency, as illustrated by the two tool types employed in algae-scooping. Indeed, in terms of structure and properties, chimpanzees' choice of algae-scooping tools seemed to reflect an assessment of and adaptation to the condition of the goal, i.e. density of the algae. However, this relationship still remains to be tested quantitatively.

At Taï, few tool modifications were observed once tool-use behaviour was in progress (Boesch and Boesch, 1990), whereas at Mahale, standardisation of the tools resulted from successive improvements made to the tool during use (Nishida and Hiraiwa, 1982). At Bossou, further tool modification was observed at low frequencies during ant-dipping, and was frequently observed during tool-assisted predation, whereas none was observed during algae-scooping. Most of these alterations involved further bark stripping of woody tools, although nearly half were also concerned with shortening the tool and some with modifying the shape. The task with the highest frequency of further tool modifications was prising an animal out of a tree hole. This task involves the insertion of the tool into a cavity and the required attributes of the tool, i.e. shape, width, length, for such a behaviour are not as predictable as for ant-dipping or algae-scooping. It also seems that during algae-scooping, where the target is most visible and/or the least embedded, the chimpanzees could more easily evaluate the task at hand, as potentially reflected by their different choice of raw material as a function of algae density at the pond surface.

In terms of tool manufacturing, bark-stripping at Bossou was clearly intentional. Bark-stripping of woody tools was, however, not consistent across all three tool-use behaviours. For algae-scooping and tool-assisted predation, all woody tools were systematically stripped of some of their bark, while for ant-dipping, tree- or vine-based wands were not always stripped of their bark. Bark-stripping is an interesting tool-making operation since it has no obvious function and yet is faithfully performed for two of the tool-use behaviours, but not for ant-dipping. It remains unclear what benefits or advantages bark-stripping can confer to a chimpanzee engaged in a stick- or stalk-use task. In some circumstances, as proposed by McGrew *et al.* (1979), it may facilitate swiping, whether through the hand or through the lips. However, I suggest that this tool modification may reflect a cultural behavioural pattern, socially transmitted and/or conventionally reinforced only in the context of certain tool-use tasks.

In their study of tools employed by chimpanzees in the Lopé Reserve, Gabon, Tutin *et al.*'s (1995b) found that tool length was adapted to the specific tool task undertaken, although raw material selection, bark-stripping and fraying varied little across the various stick-use behaviours observed. In contrast, at Bossou, more differences emerged between stick- or stalk-tools employed for different tasks, encompassing plant types chosen, bark-stripping, length, width and width to length ratio. Algae-scooping tools were significantly longer than tools employed for ant-dipping or tool-assisted predation. Assuming that algae-scooping evolved partly to avoid contact with water, then the tools clearly need to be long to reach for the floating algae, while minimising contact with water. But water avoidance as a possible influence on tool length was not consistent across all individuals. In 1995, one adult male, Tua, was recorded occasionally algae-scooping while standing in the water, while all the other individuals scooped from the edges of the pond. Tua also often inserted his hand, as well as the tool, into the water, a behaviour also sometimes seen in other members of the community.

In addition, algae-scooping tools were wider and exhibited a greater width to length ratio than ant-dipping wands; the former were more robust probably in order to bear the weight of the algae. Prising/expelling tools, although not longer than ant-dipping tools, were clearly wider and sturdier and therefore also adapted for their function.

Inter-site comparison of tools employed in driver ant feeding

Brush manufacture was rarely noted for either Bossou and Seringbara and never at Yealé. Tool fraying is therefore uncommon in the context of driver ant feeding in this region. Moreover, although one observation of intentional tool fraying was made at Bossou, most such tool modification seems to be an artefact of tool wear caused by repeated friction. In addition, no differences emerged in end use across the three sites, with approximately half of the tools employed at both ends at each of those sites.

Wands used at Bossou were generally shorter than tools used for ant-dipping at Yealé. However, tool sample size at Yealé was small, and therefore the trend requires confirmation. One species of driver ants available at this site was *Dorylus victoriae* (Santschi), which was not found at Bossou, but resembles *Dorylus nigricans*, since it also belongs to the *Nigricans* group. Humle and Matsuzawa (2002) showed that the type of *Dorylus* ant species dipped for, as well as ant condition, i.e. nests versus migrating, influence tool length in ant-dipping at Bossou (see *Chapter 6* for details). This difference in wand length between Bossou and Yealé could, thus, potentially be explained on the basis of the differences in driver ant species consumed by the chimpanzees at the two sites and/or the fact that all tools from the Nimba site were retrieved from abandoned nest sites. However, not all species of *Dorylus* ants found and consumed at either Yealé or Seringbara have yet systematically been sampled.

No difference in wand length was uncovered between Seringbara and Bossou. Nevertheless, wands at Seringbara, tended to be wider, with a greater width to length ratio than those at Bossou. No differences in tool length, width or ratio emerged between Seringbara and Yealé. Although wands employed at the Nimba sites were more similar to each other than those from Bossou, driver ant feeding at Seringbara was notably different by the presence of another set of tools, i.e. 'digging tools', presumably used in excavating the top soil of the ants' nest. These 'digging' tools were distinctly wider and had a greater width to length ratio than wands recovered from either Seringbara, Bossou or Yealé.

The possible existence of a 'digging' tool in driver ant feeding at Seringbara is reminiscent of accounts of the use of perforating tools for digging a hole into termite mounds to facilitate the insertion of a slender probe when fishing for *Macrotermes spp.* termites. This behaviour has only been observed in the central African subspecies of chimpanzees (*Pan troglodytes troglodytes*) (Suzuki *et al.*, 1995; Bermejo and Illera, 1999). The use of a tool-set for termite-fishing has been reported at several study sites including Campo, Cameroon (Sugiyama, 1985), Belinga, Gabon (McGrew and Rogers, 1983), Ndoki (Suzuki *et al.*, 1995) and the Lossi forest, Congo (Bermejo and Illera, 1999), Ndakan and Bai Hokou, Central African Republic (Fay and Carroll, 1994). However, at all other study sites where termite-fishing occurs, no perforating tool has ever been discovered and the chimpanzees rely only upon slender probes, which they insert into openings in the termite mound to extract the termites (McGrew *et al.*, 1979; McGrew, 1992). Although driver ant feeding was not directly observed at Seringbara, these 'digging' tools were very different from the associated dipping wands also found at deserted driver ants' nests. Interestingly, Sugiyama *et al.* (1988) had previously reported and speculated on the possible discovery of one such tool-set at Bossou, but none has been made since.

With regards to termite-fishing, no apparent ecological difference in mound formation or structure, or in prey behaviour, can explain the difference in termite-fishing technique between the central African subspecies of chimpanzee and its two neighbours, the eastern and the western subspecies (Suzuki *et al.* 1995). However, it seems that, in contrast to the other two subspecies, the central subspecies fishes for termites all year round. The perforating stick may thus be helpful in gaining access to the termites deep inside the mound outside the termite swarming season when natural tunnels are unavailable by acting as a stopper enabling reuse of a hole previously used (Suzuki *et al.*, 1995). Thus, although not yet established, there may still be an environmental explanation for this difference in termite-fishing technique. Nevertheless, it has also been suggested that the difference could reflect a cultural difference between these chimpanzee populations (McGrew, 1992).

Finally, if indeed the 'digging' tools constitute a tool-set with dipping wands, then their presence at Seringbara may be due to some environmental differences in driver ants' nest structure, soil composition or *Dorylus* species. Such differences could account for the absence or extreme rarity of 'digging' tools at the two neighbouring sites and particularly favour their use at Seringbara. If these tools proved not to be used in a digging context but rather represent another type of sturdier dipping wand, then the intra-site variability in wand length and width and the resulting significant difference with wands from either Bossou or Yealé would still require some explanation. One species of driver ants available at Seringbara was identified as *Dorylus molestus* (Gerstaecker), which had previously been thought to occur at Bossou but which was not identified in any of the samples collected (Humle and Matsuzawa, 2002) (see *Chapter 6* for details). Possible environmental differences in and influences on ant feeding will be explored in the future, but until then this difference remains unexplained and could potentially represent a cultural variant, whether at the level of a tool-set or a difference in tool-choice, between neighbouring communities of chimpanzees in this region.

Conclusion

Tool-choice and tool-making in chimpanzees clearly reflect the function of the task being performed. As proposed by Boesch and Boesch (1990), there also appears to be a link between selectivity in raw material and the number of tool modifications applied to the stick- or stalk-tools before initiating the task. The uniformity of this relationship within a single chimpanzee community across different stick- or stalk-use behaviours may well represent a cultural community-wide pattern of behaviour. Further studies of stick- or stalk-use behaviours and the tool-manufacturing process within other chimpanzee communities are required though before such a pattern of cultural variation can be confirmed.

In addition, this study indicated that the frequency of further tool modifications, while the behaviour is in progress, also closely depends on whether the chimpanzee is able to foresee the tool requirements before initiating the task at hand.

Although tools employed for a same purpose between chimpanzee communities may show similarities, such as straightness, these are likely be imposed by environmental or task constraints. Nevertheless, tools used for a same purpose across different chimpanzee communities may also differ in many respects. In their study of differences in tools used to obtain termites (*Macrotermes* sp.) between three populations of chimpanzees, McGrew *et al.* (1979) proposed bark-peeling, end use and plant type choice to represent cultural preferences, prevailing over environmental demands. This study confirms that plant type choice and degree of bark-stripping may well represent cross-cultural differences; whereas variables such as tool length and width may rather be environmentally determined.

Although no evidence for differences in end use, i.e. whether only one or both ends of the tool are employed, between Bossou, Yealé and Seringbara emerged in this study; this does not necessarily preclude this aspect of tool-use from being a possible cultural variant. End-use was shown though to be highly dependent on plant type material used and possibly the distal and proximal diameter of the tool.

Finally, more detailed studies at different sites focusing on tool-choice and tool-making are urgently required to elucidate their propensity for cultural variation.

Chapter 8

Laterality in hand use and efficiency in tool-use

8.1 Introduction

The terminology related to the topic of laterality in hand use employed in the following chapter will follow that proposed by McGrew and Marchant (1996) (See Table 8.1 and Fig 8.1).

Table 8.1 Terminology employed when addressing laterality of hand function in terms of tasks and subjects (from McGrew and Marchant, 1996).

	SUBJECT(S)	
	Within	**Across**
TASK(S)		
Within	Hand preference	Task specialisation
Across	Hand specialisation	Handedness

Laterality of function, whether behavioural or physiological, has been presented as being crucial to the understanding of the evolution of human cognition (Corballis, 1989; Bradshaw and Rogers, 1993) and language (Frost, 1980, Corballis, 1989, 1991; Greenfield, 1991). Humans (*Homo sapiens*) have long been known to be overwhelmingly right-handed (90%) at the species level (Annett, 1972). Manual specialisation has been proposed as the first step in the evolution of left-hemisphere specialisation that is characteristic of humans and thought to be an important neural and functional development that sets humans apart from other animals (McNeilage *et al.*, 1987).

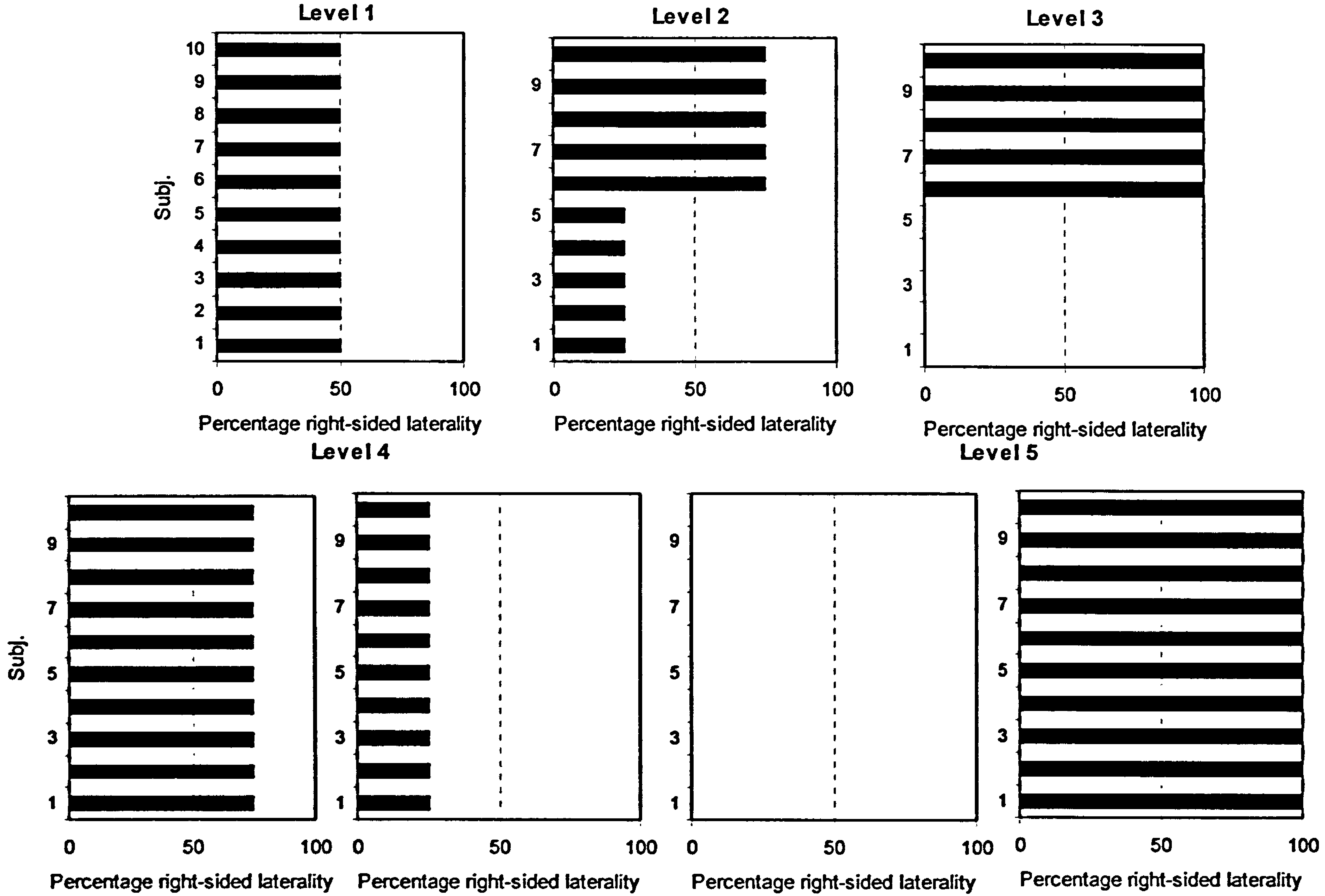
McGrew and Marchant (1994) showed that the number of reported left-handers in a given human population varies between 0-23%. In addition, Marchant *et al.*'s (1995) study of human handedness among three traditional cultures based on cinematic archives revealed that common non-tool-use activities, involving both object and non-object manipulation, were unlateralised. In contrast, less skilled tool-use with a power grip showed Level 4 laterality and only skilled tool-use with precision grip was at level 5 with 55% of the 58 individuals observed being exclusive right-handers and 38% ambilateral (see Fig. 8.1 for definition of Levels).

Until 1987, relatively few studies had addressed the issue of laterality in hand use in non-human primates. Many were anecdotal or flawed by having too few subjects and by failing to acknowledge the problem of independence of data points, thus presenting inflated sample sizes, yielding significant differences where possibly none existed (McGrew and Marchant, 1997a). The issue of laterality in non-human primates experienced a resurgence following MacNeilage *et al.*'s (1987) provocative and stimulating reassessment of the behavioural laterality of hand function in the order Primates. The authors put forward the so-called "postural origins theory" which aimed at predicting population-level handedness, as well as explaining the evolutionary origins of right-handedness in the Order Primates. This theory, which as since been disproved, proposed that non-human primates show a left-hand specialisation for visually guided reaching, while exhibiting a right-hand specialisation for manipulation among the more recently evolved terrestrial primates, and for postural support and stabilisation in more primitive, arboreal primates.

Laterality in hand use among chimpanzees

Most major studies of laterality of hand use in apes have focused on chimpanzees and on captive subjects rather than wild ones. Furthermore, almost all wild great ape studies on laterality in hand use have concentrated on the chimpanzee (McGrew and Marchant, 1997a). Most field studies have focused on skilled object manipulation, such as tool-use, while most captive studies have focused on simpler motor patterns such as reaching (McGrew and Marchant, 1996). The majority of these

Fig 8.1. Levels of lateralisation illustrated through hypothetical, extreme distribution of ten subjects (from McGrew and Marchant, 1996). *Level 1*: All subjects ambilateral; *Level 2*: Half the subjects significantly lateralised to the left and half to the right; *Level 3*: Half the subjects exclusively to the left and half to the right; *Level 4*: Either all subjects significantly to the left or to the right; *Level 5*: All subjects exclusively to the left or to the right.



studies present no evidence for overall dominance of the right hand or the left hand (Nishida and Hiraiwa, 1982; Marchant, 1983; Heestand, 1986; Boesch, 1991a; Hopkins, 1993; Sugiyama *et al.*, 1993b; Tonooka and Matsuzawa, 1995; Marchant and McGrew, 1996). Indeed, so far, no compelling evidence exists in chimpanzees or other non-human primates of population-level handedness or even task specialisation (McGrew and Marchant, 1997a), although a few captive studies suggest otherwise (e.g. Hopkins, 1994b).

However, wild chimpanzees were found to be individually highly lateralised for tool-use tasks, which, compared to simple reaching tasks, require greater motor complexity. Level 3 laterality (see Fig. 8.1) was seen in tool-use activities such as wadge-dipping (Boesch, 1991a), nut-cracking (Boesch, 1991a; Sugiyama *et al.*, 1993b; Matsuzawa, 1996), termite-fishing and food pounding (Marchant and McGrew, 1996). For example, in Boesch (1991a)'s study at Taï, Côte d'Ivoire, where wild chimpanzees use stone or wooden hammers to crack five different species of nuts, 49% of adults (22/45) used one hand exclusively to hammer nuts. Sugiyama *et al.* (1993b) and Matsuzawa (1996) recorded a similar pattern of laterality in the wild chimpanzees of Bossou. At Bossou, all adult chimpanzees observed nut-cracking (N=14) consistently used the same hand to crack open oil-palm nuts (*Elaeis guineensis*) (Sugiyama *et al.*, 1993b; Matsuzawa, 1996, 1999). Moreover, McGrew *et al.* (1999) published a study on manual laterality among the chimpanzees of Gombe, cracking *Strychnos* fruit using an anvil stone, and also found Level 3 laterality of function in anvil use (see Fig 8.1). Finally, none of the studies focusing on tool-use and laterality in hand use in the wild revealed task specialisation whether to the left or to the right (McGrew and Marchant, 1997b).

Captive studies of laterality in hand use in tool-use tasks are fewer. Hopkins *et al.* (1993) showed that for aimed throwing, 12 of 21 captive chimpanzees of all ages normally made exclusive use of one hand. However, Marchant's (1983) study of 27 captive chimpanzees living on islands in Lion Country Safari Park, Florida, indicated that subjects were only mildly lateralised for throwing. However, this study, in contrast to Hopkins *et al.*'s (1993), included bouts of non-aimed throwing, which is considered to require less skill than aimed throwing. Therefore, the limited results from captive studies focusing on more complex tasks are congruent with findings from the wild, suggesting high levels of individual preference in hand use and often exclusive use of one hand, but lacking evidence for task specialisation.

One study of wild chimpanzees failed to show a high level of individual lateralisation during a tool-use task. At Mahale in Tanzania, Nishida and Hiraiwa (1982) showed that most individuals involved in fishing for arboreal wood boring ants (*Camponotus* spp.) were ambilateral. However, the data set was small and based on relatively few bouts of the behaviour. McGrew and Marchant (1996), thus, suggested that only terrestrial tool-uses so far present patterns of Level 3 lateralisation. However, this lateralisation in wild chimpanzees is expressed by strong individual hand preferences rather than task specialisation across individuals (see Table 8.1).

For bouts of simple reaching, studies indicate that wild chimpanzees are relatively unlateralised (Boesch, 1991a; Sugiyama *et al.*, 1993b; Marchant and McGrew, 1996; McGrew and Marchant, 2001). However, studies in laboratories and zoos reveal a more heterogeneous picture. Simple reaching to pick up food items may be unlateralised (Heestand, 1986); mildly lateralised (Marchant, 1983; Steiner, 1990; Hopkins, 1993; Christel, 1994; Hopkins, 1995b; Tonooka and Matsuzawa, 1995), highly lateralised but not exclusively so (Finch, 1941; Aruguette *et al.*, 1992; Hopkins, 1994a; Colell *et al.*, 1995; Lacreuse *et al.*, 1999), or highly lateralised, including nearly 20% of the subjects displaying exclusive hand use (Hopkins, 1995b), depending on the population studied. However, it must be noted that many of these studies cited above have been plagued by methodological problems and their conclusions has since been questioned (*cf.* McGrew and Marchant, 1997a; Palmer, 2002).

Nevertheless so far, studies of laterality in both captive and wild chimpanzees hint towards higher lateralisation (Level 3) for complex behaviours, and ambi-preference (Level 1) for simpler reaching tasks, although some may also show Level 2 laterality.

Only a few studies have focused on hand specialisation and the inter-correlation in hand use across tasks. Hopkins (1994b) showed in a study of captive chimpanzees at the Yerkes Primate Research Center, Atlanta, USA, that four measures of hand preferences (quadrupedal reaching, bipedal reaching, bimanual feeding and throwing) were positively significantly correlated with each other, while one measure, coordinated bimanual actions, did not correlate with any of the remaining measures. In Sugiyama *et al.*'s (1993b) study of the Bossou chimpanzees, all 10 subjects who showed a hand preference in food picking exhibited exclusive use of that same hand for hammering nuts. McGrew *et al.* (1999) explored laterality at Gombe, Tanzania, within individuals across two tasks - *Strychnos* pounding and termite-fishing - and found a remarkable congruence in hand use at the individual level. Boesch (1991a) also compared individual hand preferences in skilled object manipulation across tasks – hammer use in nut-cracking and wadge-dipping – among 16 Taï chimpanzees. However, he did not find any consistency across tasks. Indeed, only 3 of the 16 chimpanzees showed the same level of consistency, i.e. always left, significantly left, ambi-preferent, significantly right, always right (c.f. McGrew and Marchant, 1999), for both activities. Three reversed their hand preference across tasks, while the remaining 10 did not vary significantly. Therefore, although there is some evidence in chimpanzees for hand specialisation across tasks, the evidence remains weak.

Laterality and efficiency in tool-use behaviour

Although a few studies in the wild have focused on exclusivity of hand use, most studies of laterality in non-human primates have primarily been concerned with preference in hand use at the population level, based on the benchmark of human right-handedness. However, the selective advantages of lateralisation have rarely been addressed. Although not as lateralised as was once thought, *Homo sapiens* nevertheless evolved an extreme degree of lateralisation in structure and function (Hopkins, 1996). How has natural selection acted upon this trait, which seems to be highly derived? What are the benefits of being lateralised? Are more lateralised individuals fitter than ambi-preferent ones? As McGrew and Marchant (1997a, p.201) pointed out: "Why should any primate constrain its manipulatory options by biasing its manual functions?[...] Notable benefits must be gained via natural selection if it favours such a handicap."

Unfortunately, only a handful of studies have addressed the efficiency of performance in hand use and only a few have been carried out on chimpanzees. Butler *et al.* (1995) studied the relative efficiency of preferred and non-preferred patterns of lateralised feeding on bamboo in the gentle lemur (*Hapalemur griseus*) and found that preferred patterns of bamboo processing were done faster than non-preferred ones. Fragaszy and Mitchell (1990) found, in capuchin monkeys (*Cebus apella*) performing unimanually or bimanually, a negative correlation between latency to perform a problem-solving task and the degree of hand preference. Hopkins *et al.* (1992) found that rhesus macaques (*Macaca mulatta*), who preferred their right hand , performed better than subjects who preferred their left hand, during a video game joystick task. Rigamonti *et al.* (1997) showed in pigtailed macaques (*Macaca nemestrina*) that the preferred hand made fewer errors in a simulated foraging task, which involved removing embedded food pellets, than the non-preferred hand. King (1995) showed that cotton-top tamarins (*Saguinus oedipus*) reaching to get food-items from a moving turntable were more accurate with their preferred hand, and the more lateralised individuals made fewer errors. Finally, King and Landau (1993) found that in squirrel monkeys (*Saimiri* sp.) reaching to catch live goldfish from a pool, more lateralised individuals caught more fish than their less lateralised counterparts.

McGrew and Marchant (1999) explored the extractive profiency of wild chimpanzees during episodes of termite-fishing at Gombe. Gombe chimpanzees had previously been noted to vary in the extent of lateralisation on this tool-use task (McGrew and Marchant, 1996). Three aspects of payoff in termite fishing, i.e. efficiency, rate of success and error rate, were contrasted between two subsets of chimpanzees, those observed exclusively to use one hand or the other versus those who used both. The authors tested the hypothesis that chimpanzees using only one hand were more efficient and successful and less error-prone than those using both hands, based on the assumption that more lateralised individuals had a more skilful and practised hand. They found that exclusively lateralised individuals were more efficient, gathering more prey per unit effort, than incompletely lateralised chimpanzees. However, the former were not more successful or less error prone than the latter. Thus, this study partly supports the suggestion that "more energetically efficient foragers will be advantaged by natural selection, thus resulting in progressively greater lateralisation over evolutionary time" (McGrew and Marchant, 1999, p.510).

Only two other studies on wild chimpanzees have addressed the issue of relative efficiency in a tool-use behaviour in relation to lateralisation. Nishida (1973) recorded the relative efficiency of an ambilateral sub-adult female chimpanzee fishing for arboreal wood-boring ants (*Camponotus* spp.) and uncovered no difference in the duration of fishing cycles between her right versus left hand. Günther and Boesch (1993) carried out a detailed video analysis of the energetic efficiency of nut cracking based on a right-preferent adult male. However, both these studies failed to provide data on more than one subject and, therefore, to address variation in efficiency across individuals exhibiting different levels of lateralisation.

Human children (Rudel *et al.*, 1984), adolescents (Deuel and Moran, 1980), and adults (Annett, 1970) also routinely perform better with their preferred hand than their non-preferred hand in a range of manual tasks.

8.2. Aims

-Age-class differences in efficiency on three tool-use behaviours, i.e. ant-dipping, nut-cracking and pestle pounding, were explored. Several measures reflecting efficiency in performance were employed and compared between adults and sub-adults. The hypothesis being tested here is that adults are more efficient, successful and less error prone at performing these behaviours than sub-adults.

-Laterality in hand function was analysed within and between the three tool tasks. Age differences in laterality were also explored. The main questions addressed here were: Is there any evidence for task specialisation or hand specialisation among the chimpanzees of Bossou? What is the level of lateralisation exhibited by ant-dipping and pestle pounding? How does it compare with nut-cracking which is recognised as the most cognitively complex task of the three?

-For tool-use behaviours providing a sufficient sample size for comparison, efficiency in behaviour, between those individuals who were exclusive in their hand use and those who were not, was compared. The hypothesis being tested here is that exclusive handers are more efficient, successful or less error prone in performing the task than non-exclusive handers.

8.3 Method and data analysis

Laterality data on hand use were obtained for three tool-use behaviours observed among Bossou chimpanzees based on both observations and video recordings. These behaviours included: (1) ant-dipping for driver ants (*Dorylus spp.*) (2) nut-cracking of oil-palm nuts (*Elaeis guineensis)* and (3) pestle pounding. For a detailed description of these behaviours refer to *Chapter 2* for nut-cracking and pestle pounding and *Chapter 6* for ant-dipping. Most of the data, collected between June-August 1995, June-September 1997 and August-October 1999, were obtained through *ad lib.* behavioural sampling. Thus, 5 non video-recorded sessions were obtained for ant-dipping and 15 for nut-cracking.

Between June and September 2000 and June and September 2001, video records were made of these behaviours on an opportunistic basis using a Sony DCR-TRV20 digital camera, and in October 1997, a few ant-dipping and nut cracking sessions were filmed using a Sony Hi8 video camera. Some video data of ant-dipping were donated by G.Yamakoshi. These were collected between August and October 1999 using a Sony DCR-TRV9 digital camera, while one ant-dipping session was recorded in August 1999 by G. Ohashi.

Age-class categories followed those employed by Sugiyama (1999): 1) Infant (1-3 years old); 2) Juvenile (4-7 years old); 3) Adolescent (8-11 years old) and 4) Adult (>11 years old). However, due to an insufficient number of individuals within each age-class, two broader age categories were compared: 1) Adults versus 2) Sub-adults, comprising adolescents and juveniles.

To ensure independence of data points, only bouts of tool-use or of reaching events, rather than each individual act, were incorporated into the data analysis (*sensu* McGrew and Marchant, 1996). As previously described in *Chapter 6*, a *session* is defined as a period during which at least one chimpanzee is engaged in tool behaviour; the session is terminated when the last remaining chimpanzee of the subgroup ends tool-use. A *bout* is "a period during which an individual is engaged in tool-using behaviour", represented by elements of the tool-task being performed, separated by intervals when no tool is held (when relevant), the hand performs an intervening activity, such as self-grooming or suckling, or when the chimpanzee changes position (McGrew and Marchant, 1992, p.115).

For single-handed bouts, each individual contributing enough data (minimum of 6 bouts) was assigned to a laterality class (*sensu* McGrew and Marchant, 1996). Classes 'all left' and 'all right' refer to exclusive use of that hand for a given task; 'significant left' and 'significant right' refer to a statistically significant preference for that hand in that task; 'ambilateral' refers to the interchangeability of the two hands whereby there is no statistical difference between right and left (McGrew and Marchant, 1996). Such categorical classification was established on the basis of a Binomial test, whose standard measure is the *z*-score, (Siegel and Castellan, 1988) for samples sizes from 6-10, and a chi-square test for samples of 10 and above (Byrne and Byrne, 1991). All statistical tests performed on the data were two-tailed and the level of significance was $p=q=0.05$.

For all statistical analyses, the data were checked for normality using a normality probability plot and a Kolmogorov-Smirnov test. Non-parametric or parametric tests were then employed as appropriate. Independent sample *t*-tests were adjusted, if equal variance between the samples could not be assumed, as tested by a Levene's test for equality of variance.

One adult female, Fana, was excluded from the data set since she has a dislocated left shoulder, which severely limits the extent to which she can use her left arm. She was, nevertheless, observed to perform all three tool-use tasks considered here, relying on exclusive use of her right hand. No sex comparisons were carried out due to an insufficient sample set of adult males (N=2) within the Bossou community

To look at efficiency in relation to laterality within the three tool-use behaviours analysed, two subsets of chimpanzees, those exclusively committed to one hand or the other versus those who were not, were compared. Only one-handed bouts were considered in this analysis. Different measures reflecting foraging success were calculated, appropriate to the tool-task being analysed. These measures were based on the video data, which were more accurate than the observational data. Thus, observational data were only used to provide additional information on individual laterality in hand use. All of the video data were analysed two or three times by myself and, for ant-dipping only, 14 of the 24 sessions were also analysed by a second observer blind to the hypotheses being tested. In this case, any divergences in scoring were reviewed by both observers until a consensus was reached.

Ant-dipping

For statistical purposes, only data from individuals, for which a minimum of 6 bouts and 20 dips (to avoid small sample size effects) were recorded, were retained for analysis (see Table 8.2). Observational data served to complement laterality data from the video recordings (see Table 8.2).

The following measures reflecting foraging success were calculated for each individual chimpanzee:

- *Dipping rate*:

The rate of dipping (No. Dips/Min.) was calculated as the ratio of the total number of dips over the total time spent ant-dipping in minutes.

- *Efficiency*:

Ant-dipping efficiency, i.e. the number of ants gathered per minute, was calculated for each individual chimpanzee based on the assumption that each dip yielded an average of 50 ants (refer to *Chapter 6* for origin of this value). The equation used was as follows:

$$\textit{Ants/Min.} = (\text{Dips/Min.}) * [(\text{Successful dips} * 50)/(\text{Total No. of Dips})]$$

- *Error rate*:

$$\textit{\%ER} = [(\text{Total No. of withdrawals yielding no ants})/\ (\text{Total No. of withdrawals})] * 100$$

Table 8.2. List of individuals included in the ant-dipping analysis (in parentheses: data acquired from observations rather than video).

Name	Age Class	Sex	No. Sessions	No.Bouts	No. Dips	Total Time Dip (sec.)
Foaf	Adult	Male	8	15	37	1329
Jire	Adult	Female	3	6	34	1198
Kai	Adult	Female	3 (2)	6 (3)	34	864
Nina	Adult	Female	1	12	27	941
Tua	Adult	Male	5	9	69	1539
Velu	Adult	Female	3	9	54	1311
Yo	Adult	Female	10 (2)	79 (5)	290	8470
Fotayu	Adolescent	Female	3 (1)	7 (13)	23	2240
Nto	Adolescent	Female	3	49	65	3644
Vuavua	Adolescent	Female	5(1)	30 (8)	66	3515
Vui*	Adolescent	Male	1(1)	5(3)	8	290
Yolo	Adolescent	Male	7	48	129	5008
Juru	Juvenile	Female	11(1)	76 (11)	195	7957

*Not included in the foraging success analysis since performed less than 20 dips, but considered when exploring laterality in hand use since number of bouts is greater than or equal to 6.

Nut-cracking

Only individuals who cracked at least 10 nuts and for which a minimum of 6 bouts was recorded were retained for analysis (see Table 8.3). Although two individuals did not have 6 bouts on video, they were still included in the analysis, supplementing their data set with observational data (see Table 8.3).

Table 8.3. List of individuals employed in the nut-cracking analysis (in parentheses: data acquired from observations rather than video).

Name	**Age Class**	**Sex**	**No. Sessions**	**No.Bouts**	**Total No. of Nuts**	**Time Crack (sec.)**
Foaf	Adult	Male	17 (7)	58 (10)	526	11093
Jire	Adult	Female	6 (2)	33 (26)	78	1246
Kai	Adult	Female	2 (1)	4 (3)	18	363
Pili	Adult	Female	1(4)	2(41)	10	316
Tua	Adult	Male	5 (4)	21 (17)	10	177
Yo	Adult	Female	3 (1)	46 (34)	109	3690
Vuavua	Juvenile/Adolescent	Female	9(1)	35(3)	76	2430
Vui	Adolescent	Male	11 (8)	60 (45)	82	2139
Fotayu	Juvenile	Female	2 (2)	5 (11)	36	1136
Nto	Juvenile	Female	2 (1)	17 (10)	17	1320
Yolo	Juvenile/Adolescent	Male	11 (4)	47(17	166	5442

Four individual measures of foraging success during episodes of nut-cracking were calculated:

- *Hits per nut*: Average Number of hits required per nut cracked (*sensu* Boesch and Boesch,1981)
- *Nuts per minutes*: Number of nuts (includes empty nuts and nuts yielding a kernel within) cracked per minute (*sensu* Boesch and Boesch, 1981)
- *Rate of success*: Number of nuts, yielding an edible kernel, cracked per minute
- *Error rate*: Number of bad nuts, i.e. yielding a rotten kernel or none at all, divided by the total number of nuts cracked.

Pestle-pounding

For pestle pounding, only individuals exhibiting a minimum of 6 pounding episodes and 10 extracting bouts were used to calculate measures reflecting foraging success (see Table 8.4)

Table 8.4. List of individuals employed in the pestle pounding analysis.

Name	Age Class	Sex	No. Sessions	No. Pound Bouts	No. Extract Bouts	Total Time (sec.)
Foaf	Adult	Male	2	9	10	527
Jire	Adult	Female	4	17	17	1065
Kai	Adult	Female	10	47	33	3272
Nina	Adult	Female	8	53	48	5367
Tua	Adult	Male	6	30	19	1949
Velu	Adult	Female	7	16	14	1574
Fotayu	Adolescent	Female	12	71	54	5011
Nto	Juvenile/Adolescent	Female	10	31	36	3126
Poni	Adolescent	Male	2	16	17	882
Vua	Adolescent	Female	3	13	8	994
Juru	Juvenile	Female	28	136	176	13121

The following measures were used as estimates of foraging success in pestle pounding:

- *Pounding rate*: Number of pounds per total time spent pounding in minutes. This measure aims to reflect individual ability for pounding rapidly and effectively.
- *Number of pounds per extraction minute*: The assumption for this measure is that the fewer pounds required per extraction minute, the more efficient the individual.
- *Time spent extracting per extraction*: Time spent extracting begins when the chimpanzee inserts one arm into the excavated cavity to extract the softened palm heart and ends when it stops consuming on the palm product thus obtained from this single bout of extraction. Time spent extracting per pestle pounding bout reflects the quantity of product obtained: longer times will mean a larger handful of product, which also takes longer to consume. Actual time spent extracting per bout was found to be significantly positively correlated with time spent eating on the mashed palm heart for each the 11 subjects analysed (see Table 8.5).

Table 8.5. Correlation between actual time spent extracting (sec.) and time spent feeding (sec.) per bout of pestle pounding for each the 11 subjects included in the analysis.

Name	**Two-tailed Spearman Rank Correlation**
Foaf	R_s=0.986; N=6; ρ<0.001
Fotayu	R_s=0.928; N=6; ρ<0.01
Jire	R_s=0.886; N=6; ρ<0.05
Juru	R_s=0.986; N=6; ρ<0.001
Kai	R_s=0.986; N=6; ρ<0.001
Nina	R_s=0.812; N=6; ρ=0.05
Nto	R_s=0.943; N=6; ρ<0.01
Poni	R_s=0.829; N=6; ρ<0.05
Tua	R_s=0.943; N=6; ρ<0.01
Velu	R_s=0.996; N=6; ρ<0.001
Vuavua	R_s=0.900; N=6; ρ<0.05

8.4. Results

Age-class differences in efficiency

Ant-dipping

No differences on total ant-dipping duration (t(10)=-0.358; *n.s.*) and on total number of dips performed (t(10)=-1.502; *n.s.*) emerged between adults (N=7) and sub-adults (N=5) (see Table 8.2). It is in this context that the two age categories were compared on ant-dipping efficiency, success and error rate thus focusing on relative performance rather than absolute frequency (see Table 8.6).

Table 8.6. Ant-dipping performance measures for each individual chimpanzee.

Name	Age Class	Sex	Dips/Min	Ants/Min	%Error Rate
Tua	Adult	Male	2.7	133.2	1.5
Velu	Adult	Female	2.5	124.2	0.0
Kai	Adult	Female	2.4	118.6	0.0
Yo	Adult	Female	2.1	101.8	1.4
Nina	Adult	Female	1.7	86.5	0.0
Jire	Adult	Female	1.7	85.6	0.0
Foaf	Adult	Male	1.7	83.9	0.0
Yolo	Adolescent	Male	1.6	74.6	3.9
Vuavua	Adolescent	Female	1.1	54.9	3.0
Nto	Adolescent	Female	1.1	50.5	6.2
Fotayu	Adolescent	Female	0.6	31.0	0.0
Juru	Juvenile	Female	1.5	71.6	3.1

Adults displayed a significantly greater dipping rate (dips/min.) than sub-adults (see Table 8.7). In addition, adults gathered significantly more ants per minute and were less error prone than sub-adults (see Table 8.7). Thus, on all three measures reflecting foraging success, adults were superior to sub-adults.

Table 8.7. Comparison of ant-dipping performance between adults and sub-adults.

Measure	Age category	No.	Mean	Range	SD	T-Test
Dips/Min.	Adult	7	2.1	1.7-2.7	0.4	t(10)=3.964;
	Sub-adult	5	1.2	0.6-1.6	0.4	ρ<0.01
Ants/Min.	Adult	7	104.8	83.9-133.2	20.5	t(10)=4.248;
	Sub-adult	5	56.5	31.0-74.6	17.7	ρ<0.01
%ER	Adult	7	0.4	0-1	0.7	t(10)=-3.229;
	Sub-adult	5	3.2	0-6	2.2	ρ<0.01

Overall, there was a significant degree of concordance within individuals in their rank in foraging success based on the measures used for ant-dipping (Kendall coefficient of concordance, k=3; df=11; w=0.732; ρ<0.05). However, percentage error rate was not correlated with either the number of ants harvested per minute (two-tailed Pearson rank Correlation: R=-0.412; N=12; *n.s*) or the number of dips per minute (two-tailed Pearson rank Correlation: R=-0.376; N=12; *n.s*).

Nut-cracking

Six adults and 5 sub-adults were compared in their performance measures for nut-cracking (see Table 8.8). The variables used for the calculation of the measures did not differ significantly between adults and sub-adults (total nut-cracking duration: t(9)=0.157; *n.s.*; number of hits: t(9)=-0.145; *n.s.*; number of nuts: t(9)=0.533; *n.s.*; number of good nuts cracked: t(11)=0.516; *n.s.*) (see Table 8.3). Therefore, although the data were collected *ad lib,* when comparing the two age-groups, the issue addressed was once again relative performance rather than absolute frequency.

Table 8.8. Nut-cracking performance measures for each individual chimpanzee who cracked a minimum of 10 nuts.

Name	**Age Class**	**Sex**	**Nuts/Min.**	**Good Nuts/Min.**	**Hits/Nut**	**%Error rate**
Jire	Adult	Female	3.8	2.5	3.5	34.6
Tua	Adult	Male	3.4	2.4	4.4	30.0
Kai	Adult	Female	3.0	1.3	3.1	55.6
Foaf	Adult	Male	2.8	2.5	2.3	13.3
Pili	Adult	Female	1.9	1.9	5.0	0.0
Yo	Adult	Female	1.8	1.5	4.7	14.7
Vui	Adolescent	Male	2.3	1.8	3.6	19.6
Yolo	Juvenile/Adolescent	Male	1.8	1.6	5.8	10.8
Vuavua	Juvenile/Adolescent	Female	1.9	1.4	5.5	25.0
Fotayu	Juvenile	Female	1.9	1.4	5.1	25.0
Nto	Juvenile	Female	0.8	0.5	6.3	35.3

Adults cracked significantly more nuts per minute than sub-adults (see Table 8.9). However, adults failed to crack significantly more good nuts per minute than sub-adults (see Table 8.9). In addition, sub-adults required significantly more hits per nut than adults, while there was no significant difference in error rate between them (see Table 8.9).

Table 8.9. Comparison of nut-cracking performance between adults and sub-adults.

Measure	**Age Category**	**No.**	**Mean**	**Range**	**SD**	**T-Test**
Nuts/Min.	Adult	6	2.8	1.8-3.8	0.8	t(11)=2.448;
	Sub-adult	5	1.7	0.8-2.3	0.6	**ρ<0.05**
Good nuts/Min	Adult	6	2	1.3-2.5	0.5	t(11)=2.164;
	Sub-adult	5	1.3	0.5-1.8	0.5	ρ=0.059
Hits/Nut	Adult	6	3.8	2.3-5.0	1.1	t(11)=-2.276;
	Sub-adult	5	5.3	3.6-6.3	1.0	**ρ<0.05**
%Error	Adult	6	24.7	0-55.6	19.6	t(11)=0.163;
	Sub-adult	5	23.1	10.8-35.3	8.9	*n.s.*

There was a significant degree of concordance within individuals in their rank in foraging success based on the measures used (Kendall coefficient of concordance, *k*=4; *df*=10; *w*=0.483; ρ<0.05). The measure of nuts cracked per minute was significantly correlated with good nuts per minute (two-tailed Pearson rank Correlation: R=0.806; N=11; ρ<0.01) and number of hits per nut (two-tailed Pearson rank Correlation: R=-0.751; N=11; ρ<0.01). The number of hits per nut was also correlated with the number of good nuts cracked per minute (two-tailed Pearson rank Correlation: R=-0.654; N=11; ρ<0.05). However, none of these measures correlated significantly with percentage error rate (two-tailed Pearson rank Correlation: nuts/min: R=0.328; N=11; *n.s.*; good nuts/min.: R=-0.273; N=11; *n.s.* and hits/nut: R=-0.200; N=11; *n.s.*).

Pestle pounding

Six adults and 5 sub-adults were compared (see Table 8.4). The variables employed in the calculation of the performance measures did not differ significantly between the two age categories (Time pounding: t(9)=-1.025; *n.s.*; No. of pounds: t(9)=-0.714; *n.s.*; Time extract: t(9)=-0.995; *n.s.*; No. of extractions: t(9)=-1.384; *n.s.*). The analysis was therefore once again based on relative performance rather than absolute frequency (see Table 8.4).

Table 8.10. Pestle pounding performance measures for each individual chimpanzee.

Name	Age Class	Sex	Pounding rate	No. Pounds per Extraction Time (min.)	Time per Extraction (sec.)
Velu	Adult	Female	63.8	11.1	53.9
Tua	Adult	Male	60.0	11.9	47.3
Kai	Adult	Female	54.9	7.05	46.2
Nina	Adult	Female	60.7	17.0	42.7
Jire	Adult	Female	60.0	19.0	30.8
Foaf	Adult	Male	63.2	17.0	23.6
Nto	Juvenile/Adolescent	Female	45.4	17.2	29.2
Vua	Adolescent	Female	60.0	28.5	34.0
Fotayu	Adolescent	Female	51.2	11.8	27.7
Poni	Adolescent	Male	60.0	11.9	19.9
Juru	Juvenile	Female	53.0	5.9	33.6
Nto	Juvenile	Female	39.7	30.9	24.5

No significant difference between the two age categories was observed in the three measures of performance used. However, there was a tendency for adults to show a higher pounding rate than sub-adults (see Table 8.11). In addition, adults tended to spend more time extracting per extraction than sub-adults (see Table 8.11).

Table 8.11. Comparison of pestle pounding performance between adults and sub-adults.

Measure	Age category	No	Mean	Range	SD	T-Test
Pounding Rate	Adult	6	60.4	54.9-63.8	3.1	t(9)=2.255;
	Sub-adult	5	53.9	45.4-60.0	6.2	p=0.051
No. pounds/ Extraction Minute	Adult	6	13.8	7.0-19.0	4.6	t(9)=-0.304;
	Sub-adult	5	15.1	5.9-28.5	8.5	*n.s.*
Time/Extraction (sec.)	Adult	6	39.6	23.6-53.9	12.8	t(9)=2.115;
	Sub-adult	5	28.9	19.9-34.0	5.7	*n.s.*

There was no significant concordance between individual ranks across the three measures of performance used (Kendall coefficient of concordance, *k*=3; *df*=11; *w*=0.160; *n.s.*). Moreover, none of the performance measures used were significantly correlated with each other (two-tailed Pearson rank Correlation: pounding rate and number of pounds per extraction time: R=0.214; N=11; *n.s.*; pounding rate and time spent per extraction: R=0.21; N=11; *n.s.*; number of pounds per extraction time and time spent per extraction: R=-0.279; N=11; *n.s.*).

Laterality in hand function within and between tool tasks

Ant-dipping

Table 8.12. shows the raw frequencies for all 14 subjects presenting enough data to carry out individual statistical testing. Seven of the 14 (50%) subjects showed hand preferences: 5 to the right and 2 to the left (see Table 8.12). For those individuals showing a hand preference in ant-dipping, there was a tendency to use the right hand; however, this trend fell short of significance (Binomial test; *n.s.*). Of these individuals, 1 used the right hand exclusively and 2 used the left exclusively, thus only 21% showed exclusivity in hand use (see Table 8.16). Seven (50%) individuals were ambi-preferent.

But considering that handedness might vary according to the age of the individual (Boesch, 1991a), handedness among adults only was further analysed. Five of the 7 (71%) adults showed hand preference in ant-dipping, one exclusively to the right and two significantly towards the right, and two exclusively to the left (see Tables 8.12 and 8.16). Thus, 43% of adults showed exclusive use of one hand when engaged in ant-dipping.

There was no difference in the number of adults and sub-adults exhibiting either exclusivity in hand use or significant preference in hand use (see Table 8.12).

Table 8.12. Relative frequency of left or right hand use and handedness index for ant-dipping.

Name	Age Class	Right Bout	Left Bout	Significance	Lat. Class
Velu	Adult	9	0	**	1
Yolo	Juvenile(Adolescent)	11 (37)	0(11)	***	2
Yo	Adult	77	7	***	2
Tua	Adult	8	1	*	2
Juru	Juvenile	53	23	**	2
Fotayu	Juvenile(Adolescent)	4(7)	9(0)		3
Jéjé	Infant	5	1		3
Vuavua	Juvenile(Adolescent)	4(15)	4(15)		3
Foaf	Adult	8	7		3
Nto	Adolescent	26	23		3
Vui	Adolescent	4	4		3
Nina	Adult	6	6		3
Jiré	Adult	0	6	*	5
Kai	Adult	0	9	**	5

Laterality Class: 1: all right, 2: significant right; 3: ambi-preferent; 4: significant left; 5: all left, based on two-tailed binomial test for n: 6-10 and chi-square test for n>10 with $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$.

Nut-cracking

Nut-cracking contrasted markedly with ant-dipping with regards to laterality in hand function. Table 8.13 shows the raw frequencies for all 13 individuals for which a minimum of 6 bouts was recorded. All subjects, regardless of age-class, showed significant hand preferences: 7 to the right and 6 to the left (see Table 8.16). Of these, 6 used the right hand exclusively and 4 employed the left exclusively. Only one adult, Foaf, did not show exclusivity in hand use, however he was significantly biased to the right. Finally, there was no evidence for task specialisation towards either the right or the left (Chi-square test: $\chi^2(1, N=13)=0.077$; *n.s.*), but there was a strong lateralisation in hand use, whereby 77% (10/13) of the subjects showed exclusive use of one hand (Chi-square : $\chi^2(1, N=13)=3.769$; $p=0.052$).

Table 8.13. Relative frequency of left or right hand use and handedness index for nut-cracking.

Name	Age-Class	Right Bout	Left Bout	Significance	Lat. Class
Kai	Adult	7	0	*	1
Pili	Adolescent(Adult)	31(12)	0(0)	***	1
Velu	Adult	7	0	*	1
Na	Adolescent	29	0	***	1
Fotayu	Juvenile	16	0	***	1
Nto	Juvenile	27	0	***	1
Foaf	Adult	66	2	***	2
Vuavua	Juvenile(Adolescent)	5(0)	18(15)	***	4
Vui	Adolescent	3	102	***	4
Yolo	Juvenile(Adolescent)	0(0)	18(46)	***	5
Jire	Adult	0	59	***	5
Tua	Adult	0	38	***	5
Yo	Adult	0	80	***	5

Laterality Class: 1: all right, 2: significant right; 3: ambi-preferent; 4: significant left; 5: all left, based on two-tailed binomial test for n: 6-10 and chi-square test for n>10 with *$p<0.05$; **$p<0.01$; ***$p<0.001$.

In terms of the ontogeny of laterality in nut-cracking, Yolo maintained exclusive use of the left hand both as a juvenile and as an adolescent, while Pili was exclusive in the use of her right hand both as an adolescent and an adult (see Table 8.13). Vuavua showed significant preference for the right hand as a juvenile and went on to express exclusive use of the right hand as an adolescent (see Table 8.13). Thus, for nut-cracking, it appears that maturation for a preference in hand use emerges early on and then develops into exclusivity in hand use for that preferred hand.

Pestle pounding

Laterality data on hand use for pounding and extracting during pestle pounding (minimum of 6 bouts) were obtained respectively on 11 and 13 chimpanzees (see Tables 8.14 and 8.15). While pounding, the tool was held either single-handedly or using both hands; in the latter case a distinction was made between which hand was positioned above the other (see Table 8.14). All individuals displayed single-handed bouts, while 5 out of 11 (45%) individuals were observed also to pound two-handedly (see Table 8.14). Two of the 3 subjects who exhibited more than 6 bouts of two-handed method demonstrated strict use of the same hand above the other (see Table 8.14). For two of the chimpanzees who performed more than 6 two-handed bouts, i.e. Kai, Velu, Juru,, the hand placed above the other was also the preferred hand when performing single-handed bouts (see Table 8.14).

If one considers single-handed bouts only, 4 out the 11 (36%) subjects (or 3/6 adults) were exclusive in their hand use, 3 (27%) (or 0/6 adults) showed a significant preference in hand use and 4 (36%) (or 2/6 adults) were ambi-preferent. Therefore, 64% of subjects were strongly laterised when pestle pounding; however, only 50% of adults (3/6) showed this pattern. Overall, no evidence for task specialisation emerged with 5 chimpanzees being right-preferent and 2 left-preferent (Binomial test; *n.s.*).

Table 8.14.Relative frequency of left-, right- and two-handed pounding bouts, based on video recordings (R/L: Right hand above left hand; L/R: Left hand above right).

Name	Age Class	Sex	Right	Left	R/L	L/R	Significance	Lat. Class
Jire	Adult	Female	16	0	0	1	***	1
Nina	Adult	Female	53	0	0	0	***	1
Nto	Juvenile(Adolescent)	Female	18 (12)	0 (1)	0	0	***	2
Juru	Juvenile	Female	82	9	36	9	***	2
Fotayu	Adolescent	Female	48	23	0	0	**	2
Foaf	Adult	Male	7	2	0	0		3
Poni	Adolescent	Male	10	5	0	1		3
Tua	Adult	Male	14	16	0	0		3
Velu	Adult	Female	3	3	10	0		3
Vua	Adolescent	Female	0	13	0	0	***	5
Kai	Adult	Female	0	14	0	33	***	5

Laterality Class and Significance (based on single handed bouts) : 1: all right, 2: significant right; 3: ambi-preferent; 4: significant left; 5: all left, based on two-tailed binomial test for n: 6-10 and chi-square test for n>10 with *ρ<0.05; **ρ<0.01; ***ρ<0.001.

Two individuals, a mother/offspring pair – Yo and Yolo – were never observed pounding. They were nevertheless observed extracting and consuming palm heart without pounding either after removing young palm fronds from the centre of the palm crown thus clearing access to the palm cavity or after climbing a palm tree which had previously been pestle pounded by another chimpanzee.

For palm extraction, 6 out of 7 (86%) adults showed a significant preference for one hand over the other (see Table 8.15). Four were exclusively right handed, one showed a significant preference for the right hand, and another for the left (see Tables 8.15 and 8.16). Four of the 6 (67%) sub-adults also showed significant use of one hand: 3 were significantly right handed, while one was significantly left handed (see Tables 8.15 and 8.16). Overall 10 out of 13 (77%) individuals showed significant lateralisation for extraction (Chi-square test: $\chi^2(1, N=13)=3.769$; $\rho=0.052$) and 5 (38%) of the subjects were exclusive in their hand use. This lateralisation showed a tendency for a right hand bias with 8 individuals being right-preferent, while only 2 were left-preferent.

There was no statistically significant difference between adults and sub-adults in the number of individuals exhibiting exclusivity in hand use (Fisher's Exact test: *n.s.*) or in the number of right- versus left-preferents for either pounding or extracting (Fisher's Exact test: *n.s.*) (see Table 8.14 and 8.15).

Table 8.15 Relative frequency of left or right hand use and laterality index for bouts of palm heart extraction during pestle pounding.

Name	Age Class	Sex	Right	Left	Significance	Lat. Class
Jire	Adult	Female	17	0	***	1
Nina	Adult	Female	48	0	***	1
Tua	Adult	Male	19	0	***	1
Velu	Adult	Female	14	0	***	1
Yolo	Adolescent	Male	10	0	***	1
Poni	Adolescent	Male	16	1	***	2
Fotayu	Adolescent	Female	51	3	***	2
Yo	Adult	Female	13	3	*	2
Vua	Adolescent	Female	7	1		3
Foaf	Adult	Male	7	3		3
Juru	Juvenile	Female	98	78		3
Nto	Juvenile (Adolescent)	Female	2(0)	19(15)	***	4
Kai	Adult	Female	1	32	***	4

Laterality Class: 1: all right, 2: significant right; 3: ambi-preferent; 4: significant left; 5: all left, based on two-tailed binomial test for n: 6-10 and chi-square test for n>10 with *$\rho<0.05$; **$\rho<0.01$; ***$\rho<0.001$.

Congruence in laterality across tasks

Table 8.17 displays the laterality of hand use for each individual chimpanzee, presenting a minimum of 6 single-handed bouts for each behavioural task analysed. There was no overall significant concordance in laterality class within individuals across the four tasks (Kendall coefficient of concordance, *k*=4; *df*=7; *w*=0.245; *n.s.*).

Ant-dipping and extracting showed no significant consistency in hand use based on the three categories of laterality used in Table 8.17 (two-tailed Pearson rank Correlation: R=-0.322; N=12; *n.s.*). Indeed, among the 12 individuals for which this comparison was feasible, only 5 matched their hand preference across these two behaviours, while 6 did not differ significantly and one reversed her preference (see Table 8.17). For the 7 adults in this sample set, 4 matched in their preference and 2 did not differ significantly, while one reversed her preference. Among the 5 sub-adults in the sample, 1 matched in their preference and 4 did not vary significantly.

When comparing pounding and extracting, these two behaviours did not exhibit a significant degree of consistency in hand use (two-tailed Pearson rank Correlation: R=-0.032; N=11; *n.s.*). Among the 11 subjects for which comparative data were available, 4 matched in their preferred choice of hand, 6 did not differ significantly between the two behaviours and one showed a reversal in preference (see Table 8.17). If one considers adults only, among the 6 adults, 3 matched in their preference and 3 did not differ significantly. Thus adult chimpanzees did not show any reversal in preference in hand use between pounding and extracting, although they failed to show a convincing level of consistency in hand use between the two behaviours.

For ant-dipping and pounding, 7 out of 10 subjects (4/6 adults) did not differ significantly in their hand use, while 2 (1/6 adults) expressed the same preference in hand use and one adult reversed hand preference (two-tailed Pearson rank Correlation: R=-0.342; N=10; *n.s.*).

Nut-cracking differed the most in terms of hand use within individuals when compared to the other three behaviours. It showed the least number of matches and the greatest number of reversals (see Table 8.17): when compared with ant-dipping, 4 out of 11 subjects (3/6 adults) reserved their hand preference, 5 (1/6 adults) did not change significantly and 2 (2/6 adults) were consistent in their hand use (two-tailed Pearson rank Correlation: R=-0.314; N=11; *n.s.*). For extracting and nut-cracking, 6 out 11 (4/6 adults) individuals expressed opposite preferences in hand use, while 3 (1/6 adults) matched their preference and 2 expressed no significant difference in hand use (1/6 adults) (two-tailed Pearson rank Correlation: R=-0.17; N=11; *n.s.*). Nut-cracking shared the greatest proportion of consistency in hand use with pounding with 3 out of 9 chimpanzees exhibiting the same preference in hand use. However, none of the adults showed this pattern. Indeed, 3/5 adults failed to demonstrate a significant difference in hand use, while 2/5 reversed theirs. Thus, 3 out of the 4 sub-adults completely matched their hand preference for pounding and nut-cracking. Regardless, overall there was no significant concordance between nut-cracking and pounding in laterality of hand use (two-tailed Pearson rank Correlation: R=-0.090; N=9; *n.s.*).

Population level handedness

Table 8.18 provides information on the percentage of right versus left hand use based on bouts of behaviour for each task at the level of the individual, as well as an overall average percentage use of the right or the left hand for each individual analysed across a minimum of 3 tasks. Based on these data, no significant right-hand bias emerged at the population level, although as can be observed in Table 8.17 and 8.18, there was an overall population tendency for a right-hand bias (Wilcoxon Signed Rank test: N=14; z=-1.712; ρ=0.087).

Laterality and efficiency in behaviour

Ant-dipping and nut-cracking

Given the significant age differences in foraging success for both nut-cracking and ant-dipping, laterality in hand use and efficiency across these two tool-use tasks could only be explored by looking at the two age categories separately. Unfortunately, statistical analysis was not feasible, as there were too few subjects within each age category to compare exclusive and non-exclusive handers (see Tables 8.12 and 8.13).

Pestle pounding

For pestle pounding, however, no significant differences emerged in performance in behaviour between the two age categories. Therefore, an analysis could be carried out comparing those individuals who showed complete preference for one hand and those who were not exclusive. Exclusivity in hand use was established on the basis of single-handed bouts only.

Four subjects – 3 adults and 1 sub-adult - were exclusive in their hand use for single handed pounding, 2 to the right and 2 to the left, while 7 – 3 adults and 4 sub-adults - were non-exclusive (see Table 8.14). Variables employed in the calculation of the efficiency measures for pestle pounding did not differ significantly between exclusive handers and non-exclusive while pounding (Time pound: t(9)=0.407; *n.s.*; Total number of pounds: t(9)=-1.007; *n.s.*; Time extract: t(9)=-0.201; *n.s.*; Total number

Table 8. 16. Laterality of hand use across three tool-use behaviours: Individual hand preference based on statistical significance.

Tool-Use	Age-class	Left Only	Sign. Left	Ambi-preferent	Sign. Right	Right Only
Ant-Dipping	Adult	2	0	2	2	1
	Sub-adult	0	0	5	2	0
	Total	**2**	**0**	**7**	**4**	**1**
Nut-Cracking	Adult	3	0	0	1	2
	Sub-adult	1	2	0	0	4
	Total	**4**	**2**	**0**	**1**	**6**
Pounding (single-handed bouts only)	Adult	1	0	3	0	2
	Sub-adult	1	0	1	3	0
	Total	**2**	**0**	**4**	**3**	**2**
Extracting	Adult	0	1	1	1	4
	Sub-adult	0	1	2	2	1
	Total	**0**	**2**	**3**	**3**	**5**

Table 8.17. Individual preferences in hand use across the four behaviours analysed (Adults in **bold**). (R: Right-preferent; L: Left-preferent; A: Ambi-preferent; *: Exclusive in hand use; (-): based on data from Matsuzawa (1999); X: never observed performing behaviour).

	Name															
Behaviour	**Foaf**	Fotayu	**Jire**	Juru	**Kai**	**Nina**	Nto	Poni	**Tua**	**Velu**	Vuavua	Vui	**Yo**	Yolo	**Pili**	Na
Nut-cracking	R	(R*)	L*		R*	X	R*	(R*)	L*	R*	L	L	L*	L*	R*	R*
Ant-dipping	A	A	L*	R	L*	A	A		R	R*	A	A	R	R		
Pounding	A	R	R*	R	L*	R*	R	A	A	A	L*		X	X		
Extracting	A	R	R*	A	L	R*	L	R	R*	R*	A		R	R*		

Table 8.18. Percentage of right- or left-hand bouts for each task for which data were available and overall average across a **minimum** of 3 tasks for each individual chimpanzee.

	Ant-dip		**Nut-crack**		**Pestle pound**		**Extract**		**Overall**	
Name	**Right**	**Left**	**Right**	**Left**	**Right**	**Left**	**Right**	**Left**	**Right**	**Left**
Foaf	53.3	46.7	97.1	2.9	77.8	22.2	70.0	30.0	**74.5**	**25.5**
Fotayu	55.0	45.0	100.0	0.0	67.6	32.4	94.4	5.6	**79.3**	**20.7**
Nto	53.1	46.9	100.0	0.0	96.8	3.2	5.6	94.4	**63.8**	**36.2**
Velu	100.0	0.0	100.0	0.0	50.0	50.0	100.0	0.0	**87.5**	**12.5**
Tua	88.9	11.1	0.0	100.0	46.7	53.3	100.0	0.0	**58.9**	**41.1**
Jiré	0.0	100.0	0.0	100.0	100.0	0.0	100.0	0.0	**50.0**	**50.0**
Kai	0.0	100.0	100.0	0.0	0.0	100.0	3.0	97.0	**25.8**	**74.2**
Vuavua	50.0	50.0	13.2	86.8	0.0	100.0	87.5	12.5	**37.7**	**62.3**
Juru	69.7	30.3			90.1	9.9	55.7	44.3	**71.8**	**28.2**
Nina	50.0	50.0			100.0	0.0	100.0	0.0	**83.3**	**16.7**
Poni					66.7	33.3	94.1	5.9	**80.4**	**19.6**
Yo	91.7	8.3	0.0	100.0			81.3	18.8	**57.6**	**42.4**
Yolo	81.4	18.6	0.0	100.0			100.0	0.0	**60.5**	**39.5**
Vui	50.0	50.0	2.9	97.1					**26.4**	**73.6**
Na			100	0					-	-
Pili			100	0					-	-

of extractions: t(9)=-0.132; *n.s.*). Therefore, this analysis was concerned with relative performance rather than absolute frequency. Across the three measures of foraging success, there was no significant difference between exclusive and non-exclusive handers (see Table 8.19).

For the extraction task, 4 chimpanzees – 4 adults - were exclusive in their hand use, all 4 to the right, while 7 – 2 adults, 3 adolescents and 2 juveniles – were non-exclusive. There was again no significant difference in the variables used in the calculation of the one efficiency measure relevant to this task, i.e. time spent in seconds per extraction, between exclusive and non-exclusive handers (Time spent extracting: t(10)=0.596; *n.s.*; Total number of extractions: t(10)=0.894; *n.s.*). For this behaviour, exclusive handers were found to spend significantly more time extracting per extraction than non-exclusive-handers (see Table 8.19).

8.5 Discussion

Age differences in efficiency

For all measures used to reflect efficiency in ant-dipping, significant age differences emerged suggesting that adults were better at ant-dipping than sub-adults. Adults were more efficient, more successful and less error prone than juveniles and adolescents. Thus, although individuals as young as 32 months old (refer to *Chapter 6*) can perform the appropriate sequence of behaviour for ant-dipping, it takes years of experience for an individual to become an efficient and successful ant-dipper.

In addition, adults were more efficient and generally more successful than sub-adults at nut-cracking, although no significant difference in error rate emerged. The difference in performance between adults and sub-adults for nut-cracking was not as

Table 8.19. Comparison of efficiency measures of pestle pounding between exclusive versus non-exclusive handers for single-handed bouts of pounding and extracting.

Task	Efficiency measure	Category	No.	Mean	Range	SD	T-Test
Pounding	Pounding Rate	Non-Exclusive	7	57.9	45.2-63.8	6.3	t(9)=0.327; *n.s.*
		Exclusive	4	56.7	51.2-60.7	4.5	
	No. Pounds per Extraction	Non-Exclusive	7	14.7	5.9-28.5	7.2	t(9)=0.259; *n.s.*
		Exclusive	4	13.7	7.0-19.0	5.4	
	Time extract (sec.) per Extraction	Non-Exclusive	7	34.5	19.9-53.9	12.2	t(9)=-0.333; *n.s.*
		Exclusive	4	36.8	27.7-46.2	9.0	
Extracting	Time extract (sec.) per Extraction	Non-Exclusive	7	30.6	19.9-46.2	8.5	t(9)=-2.329 $\rho<0.05$*
		Exclusive	4	43.7	30.8-53.9	9.7	

Statistical significance: *$\rho<0.05$

pronounced as for ant-dipping, although nut-cracking is considered to be a more complex and sophisticated tool-use behaviour requiring both bimanual and asymmetric manipulation, and power control (Boesch and Boesch, 1983). None of the sub-adults exceeded adults in ant-dipping rate or ants gathered per minute, and sub-adults were overwhelmingly more error prone than adults (see Table 8.5). For nut-cracking, some sub-adults showed similar levels of efficiency and success to adults and there was no difference in error rate between the two age classes (see Table 8.7). However, ant-dipping is a more 'precarious' tool-use behaviour, being aimed at biting ants, which cause discomfort to the ant-dipper. Indeed, as reported in *Chapter 6*, sub-adults are sensitive to bites from driver ants and, compared to adults, prefer to dip in contexts of reduced biting risk. It should also be noted that the tool-use behaviours showed individual variability in foraging success, even among adults.

Finally, for pestle pounding, no obvious difference in performance emerged between adults and sub-adults. However, adults tended to exhibit a higher rate of pounding than sub-adults and to spend more time during each extraction removing and consuming the palm heart product thereby obtained. The measures of efficiency used for this behaviour may not reveal differences in performance between adults and sub-adults. Pestle pounding is comprised of two main sequences of actions, pounding and extracting, which may each in turn influence performance and efficiency and the final amount of product collected. In addition, sub-adults may have less strength than adults for pounding effectively, which would limit the amount of product they are able to obtain. Since the chimpanzees often have to insert their arm up to the shoulder to access the pulped palm heart within the crown cavity (Yamakoshi and Sugiyama, 1995), the smaller sub-adults may not be able to remove as much product as adults.

Laterality of hand use across the four tasks

For ant-dipping, when considering the overall data, chimpanzees at Bossou presented a tendency for Level 2 performance with 50% (7/14) of individuals showing a significant hand preference in this tool-use behaviour (see Fig. 8.1). They failed to show convincing Level 3 laterality, with only 21% (3/14) of individuals showing exclusive use of one hand over the other. Although there were no significant differences between adults and sub-adults, the pattern of lateralisation at the population level differed slightly when considering the adult data only. Forty two percent (3/7) of adults were exclusive in their hand use, while 29% were either incompletely lateralised or ambi-preferent, thus exclusivity in hand use was the predominant category among adults. Unfortunately, the small sample failed to reveal statistical predominance in exclusivity in hand use among adults. Thus, ant-dipping among the chimpanzees of Bossou cannot be classed as Level 3 until more data on adults can be obtained. In addition, there was no significant evidence for task specialisation, although there was an overall tendency for right hand preference. But this tendency was not substantiated by the adult data whereby, among those showing a hand preference, only 3 out of 5 adults (60%) showed a right hand bias. Finally ant-dipping at Bossou exhibited Level 2 laterality in hand function with 71% (5/7) of the adults exhibiting a significant hand preference.

Bossou chimpanzees showed Level 3 laterality of function for nut-cracking with 86% (6/7) of adults showing complete lateralisation in hand use for this task. However, there was no evidence for task specialisation or significant difference between the adult and sub-adult sample in laterality of hand use. Nevertheless, maturation in handedness appears to be characterised by the development of a preference in hand use that eventually develops into exclusive use of that same hand during late juvenility or early adolescence. Such a pattern of ontogeny, showing increased lateralisation with age, at least up to adulthood, has been reported from other studies of non-human primates; however, most of these have been cross-sectional (e.g. lemurs: Ward *et al.*, 1990; Hylobates: Stafford *et al.*, 1990; captive chimpanzees: Hopkins and Leavens, 1997) rather than longitudinal (captive chimpanzees: Bard *et al.*, 1990; Hopkins, 1995b; Hopkins and Bard, 1993). However, Boesch (1991a) and McGrew and Marchant (1992) showed that for nut-cracking and termite fishing respectively, younger chimpanzees exhibited a greater degree of lateralisation than adults; the results from the present study do not support such a pattern.

Pounding the centre of the palm crown with the aid of a palm frond, during pestle pounding, was performed either using both hands or single-handedly, the latter being the method most frequently observed. Not all chimpanzees employed the two-handed technique, which was preferentially performed by two adult females - Kai and Velu – and commonly observed in a single juvenile female - Juru. During two-handed bouts, these three individuals clearly showed preferences for which hand was placed above the other. In addition, for the two individuals who exhibited a hand preference for single-handed bouts, the preference was for the hand that was placed above during two-handed bouts. Based on single handed-bouts, however, this tool-use behaviour exhibited Level 2 laterality on the grounds that 64% (7/11) of the subjects or 50% (3/6) of the adults showed significant preference for one hand over the other. Only 36% (4/11) of the chimpanzees or 50% (3/6) of the adults were exclusive in their hand use for single-handed pounding bouts. In addition, there was no evidence for task specialisation, although there was a tendency for right-preference. Finally, there was no significant difference between adults and sub-adults in laterality of hand use for pounding.

Although part of the pestle pounding sequence, extraction does not involve any tool manipulation. Nevertheless, Bossou chimpanzees showed clear Level 2 laterality in this behaviour, with 77% (10/13) of individuals and 86% (6/7) of adults showing a significant hand preference, slightly more than for pounding. Moreover, 57% (4/7) of the adults showed complete lateralisation in hand use while extracting, suggesting Level 3, but the sample size was too small to reveal statistical significance. One may argue that the hand employed in extracting may be influenced by which hand was used while pounding; however, there was no significant relationship in laterality between pounding and extracting.

For extraction, a strong tendency for a right-hand bias emerged with 62% (71% of adults) of the subjects showing a right-preference, classifying this behaviour as Level 2 and on the border of Level 4 performance in hand use. However, extraction failed to show any overall statistical evidence for task specialisation. Once again, unfortunately, the small sample size of subjects available at Bossou impaired any significant statistical inferences about trends.

During extraction, the chimpanzee was required to insert most of or the whole of its arm up to the shoulder into the deep hole or central cavity to gain access to the pulped apical meristem (Yamakoshi and Sugiyama, 1995). The chimpanzee was then obliged to rely on active touch in order to extract the softened palm heart. Such a task is analogous to haptic tasks conducted in captivity, which requires subjects to rely on active touch to discriminate objects or retrieve food items from opaque containers. Only one such study has been conducted on chimpanzees: Lacreuse *et al.* (1999) found that 20 chimpanzees from the Yerkes Primate Center exhibited a significant right hand preference when attempting to recover food from an opaque bucket enclosed in a metal frame attached to the mesh on the inside of the home cage. The same group of chimpanzees showed no task specialisation for a simple reaching task or a bimanual task involving extracting peanut butter from the inside of a PVC tube, a task which required simultaneous use and co-ordination of both hands. Thus the right-hand bias found among the wild chimpanzees of Bossou for extraction, as an analogue of the haptic task used in captivity, tenuously supports Lacreuse *et al.*'s (1999) finding of a right-hand preference for such tasks in chimpanzees.

Sugiyama *et al.* (1993b) showed that Bossou chimpanzees manifest Level 1 laterality of function during bouts of feeding involving simple reaching for food and bringing it to the mouth. It has generally been thought that Level 3 performance is characteristic of tool-use behaviours of wild chimpanzees (McGrew and Marchant, 1996, 1997; McGrew *et al.*, 1999), with the exception of ant-fishing at Mahale (Level 1: Nishida and Hiraiwa, 1982). However, among the four tasks analysed here, only one, nut-cracking revealed convincing Level 3 performance, while pounding and ant-dipping both showed Level 2. Thus of the three tool-use contexts studied among the chimpanzees of Bossou, only the most complex, nut-cracking, was typified by convincing Level 3 laterality in hand use.

Extracting whilst pestle pounding did not involve any tool manipulation yet still showed a significantly greater level of lateralisation than simple reaching, with a high degree of exclusivity in hand use and slight indications of task specialisation. Other behaviours not involving subsistence technology have also been reported to display high levels of hand preference in wild apes, and even lateral bias. Several hierarchically structured behaviours (*sensu* Byrne and Russon, 1998), targeted at gaining access to food types that require skilled, elaborate and often bimanual processing, fluctuate between Levels 2 and 3, and even 4 and 5 (e.g. wild chimpanzees: Corp and Byrne, 2002; wild gorillas: Byrne and Byrne, 1991).

Hand specialisation and population level handedness

There was no evidence of hand specialisation amongst the chimpanzees of Bossou. Indeed, there was no concordance in laterality of hand use across the four tasks. Ant-dipping and palm heart extraction showed little consistency in hand use. Moreover, there was no significant correlation between pounding and extracting. Nut-cracking contrasted the most with ant-dipping and extracting, with respectively 50% (3/6) and 67% (4/6) of adult subjects expressing reversed hand preferences. Nut-cracking and pounding also failed to show a high level of concordance among adults; however, 3 of the 4 sub-adults matched their hand-preferences for these two behaviours.

Discrepancy in hand use between tasks may relate to their varying manipulatory demands (Boesch, 1991a; McGrew *et al.*, 1999). Nut-cracking and pestle pounding require elaborate motor skills, involving series of precise downward pounding actions and the manipulation of an awkward tool, particularly for sub-adults who may be physically limited in their ability to manipulate stones or palm fronds. However, adults failed to show a high degree of consistency in hand use between these two tool-use tasks. Nut-cracking differs from pounding in requiring complementary use of both hands, since one hand is employed for hammering while the other is used to place the nut on the anvil, a sequence of actions not observed in pounding. This difference in task complexity may be sufficient to explain lack of hand concordance between nut-cracking and pounding by adults. However, sub-adults may be more likely to use the same preferred hand for both tasks possibly to facilitate their acquisition and/or efficiency. However, more data will be required to further test a concordance in hand use between nut-cracking and pounding among sub-adults, before testing hypotheses to explain any dichotomy between adults and sub-adults.

At the population level, although not statistically significant, there was a tendency for a right hand bias being expressed within the Bossou community.

Efficiency in behaviour and exclusivity in hand use

The significant differences between adults and sub-adults for both ant-dipping and nut-cracking clearly demonstrate the need for caution when considering data from sub-adults regarding the issue of laterality of hand function and efficiency in behaviour. Other authors have pointed out that sub-adult data may not reflect adult performance (Boesch, 1991a; McGrew and Marchant, 1992; Tonooka and Matsuzawa, 1995).

McGrew and Marchant (1999) showed that individual chimpanzees who were completely lateralised, using only one hand or the other for termite fishing at Gombe, Tanzania, were more efficient (gathering more prey per unit effort) than those who were incompletely lateralised. However, exclusive handers were neither more successful nor less error prone. Five among the 11 chimpanzees observed by McGrew and Marchant (1999) were sub-adults and no information was provided as to how many of these were exclusive in hand use. If a high proportion of sub-adults were incompletely lateralised, their results could be an artefact of age differences in efficiency.

No significant differences between adults and sub-adults were found in the three measures of efficiency in performance for pestle pounding and in exclusivity in hand use. An analysis of the influence of exclusive laterality on performance was thus carried out on both adults and sub-adults. Based on single-handed pounding bouts, no difference emerged on any of the three measures between those individuals that were exclusive handers and those that were not. However, for extracting, exclusive handers were found to spend more time extracting per extraction. Since extraction time per extraction reflected the amount of product obtained, completely lateralised individuals appeared to be more efficient at extracting the crushed palm heart.

Although I could not explore the issue of laterality in hand use and foraging success for either ant-dipping or nut-cracking due to an insufficient number of adult or sub-adult subjects, data for extracting suggested that exclusive handers might have some advantage relative to unlateralised individuals. This result supports the argument that individuals who exhibit Level 3 performance or invest motor skill in only one hand may indeed benefit from a greater pay-off. However, McGrew and Marchant (1999) asked whether such a difference could lead to a genuine ecological advantage in foraging. Yamakoshi (1998) demonstrated that the Bossou chimpanzees depend strongly on tools for their subsistence. The availability of keystone resources, such as oil-palm (*Elaeis guineensis*) nuts and the apical meristem, i.e. the palm heart, are essential for these chimpanzees during periods of fruit scarcity. Therefore, greater foraging efficiency for these food items is likely to have some influence on individual fitness, which could conceivably result over evolutionary time in natural selection for increased lateralisation.

Continued collection of video recordings of nut-cracking, ant-dipping and pestle pounding behaviours from Bossou will provide data from a greater sample of adults and allow for this issue of efficiency and laterality in hand use to be more comprehensively addressed.

Conclusion

The results from this study support the prevalence of an evolutionary drive for increased individual hand preference, resulting in varying proportions of subjects being exclusive in hand use, for tool-use behaviours and haptic tasks. Many other foraging behaviours that require complex processing techniques and/or simultaneous and complementary use of both hands also fit this pattern (e.g. Byrne and Byrne, 1991; Colell *et al.*, 1995; Hopkins, 1995b).

Such an evolutionary drive may have been prompted by the foraging payoffs gained from performing a complex task while attributing specific roles to each hand or employing one hand exclusively when engaged in unimanual tasks. The picture that emerges in wild chimpanzees so far supports this hypothesis. Nevertheless, more studies exploring the relationship between laterality of hand function and foraging efficiency for behaviours expressing exclusivity in hand use across several tasks are needed. Such studies should take care to control for efficiency differences between adults and sub-adults, thus making sure that results are not confounded by the poorer foraging success of younger subjects.

The evolutionary forces having brought about a right-hand bias in humans remain unclear. In this study, Bossou chimpanzees failed to show any evidence for task specialisation. Bossou chimpanzees nevertheless showed an overall tendency for a population right-hand bias. Only two studies of laterality in hand use in chimpanzees have reported evidence for population-level handedness and interestingly both were biased to the right. Hopkins' (1994a) study of 140 captive chimpanzees from the Yerkes Primate Center, eating with one hand while holding other food with the other hand (bimanual feeding) revealed that 53% of the subjects were lateralised and that 66% of these were right sided. Furthermore, to explore more specifically the issue of co-ordinated bimanual hand use, Hopkins *et al.* (1995b) tested 110 chimpanzees from Yerkes for hand use while extracting peanut butter from the inside of a PVC tube, a task requiring simultaneous use and co-ordination of both hands. Overall, a significant population-level right-hand bias was again uncovered, with 67% of the lateralised subjects exhibiting a right-hand preference. However, recently, Palmer (2002) demonstrated that the above studies were flawed by the statistical methodology employed and that no right-hand bias is to be suggested after re-analysis of the data.

Therefore, the current evidence for population-level right-handedness in chimpanzees remains equivocal.

Toth (1985) showed by analysing flaked tools that hominids as early as 1.9 million years ago were already biased towards the right (57:43). The proportion of right- to left-handers in the population only increased significantly by around 0.4 million years ago (61:39), which corresponds roughly to an increase in the sophistication of the early hominid tool kit (Isaac, 1972, 1976). Although these studies are bedevilled by the pooling fallacy, these findings preliminarily suggest an increase in right-hand bias over evolutionary time. Right-handedness may have been selected for because of increasing selection for cultural conformity (Steklis and Marchant, 1987) and of increasing advantage in skill acquisition. Indeed, the distribution of handedness in early hominids might have evolved to facilitate the learning of manual activities through imitation and teaching (Michel and Harkins, 1985), especially as bimanual tasks, such as tool-manufacturing, became increasingly sophisticated. But other tasks involving hierarchically complex bimanual processing techniques or requiring haptic skills, for which no archaeological artefacts remain, may also have played an important role in the evolution of right-handedness in humans.

However, it is important to consider that there is also some evidence for genetic heritability for the degree of handedness among humans (Francks *et al*, 2003). Investigations of whether laterality follows family lines in non-human primates have, however, generally failed to reveal any correlation (wild bonnet macaques: Brooker *et al.*, 1981; Guinea baboons: Vauclair and Fagot, 1987; Japanese macaques: Takeda, 1994; wild mountain gorillas: Byrne and Byrne, 1991; captive tufted capuchin monkeys: Westergaard and Suomi, 1996). Nevertheless some evidence is emerging in chimpanzees. Indeed, Hopkins *et al.* (1993) conducted an exhaustive study of heritability of hand preference in 76 captive chimpanzees from the Yerkes Primate Center and found both paternal and maternal effects on offspring's hand bias regardless of rearing conditions. Further evidence for a genetic influence on the expression of hand preferences in chimpanzees is provided by Hopkins *et al.* (2001). Matsuzawa (2001) additionally revealed that, although hand preference was not always congruent between mothers and their offspring for nut cracking at Bossou, it was consistent without exceptions among 9 sibling pairs.

Laland *et al.* (1995) produced a gene-culture model of human handedness, which fits the data from 31 studies in humans. Finally, it is possible that laterality in hand use in modern humans may well indeed reflect an interaction between selection for more elaborate and faithful social learning processes, generating some form of cultural convention, and genetic evolution during the course of the evolution of hominids.

Chapter 9

Discussion

In discussing the data presented in this thesis, it is important to distinguish between those questions that can be answered, those for which only partial answers can be provided and those that remain unanswered, but can now be explored in future studies with greater focus based on testable hypotheses. This thesis covers a wide range of behaviours observed in wild chimpanzees at Bossou and Nimba. The underlying theme throughout the thesis is the issue of behavioural variation in chimpanzees, flirting intermittently with the concept of culture, and then only from environmental, functional and adaptive perspectives rather than from a social learning standpoint.

9.1. Environmental determinants of behavioural variation and adaptive function

An ecological approach to the study of behavioural variation among chimpanzees in the wild can provide a wealth of insights into the relationships between environmental parameters and behaviour and shed light on variables that may reflect underlying social cultural influences on behaviour. This approach has successfully been applied to previous studies of chimpanzees' feeding behaviour (e.g. Nishida *et al.*, 1983), tool-use (e.g. McGrew *et al.*, 1979; Uehara, 1982; Collins and McGrew, 1987, 1988; Boesch *et al.*, 1994; McGrew *et al.*, 1997) and nesting behaviour (e.g. Baldwin *et al.*, 1981). Although it often remains difficult to dissect accurately and satisfactorily what factors are at stake, with studies often yielding as many unanswered questions as answers, they constitute an essential first step in separating important information from the noise surrounding complex behaviour and in identifying paths and hypotheses that warrant further exploration and testing.

Unfortunately, there are few long-term study sites of wild chimpanzees across Africa where pertinent hypotheses pertaining to variation in behaviour can be addressed systematically and comprehensively. In addition, comparative studies of behavioural patterns in chimpanzees have mostly concerned geographically distant communities. Therefore, there has been relatively little scope for exploring the issue of diffusion of behaviour between neighbouring communities. In this context, a detailed within-community study of behaviours observed at Bossou supplemented by data gathered from adjacent communities in the Nimba Mountains is proving promising.

In *Chapter 4*, nesting behaviour, a material skill observed in all species of great apes, was explored at Bossou and the two Nimba sites. A significant influence of some environmental variables emerged, especially diameter of nesting tree at breast height (DBH), with regard to nesting parameters including number of nests per tree, number of trees used in integrated nests and nest height, explaining much of the variation observed between the three sites. A remarkable degree of similarity was revealed in nest parameters between the two Nimba sites with respect to habitat type choice, tree species preference, nest height, tree DBH and height to DBH ratio, when controlling for habitat type. However, further hypotheses aimed at explaining these similarities and the significantly greater frequency of ground nests and nest integration at the Nimba sites remain to be examined to determine whether these patterns are environmentally or socially determined. In addition, more detailed studies of nest building at other sites are required to achieve a greater understanding of factors influencing nesting behaviour by testing to what extent similar hypotheses can explain variation in nesting between and within communities.

In *Chapter 5*, an ecological approach to inter-community variation in behaviour was adopted to investigate differences and similarities in the use of the oil-palm tree

(*Elaeis guineensis*), a common tree species in many chimpanzee habitats across Africa and whose uses at Bossou are remarkably diverse. This study overall failed to identify proximate environmental variables underlying observed variations in frequency of specific uses between the three study sites. Assuming individual interchange between these communities and the involvement of social learning in the intra-community transmission of at least some these uses, based on studies of nut-cracking at Bossou (Inoue-Nakamura and Matsuzawa, 1997), this result raises interesting questions about diffusion of behaviour between chimpanzee communities. For example, what effects do local social and environmental conditions have on the transmission of cultural behaviours between communities? How might patterns of social interaction affect the dynamics of transmission? Responses to these questions must await future studies.

Continued habituation of the Nimba chimpanzees will lead to better knowledge of their feeding behaviour, ranging patterns and social structure, and may additionally allow us to detect the presence of chimpanzees originally native to Bossou, either via genetic means or direct observation, and to monitor future migratory patterns between these communities. All these data, as well as continued longitudinal data collection on the role of social learning in the acquisition of pestle pounding (in progress) and related oil-palm use behaviours among Bossou chimpanzees, will hopefully elucidate the differential patterns of oil-palm use between these three study sites.

Kummer (1971) stipulated three means by which behavioural differences across animal populations of a same species might arise: 1) genetically transmitted propensities that are largely independent of environmental effects on their expression in ontogeny; 2) similarly structured transactions between individuals and their environment in one community that differ from transactions in another community; 3) transmission of behavioural patterns through social learning from one individual to another, according to the norms of the community in which they live. Concerning behavioural variation between neighbouring communities that experience individual interchange or have presumably done so until only very recently, underlying genetic differences are unlikely to account for differences in behaviour. However, when addressing the question of individual transaction between organism and the environment rather than the effect of social mediation on behaviour, the picture that emerges is rather more complex. Indeed, Laland *et al.* (1993, p.260) have suggested that the spread of cultural traits "may be best modelled as the interaction of biased cultural transmission, [which occurs when, given a choice between alternative modelled variants, individuals are more likely to adopt some variants than others (Boyd and Richerson, 1985)] and individual learning". Several studies in non-human animals provide support for this assumption (e.g. Sherry and Galef, 1984; Lefebvre and Palameta, 1988; Laland and Plotkin, 1990, 1991).

The findings from the micro-ecological and preliminary ontogenic study of ant-dipping at Bossou, reported in *Chapter 6*, suggest that environmental variables can influence acquisition and performance in sub-adults, including variables such as dipping position, tool length and technique employed. Furthermore, some of the results suggest that the chimpanzees adapt their behaviour not only to minimise risk of getting bitten but also to increase efficiency. Although the involvement of social learning in the acquisition of ant-dipping in these chimpanzees has yet to be ascertained, the results suggest that social learning and individual learning may act in concert, allowing efficiency in performance and flexibility in behaviour in the face of variable conditions and exposure to risk. Continued longitudinal records of ant-dipping behaviour at Bossou across all members of the community and studies at the two Nimba sites should shed additional light on the dynamics of acquisition and transmission of this behaviour.

Ontogeny is a very different process for different animal species. For some species, it is essential that the young be almost fully functional from birth, to maximise their chances of surviving to the age of reproduction, whereas for other species a long ontogeny, with a combination of individual and social learning, is the life-history strategy employed (Tomasello, 1999). With regard to species with a long period of development, such as the chimpanzee, it is likely that age and critical learning periods affect transmission of different behavioural traits. These windows of cognitive receptivity to learning experiences appear to be directly related to the cognitive development of the young within its social and physical environment. Matsuzawa (1994, 1999a) provided some evidence that the age of acquisition of a tool-use behaviour in wild chimpanzees depends on the tool task and the level of complexity involved and that critical learning periods are important in the eventual ability of the young to perform these tasks. In *Chapter 8*, it emerged that tool-use behaviours, such as ant-dipping, pestle pounding and nut-cracking, take years of practise before sub-adults attain an adult's level of efficiency. However, differences in age of acquisition of tool-use tasks at the community- and individual-level, and identification of critical learning periods need be determined and comprehensively studied.

Finally, the transmission of cultural traits and preferences within and between adjacent chimpanzee communities is likely to be affected by developmental, experiential, social and ecological factors. These factors are not easily dissectible, however, and we have a huge challenge before us if we are to understand the interactions between these processes.

9.2. Culture in chimpanzees in perspective

Four decades of field studies of wild chimpanzees in Africa have revealed substantial differences in behavioural repertoires between subspecies, populations and communities (c.f. McGrew, 1992; Whiten *et al.,* 1999, 2001). The list of these differences is extensive and comprises a multitude of behaviours encompassing tool-use, feeding, and the social and communication domains (e.g. McGrew *et al.*, 1979; Nishida *et al.*, 1983; McGrew, 1985, 1992, 1998; Nishida, 1987; Sugiyama, 1993, 1997) (see *Chapter 1* for more details). Whiten *et al.* (1999, 2001) identified 39 candidate behavioural patterns as potential cultural variants on the grounds that they occur sufficiently frequently at one or more sites to be consistent with social transmission, yet absent at one or more others, where environmental explanations can be rejected.

Although useful in identifying potential cultural variants and illustrating the breadth of behavioural variation observed in chimpanzees, extensive cataloguing is unproductive on its own. Such an exercise may generate confusion as to the level at which cultural variation might be observed, and more studies are required to elucidate what elements of behaviour might be socially mediated and which of those might rather reflect environmental affordances and reinforcements. In *Chapter 7*, a detailed and precise study of tool-choice and tool-manufacture across three stick- and stalk-use behaviours at Bossou revealed that chimpanzees bias their choice of raw material and tool length within the requirements of the task at hand. These demands may vary during the course of the task, as suggested by observations of algae-scooping, or with environmental conditions as demonstrated in *Chapter* 6 for ant-dipping. In addition, some evidence was provided to support the hypothesis that tool-modification whilst performing the task is a function of the predictability of what attributes are required of the tool for it to be useful. Nevertheless, some aspects of tool-manufacture, such as bark-stripping, which varies significantly between tasks and across communities, remain unexplained when exploring tools employed in an identical task across the three sites such as ant-dipping. Variations in tool-choice and tool-manufacture for a same task between communities therefore require further analysis.

Finally, if we are to advance in the field of "cultural primatology" and further our understanding of the nature of cultural processes in biological systems, we need more studies into (a) the diffusion processes and mechanisms of transmission within and between communities, (b) the structure and expression of these cultural variants at the individual level, and (c) variation as it relates to adaptive function. A few diffusion and transmission chain studies have been carried out in pigeons and in species of fish and rats, in the field and in the laboratory (e.g. Helfman and Schultz, 1984, Warner; 1988; Laland and Plotkin, 1990; Lefebvre and Giraldeau, 1994; Terkel, 1996; White and Galef, 2000). However, individual fish, birds or rodents can be relatively easily transferred between populations or habitats, and their environment can more easily be modified and controlled; in contrast such manipulations cannot be easily done with non-human primates. In order to obtain the relevant data in non-human primates from the field, patience and long-term studies are required. However, field experiments as conducted by Matsuzawa and colleagues (e.g. Matsuzawa *et al.*, 2001, see *Chapter 1* and *2* for details) can also generate useful data for addressing such topics. In addition, well-designed complementary studies in captivity, controlling environmental and social conditions, will certainly continue to make useful contributions.

9.3. Where do we go from here?

Studies of behavioural variation, particularly socially learnt patterns of behaviour, within and between chimpanzee communities have generally suffered from a lack of a coherent theoretical framework, ongoing circular debates about social learning processes and mooted definitions of the concept of culture and the difficulties of studying a complex species in its natural habitat.

By employing an operational definition of culture as provided by Parker and Russon (1996) and further refined by Laland and Hoppitt (in press) (see *Chapter 1*), which is neither too narrow nor too broad and applicable to non-human animals, we have the opportunity to investigate issues which have until now rarely been addressed, "including the relationship between individual and social learning, the dynamics of social transmission, and the adaptive consequences of [cultural] behaviour" (Laland *et al.*, 1993, p.271).

Concepts from the quantitative theory of biological evolution have been used to construct a quantitative theory for the evolution of cultural traits in humans. Indeed, many social scientists and biologists have argued that culture can be viewed as an evolutionary system in its own right, cultural variants being generated, selected, and socially transmitted (Dawkins, 1976; Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985). This paralleling of conceptual frameworks has been criticised; however, it has helped to generate models and predictions, that provide a quantitative basis for the study of cultural transmission of traits, a topic whose analysis had remained for too long qualitative (Cavalli-Sforza *et al.*, 1982).

In this context, the dual inheritance theory (Richerson and Boyd, 1985), also referred to as gene-culture co-evolutionary theory (Feldman and Cavalli-Sforza, 1981), proposes that, in humans, cultural and genetic evolution are interlinked processes that may selectively influence each other. There is a growing view among biologists, psychologists and even anthropologists that recognising the interaction between biological and cultural evolution may be central to shedding light on hominid evolution (c.f. Laland and Brown, 2002).

A classic example of gene-culture co-evolution is the evolution of the ability of adult humans to consume dairy products, which have been a component of the diet of some human populations for over 6,000 years. Unlike children, who have no difficulties in consuming milk, adults vary considerably in their ability to digest it. In fact, adults across many populations around the world suffer from sickness and diarrhoea when consuming dairy products. Their inability to digest milk and related products is linked to either the insufficient activity levels of the enzyme lactase or the absence of its genetic expression in their bodies. This enzyme enables the break down of the sugar lactose which is contained in dairy products. A significant correlation has been uncovered between the incidence of the genes for lactose absorption and the history of dairy farming in human populations. More than 90% of adults from populations with a long history of dairy farming express those genes, while typically less than 20% from populations without dairy traditions (Durham, 1991). Feldman and Cavalli-Sforza (1989) used a gene-culture co-evolutionary model to investigate the evolution of lactose absorption, assuming its expression is based on a single genetic locus. Their model showed that the frequency of the allele allowing adult milk digestion in any given population depended critically on the probability that the children of dairy product consumers also became milk consumers, i.e. cultural transmission of dietary habits. Thus, this analysis provides a substantiated account for both the spread of lactose absorption and the cultural-related variability in its incidence.

However, research into gene-culture co-evolution remains heavily dependent on the development of models, with so far only a few applied studies testing relevant predictions and hypotheses (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Richerson and Boyd, 1989; Durham, 1991; Laland, 1992; Laland and Kendal, in press). In addition, since there is still some reluctance to recognise forms of culture in non-human animals as stable enough to co-direct genetic evolution, this approach has unfortunately so far only really been applied to humans.

Chapter 8 provides an analysis of individual and community-level patterns of laterality in hand-use across three tool-aided behaviours. Few studies have been able to provide data across tool-tasks in the wild or to address the issue of the selective advantages of lateralisation in hand-use with respect to behavioural efficiency. The latter was only partially investigated and, although some evidence emerged to support this hypothesis, it requires stronger support. In addition, individual laterality in hand-use proved not to be congruent between tasks, as in no evidence for hand specialisation emerged, and at the community-level, there was also no strong evidence for task specialisation. However, this study confirms the hypothesis that complex behaviours that involve a hierarchical structure of actions or object associations, such as bimanual processing or nut-cracking, are associated with higher levels of laterality. The data also suggest that haptic tasks may have played an important evolutionary role in driving population-level handedness. Although it is generally recognised that chimpanzee handedness is weaker than that observed in humans, a tendency for a right-hand bias emerged from this study concordant with findings emerging from handedness data indirectly gathered on early hominids (Toth, 1985).

It has been argued that the basis for the quantitative difference in handedness between humans and chimpanzees might reflect the role of culture in shaping behaviour (Steklis and Marchant, 1987). Indeed, Hopkins (1996, p.455) proposed that "human right-handedness may reflect an elaboration of this biological disposition through cultural transmission and modification". The recently emerging evidence for an underlying genetic basis for handedness in both humans and in chimpanzees (humans: c.f. Laland *et al.*, 1995; chimpanzees: Hopkins *et al.*, 1993; Hopkins, 1997; Hopkins *et* *al.*, 2001) suggests that right-handedness in humans, as a derived trait, may therefore ultimately represent a good example of a product of gene-culture co-evolution, as suggested by Laland *et al.* (1995).

Researchers in gene-culture co-evolution have focused much attention on how information is spread within human populations. When the mode of transmission is from parent to offspring it is termed vertical and the natural discrete unit is the generation (Cavalli-Sforza and Feldman, 1981). Transmission between members of the same generation is termed horizontal, and oblique transmission goes from non-parental individuals of the parental generation to members of the filial generation (Cavalli-Sforza *et al.*, 1982). Some theoretical predictions based upon these different modes of transmission have been produced for humans. According to Cavalli-Sforza *et al.* (1982), in humans, through teaching, oblique transmission increases homogeneity within a population and creates greater variation between populations in space and time than does vertical transmission. If the ratio of transmitters per recipient is many-to-one, the rate of evolution (change of trait frequency with time) is slow, and variation within and between populations is low. If, as in the case of teaching, transmission is one-to-many, cultural change is expected to be rapid and within-population variation low. Transmission from parent to offspring is predicted to produce moderate rates of change and relatively high within- and between- population heterogeneity. However, specific cultural traits may be transmitted in several ways, thereby complicating quantitative analysis of such mechanisms and affecting the dynamics of the evolution of a particular trait within a population. Studies testing the predictions emanating from similar models adapted to the study of non-human animals may prove useful for understanding patterns of diffusion of behaviour within and between populations or communities (Laland *et al.*, 1993).

In this context, Laland *et al.* (1993) proposed two main types of social transmission in animals: 1) "traditional" (relatively slow diffusion, weak effects of individual learning, high fidelity of vertical transmission) and 2) "highly horizontal" (rapid, ephemeral, and horizontally transmitted with a strong effect of individual learning and decision-making effects, and low transmission fidelity). Population and field studies have found much evidence for rapid, horizontally transmitted behaviours (see Galef and Giraldeau, 2001 for review). Only a few traits in non-human animals appear to be vertically transmitted and most examples can be found among primates (Kawai, 1965; Itani and Nishimura, 1973) and particularly among the great apes (e.g. chimpanzees: Boesch, 1991b; Inoue-Nakamura and Matsuzawa, 1997; Matsuzawa *et al.*, 2001; gorillas: Byrne and Byrne, 1993; orangutans: Russon and Galdikas, 1995). A prediction based on these types of transmission processes is that, for example, traditional social transmission causes individuals to track environmental variability less effectively than individual learning because the social learner's behaviour is by definition shaped by that of the previous generation (Laland *et al.*, 1993). A wealth of testable predictions, amenable to empirical testing, pertaining to the role of social and individual learning in the context of environmental variability, modes of transmission and the fidelity of transmission of behaviour in animals can thus be generated.

Finally, the evolutionary insight that can be acquired from such studies, testing similar predictions across a wide range of species, can potentially be enormous. Indeed, the adaptive consequences of social transmission in animals have hardly been addressed empirically, although important evolutionary effects have been proposed. Much model analysis of the complex interaction between culturally and genetically transmitted information has focused on the general question of the adaptive advantages (and disadvantages) of the social transmission of behaviour (Boyd and Richerson, 1985;

Laland *et al.*, 1993). The diffusion of a learned trait through a population may modify some of the physical and social conditions that cultural organisms have to deal with, i.e. niche construction, thus affecting the course of their genetic evolution, by accelerating or decelerating evolutionary rates (cf. Laland *et al.*, 1993; Laland *et al.*, 2000).

9.4. Culture in non-human animals: analogous or homologous to culture in humans?

Galef (1995) argues that human and animal cultures should be viewed as analogues rather than homologues. He also maintains that animal social learning results from mechanisms (e.g. local enhancement, social facilitation) that are different from those in human culture (i.e. imitation, teaching). Tomasello (1999) further argues that the learning skills of wild chimpanzees are sufficient to create and maintain within-community traditions, but insufficient to create and maintain human-like cultural activities. In other words, he argues that chimpanzees do not display the ratchet effect or cumulative cultural evolution. However, as discussed in *Chapter 1*, cultural learning in humans does not necessarily require imitation or teaching: other social learning processes can produce the transmission and diffusion of cultural behaviours. Regardless, chimpanzee culture and human culture are distinct. However, the population-level differences in behavioural patterns in chimpanzees strongly resemble those observed in human societies, in which cultures display a multiplicity of variations in technology and social customs (Whiten *et al.*, 1999).

As pointed out by McGrew (1981), when studying primates and more particularly great apes, viewing evolution as a continuum should be avoided, since humans have evolved separately from our closest relative, the chimpanzee, for more than 5 million years. Nevertheless, I will argue similarly to Laland *et al.* (1993) that aspects of human and animal social learning are likely to be convergent if not homologous, and I will agree with Harris (1964), who asserted that the differences between human and non-human cultures are a matter of degree and not kind.

Our understanding of culture in modern humans spans more than 10,000 years while our knowledge of culture in chimpanzees in their natural habitat has only been acquired in the last 40 years. Moreover, as Boesch (1996a) suggested, let us not lose sight of the fact that wild chimpanzees with their suspected limited migratory potentials (Morin *et al.*, 1994) live in generally stable ecological and social environments and that the need for rapid adaptation is limited. There is no wonder that examples of cumulative technical progress and innovations in chimpanzees are rare. Such a pattern is also similar to what studies of our early ancestors have revealed, i.e. highly stable and rudimentary cultural products for most of the history of *Homo habilis*, *Homo erectus* and for early *Homo sapiens* (Davidson and Noble, 1993). In addition, "how many studies, however long-term, of traditional peoples *in situ* have ever reported spontaneous invention of new tools?...[so] why should we expect to be lucky enough to see notable changes in the material culture of apes in [four] decades?" (McGrew, 1994, p.73).

Finally, studies of chimpanzees and other animal species, exploring the interaction between social and individual learning, within and between population variability in a range of behaviours, the dynamics of the diffusion of socially mediated behaviours within and between communities or populations and the social and biotic contexts in which these processes occur, have really only begun. These studies will continue to contribute to our understanding of the nature and roots of cultural processes in biological systems and of cultural evolution in humans. In spite of this effervescence of ideas and the development of approaches that are slowly bridging the gaps between different fields of science, let us not forget that we may never be able to arrive at answers if we do not also focus our attention and energy on conserving those species, particularly the great apes, that are still likely to provide us with the best clues as to our origins.

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