Human-chimpanzee coexistence at Bossou, the Republic of Guinea: A chimpanzee perspective

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List of Colour Plates

Declaration

I declare that the work undertaken and reported within this thesis is my own and has not been submitted in consideration of any other degree or award.

Kimberley Jane Hockings

Abstract

The increasing rate of human population growth has expanded the human-primate interface, with more conversion of natural primate habitat to agricultural land. Elevated levels of crop-raiding by primates are a by-product of natural resources becoming less available, and the nutritional riches of agricultural production becoming increasingly known to the primates. It was the aim of this thesis to focus on the Bossou chimpanzees' *(Pan troglodytes verus)* perspective of their habitat in the Republic of Guinea, West Africa, the risks and opportunities presented by a human-dominated landscape, and to detail their day-to-day coexistence with humans. I combined a variety of data collection techniques, from focal, scan and *ad libitum* behavioural sampling of the chimpanzees' daily activities, to broad ecological and habitat surveys.

The chimpanzees rely on cultivated foods, and thus are forced to respond to humans. However, significant variation in the importance of various cultivars in the chimpanzees' diet exists; certain cultivars are mostly fallback foods, while others are preferred food items and taken according to their availability in orchards and fields. The usage patterns of wild and cultivated foods by the chimpanzees of Bossou are thus inextricably connected. Whilst engaged in crop-raiding the chimpanzees exhibit several behavioural adaptations, namely a decrease in vocalisation levels, and increases in the transportation of food and specific vigilance behaviour. Adult males and adult male-only parties crop-raid more than other age- and sex-classes/compositions, and are more likely to take risks by raiding in exposed environments with increased risk of human confrontation. The use of human cultivars also affects the socio-sexual behaviour of the chimpanzees: chimpanzees appear to share the fruits of their risky labours (crop-raiding) as a food-for-sex strategy, which allow adult males to

advertise prowess and enhance affiliative relationships with reproductively valuable females (Hockings et al., in prep). In addition, behavioural adaptations to other anthropogenic high-risk situations such as road-crossing were found, with the chimpanzees exhibiting impressive levels of socio-spatial flexibility and cooperation (Hockings et al., 2006). The chimpanzees' level of anxiety (as measured by rough self-directed scratching) increases when dealing with some of the challenges posed by their physical and social environment. The chimpanzees of Bossou have been forced to adapt ecologically and behaviourally to the various costs and benefits of living in a human-dominated environment.

Publications and Presentations

Publications

Hockings, K.J., Anderson, J.R., and Matsuzawa, T. (2006) Road-crossing in chimpanzees: a risky business. *Current Biology* **16,** 668-670.

Hockings, K.J., Anderson, J.R., and Matsuzawa, T. (2006) Temporal patterns of crop-raiding in the Bossou chimpanzees, Guinea, West Africa *(Pan troglodytes verus)*: relation to wild food availability [Abstract]. *International Journal of Primatology* **27** (S1), 403.

Hockings, K.J. (2006) Book review: The chimpanzees of the Budongo Forest: Ecology, behaviour and conservation. *Primate Eye* **89**, 28-29.

Hockings, K.J. (2006) Report: IPS 2006. *Primate Eye* **90**, 26.

Hockings, K.J., Humle, T., Biro, D., Sousa, C., Anderson, J.R., Matsuzawa, T. (2007) Chimpanzees share forbidden fruit (in prep).

International Conference presentations

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3. Hockings, K.J., Anderson, J.R., and Matsuzawa, T. (2006) Road-crossing in chimpanzees: a risky business. Invited paper presented in symposium in the 4th International Workshop for Young Psychologists, Kyoto, Japan, September.
4. Hockings, K.J., Anderson, J.R., and Matsuzawa, T. (2006) Temporal patterns of crop-raiding in the Bossou chimpanzees, Guinea, West Africa *(Pan troglodytes verus)*:

relation to wild food availability. Poster presented at the XXI Congress of the International Primatological Society, Entebbe, Uganda, June.

5. Hockings, K.J., Anderson, J.R., and Matsuzawa, T. (2006) Road-crossing in chimpanzees: a risky business. Invited paper presented in the Bossou and Nimba annual meeting, Inuyama, Japan, April.
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3. Hockings, K.J., Anderson, J.R., and Matsuzawa, T. (2006) Road-crossing in chimpanzees: a risky business. Invited paper presented in the Behaviour and Evolution Research Group internal seminar, Stirling, Scotland, October.
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Chapter 1

The Human-Primate Frontier

The Human-Primate Frontier

"The Bossou chimpanzees will never leave the forests surrounding our village; they are our ancestors and are different from other chimpanzees. We let them feed from our fields so they will never go hungry".

Elderly Bossou villager

This is the first study to assess the range of adaptations by the Bossou chimpanzees *(Pan troglodytes verus)* living in the Republic of Guinea, West Africa to an increasingly human-influenced environment. This thesis focuses on the chimpanzees' perspectives on their environment and their coexistence with humans. To this aim I will answer questions on the importance of cultivars in the chimpanzees' diets and their behavioural adaptations to potentially high-risk situations such as crop-raiding and road-crossing. Additionally, rough scratching, a self-directed behaviour, will be analysed to evaluate quantitatively the chimpanzees' levels of anxiety as they deal with some of the challenges posed by their environment.

1.1 Culture and coexistence

Humans and wildlife have interacted for millennia, coexisting in many different ways. As our evolutionary cousins, non-human primates form an integral part of human mythologies, diets and scientific concepts. In Asia, Africa and America there are a number of agricultural, religious and cultural practices that result in a degree of protection for some primate species. Curu, a privately owned ranch and wildlife refuge in Costa Rica, is a highly successful example of commensalism between both human and non-human primates: capuchin monkeys *(Cebus capucinus)* bring in tourist revenue, and as they are perceived to have a beneficial pruning effect on crops, they live uninterrupted off the surrounding land (Baker and Schutt, 2005). At some forested temple sites in Bali, the sympatric relations between macaques *(Macaca fascicularis)* and humans have existed for such a long time that the area itself is considered a 'monkey forest'. The forest and the monkeys receive some protection due to the potential religious upheaval of disturbing the temple, beliefs about interrupting the dead and risking exposure to demons (Fuentes, Southern and Suaryana, 2005). Traditionally, non-human and human primates on the Mentawai Islands in Sumatra both relied on the forests for their survival; many Mentawai clans had taboos against hunting the gibbons *(Hylobates)*, but considered colobines *(Nasalis)* as good quality food. The non-human primates were seen as both 'cousins' and magical sources of spirit and life force, and were believed to play integral roles in the system governing the Mentawai life cycle (Fuentes, 2002). For the Guaja people of Brazil, monkeys form a significant part of the diet and also their cultural identity, being a fertility symbol for women and a target as young boys practice their hunting calls (Cormier, 2002). In Guaja animalistic beliefs, all forms of plant and animal life, especially monkeys, have souls and are woven into a comprehensive kinship system. In Japan, the Japanese macaque *(Macaca fuscata)* has positive religious associations as one of the animal reincarnations of the Buddah; however, in sharp contrast, monkeys also appear as morally dubious or unfavourable animals in Japanese folklore (Knight, 1999).

As chimpanzees are phylogenetically our closest living relatives they occupy a special importance in terms of their complex relationship with humans, spanning the border of the human-animal dichotomy (Yamakoshi, 2005). People around the Budongo Forest Reserve have positive perceptions of chimpanzees *(Pan troglodytes schweinfurthii)* as they believe that many of the behaviours that they exhibit are comparable to those of humans; however chimpanzees rarely raid domestic crops in this area (Hill, 2005; Reynolds, 2005; Webber, 2006). The villagers of Bossou (Republic of Guinea) regard the chimpanzee as a sacred totem and a reincarnation of their ancestors (Kortlandt, 1986; Yamakoshi, 2005). As a result of such beliefs, humans and chimpanzees have been close neighbours for many generations (see Chapter 2 for more details).

Pockets of primates may be offered protection by such beliefs, and some authors suggest that it is within these attitudes that conservation efforts have the greatest chance of being successful (Lee and Priston, 2005). This viewpoint is shared by Yamakoshi (2005), who believes that the integration of past and present human-chimpanzee relations is indispensable in the development of policies for natural resource conservation in Bossou. Perceptions of, and behaviours towards, non-human primates will depend upon the costs and benefits of interactions and the level of competition for resources. However, the long-term sustainability of human-primate coexistence is questionable.

1.2 Increasing human population

The high rate of human population growth worldwide is leading to ever-increasing encroachment on wildlife habitats as a large proportion of the human population relies on the land for survival. As the demand for agricultural terrain increases, more areas are being cultivated in direct proximity to the forest edge, causing the geographical ranges of many species to shrink and fragment. As a consequence of heightened forest degradation and land cultivation, human and non-human species are increasingly coming into direct contact and competition (Lee et al., 1986), and thus various aspects of human-wildlife relationships need to be re-examined (Yamakoshi, 2005). Crop-raiding by wildlife is one of a range of adaptations to a loss of natural habitat, allowing greater access to an array of energy-rich food. Many non-human species have adapted their feeding repertoire to include crop-raiding as part of their ecological strategy (Naughton-Treves, 1998). People often feel threatened by wildlife due to fears about crop loss and also personal safety (Hill, 1998; Lee and Priston, 2005). A sobering outcome of primates feeding off agricultural land is that farmers will often kill the animals in order to protect their crops; this has even resulted in losses among protected species (e.g. mountain gorillas on the periphery of the Bwindi Impenetrable National Park, (Bell, 1984)). Whilst conflict between agriculturists and wildlife has always existed, the degree of conflict has rapidly escalated over the last 30 years (Hill, 1997; Saj et al., 2001).

1.2.1 Use of terms

It is important not to automatically assume that conflict always results when a wild species crosses into agricultural land to raid crops, (Siex and Struhsaker, 1999). The term conflict, which is regularly used to describe these associations, may in fact provoke the situation into one of hostility (Lee, 2004). It is necessary to accurately determine whether human-wildlife relationships actually lead to a conflict situation, before making negative assumptions (Priston, 2005). In relation to this last point, the terms ‘pest’ or ‘weed’, referring to an ability to thrive in ecologically disturbed areas, should be assigned to primates with great caution so as not to invoke unwarranted negative perceptions of certain species and unsupported assumptions of population resilience (Paterson, 2005). Support for primate conservation in habitat countries will suffer if farmers increasingly come to see primates as agricultural pests (Malik and Johnson, 1994; Chalise and Johnson, 2005). It has also been argued that referring to wildlife feeding on human cultivars as ‘crop-raiding’ will elicit or exacerbate negative perceptions, and therefore the term resource competition may be more appropriate. However, the term resource competition is ambiguous, as humans and wildlife share and compete for different resources in various ways. Competition can arise over access to land and ‘non-cultivar’ resources, such as wild foods. For consistency with past research the expression crop-raiding will be employed in this thesis to describe crop feeding forays.

1.3 Factors affecting crop-raiding

Factors contributing to a farmer’s risk of sustaining animal-induced crop damage are multiple. Proximity of the farm to the forest boundary, and the existence of neighbouring farms on the intervening land are both reliable predictors of vulnerability to crop-raiding; greater distances from the forest and the presence of neighbouring farms reduce susceptibility (Hill, 1997, 2000; Priston, 2005; Ross and Warren, 2006).

Guarding crops against damage by wildlife is a common practice throughout the agriculture-wildlife interface; it may also discourage crop-raiding (Hill, 2005). Variation exists in the measures taken by different groups of people, with preferences often related to effectiveness and practicality (Chalise and Johnson, 2005; Hill, 2005). Traditional methods (e.g. building fences, chasing wildlife away, throwing stones and shouting) to prevent primate crop-raiding have limited success, as the adaptive responses of many primate species make such deterrence mechanisms uneconomical and ineffective in the long term (Chalise and Johnson, 2005).

Raiding intensities may vary as a function of local crop assemblages, planting patterns and crop ripening periods, with certain cultivars and developmental stages being preferentially consumed (Naughton-Treves, 1998). Availability and fluctuations in preferred forest foods may affect crop-raiding incidences, as certain species have been observed to forage on cultivars as a temporary replacement in times of fruit scarcity (Hill, 1997; Naughton-Treves et al., 1998; Saj et al., 2001; Humle, 2003a; Reynolds, 2005).

Although evidence suggests that forest fruit availability may affect crop-raiding levels, cultivar consumption may also be a preferential means of accessing a high-energy food source. Therefore the ecology of the raiding species involved will impact upon human use of a complex agro-forestry system, which is characterised by considerable temporal and spatial variability (Hill, 2000; Hill et al., 2002). Population and species differences in the intensity of crop-raiding are likely to reflect the relative costs and benefits of feeding on cultivated and non-cultivated foods.

1.4 Primates as crop-raiders

Primates in particular pose severe problems as crop-raiders (Strum, 1984, 1987; Newmark et al., 1994; Naughton-Treves et al., 1998) owing to their ecological flexibility and behavioural plasticity, along with the large quantity of crops that they may damage and consume. Nearly all families of primates have been noted to include cultivars in their feeding repertoire (Hill, 2005), and the species involved may exhibit dietary preferences according to body size, dexterity, and extent of food-processing capabilities (refer to Appendix A: crop-raiding species of primates, location, human perceptions and conflict context (adapted from Priston, 2005; Lee and Priston, 2005)). Around African and Asian Reserves, primates are considered responsible for over 70% of the damage events and 50% of the area damaged (Naughton-Treves, 1998; Hill, 2000). This has resulted in some primate species being identified as a serious menace to agriculture in many tropical countries (Mascarenas, 1971), and in the development of control or eradication programmes.

Certain primate species prosper in, and have adapted to, areas of human-wildlife interface; the exploitation of crops has allowed populations of these species to colonise new sites. Crop-raiding is a foraging strategy and therefore has dynamic costs and benefits. In some cases access to human foods has resulted in increased local population levels (Strum 1987), as illustrated by widespread complaints about members of the *Macaca* genus in Asia, and *Papio* and *Cercopithecus* genera in Africa. These genera share traits that enable them to successfully exploit the agricultural landscape surrounding them: they live in complex social organisations, are highly omnivorous, and are semi- or primarily terrestrial with the ability to use arboreal habitats (Sillero-Zubiri and Switzer, 2001). All macaque species crop-raid, albeit at different intensities; this has led to four species being classified as ‘weeds’ (Priston, 2005). Rhesus macaques *(Macaca mulatta)* in India had adapted to areas inhabited by humans to such an extent that they actively sought out these regions even after being translocated to a forest abundant in wild foods (Southwick and Siddiqi, 1994; Southwick and Malik, 1998). Olive baboons *(Papio anubis)* living in the Budongo Forest Reserve have been described as ‘public enemy number 1’ due to high levels of crop-raiding reported by local farmers (Reynolds, 2005). They were perceived to be more destructive than other species, to come in greater numbers and to be especially persistent (Hill, 2000). Like the baboon, the vervet monkey *(Cercopithecus aethiops)* is a successful agricultural ‘pest’, being particularly problematic in areas of forest fragments, plantations and semi-urban areas (Hill, 1997, 2005; Saj et al., 2001). In Gashaka Gumti National Park in Nigeria, both tantalus monkeys *(Cercopithecus aethiops tantalus)* and olive baboons in particular were reported as posing the greatest crop-raiding problem to farmers (Ross and Warren, 2006). Mangabeys *(Cercocebus)* commonly take cash food crops, and even galagos *(Galagonidae)* are perceived as ‘pests’ of cashew nuts on the Kenyan coast (Bell, 1984). Capuchin monkeys *(Cebus capucinus)* are regarded the most problematic crop feeder of the four monkey species found in Costa Rica, and their foraging technique has been referred to as ‘destructive’ (Baker and Schutt, 2005). In addition to common crop-raiding species there are growing numbers of complaints about ecologically more specialised primates such as the endangered Zanzibar red colobus *(Procolobus kirkii)* and the Angolan black and white colobus *(Colobus angolensis)* feeding in agricultural areas (Siex and Struhsaker, 1999; Wakuluzu, 1999). Long-term studies have shown that subpopulations of the critically endangered western purple-faced langur *(Semnopithecus vetulus nestor)* have adapted to a diet high in ripe fruit, a feature which is not recorded for any other colobine; these langurs have become dependent on fruits cultivated by humans (Mittermeier et al., 2006).

Naughton-Treves et al. (1998) found that abundance of forest fruit in Kibale did not diminish primate appetite for maize, although the primate pattern of foraging on bananas suggests that wildlife species use some crops as fallback foods during times of wildfood scarcity. Baboon troops in Kenya were shown to respond in different ways to critical periods of fruit abundance; they either migrated, shifted home range, or sporadically crop-raided (Musau and Strum, 1984). Hamadryas baboons in Saudi Arabia were especially likely to raid crops in very arid areas where non-cultivated foods were scarce, although when the relative costs of harassment by humans got too high then crop-raiding declined (Biquand et al., 1992). Crop-raiding by vervet monkeys in Barbados increased over a 14-year period in response to a reduction in natural food-rich areas; the monkey population remained constant (Boulton et al., 1996). Siex and Struhsaker (1999) found that red colobus consumption of cultivated coconuts was greatest in areas of high red colobus density and low availability of alternative food resources.

It appears that crop-raiding by primates is most likely to occur when a loss in natural habitat is coupled with enhanced access to a high-energy alternative, namely human crops (Strum, 1987; Pirta, 1997; Hill, 2000, 2005). Although it is still possible for some primates to subsist within habitats fragmented by agriculture, the long-term survival of primates in human-dominated areas is precarious (Cowlishaw and Dunbar, 2000; Siex, 2005) with even seemingly successful species suffering significant population declines (Saj et al., 2001).

1.4.1 Crop-raiding by the great apes

Although less common than crop-raiding by monkeys, crop-raiding by the great apes is being increasingly reported (Naughton-Treves et al., 1998; Biryahwaho, 2002). The gorillas of Bwindi *(Gorilla gorilla berengei)* have begun visiting farms and plantations as a result of increased habituation levels, and gorillas in Gabon *(Gorilla gorilla gorilla)* have been recorded raiding crops such as cassava; farmers now perceive this highly endangered great ape to be a problem species (Lahm, 1996; Hill, 2005). Orangutans in Borneo *(Pongo pygmaeus)* are persecuted as crop pests as some take to raiding oil-palm plantations and feeding on the young palms during shortages of natural food (Salafsky, 1993; Anne Russon, pers. comm. 2005; Goossens et al., 2006). The Sumatran orangutan *(Pongo abelli)* is also coming increasingly into conflict with people. Due to habitat loss through encroachment and the conversion of land for agriculture, a decline in forest fruits has forced this critically endangered great ape to feed from fruit crops and oil-palm plantations surrounding the forest, where it is often killed (SOCP, 2002). Bonobos *(Pan paniscus)* at Kokolopori (Demographic Republic of Congo) live in close proximity to villages and crop-raid pineapple, sugarcane, palm pith and banana (Georgiev, pers. comm. 2007); as increasingly important amounts of climax forest are lost and fragmented, crop-raiding in bonobos is likely to increase (Dupain and Elsaker, 2001; Myers-Thompson, 2001).

Compared to other great apes, chimpanzees have a flexible social system and a more eclectic diet, and they appear better able to adapt to areas of secondary vegetation bordering human habitation (Yamakoshi, 2005). Chimpanzees bordering agricultural land and human settlements are frequently reported to crop-raid and compete with humans over natural resources. There are six long-term chimpanzee research sites in Africa where most of the systematic data on wild chimpanzees have been collected: in East Africa, Budongo, Kibale, Gombe, Mahale, and in West Africa, Tai and Bossou. For the most part, chimpanzees inhabiting large protected areas such as the Tai National Park in the Ivory Coast and Mt. Assirik in Senegal do not raid crops (Boesch and Boesch-Acherman, 2000; Humle, 2003a); crops are generally not available and sizeable home ranges provide sufficient wild food resources. It is interesting to compare populations in East and West Africa; cultural differences between populations have not been investigated in relation to crop-raiding behaviours, but geographical variations might well exist.

In East Africa, Hill (1997) reports that chimpanzees in the Budongo Forest, Uganda (moist semi-deciduous tropical forest) do not crop-raid as much as other species such as baboons, although different chimpanzee communities within the reserve do vary in their crop-raiding propensities (Reynolds, 2005). The Sonso chimpanzees that inhabit the main Budongo Forest block occasionally raid crops, namely mango from surrounding orchards and sugarcane from commercial fields on the forest edge. Bates (2005) found that sugarcane crops were one of the most important food species contributing to the Sonso chimpanzees’ diet, despite there being plentiful food within the forest, and hypothesised that the loss of food trees within the forest would exacerbate the problem of crop-raiding. However, the Nyakafunjo chimpanzees, who live in closer proximity to human settlements, exhibit higher crop-raiding levels than their Sonso neighbours, possibly due to recent reductions in home range size. The newly studied Kasokwa forest chimpanzees inhabit a riverine strip of forest to the south of Budongo. This small community subsists mainly on forest foods, but on occasion, due to forest food shortages, the apes engage in crop-raiding activities, feeding upon papaya, mango and sugarcane (Reynolds, 2005); reported crop-raiding levels in the Kasokwa population may be underestimated. Approximately 30km south of Budongo, chimpanzees at Bulindi in the Hoima District of Uganda, also live in very small forest patches and regularly raid human cultivars including sugarcane (McLennan, pers. comm. 2007). The chimpanzees of Kibale National Park, Uganda (moist semi-deciduous and evergreen forest) feed upon maize and cause significant amounts of damage to banana plantations; they are thus viewed as a problem species by farmers (Naughton-Treves et al., 1998). Although quantitative data are lacking, the loss of forested habitat in the southern region of Gombe National Park in Tanzania has encouraged one community of chimpanzees to raid crops such as bananas, mango and palm fruits situated on the forest edge, and in the Mahale Mountains in Tanzania, chimpanzees consume sugarcane, banana pith, oil-palm nuts and maize (Nishida, 1972). Yamagiwa et al. (1992) note that even though chimpanzees in the montane forest of Kahuzi-Biega National Park exist at low population densities due to the low diversity and availability of fruits, hostility between local people and chimpanzees in this region of Demographic Republic of Congo is heightening due to the latter’s increased raiding of staple foods such as maize and plantain bananas. Additionally, Biryahwaho (2002) notes that crop-raiding by chimpanzees around Bwindi exists, but is relatively infrequent.

In West-Central Africa, Lahm (1996) records that chimpanzees in Gabon *(Pan troglodytes troglodytes)* occasionally feed upon cultivars, but no quantitative measures are given. The Fongoli community of savannah-dwelling chimpanzees *(Pan troglodytes verus)* in South-Eastern Senegal (West Africa) overlap substantially with humans in their use of forest resources. They have peacefully coexisted due to a cultural taboo against the hunting of chimpanzees, but concerns over rising levels of crop-raiding in the Tomboronkoto region threatens such relations. Pruetz (2002) suggests that humans and chimpanzees in this region consume approximately 17 species of plants in common; the fruit from the forest liana *Saba senegalensis* is important for the chimpanzees during periods of fruit scarcity and serves as a 'cash crop' for humans during periods of hardship. Due to the unsustainable harvesting of these fruits by humans, wild fruit availability may be reduced to such an extent that the chimpanzees will be forced to seek alternatives, including increasing consumption of cultivated crops.

Dunnett et al. (1970) reported that chimpanzees in the Kanka Sili area of Guinea often fed on rice and millet from small subsistence farms, and grapefruit from commercial plantations, although there is no current information on this community. The chimpanzees of Bossou, Republic of Guinea (dominated by secondary and scrub forest), have been the subject of complaints by local farmers who report that this species in particular frequently raids a wide array of domestic crops, including cassava, maize, pineapple, orange and papaya. Humans and chimpanzees are not only neighbours in this area, but their coexistence is preserved by a delicate ecological equilibrium of resource use (Yamakoshi, 2005). This population of chimpanzees may be comparable to the Kasokwa community in Budongo, as both have small group sizes and restricted home ranges. In the village of Yeale, Nimba Mountains (Ivory Coast), chimpanzees regularly raid cacao fields and have been reported to feed on papaya, pineapple, oranges and cassava which are grown in close proximity to the forest edge. Humle (2003a) proposes that instances of crop-raiding in this population tend to be correlated with low natural fruit availability; when fruits are abundant within the reserve chimpanzees are rarely observed in proximity to the village.

Of all the great apes, chimpanzees are the most frequent crop-raiders. They are opportunistic frugivores and their ability to adapt to new situations has allowed them to successfully exploit agricultural land that is impinging on their natural habitat. Although the Bossou chimpanzees are afforded some protection and tolerance due to cultural beliefs of the local Manon people, their future is uncertain. Across Africa and Asia, as habitat destruction and fragmentation continue at an alarming rate, an increasing number of great ape populations will be forced into the human-primate interface and become increasingly at the mercy of neighbouring human beings. The objective of many crop-raiding studies is to minimise human-wildlife conflict by suggesting ways to reduce crop loss. The aim of the present study is to bring together aspects of the Bossou chimpanzees' behaviour and ecology to gain a better understanding of crop-raiding and other human-influenced behaviours in this community, with the future aim of extending this kind of approach to other populations. Comparisons across sites will determine the kinds of features that are site-specific, which factors if any might be habitat- or species-specific, and whether there are any common aspects of farmer-wildlife conflict (Hill et al., 2002).

1.5 Thesis structure

Two broad research goals were addressed in this thesis. The first was to establish the ecological determinants of crop-raiding in the chimpanzees of Bossou. The second was to document some behavioural adaptations by the chimpanzees to a heavily human-influenced environment. Chapter 4 describes the availability of wild and cultivated foods, and Chapter 5 uses these data to examine the impact of both cultivated and fallback foods upon the feeding ecology of the Bossou chimpanzees. In Part one of Chapter 6, the influences of cultivars on the chimpanzees' sociality and behaviour are explored; Part two describes the role of human cultivars in the socio-sexual behaviour of the chimpanzees. Chapter 7 evaluates the chimpanzees' socio-spatial organisation during anthropogenic risky situations, and Chapter 8 quantifies (using self-directed behaviour) the chimpanzees' levels of anxiety when dealing with some of the challenges posed by their environment and coexistence with humans. To conclude, Chapter 9 draws together the main findings of the study, and conservation recommendations and implications are discussed.

Chapter 2

The Study Site and Bossou Chimpanzee Community

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2.1 Location of the study site

The Republic of Guinea lies on the west coast of Africa, covering an area of 245,857 km². Guinea shares borders with Guinea Bissau, Senegal, Mali, Ivory Coast, Liberia and Sierra Leone. It can be divided into four main regions: coastal, flat, high and forest. The village of Bossou is situated in the forest region in south-eastern Republic of Guinea (latitude 7° 38'71.7 N; and longitude 8° 29'38.9’ W), approximately 10 km from the Nimba Mountain range (see Figure 2.1).

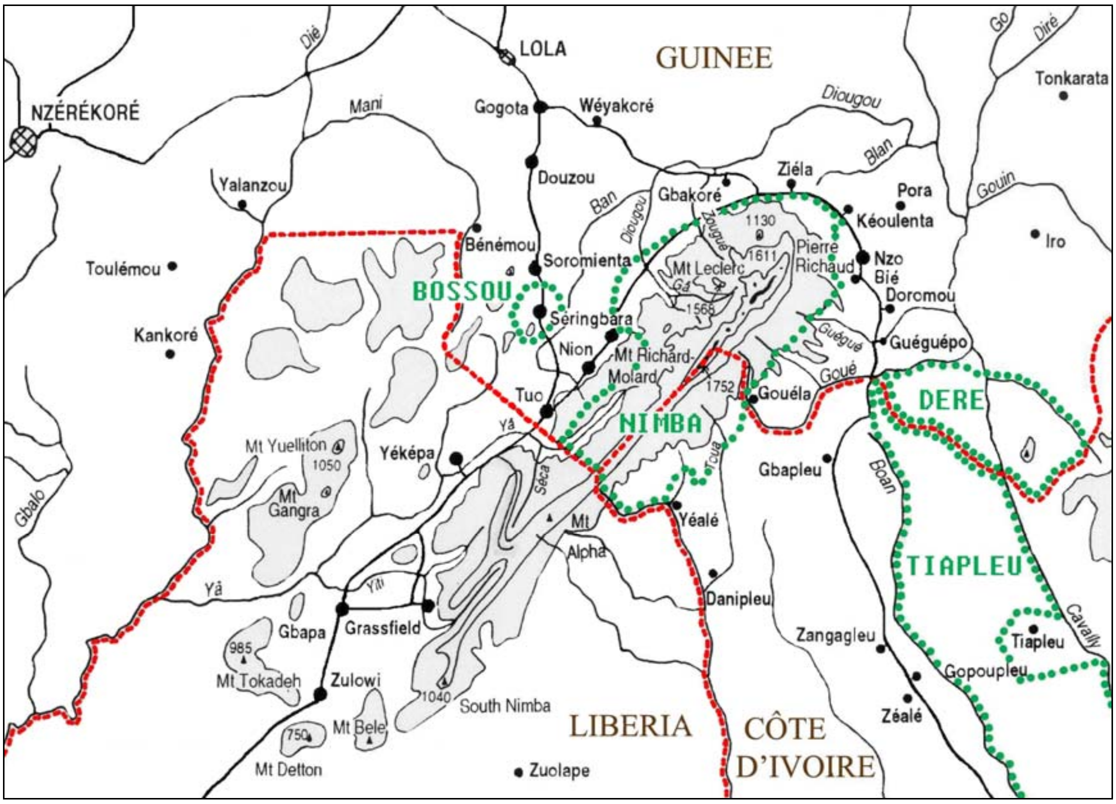


Figure 2.1. A map of the field study site Bossou in the Republic of Guinea, and the neighbouring Nimba Mountain range. The Green lines show areas where research is currently being conducted by KUPRINT (Kyoto University Primate Research International Team), and the red lines illustrate the main roads in the area (Map drawn by T. Humle, N. Granier and L. Martinez).

2.2 Climatic Variables

The climate at Bossou is classified as tropical wet seasonal (Richards, 1996). From data collected during the course of this study in 2005 (see Figure 2.2, see p.31), Bossou has a clear wet season (from March to October) and dry season (from November to February); this is consistent with past records (Yamakoshi, 1998; Takemoto, 2002; Humle, 2003b). Wet months are classed as those when rainfall exceeds 100mm (taken as an approximate guide to evaporation in the tropics) and dry months when rainfall falls below 100mm. Total rainfall from the 1st January to the 31st December 2005 was 3,437.75 mm, which is much higher than the 1779.4mm previously reported by Humle (2003b) and 2190 mm by Takemoto (2002; data collected from 1995 to 1998). During the months of July and August rainfall levels were particularly high. The average annual temperature was 26.9 °C, ranging from a minimum of 12.3°C to a maximum of 36.9°C, with the greatest range difference observed in the months of January and February.

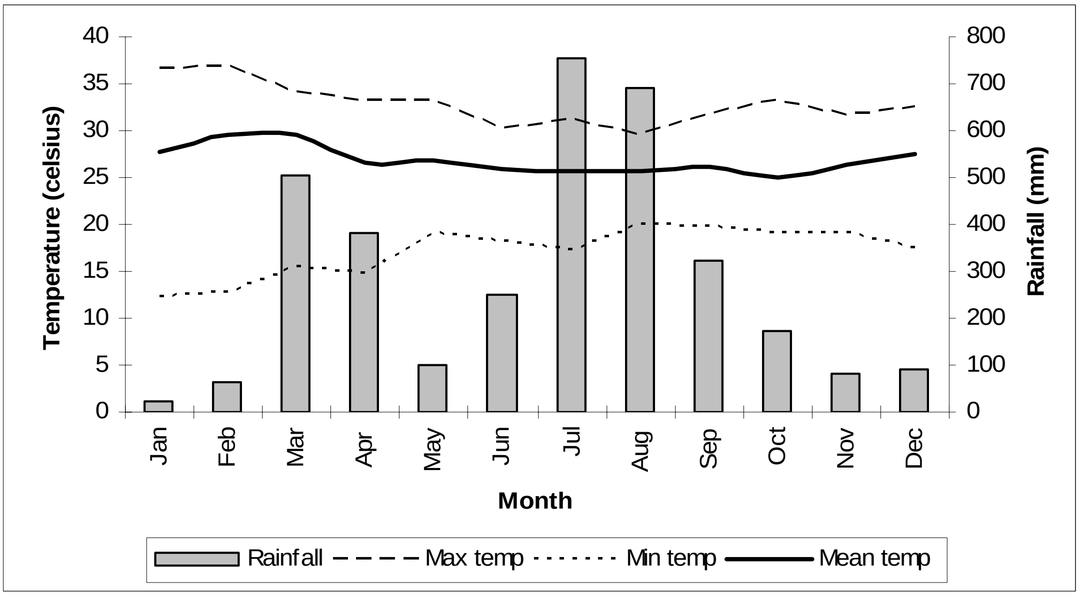


Figure 2.2. Rainfall and temperature data from Bossou, Guinea, between January-December 2005 (longterm data not available).

2.3 Vegetation

The small hills (70-150m high) that constitute the chimpanzees' home range are covered in primary and secondary forest, cultivated and abandoned fields, and orchards. At the foot of these hills a mixture of cultivated and abandoned fields, secondary, riverine and scrub forests dominate the landscape for approximately 6 km in all directions.

Primary forest accounts for 1km² and is predominantly located at the summit of the largest hill (Gban). The main body of forest is mostly characterised by secondary and scrub forest due to abandoned cultivation. There is a noticeable occurrence of certain tree species within the secondary forest including the umbrella tree *(Musanga cecropioides)*, the oil palm tree *(Elaeis guineensis)* and the bush pineapple *(Myrianthus arboreus)*. Terrestrial herbaceous vegetation of the families Marantaceae and Zingiberaceae is found throughout.

2.4 Human impact

In general, human interference in forested ecosystems in the Republic of Guinea is extensive; the area around the village of Bossou is no exception. There are approximately 2000 people living in Bossou, although numbers have fluctuated due to the establishment of temporary refugee camps during civil wars in Liberia and the Ivory Coast (Humle, 2003a; Yamakoshi, 2005). Although Bossou has been declared a reserve area, the majority of people living there are subsistence farmers practising slash and burn agriculture. Consequently the chimpanzees' home range is fragmented and surrounded by cultivated and abandoned orchards, fruit trees, fields and farms. The locals rely heavily on rice and cassava for carbohydrate intake, but also produce a wide variety of fruits including pineapple, papaya, orange, mandarin, mango and avocado for their own consumption and retail. Both humans and chimpanzees rely heavily on oil-palms, but due to this species' high density and status as a communal resource, competition remains low (Yamakoshi, 2005). Although it was previously thought that deforestation and the subsequent cultivation of the forested hills began relatively recently, video footage from the 1960's shows extensive deforestation on the slopes of the largest hill, Gban (Yamakoshi, pers. comm.). This reinforces the view that the chimpanzees and the local population have coexisted in close proximity for generations.

The village of Bossou and the chimpanzees' home range are dissected by one large road (approximately 12m wide) that stretches from the Guinea-Liberia border through into the forested region of Guinea. This road was expanded in December 2004 and is frequently used by large trucks, cars, motorbikes and pedestrians. A narrower dirt road (approximately 3m wide) branches off from the large road; the smaller road is used by pedestrians. The chimpanzees must cross both roads to move from one forested area to the next. Both roads have forest cover up to the edges, and are separated by a middle zone of secondary forest and coffee plantations. The chimpanzees typically cross the two roads at specific points that the group has used for decades (Matsuzawa, 2006).

Illegal hunting and poaching occur within the forests of Bossou; gunshots are often heard and traps are frequently confiscated by guides (pers. obs.). The forests currently sustain relatively few large mammals, as many have fallen victim to past hunting activities. Although chimpanzees are not hunted, mammalian species that are directly targeted include the red-flanked duiker *(Cephalophus rufilatus)* and the cane rat *(Thrynomys swinderianus)*. The Bossou chimpanzees have been observed dismantling traps that are found in their home range; it is conceivable that their knowledge of how to detect and dismantle these traps is passed on to younger members of the community (Ohashi, 2005).

2.5 Local beliefs

The village of Bossou is home to the Manon people who hold the neighbouring chimpanzees sacred as the reincarnation of their ancestors, and believe that their ancestors' souls rest on the sacred hill of Gban (Kortlandt, 1986). As the chimpanzee is a totem of the most influential family of Bossou, it is strictly forbidden to hunt or eat the chimpanzee (Yamakoshi, 2005). Yamakoshi (2005) proposes that Gban was important for village protection during years of tribal conflict; the current peaceful coexistence between man and chimpanzee may have historical war roots. The chimpanzees regularly crop-raid and are known to occasionally attack villagers (Yamakoshi, 2005). People's reactions to crop-raiding vary in the village; some tolerate it as they believe the chimpanzees have a right to feed off a small amount of their crops, whilst others actively chase and throw stones at any chimpanzees seen near to their farm. Due to the increase in purchasable imports and the depreciation of the Guinean franc, crop-raiding that may have been tolerated in the past is now often seen as problematic. The people and chimpanzees come into contact regularly either by the road side or around cultivated areas, and many villagers are afraid of the chimpanzees (pers. obs.). However, due to the local people's strong cultural beliefs, humans and chimpanzees have been able to cosurvive in such close proximity over many generations.

2.6 History of research at Bossou

Zoologist M. Lamotte was the first to announce Bossou as a valuable chimpanzee field site, in 1942 (Kortlandt, 1986). Following this, Kortlandt visited on several occasions during the early 1960's, conducting research on the Bossou chimpanzee community (Kortlandt, 1962). Bossou was first established as a long-term chimpanzee field site in

1976 by Sugiyama from the Primate Research Institute, Kyoto University, Japan, and research has continued ever since.

A wide range of research has been conducted at Bossou; which has focused predominantly on chimpanzee tool use and cultural behaviours, population dynamics and life history. The Bossou chimpanzees habitually use pairs of stones as a hammer and anvil to crack open the hard shells of oil palm nuts to obtain the kernel inside (Kortlandt, 1987; Biro et al., 2003; Biro et al., 2006; Matsuzawa, 2006). Additionally, they use tools in an exclusive range of behaviours including pestle-pounding and algae scooping (Ohashi, 2006). The Bossou chimpanzees regularly engage in ant-dipping, some characteristics of which appear to be unique to this community (Humle, 1999, 2003b, 2003c, 2006; Humle and Matsuzawa, 2001).

The nearest neighbouring chimpanzee community lives in the Nimba mountains, where habituation and research is at a preliminary stage (Koops et al., 2006). Conservation activities concerning the planting of a green corridor to join together the fragmented forests of Bossou and the Nimba Mountains were first touched upon by Hirata in 1998. Progress on this commendable long-term conservation plan continues, with completion estimated in the near future. Aside from the green corridor project, considerable effort has been made to protect the Bossou chimpanzees and the forests in which they live, although research with specific conservation objectives is lacking.

Although there have been some studies on the Bossou chimpanzees' ecology and feeding behaviour (Sugiyama and Koman, 1992; Yamakoshi, 1998; Takemoto, 2002), there is still much that remains unexplored. Future research conducted on the Bossou community may have important implications, acting as a template for conservation efforts for other populations living in fragmented disturbed habitats.

2.6.1 Subsistence behaviour

Sugiyama (1992) made a preliminary list of all flora present in Bossou, and reported that due to extensive habitat destruction, 55% of tree species identified are located mostly in secondary forest. He stated that the chimpanzees feed upon 200 different plant species and 246 items (parts of plants); representing approximately 30% of the available species in their habitat. Yamakoshi (1998) stated that the Bossou chimpanzees spend on average 60.5% of their annual feeding time on fruits; and that certain fruit items vary in their importance depending upon the season. Yamakoshi (1998, 2005) also highlighted that chimpanzees rely heavily upon human-influenced habitats, including secondary forest, scrub forest, orchards and cultivated fields, during the fruit-scarce season. He demonstrated that aseasonal secondary forest specialists such as the umbrella tree and palm tree also act as important fallback foods during periods of fruit scarcity, and may partly explain how a group of large mammals is able to survive in such small patches of forest. However, chimpanzees may be forced to decrease their dietary diversity to cope with such periods of low fruit abundance (Takemoto, 2002)

Sugiyama and Koman (1992) noted that chimpanzees at Bossou feed on 29 species of cultivated foods, taken from both abandoned and maintained fields and orchards; these foods are fully integrated into their dietary repertoire. Takemoto (2002) supplies the only quantitative record of cultivar feeding in this population of chimpanzees, showing that 6.4% of their annual diet is composed of cultivars which are largely eaten during some months of low fruit abundance. Oranges *(Citrus aurantifolia)* make up 55.5% of all cultivated fruit consumed, while other notable cultivars include mandarin *(Citrus reticulata)*, papaya *(Carica papaya)*, banana *(Musa sinensis)* and maize *(Zea mays)*; see Chapter 5 for additional data.

Leaves and woody pith are also significant natural foods, comprising approximately 10.8% and 10.1% of total chimpanzee feeding time respectively. Additionally, flowers, gum, seeds and roots form some of the plant items frequently consumed at Bossou, and other less commonly consumed items include mushrooms, algae and bird eggs. Insects, including termites (*Isoptera*) and ants (*Dorylus* sp. and *Oecophylla longinoda*) are habitually eaten by the chimpanzees as are insect eggs, larvae and to a lesser extent bees and beetles. Feeding on mammalian matter is infrequent, probably due to the scarcity of such species in their habitat, but observations confirm the occasional consumption of tree pangolin *(Phataginus tricuspis)* and the opportunist feeding of expelled chimpanzee placenta by several members of the group (pers. obs., 2004).

2.6.2 Demography

The chimpanzees of Bossou conform to the typical chimpanzee fission-fusion social pattern (Nishida, 1968; Goodall, 1986; Sugiyama, 2004; Matsuzawa, 2006). Bossou chimpanzees form very cohesive groups compared with other reported communities (Sugiyama and Koman, 1979), and inter-female and male-female relationships are highly affiliative (Sugiyama, 1988). Semi-isolation of this community and low levels of female dispersal (Sugiyama, 1981, 1984) may have resulted in high relatedness amongst individuals and consequently strong associations. Sakura (1994) reported that many aspects of party formation patterns at Bossou were comparable to those observed at other long-term chimpanzee field sites, where food supply, presence of maximally swollen females and infants, and presence of predators were all influencing factors. Sakura noted the low correlation between party size and the feeding ratio of a party (number of feeding animals in a party/total number of animals in the party), possibly a result of low inter-individual feeding competition. In parallel with other chimpanzee populations, strong seasonal fluctuations in party size exist, and the presence of maximally swollen females causes higher aggregation amongst males. Sakura also remarked upon some interesting group changes during ‘high risk’ road-crossings: the chimpanzees formed significantly larger parties that more frequently included the alpha male, compared with baseline periods.

Sugiyama (1994, 2004) found that the mean interbirth interval of the Bossou chimpanzees is 5.1 years (excluding cases where the previous infant had died within its first 3 years) and weaning occurs at around 4 years of age (Matsuzawa, 2006). Females at Bossou give birth when 12 to 14 years old, although a female has been recorded giving birth at 9.6 years; this is younger than records from other chimpanzee populations.

In sum, the Bossou community displays some unique demographic features and population dynamics, possibly explainable by their continual access to high-quality foods such as cultivars and semi-isolation from neighbouring communities. Such differences lead to hypotheses regarding the presence and transmission of cultural behaviours within and between populations.

2.7 The Bossou chimpanzee community

There are 4 identified sub-species of robust chimpanzee: Eastern chimpanzee *Pan troglodytes schweinfurthii,* Central chimpanzee *P. t. troglodytes,* Nigerian chimpanzee *P. t.*

vellerosus and the Western chimpanzee *P. t. verus*; the Bossou chimpanzees are of the Western sub-species (Grubb et al., 2003; Matsuzawa, 2006; Oates, 2006). There are an estimated 38,000 *P. t. verus* throughout West Africa, a large proportion of which live in the Republic of Guinea (Butynski, 2001).

Chimpanzees live in a group called a community, consisting of several adult males and (usually) more females. Matsuzawa (2006) defines the following age-categories: infants (0 to less than 4 years old), juveniles (4 to less than 8 years old), adolescents (8 to less than 12 years old), adults (12 to less than 36 years old), and elders (greater than 36 years old). The age category may be slightly different between the sexes and among different communities (Matsuzawa, 2006).

Chimpanzees have a patrilineal society; females normally emigrate at puberty whereas males tend to stay in their natal community (Goodall, 1983; Boesch and Boesch-Achermann, 2000). During the past 30 years of research, all the females born into the Bossou community left before or following their first birth (Matsuzawa, 2006). During this study, (May 2004-December 2005) a 13-year old adult female chimpanzee (Fotayu) with her 3-year old infant (Fokaye) emigrated from the Bossou community (Table 2.1). In contrast to other sites, Humle (2003b) proposes that due to the unexplained disappearance of some males from Bossou, it is very likely that both females and males emigrate from their natal community. This could be influenced by intra-group male-male competition and the habitat structure of Bossou (Sugiyama, 1999).

Since 1976 the Bossou chimpanzee community has remained at approximately 20 individuals; Figure 2.3 clearly shows that the Bossou community is now an ageing population. During this study the Bossou community size ranged from 12 to 14 individuals; birth and disappearance dates are shown in Table 2.1. The social rank of the Bossou males has varied over the years, but during this study the relative status of the alpha male (Yolo), the second-ranking male (Foaf) and the third-ranking male (Tua) was stable (Biro et al., 2003; Sugiyama, 2004).

Table 2.1. The Bossou community during the study period (May 04-December 05).

Name	Abbr.	Sex	Rank	Birth date	Status
Yulo	YL	m	Alpha male	Middle 1991	Present
Foaf	FF	m	Second male	Late 1980	Present
Tua	TA	m	Third male	Unknown (adult in 1976)	Present
Yo	Yo	f	Alpha female	Unknown (adult in 1976)	Present
Jire	Jr	f		Unknown (adult in 1976)	Present
Pama	Pm	f		Unknown (adult in 1976)	Present
Fana	Fn	f		Unknown (adult in 1976)	Present
Velu	Vl	f		Unknown (adult in 1976)	Present
Fotayu	Ft	f		Middle 1991	Disappeared Dec-04
Fanle	Fl	f		Oct-97	Present
Jeje	JJ	m		Dec-97	Present
Peley	PE	m		Apr-98	Present
Fokaye	FK	m		Jun-01	Disappeared Dec-04
Joya	Jy	f		Sep-04	Present

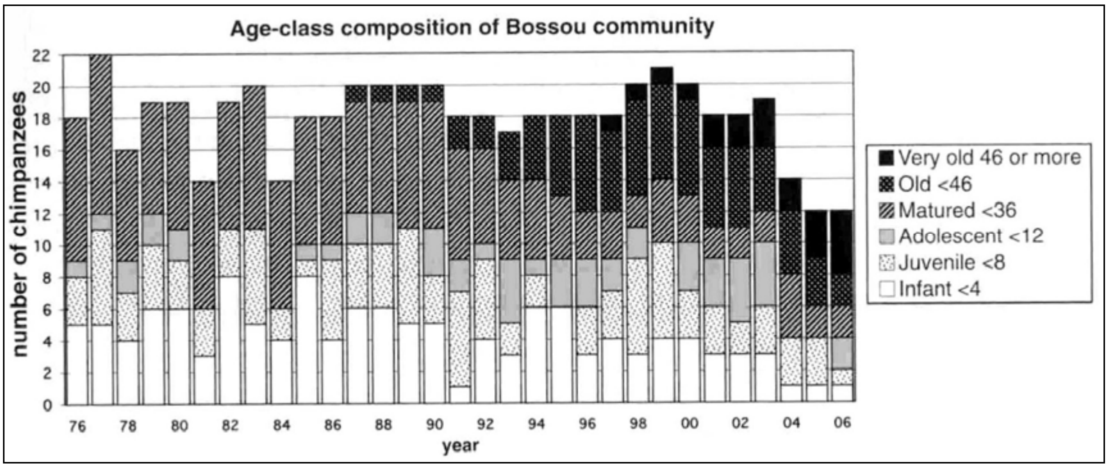


Figure 2.3. Demography of chimpanzees in the Bossou community. The number of chimpanzees in each age category is plotted against years since 1976 (taken from Matsuzawa, 2006).

Chapter 3

Study Methods

Study Methods

3.1 Overview of methods

Data collection used a variety of methods including line transect fruit availability surveys, cultivar availability questionnaires and surveys and focal, scan and *ad libitum* behavioural sampling. Focal sampling was used to collect data on an individual's feeding patterns and associated behaviours, and to reduce observational biases that might arise from females being more fearful of human observers. Additionally, within the same observation period, I used scan sampling and *ad libitum* sampling to record various social and behavioural data. In this chapter I will explain the procedures employed in data collection and analysis.

3.2 Study Period

Phenological data were collected continually for 20 months, from May 2004-December 2005. Behavioural data collection for this research was carried out in three periods: May 2004-October 2004, January 2005-April 2005 and November-December 2005, for a total of 12 months. These periods were chosen to ensure that chimpanzee observations were recorded during every month of the year. Within this time I recorded 187 focal samples, totalling 1,673 hours of focal observation upon which this thesis is largely based (see Table 3.1). The total observation time in months of low wild fruit availability (May to November; 4177 hours: 49.7% of total time) and high wild fruit availability (December to April; 4214 hours: 50.3% of total time) were very similar (see Chapter 4). See Appendix B1 for further details on observation biases.

Table 3.1. The number of focal samples, mean focal time (hours), total focal time (hours) and total scan time (hours) for each member of the Bossou community. Focals were not conducted on juveniles (*) and infants were excluded from observations.

Chimpanzee	Sex	No. of samples	Mean ±SE	Focal time (hours)	Scan time (hours)
YL	m	20	9.6 ± 0.5	192.4	841.3
FF	m	23	8.9 ± 0.6	213.8	913.8
TA	m	19	9.7 ± 0.4	183.9	729.3
Yo	f	24	9.2 ± 0.4	219.3	772.8
Jr	f	25	9.2 ± 0.5	220.5	795.7
Pm	f	20	9.0 ± 0.3	180.1	653.8
Fn	f	22	9.2 ± 0.5	202.6	705.1
Vl	f	24	8.5 ± 0.5	203.4	497.1
Ft	f	10	5.7 ± 0.9	57.1	193.7
PE*	m				756.3
JJ*	m				826.2
Fl*	f				706
Totals		**187**		**1673**	**8391**

3.3 Habituation and visibility levels

The Bossou chimpanzees have been studied intensively since 1976 (for a historial perspective, see Matsuzawa, 2006) and are well habituated to being observed. By the beginning of the study all community members were easily identifiable by KH and guides. As female chimpanzees were sometimes timid in the presence of observers, particular attention was paid to reducing noise levels and maintaining an appropriate distance so as to minimise intrusiveness. Where possible, the chimpanzees were observed from a minimum distance of 7m. This was done to minimise any risk of disease transmission, avoid displacing group members, and prevent interference with their ongoing behaviours.

Visibility levels in the forest were generally good. It could sometimes be difficult to get clear observations in dense secondary and scrub forests; areas of thicket in and around agricultural fields proved particularly challenging. In such places the guides used small secateurs to cut through obscuring vegetation; the chimpanzees exhibited no observable signs of fear or alarm at such activities.

3.3.1 Location of chimpanzees

The following techniques were employed, often in combination, to locate the chimpanzees:

- Nest-to-nest follows: on occasion chimpanzees were found in the same nest the following morning.
- Tracks: these included foot and hand imprints, food remains, and bent or broken vegetation.
- Direction of chimpanzee vocalisations: we often waited at elevated locations to listen for vocalisations from the surrounding hills.
- Waiting by specific fruiting trees and surveying frequently used spots.
- Asking local villagers if they have recently heard or seen the chimpanzees.
- Opportunistic discoveries.

Locating the chimpanzees was easier in the dry season than the wet season. This was mainly due to larger party sizes, higher fruit availability, increased vocalisation rates and reduced ambient noise levels. Walkie-talkies were used for communication between guide parties to assist in the location of chimpanzee parties and specific individuals.

3.4 Rainfall and temperature

Precipitation data (mm) at the study site were collected daily at 1700h from a rainfall gauge located in an open area. The mean, maximum and minimum daily temperatures (C^o) were also collected during the research period. The thermometer was placed under a waterproof shelter on the edge of the forest close to camp, and readings were taken at 1730h.

3.5 Phenology

The resident botanist, Paquille Cherif, had very good knowledge of the flora at Bossou, and knew both the local Manon and scientific names. Paquille and I (when present) collected phenology data together, confirming all transect trees (see Chapter 4, p.47). Paquille was present for the first 18 months of this study but not for the final 2 months. Paquille and I trained another guide, Henry Gbergbe, in botanical and transect methods for 12 months prior to Paquille's departure.

A total of six belt transect lines (total of 4739m) were set up in May 2004 to monitor all tree species (see p.47); for comparative purposes, transect methods replicated those of Takemoto (2002, 2004). Transect placement is dependent on the objective of the study (Morgan, 2000). As the chimpanzees' home range is enclosed by savannah, cultivated fields and shrub land, the transect lines were purposefully established in the three principal hill forests (Gban including Seiba, Guein and Gboton). Using a compass to ensure accurate navigation, the transects were made in north-to-south and east-to-west directions from the summit of each hill until reaching a road or cultivated field. Due to the restricted home range of the chimpanzees, this purposeful method was considered appropriate for maximising the area and number of trees sampled. Additionally, the transect lines passed through all the habitat types present in the Bossou home range, and the trees sampled are presumed to be representative.

The transects were monitored twice per month from May 2004 to December 2005, although only once during May 2004 due to the study establishment phase (20/05/04 to 29/05/04). Each transect line was 10m wide, and included every tree greater than 5cm in diameter at breast height (DBH); lianas were also included. Mango trees *(Mangifera indica)* which are fed on frequently by the chimpanzees, were the only cultivar included in the transects. For trees with buttresses, diameter was measured directly above the buttress, as the inflated diameter is unlikely to reflect the tree’s fruit production (Chapman et al., 1992). For trees with multiple large trunks, each trunk was measured separately and the basal area for each summed. Certain species had many small trunks and if any DBH was smaller than 5cm it was not included.

Trees that were either cut down or that died during the 18-month study were not included in analysis. The effect of excluding this small number of trees on the total density and basal area is assumed to be negligible. Additionally, any trees that grew to more than 5cm DBH during the study period were not included, although it should be acknowledged that personal observations confirm that certain species with a small DBH and rapid growth rate can produce fairly large amounts of fruit.

Every 2nd and 4th week (Humle, 2003b), the transects were monitored for fruit and flower availability by at least two observers, using binoculars. The results were written down by a member of the transect team. Each tree was coded for fruit (ripe and unripe) and flower availability on a scale of 0 to 4 (0 is absent; 1 is between 1 and 25% of the canopy covered; 2 is 26 to 50% cover, 3 is 51 to 75% cover, and 4 is 76 to 100% cover). If a tree was dead or had been cut down, this was recorded.

3.6 Cultivar availability

The seasonality of cultivars was recorded as availability on each respondent’s farm; thirty seven interviews in total were carried out over two weeks at the end of the third study period (December 2005). Ideally, to monitor temporal variations in cultivar availability, a representative number of cultivar trees or crop fields would be sampled. However, due to time restraints and the range of cultivars that the chimpanzees consume, this was not practicable. Additionally, due to the guaranteed harvesting of ripe fruits by farmers, if the above method was employed it would have resulted in an inevitable underestimation of ripe fruits present; it was not possible to monitor the cultivars with sufficient regularity to avoid such likely inaccuracies. However, to check for correlations with questionnaire data, monthly production levels of cultivars, including pineapple, papaya, banana, oil-palm fruit, and cassava, were monitored for one year on a large farm in Bossou. Additionally, mango availability in both the village and the forest was recorded, using the same method as outlined for transect recordings.

A list of all the families cultivating in the Bossou area was compiled and families were randomly selected on this list. The questionnaire employed during the interview asked villagers about monthly variations in ripe crop abundance and the planting and harvesting patterns of the crops produced by the respondent’s family. The cultivar availability questionnaire aimed to collect standardised information from a relatively large number of individuals in Bossou, in order to generalise from the sample to the Bossou population (see Bulmer and Warwick, 1983). A potential problem with questionnaires is that respondents, rather than appearing uncooperative or non-knowledgeable, may prefer to give potentially incorrect information. To avoid this, knowledge of a topic should be ascertained before asking questions on it (Bulmer and Warwick, 1983). All the respondents were farmers from the Bossou area, answering questions on the crops that they produced.

There is often a problem in obtaining accurate estimates of crop yield when crops are sold in variable units, harvested opportunistically and consumed as needed. Respondents may therefore find it difficult to recall exact amounts when no records are kept (Casley and Lury, 1986). For this reason a very simple measurement index was adopted for data collection. The respondent rated the monthly presence of each specific cultivar for the preceding year (2005), grading from 0-2 where 0 was no availability, 1 was low availability and 2 was high availability. The cultivars examined in the questionnaire were selected according to prevalence in the chimpanzees' diet, and included banana, cacao, cassava, maize, mandarin, mango, oil-palm, orange, papaya, pineapple and rice. The respondents were asked about the planting, harvesting and location of specific crops (paddy, forest or savannah) on their farm. Only cultivars that required a planting regime, such as banana, cassava, maize, pineapple and rice were included in this part of the questionnaire.

Interviews lasted approximately 20 minutes, and answers were recorded on pre-printed sheets. The respondents were not prompted, and to ensure accuracy of questionnaire transcriptions, relevant details were discussed with the translators, Bossou guides Marcel Dore and Henry Gbergbe, prior to the interview. Where possible, the questions were also asked in French, to reduce misinterpretation. This study did not have to deal with problems of a courtesy bias as there were no obvious right or wrong answers, and no answer received a particularly positive or negative reaction by the interviewer (see Priston, 2005).

The number of respondents that grow a crop on their farm gives an indication of its spatial availability within the chimpanzees' core area. However, exact counts of cultivated trees, orchards and fields on the three main hills (Gban, Guein and Gboton) and up to 50 metres from the forest edge were conducted. In addition, a map was drawn to visually illustrate fields of cultivars and orchards within and around these hills (extends to show cultivars greater than 50 metres from the forest edge).

3.7 Chimpanzee behavioural sampling

All behavioural data were always recorded by KH using a double-sided check sheet and pen (see Appendix B2); guides were used to assist with tracking the chimpanzees and identifying the names of foods. All the guides were familiar with, and to, the chimpanzees. The same guides were used as much as possible, but due to sickness and family obligations, other guides sometimes assisted. Additionally, during the months of January and December 2005, other research experiments on nut-cracking were conducted under naturalistic conditions within the chimpanzees' core area.

3.7.1 Focal individual sampling

Focal individual sampling is the observation and behavioural recording of one individual for a specified period of time (Martin and Bateson, 1986). A focal individual was randomly selected from a predetermined list each day prior to the observation session and followed from 0630h to nest. Only adults (n=9) were selected as focal individuals. If the focal individual was out of sight, no records were made. Each individual was randomly sampled two times per month when possible (once in the first half and once in the second half of the month): if there were 'spare days' left at the end of the month, individuals with the least observation time were sampled again. If the predetermined focal individual was not located by midday (after approximately 5.5 hours of searching) then the next focal individual was selected from the predetermined list. If the target individual was lost, extensive searching usually resulted in resumption of contact. However, if the chimpanzee could not be found in spite of extensive searching, then depending on the time of day, a new focal individual was chosen using the method outlined above.

I used instantaneous point sampling to record the activity and behaviour of the focal individual; continuous recording of the focal individual would have compromised the accuracy of other data collected (Martin and Bateson, 1986). Every 5 minutes, the ongoing behaviour of the focal individual was recorded; behaviours were mutually exclusive and the recording process took approximately 10 seconds. Behaviours were initially divided into 4 main categories: feeding (including food preparation), moving, resting and social, with each of the behaviours being more specifically categorised (see Appendix B3). These behaviours were based on an ethogram of the Mahale chimpanzees published by Nishida et al. (1999), although as this ethogram is extremely detailed, several behaviours were clumped. In addition to behaviour, the individual's location was noted as terrestrial or arboreal. The criterion for terrestrial behaviour was whether or not the individual placed at least one of its feet on the ground (Takemoto, 2004). If it was raining, this was also recorded.

If the focal individual was feeding on either wild or cultivated foods, the method of food acquisition, the food type and part, the food classification and the GPS location were recorded. Location information was obtained using the waypoint function on a hand held Garmin II+ GPS device. If the individual was preparing a food source prior to feeding, the food type, part and classification were again recorded. When feeding on cultivated foods, the first chimpanzee to enter the field or orchard was recorded. Human presence (auditory and visual clumped together), guard level [classified from '**a** to **c**', where '**a**' is abandoned, '**b(i)**' is guarded but tolerated (stones are never thrown and chimpanzees are never chased), '**b(ii)**' is guarded but not tolerated (stones are thrown and/or chimpanzees are chased), and '**c**' is supplied (chimpanzees are offered food by researchers conducting nut-cracking experiments)]. Hours of guarding would have been a preferred measure for **b(i)** and **b(ii)**, but this would have been difficult to obtain accurately. Other physical deterrent mechanisms such as fences and traps are not considered, as these were used to restrict access by other animals like the cane rat, not by chimpanzees. The location in which the food was acquired was also noted as either in the forest or the village; if feeding occurred in the village the distance from the nearest forest edge was estimated. Whether the focal individual ‘transported’ the food acquired in one place to another place before feeding (e.g., from the source tree or patch to consume elsewhere) was also noted.

3.7.2 Scan sampling

Scan sampling involves rapid scanning of the whole party at regular intervals (Martin and Bateson, 1986). Scan samples were made using the same 5-minute mark as focal samples to record the composition of the party associated with the focal individual’s behaviour. In accordance with previous studies at Bossou, a party was classified as within a 30-m radius from the focal individual; beyond this, visibility was restricted (Sugiyama and Koman, 1979; Sakura, 1994). The radius around the focal individual was increased qualitatively to ensure that party size was not underestimated; this only occurred rarely (Sakura, 1994; Bates, 2005).

‘Party spread’ and ‘proximity of nearest neighbour’ were also recorded on the 5-minute mark. ‘Party spread’ was defined as the furthest distance (in metres) between 2 individuals within the party, and ‘proximity of nearest neighbour’ was the distance (metres) of the closest chimpanzee to the focal individual; infants were excluded from observations.

Distance estimation tests were conducted three times on KH, once at the beginning of each data collection phase (Martin and Bateson, 1986). KH estimated a series of arboreal (n=10) and terrestrial (n=10) distances in different types of forest and in more open areas which were subsequently measured. Arboreal distances proved slightly more difficult, but were measured by extending the location points to the ground and then measuring whilst taking into account any slope. KH recorded all distances during this study and was able to estimate distances to within a high accuracy in both arboreal and terrestrial conditions during all 3 test phases (see Appendix B4).

3.7.3 Ad libitum observations

During *ad libitum* data collection no systematic constraints are placed on what is recorded and when (Martin and Bateson, 1986). *Ad libitum* samples included the name of the individuals involved and the time of day, so that records could be associated with other data gathered.

(a) Feeding

Whilst remaining with the focal animal, all-occurrence feeding by all adult chimpanzees was noted. This included the time of feeding, name of feeding individual, food type and part, and whether the individual vocalised when feeding (only includes pant-hoots made within a food patch or tree, from up to 10 seconds before feeding started until feeding finished). Bipedal standing for two seconds or more and assuming an elevated position when crop-raiding were recorded as vigilance behaviours. Note that all occurrences of feeding by infant and juvenile chimpanzees was not recorded, as they would often experiment and play with food without ingesting it. When the chimpanzees were observed feeding on cultivars, much of the same information was recorded as with focal sampling. The start and finish times of feeding were noted as well as guard level, first chimpanzee to enter, human presence, location, distance from forest edge and whether the chimpanzee vocalised. Both the adults and juveniles were included in these records.

(b) Road-crossing

All occurrences of road-crossing and road-crossing progression orders from January to April 2005, and November to December 2005 were recorded (for complete methods see Chapter 7).

(c) Self-directed behaviours (SDB's)

All occurrences of rough self-scratching were recorded as a measure of SDB; full method details are given in Chapter 8.

3.8 Analyses

All data were analysed using SPSS version 13, and details of the statistical tests used can be found in the relevant chapters. The data were checked for normality and parametric statistics were employed where appropriate. If data were not normally distributed and could not be transformed, non-parametric tests were used. One-tailed or two-tailed tests were employed in accordance with the original hypotheses; one-tailed tests are highlighted throughout. The critical significance level was set at 5%.

Chapter 4

Patterns of Wild Food and Cultivar Availability

Patterns of Wild Food and Cultivar Availability

4.1 Introduction

Fruit production in tropical forests is highly seasonal and periods of fruit scarcity are common (Tergborgh, 1986; Yamakoshi, 1998; Fawcett, 2000). Different plant species present varying patterns of food abundance and scarcity; some produce fruits that are available throughout the year, others produce fruits consistently at the same time each year, and particular plants have no obvious fruiting pattern.

A variety of factors have been proposed as driving the phenological patterns of tropical rain forests, such as temperature, rainfall and sunlight levels (Richards, 1996; Fawcett, 2000; Chapman et al., 2005). Fruiting can be triggered by climatic changes which act as signals (e.g. fruits are produced when the water need to produce them is abundant), or can be direct responses to climatic conditions such as temperature (Tutin and Fernandez, 1993; Chapman et al., 2005). Regardless of the mechanisms influencing fruiting, climatic patterns are likely to be crucial in setting the timing of fruiting events (Chapman et al., 2005). It is probable that the planting and fruiting of certain cultivars is also determined by these same climatic factors, and may show synchrony with wild fruit availability.

Forest fallback or keystone plant resources, which are by definition available consistently all year-round or when main foods are scarce (Tergborgh, 1986; Tutin and White, 1998), clearly play a critical role in sustaining organisms. Tergborgh (1986) notes that these fruits are generally inferior in quality as measured by lower calorie and mineral content; however, other studies present data on the nutritional adequacy of fallback foods (Yamakoshi, 1998). Cultivars also have diverse patterns of availability, and are additionally high in nutritional content but low in toxins. Whether there is any discernable relationship between use of nutrient-rich cultivars and fallback forest fruits by chimpanzees remains to be established.

Although the diets of chimpanzees are diverse, they are dominated by ripe arboreal fruits (Wrangham, 1977; Goodall, 1986; Tutin, 1991; Matsuzawa, 2006); it is therefore necessary to monitor ripe fruit phenology patterns when answering questions on chimpanzee ecology. Few studies of habituated chimpanzees include phenological data on both wild and cultivated fruits; much work may therefore be overlooking an integral part of the ecology of these apes (Naughton-Treves et al., 1998). An understanding of availability patterns of both categories of food is essential for answering questions on the importance of cultivars in the Bossou chimpanzees' diet, for example: Do cultivars act as additional fallback foods for the chimpanzees in times of fruit scarcity, or are they simply preferred all year round due to their superior nutritional content?

The objective of this chapter is to describe the monthly variations in availability of wild and cultivated fruits for the Bossou chimpanzees, linking food availability in croplands and adjacent forest to their use, for analyses and discussion in the following chapters.

4.1.2 Monitoring forest fruit availability

Chapman et al. (1994) highlight the difficulty of accurately quantifying fruit abundance in tropical forests. Estimates of fruit abundance derived from fruit traps were not correlated with approximations from either systematic area-based phenology transects or non-systematic fruit trails of key fruiting species; however the latter two were positively correlated. The choice between these latter two methods will depend upon the existing knowledge of key species for inclusion in the trail and the amount of time that is available for sampling (Blake, 1990; Chapman et al., 1992, 1994).

Monitoring phenology transects involves the establishment of areas in which trees are routinely monitored for the presence of fruit. The most common method to assess the size of the fruit crop on individual trees is to assign a relative rank using exact scores on an integer scale (Chapman et al., 1994). Tree size is measured by diameter at breast height (DBH), as it is assumed that the size of the tree reflects the tree's ability to produce fruit. A fruit availability index for each tree is then calculated from the fruit crop score and DBH. Compared to other parameters such as crown volume, DBH was found to be the most accurate estimator of fruit abundance and displayed low levels of inter-observer variability (Chapman et al., 1992; Fawcett, 2000).

In tropical forests the upper canopy is often obscured and in areas of dense secondary forest the trees are often entwined, making it time consuming to get an accurate recording of fruit availability. The accuracy of estimating fruiting patterns will increase with the proportion of the animal's home range that is sampled; a representative section of all vegetation types should also be included. If only key species are monitored, knowledge of their densities will be necessary to extrapolate the results to general fruit availability (Chapman et al., 1994; Fawcett, 2000). As all the plant species that were present on transects were monitored, density measurements were not conducted. The consumption of wild ripe fruits by animals may affect scoring on transects, a potential problem noted in monitoring wild fruit availability (Fawcett, 2000). However, as described in Chapter 2, the forests of Bossou do not contain many other frugivorous animals or birds (local inhabitants, pers. comm. 2004; pers. obs. 2004-2005), so such effects should be negligible.

4.1.3 Hypotheses

(a) Forest fruit and cultivar availability will vary throughout the year.

(b) Certain wild fruits will be present year-round and during periods of wild fruit scarcity.

4.2 Methods and analyses

For complete methods, see Chapter 3.

4.2.1 Wild fruit availability

The following formula was used to calculate the fruit availability index (FA Index), which assumes circular cross-section of trunks (modified from Takemoto, 2004):

$$\textbf{FA Index} = [\sum (\mathbf{Pi} \times \mathbf{Fi})] \;/\; [\sum (\mathbf{Pi} \times 4)] \times 100$$

Pi is the basal area of the tree (cm²). **Fi** is the fruiting score of the tree (0-4).

Fruiting score: 0 is absent; 1 is between 1 and 25% of the canopy covered; 2 is 26 to 50% cover, 3 is 51 to 75% cover, and 4 is 76 to 100% cover.

The plant species present on the transects were divided into two groups (Fawcett, 2000):

- ‘Community-wide species’: all monitored plant species on the transects.
- ‘Chimpanzee food species’: chimpanzees were observed consuming the fruit of these species by KH during the study period.

Monthly FA Index values of food availability were calculated by taking the mean of the FA Index values for the two surveys. The beginning of the month refers to values from the first monthly monitoring session in week 2, and the end of the month refers to the second session in week 4.

The data were checked for normality using a normality probability plot and parametric linear regression analyses were used to test for relationships between community-wide and chimpanzee food species availability.

4.2.2 Cultivar availability

To get an indication of the spatial availability of cultivars, the presence of all cultivars on the three main hills (Gban, Guein and Gboton) and up to 50 metres from the forest edge were assessed. To understand the temporal availability of cultivars, villagers who owned farmland within or around Bossou answered questionnaires on the planting patterns of the cultivars they produced and the monthly availability of cultivars on their farms. This was done using a simple measurement index from 0 to 2 (0: no availability; 1: low presence; 2: high presence). A score of general availability was calculated by combining the low and high monthly presence values of cultivars, thus percentage availability of cultivar refers to the percentage of respondents who rated that cultivar to be available.

Monthly cultivar availability data were checked for normality using a normality probability plot and parametric analyses were used. Regression analyses were conducted to test for the best predictor of cultivar availability (dependent variable); independent variables included community-wide ripe FA Index, chimpanzee food species FA Index, rainfall, rainfall (including 1 month lag) and mean, maximum and minimum temperatures. When multiple variables were tested, stepwise regression analyses were used to assess the significance of each variable.

Systematic recordings of cultivars were also conducted, and are correlated with questionnaire availability where appropriate. Monthly production levels of certain cultivars, including pineapple, papaya, banana, oil-palm fruit, and cassava, were monitored for one year on a large farm in Bossou. Additionally, mango availability in both the village and forest was recorded using the method outlined for transect recordings.

4.3 Results

4.3.1 Phenology patterns and wild food availability

In total, 3611 trees from 149 community-wide species were sampled across transects, and of those, 1596 trees from 59 species were chimpanzee food species (see Appendix C1 for a comprehensive list). As expected, mean DBH was an indicator of forest maturity, with more heavily cultivated and more recently deforested areas having a smaller mean DBH (see Appendix C2), i.e., trees present on Gban (a mixture of primary and secondary forest) were generally larger than Gboton (secondary forest only). Additionally, 31 trees from 24 species (of which 11 trees from 7 species were chimpanzee food species) were cut or died during the study period; all were located in areas of secondary forest and 50% of these were located on Gboton (see Appendix C3). Most of them were classified as small trees (less than 10m in height at maturity), with a mean DBH of 8.75cm, which is smaller than the community-wide mean DBH of 14.3 cm.

The monthly fluctuations in flowers, unripe fruit and ripe fruit of community-wide species and chimpanzee food species are shown in Figure 4.1 (a) and (b) respectively. Discussions on the temporal variations of each phenophase follow, with particular emphasis on ripe fruit availability.

Plate 4.2. Transect monitoring on Guein by KH and guide.

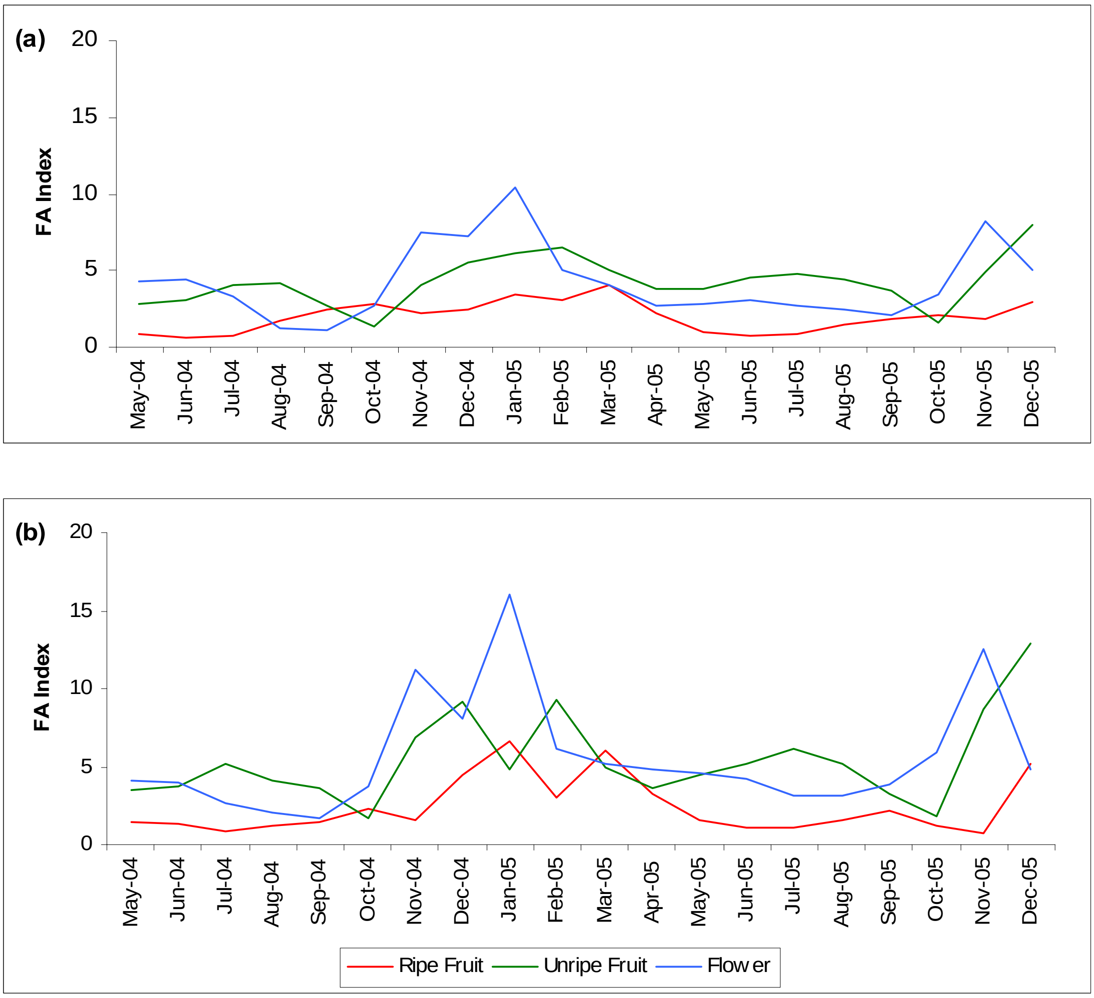


Figure 4.1. (a) The monthly availability of ripe fruit, unripe fruit and flowers in community-wide species (b) The monthly availability of ripe fruit, unripe fruit and flowers in chimpanzee food species.

Flowers

Monthly FA Index values showed flower availability of community-wide and chimpanzee food species were positively associated over the study period (linear regression; $r^2 = 0.89$, $p<0.01$). Flower production was greatest from November 04 to January 05, with another increase at the same time the following year (November 05), for both community-wide species and chimpanzee food species.

Unripe Fruit

The availability of unripe fruit for community-wide and chimpanzee food species was positively associated in terms of monthly values ($r^2 = 0.76$, $p<0.01$). Community-wide unripe fruit availability increased at the end of November and remained high until the end of March, while a drop in unripe fruit abundance was observed at the beginning of February for chimpanzee food species.

Ripe Fruit

There were significant associations between patterns of ripe fruit availability for community-wide and chimpanzee food species over this 20-month period ($r^2 = 0.63$, $p<0.01$). Ripe fruit availability varied throughout the year for both measures, peaking between December 04 and April 05, and increasing again in December 05. This period of 'abundance' (December to April) was especially clear for chimpanzee food species (see Figure 4.1 (b)); the rest of the year (May to November) ripe fruit availability was consistently low (FA Index values: mean ±SE, *high* vs *low;* 4.8 ± 0.6 vs 1.4 ± 0.1). Focussing on chimpanzee food species, the bi-monthly values show specifically that ripe fruit availability was low at the beginning of December 04, increasing by the end of December 04 and remaining high until the beginning of April 05. This rapid increase was partly attributable to the abundance of ripe *Antiaris africana;* however, the overall number of species producing ripe fruit was also significantly positively correlated with ripe fruit for all chimpanzee food species ($r^2 = 0.70$, $p < 0.01$).

Overall ripe fruit availability was higher during the dry season (November to February) than the wet season (March to October), with a delay of around one month between the November reductions in rainfall and the December increases in ripe fruit availability (Figure 4.2).

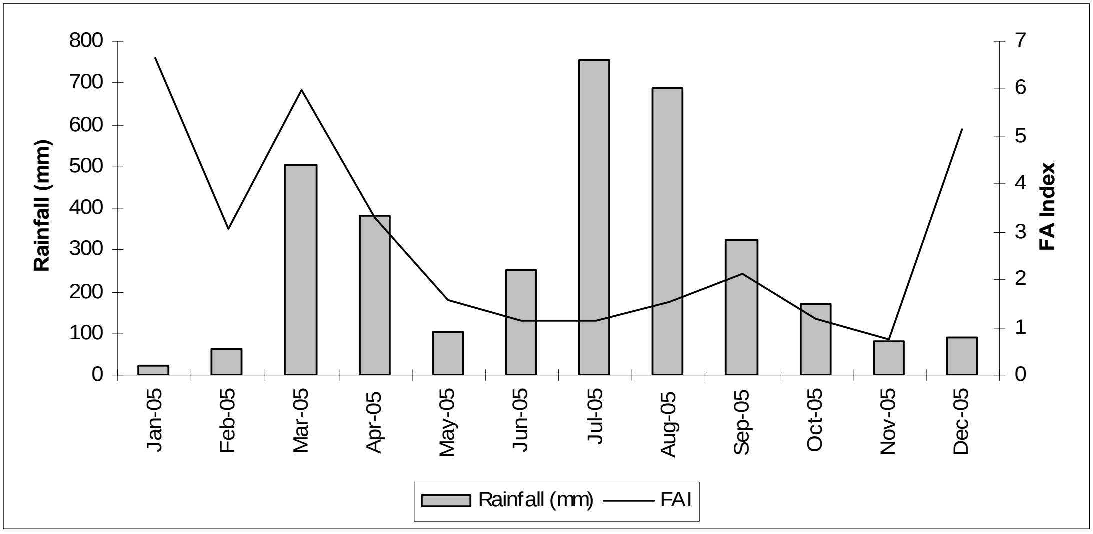


Figure 4.2. Ripe fruit availability of chimpanzee food species, and rainfall for 2005.

Correlations between community-wide fruit availability and chimpanzee food species fruit availability over this 12-month period were significant ($r^2 = 0.71$, $p < 0.01$). Community-wide fruit availability and chimpanzee food species fruit availability were separately tested against rainfall, and mean, maximum and minimum temperature. Mean temperature accounted for 58.5% ($p < 0.01$) of the variance in community-wide fruit availability and 49.6% ($p < 0.05$) in chimpanzee food species fruit availability over the 12-month period.

4.3.2 Fallback resources

Associations between community-wide ripe fruit availability and oil-palm *(Elaeis guineensis)* ripe fruit availability and umbrella tree *(Musanga cecropioides)* ripe fruit availability were not significant (r^2= 0.08, ns; r^2= 0.01, ns respectively). Similarly, regressions were not significant between chimpanzee food species and availability of oil-palm ripe fruit and umbrella tree ripe fruit (r^2= 0.05, ns; r^2= 0.00, ns respectively); these 2 species therefore cannot explain variance in ripe fruit availability at either community or chimpanzee food species level. Both the oil-palm (see also Section 4.3.3) and the umbrella tree produced ripe fruit throughout the year, including during periods of general low fruit availability, with each species producing fruit in every phenological sample; this highlights their potential value as fallback resources. A commonly occurring fig species (*Ficus sur)* also produced ripe fruit throughout the year, but at low levels.

Plate 4.3. Chimpanzee feeding on the fruit of the Umbrella tree *(Musanga cecropioides)*.

4.3.3 Cultivar availability

The availability of cultivars to the chimpanzees is the combination of the spatial arrangement and temporal abundance within a given location at a given time. Only cultivars that were frequently consumed by the Bossou chimpanzees were included in analyses (see Table 4.1).

Table 4.2 shows the number of orchards, farms and fields (collectively defined as plots) growing each cultivar in the monitored area (within the forest and up to 50-m from the forest edge), and the mean count of trees and plants present within each plot. Figure 4.3 maps the plots within and surrounding the three hills (extends to show cultivars greater than 50-metres from the forest edge).

Table 4.1. List of cultivars consumed and parts eaten by the chimpanzees at Bossou during the study period; FT: fruit, LF: leaf, PI: pith, GM: gum, FL: flower, NT: nut, TB: tuber, BK: bark, WT: woody tissue. Cultivars that are frequently consumed by the chimpanzees are in bold. The term pith is used to describe the pith (the central core of the stem), the petiole (the stalk upon which the leaf stands) and the stem (the main axis of a vascular plant). Although the nut is effectively the seed of a plant, the term nut is employed throughout this thesis. Grains will be recorded as fruit (i.e. maize fruit).

Common name	**Species**	**Family**									
			FT	**LF**	**PI**	**GM**	**FL**	**NT**	**TB**	**BK**	**WT**
Avocado	*Persea americana*	Lauraceae		x							
Banana	***Musa sinensis***	**Musaceae**	x		x						
Cacao	***Theobroma cacao***	**Sterculiaceae**	x								
Cassava	***Manihot esculenta***	**Euphorbiaceae**					x		x		
Grapefruit	*Citrus grandis*	Rutaceae	x								
Maize	***Zea mays***	**Graminae**	x								
Mandarin	***Citrus reticulata***	**Rutaceae**	x								
Mango	***Mangifera indica***	**Anacardiaceae**	x								
Oil-palm	***Elaeis guineensis***	**Palmae**	x		x	x	x	x			x
Okra	*Hibiscus esculentus*	Malvaceae	x	x	x		x				
Orange	***Citrus aurantifolia***	**Rutaceae**	x								
Papaya	***Carica papaya***	**Caricaceae**	x	x	x					x	x
Pineapple	***Ananasa comosus***	**Bromeliaceae**	x		x						
Raphia-palm	*Raphia gracilis*	Palmae				x					
Rice	***Oryza sp.***	**Graminae**			x						
Sugar Cane	*Sacchrum officinarum*	Poaceae			x						
Yam	*Dioscorea sp.*	Dioscoreaceae							x		

Table 4.2. The number of orchards, farms or fields (plots) within the monitored areas containing each specific cultivar, and the mean ± SE of exact counts of trees or plants within each plot. Only cultivars frequently consumed by the chimpanzees were included.

	Gban	Guein	Gboton	Total	Mean ± SE
Papaya	5	0	1	6	4.5 ± 0.9
Banana	12	5	12	29	38.2 ± 7.5
Orange	5	3	5	13	2.8 ± 0.5
Mandarin	4	2	1	7	2.1 ± 0.8
Pineapple	2	0	1	3	6 ± 3
Mango	7	9	23	38	7.3 ± 2.6
Rice	7	0	3	10	
Maize	3	0	1	4	
Cassava	4	0	8	12	
Cacao	0	1	0	1	
Oil-palm	5	0	0	5	17.4 ± 7.9

Plate 4.4. Chimpanzee feeding remains of sweet cassava tuber *(Manihot esculenta)*.

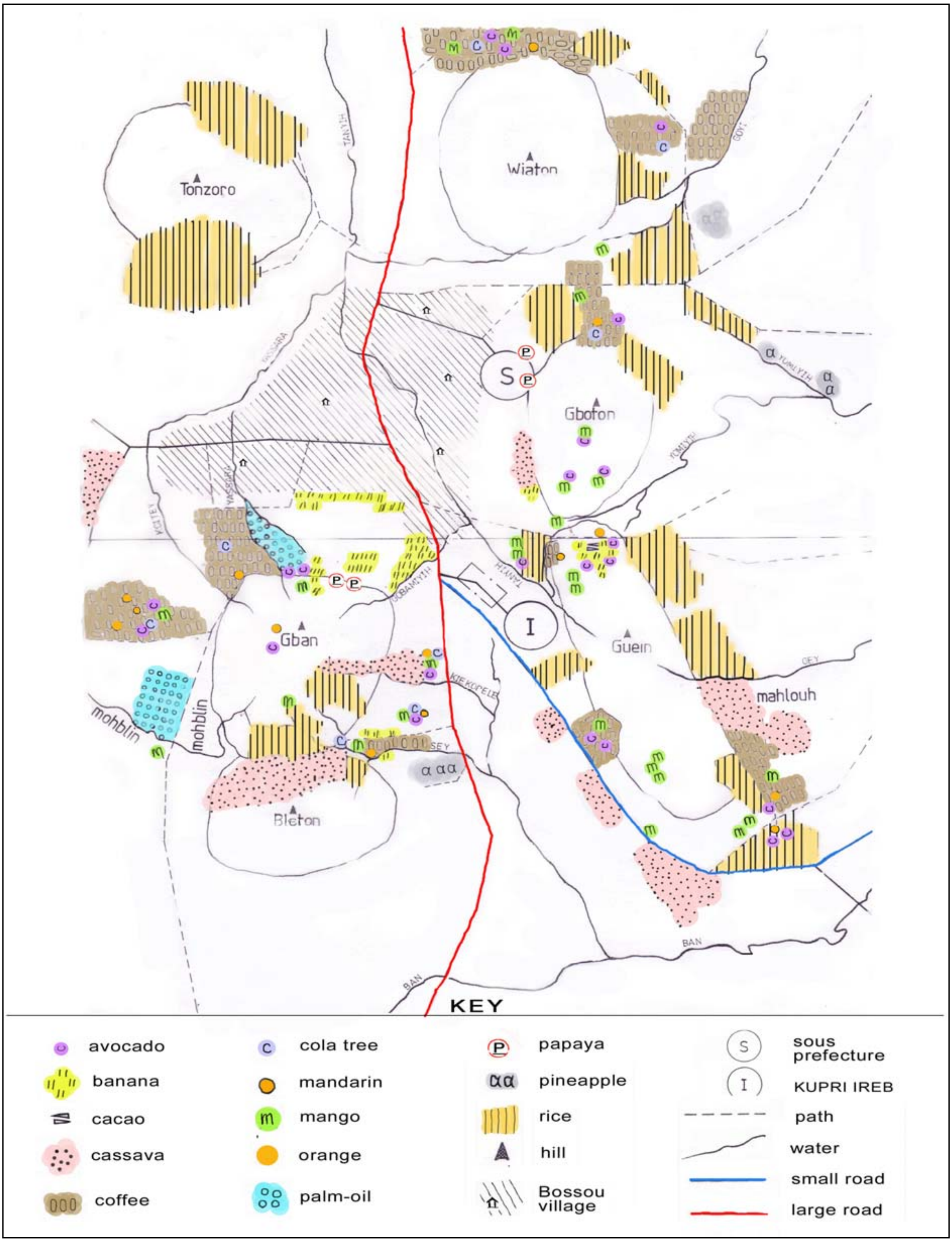
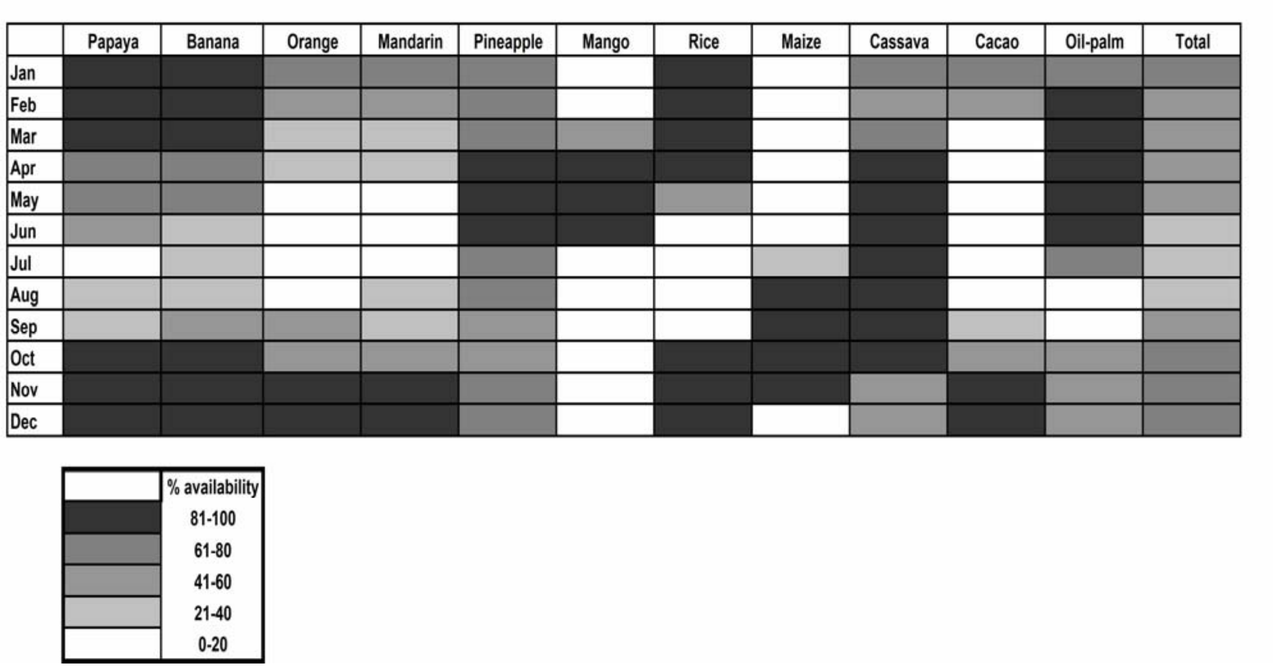


Figure 4.3. Map showing the presence of different cultivars within and surrounding the Bossou chimpanzees' core area (originally illustrated by Marcel Dore, modified by S. Hockings). Maize is not included in the map as it is usually cultivated in fields with cassava and rice.

Planting pattern and monthly availability of each cultivar



	Papaya	Banana	Orange	Mandarin	Pineapple	Mango	Rice	Maize	Cassava	Cacao	Oil-palm	Total
Jan	■	■	▓	▓	▓	□	■	□	▓	▓	▓	▓
Feb	■	■	▒	▒	▓	□	■	□	▒	▒	■	▒
Mar	■	■	░	░	▓	▒	■	□	▓	□	■	▒
Apr	▓	▓	░	░	■	■	■	□	■	□	■	▒
May	▓	▓	□	□	■	■	▒	□	■	□	■	▒
Jun	▒	░	□	□	■	■	□	□	■	□	■	░
Jul	□	░	□	□	▓	□	□	░	■	□	▓	░
Aug	░	░	□	░	▓	□	□	■	■	□	□	░
Sep	░	▒	▒	░	▒	□	□	■	■	░	□	▒
Oct	■	■	▒	▒	▒	□	■	■	■	▒	▒	▓
Nov	■	■	■	■	▓	□	■	■	▒	■	▒	▓
Dec	■	■	■	■	▓	□	■	□	▒	■	▒	▓

	% availability
■	81-100
▓	61-80
▒	41-60
░	21-40
□	0-20

Figure 4.4. The monthly availability of cultivars rated by questionnaire respondents. Respondent's ratings of low and high availability were combined for analyses (see Appendix C5 for separate values).

Figure 4.4 shows the temporal availability of cultivars that are frequently consumed by the chimpanzees. To determine which climatic and phenological variables could best predict the monthly percentage availability of individual cultivars (see Table 4.3), community-wide and chimpanzee food species FA Index values were used in linear regressions in addition to rainfall, rainfall including a 1-month lag, and the mean, maximum and minimum temperatures (see Appendix C4 for complete tables). As the respondents were asked about availability during 2005, phenological and climatic data from January 05 to December 05 were used in analyses. All analyses involving wild fruit availability use ripe fruit index values, and percentage availability of cultivar refers to the percentage of respondents who rated that cultivar to be available (low and high availability combined).

Table 4.3 Significant results of linear regressions predicting the percentage availability of individual cultivars in relation to wild fruit availability (FA) of community-wide species (CW), chimpanzee food species (Ch Fd), rainfall, rainfall 1-month lag, and mean, minimum and maximum temperatures.

	FA Index CW	FA Index Ch Fd	Rainfall	Rainfall lag	Mean temp	Min temp	Max temp	R^2
Papaya	**0.005**	**—**	**0.009**	**—**	**—**	**—**	**—**	**0.793**
Banana	**0.004**	**—**	**0.004**	**—**	**—**	**—**	**—**	**0.820**
Orange	**—**	**—**	**0.019**	**—**	**—**	**—**	**—**	**0.438**
Mandarin	**0.039**	**—**	**—**	**—**	**—**	**—**	**—**	**0.361**
Pineapple	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**0.621**
Mango	**—**	**—**	**—**	**—**	**—**	**—**	**—**	**0.372**
Rice	**0.001**	**—**	**0.005**	**—**	**—**	**—**	**—**	**0.843**
Maize	**—**	**—**	**—**	**—**	**—**	**0.013**	**—**	**0.480**
Cassava	**0.005**	**—**	**0.051**	**—**	**—**	**—**	**—**	**0.563**
Cacao	**—**	**—**	**0.026**	**—**	**—**	**—**	**—**	**0.407**
Oil palm	**—**	**—**	**—**	**—**	**—**	**0.023**	**—**	**0.417**

Papaya

Papaya was grown in six separate plots within the monitored area (see Table 4.2). Twenty-six questionnaire respondents reported growing papaya, all of which was grown outside of the forest and at varying distances from the forest edge. Papaya was available all year round in respondents' farms and orchards (see Figure 4.4); ripe fruit was highly available during the dry months from November to February (see Appendix C5). Ripe fruit abundance derived from systematic recordings of papaya trees on the farm were highly correlated with estimates by questionnaire respondents (r_s= 0.65, n=12, $p<0.05$; see Appendix C6 for complete results). Rainfall and forest fruit availability together accounted for up to 79.3% of variations in papaya availability (see Table 4.3). Papaya leaf, petiole, bark and woody tissue were also available year-round.

Banana

Sweet banana plants were grown in both paddy (n=3) and forest or savannah fields (n=25), with all locations having a very similar planting pattern. Banana plots were found extensively throughout the forest and village in the monitored area, with a comparatively high number of plants grown per plot (see Table 4.2). The majority of respondents said that planting occurred throughout the year and banana plants took 12 to 18 months to reach maturity. Sweet banana fruits and pith were available throughout the year, with high fruit availability from September to February; fruit abundances derived from the farm survey were highly correlated with estimates by questionnaire respondents (r_s= 0.86, n=12, p<0.01; see Appendix C6). Banana availability could be predicted by both rainfall and community-wide fruit availability levels; explaining up to 82% of variance (see Table 4.3).

Orange

Orange trees were located on 13 plots throughout the village and forest in the monitored area with relatively few trees per plot (see Table 4.2). Oranges were available on fourteen of the respondents' farms from October to January. Orange availability was best predicted by rainfall which accounted for up to 43.8% of variance (see Table 4.3).

Mandarin

Mandarin trees were located on 7 plots within and outside the forest with relatively few trees per plot (see Table 4.2). Mandarin (n=12) availability showed a similar pattern to orange availability, with highest presence from October to January, and community-wide forest fruit availability explaining 36.1% of observed variance (see Table 4.3).

Pineapple

Ten respondents reported that they cultivated pineapples in forest and savannah areas; however there were only three very small pineapple plots within the monitored area. The majority of farmers said that it was possible to plant pineapples at any time of the year, although 6 respondents planted at the beginning of the rainy season. Respondents reported that harvesting of pineapple occurred 11 to 19 months after planting. Pineapple fruit and pith were available throughout the year, although availability was low from September to November and none of the tested variables predicted pineapple availability (see Table 4.3).

Availability results from the questionnaires and recordings from the farm survey were highly correlated (r_s= 0.80, n=12, p<0.01; see Appendix C6).

Simple-sugar (SS) fruit cultivars

Excluding mango from analyses (as abandoned mango trees are found extensively throughout the forest) the monthly availabilities of other SS fruits (papaya, banana, orange, mandarin and pineapple) were summed to give an overall monthly mean availability value for SS fruits. SS fruits were available at higher levels from October to April; the rest of the year abundance was relatively low (mean ± SE: 75 (± 5.5) vs 34 (± 3.4)).

Mango

Mango trees were found extensively and abundantly within the monitored areas in 38 plots, both within the forest and village (see Table 4.2). Mango ripe fruit (n=34) was available in Bossou from March to June, with high abundance during the month of May. Mango availability was not predicted by any of the phenological or climatic variables (see Table 4.3). Ripe fruit abundances derived from systematic recordings of mango trees were highly correlated with estimates by questionnaire respondents (r_s= 0.89, n=12, p<0.01; see Appendix C7).

Rice

Rice was divided into three types depending on the location of the field: paddy, forest or savannah. All respondents cultivated rice and 10 respondents had rice fields in more than one location. Firstly, paddy rice was planted between May and July, with 15 out of the 20 respondents planting in June. Paddy rice was harvested between November and January, with the majority of villagers harvesting in December. Forest and savannah rice were planted at similar periods between April and May, and harvested between September and November. There were ten rice plots within the monitored area, and the monthly availability of rice is displayed by combining paddy, forest and savannah rice (see Table 4.2). Chimpanzees only feed on the mature sugary pith of rice which was available just before, during and after the harvesting period. The community-wide FA Index and rainfall were the best predictors of rice availability, explaining up to 84.3% of the observed variance (see Table 4.3); rice was available during the dry season when forest fruits were abundant.

Carbohydrate, protein, lipid (CPL) cultivars

Maize

Maize (n=17) was cultivated either in the forest or savannah, and was frequently grown in fields with rice or cassava. Despite this only four monitored fields contained maize. Planting occurred at the onset of the rains between April and May, and harvesting fell between the months of July and October. Maize was available from July to December, and highly available in the months of September and October (see Appendix C5), with up to 48% of the variance in maize availability being explained by variations in the minimum temperature (see Table 4.3).

Cassava

All 37 questionnaire respondents cultivated sweet cassava, which is a staple carbohydrate for the people in this region. There were twelve plots throughout the monitored area which grew cassava. Cassava was cultivated in either the forest or savannah, but the location did not affect planting patterns. Planting occurred between March and May and was equally distributed across these 3 months. The period of growth until maturity was between 10 and 17 months. Cassava root was available year-round, although availability results from questionnaire respondents and the farm survey did not significantly correlate (r_s= 0.36, n=12, ns; see Appendix C5). Community-wide fruit availability best predicted cassava availability, predicting up to 56.3% of the variance, although rainfall approached significance (see Table 4.3); cassava was highly available during the wet season when forest fruits were scarce.

Cacao

The availability of ripe cacao fruits (which contain high levels of fat) was highest from October through to January (n=9) and fruits became abundant during the dry season; cacao availability was best predicted by rainfall which explained up to 40.7% of the variance (see Table 4.3). However, cacao trees were only present in one plot within the monitored areas (see Table 4.2).

Oil-Palm

Oil-palm fruit was cultivated in five plots within the monitored areas (see Table 4.2). Oil-palm fruit was available year round on respondents' farms (n=12), with high availability from March to May; up to 41.7% of the variance in oil palm fruit availability was attributable to changes in the minimum temperature (see Table 4.3). Ripe fruit abundances derived from the farm survey were highly correlated with estimates by questionnaire respondents (r_S= 0.80, n=12, p<0.01; see Appendix C5). Oil-palm pith, flowers, nuts (seeds), gum and woody tissues were also available year round, with flowers and nuts being most abundant prior to and following periods of high fruit availability, respectively.

4.4 Discussion

The aim of this chapter was not to provide a detailed ecological analysis of the forests of Bossou, but instead to offer enough background information to allow examination of the chimpanzees' foraging activities. There is marked seasonal variation in the availability of ripe fruit at Bossou. Consistent with past findings, months of high wild fruit availability at Bossou are from December through to April, whereas low fruit availability months are from May to November (Yamakoshi, 1998; Takemoto, 2002). Bossou exhibits regular annual peaks in fruit production. Over this study period, the 2004 December increase in ripe fruit availability is mirrored by a similar increase in December 2005.

Although the exact mechanisms influencing fruiting cannot be established from such a short study, analyses suggest that ripe fruit availability, for both community-wide and chimpanzee food species is most closely linked to variations in mean temperature. Long-term studies at other study sites have revealed inter-annual variations in fruit production (Tutin et al., 1997; Chapman et al., 1999, 2005), although it was outside the scope of this study to address questions about long-term changes.

Secondary forest specialists including the oil-palm tree and umbrella tree produced fruit year-round, and were confirmed as potential fallback foods for the chimpanzees. Both species are abundant in the regenerating secondary forest of Bossou, and past research has revealed the importance of their fruits in the chimpanzees' diet; large amounts of the pith of oil-palm were also consumed when fruits were scarce (Yamakoshi, 1998; Takemoto, 2002; Humle and Matsuzawa, 2004). Other researchers have observed the importance of certain fig species as fallback foods for chimpanzees during periods of general fruit scarcity (Terborgh, 1986; Wrangham et al., 1996; Fawcett, 2000); phenology results from this study indicate that one species of fig in particular *(Ficus sur)* produces fruit all year round, albeit at relatively low quantities.

Due to the wet climate at Bossou, a wide range of cultivars are grown, and the climate dictates the planting regimes and fruiting patterns of these cultivars; it appears that the environmental cues for fruiting may be particular to each species. Despite chimpanzee fruit availability showing the same phenological patterns of production as community-wide fruit availability, this measure was a much less accurate predictor of cultivar availability. This may simply be a result of the short duration of the study, or the lack of synchrony between the certain high fruiting chimpanzee food species and cultivars. Considerable variability in the spatial and temporal availabilities of different cultivars exists and this must be taken into account when looking at cultivar usage by the chimpanzees. Certain cultivars, e.g. mango, have a very precise and short-lasting fruiting period, whereas others e.g. cassava, are available for most of the year. The availability of different cultivars both during periods of fruit scarcity and year-round promotes the possibility that these species may also act as fallback foods for chimpanzees. This analysis illustrates the availability of potentially important fallback foods, both wild and cultivated, to the chimpanzees. Estimates of food availability derived by questionnaires and systematic recordings were highly correlated for all monitored cultivars except cassava. Unlike fruits on the farm survey, cassava tuber was only unearthed when needed, which possibly accounts for the observed discrepancies. This analysis highlights the accuracy and usefulness of questionnaires when investigating temporal variations in a large number of cultivated species, as they are less time consuming than systematic recordings.

Chapter 5

Crop-Raiding: an Ecological Approach

Crop-raiding: an Ecological Approach

"Tropical forests, from the point of view of their animal inhabitants, are not what they seem to the outside observer; scarcity and abundance is the key consideration to understanding their ecology". Terborgh, 1986, p.331

5.1 Introduction

Availability of, and fluctuations in, wild forest foods may affect crop-raiding levels. Particular crops might be crucial for the Bossou chimpanzees' subsistence, while others are exploited because they are more palatable or nutritious than wild foods. The aim of this chapter is to characterise the Bossou chimpanzees' feeding strategies in relation to fluctuations in fruit availability, by bridging the gap between wild food foraging and crop-raiding. This chapter will explore the utilisation of all crop types by the Bossou chimpanzees, and discuss the ecology of fallback foods in the context of crop-raiding.

Wild chimpanzees are omnivorous, but their diet is dominated by ripe fruit, which accounts for 50 to 65% of their time spent feeding (Wrangham, 1977; Goodall, 1986; Tutin et al., 1997; Yamakoshi, 1998; Pruetz, 2006). Chimpanzees are known to prefer foods with high sugar levels, and numerous studies indicate that primates select specific foods to meet their nutritional requirements and metabolic demands: fruits are rich in simple-sugars but deficient in proteins and fats; leaves serve as an important protein source to chimpanzees; pith contains sugars, protein and fermentable fibre; and nuts are high in protein, minerals and fats (Rogers, 1990; Reynolds et al., 1998; Fawcett, 2000; Laska et al., 2000; Rode et al., 2003). Less commonly discussed, yet still exploited by chimpanzees are the subterranean parts of plants, including the underground storage organs (USOs), which provide an alternative energy source, in the form of carbohydrates (Laden and Wrangham, 2005).

Optimal foraging theory predicts that an individual should increase foraging efforts by making dietary changes when main foods are scarce in order to maximise the quality of their nutritional intake; individuals are expected to reduce selectivity by feeding on a broader range of lower quality food items (Begon et al., 1996). However, it is unclear whether fruit scarcity correlates with changes in the overall dietary diversity of chimpanzees. Some chimpanzee research shows that dietary diversity increases and selectivity decreases as a response to wild fruit scarcity (Isabirye-Basuta, 1989; Fawcett, 2000), whereas other studies demonstrate no relationship between dietary diversity and fruit availability (Kuroda et al., 1996; Yamakoshi, 1998; Takemoto, 2000).

As most plant species exhibit periods of scarcity, fruit specialists in general are under considerable pressure to show dietary flexibility to survive fruit bottlenecks (Milton, 1981; Robinson, 1986; Terborgh, 1986; Yamakoshi, 1998); as indicated in Chapter 4, fallback foods perform a vital role in sustaining primates through such periods (Terborgh, 1986). During times of wild fruit scarcity, chimpanzees have been observed consuming higher quantities of leaves (Nishida, 1976), bark (Nishida 1976), terrestrial herbaceous vegetation (THV) pith (Wrangham et al., 1991; Wrangham et al., 1998; Yamakoshi, 1998), and oil-palm fruit (McGrew, 1992; Tutin et al., 1997; Yamakoshi, 1998). Laden and Wrangham (2005, p.13) proposed that “the evolution of hominids from the last common ancestor shared with chimpanzees depended partly on the substitution of USOs for herbaceous vegetation as fallback foods”. Current data suggest that edible USO diversity and abundance is higher in savannahs than in rainforests (Laden and Wrangham, 2005). The occupation of savannahs by early hominoids therefore meant that when preferred foods were scarce, a new type of fallback food was required; this hypothesis has not been explored in relation to the usage of USOs by wild chimpanzees. Additionally, certain chimpanzee communities engage in hunting, a high-risk activity, to compensate for seasonal food shortages (Teleki, 1973; Takahata, 1984; Stanford, 1998). When wild forest fruits were scarce, hunting incidences by communities of chimpanzees at Gombe and Mahale increased; the chimpanzees of the Mahale Mountains engaged in as many as 60% of annual hunts during 2 months when wild fruits were most scarce. Crop-raiding may be a comparable strategy for fallback nutrition. However, in sharp contrast, the chimpanzees at Ngogo in Kibale National Park hunted primarily during times of food abundance rather than scarcity (Mitani and Watts, 2001).

Cultivars afford greater digestibility, lower toxicity and increased foraging efficiency over natural foods (Robinson, 1986; Strum, 1994) and thus constitute an attractive resource. When analysing the feeding ecology of primates, many studies have failed to take fully into account the importance of crop-raiding (Richard et al., 1989; Naughton-Treves et al., 1998; Bates, 2005; Linkie et al., 2007). Animals that raid domestic cultivars will not forgo feeding on wild food resources but instead add the crops to their ecological strategy; a field or orchard of ripe crops may be viewed as equivalent to a mass fruiting event (Strum, 1987; Naughton-Treves et al., 1998; Yamakoshi, 1998).

Siex and Struhsaker (1999) documented that the consumption of cultivated coconuts by wild colobus monkeys was highest in areas with low availability of alternative food resources. However, abundant forest fruit did not diminish the Kibale chimpanzees' appetite for protein-rich maize; whereas increased consumption of banana pith was associated with forest fruit shortages (Naughton-Treves et al., 1998). It was therefore suggested that particular crops are critical for the chimpanzees' subsistence during periods of wild fruit scarcity, while others are exploited simply because they are tastier than wild foods. Greengrass (2000) described how the Gombe chimpanzees fed on banana, mango and other cultivated fruit, situated on the forest edge, due to a loss of habitat that had previously provided all their dietary requirements. Comparable to the chimpanzees of Gombe, the Bossou chimpanzees inhabit a very small and semi-isolated range which may well have contributed to their extensive usage of human cultivars. Sugiyama and Koman (1992) noted that chimpanzees at Bossou consume 29 species of cultivated plants, and Takemoto (2002) reported that cultivated fruits comprised 6.4% of their annual diet; both reports suggest that cultivars are fully integrated into the Bossou chimpanzees' dietary repertoire.

These studies touch upon the importance of access to wild fruits for determining levels of crop-raiding, underlining the likelihood that the two are closely linked. It is foreseeable that crop-raiding by the great apes will become more widespread and prevalent throughout Africa, as levels of deforestation and human population growth rates continue to soar. Effective management schemes require understanding the complete ecology of the raiding species involved.

5.1.2 Hypotheses

(1) Temporal variations in crop-raiding

- (a) Depending on the cultivar, cultivar feeding will be affected by wild fruit availability and/or cultivar abundance.
    - During periods of wild fruit scarcity, levels of crop-raiding for simple-sugar (SS) fruits will increase due to chimpanzees' high dependence on fruit.
    - Both cultivar and wild forest fruit availabilities will affect carbohydrate, protein, lipid (CPL) raiding levels (as CPL wild foods are less abundant than fruits throughout the chimpanzees' home range).
- (b) Chimpanzees will minimise risks associated with crop-raiding, by preferentially selecting low-risk situations.

(2) Synthesis of wild and cultivated foods.

- (a) Oil-palm raid levels will be affected by a combination of supplied, abandoned and wild consumption of oil-palm.
- (b) Crop-raid levels will be negatively correlated with wild food consumption, and will follow fallback food usage patterns.
- (c) Cultivar feeding will contribute towards maintenance of high dietary diversity during periods of wild fruit scarcity.

5.2 Methods and analyses

For complete methods, see Chapter 3.

Phenology and cultivar availability

All measures of crop-raiding were tested against the same wild fruit availability values (FA Index of chimpanzee food species) for exactly the same months. Cultivar availability values varied depending upon the cultivar type as some cultivars were seasonal whereas some showed year-round availability (see Chapter 4); it was assumed that no inter-annual monthly variation existed in cultivar availability. When monthly cultivar availabilities were clumped, the mean of the availability values was calculated.

Observation times

***Ad libitum* events**: monthly observation times were calculated by pooling the presence data for each individual from the 5-minute scan samples.

Focal durations: As wild food feeding durations were not measured during *ad libitum* samples, monthly focal animal observation times were used when calculating the duration of feeding on wild foods.

It should be noted that during the study period the alpha male, second male and third male consorted with females outside the normal home range on several occasions; analysis of total monthly presence data took account of individual absences. The time of day was divided into 3 periods for analyses: morning (0700h-1059h), midday (1100h-1459h), and afternoon (1500h-1859h).

Definitions: Crop-raiding events, bouts and duration

Crop-raid 'event': Each foray by a single individual to obtain cultivated food, defined by exit from and return to natural vegetation (Naughton-Treves et al., 1998).

Crop-raid 'bout': All events that occurred within 10 minutes of each other; the termination of a bout occurred when the time-lag before the next event was greater than 10 minutes. A bout could consist of numerous raid events and it was possible for several bouts to take place during any one day.

Total duration: Collective time spent feeding on cultivars by all individuals.

Occasionally a chimpanzee would feed on more than one cultivar during an event. If this occurred, events were separated when analysing individual cultivars, and clumped when analysing combinations of cultivars; total frequencies were therefore not affected. When multiple cultivars were consumed within a bout; these would be classified as mixed feeding bouts and as either predominantly simple-sugar (SS) bouts or carbohydrate/protein/lipid (CPL) bouts. Some cultivars were present on routes commonly used by the chimpanzees, so that they frequently encountered these foods even though not actively searching for them. Data were not collected on such occasions when cultivars were encountered and not eaten.

Crop-raiding rates

Crop-raiding rates were calculated by dividing the number of observed raiding events or bouts by the combined *ad libitum* observation times for each individual per month, to give crop-raid rate per hour; this rate was then multiplied by 100. When calculating wild food feeding durations, focal observation times were used instead. One-tailed or two-tailed tests were employed in accordance with the original hypotheses; one-tailed tests are highlighted throughout.

The term ‘primary factors’ is used to describe the nutritional factors that may influence a chimpanzee’s choice to crop-raid, i.e. wild fruit, cultivar availability and cultivar type. The term ‘secondary factors’ is employed when discussing factors that are directly influenced by humans, i.e. location of the resource and human presence.

Crop preferences

To determine if certain cultivars were preferred over others, an approximate measure of relative preference was employed using a preference index (Kagoro-Rugunda, 2004; Priston, 2005). The rates at which a certain cultivar (or group of cultivars) was raided were clumped and expressed as a percentage of total rates (for comparative reasons, mango was also included). For each cultivar the corresponding monthly availabilities were also pooled to obtain a percentage of total cultivar temporal availability (spatial availability not incorportated).

$$\text{Preference Index } i \text{ (PI)} = \frac{\text{Rate of events } i}{\text{\% availability } i}$$

Guard levels

As discussed in Chapter 3, cultivars were divided into 3 groups depending on where they were obtained (see Table 5.1):

(a) Abandoned: cultivars that are not regularly guarded.
(b) Guarded: cultivars that continue to be guarded.
(c) Supplied: cultivars supplied during nut-cracking experiments.

Table 5.1. Classification of groups of cultivars and colour code. Please note that when analyses include wild foods, 'non-raid' refers to feeding from wild, abandoned and supplied sources.

	Abandoned	Guarded	Supplied
Crop-raid		x	
Non-raid	x		x
Total cultivar feeding	x	x	x

Dietary Diversity

Standardised Shannon-Wiener indices were calculated as a measure of dietary diversity to take into account the relative proportion of each species in the diet (Krebs, 1989; Begon et al., 1996; Newton-Fisher, 1999):

$$J' = -(p.\ln p + p.\ln p + \ldots\ldots. + p.\ln p)/\ln n$$

where n is the number of species consumed and p is the proportion of each species in the diet.

5.3 Results: Temporal variations in crop-raiding

5.3.1 Crop-raiding frequencies

In total, 786 crop-raiding events and 332 non-raiding events on cultivars were observed during the 12-month study period. Raided cultivars contributed to 8.8% of total feeding time (monthly range: 1.8 – 16.6 %, SD ± 4.8), and total cultivars comprised 14% of total feeding time (monthly range: 3.6 – 26.3 %, SD ± 6.9). Table 5.2 shows the frequencies of crop-raiding and total cultivar consumption by the chimpanzees. Total cultivar consumption of all species and parts are included in clumped analyses, but certain cultivars (Table 5.2 non bold font) will not be specifically discussed as they were fed on infrequently or in very small quantities.

Okra leaves were fed on quite often but only one or two small leaves were ever taken. Sugarcane was only observed on the one farm where the feeding events took place, and yam was very rarely taken. Grapefruit was not grown by villagers but one abandoned tree was present within the Bossou forest. Also, for chimpanzees to feed on raphia-palm gum or ‘palm-wine’, a person must have set up the specialised equipment to drain the gum from the tree; therefore the chimpanzees did not consume palm-wine frequently.

Table 5.2. Crop-raid and non-raid event frequencies for each cultivar and part (FT: fruit, LF: leaf, PI: pith, TB: tuber, NT: nut, FL: flower, GM: gum) during the study period. Numbers in brackets indicate the frequency where more than one part of the specified cultivar was consumed in a single event, and + (raided), * (non-raided) indicate the parts. SS cultivars (•) and CPL cultivars (∞) are highlighted. In addition to the results presented, there were 5 events where multiple SS cultivars were raided and 2 where multiple CPL cultivars were raided.

CULTIVAR			**EVENTS**	
Common name	**Scientific name**	**Part**	**Raid**	**Non-raid**
Papaya	***Carica papaya***	FT•	126(4)+	0
		LF∞	69+	0
Banana	***Musa sinensis***	FT•	62(3)+	23(2)*
		PI∞	63+	26*
Orange	***Citrus aurantifolia***	FT•	86	3
Mandarin	***Citrus reticulata***	FT•	18	0
Pineapple	***Ananasa comosus***	FT•	21	3
Mango	***Mangifera indica***	FT•	0	149
Rice	***Oryza sp.***	PI•	81	0
Maize	***Zea mays***	FT∞	48	0
Cassava	***Manihot esculenta***	TB∞	74	26
Cacao	***Theobroma cacao***	FT∞	34	0
Oil-palm	***Elaeis guineensis***	FT∞	57(1)+	24(14)*
		NT∞	8	53*
		FL∞	1	0
		PI∞	0+	0
	Coula edulis	NT∞	0	5
Okra	*Hibiscus esculentus*	LF∞	18	0
		FL∞	1	0
Raphia-palm	*Raphia gracilis*	GM∞	10	0
Sugarcane	*Saccharum officinarum*	PI•	1	0
Avocado	*Persea americana*	LF∞	0	2
Yam	*Dioscorea*	TB∞	0	1
Grapefruit	*Citrus grandis*	FT•	0	1

5.3.2 Combined cultivars

Combined crop-raiding levels (includes all raided cultivars and parts)

Figure 5.1 (a) shows the monthly crop-raid event rates for individual and groups of cultivars. Combined crop-raiding event and bout rates showed negative correlations with wild fruit availability, but these failed to reach significance (*event*: r_s=-0.42, n=12, ns; *bout*: r_s =-0.34, n=12, ns). The combined raided monthly feeding durations and event rates showed a strong positive correlation (r_s= 0.92, n=12, $p<0.01$), and the negative correlation between combined raided monthly feeding durations and wild fruit availability approached significance (see Figure 5.1 (c); r_s=-0.47, n=12, p=0.06). Total crop-raiding rates showed a positive relationship with cultivar availability, but this again failed to reach significance (*event*: r_s= 0.42, n=12, ns; *bout*: r_s= 0.15, n=12, ns). When comparing periods of high and low fruit availabilities, crop-raid events ($X^2(1) = 80.92$, $p<0.01$) and bouts ($X^2(1) = 19.96$, $p<0.01$) were significantly higher when wild fruits were scarce.

Combined total cultivar-feeding (includes total cultivars and parts)

Figure 5.1 (b) shows the monthly total cultivar feeding event rates for individual cultivars. Total cultivar feeding event and bout rates did not correlate with wild fruit availability (*event*: r_s= -0.15, n=12, ns; *bout*: r_s= -0.09, n=12, ns) or cultivar availability (*event*: r_s= 0.29, n=12, ns; *bout*: r_s= 0.01, n=12, ns). Additionally, no correlation was observed between combined total monthly feeding durations and wild fruit availability (see Figure 5.1 (c); r_s= -0.047, n=12, ns); total monthly feeding durations and event rates showed strong positive correlations (r_s= 0.95, n=12, $p<0.01$). However, cultivar feeding events ($X^2(1) = 32.43$, $p<0.01$) and bouts ($X^2(1) = 13.81$, $p<0.01$) were much more frequent during months of low compared to high wild fruit availability.

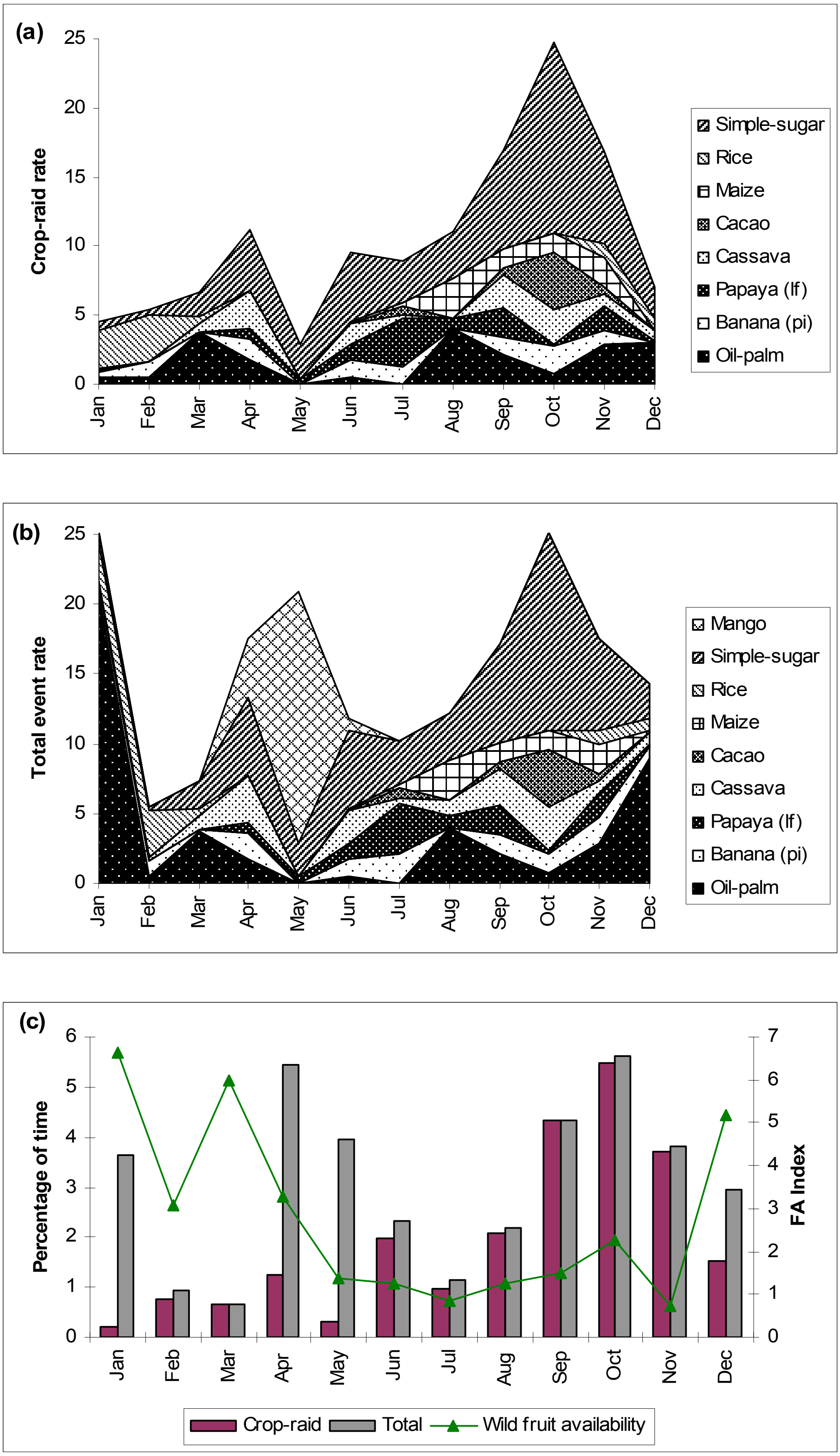


Figure 5.1. Monthly (a) crop-raid event rates (b) total cultivar feeding event rates and (c) percentage of total observation time spent crop-raiding and total cultivar feeding in relation to wild fruit availability.

During most months, SS and CPL cultivars were raided in fairly similar proportions (see Table 5.2 for the classification of each cultivar); chimpanzees may exploit a wide range of cultivars to balance their nutritional intake (refer to Figure 5.2 (a)). However, as can be seen in Figure 5.2 (b), during April and May, very high feeding rates were observed on non-raided SS fruits, and in January a similar pattern was observed for CPL cultivars. As the influence of secondary factors might also vary depending on the cultivar type, these will be discussed throughout.

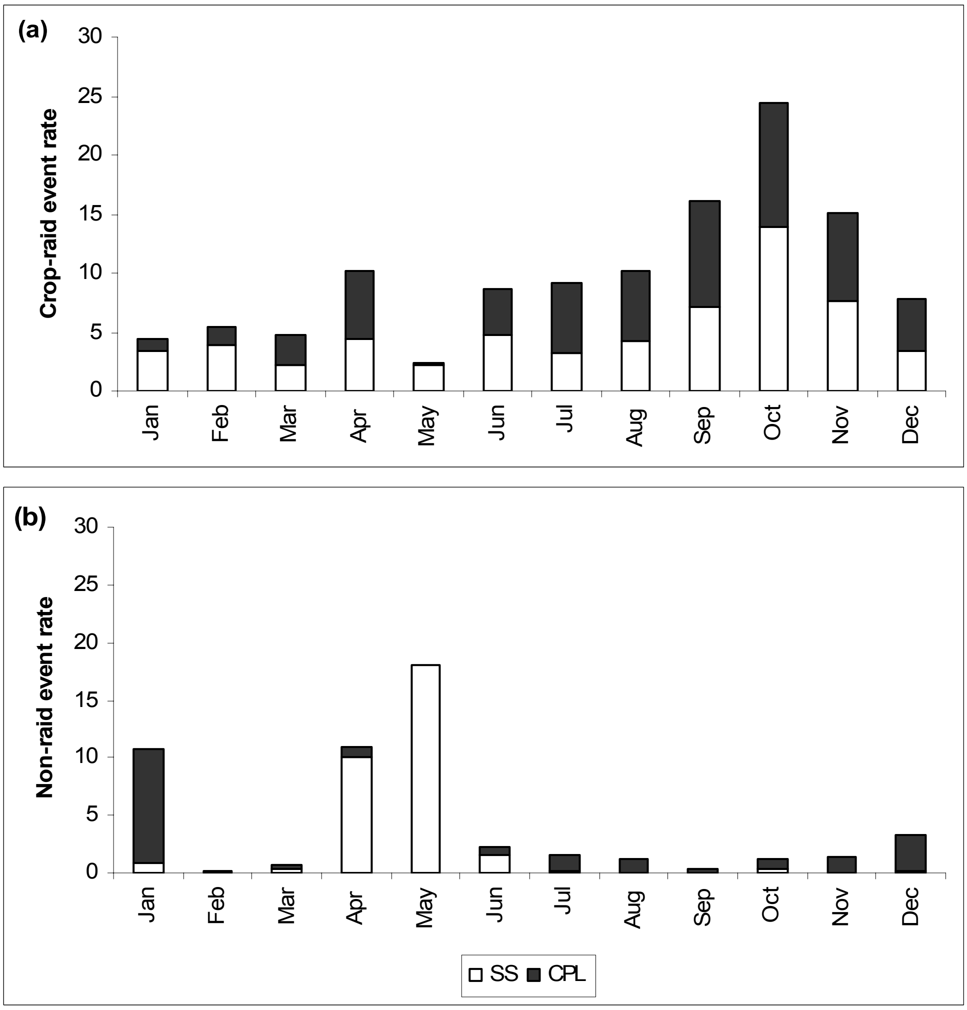


Figure 5.2. Combined monthly (a) crop-raid event rates and (b) non-raid event rates, divided into SS foods and CPL foods.

5.3.3 Simple-sugar (SS) fruits

Analyses

As chimpanzees feed heavily on ripe fruits (see p.84), relationships between wild fruit availability, cultivated fruit availability and crop-raiding levels of SS fruits were analysed. The 320 recorded crop-raiding events for SS fruits (papaya, banana, orange, mandarin and pineapple combined) were used in analyses. Abandoned banana and mango fruits, a result of past cultivation within the forest, were also consumed by chimpanzees during the study period. Indeed, the only mango the chimpanzees were observed feeding on were from abandoned trees in the forest, and people were never present. It was assumed that the risks associated with feeding on abandoned cultivars was the same as that of feeding on wild fruits, and therefore these instances were not included in clumped SS fruit crop-raiding analyses.

Results

Events

Temporal variations in SS fruit-raiding were observed (Figure 5.3 (a)): when forest fruits were scarce higher rates of raiding occurred (one-tailed: r_s= -0.53, n= 12, p<0.05). The availability of SS cultivars did not significantly influence the rate of raid events (Figure 5.3 (b)), thus chimpanzees were not feeding on cultivars simply because they were abundant (r_s= -0.15, n= 12, ns). However, ripe fruits were taken significantly more than unripe fruits during raids (251 out of 321 events; binomial: p<0.01). Chimpanzees did not exhibit a particular preference to raid SS fruits over other cultivars (PI= 0.91). Crop-raiding rates were highest from September to November, with rates peaking in October; during these periods, forest fruit availability was low and SS cultivar availability had started to increase.

From June to August, SS fruit availability was substantially lower, possibly limiting crop-raiding levels.

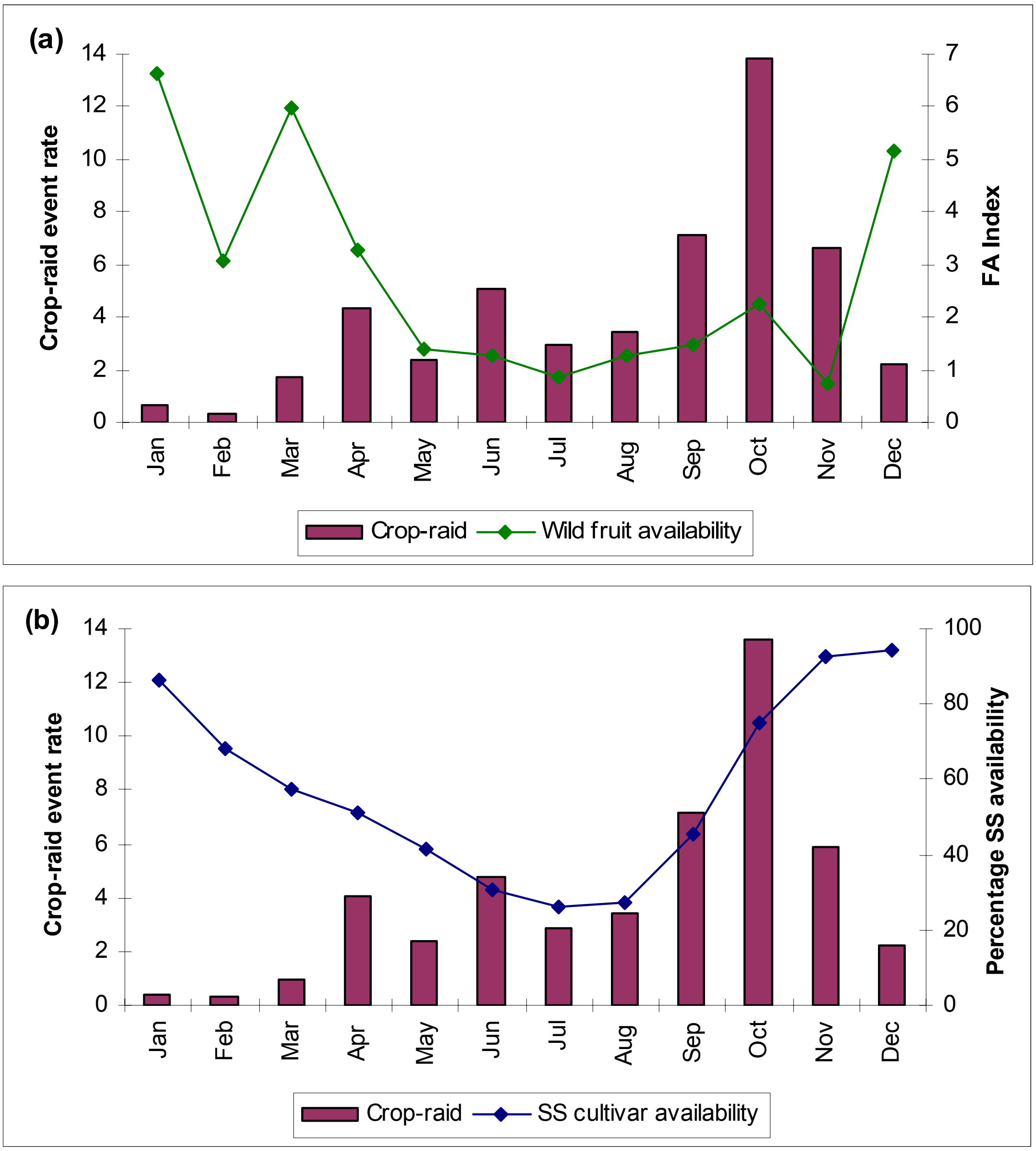


Figure 5.3. Monthly crop-raiding event rates for SS cultivars plotted against (a) wild fruit availability and (b) cultivar availability.

Bouts

The correlation between wild fruit availability and rate of SS-raiding bouts approached significance (one-tailed: r_s= -0.43, n=12, p=0.08), whereas cultivar availability was not significantly correlated with the rate of SS-raiding bouts (one-tailed: r_s= -0.37, n=12, ns).

When months were divided into those of low wild fruit availability (May to November) or high wild fruit availability (December to April) the frequency of SS-raiding bouts was significantly greater during periods of low compared to high wild fruit availability (see Table 5.3: Wild FA underlined).

Durations

There was a significant negative correlation between total monthly SS-raid durations and wild-fruit availability (one tailed: r_s= -0.50, n= 12, p<0.05); when wild fruits were scarce the total feeding durations on raided SS fruits increased.

Secondary factors

The effects of secondary factors on the frequency of SS-raiding bouts during periods of low and high wild fruit availability were tested. This assessed whether other factors (in addition to forest fruit availability) influenced observed SS-raiding variations. These analyses were conducted on independent crop-raiding bouts, as secondary factors mostly remained constant throughout events within the same bout; any bouts where changes in secondary factors occurred were excluded. Variations in the frequency of crop-raiding bouts during periods of low and high wild fruit availability could not be explained by differences in people presence, location, time of the day or guard levels (all results presented in Table 5.3). Chimpanzees did not travel further from the forest edge to crop-raid during periods of low wild fruit availability (Mann-Whitney U-test: Z = -1.04, ns).

More crop-raiding bouts occurred when people were not present compared to when people were present, and also in the village as opposed to the forest. Crop-raiding events were equally likely to take place at different time periods and irrespective of guard level (see underlined results in Table 5.3).

Table 5.3. Chi-squared tests conducted on SS crop-raiding bouts: People: presence vs absence; Location: village vs forest; Time: morning vs midday vs afternoon; Guard: low vs high; Wild FA: low vs high wild fruit availability. Significant results including Bonferroni corrections are highlighted.

People	Location	Time	Guard	Wild FA
Pres/Abs	Vill/For	Am/Mid/Pm	Low/High	Low/High
$X^2(1)=14.54$ **$p<0.01$**	$X^2(1)=38.38$ **$p<0.01$**	$X^2(2)=4.62$ $p=0.099$	$X^2(1)=5.76$ $p=0.016$	$X^2(1)=22.78$ **$p<0.01$**
People	$X^2(1)=9.10$ **$p<0.05$**	$X^2(2)=2.67$ $p=0.264$	$X^2(1)=1.63$ $p=0.244$	$X^2(1)=2.03$ $p=0.21$
Location		$X^2(2)=0.97$ $p=0.616$	$X^2(1)=3.54$ $p=0.082$	$X^2(1)=2.25$ $p=0.148$
Time			$X^2(2)=4.28$ $p=0.118$	$X^2(2)=0.49$ $p=0.78$
Guard				$X^2(1)=4.53$ $p=0.048$
Wild FA				

5.3.4 Other simple-sugar cultivars

Mango

As can be seen from Figure 5.4 (a), forest fruit availability was not correlated with observed mango feeding rates (*event*: r_s= -0.07, n=12, ns; *duration*: r_s= -0.04, n=12, ns). The highly seasonal availability of mango significantly affected the rate and duration of feeding events (Figure 5.4 (b); *event*: r_s= 0.84, n= 12, p<0.01; *duration*: r_s= 0.82, n=12, p<0.01); chimpanzees fed on mango especially when they were abundant. Feeding rates peaked during the month of May when mango abundance was high and wild fruit availability was low, and feeding principally occurred on ripe rather than unripe fruits (119 out of 149 events; binomial: p<0.01). Mango was preferentially selected over other SS cultivars by the chimpanzees, presumably as it has no associated risks and was highly palatable (PI= 4.09); the high rate of mango consumption during the month of May resembles a high wild fruit availability month.

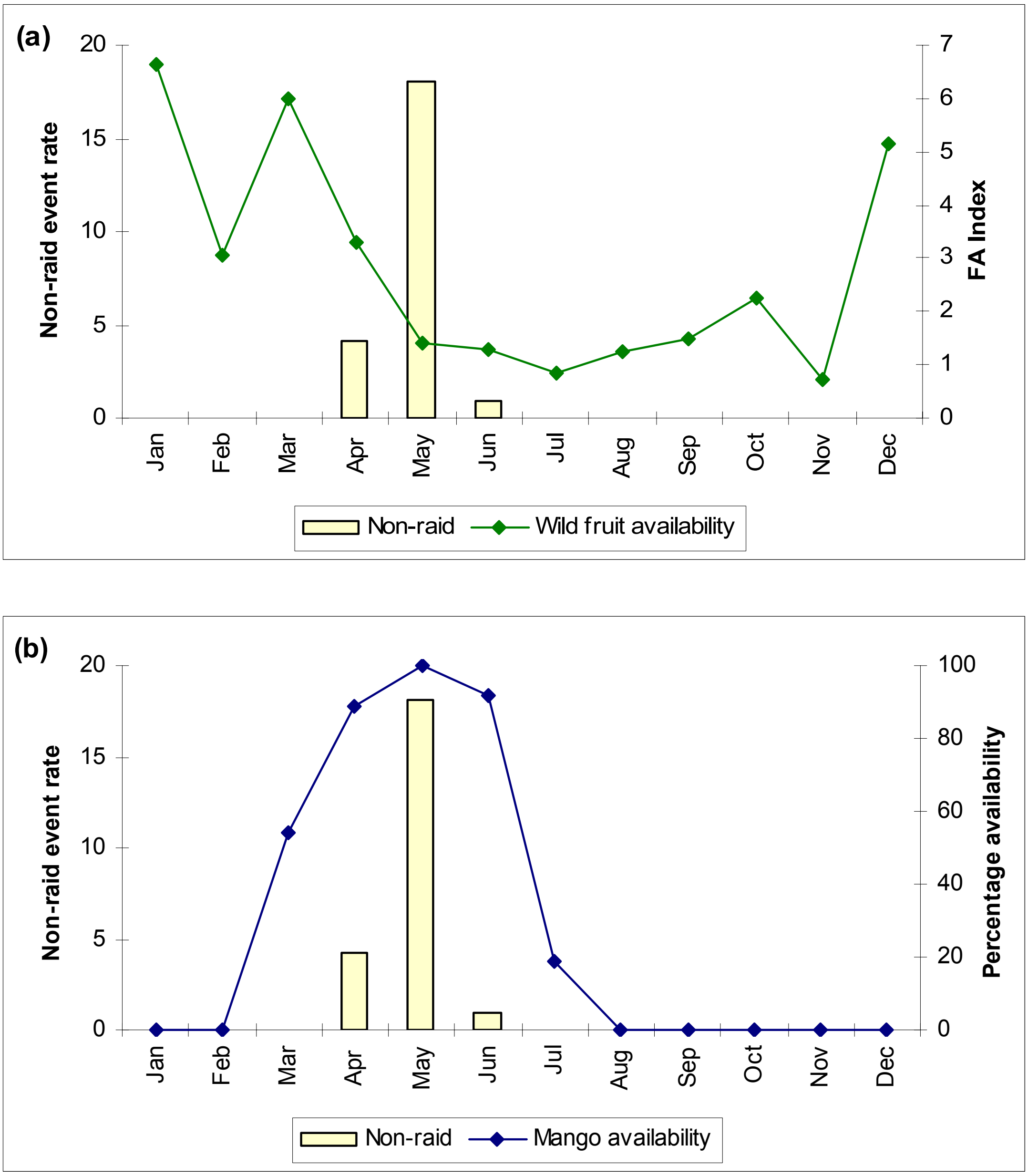


Figure 5.4. Monthly feeding event rates for mangoes plotted against (a) wild fruit availability and (b) mango availability.

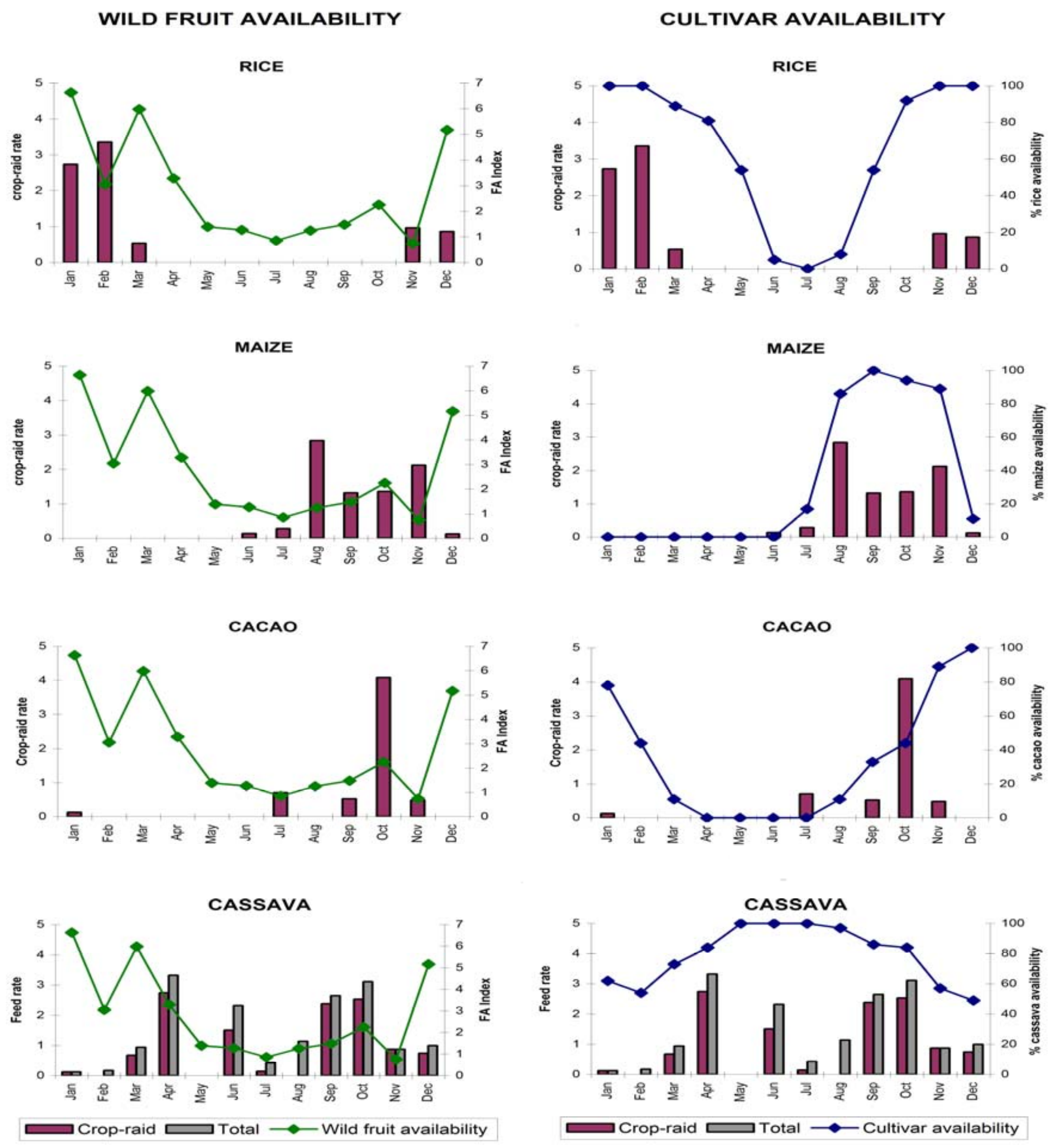


Figure 5.5. Crop-raid rates and total feeding rates on rice, maize, cacao and cassava plotted against wild fruit availability (left side panels) and cultivar availability (right side panels).

Rice

Rice pith was fed on both prior to and after rice grain harvesting (Plate 5.2). Fields were often left abandoned after harvesting took place; despite this, the term crop-raiding will be used to describe all feeding on rice pith. Crop-raiding rates for rice pith were highest during November to March (coinciding with high wild fruit availability), in particular during the months of January and February (see Figure 5.5). Raiding rates positively correlated with high rice availability (*event*: $r_s = 0.84$, n= 12, $p < 0.01$; *duration*: $r_s = 0.84$, n=12, $p<0.01$) but showed no relationship with wild fruit availability (*event*: $r_s = 0.41$, n= 12, ns; *duration*: $r_s = 0.33$, n=12, ns).

In total, 22 raiding bouts and 81 raiding events were recorded. Over 90% of crop-raiding bouts took place in the forest, a likely reflection of the abundance of rice fields throughout the chimpanzees' home range. As rice is a staple carbohydrate for the local people, crop-raiding by chimpanzees before harvesting is generally not tolerated. Over two-thirds of crop-raiding bouts occurred in highly guarded fields, where an equal number of raids took place before and after harvesting. Most bouts that occurred after harvesting were in low-guarded fields (6 out of 7 bouts), and at equal frequencies when people were present and absent. When raids did take place before harvesting, in both guard conditions, people were never present. Rice pith showed a relatively low preference index (PI= 0.67) which may have been influenced by both high guard levels and high wild fruit availability.

Plate 5.2. Bossou female chimpanzee feeding on rice pith after rice grain harvesting.

5.3.5 Complex carbohydrate/protein/lipid (CPL) cultivars

Maize

Maize availability was highly seasonal, peaking mainly from August to November. Crop-raiding event rates were high throughout these months, being positively correlated with maize availability (see Figure 5.5; *event*: $r_s = 0.87$, n=12, $p<0.01$; *duration*: $r_s = 0.83$, n=12, $p<0.01$). However, as crop-raiding was most pronounced during months of fruit scarcity, rates also showed a significant negative correlation with wild fruit availability (see Figure 5.5; *event*: $r_s = -0.70$, n=12, $p<0.01$; *duration*: $r_s = -0.76$, n=12, $p<0.01$). Bouts of crop-raiding on maize were observed on 10 occasions, giving a total of 48 events. The chimpanzees showed a strong preference for ripe maize (45 out of 48 events; binomial: $p<0.01$). Raiding took place in both the forest and the village, with 60% of bouts occurring in highly guarded fields in the forest. Despite high guard levels, maize showed a relatively high preference index relative to other CPL cultivars (PI= 0.91).

Cacao

Crop-raiding on cacao was not correlated with wild fruit availability (Figure 5.5; *event*: $r_s = -0.28$, n=12, ns; *duration*: $r_s = -0.28$, n=12, ns) or cultivar availability (Figure 5.5; *event*: $r_s = 0.22$, n=12, ns; *duration*: $r_s = 0.22$, n=12, ns). A total of 15 bouts and 34 events of cacao crop-raiding occurred in the same small forest plantation; people were never present when raids took place and preference was relatively high (PI= 0.90), possibly due to low guard levels. In 82% of events, ripe cacao was preferred to unripe cacao (binomial: $p<0.01$).

Cassava

As can be seen in Figure 5.5, event rates and durations of raiding for cassava tuber (USO) showed no correlation with either wild fruit availability (*event*: $r_s = 0.06$, n=12, ns; *duration*: $r_s = -0.03$, n=12, ns) or cassava availability (*event*: $r_s = -0.02$, n=12, ns; *duration*:

r_s= -0.01, n=12, ns). As cassava was available year-round, raided and non-raided event rates were calculated for both periods of low and high wild fruit availability. Although cassava-raiding frequency appeared greater during periods of wild fruit scarcity, no significant relationship existed ($X^2(1) = 1.95$, ns). When crop-raiding frequencies were combined with feeding frequencies on non-raided cassava, higher cassava feeding levels were observed during periods of fruit scarcity ($X^2(1) = 4.65$, $p<0.05$). The month of April (end of high wild fruit availability period) saw the highest levels of cassava consumption, which may reflect the lack of availability of other cultivars. In comparison, throughout the months of May, July and August, when feeding rates on mango, papaya leaf and maize were high, virtually no cassava raiding was observed; access to other cultivars may therefore explain why temporal variations did not reach significance. Another point to consider is that cassava feeding levels may have been reduced during the dry season (coincidentally when wild fruit was highly available), due to the difficulty of extracting the tubers from the ground (Laden and Wrangham, 2005).

There were 19 observed cassava-raiding bouts and 74 events, most of which occurred in the forest, fell in the highly guarded category or were carried out when people were absent; 10 out of the 19 bouts satisfied all three conditions. However, on an event basis, during the season of wild fruit scarcity, chimpanzees were significantly more likely to crop-raid in highly guarded fields ($X^2(2) = 19.69$, $p<0.01$) and when people were present ($X^2(1) = 5.83$, $p<0.05$) compared to periods of high wild fruit availability. All 14 non-raided cassava feeding bouts took place in the forest where people were absent. Mature cassava tubers were always selected in both raided and non-raided conditions. Chimpanzees did not exhibit a particularly high preference for cassava over other cultivars (PI= 0.77). The frequency of feeding on cassava tubers may be underrepresented due to restricted observations, as mature cassava plants were generally taller than a chimpanzee, and abandoned cassava was often found in areas of dense thicket.

Papaya leaf

Crop-raiding on papaya leaf (including pith) showed a strong negative correlation with wild fruit availability (Figure 5.6; *event*: $r_s = -0.82$, $n=12$, $p<0.01$; *duration*: $r_s = -0.75$, $n=12$, $p<0.01$). This good protein source was thus raided when forest fruit was scarce. Only 4 crop-raiding bouts were observed where papaya leaf alone was consumed, compared to 19 bouts where both papaya fruit and leaf were consumed. Focussing on raiding events, chimpanzees did not specifically choose young leaves of papaya; mature leaves were consumed in 70 out of 73 events (binomial: $p<0.01$). People were present in 62 out of the 73 raiding events.

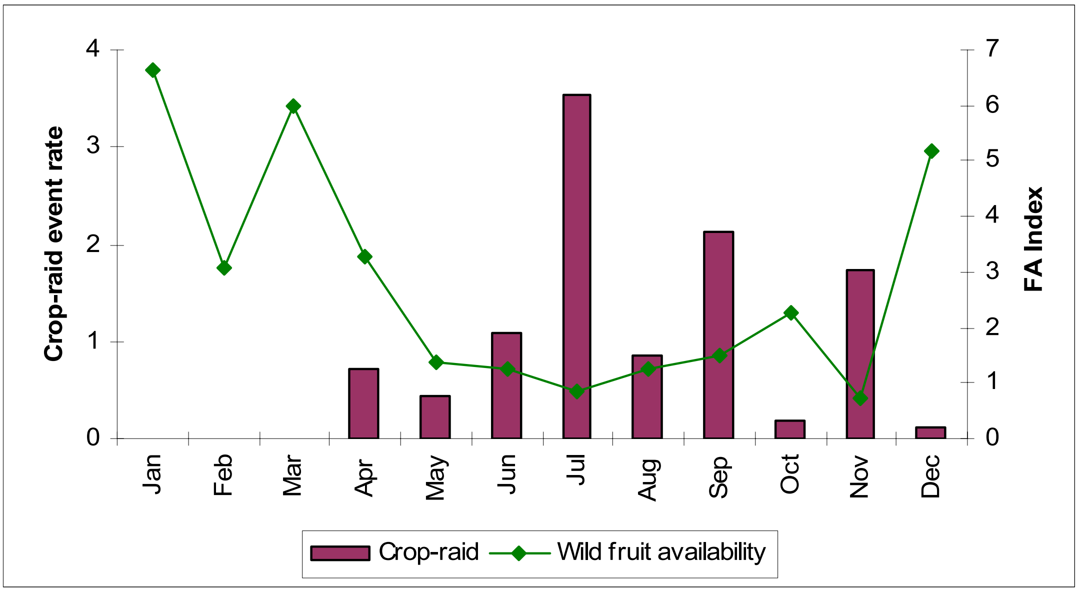


Figure 5.6. Crop-raiding rate on papaya leaf plotted against wild fruit availability.

Banana pith

Although negative correlations existed between wild fruit availability and both raiding on banana pith (Figure 5.7; *event*: r_s= -0.12, n=12, ns; *duration*: r_s= -0.41, n=12, ns) and total consumption rates of banana pith (Figure 5.7; *event*: r_s= -0.31, n=12, ns; *duration*: r_s= -0.33, n=12, ns), the results did not reach significance. However, banana pith-raid rates were significantly higher during periods of wild fruit scarcity ($X^2(1) = 3.85$, $p<0.05$), although no associations were observed between total feeding rates and wild fruit availability ($X^2(1) = 1.29$, ns). As with cassava, the chimpanzees were not observed feeding on banana pith during the months of May or August, when mango and maize were highly abundant.

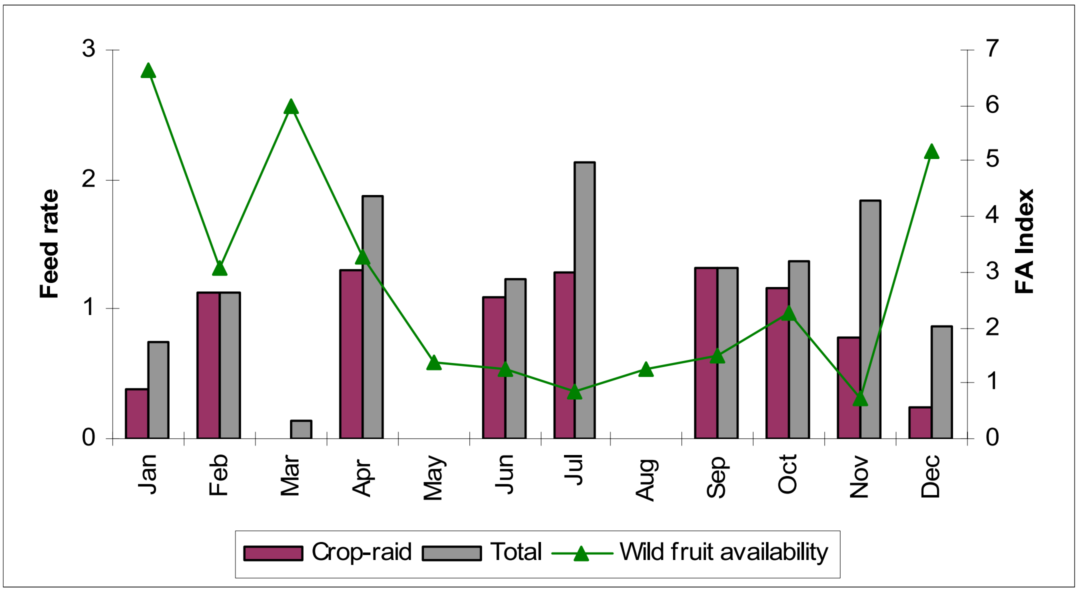


Figure 5.7. Crop-raiding rates and total feeding (raided and abandoned) rates on banana pith plotted against wild fruit availability.

5.3 Results: Synthesis of wild and cultivated foods.

5.3.6 Oil-palm utilisation

To gain a comprehensive understanding of oil-palm usage by the Bossou chimpanzees, it is necessary to consider feeding events in wild, supplied (see Plate 5.3) and raided conditions. Oil-palm fruits were often cut down by villagers throughout the chimpanzees’ home range, covered by palm leaves for protection, and collected some time afterwards. Although this mostly occurred within the forest, due to the high commercial value of palm-oil (Humle, 2003b), the villagers did not tolerate the chimpanzees feeding on the harvested oil-palm fruits; such events were therefore classified as raiding.

Plate 5.3. Adult and juvenile females cracking open supplied oil-palm nuts.

The chimpanzees obtained different oil-palm parts from different sources (Figure 5.8). Fruits were predominantly consumed from the wild, but also from supplied and raided sources, nuts were mostly obtained from the supplied source, and pith was nearly always consumed in the wild. Pith was not supplied during the nut-cracking experiments so could not be consumed from this source; however pith-raiding, although possible, only occurred once and pith was taken along with fruit.

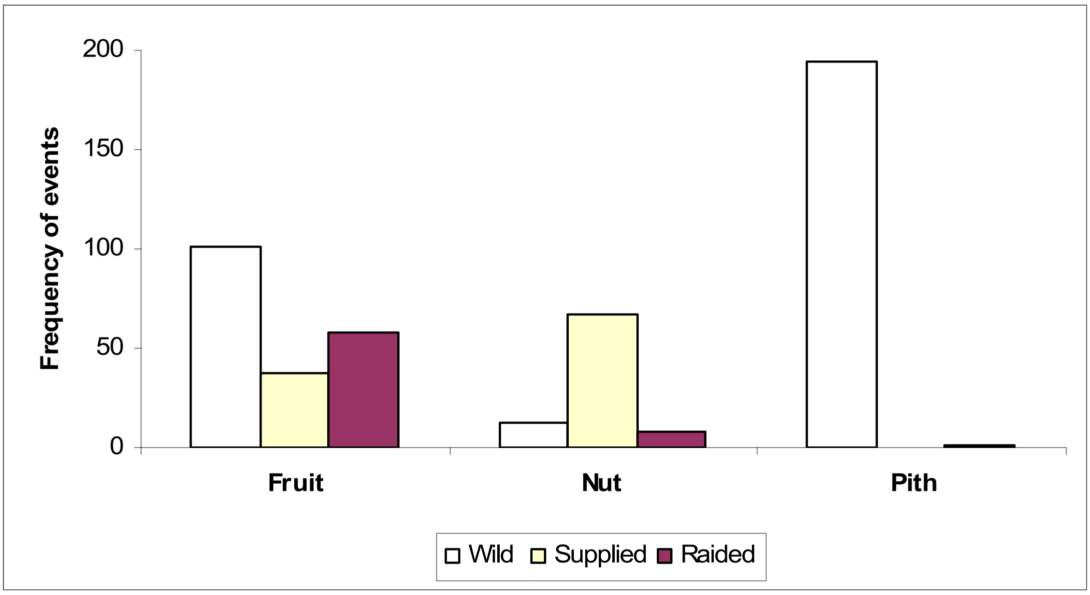


Figure 5.8. The total frequency of oil-palm feeding events (wild, supplied and raided) of fruit, nut and pith during the study period.

Oil-palm fruits were available year-round (refer to Chapter 4), and yielded the lowest preference index of all raided cultivars (PI= 0.59). Temporal variations were observed in the frequencies of oil-palm fruit consumption (Figure 5.9 (a)), with highest overall feeding rates during January, when fruits were supplied. Contrary to predictions, no correlations were found between event rates for wild, supplied and raided oil-palm fruit, or with wild fruit availability (see Table 5.4). However, combined consumption of wild and raided fruits was significantly higher during periods of wild fruit scarcity than abundance ($X^2(1) = 8.61$, $p<0.01$). For additional results, refer to the fallback foods section. Oil-palm nuts were consumed at consistently low levels throughout the year except when they were supplied during December and January (see Figure 5.9 (b)).

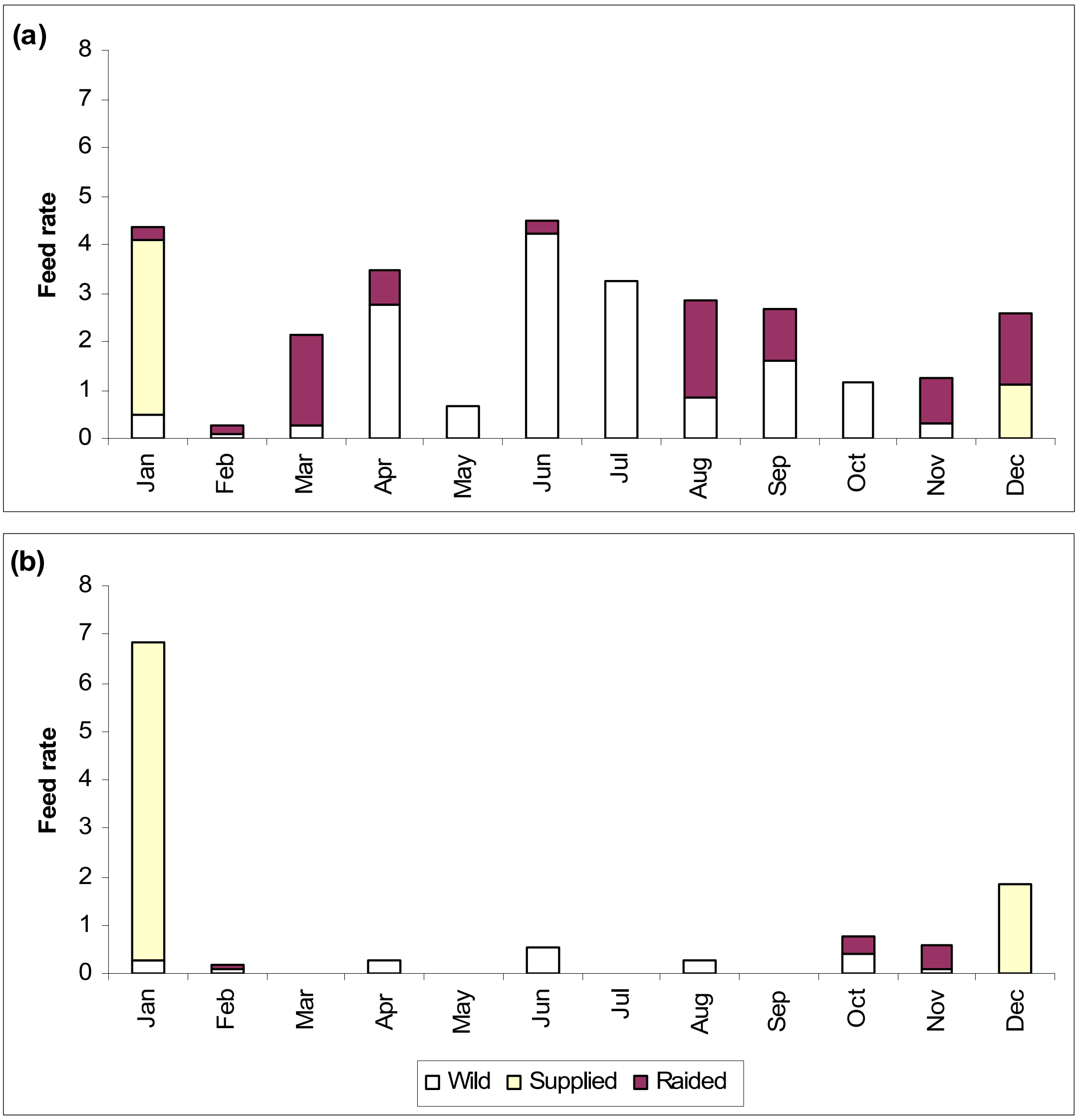


Figure 5.9. Monthly feeding rates on wild, supplied and raided oil-palm (a) fruit and (b) nut.

Table 5.4. Correlations between wild fruit availability, and wild, supplied and raided oil-palm fruits. Bonferroni corrections included.

	Wild	Supplied	Raided
FA Index	r_s= -0.44 ns	r_s= 0.59 ns	r_s= 0.13 ns
Wild		r_s= -0.43 ns	r_s= -0.30 ns
Supplied			r_s= 0.10 ns
Raided			

5.3.7 Wild feeding

Wild food feeding durations were not measured during *ad libitum* samples, so feeding duration data were taken from focal samples. As *ad libitum* event rates and *ad libitum* durations were shown to correlate strongly for both combined crop-raiding and combined total cultivar feeding, both event rates and feeding duration results were used in analyses of feeding on wild and cultivated foods.

Within-food parts

Over 80% of fruit feeding events and total fruit feeding time occurred in the wild, 13.4% and 9.8% were in raided conditions (events and total time respectively), and approximately 5% concerned abandoned sources (Table 5.5). Compared to fruit, a slightly higher percentage of leaves and pith were consumed in the wild than were raided, and all tubers consumed were from abandoned and raided sources.

Table 5.5. The percentage of feeding events and durations (in brackets) for each food part consumed in supplied, abandoned, raided and wild conditions.

	Supplied	Abandoned	Guarded	Wild
Fruit	1.1 (0.2)	5.2 (4.5)	13.4 (9.8)	80.3 (85.5)
Leaf	0	0	8.3 (6.5)	91.7 (93.5)
Pith	0	1.9 (1.1)	10.1 (5.0)	88 (94)
Tuber	0	25.5 (21.6)	74.5 (78.4)	0 (0)
Nut	67.7 (76.9)	0	9.1 (15.3)	23.2 (7.7)
Gum	0	0	5.6 (6.8)	94.4 (93.2)
Flower	0	0	11.1 (0)	88.9 (100)
Bark	0	0	0	100 (100)
Insect	0	0	0	100 (100)
Animal	0	0	0	100 (100)
Woody tissue	0	0	0	100 (100)
Other	0	0	0	100 (100)

Between-food parts

The chimpanzees were recorded feeding on a total of 123 identified plant species and 188 plant items during *ad libitum* samples (for complete lists, see Appendix D1). Additionally, the chimpanzees habitually fed on other food items including honey, algae and mushrooms, and insects such as ants, ant larvae and wasps nests. There was one observation of a chimpanzee opportunistically eating a mouse and on one occasion several chimpanzees fed opportunistically on placenta.

The chimpanzees ate fruit in over half of all recorded feeding events and durations (raids and all combined, Figure 5.10 (a)), highlighting that, despite fluctuations in availability of wild ripe fruit, chimpanzees maintain a high proportion of ripe fruit in the diet (*event***:** mean: 51.9%, range: 45.7 - 60.3, SD ± 4.6; *duration***:** mean: 60.3%, range: 46.4 – 75.6, SD ± 8.0). Pith was frequently consumed (*event***:** mean: 21.5%, range: 11.8 - 27.9, SD ± 4.3; *duration***:** mean: 15.2%, range: 10.8 – 24.6, SD ± 4.7), and leaves were consumed at a similar proportion to pith (*event***:** mean: 16.9%, range: 8.2 – 16.9, SD ± 4.2; *duration***:** mean: 17.2%, range: 6.5 – 25.2, SD ± 5.1). Over 80% of monthly feeding events and durations concerned fruit, leaf and pith, and these food parts were subsequently divided into raided events and all other events (from wild, supplied and abandoned sources, Figure 5.10 (b)).

The monthly frequencies of non-raided fruit feeding events correlated negatively with monthly raided fruit events (r_s= -0.755, n=12, p<0.01) and durations (r_s= -0.586, n=12, p<0.05); as hypothesised, chimpanzees supplement wild fruits with cultivated fruits. On a daily basis (data collected from focal follows of 5 hours of more), there was also a significant negative correlation between wild feeding time and cultivar feeding time (linear regression: r^2= 0.047, p<0.05). However, no significant correlations were found between non-raided and raided leaf consumption (*event*: r_s= 0.417, n=12, ns; *duration*: r_s= 0.116, n=12, ns) and non-raided and raided pith consumption (*event*: r_s= 0.182, n=12, ns; *duration*: r_s= 0.35, n=12, ns).

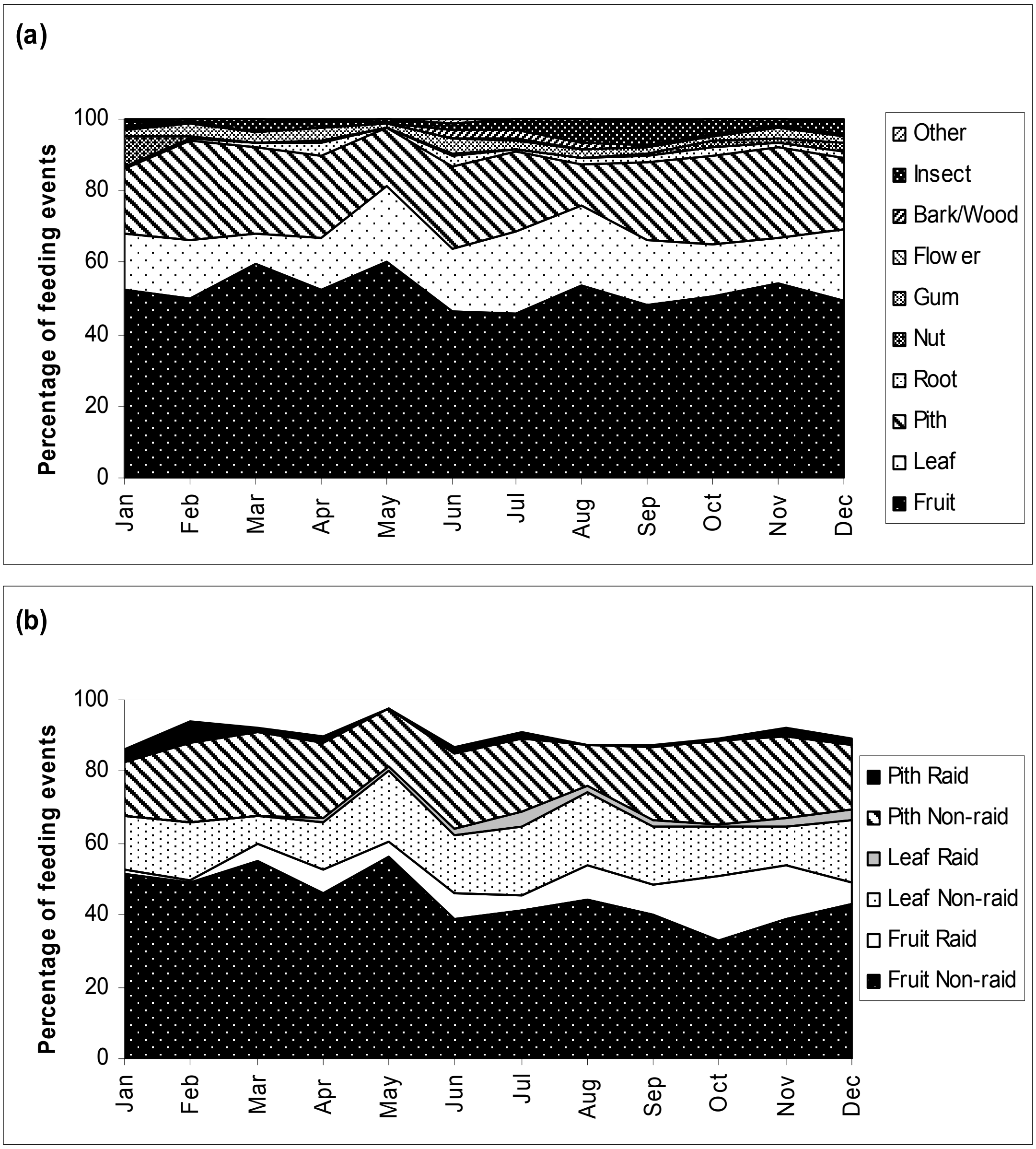


Figure 5.10. The monthly percentages of feeding events for (a) each food part that was consumed in supplied, abandoned, raided and wild conditions combined and (b) raided and all (wild, abandoned and supplied) fruit, leaf and pith feeding events.

5.3.8 Fallback foods

As previously discussed, oil-palm pith and umbrella tree fruit are recognised fallback foods for the Bossou chimpanzees during periods of fruit scarcity (Chapter 4). Since mango availability within the forest had a large effect on crop-raiding rates, wild fallback feeding rates and durations were correlated against combined crop-raiding rates. As hypothesised, feeding on umbrella tree fruit (*event*: r_s= 0.629, n=12, p<0.05; *duration*: r_s= 0.580, n=12,

$p<0.05$) and oil-palm pith (*event***:** $r_s= 0.671$, n=12, $p<0.05$; *duration***:** $r_s= 0.655$, n=12, $p<0.05$) showed the same usage patterns as raided cultivars. To better understand the function of cassava tuber in the chimpanzees' diet, analyses between feeding rates and combined crop-raiding rates (cassava excluded) were conducted; cassava tuber, like wild fallback foods, showed the same usage patterns as raided cultivars (*event*: $r_s= 0.818$, n=12, $p<0.01$; *duration*: $r_s= 0.893$, n=12, $p<0.01$). Due to periods of supplied oil-palm fruits, correlations between wild and raided oil-palm fruit usage combined, and combined crop-raiding rates (oil-palm fruits excluded) were tested. Although correlations were positive, they failed to reach significance (*event*: $r_s= 0.385$, n=12, ns; *duration*: $r_s= 0.524$, n=12, ns).

5.3.9 Dietary diversity

To investigate monthly and seasonal changes in the dietary diversity of the Bossou chimpanzees, the number of identified plant species consumed, and standardised Shannon-Wiener indices (J') were calculated. The Shannon-Wiener index is a more sensitive measure of dietary diversity than basic counts of the number of plant species consumed; it considers the relative proportion of each species in the diet, measuring diversity on a scale of 0 to 1 (see Appendix D2 for complete test results).

The chimpanzees had a diverse diet in all study months (monthly median = 53 sp., range = 32-65) and there was little variation when comparing periods of low and high fruit availability [*low*: median = 51 (32 – 61) sp.; *high*: median = 54 (50 – 65) sp.; U = 17, n*low* = 7, n*high* = 11, Z = -0.081, ns). The monthly number of species consumed showed no correlation with wild forest fruit availability ($r_s= 0.263$, n=12, ns). The mean index of diversity was very high at 0.84 (SD ± 0.04), again with very low levels of variation between periods of low and high fruit availability [*low*: mean J'= 0.84 (range: 0.78 – 0.89); *high*: mean J'= 0.84 (range: 0.78 – 0.88)]. These indices showed no correlation with availability of wild forest fruit (Figure 5.11; r_s= 0.259, n=12, ns) showing the Bossou chimpanzees did not change their dietary diversity when wild fruits were scarce.

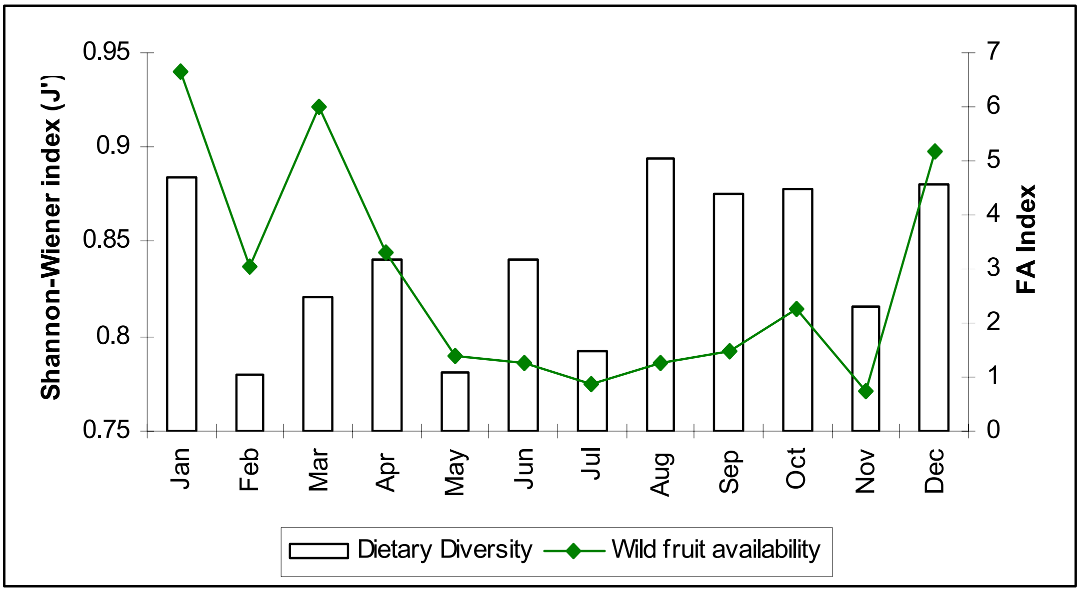


Figure 5.11. Temporal variations in dietary diversity (standardised Shannon-Wiener Index) and wild-fruit availability (FA Index).

5.4 Discussion

Predicting foraging behaviour in biologically complex systems is very difficult; a chimpanzee's choice to crop-raid will be influenced by a multitude of factors (Naughton-Treves, 1997). The combined availability of abandoned and guarded cultivars, provisioning with palm nuts for research purposes and the abundance of wild foods all affected the food available to the Bossou chimpanzees and thus influenced crop-raiding levels. This work attempts to tease apart these variables to best establish the primary and secondary forces driving or otherwise influencing the chimpanzees' decisions to crop-raid. Table 5.6 summarises the primary factors influencing crop-raiding rates.

Table 5.6. Summary of the use of cultivars in response to wild fruit availability and respective cultivar availability (✓: correlation present; ✗ correlation absent) and preference index for each cultivar.

Cultivar	Wild fruit availability	Cultivar availability	Preference index
SS-fruit	✓	✗	0.91
Mango	✗	✓	4.09
Rice	✗	✓	0.67
Maize	✓	✓	0.91
Cacao	✗	✗	0.90
Cassava	✗	✗	0.77
Papaya leaf	✓	-	-
Banana pith	✗	-	-
Combined crop-raid	✗	✗	-
Total cultivar feeding	✗	✗	-

Like other communities the Bossou chimpanzees had a broad diet dominated by fruit, although unlike most other communities they consumed large quantities of cultivars (Newton-Fisher, 1999; Tutin et al., 1991; Wrangham et al., 1996; Fawcett, 2000). The chimpanzees 'optimally' utilised a large and nutritionally balanced range of cultivars throughout the year, which functioned to complement their wild diet and contributed to a continuously high monthly dietary diversity. This study shows that cultivars are fully integrated into the Bossou chimpanzees' dietary repertoire and during this study the chimpanzees did not experience any period of serious food shortage. The Bossou chimpanzees rarely fed on unripe or immature crops and they exhibited a strong preference for mango fruits compared to other cultivars. This probably reflects the chimpanzees' preference for a low-risk, highly palatable cultivar, but PI values also reflect variations in farmers' tolerance of crop-raiding. The raiding of CPL crops, which form a predominant part of the diet of the local people, was generally less accepted by farmers. It would be interesting to observe inter-annual variations in crop-raiding levels and crop preferences, as wild fruiting patterns and crop-yields have a tendency to fluctuate from year to year. Even though overall crop-raiding and cultivar feeding rates were significantly higher during periods of wild fruit scarcity, total crop-raiding levels correlated weakly with both wild fruit and cultivar availability. Certain cultivars were raided in direct response to wild fruit scarcity whereas others were raided according to their availability; this illustrates the importance of analyses of individual and specific groups of cultivars. Such variations also illustrate the importance of crop choice by farmers when establishing land management techniques for alleviating human-primate conflict.

5.4.1 Simple-sugar fruits

As predicted, forest fruit availability was the primary factor influencing SS fruit crop-raiding rates. Cultivated fruits acted as fallback foods for the chimpanzees during periods of fruit scarcity; however, the low availability of SS cultivars from June to August may have diminished the incidence of crop-raiding during this period. Throughout the month of May, the high availability of mango amounted to a superabundance of wild fruit, and as there were no risks incurred by harvesting them, lower SS fruit-raiding rates were observed.

Secondary factors did not significantly contribute to temporal variations in crop-raiding levels. However, as hypothesised, chimpanzees preferentially crop-raided under certain secondary conditions. Crop-raiding occurred more than expected in the village, where SS fruits were predominantly grown, and when people were absent. This is understandable as the perceived risk of raiding would have been greater when people were present in such exposed areas. Even though the chimpanzees are totemic to local people and are therefore not killed, they are often chased away with noise and sometimes with the use of stones. The chimpanzees probably associate certain areas as higher risk than others, but are likely to fear human presence to a certain extent in any exposed area.

5.4.2 Other cultivars

Rice pith raiding was strongly correlated with its availability, and fully grown piths were raided by the chimpanzees at around the time when rice grains were ready for harvesting. Before harvesting, the presence of people in rice fields acted as a strong deterrent against crop-raiding, and may have had a lasting influence in limiting feeding in highly guarded areas even after harvesting.

It appears that maize-raiding by the Bossou chimpanzees was driven by high maize availability and increased by wild fruit scarcity, making it a very risky for farmers to grow maize near or within the forest. The chimpanzees' strong preference for protein-rich maize conforms to the widespread view that wildlife raid crops whenever they are available due to their higher nutritional value (Maples et al., 1976; Bell, 1984; Naughton-Treves et al., 1998).

Cacao was not raided in response to wild fruit or cultivar availability. However, the latter case may be an artefact of chimpanzees only raiding from one site; raiding rates may well be linked to cacao availability at the one site where raiding took place.

The raiding of papaya leaf in response to wild fruit scarcity may have been a side-effect of increased levels of SS fruit-raiding. However, it is also likely that papaya leaf provided the chimpanzees with a required protein source during periods of scarcity. Papaya leaf, which contains proteolytic enzymes, has also been acknowledged for its medicinal properties as an anthelmintic and in the treatment of malaria and digestive disorders. This possibly explains the selection of older and tougher leaves instead of the normally preferred young leaves. According to Huffman et al. (1998, p.113) "there is a fine line between what may be ‘medicine’ and what may be ‘food’ in primates, making the difference often seem transparent”. This highlights the possible medicinal usage of papaya leaf by chimpanzees and should be explored further using a multidisciplinary approach, wherein the biological activity of papaya leaf is assessed against chimpanzee parasite species (Huffman, 2001).

Banana pith-raiding did not significantly correlate with forest fruit availability, although bananas were raided at higher frequencies during periods of wild fruit scarcity; this shows some consistency with the usage of banana pith by the Kibale chimpanzees (Naughton-Treves et al., 1998). High-fibre banana pith may function as a fallback food, although it was not always taken in preference to alternative available cultivars. It is also plausible that banana pith acted as an additional water source for the chimpanzees during the dry season (high wild fruit availability), dampening seasonal effects.

Although cassava-raiding was not related to wild fruit availability, like wild fallback foods, it exhibited the same usage patterns as other raided cultivars. Cassava dominates the diets of the Bossou farmers during the wet season (low wild fruit availability), which may explain why chimpanzees showed higher levels of crop-raiding in the presence of people during such periods. However, a greater than expected frequency of raids in highly guarded fields was also observed, supporting the hypothesis that chimpanzees are willing to take greater risks when wild fruits are scarce. Byrne et al. (1993) documented that during the harshest times of year principal fallback foods for baboons were often underground. Laden and Wrangham (2005) proposed that a key change in the evolution of hominoids from the last common ancestor shared with chimpanzees was the substitution of USOs for herbaceous vegetation as fallback foods. This research has shown that when available to them, chimpanzees show a propensity to exploit USOs, although to a much lesser extent than other plant parts. From this standpoint it would be interesting to compare the usage of fallback foods and in particular USOs by savannah- and forest-dwelling chimpanzees.

5.4.3 Wild fallback foods

Other previously recognised wild fallback foods, including umbrella tree fruit and oil-palm pith, showed the same usage patterns as raided cultivars, again highlighting the function of both wild and cultivated fallback foods in the chimpanzees' diets. An effort should be made to conserve these secondary forest species, as they almost certainly buffer crop-raiding rates during periods of wild fruit scarcity. Oil-palm fruit did not emerge as a specific fallback food during this study, although raid and wild feeding rates were significantly higher during periods of wild fruit scarcity. Oil-palm fruits were also consumed frequently, especially from the wild, during June and July when general cultivar availability was low. Interestingly, Yamakoshi (1998) did identify oil-palm fruit as a fallback food for the chimpanzees of Bossou; however, at the time of his study oil-palm fruits were not supplied, and cultivars were possibly not such a predominant part of the diet.

5.4.4 Culture in crop-raiding

According to Humle (2003b), cultures are defined as dynamic behavioural traditions that are 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. Numerous dietary and behavioural traditions have been established among different populations of chimpanzees (Nishida et al., 1983; McGrew, 1992; Whiten et al., 1999). The major dietary differences between the chimpanzees of Gombe and Mahale were compared, revealing variation in the frequency that commonly occurring plant species were consumed and processed (Nishida et al., 1983). Additionally, not all species of edible nut are cracked by different populations of chimpanzees where nut-cracking behaviour is present within the population, and the nut species are available (Sugiyama, 1981; Anderson et al., 1983; Boesch and Boesch, 1990; Humle and Matsuzawa, 2001). Culture has not been explored with respect to the exploitation of cultivars. The process of acquisition and propagation of new feeding habits within a population is an important factor when considering the possibility of culture in chimpanzee crop-raiding. In 1983, after 16 years of observation, Takashi (1983, p.273) observed the chimpanzees of Mahale feeding on mango fruits for the first time. He stated that “the consumption of mangoes eventually could be fixed in their dietary tradition, through repeated occasions of tasting fruit, by becoming familiar with the fruit en route [in] their daily ranging”.

Certain cultivars were preferred by the Bossou chimpanzees, raising the possibility that different chimpanzee populations exhibit material and behavioural cultural patterns in their usage of cultivated foods. For example, during the study period the Bossou chimpanzees were not observed feeding on guava or avocado fruits, even though these are readily eaten by captive chimpanzees (de Nijs, 1995; Matsuzawa, pers. comm.); avocado trees were widely available and a guava tree was present in a regularly visited orchard. In contrast, sugarcane was rare throughout the chimpanzees’ home range but, when encountered, was preferentially raided compared to other cultivars. Taking the density and distribution of cultivars into account, information from primate communities in a wide range of habitats is needed to distinguish between site-specific and species-specific traits.

In conclusion, the usage patterns of wild and cultivated foods by the Bossou chimpanzees are inextricably connected. Although crop-raiding in Bossou has probably long existed, quantitative data have shown an increase over the last decade (Takemoto, 2002). Is this a reflection of recent deforestation or increased cultivation within the home range, or have the chimpanzees merely become more ‘habituated’ to raiding cultivars? As this chapter has discussed, there are a multitude of factors that contribute to a chimpanzee’s decision to crop-raid. On a broader level, questions regarding long-term changes also need answering if we are to establish durable human-primate conflict mitigation strategies.

Chapter 6- Part One

Crop-raiding: a Behavioural Approach

Crop-raiding: a Behavioural Approach

6.1 Introduction

The previous chapter explored the ecological contexts of chimpanzee crop-raiding. This chapter aims to describe the influence of cultivars on the chimpanzees' activity budgets and the chimpanzees' social and behavioural adaptations surrounding crop-raiding. Understanding the behaviour of primates whose home ranges border agricultural land and human settlements is central to answering questions about how they perceive and adjust to such environments.

Seasonal fluctuations in resource abundance are reported to cause primates to change their activity budgets. Oates (1987) summarised the available evidence and showed that in times of food scarcity, species that rely on fruit normally increase the time spent searching for food, whereas species that rely on foliage decrease their level of activity in order to minimise energy expenditure. Travel costs are greater during periods of wild fruit scarcity, and therefore individuals can reduce energy expenditure by decreasing time spent travelling and increasing time spent resting and feeding (Wrangham, 1977; Gillespie and Chapman, 2001). Doran (1997) explored seasonal variations in the feeding ecology of the chimpanzees of Tai, and reported that individuals responded to a minor dry season by spending significantly longer feeding. It is possible that daily energy requirements only determine foraging time during fruit scarcity, whereas during fruit abundance foraging time is determined by the digestive capacities of the individuals. Fawcett (2000) concluded that when food is scarce, the chimpanzees of Budongo spend less time resting and moving; in contrast Bates (2005) found no evidence that the same community of chimpanzees changed their activity budgets to compensate for low fruit availability. This discrepancy highlights the possibility of inter-annual variation in response to fruit availability, or the possible influence of other factors, including social ones. The inclusion of predictable, high energy, human-produced food in the diet can have a pervasive impact on the activity budgets of primate groups, altering both activity patterns and sociality. Access to human food, has been shown to result in both a higher proportion of time resting and a lower proportion of time feeding by baboons (Saj et al., 1999; Strum, 1984), and an increase in the rate of aggressive and competitive interactions in vervet monkeys (Lee et al., 1986).

An alternative strategy to changing activity budgets is to alter daily range length. Concurrent with the 'ecological constraints model' (Chapman, 1990), whereby individuals in larger parties need to travel further for resources, research shows that when foods are scarce the chimpanzees of Tai reduce their travel distance to reduce energy expenditure (Doran, 1997; Boesch and Boesch-Achermann, 2000). However, other chimpanzee populations have been found to expand their home range during periods of fruit scarcity, despite the energetic demands of travel (Yamagiwa, 1999).

In addition to feeding competition and resource availability, sexual dimorphism may contribute to sex differences in primate foraging strategies, as the sexes experience different selective pressures for energy acquisition and expenditure (Bean, 1999). Both Ghiglieri (1984) and Fawcett (2000) found that male chimpanzees spent significantly more time feeding and travelling than females; however both studies were characterised by acknowledged sampling biases. In contrast, Doran (1997) found no differences in time spent feeding, resting and moving between chimpanzee sexes. If sex differences in feeding behaviours do exist, the individuals requiring the greatest nutritional intake may exhibit a greater propensity to crop-raid, replacing lower-quality fallback foods with cultivars. Interestingly, Strum (1984) found that adolescent male baboons were especially likely to become raiders, possibly because the increased nutritional content of crops, predominantly maize, could help them grow faster; once full size was attained, their raiding behaviour declined. Similarly, Priston (2005) found that adult males were heavily over-represented in raiding parties of Sulawesi macaques, and that they were more willing to take risks than other group members. The risks associated with human food acquisition have been used to explain the low consumption of human food by female monkeys, especially those with dependent offspring (Saj et al., 1999; Priston, 2005).

In adaptation to the costs and benefits of group-living, chimpanzee social systems are characterised by a fission-fusion pattern of organisation, in which individuals of a community separate to form small temporary parties (Nishida, 1968; Goodall, 1986; Boesch, 1991). According to Lehmann and Boesch (2004), party size and composition in chimpanzees depend upon three main factors: food availability, the presence of maximally swollen females, and the activity of the party. Some authors have argued that the potential risk of encountering predators is the main factor underlying party formation (Tutin et al., 1983; van Schaik, 1983; Dunbar, 1988). The social organisation of chimpanzees in human-influenced risky situations such as crop-raiding and road-crossing may be comparable to some aspects of their strategies for predator avoidance (Sakura, 1994; Takemoto, 2002; Hockings et al., 2006).

According to the ecological constraints model, party size should be strongly correlated with food availability to reduce feeding competition between party members: large parties form to exploit rich food patches and divide when fruits are scarce (Wrangham, 1977;

Isabirye-Basuta, 1988; Wrangham et al., 1992; Sakura, 1994; Fawcett, 2000). However, the importance of food availability as a determinant of party size has been questioned (Stanford, 1995; Boesch, 1996; Hashimoto et al., 2001). Both sexual and non-sexual social factors have also been reported to affect chimpanzee party formation; for example kin and allies remain together, and sexually receptive adult females attract males, further increasing party size (Goodall, 1986; Matsumoto-Oda, 1999; Wallis and Reynolds, 1999; Newton-Fisher et al., 2000; Wrangham, 2000).

Chimpanzees in the Tai forest suffer from heavy predation by leopards and show specific social responses to such risks (Boesch, 1991). Boesch (1991, p.236) reports that "Tai chimpanzees are mostly found in parties with the best defence capacities (mixed and all-male) that allow both sexes to profit from others' support". In contradiction to theories linking larger parties with improvements in predator detection (Hamilton, 1971; Dunbar, 1988), when predation pressure increased, the Tai chimpanzees decreased their party size. This may be because greater noise levels by large parties may increase the likelihood of detection by predators, and because dense forest decreases the advantage of increased vigilance as a function of party size. However, the benefits of large party sizes during crop-raids, where cultivars are plentiful and mostly located in open areas, may result in less seasonal variation in party sizes, and larger overall parties.

Research comparing subsistence-related behavioural adaptations of chimpanzee populations living in both pristine and human-degraded environments contributes to revealing these primates' propensity for behavioural flexibility in unpredictable environments. This has important implications for understanding primate behavioural innovation, as unpredictability in both ecological and social contexts is key to setting the conditions for innovation (Reader and Layland, 2001; Lee, 2003; Reader and MacDonald, 2003). However, when a group of primates has been feeding off domestic crops for a long period, as observed with the chimpanzees of Bossou, crop-foraging will be well established in their ecological strategy, and they are expected to adjust their behavioural repertoire accordingly.

Few data exist on behavioural adaptations of primates in the context of crop-raiding. Maples et al. (1976) reported that several aspects of the movements and organisation of crop-raiding yellow baboon populations in Kenya were of particular advantage for crop-raiding, and significantly different to those of non-raiding populations. Baboons located near the edges of farms showed enhanced vigilance behaviours compared to the baboons that were protected by forests, thereby reducing the potential costs associated with crop-foraging. Furthermore, one baboon troop divided into subunits to conduct simultaneous raids, and possibly used vocalisations to distract the farmers' attention whilst other individuals crop-raided, though it remains unclear whether diversionary tactics are used by baboons when crop-raiding. It is interesting to note that in Kibale, the chimpanzee sexes varied in their vocal behaviour in anticipation of potentially risky intergroup encounters: females adopted a 'keep quiet' strategy even when accompanied by adult males. Also, larger parties of adult males were more likely to countercall than smaller parties of males (Wilson et al., 2001). Priston (2005) reported that Sulawesi macaques showed vigilance behaviours when crop-raiding, and also decreased risks by transporting food obtained in cultivated areas back to the relative safety of the forest. However, Priston (2005) made no inferences regarding the use of diversionary tactics or cooperative behaviours by the monkeys during raids. Cooperation, defined as 'joint action for mutual benefit' (Gilby et al., 2006), by adult male chimpanzees has been documented in a wide array of risky situations in the wild, including hunting (Boesch, 1994; Boesch and Boesch-Achermann, 2000), border patrols (Wilson et al., 2001) and road-crossing (Hockings et al., 2006). Cooperative behaviours may prove beneficial during crop-raids by increasing protection and access to resources.

6.1.2 Hypotheses

(1) Daily activity patterns

- (a) Cultivar consumption will contribute to an increase in time spent resting and a decrease in time spent feeding.
- (b) Males will spend more feeding time than females on cultivars compared to wild fallback foods.

(2) Party formation

- (a) Party size during crop-raids will be greater than during wild feeds.
- (b) Party composition will vary depending on the degree of risk associated with cultivar feeding.
- (c) Chimpanzees will decrease group spread and increase inter-individual proximity during crop-raids.
- (d) The presence of all three adult males will lead to increased raiding and raiding in higher risk situations.

(3) Behavioural adaptations to crop-raiding

- (a) Chimpanzees will vocalise less when crop-raiding than when feeding on wild foods.
- (b) Chimpanzees will more frequently transport raided food than wild food.
- (c) Chimpanzees will show heightened vigilance behaviours when crop-raiding.

6.2 Methods and analyses

As various sampling procedures were employed during this study, they are specified throughout. Please refer to Chapter 3 and Chapter 5 (p.68-69) for definitions of crop-raiding bouts, crop-raiding rates, guard levels and secondary factors.

Activity patterns

Activity budgets were calculated using focal data. From the 187 focal samples (mean observation time: 8.95hrs, S.D ± 2.37), days of 5 or more hours of observation time were selected (n=169, mean: 9.6hrs, S.D ± 1.46). During months of low wild fruit availability, chimpanzees made their nests earlier and were often more difficult to find and follow, a higher cut-off observation time may have resulted in observation biases between months.

Description of analysed factors:

Sex: Male or female focal days.

Maximally swollen: To understand the effects of a maximally swollen female on the group dynamics of the small Bossou community, the presence of a maximally swollen female in the group was recorded, rather than the variations in the activity budget of the maximally swollen female herself.

Cultivar consumed: Cultivars consumed or not by the focal individual on that day.

Season: High or low wild fruit availability.

Party size

All focal follows were included in analyses of party size, and included all juveniles and infants unless otherwise stated (party sizes including and excluding immatures were positively correlated: see Appendix E1). Due to the emigration of an adult female and her infant, and a birth within the Bossou community, the maximum group size varied over the study period (see Chapter 2). Therefore, where stated, party size was calculated as a percentage of maximum group size. Also, where appropriate, maximum group size was included as a covariate for statistical analyses, and data were compared on a daily basis using matched samples.

Variations in party size and composition in relation to specific groups of cultivars and secondary factors were statistically tested where possible. However, statistical tests were not always feasible due to small sample sizes. Data on party compositions during crop-raids were analysed using ‘bouts’, as it was possible for more than one crop-raiding bout to take place on any individual day.

Party composition was divided into the following four groups:

Male-only: parties only containing adult males.

Mixed: parties consisting of at least one adult male, adult female and immature.

Male and Other: parties consisting of at least one adult male, and either at least one adult female or immature.

No Male: parties with no adult male.

Behaviours associated with crop-raiding

The term ‘vocalisation’ here only refers to a ‘pant-hoot’ vocalisation.

‘Wild fruits’ refers to all non-cultivar fruits consumed by the chimpanzees, and ‘Large fruit trees’ refers to fruits consumed from larger fruiting trees, as described in Appendix E2.

6.3 Results: Daily activity patterns

From focal follows of five hours or more, the Bossou chimpanzees fed throughout the day, with feeding peaking between 1600h and 1655h (see Figure 6.1). The chimpanzees spent most of the midday period resting, and were engaged in feeding behaviours for 22.5% of the day, on average for 129 minutes (SD ± 40.3 mins). Of that daily feeding time, males spent significantly longer than females feeding on cultivars (one-way ANOVA; $F_{1,167} = 24.0$, $p<0.001$). Males spent on average 25.6 minutes per day feeding on cultivars (range: 0-105 mins, SE ± 3.7mins), whereas females spent only 9.5 minutes per day (range: 0-55 mins, SE ± 1.4mins).

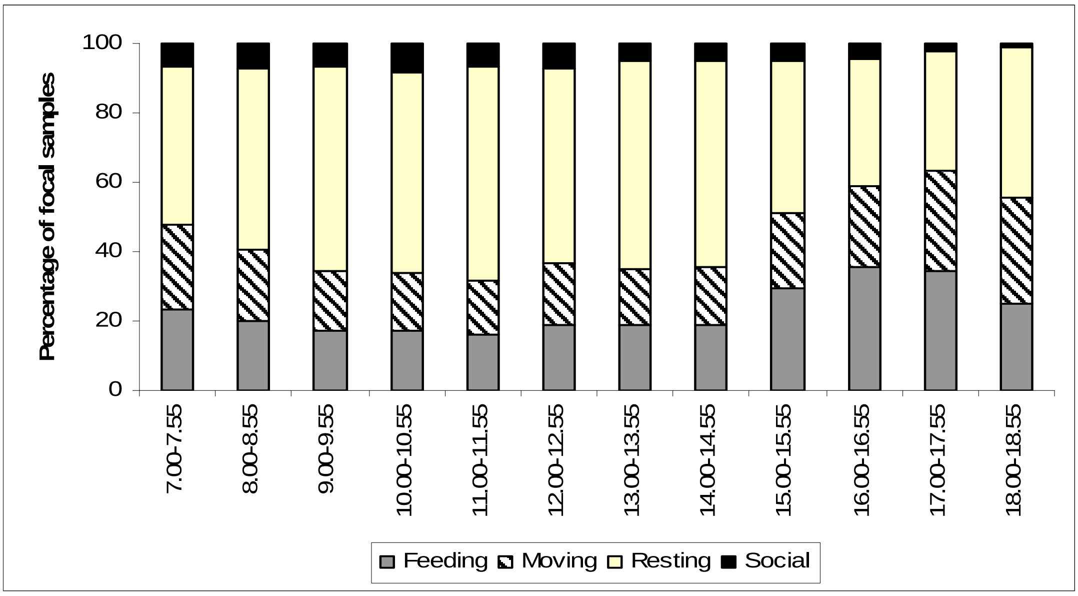


Figure 6.1. The percentage of focal samples engaged in each activity throughout the day.

Multivariate ANOVA assessed the behavioural categories (proportion of time feeding, resting, moving and socialising) as a function of sex classes, season, reproductive state and cultivar consumption. There were significant main effects of season, sex and cultivar consumption ($F_{1,153} = 4.73$, $p<0.05$). During periods of high wild fruit availability males spent significantly more time resting when cultivars were consumed than when they were not consumed. Additionally, on days when cultivars were consumed, both sexes spent a significantly greater proportion of the day feeding ($F_{1,153} = 6.79$, $p<0.01$) and moving ($F_{1,153} = 6.42$, $p<0.05$). When a female in the group was maximally swollen, males engaged in more social behaviours ($F_{1,153} = 6.42$, $p<0.05$) and the group in general spent less time feeding ($F_{1,153} = 5.79$, $p<0.05$). Activity budgets were not significantly affected by any other factors.

Cultivar feeding during wild fruit scarcity (Figure 6.2 (a)) appears more clumped than during periods of wild fruit abundance (Figure 6.2 (b)), with chimpanzees repeatedly visiting the same sites to raid. In combination with the above data on activity budgets, chimpanzees may be travelling further to obtain cultivars. Although it appeared that the chimpanzees travel more frequently to feed on the third hill Gboton during periods of wild fruit scarcity, only very small differences in core area usage were observed during these two periods (see Appendix E3 for Kernel analyses).

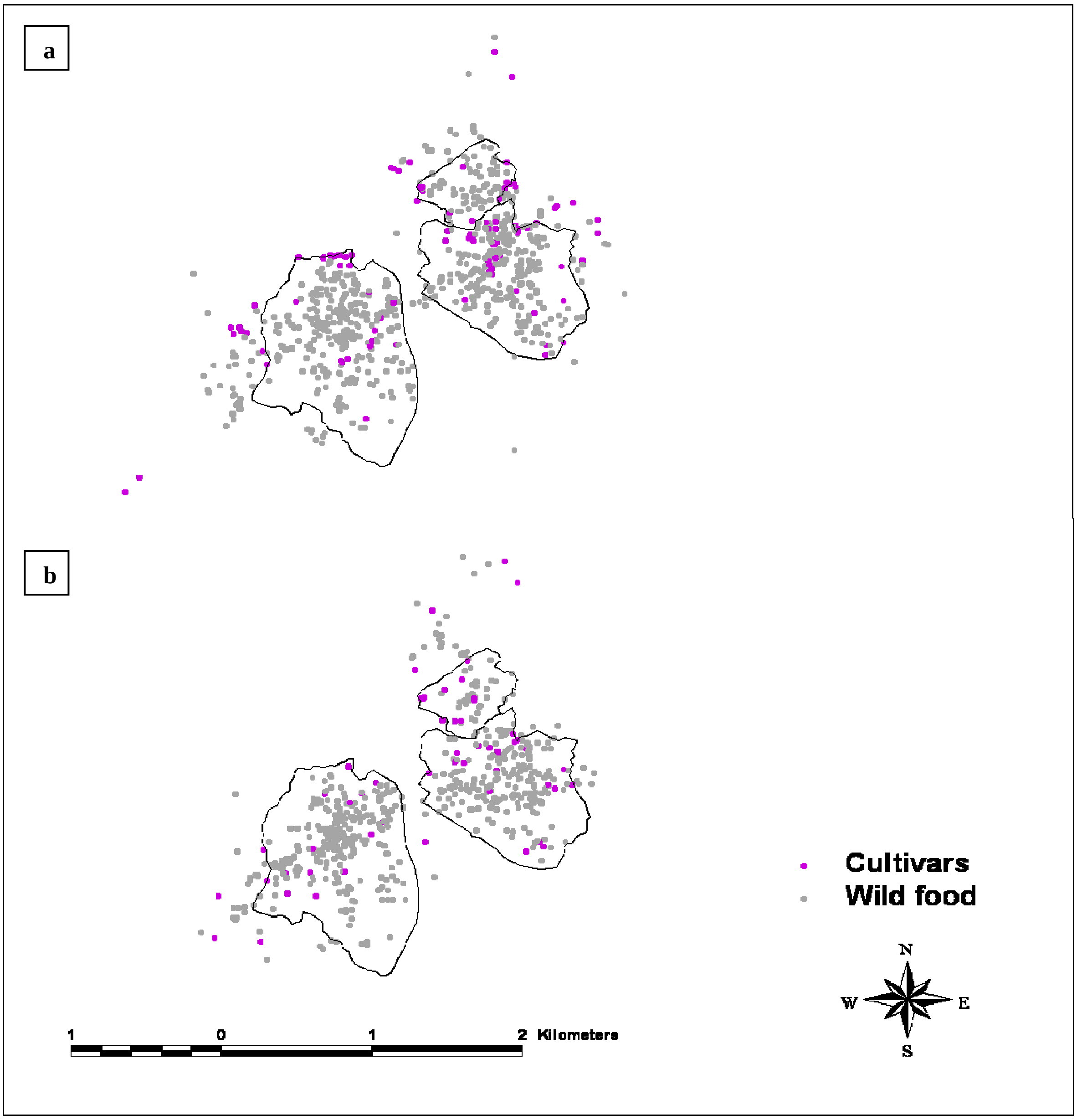


Figure 6.2. GPS locations when feeding on different sources by focal individuals during periods of (a) wild fruit scarcity (n=851) and (b) wild fruit abundance (n=626).

6.3.1 Crop-raiding and fallback foods

To establish whether males and females exploited wild and cultivated fallback foods in different ways, all-occurrence feeding rates of raided cultivars, umbrella tree fruit and oil-palm pith were calculated for both adult males and females. Males and females consumed wild fallback foods at similar rates (see Figure 6.3); however, cultivated food exploitation rates were much higher for males than females, contributing to higher overall fallback feeding rates for males. Additionally, males ate relatively greater proportions of cultivars than wild fallback foods especially during periods of wild fruit scarcity (June to November), whereas females relied more on wild fallback foods.

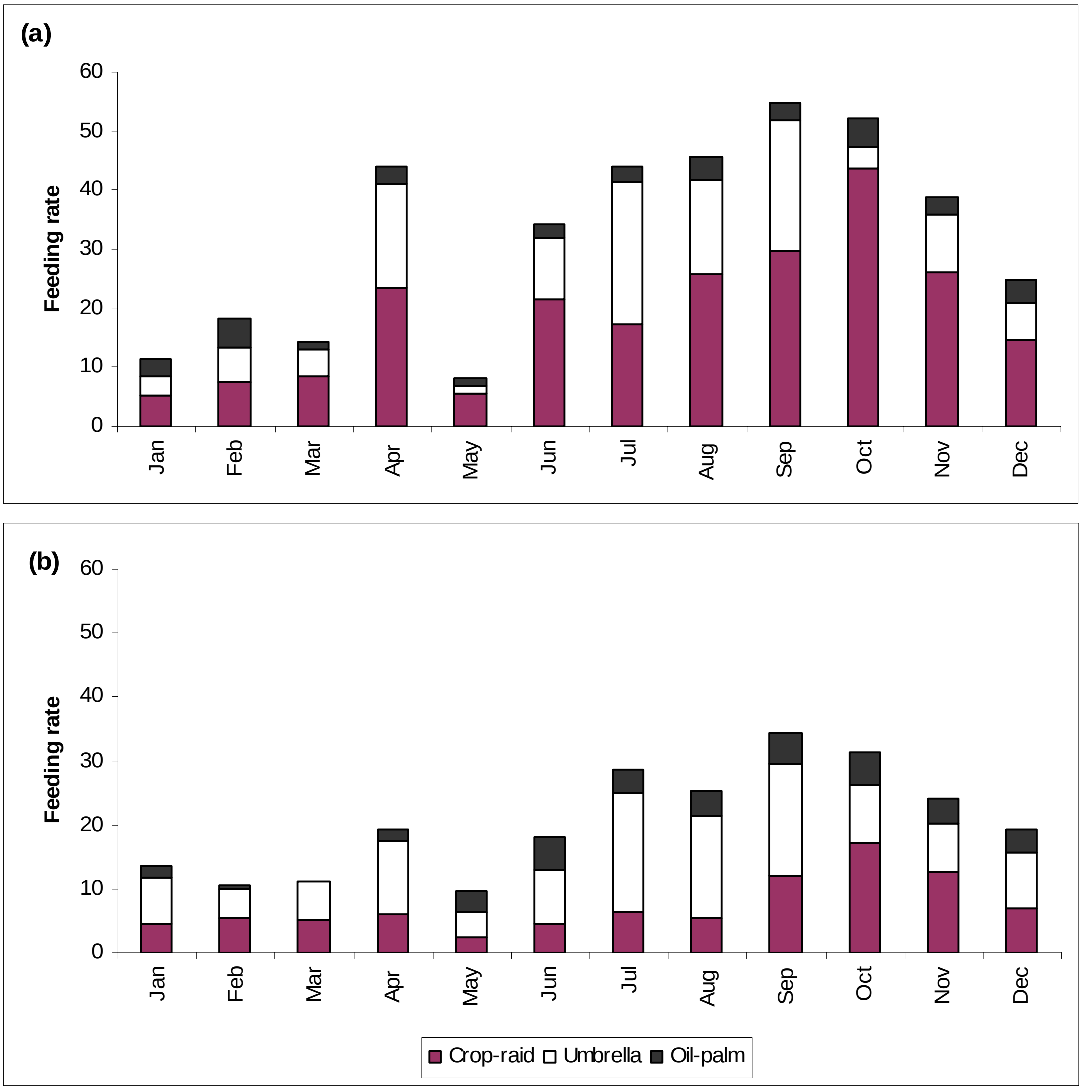


Figure 6.3. Feeding event rates from all-occurrence data for crop-raiding, umbrella tree fruit and oil-palm pith for (a) adult males and (b) adult females over the study period.

6.3 Results: Party formation

Based on all focal follows, mean party size was 4.9 individuals (SD ± 0.9). A one-way ANOVA (with maximum group size as a covariate) showed that mean party size significantly increased when a female within the core area was maximally swollen ($F_{1,178}$ = 11.37, $p<0.001$), and significantly decreased when a male and a female consorted outside the core area ($F_{1,178}$ = 12.00, $p<0.001$). Party size was not significantly different as a function of the sex of the focal individual ($F_{1,178}$ =1.22, ns).

Additionally, no significant correlation existed between mean monthly party size (as a proportion of maximum group size) and wild fruit availability (see Figure 6.4 (a); r_s= 0.22, n=12, ns), although party sizes were smallest during periods of fruit scarcity. As chimpanzees predominantly raided simple-sugar (SS) fruits, the relationship between party size and SS cultivar availability was tested. There was a significant positive correlation between mean party size (as a proportion of maximum group size) and SS cultivar availability (see Figure 6.4 (b); r_s= 0.62, n=12, $p<0.05$). See Appendix E4 for monthly variations in number of adult males present during focal observations.

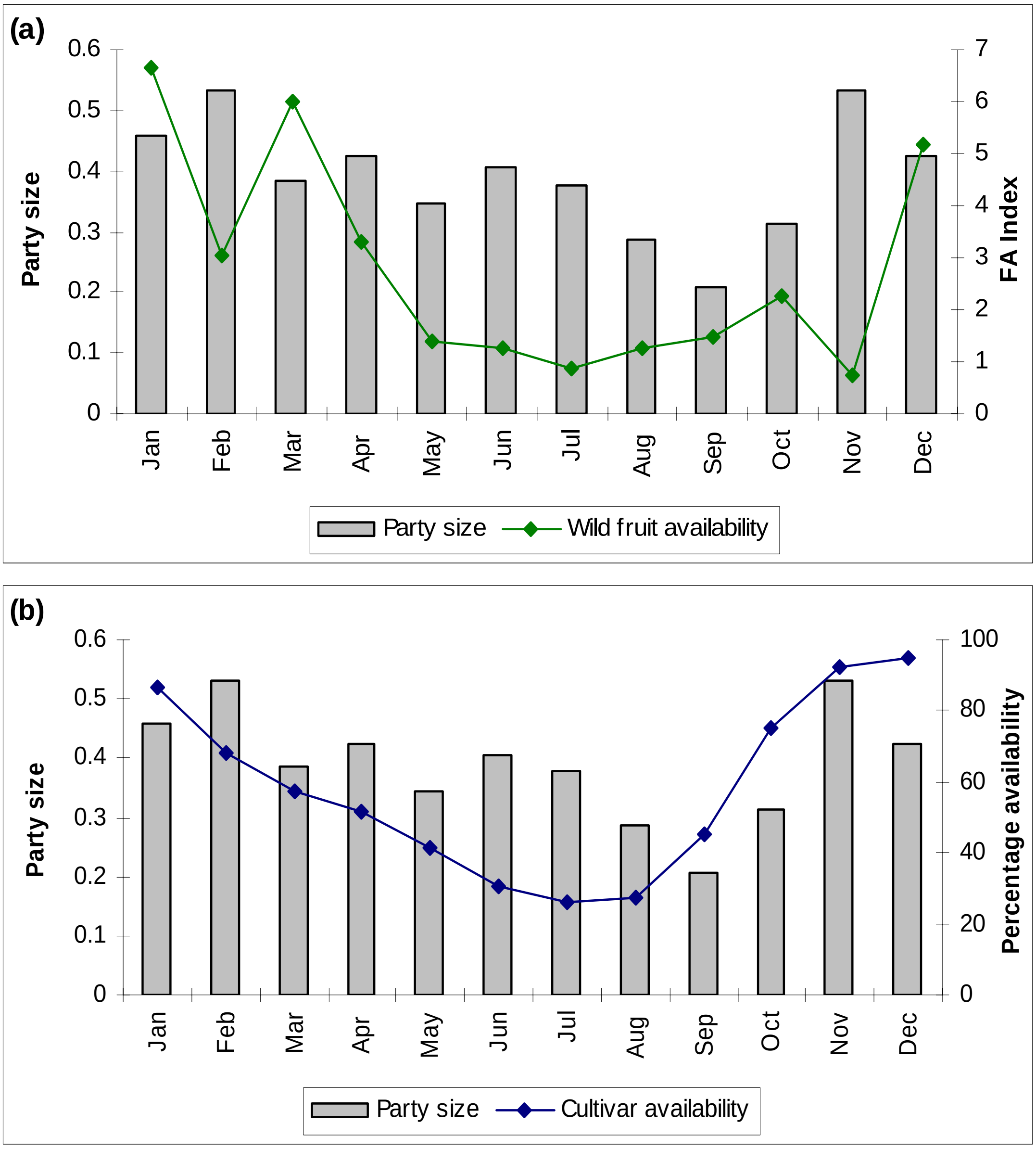


Figure 6.4. Monthly variations in mean party size as a proportion of maximum group size (all community members) plotted against (a) wild fruit availability, and (b) SS cultivar availability.

Daily mean party sizes when feeding on wild and raided sources were compared: party sizes were slightly larger when feeding on raided than on wild foods, although this failed to reach significance (means: 4.8 vs 5.2 individuals, t-test; $t_{88}=-1.82$, $p=0.073$).

Party composition during crop-raiding bouts was significantly affected by the location of the cultivar (forest vs village, $X^2(3) = 36.40$, $p<0.001$); male-only parties were much more common during village crop-raids than during raiding bouts in the forest (see Figure 6.5).

The effects of other secondary factors during crop-raiding bouts were varied. For example, people presence had a significant effect on party composition ($X^2(3) = 13.10$, $p<0.01$): parties with no males raided in the presence of people significantly less than expected by chance. In contrast, guard level did not affect party composition during raiding bouts ($X^2(3) = 5.80$, ns). Within forest raids, vegetative cover was mostly cultivar-dependent, which may in turn have influenced visibility and perceived risk.

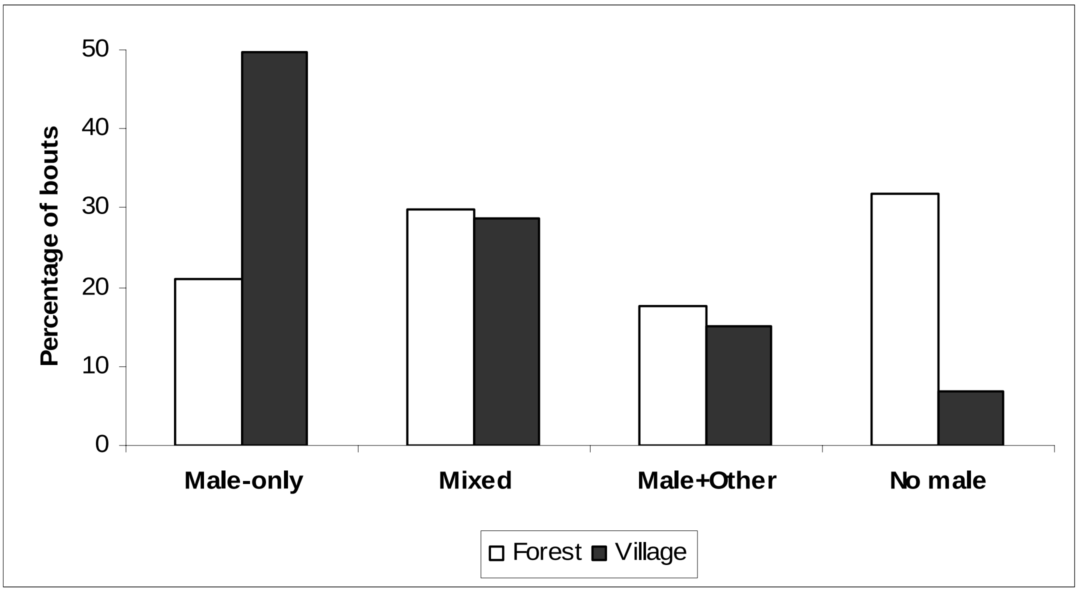


Figure 6.5. Party compositions during crop-raiding bouts in the forest and the village.

Simple sugar cultivars

To analyse SS-raiding bouts, a one-way ANOVA was used to determine if party size was affected by secondary factors, including maximum group size as a covariate. When guard level was low, chimpanzees were significantly more likely to crop-raid in larger parties when people were present than absent ($F_{1,120} = 16.14$, $p<0.05$), although location did not affect party size ($F_{1,120} = 0.04$, ns). However, there were significant differences between party compositions depending on location ($X^2(3) = 25.71$, $p<0.001$), people presence ($X^2(3) = 11.50$, $p<0.001$) and guard level ($X^2(3) = 8.32$, $p<0.05$; not significant if Bonferroni correction is applied). More specifically, male-only parties were significantly more likely than any other party composition to crop-raid in highly guarded areas ($X^2(1) = 7.06$, $p<0.01$), when people were present ($X^2(1) = 7.06$, $p<0.01$), and in the village ($X^2(1) = 10.98$, $p<0.001$). Chimpanzees were observed travelling a maximum of 120 metres from the forest edge to crop-raid, and males travelled significantly further than other age- and sex-classes from the forest edge to crop-raid (Mann-Whitney U-test: $Z = -3.71$, $p<0.001$). When no adult males were present, females and immatures were less likely to crop-raid SS fruits in the presence of people than when people were absent ($X^2(1) = 6.97$, $p<0.01$). Despite these differences, all age-and sex-parties were equally likely to raid ripe SS fruits compared to unripe fruits ($X^2(3) = 0.96$, ns).

When feeding on mango fruits, which presented little associated risk, no-male and mixed-party compositions were much more common than in raids on other SS fruits (Table 6.1). Additionally, over 80% of rice-raiding bouts were of mixed or no-male composition, with only 1 out of 22 bouts being male-only; party compositions were different to those seen in other SS raids. The chimpanzees would feed on the edge of rice fields where they were able to quickly re-enter the forest, and rarely fed in the centre of the field.

Carbohydrate, protein, lipid cultivars

Similarly to rice raids, 40% of maize raiding bouts involved mixed-party composition, although in contrast, 40% of bouts involved male-only parties, likely due to exposure associated with raiding in the village (see Table 6.1). Party sizes were larger during forest compared to village raids (5.8 vs 3.7 individuals; statistical tests were not conducted due to small sample size); this may reflect the increased risk of raiding maize in exposed areas near the village. The forest location and protective cover of the small cacao plantation probably resulted in this resource being sought out by females and immatures in 40% of all recorded bouts.

The mean party size was larger during cassava raids compared to abandoned cassava feeds (means: 3.9 vs 1.9 individuals); and party composition also differed between abandoned and cultivated categories (statistical tests not conducted due to small sample size). Frequency of male- and female-only parties increased and party size decreased when feeding on abandoned cassava. This latter effect may have been due to a high abundance and density of cassava in cultivated areas, allowing more individuals in mixed-parties to feed. Cassava plants also provide some protective cover, leaving the chimpanzees less exposed. Areas of abandoned cassava, which occur at lower densities than cultivated cassava, may be sought out by females as low-risk and high-calorie feeding patches.

Party compositions during papaya leaf-raiding bouts were not analysed as papaya leaf was predominantly raided in conjunction with papaya fruit. However, as with fruits, adult males consumed papaya leaf at significantly higher rates than other age-sex classes (43 out of 73 events; binomial: $p<0.01$).

Considering all oil-palm parts together, adult males and females appear to use oil-palm resources differently. Males fed predominantly from wild and raided sources, and females fed from supplied sources at significantly higher frequencies than expected ($X^2(2) = 9.22$, $p<0.01$); females thus exploited the fruits and nuts which were supplied in high quantities with no associated risks.

Table 6.1. The composition of parties (percentage of total) during cultivar feeding bouts, as a function of cultivar and location (forest, village, abandoned and guarded).

		Party Composition %			
Cultivar	**Location**	**Male-only**	**Mixed**	**Male + Other**	**No male**
SS fruits	Forest	32.5	30	25	12.5
	Village	56.8	22.7	10.2	10.3
Mango	Forest	29.4	41.2	8.8	20.6
Rice	Combined	4.5	40.9	13.6	41
Maize	Combined	36.4	36.4	9.1	18.1
Cassava	Abandoned	35.7	21.4	7.1	35.8
	Guarded	21.1	47.4	15.8	15.7
Cacao	Forest	20	20	20	40
Oil-palm	Forest	3.7	51.9	18.5	25.9
	Village	37.5	25	25	12.5
Banana pith	Forest	27.3	15.9	11.4	45.4

6.3.2 Party spread and proximity

The mean daily spread of the party was compared when feeding arboreally and terrestrially (all guard levels combined). Party spread was significantly greater when feeding arboreally (means: 17.1 vs 15.1 m: $t_{141} = -2.20$, $p<0.05$). The same analysis was conducted for the proximity of nearest neighbour to the focal individual; the distance between individuals decreased when feeding terrestrially (7.1 vs 4.9m: $t_{147} = -5.74$, $p<0.001$). Bossou chimpanzees decrease the party spread and increase the proximity between individuals when feeding terrestrially.

As chimpanzees often transported raided food from where it was obtained arboreally to a terrestrial location, arboreal spread and proximity data were analysed in relation to guard level. Food that was 'supplied' was always provided terrestrially and within a restricted area, therefore this condition was not analysed. Spread and proximity data were compared for each day using a one-way ANOVA; however, as focal chimpanzees fed on both abandoned and raided foods on the same day on only two occasions, analyses comparing these two conditions were not possible. As can be seen from Figure 6.6, arboreal party spread was significantly greater when feeding on wild foods compared to raided foods ($t_{20} = 4.58$, $p<0.001$) and the chimpanzees maintained closer proximity when feeding on raided cultivars ($t_{24}=2.06$, $p<0.05$), although party sizes were slightly larger when raiding. In contrast, no significant differences existed when party spread (16.3m vs 18.4m: $t_{14} = -0.87$, ns) and proximity (6.5 vs 4.4m: $t_{15} = 1.79$, ns) were compared during arboreal wild and abandoned feeds. It is therefore unlikely that physical differences in wild and cultivated trees caused this effect.

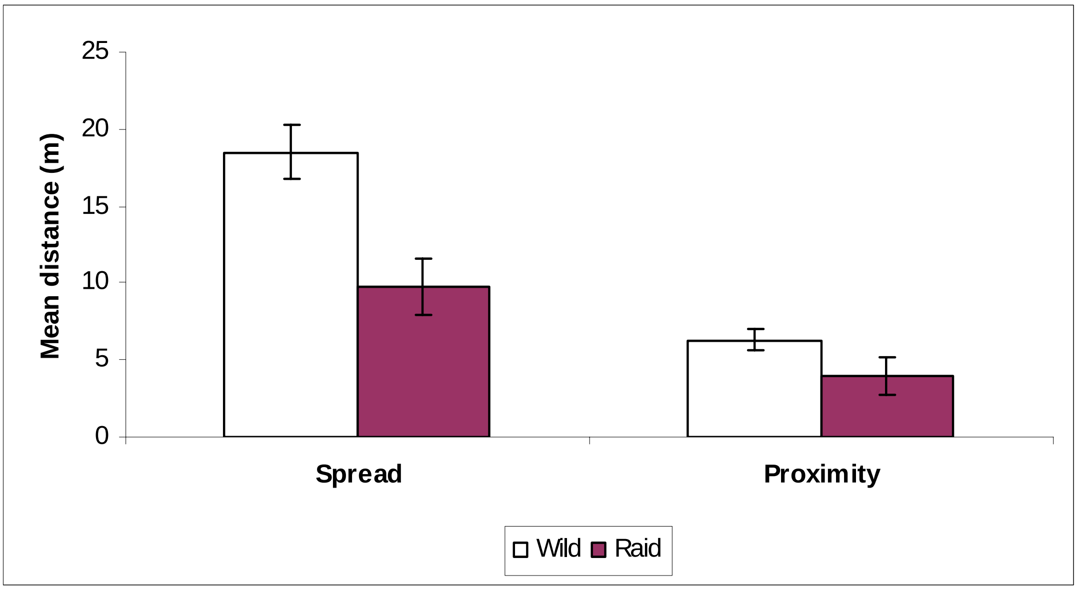


Figure 6.6. The mean party spread and proximity of nearest neighbour when feeding under arboreal wild and raided conditions.

6.3.3 Number of adult males

As sex differences in propensity to crop-raid have been established, only focal days with males were selected. To test whether the number of males present reduced the perceived cost of raiding, raid and wild conditions were compared. There were significant differences between the proportion of feeding time devoted to wild feeds and raids in relation to the number of males present ($X^2(2) = 13.01$, $p<0.001$); a single male spent significantly longer feeding on wild foods than raided foods, whereas when all three males were present, they spent significantly longer feeding on raided than wild foods. When all three adult males were together, 10.8 focal hours were spent feeding on cultivars, compared to only 4.2 hours for one adult male, and 5.8 hours for two adult males.

As can be seen in Figure 6.7, as the number of adult males in a raiding party increases, so does the amount of time feeding on cultivars in the presence of people (only including adult males; $X^2(2) = 13.01$, $p<0.001$). Also, when all three males were present in a raiding party, they spent much longer feeding on raided cultivars obtained further from the forest edge, than when one or two adult males were present (*one* male, mean: 6.9m, SD ± 1.1; *two* males, mean: 6.9m, SD ± 1.2; *three* males, mean: 18.3m, SD ± 4.9). However, the amount of feeding time on cultivars obtained from highly guarded areas was not affected by the number of adult males present ($X^2(2) = 1.42$, ns).

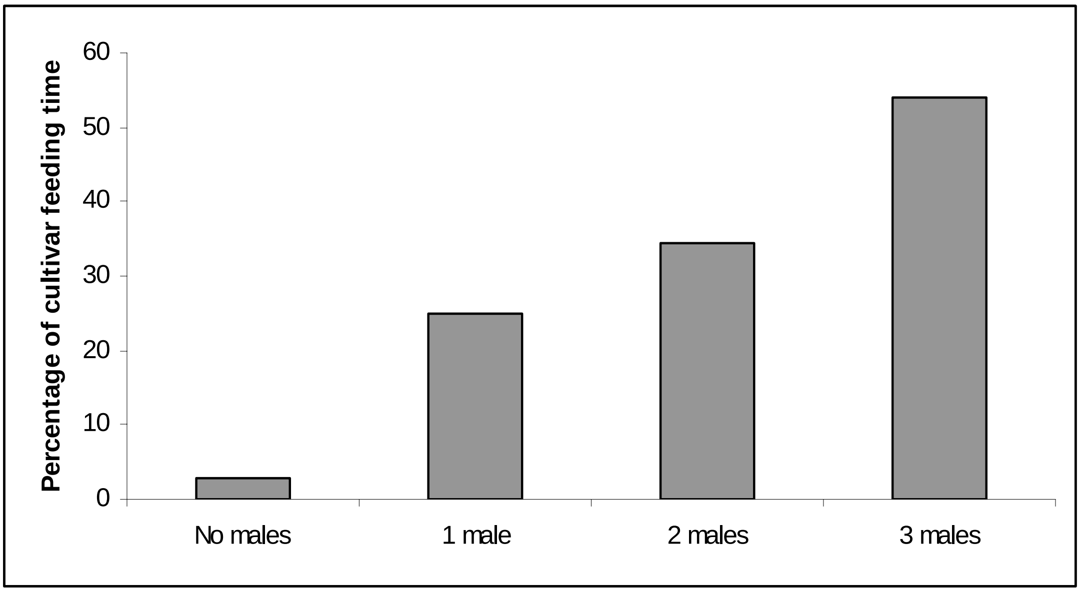


Figure 6.7. The percentage of focal crop-raid feeding time as a function of number of adult male chimpanzees whilst in the presence of humans.

6.3 Results: Behavioural adaptations to crop-raiding

6.3.4 Vocalisations

As chimpanzees vocalised significantly more when feeding on wild fruits compared to other wild food types ($X^2(1) = 167.80$, $p<0.001$), pant-hoot vocalisation frequency was calculated from all-occurrence feeding observations concerning fruits. Chimpanzees vocalise predominantly when arriving at a food source (Goodall, 1986). To eliminate any possible bias, feeding durations on wild and cultivated foods were compared: in a preliminary analysis, no significant difference was found between mean focal event duration for large fruit trees and fruit cultivars (Mann-Whitney U test, $Z = -1.48$, ns), Therefore when comparing wild and cultivar feeding, feeding events were used in analyses.

Wild and cultivated fruits

When feeding on wild fruits, the chimpanzees vocalised in 15% of feeding events (445 out of 3002 events). When only ‘large fruit trees’ were included, the vocalisation occurrence increased to 20%, which was significantly more than during fruit raids (all cultivated fruits included), when the chimpanzees vocalised during only 9% of events ($X^2(1) = 10.35$, $p<0.001$). Both sexes vocalised less in raid compared to wild feeding conditions, with females rarely vocalising when raiding (see Figure 6.8).

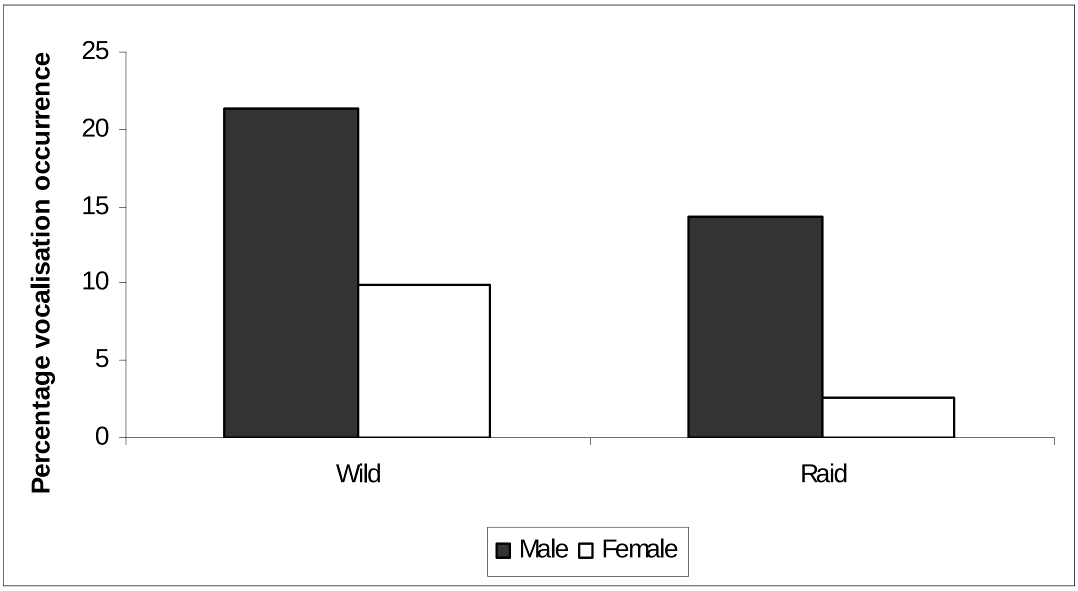


Figure 6.8. The percentage of events during which males and females vocalised during wild and raid fruit feeding situations.

Absence or occurrence of vocalisations during raiding bouts was analysed, since a vocalisation during any raiding bout would alert the farmers to the chimpanzees' presence. Chimpanzees vocalised during bouts of raiding for SS fruits, whereas they rarely vocalised when feeding on other cultivars (see Table 6.2).

Table 6.2. Frequency of crop-raiding bouts accompanied by vocalisations or not when feeding on different food parts; FT: fruit (SS) including Simple-Sugar, LF: leaf, PI: pith, TB: tuber. Frequencies were not included if multiple food parts were consumed during the same bout.

	VOCALISATION	
Food part	**No**	**Yes**
FT (SS)	130 (108)	23 (20)
LF	8	0
PI	51	0
TB	18	1

As almost all vocalisations whilst crop-raiding occurred during SS bouts, these were used in subsequent analyses. During SS raiding bouts, vocalisation was not affected by location ($X^2(1) = 2.16$, ns) or people presence ($X^2(1) = 3.06$, ns); chimpanzees did not significantly vary their vocalisation rates according to degree of risk. The association with number of adult males present and vocalisation absence or presence approached significance (see Figure 6.9; $X^2(3) = 6.72$, p=0.08): females and immatures never vocalised when adult males were absent, whereas vocalisation frequencies increased when two or three males were present during crop-raids. However, no effect of overall party size on vocalisation frequency was found (Mann Whitney, Z = -1.13, ns).

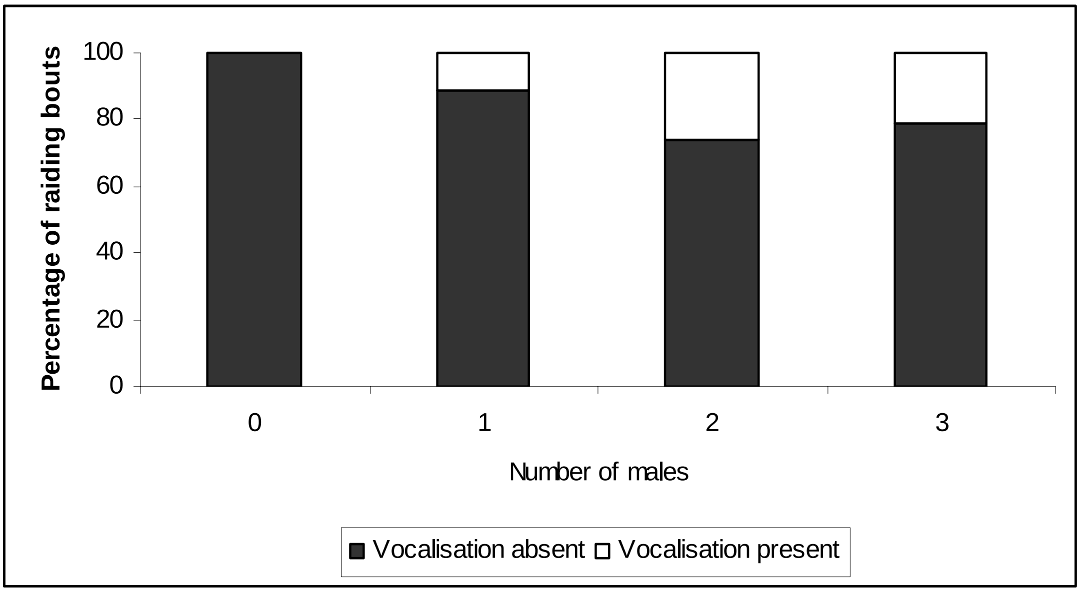


Figure 6.9. The presence or absence of vocalisations and the numbers of adult males present during SS-raiding bouts.

6.3.5 Transportation of foods

From focal data, food was transported during 40% of raid feeding duration compared with only 1.8% of wild feeding duration (see Table 6.3). Abandoned and supplied feeding conditions showed similarly low transportation frequencies compared to raid feeding samples. When chimpanzees transported food, it was mostly carried in one hand while the chimpanzee moved tripedally, but depending on the size of the food it was also transported in the mouth.

Table 6.3. The percentage of focal feeding duration during which food was transported or not transported from the tree or food patch.

	Transport food	
	No (%)	**Yes (%)**
Wild	98.2	1.8
Abandoned	99	1
Supplied	100	0
Raid	59.7	40.3

I used a one-way ANOVA to assess whether distance from forest edge influenced the transportation of raided cultivars (data taken from focal 5-minute samples). As can be seen from Figure 6.10, the chimpanzees were significantly more likely to transport cultivars that were located further from the forest edge ($F_{1,395} = 37.61$, $p<0.001$). However, both sexes were equally likely to transport raided cultivars ($X^2(1) = 1.64$, ns).

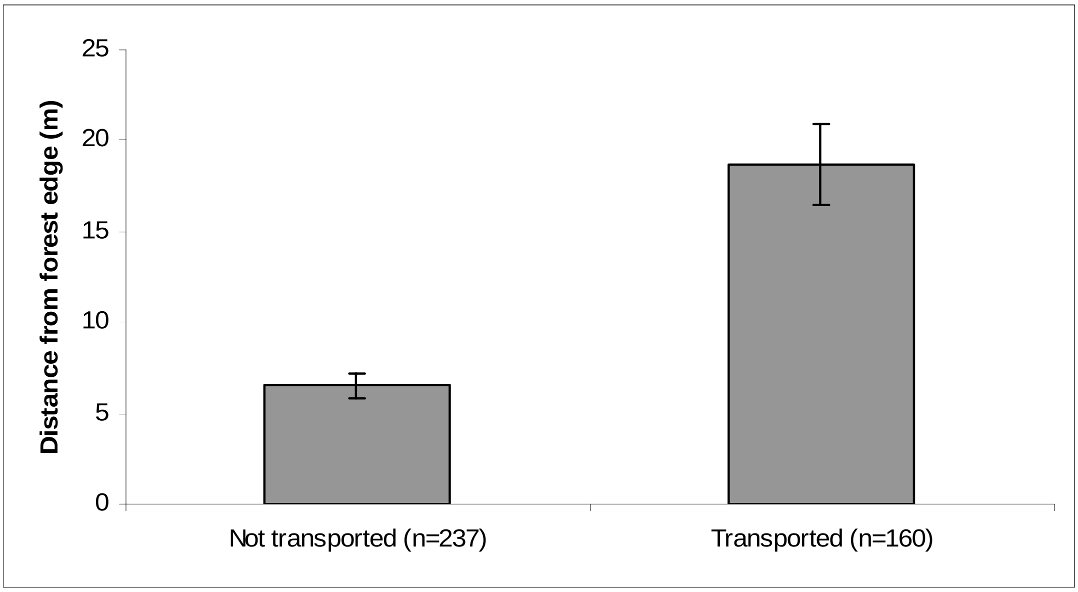
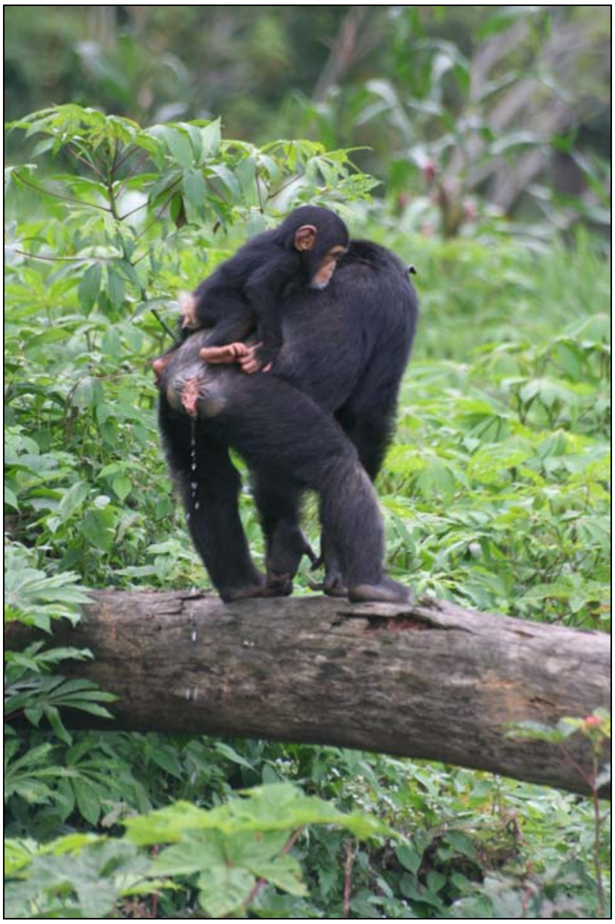


Figure 6.10. The mean distance of cultivars from the forest edge (m) that were transported or not transported.

6.3.6 Vigilance

Vigilance behaviours such as visual scanning when crop-raiding were difficult to distinguish quantitatively from vigilance behaviours within and around the forest itself. However, before or during raids, if the chimpanzees' field of observation was limited or an unexpected noise was heard, they would sometimes take-up an elevated position, either by climbing onto an elevated substrate or by standing bipedally, to scan the surrounding area. Chimpanzees were observed climbing to an elevated position on 7 occasions, 5 times on fallen logs in the cassava or maize field where the raid was taking place. On 5 out of the 7 occasions, vigilance behaviour was performed by females and juveniles when adult males were not present (see Plate 6.2). Bipedal standing was observed 9 times prior to and during crop-raids; males sometimes did this when they were raiding far from the forest edge. Bipedal standing was also observed 3 times during large road-crossings. However, bipedal standing was also seen during male displays, and sometimes when one individual located another individual nearby whose presence was obscured by vegetation.

Plate 6.2. Adult female with infant displaying climbing onto fallen tree in cassava field.



6.4 Discussion

6.4.1 Activity budgets

As hypothesised, cultivar consumption had a pervasive influence on the chimpanzees' activity budgets. During periods of wild fruit abundance, males spent more time resting on days when cultivars were consumed than when they were not; abundant and spatially concentrated cultivars contributed to an increase in proportion of time spent resting by males. However, contrary to predictions, when cultivars were consumed, both sexes spent a greater proportion of their day feeding and moving. From this finding alone, it is not possible to confirm whether chimpanzees travelled further to feed on cultivars or as a result of increased energy due to cultivar consumption. However, the GPS maps suggest that chimpanzees travel repeatedly to the same cultivated areas during periods of wild fruit scarcity. The chimpanzees' core feeding areas did not vary greatly according to wild fruit availability, and were focussed at the summits of Mont Gban and Guein. This raises some interesting questions regarding the use of mental maps by chimpanzees. Bates (2005) showed that chimpanzees at the Budongo Forest were more likely to travel further to crop-raid sugarcane than to any other resource, suggesting spatial knowledge of their environment. Using cultivars to evaluate whether chimpanzees employ mental representations of space to plan and direct their daily foraging routes poses an interesting line of future enquiry. It would also be interesting to test whether chimpanzees consume higher quantities of cultivars and alter their activity budgets during consortships as a function of higher cultivar density, less wild food, and changes in party composition.

Both sexes equally consumed wild fallback foods in response to food shortages; however males used cultivars to supplement theses fallback foods to a greater extent. Despite this sex difference, there was no evidence that the chimpanzees of Bossou altered their activity budgets in response to prolonged food shortage. Instead, they adapted their activity budgets to include cultivars as part of their ecological strategy.

6.4.2 Party formation

Party size and composition were affected by a complex interplay of ecological and social factors. There was no evidence that forest fruit availability overall dictated party size, although the smallest mean monthly party sizes were found during the low wild fruit availability season. However, party size was positively correlated with SS cultivar availability, highlighting the potential influence of cultivars on party size. Additionally, party size was reduced during consortship periods as group members left the core area, and increased when a female within the core area was maximally swollen.

Fluctuations in the size of temporary parties, particularly whilst feeding, should reflect variations in costs and benefits of group living. Following predictions, the Bossou chimpanzees formed slightly larger parties when feeding on raided compared to wild foods, presumably thereby increasing overall vigilance and the protective capability of the party. Wild conditions were possibly considered safer, particularly by females and immatures, who typically fed in smaller parties; this also reduced potential feeding competition. As cultivated foods were mostly found at high densities, feeding competition when crop-raiding was less likely to dictate party size, whereas degree of risk from secondary factors was probably more influential.

Party compositions during crop-raids varied depending on secondary factors associated with specific cultivars. Certain secondary factors, including location and people presence, influenced the degree of risk associated with raiding due to increased exposure and risk of human confrontation, and had pervasive effects on individuals' initiation of crop-raiding. In general, male-only parties were more common when the degree of risk increased, suggesting a perception of the need for greater security, whereas females and immatures rarely raided in exposed areas in the absence of an adult male. More specifically, SS fruit-raiding by adult male-only parties was associated with greater exposure and risk: male-only parties were again more likely than other party compositions to raid in the village, to take more risks by raiding further from the forest edge, and raid in more highly guarded situations. Interestingly, in a comparison restricted to forested locations, a higher proportion of 'no-male' parties were found feeding on abandoned mango fruits compared to raided SS fruits. Males and females also exploited oil-palm differently; females fed mostly from supplied sources which had no associated risks (even though the supplied period fell in the period of wild fruit abundance), whilst males fed relatively more on higher-risk, raided trees.

The spread of the party and the proximity of nearest neighbour give some indication of the cohesiveness of parties in various feeding conditions. The chimpanzees reduced party spread and increased proximity when feeding terrestrially, suggesting that either they felt more vulnerable when feeding terrestrially, or feeding competition was relaxed when consuming terrestrial foods such as THV. The chimpanzees also showed reduced party spread and remained closer to their nearest neighbour when feeding on raided rather than wild foods; however, such patterns did not exist when comparing party spread and proximity when using wild and abandoned food sources.

Lehmann and Boesch (2004) showed that over a period of ten years, a decrease in the community size of the chimpanzees of Tai led to increased party cohesion. The cohesive nature of the Bossou chimpanzees, as proposed by Sugiyama and Koman (1979), may be a result of the small community size and high proximity to the village, with corresponding repeated exposure to human confrontation.

A positive association existed between the number of adult males and the proportion of time that they spent feeding on raided compared to wild foods. When all three males were present, a significantly greater proportion of time was spent feeding on raided foods. Conversely, when only one or two males were present, more time was spent feeding on wild foods. The absolute focal feeding time devoted to raided cultivars was also greater when all three males were present. Additionally, as the number of males in a raiding party increased, so did the likelihood that they would raid in the presence of people and further from the forest edge. The perceived risk associated with crop-raiding may have been reduced by having more adult males present, and the presence of cooperative partners may have increased the readiness to crop-raid. Although there is some debate over the extent to which male chimpanzees hunt cooperatively (Boesch and Boesch-Achermann, 2000; Mitani and Watts, 2001; Gilby, 2006), it is worth remembering that they may decide to hunt for social as well as simple energetic reasons (Teleki, 1973; Mitani and Watts, 2001). Crop-raiding certainly provides energetic benefits, but as has been proposed for hunting, it can also provide males with opportunities to ‘show off’ their boldness (Teleki, 1973; Stevens and Gilby, 2004), especially when other individuals get access to some of the food (see Chapter 6 – Part Two).

6.4.3 Behaviours associated with crop-raiding

As the conversion of forested habitats to agricultural fields continues; the potential for the acquisition and propagation of new feeding habits within primate populations increases (Takasaki 1983). In the case of the Bossou chimpanzees, such adaptation includes behaviours to cope with the risks associated with crop-raiding.

Chimpanzees may suppress vocalisations as a tactic to avoid detection by predators and other chimpanzees (Wilson et al., 2001). The Bossou chimpanzees vocalised less frequently when feeding on raided fruits compared to wild fruits, with females showing the greatest reduction; this is consistent with females being more afraid than males when raiding. The chimpanzees vocalised relatively more when feeding on SS cultivars and their vocalisation rates did not vary with the risk of raiding. In accordance with past research (Clark, 1993), adult males were the most vocal, especially when crop-raiding. Studies suggest that male pant-hoot vocalisations are directed to particular audiences within their social group specifically to maintain contact, and to recruit allies and associates (Mitani & Nishida, 1993). Adult males were less likely to crop-raid alone, but when they did, they were more likely to remain quiet; vocalisation rates increased when two or three males were present during crop-raids. Adult males may simply be more confident when other males are present. However, other chimpanzee communities reportedly use pant-hoots to advertise the presence of large parties in an effort to deter approach by extragroup chimpanzees (Nishida et al., 1985). It is possible that the Bossou adult males may be promoting their presence in an area, and intimidating human bystanders rather than other chimpanzees. The use of complex communicative behaviour in risky situations constitutes a compelling line of enquiry regarding cooperative networks in chimpanzees.

By transporting food from a risky environment to one of relative safety, the chimpanzees reduce the amount of time spent in an exposed area, and thus the likelihood of detection by people. When food was obtained in wild, abandoned and supplied conditions, it was rarely transported to another place for feeding. However, chimpanzees commonly transported raided foods back to the safety of the forest before feeding, especially when the cultivars were obtained at a greater distance from the forest edge. The Sonso community of chimpanzees at Budongo also exhibit this behaviour when raiding sugarcane (pers. obs.).

To facilitate detection of potential risks in fields or farms when crop-raiding, the Bossou chimpanzees often visually scanned the surrounding areas intently before entering. As the chimpanzees' forest is located on hills, they are already in an elevated position to scan potential cultivars in the village. It would be interesting to examine how chimpanzees might use their environment to their advantage when entering fields and orchards within the forest. Scanning behaviours were sometimes enhanced by taking up bipedal and elevated positions. In contrast, bipedal standing within the forest was less frequent than in the context of crop-raiding, and most occurrences were in a display context. Quantitative measures such as head turn rate would be useful for accurately determining the role of vigilance as a function of degree of risk.

In summary, the chimpanzees of Bossou crop-raided in larger parties with protective compositions, whilst also reducing the party spread and increasing proximity between individuals. They also vocalised less, showed more food transportation and showed specific vigilance behaviours when crop-raiding. Analysing how chimpanzees adapt their social organisation and behaviours when exploiting different environments bolsters our understanding of why chimpanzees make such successful crop-raiders.

Chapter 6-
Part Two

Chimpanzees Share Forbidden Fruit

Chimpanzees Share Forbidden Fruit

6.5 Introduction

Food sharing has important implications for the evolution of cooperation, offering a means to evaluate the ‘paradox’ of altruism, whereby a recipient gains fitness benefits at the expense of a donor (Stevens and Gilby, 2004). Dunbar (1998) proposed that the increase in the size of the primate neocortex came about as a result of challenges requiring social intelligence. When individuals control a highly valued resource, there are plenty of opportunities to use that resource as a manipulative tool. Thus, even acts that appear altruistic may serve to additionally enhance one’s own fitness.

Food sharing is observed throughout the animal kingdom, albeit at varying complexities. In humans, food sharing plays a fundamental role in the organisation of traditional hunter-gatherer societies (Kaplan and Gurven, 2005; Wood, 2006); collected plant foods are generally shared with family members, whereas meat is characteristically shared with all members of the group (Silk, 2005). Hill and Hawkes (1983) showed that the sharing of meat in a hunter-gatherer society in Paraguay was part of a male’s mating and political strategy, in addition to straightforward nutritional benefits. Nonhuman primates infrequently share food out of the parent-offspring context (Feistner and McGrew, 1989); however chimpanzees provide an exception to this rule, exhibiting universal and complex food sharing behaviours (Teleki, 1973; Boesch and Boesch-Achermann, 2000; de Waal, 1989). Chimpanzees habitually share wild plant foods (Goodall, 1986; McGrew, 1996; Nakamura and Itoh, 2001), albeit at low rates, whereas, within chimpanzee communities that engage in hunting (considered a high-risk activity), meat is frequently used as a ‘social tool’ whereby alliances and affiliative relationships are cemented by gifts of meat (Mitani and Watts, 2001; Stanford, 2001). The distribution of meat in such situations is not always peaceful, and can often result in high levels of aggression (Kawanaka, 1982).

Chimpanzees may have different sharing strategies depending upon their rank. Long-term data from Mahale suggests that alpha males use meat sharing as a coalition strategy, never sharing with potential rivals such as beta and younger adult males (Nishida et al., 1992). The sharing of provisioned bananas was non-randomly dispersed between chimpanzees at Gombe. McGrew (1975) found that in 88% of non-kin sharing cases of provisioned bananas, the recipient was younger, disproving the simple explanation that adult males received food due to their dominance. Adult males predominantly shared with adult females, and male generosity was strongly correlated with aspects of female socio-sexual behaviour. In support of this, Gilby (2006) showed that a male's relationship with a female may affect his readiness to share meat with her; regular grooming partners tended to receive more meat. In chimpanzees, the 'meat-for-sex' hypothesis suggests that males share meat, either to gain immediate access to swollen females (Goodall, 1986; Stanford, 1998) or to establish an affiliative relationship with females, for increasing mating opportunities during future sexual cycles (Tutin, 1979). Additionally, as meat is energetically costly and risky to acquire for chimpanzees, sharing with others may advertise an individual's strength and prowess (Boesch, 1994), and simply possessing a desirable item may draw positive attention to an individual, enhancing its social status (Teleki, 1973; de Waal, 2000).

The social and political components of meat sharing in chimpanzees have led to insights into the evolutionary basis of human food sharing. As the majority of chimpanzees' diets consist of plant foods, it has been argued that plant food sharing is phylogenetically older and of more ecological importance than meat sharing (McGrew, 1975; Kuroda, 1984). However, until now data on the sharing behaviours of high-risk plant foods have been lacking.

Cognitively complex hypotheses to explain food sharing behaviours by donors, such as status enhancement, are difficult to test. Stevens and Gilby (2004) have underlined the importance of eliminating simpler explanations, such as harassment, prior to drawing higher-level conclusions; during meat-sharing, begging often appears aggressive and costly to meat possessors, who may be ‘forced’ to share (Gilby, 2006). Categorising non-kin food sharing according to the currency units of sharing, and the latency between sharing and the receipt of consequent benefits, may help to understand such behaviours (Stevens and Gilby, 2004).

When examining cases of food sharing, it is probable that various kinds of benefits occur simultaneously to shape the behaviour, with simpler mechanisms instigating sharing, which in turn promote the evolution of more elaborate mechanisms (Stevens and Gilby, 2004). Such explanations of food sharing assume a nutritional currency from the donor to the recipient; this may be justified when the food concerned is of high nutritional content and otherwise difficult to obtain. When natural plant foods are shared, they tend to be large, divisible, nutritionally rich and scarce (Bethell et al., 2000; Slocombe and Newton-Fisher, 2005). Assuming diminishing returns, the costs of sharing will decrease as the package size of the resource increases; large package size may therefore be a significant predictor of sharing. However, Slocome and Newton-Fisher (2005) challenge this assumption, arguing that certain instances of food sharing can only be understood within the context of social dynamics.

The Bossou chimpanzees encounter vertebrate prey infrequently, and hunting is almost never observed in this population (Sugiyama, 2004); crop-raiding may be viewed as a broadly comparable high-risk behaviour. Temporal variations in forest fruit availability have been recognised as a driving force behind rates of raiding certain cultivars, providing answers to questions such as ‘Why do chimpanzees crop-raid?’ (see Chapter 5). This chapter will explore observed patterns of food sharing, mostly in the context of crop-raiding by the Bossou chimpanzees.

6.5.1 Hypotheses

(a) Food-for-sex: adult males preferentially share with

- maximally swollen females for immediate benefit
- females of reproductive age for delayed benefit.

(b) Status enhancement: adult males will share with dominant and influential individuals.

(c) Future cooperation: adult males share with other adult males.

(d) Harassment: individuals share more with individuals who harass/beg more.

6.6 Methods and analyses

Data on chimpanzee food sharing were collected opportunistically while studying other aspects of their behavioural ecology. The names of donors and recipients were always noted, and the same information was recorded as presented in the behavioural observations section of Chapter 3.

Definitions: Begging, harassment and sharing

Begging: Any chimpanzee that approached within approximately 3 m of the possessor, but did not restrict the possessor's movement. This definition includes sitting and staring at the possessor or the food, and hold-out-hand gestures towards, but not touching, the food and/or possessor.

Harassment: Acts that restrict the possessor's movement. This definition includes touching the possessor, or placing a hand directly over the possessor's mouth, in addition to aggressive interactions (Gilby, 2006).

Sharing: "If an individual can defend a food item but allows another individual to consume part of that item it is considered to be sharing" (Stevens and Gilby, 2004, p.603). It was classified as active sharing if the food was relinquished from the mouth of the possessor, or the food was handed from the possessor to the beggar. In all cases, for 'sharing' to be recorded, it is important that the sharing individual is holding the food item when sharing takes place.

Observations

Data on plant food sharing were collected throughout the 12-month study. The data were supplemented by T.Humle, another researcher at Bossou, from observations conducted between February 2003 and December 2005. Data from Humle and KH are combined for all analyses on plant food sharing unless otherwise stated.

Sharing of wild foods between mother and infant were not recorded, as the close proximity between mother and infant made it difficult to accurately record the frequency of these events. Additionally, during feeding on wild foods, individuals tend to be more spread out than during crop-raiding, increasing the difficulty of detecting food transfers. However, all observed transfers of items of wild food between adults, both related and unrelated, were always noted.

Females were classified as being (1) of reproductive age, and (2) cycling: of reproductive age with no dependent infants. Maximally swollen females were identified by their sexual swelling and the fact that they were sexually receptive to, and mated with, adult males.

Food sharing and grooming rates

To evaluate temporal variations in food sharing, food sharing rates were calculated: monthly food sharing event frequency was divided by the total monthly chimpanzee observation time. When binomial tests were conducted, the test proportions were adjusted appropriately. Grooming rates were calculated by dividing the focal grooming frequency (mins) by the focal observation time (mins).

6.7 Results

6.7.1 Foods shared by chimpanzees

A total of 59 food sharing events (excluding transfers of wild foods from mother to infant) were observed, although no active sharing was observed. This total included only one instance of wild food sharing, which concerned the transfer of a *Ficus exasperata* leaf from an adult male to his mother. As can be seen in Table 6.4, 47 out of the remaining 58 sharing events involved the transfer of fruits, 36 of these involving the transfer of papaya (binomial: $p<0.001$).

Table 6.4. The cultivated foods and parts transferred during sharing events (n=58; wild food transfer excluded). FT (fruit), LF (leaf), PI (pith), TB (tuber) and WT (woody tissue).

	FT	LF	PI	TB	WT
Papaya	36	3	0	0	4
Orange	5	0	0	0	0
Pineapple	3	0	0	0	0
Cassava	0	0	0	3	0
Cacao	2	0	0	0	0
Maize	1	0	0	0	0

6.7.2 Occurrence of food sharing

To avoid seasonal observation biases, only food sharing rates monitored by KH during the 12-month study were correlated against wild fruit availability. Even though simple-sugar fruits were raided by chimpanzees particularly in response to wild fruit scarcity (see Chapter 5), there was no correlation between wild fruit availability and food sharing rates (r_s= 0.008, n=12, ns). However, as simple-sugar fruit cultivars were the predominant food shared during the 12-month period, simple-sugar fruit availability was tested against food sharing rates. There was a strong positive relationship (r_s= 0.711, n=12, $p<0.01$).

From data collected by myself over the 12-month study period, cultivars were shared in 2.3% of crop-raiding events (18 out of 786 events). However, as papaya was the predominant fruit shared, the percentage of papaya sharing events with respect to the overall frequency of papaya raids was analysed; this figure reached 11.5% (15 out of 130 events). This is consistent with the hypothesis that large and easily divisible foods are more often shared. However, pineapple fruit which is also large in size, but maybe not as easily divisible, was only shared on one occasion (1 out of 25 raids); this may be due to its relatively low temporal and spatial availability.

To establish whether cultivars were shared after particular high-risk crop-raiding situations, analyses from Chapter 6 were used and sharing data collected by KH were analysed. As crop-raiding behaviours of more fearful individuals may have been influenced by male presence, where appropriate, data on group compositions during crop-raiding bouts were analysed, rather than individual crop-raiding events. Male-only parties were significantly more likely to crop-raid in the village than were other group compositions ($X^2(1) = 10.98$, $p<0.001$). Males also travelled significantly further from the forest edge to crop-raid simple-sugar fruits than other group members (Mann-Whitney U-test; $Z = -3.711$, $p<0.001$). When adult males were not present, females and young were significantly less likely to crop-raid simple-sugar fruits in the presence of people compared to when people were absent ($X^2(1) = 6.97$, $p<0.01$).

Sharing was significantly more likely to occur after crop-raids in the village than the forest (18 vs 0 events; X^2 (1) = 9.54, $p<0.01$), and when cultivars were obtained at a greater distance from the forest edge (see Figure 6.11; Mann-Whitney U-test; $Z = -3.559$, $p<0.001$). Sharing was also more likely to occur after a crop-raid when people were present when the crop-raiding took place (12 vs 6 events; X^2 (1) = 5.99, $p<0.05$).

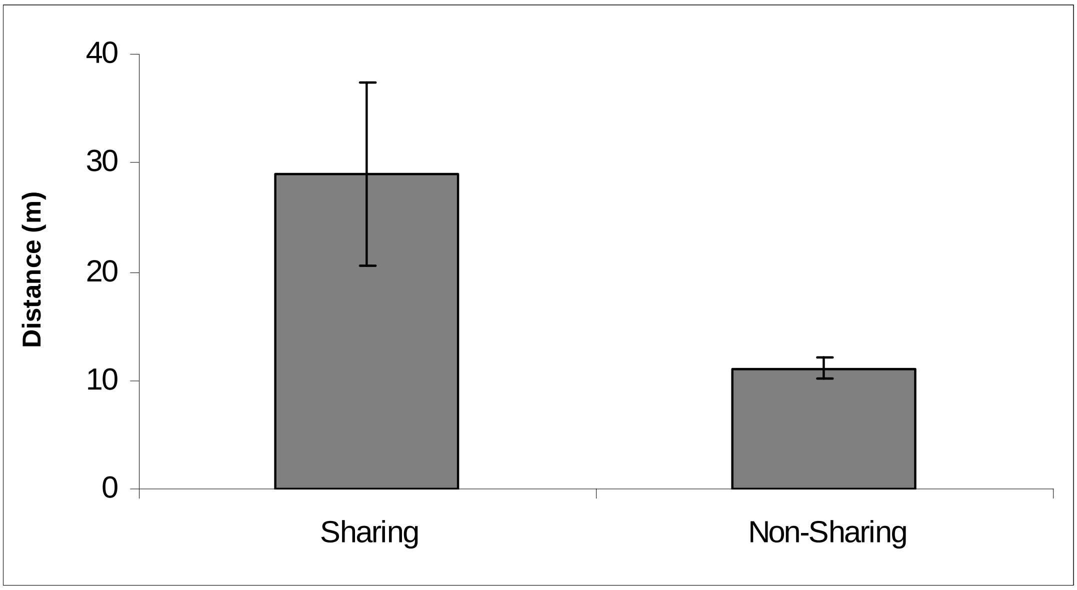


Figure 6.11. The mean distance from the forest edge during sharing and non-sharing events.

6.7.3 Who shares with whom

The main focus of the results section is on food sharing not involving mother-offspring dyads. Food exchanges between kin are only briefly discussed, as sharing behaviour between related individuals has obvious evolutionary advantages in the context of kin selection. Due to the patriarchal nature of chimpanzee society, adult males can be assumed to be related to each other along with infants and juveniles. The Bossou chimpanzee community is very small and each adult male has at some stage held the alpha position. Therefore, the overall relatedness between adult males and young is probably higher than in other communities and food exchanges between adult males and young can be explained in terms of kin selection.

Figure 6.12 summarises the cultivar sharing data. A total of 15 food sharing events were observed in the direction mother to offspring, and 5 from offspring to mother (combined in Figure 6.12). The sharing offspring were adult in 4 out of the 5 sharing events (an adult female ‘Jr’ shared with her elderly mother ‘Kai’ on 1 occasion, and adult males shared with their mothers on 3 occasions: 2 sharing events occurred from ‘YL’ to ‘Yo’, and 1 event from ‘FF’ to ‘Fn’), however there was also one recorded instance of a juvenile ‘PE’ sharing with his mother ‘Pm’. Additionally, 9 transfers were from adult males to immatures, 2 were from adult females to related immatures (non-offspring), and 1 was from an adult female to an unrelated immature. As papaya fruit was the most frequently shared cultivar, male success rate for papaya raids was calculated. In over a third of all raids involving multiple males, at least one male failed to secure a fruit. Despite this, only one instance of an adult male sharing food with another adult male was recorded: the woody tissue from a papaya tree was transferred from ‘TA’ to ‘FF’. Notably, 42.4% of all food transfers were from adult males to unrelated adult females; this increased to 65.8% when mother-offspring and offspring-mother transfers were excluded from analyses.

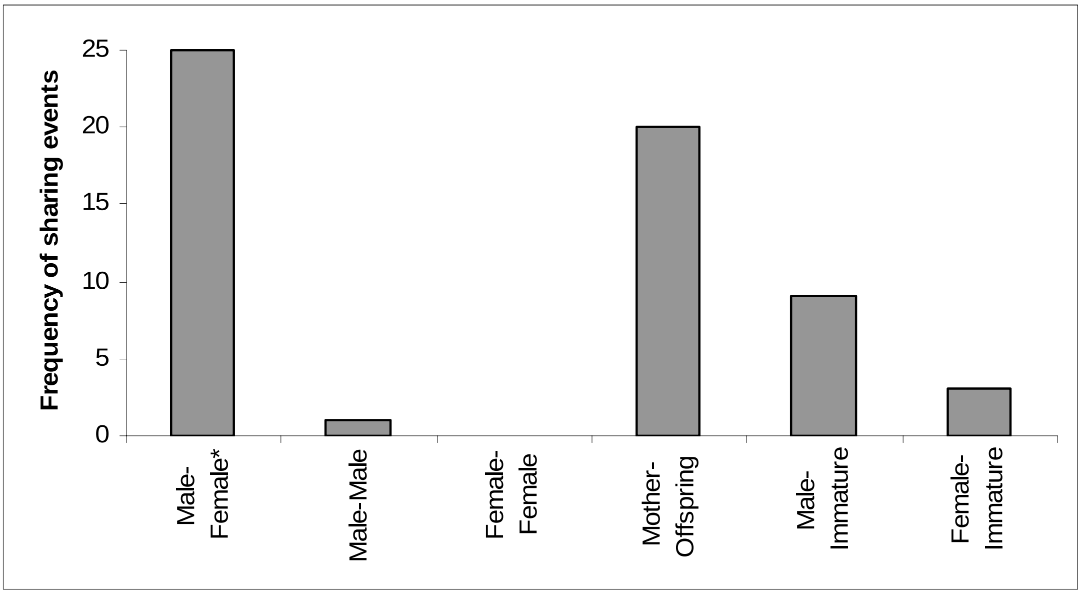


Figure 6.12. Age/sex classes of food sharing dyads. * indicates sharing between unrelated individuals. Offspring are of any age, 'male' or 'female' always refers to adult individuals, and 'immature' refers to infants or juveniles.

Mating never occurred during any crop-raiding observations, and when adult males shared with adult females, they did not show any preference for sharing with maximally swollen females; such sharing behaviours were only observed in 16% of cases. From data collected by KH, no significant difference existed between the likelihood of reproductively cycling or non-cycling females being present during papaya raids ($X^2(1) = 1.63$, ns). Additionally, presence (instead of number) of females of reproductive age, and presence of cycling females during the sharing events was considered using binomial analyses to ensure that sharing behaviour was not a result of increased association with males. Adult males were significantly more likely to share with females of reproductive age than with females of non-reproductive age (23 out of 25 events; binomial, $p<0.001$), and with cycling females then non-cycling females (18 out of 25 events, binomial; $p<0.001$).

Both the overall frequency at which adult males shared with an adult female and the overall rate that adult males shared with a particular adult female as a function of her presence during sharing events were calculated from data collected by KH (see Table 6.5). Males preferentially shared with one cycling adult female named ‘Pm’, who received food from all three males; both sharing frequency (n=8 from data collected by myself, and n=14 from total data) and rate were greater than observed for other females (see Table 6.5). ‘Fn’, the only other cycling female, received food at a greater rate than non-cycling females when her overall presence during sharing bouts was considered. Both elderly non-cycling females, ‘Yo’ and ‘Vl’, received the lowest frequency and rates of food from the males.

To explore whether certain females were socially ‘preferred’, the ratio at which each female was groomed by an adult male was analysed from focal data collected by KH (see Table 6.5). ‘Pm’, who was the major recipient of food, was also groomed more than all the other females, and ‘Vl’, the female who never received food from any adult male, was groomed much less than the other females.

Table 6.5. The frequency and ratio (frequency of events/ frequency of events the female was present) of sharing, and grooming rate, from adult males to each adult female; * indicates cycling female.

	Share freq	Share rate	Groom rate
Pm*	8	47.1	0.058
Fn*	4	36.4	0.016
Jr	4	30.8	0.050
Yo	1	7.7	0.019
Vl	0	0	0.001

‘Pm’ consorted with the adult males more frequently than other females throughout the study, consorting with a male shortly after every sharing event; however the males’ consortship rates with ‘Pm’ did not show any relationship with their frequency of sharing with her (see Table 6.6). ‘Fn’ consorted only once after sharing, and ‘Jr’ never consorted with males; she was pregnant or lactating during all of the study period and was therefore not cycling.

Table 6.6. Recipient females of reproductive-age and the adult male donor of each sharing event, the total number of sharing events per dyad, and the female's next consort partner after the sharing event. Cases when the donor was also the consortship partner are noted. 'NO' is when no consortship behaviour occurred, and 'X' refers to a kin relationship. 'Yo', an adult female, was not included as she was too old to be cycling, and another elderly female, 'Vl', was never the recipient of any sharing. On two occasions, two males 'TA' and 'YL' consorted with 'Pm' together, and are recorded individually.

				CONSORT		
Recipient	**Donor**	**Sharing events**	**YL**	**FF**	**TA**	**NO**
Pm	**YL**	2	1	1	0	0
	FF	6	4	2	0	0
	TA	6	0	4	2	0
Fn	**TA**	4	0	X	1	3
Jr	**YL**	3	0	0	0	3
	FF	1	0	0	0	1
	TA	1	0	0	0	1

6.7.4 Harassment

Unlike descriptions of meat sharing, no aggressive interactions of any kind were observed during cultivar sharing. Begging occurred, and possessors never chased beggars away. In the context of meat-sharing, Gilby (2006) refers to 'begging clusters', which commonly give rise to sharing meat with multiple individuals. During cultivar-sharing, adult males were more likely to share with a single female rather than two females within the same crop-raiding bout; on 19 occasions an adult male shared with one adult female, whereas an adult male shared with 2 adult females on only 3 occasions. However, detailed data on begging persistence and intensity were not collected.

6.8 Discussion

In agreement with other studies on wild chimpanzee populations, chimpanzee adults at Bossou very rarely transferred wild plant food. Similar to meat, cultivated plant foods were shared much more frequently. This seems paradoxical from the standpoint of the sharer, as sharing wild foods should be less costly than cultivated foods, as there are additional risks to acquiring cultivars. Indeed, for a chimpanzee making a decision about whether to crop-raid, the cultivar’s nutritional value must be weighed against the cost of obtaining it, i.e. the risks of potential failure and human confrontation during raiding. As Chapter 5 illustrated, a decrease in wild fruit abundance was a strong contributing factor towards the highly seasonal nature of crop-raiding in chimpanzees. However, cultivars were not shared in response to wild fruit scarcity, but instead were shared when they were highly available.

Adult males showed a higher propensity to crop-raid in more ‘exposed’ situations than did females and young. Although crop-raiding can be assumed to have emerged in the repertoire primarily for nutritional reasons, the fact that it provides males with access to highly desirable food commodities raises another potential benefit. Being successful in certain ‘risky’ situations may afford males opportunities to ‘show off’ their boldness and prowess, thereby intimidating rivals or attracting potential mating partners (Stevens and Gilby, 2004).

Adult males preferentially shared food with adult females, but not with other males. Even though not all three males secured cultivars during all raids, they did not share food among themselves. Therefore, for males, cultivar sharing did not serve the goal to enhance cooperative raiding behaviours and thus reduce risks. In Mahale, meat sharing is important for establishing and maintaining long-term cooperative relationships between male chimpanzees although in Gombe no such reciprocal exchanges seem to exist (Nishida et al., 1992; McGrew, 1975). It seems plausible that males at different sites differ in their tendency to cooperate, and in their methods of cooperating with other males.

There was no evidence of sharing with maximally swollen females, and mating was never observed in the immediate context of sharing, although males did exhibit a tendency to share preferentially with cycling adult females. As females were less likely to raid cultivars, the transfer of cultivars from males to females presumably resulted in a non-food currency return benefit for the males. Gaining access to maximally swollen females is highly competitive for male chimpanzees, which may possibly limit sharing after raids. Sharing the fruits of risky ventures may be part of a male’s mating strategy to advertise his boldness and enhance affiliative relationships with valuable reproductively active females. Additionally, the adult males shared food with and groomed one female preferentially; this female was in turn more likely than the other females to consort with the males over the study period, suggesting female choice (Stumpf and Boesch, 2006).

Papaya, the largest simple-sugar fruit available to the chimpanzees, was shared more frequently than other cultivars; large fruit is easily divisible and there is enough to share and still satisfy one’s own needs. It has been hypothesised that the pursuit of large food packages (especially meat) in humans is very sex-biased and that men acquire large packages to show-off and garner attention from community-members (Kaplan and Gurven, 2005); this may also be applicable to chimpanzees. The payoffs to this attention presumably come in the form of status enhancement, and increased access to females. Long-term data are needed to establish whether sharing food with females can function to enhance a male’s status and reproductive fitness, or whether sharing is rank- or individual specific.

No aggressive interactions were observed during cultivar begging episodes, with begging consisting of an individual remaining in close proximity to the possessor, and alternating stares between the possessor and the food. On occasions, a beggar would try to elicit sharing by reaching out a hand (as described by Goodall, 1986; de Waal, 1989), but the possessor often ignored the begging individual with little sign of being harassed; in contrast to meat begging, cultivar begging appears to impose no energetic costs to the possessor. Additionally, multiple individuals tend to receive meat during meat sharing occasions (Teleki, 1973; Gilby, 2006), whereas cultivars were predominantly shared with only one individual. Therefore it is unlikely that levels of harassment, by all nearby members and by frequent female grooming partners, can explain sharing behaviours. McGrew (1996) noted that male-to-female sharing patterns cannot be coercive, as females are subordinate to males; males can select the situations when sharing will take place, and the individuals with whom they share.

6.8.1 Cultural implications

Cultural traditions are crucial to understanding many aspects of chimpanzee behaviour, with patterns of cultural diversity in food sharing behaviours observed from one wild chimpanzee population to the next. Stanford (2001, p.110) states that “meat provides social as well as political motivation for the hunter, among hunter-gatherers as well as chimpanzees. The Gombe chimpanzees are utterly nepotistic and Machiavellian in their use of the prey carcass; captors share mostly with their family members, allies and swollen females. In Tai, hunters receive a share of meat regardless of the captor if they have participated in the hunt”. The sharing of cultivated foods at Bossou is again different, with males predominantly sharing with reproductively active females. These studies emphasise the complexities of food sharing behaviours, and how they are influenced by a range of social and ecological factors. Additionally, a variety of vocal and gestural signals occur in meat sharing contexts (Feistner and McGrew, 1989); Goodall (1986) described how an individual requesting meat will stare intently, at close range, into the face of the meat-eater, and reach out to touch the meat or the face and mouth of the eater, often accompanying these gestures with a soft whimper or ‘hoo’ call. Although such signals were not systematically recorded during cultivar sharing episodes at Bossou, observations suggest that this is another aspect where both parallels and differences between sites and foods in begging behaviours may well exist.

Both human and chimpanzee males occupy influential positions in the context of obtaining, sharing and controlling resources. Advanced cognitive abilities come into play after the resource has been acquired (Stanford, 2001), as both males and females in both human and nonhuman primate societies have a strong vested interest in obtaining certain foods. Stanford (2001, p.117) proposes that “studying these differences leads us to many of the most interesting features of our humanity and of the origins of human cognition”. The raiding and sharing of cultivars appear to serve both nutritional and social purposes. Adult male chimpanzees at Bossou may habitually share cultivated plant foods as a display of boldness and prowess to other members of the group. Furthermore, they preferentially share these highly prized commodities with reproductively active females; this may be a strategy to improve affiliative relations and future mating success. When chimpanzee behaviours, such as food sharing, occur in such unusual situations as meat-hunting or crop-raiding, they allow us to better understand the evolution of complex food sharing behaviours in humans, and to hypothesise about how and when such changes may have occurred in our evolutionary history. The present data suggest that sharing difficult-to-obtain food items may have played a role as important as meat-sharing in the advancement of complex food sharing behaviours in hominoids.

Chapter 7

Roads, Raids and Risk

Study 1 of this chapter was published in *Current Biology* **16**, 668-670; see Appendix F

Roads, Raids and Risk

"I remember one strange encounter I had in the jungle. A troop of chimpanzees was crossing the jungle path ahead of me, an old male, the leader, stood glaring at us from a distance of a few paces. At intervals he intensified his gruntings to hurry up the rest of the troop, cursing the stragglers. The last chimpanzee to cross was a terrified female. Suddenly the big male gave a bound towards her, seized her and shook her and grunted at her something we could not interpret. Whatever it was, it forced her to turn back into the bush. She reappeared a moment later, and now, clinging to her back with both hands and feet, was a grimacing little baby chimpanzee, which in her terror she had abandoned. Then she leaped into the air with her baby in her arms and disappeared among the foliage of the trees. All was now in order, and the old male gave a couple of triumphant grunts, made a gesture as much to say that the path was free for me, and disappeared into the jungle, the last of his troop." Guillot, 1956, p.157.

This hunter's anecdotal report is largely anthropomorphic and likely to be somewhat embellished, but serves to highlight the protective nature of the adult male chimpanzee during this high-risk encounter.

7.1 Introduction

Regularities in spatial patterns are a well-known occurrence in the animal kingdom (Browns and Orians, 1970); for example during group movements monkeys reduce the risk of predatory attacks through adaptive spatial patterning. Although increased survival is their ultimate function, at a proximate level differences among age- and sex-classes in fear or confidence may result in non-random progression orders, whereby positioning will alter as a function of perceived or anticipated danger (DeVore and Washburn, 1963; Hall and DeVore, 1965; Altmann, 1979; Rhine and Westlund, 1981; Rhine et al., 1985; Waser, 1985; Rhine, 1986; Bicca-Marques and Calegaro-Marques, 1997).

Busse (1980) reported that the majority of lion attacks on baboons in Moremi Wildlife Reserve (Botswana) were from the direction in which the group was travelling. In this context it is noteworthy that adult males in several savannah baboon troops tend to move towards the front of the group during progressions, and to a lesser degree towards the rear (Rhine and Westlund, 1981). In adult male chacma baboons, their forward tendency increases when approaching a waterhole with potential predators, with their rearward tendency also increasing when retreating from a source of danger (Rhine, 1975; Rhine and Westlund, 1981; Rhine and Tilson, 1987). Similarly, during crop-raids, Priston (2005) noted that adult male Sulawesi macaques were more likely than other age- and sex-classes to lead the raids.

Individual-, age-, and sex-based trends in spatial organisation of black-and-gold howler monkey *(Alouatta caraya)* troop progressions indicate that adult males take up the protective positions (Bicca-Marques and Calegaro-Marques, 1997), and Waser (1985) reports that the socio-spatial progressions of the gray-cheeked mangabey *(Cercocebus albigena)* across canopy gaps strongly resembled that of baboons. In contrast, analyses of a single troop of mantled howler monkeys *(Alouatta palliata)* revealed that adult females occupied the first position during party progressions more frequently than troop composition would predict (Costello, 1991).

The interplay between risk and vulnerability can produce a complex set of adaptive behaviours (Miller and Treves, 2006). Given that adult males are usually the most physically powerful group members, they might be expected to be the most willing to enter unexplored areas (Hamilton, 1971). Therefore adult males should maintain or increase frontward positions in progressions when moving into potentially unsafe areas, but they should also be more rearward in progressions moving away from frightening or potentially dangerous situations (Rhine and Tilson, 1987). Adult females are expected to spread out less systematically within the travelling party, while the more fearful and vulnerable immature individuals are expected to keep other members of the party between themselves and potential danger.

Almost nothing is known about progression orders in chimpanzees. The chimpanzees of Bossou conform to the typical chimpanzee fission-fusion pattern (Nishida, 1968; Goodall, 1986, Matsuzawa, 2006). Sakura (1994) reported that the Bossou chimpanzees formed into parties that usually included the alpha male before crossing a road; this was interpreted as being due to heightened perceived risk. Additionally, it was reported that the first individual to visually scan and cross the road was nearly always the second-ranking male, not the alpha male (Matsuzawa and Sakura, 1988). According to Takemoto (2002) when presented with a fearful situation, chimpanzees' behavioural adaptations, including party formation, may be similar to their response to encounters with predators. However the limited data available on the effects of such situations on chimpanzee behaviour are inconclusive (Itani and Suzuki, 1967). The flexibility of responses by monkeys during progression orders highlights the possibility that individuals may be cooperating (defined as joint action for mutual benefit) to maximise party protection. If the Bossou chimpanzees are found to be cooperating during high-risk activities, it would have implications regarding the importance of altruistic behaviours, which are often difficult to observe in wild chimpanzee communities.

The Bossou chimpanzees often hesitate to cross roads due to wariness of people and the risk of injury from vehicles travelling at speed, but they frequently need to do so in order to access foraging sites in their relatively constrained home range. As discussed in Chapters 5 and 6, chimpanzees regularly engage in crop-raiding at Bossou, an activity which is associated with increased exposure to risk. Opportunities to test the fear hypothesis of progression orders are quite rare in wild primates because naturally occurring fearful events are usually difficult to anticipate or predict (Rhine and Tilson, 1987). However, road-crossing and crop-raiding both provide excellent opportunities to analyse this aspect of socio-spatial organisation.

7.1.2 Hypotheses

(1) Road-crossing

(a) The chimpanzees will wait longer when crossing a large road than a small road due to greater perceived risk, although this will vary according to changes in perceived risk.

(b) The chimpanzees will evaluate the risk when crossing roads, and will organise themselves flexibly to maximise party protection.

(2) Crop-raiding

(a) The adult male chimpanzees will increase their frontward presence when crop-raiding compared to when approaching abandoned cultivars.

7.2 Methods and analyses

Road-crossing

Location

The village of Bossou and the chimpanzees' home range are dissected by one large road (12m wide at the point where the chimpanzees usually cross) that stretches from the Guinea-Liberia border through into Guinea Forestière. This road was widened in December 2004 and is frequently used by large trucks, cars, motorbikes and pedestrians. A narrower dirt road (3m wide at the place where the chimpanzees tend usually cross) branches off from the large road; the smaller road is used mainly by pedestrians (see Figure 7.1 for map of Bossou and the two roads). The Bossou chimpanzees have to cross both roads regularly to reach foraging sites in their fragmented home range and typically cross at specific points that the group has used for decades (Matsuzawa and Sakura, 1988). Both roads have forest cover up to the edges, and are separated by a middle zone of secondary forest and coffee plantations that normally takes 2 to 3 minutes to cross; except for researchers and field assistants, people were never observed in this area during the study period. The chimpanzees cross going from west to east and from east to west. When moving from west to east they must pass from the forest of Gban, onto the large road, then into the middle zone, across the small road, to reach the forest of Guein; the reverse itinerary applies from east to west.

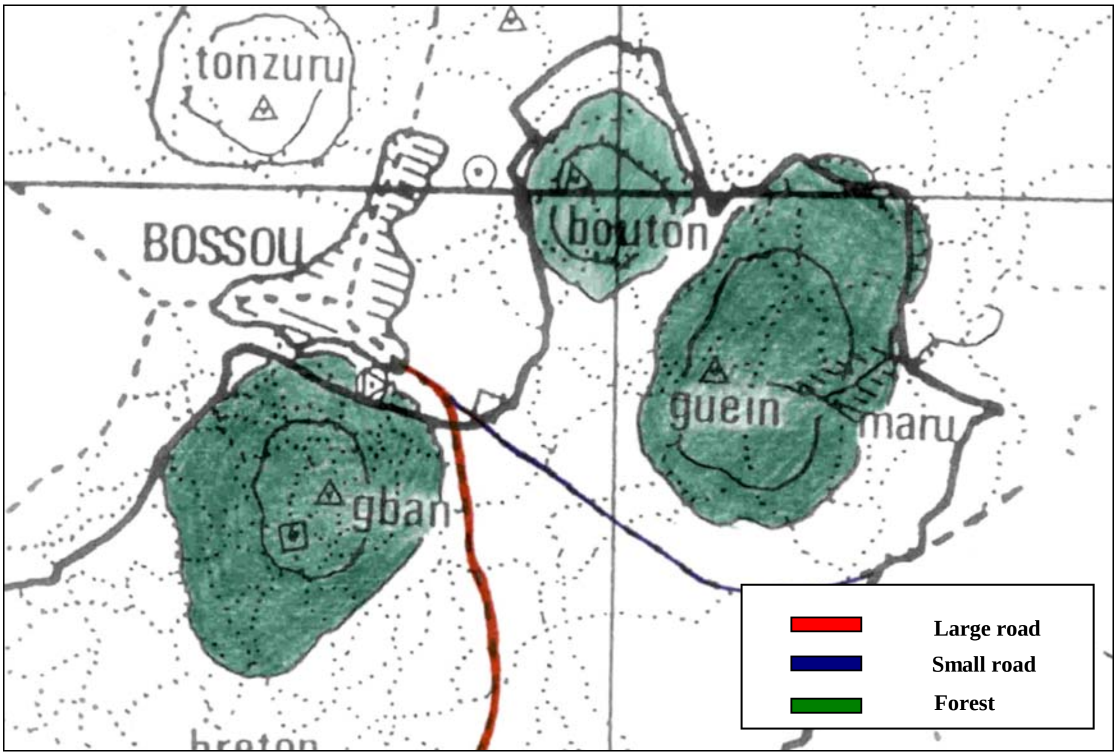


Figure 7.1. Map of Bossou showing the three main hills (forest) and the large and small roads (modified from map drawn by Yokota).

Study 1 was carried out between January and April 2005, and a follow-up study (Study 2) was carried out from November to December 2005 (approximately one year after the large road was widened). Throughout these study periods the community size remained at 12 individuals (including 3 adult males, 5 adult females, 3 juveniles and 1 infant; see Chapter 3 for details).

Procedure

Records were made of the order in which chimpanzees left the forest and moved onto the road. If an individual crossed back over the counting line (forest-road edge), it was counted only on the final progression. It was possible for chimpanzees to visually scan the road without crossing the counting line. Exact progression orders were simple to record as all individuals were well habituated and could be easily recognised as they crossed the open area, but if it was suspected that an individual was missed, that crossing event was not included in analysis. Only progressions at the chimpanzees' regular crossing points were recorded. I recorded the progression order from the counting line with one field assistant, with input from other field assistants when required. The first chimpanzee to scan the road was recorded as the *first individual to scan*. As scanning constituted an individual poking their head out of the forest to observe the road, identifying a scanning event was uncomplicated. This individual was not necessarily the first to cross the counting line. The latency between arrival of the first individual to scan and the last party-member to cross the forest-road edge was termed *waiting time.* Presence or absence (either auditory or visual) of humans and vehicles at each road-crossing event was also recorded. The field of observation was estimated for each road in both directions (east-west and west-east) where the chimpanzees left the forest and the middle zone; by taking up position just before the counting-line and measuring at chimpanzee eye-level the observable distance left and right along the road. These two distances were then summed. The frequency of pedestrians and vehicles present on both the roads from 0700h to 1829h were counted on three randomly selected non-market days and then averaged.

The expected frequency of being first to scan, cross, or being last to cross were calculated from the mean number of adult males per progression divided by the mean number of group members present (excluding the dependent infant).

Guarding behaviour was not included in the ethogram as it was not recorded in any situation other than road-crossing. In this chapter, guarding is defined as 'standing in a quadrupedal posture on the road for greater than 5 seconds without moving'.

Crop-raiding

Records were made of the first chimpanzee to enter the field or orchard. The counting line was defined as the edge of the forest to the field or orchard, and therefore changed depending on the location of the cultivar. Instances of chimpanzees visually scanning the field or orchard were not recorded due to observation difficulties from the back of the party. Also, the last individual to cross into the field or orchard was not recorded, as unlike road-crossing, crop-raiding was not obligatory and movements were often not in an easily observable progression line.

7.3 Results: Road-crossing, Study 1

7.3.1 Party waiting time

There were 19 combined road crossings where the party members remained the same when crossing the large road and then the small road; these were used to analyse the party waiting time. Waiting time was significantly longer before crossing the large road than the small road (see Figure 7.2; medians: 80 vs. 4 sec; Wilcoxon test: $T = 5$, $n=19$, $p<0.01$). The presence of people had no effect on party waiting time on the small road (Mann-Whitney U test: $Z = -0.168$, $n=19$, ns). In contrast, the presence of people ($Z = -2.059$, $n=19$, $p<0.05$) or vehicles ($Z = -2.043$, $n=19$, $p<0.01$) on the large road significantly increased party waiting times. As party size increased, so did party waiting times on both the small (Spearman rank correlation: $r_s= 0.702$, $n=19$, $p< 0.01$) and the large road ($r_s= 0.707$, $n=19$, $p<0.01$).

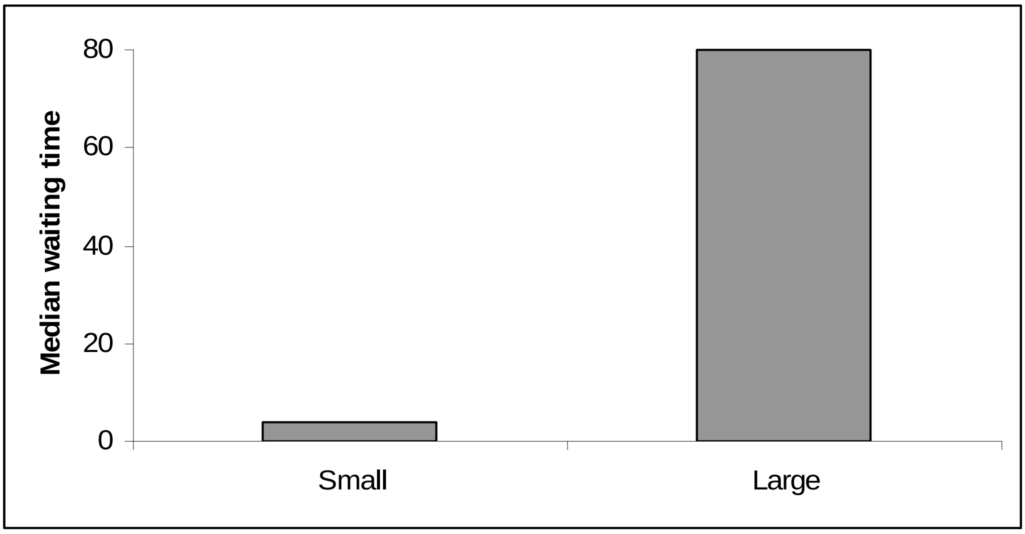


Figure 7.2. Median waiting times (seconds) on the small and large roads.

A significant effect of direction of travel emerged concerning the large road (Z = -2.083, n=19, $p<0.05$); the same effect for the small road approached significance (Z = -1.915, n=19, p= 0.06). When leaving the forest to move into more open areas, party waiting time increased. The field of observation for the small road was 67m when leaving the forest of Guein (east to west), and 30m when leaving the middle zone (west to east). The field of observation for the large road was much larger, 168m from both directions (from the forest or from the middle zone). Chimpanzees crossing times ranged from 0650 h through to 1740h (from either direction, and including all 94 crossings). Figure 7.3 shows that vehicle presence did not vary greatly throughout the day, but pedestrian numbers were lowest between 1030h and 1630h. However, there were two peaks in road-crossing times, the first from 0800h to 0930h when pedestrian numbers were high and an additional peak in road crossings from 1100h to 1330h when pedestrian numbers were low. This suggests that the chimpanzees did not always time their movements to avoid or reduce confrontation with humans.

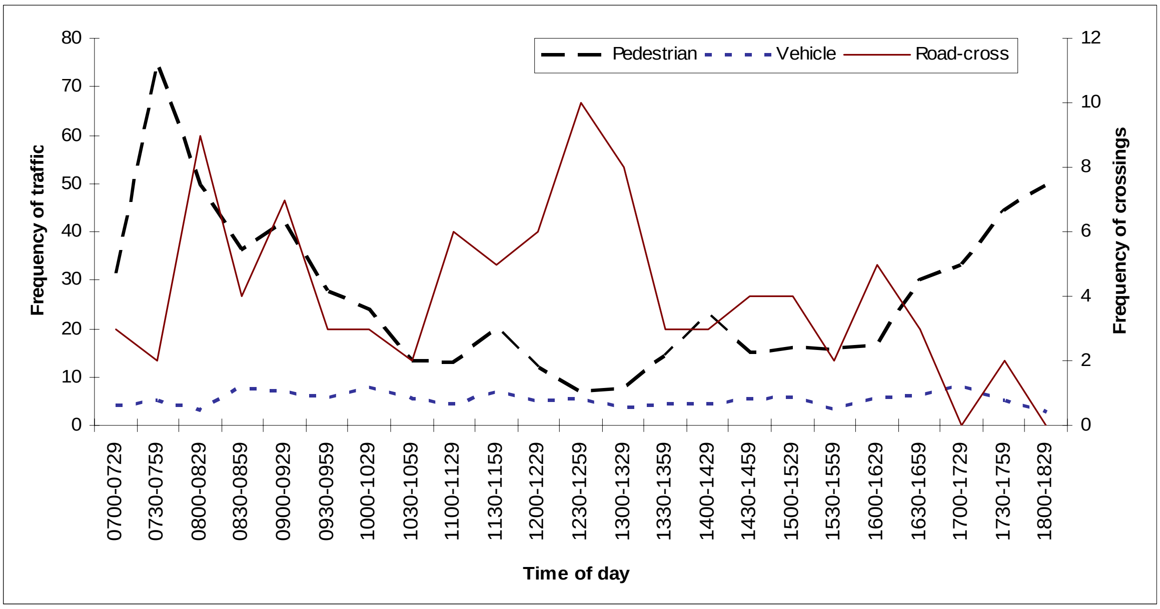


Figure 7.3. The frequency of pedestrian and vehicle traffic; both roads combined.

7.3.2 Party Composition

As described in Chapter 6, party compositions were divided into four types: male-only, mixed, male and other, and no-male. In total, 94 progression orders were recorded (50 on the large road and 44 on the small road). To analyse correctly the socio-spatial organisation of the party it was necessary to have a combination of age- and sex-classes, therefore only mixed-party progressions (at least one male, female and juvenile present) were included. When the alpha male was absent due to consortship, the frequency of mixed-party progressions decreased whereas adult male-only and male-plus-juvenile progressions increased. There was significant variation in the frequency of different party compositions when the alpha male was present, ($X^2(3) = 25.8$, $p<0.001$) but not when he was absent ($X^2(3) = 0.94$, ns). Therefore, analysis of road crossing progressions focused on 28 mixed-party progressions (17 small and 11 large road crossings), in which all three adult males were present (mean party size: 10.6 individuals, SD ± 2.1), and an additional 6 mixed-party large road progressions, where the alpha male and one other adult male were present (mean party size: 6.7 individuals, SD ± 1.5).

7.3.3 Progression order

Adult male chimpanzees led progressions across roads significantly more often than expected by party composition (Figure 7.4). An adult male was first to cross in 18 of the 28 progressions (binomial test: $p<0.001$). If the analysis is limited to adults of both sexes, the outcome is still highly significant (binomial: $p<0.005$). The first individual to scan the road was the first to cross in 88% of progressions: adult males were significantly more likely than chance to be the first to scan the road prior to crossing (binomial: $p<0.001$). However, the three males differed significantly in their frequency of being first to scan the road ($X^2(2) = 14.0$, $p<0.001$) and first to cross ($X^2(2) = 6.3$, $p<0.05$), with the second-ranking male being most likely to both scan and cross.

By comparison, adult males overall did not occupy the rearmost position more frequently than expected based on either total party composition (binomial: $p = 0.126$) or adult party composition (binomial: $p = 0.378$). As the second- and third-ranking adult males frequently led the progressions, the frequency of the alpha male being last was tested against party composition excluding the other two males; this was highly significant (binomial: $p<0.01$). The alpha male was also last in significantly more progressions than expected by adult party composition (binomial: $p<0.05$).

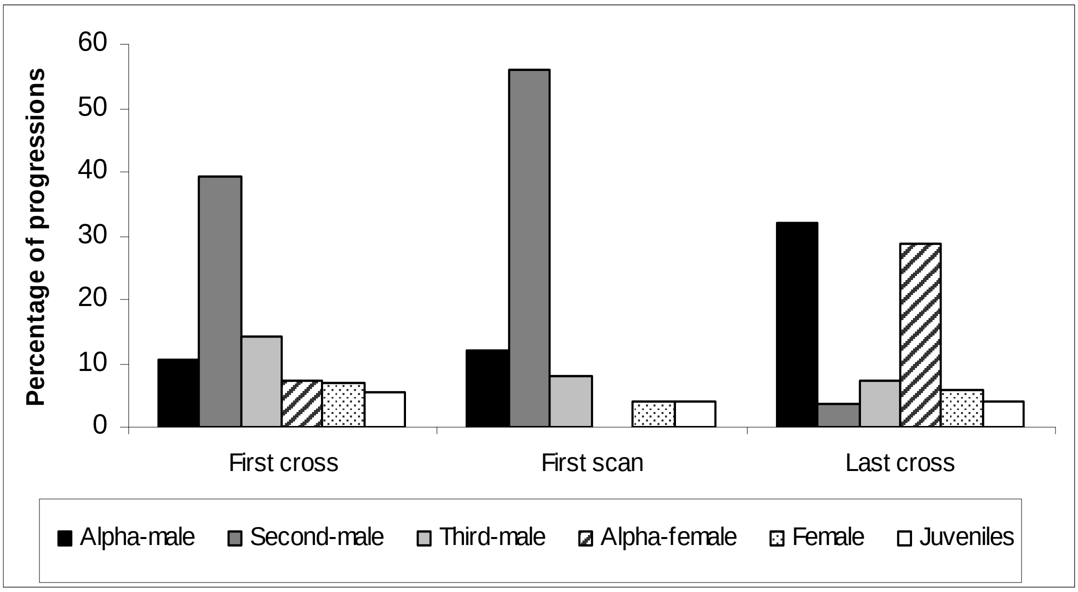


Figure 7.4. The percentages of progressions in which the three males, the alpha female (determined by the direction of pant grunts by other females) and the average non-alpha female and juvenile were first to cross, first to scan the road, and last in the progression; both roads combined.

There were too few observations for separate statistical analyses of progression orders on the two roads. The second-ranking male led in 52.9% of small road progressions, but this fell to 18.2% for large road progressions (Figure 7.5 (a)). The third-ranking male never led across the small road, but was first in 36.4% of the large road progressions. The alpha male led in a relatively low percentage of both small and large road progressions.

The second-ranking male was first to scan the small road in 52.9% of progressions; he also had the highest scanning score for the large road (45.5%, Figure 7.5 (b)). The third-ranking male was never first to scan before a progression across the small road, and he was the first to scan in only 18.2% of large road progressions. The alpha male was infrequently the first to scan on either road. The first individual to scan was the first to cross the small road in 100% of cases, compared to 70% for the large road. The second-ranking male was the first to scan on all occasions in which the first individual to scan did not become the first individual to cross.

The alpha male was last to cross in 23.5% of small road progressions; this increased to 45.5% for large road progressions (Figure 7.5 (c)). The second- and third-ranking males were infrequently last to cross either road. Each female (not including the alpha-female) was last for an average of 5.9% of small and 5.6% of large road progressions, and for each juvenile these percentages were similar (2.2% and 6.7% respectively). Interestingly, the alpha female was last in 41.2% of small road progressions, but in only 9.1% of large road progressions.

Additionally, when the alpha male was present in mixed-party progressions containing one other adult male (second-ranking male), he was first to scan and cross in 50% of large road-crossings and last in only 33%. This suggests that his rearward position at other times was not due to fear.

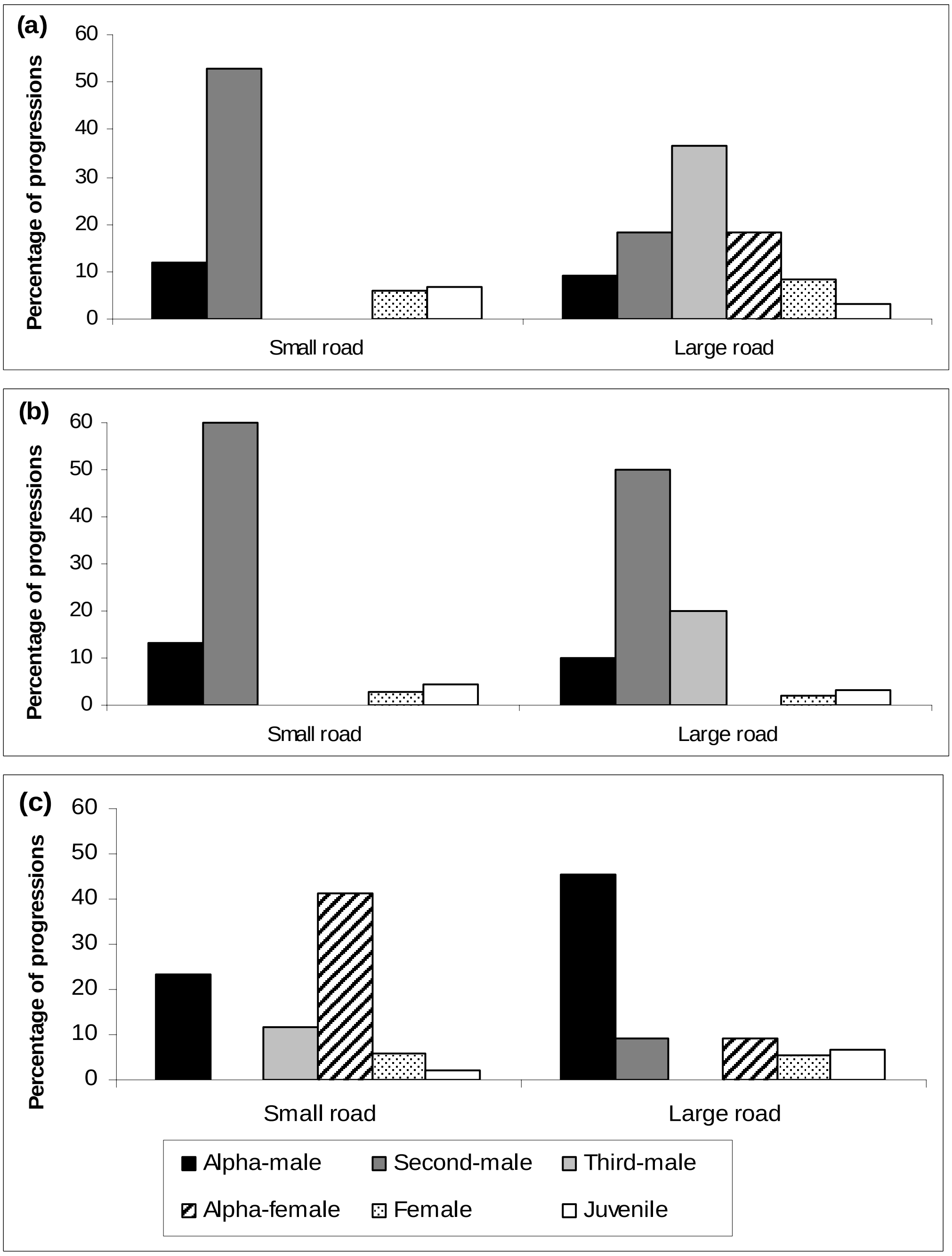


Figure 7.5. The percentages of Study 1 progressions in which the three males, the alpha female and the average non-alpha female and juvenile were (a) first to cross, (b) first to scan the road, and (c) last in the progression on the two roads.

7.3 Results: Road-crossing, Study 2

The second analysis of road-crossing progressions focused on the data from 25 mixed-party progressions (12 small and 13 large road crossings), in which all three adult males were present (mean party size: 8.6 individuals, SD ± 2.6).

7.3.4 Party waiting time

There were 9 combined road-crossings where the party members remained the same when crossing the large road and then the small road. Based on these events party waiting time remained significantly longer when crossing the large road (medians: 40 vs. 10 sec; Wilcoxon test: $T = 0$ $n=9$, $p<0.01$). Despite people being present during 8 out of the 9 large road crossings, the mean waiting time on the large road was much less than during Study 1 (40 vs 80 secs). It is possible that this difference is due to the absence of vehicles during large road crossings in Study 2. The effect of presence of people on waiting times was not analysed statistically due to the small number of samples.

7.3.5 Progression order

Consistent with Study 1, adult male chimpanzees led progressions across roads significantly more often than expected by party composition; an adult male was first to cross in 23 of the 25 progressions (binomial test: $p<0.001$). Adult males were also significantly more likely than chance to be the first to scan the road prior to crossing (binomial: $p<0.001$). Likewise, adult males did not occupy the rearmost position more frequently than expected. However, in contrast to the first study, the alpha male occupied the rear position in only 2 out of 25 road-crossing progressions.

For clarity, Figure 7.6 presents the data from Study 1 again alongside those from Study 2. The alpha male led in 33.3% of small road progressions, and this increased to 69.2% for large road progressions (Figure 7.6 (a), Study 2), whilst the second-ranking male led in 41.7% of small road crossings and 30.8% of the large road progressions. The third-ranking male led in a very low percentage of both small and large road progressions. The first individual to scan remained the first to cross the large road in 92.3% of progressions (Figure 7.6 (b), Study 2).

Similarly to Study 1, the alpha female was last in 41.7% of small road progressions, but in only 7.7% of large road progressions. The last position was taken by an adult male in 53.9% of progressions, which is again comparable to Study 1. The second- and third-ranking males increased their rearward presence when crossing the large road. However, the alpha male was last to cross in only 8.3% of small road progressions; this decreased slightly to 7.7% for large road progressions (Figure 7.6 (c), Study 2). This was different to progressions shortly after the widening of the large road, when the alpha male was rearward in 23.5% of small road and 45.5% of large road-crossings. Each female (not including the alpha female) was last for an average of 11.1% of small and 10.3% of large road progressions, and for each juvenile these percentages remained low (0% and 3.9% respectively).

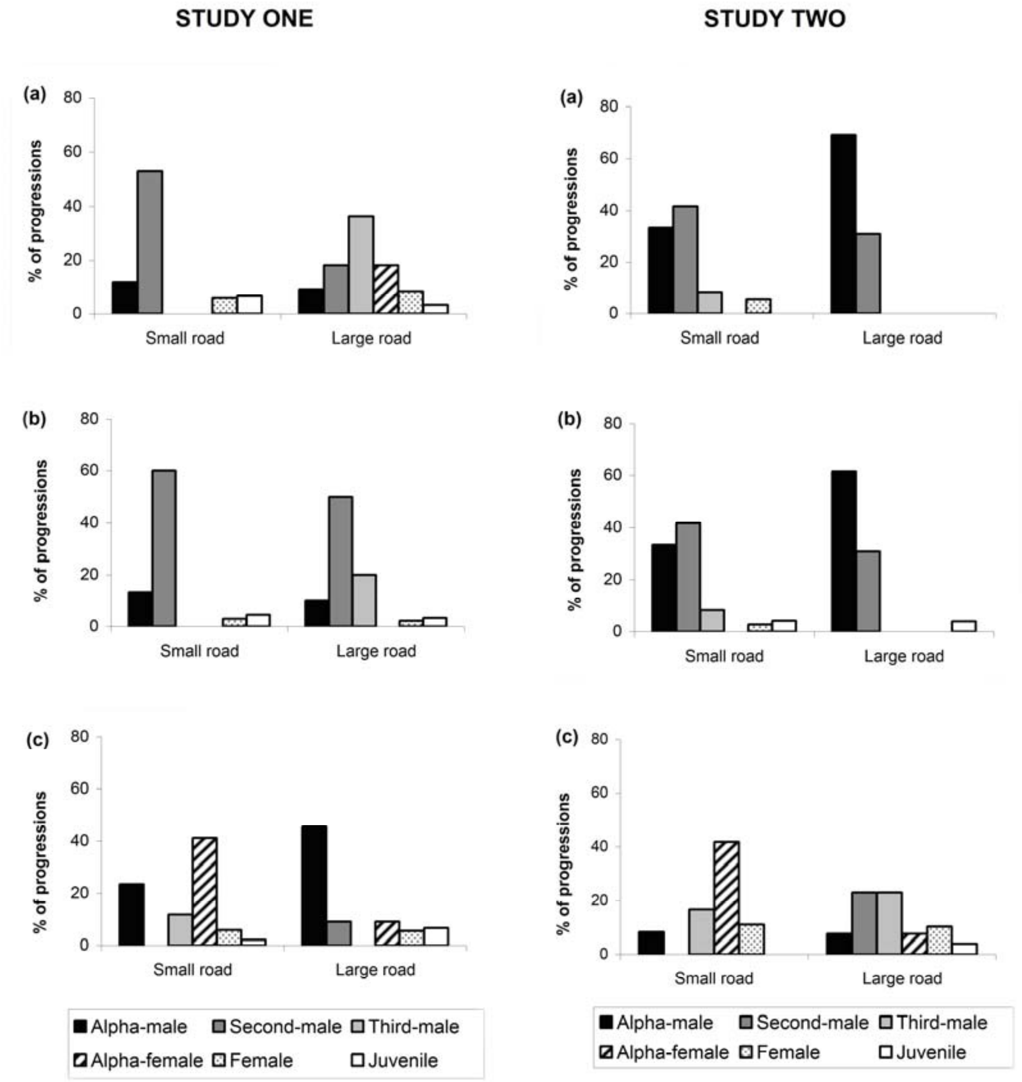


Figure 7.6. The percentages of Study 1 and Study 2 progressions in which the three males, the alpha female and the average non-alpha female and juvenile were (a) first to cross, (b) first to scan the road, and (c) last in the progression on the two roads.

7.3.6 Guarding behaviour

The occurrence of guarding behaviours whilst road-crossing was not recorded during Study 1, but during Study 2, guarding occurred on 9 out of 25 road-crossings (3 on the large and 6 on the small road). As can be seen from Figure 7.7, guarding behaviour was not always seen when people were present; however 8 out of 9 occurrences did occur when people were present on the roads (binomial test: $p<0.05$).

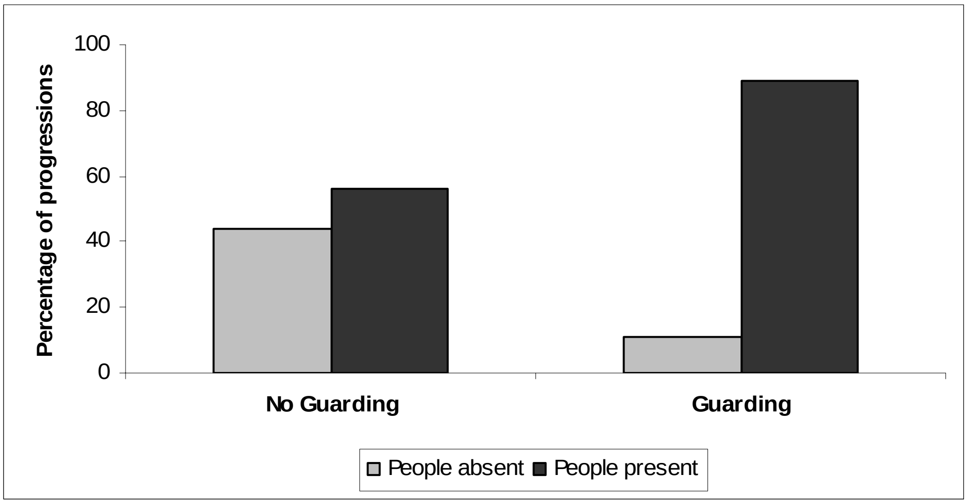


Figure 7.7. The occurrence of guarding behaviour and the presence or absence of people.

The individual to exhibit guarding behaviour was predominantly the first individual to cross the road (7 out of 9 instances). This was always an adult male, and was the alpha male in 7 out of the 9 instances. Interestingly, on 2 occasions when an adult male showed guarding behaviour, both juvenile males stood next to the adult males in a similar guard-like position.

Plate 7.2. Alpha male exhibiting guarding behaviour on the large road.

7.3.7 Timecharts

Figure 7.8 (a) illustrates a hypothetical example of a large road crossing where no observable socio-spatial organisation was employed by party members; adult males, adult females and juveniles are randomly distributed within the progression. The timechart (Figure 7.8 (b)) of an actual large road crossing visually demonstrates the complexity of the crossing (including waiting time and guarding behaviour) and the protective positioning of the adult males.

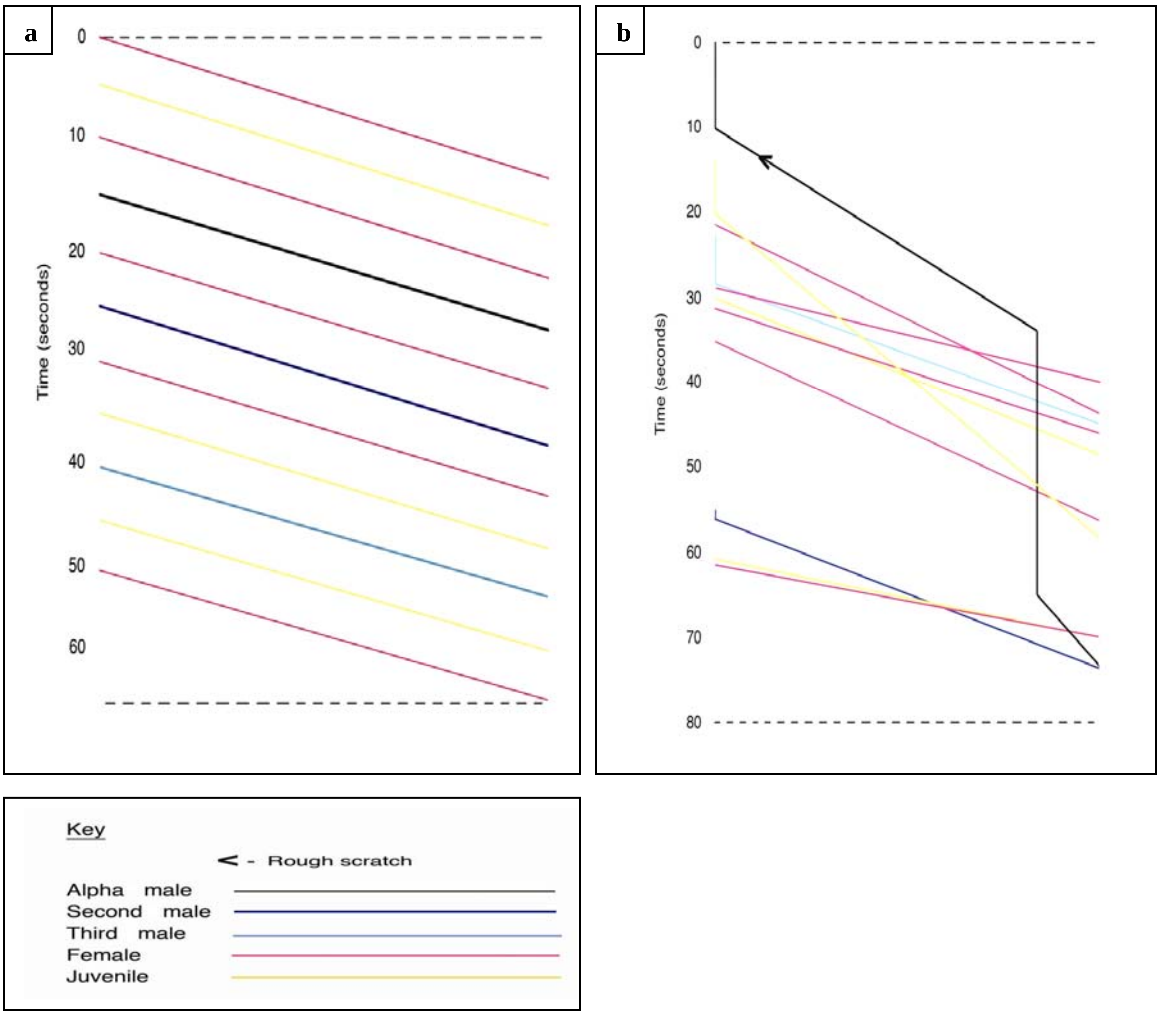


Figure 7.8. Time chart illustrating the complexity of a large road crossing progression; (a) is an example of a road-crossing with no socio-spatial organisation, and (b) is an actual large road-crossing with crossing time in seconds on the y-axis and the width of the road on the x-axis.

7.3 Results: Crop-raiding

The mean party size and number of adult males present during feeding on abandoned crops and raided crops were very similar (mean party size: 5.3 vs 5.4 individuals; mean number of males: 1.9 vs 2.0 individuals). As there was no significant difference between feeding conditions and number of males present ($X^2(2) = 0.41$, ns), the two feeding conditions were directly compared.

7.3.8 Positioning

During mixed-party raids, adult males (from one to three adult males present) were significantly more likely to take a frontward position than females and juveniles when crop-raiding than when feeding on abandoned cultivars (see Figure 7.9: $X^2(1) = 9.30$, $p<0.01$). Adult males took up a frontward position when crop-raiding during 55 out of 69 bouts (binomial, $p<0.001$; excluding dependant infants). However, adult males only took up a frontward position during 8 out of 17 bouts when feeding on abandoned cultivars.

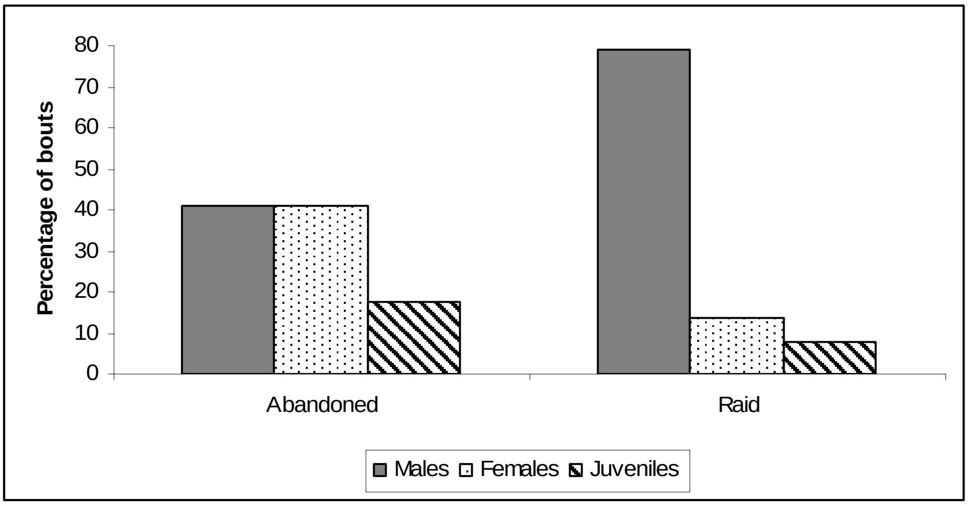


Figure 7.9. The percentage of bouts in which adult males, adult females and juveniles took the frontward position in abandoned and raid conditions.

There were only four bouts when all three adult males were present during abandoned feeding conditions, not allowing comparisons with raids.

When only the alpha- and second-ranking males were present during raids, one of them led progressions in 77.8% of raiding bouts (Figure 7.10). When all three males were present, one of them led during 83.3% of bouts. This strong frontward presence was maintained when only two males were present by the alpha male increasing his lead role.

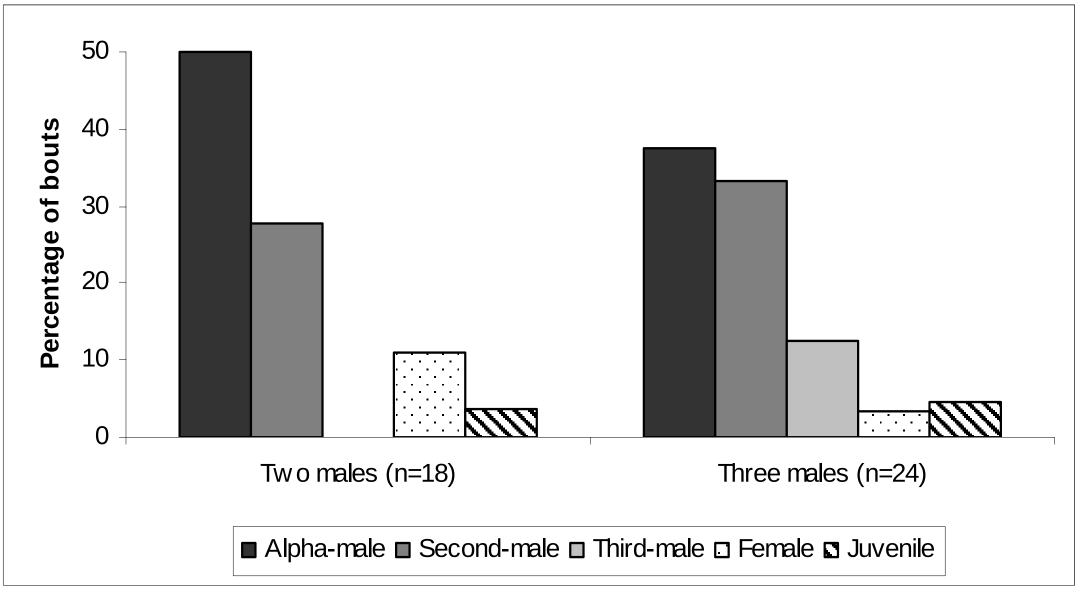


Figure 7.10. The percentages of mixed-party raid bouts in which both males (only alpha- and second-ranking males), all three males, the average female and juvenile took the forward position.

As the males were so heavily represented at the front of the party when raiding, people presence ($X^2(1) = 0.01$, ns), location ($X^2(1) = 1.0$, ns), and guard level ($X^2(1) = 0.1$, ns) did not significantly impact on their frontward presence. Interestingly, when all three adult males were present during raids, the alpha male was more likely to be the first male to enter when in mixed- compared to male-only parties despite there being more individuals in mixed parties (see Figure 7.11). Consequently, both the second- and third-ranking males were less likely to be the first to enter during mixed-party compositions.

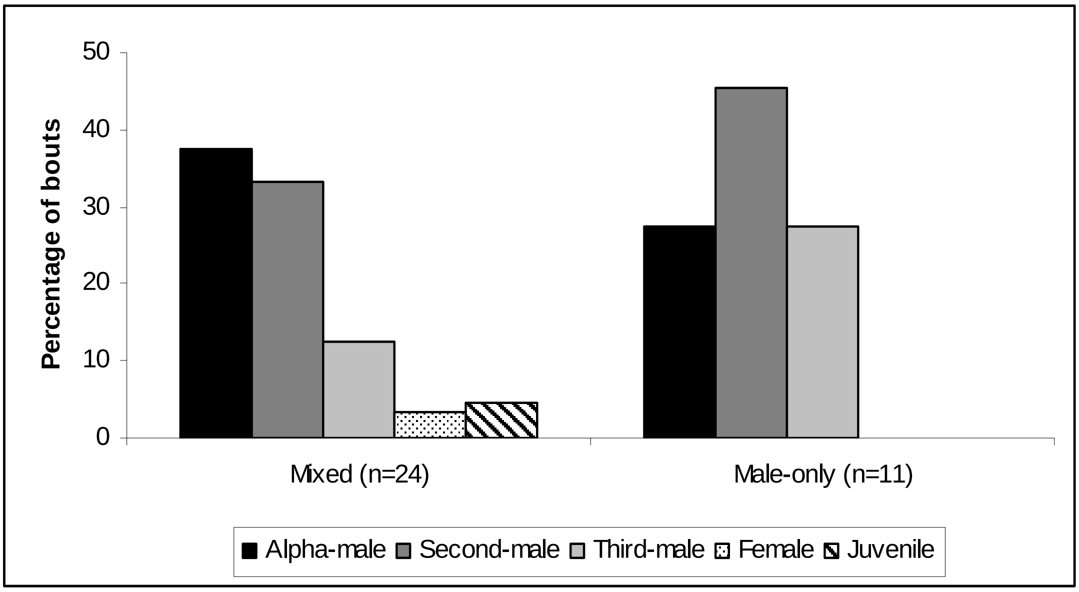


Figure 7.11. The percentage of raiding bouts in which each adult male was first to enter the field or orchard when all three males were present, in both mixed and male-only party compositions.

7.4 Discussion

7.4.1 Degree of Risk

Both crop-raiding and road-crossing are potentially risky situations for chimpanzees due to likelihood of human confrontation. The crop-raiding progression data presented here should be viewed as an extension to results presented in Chapter 6 on social and behavioural adjustments during crop-raids (see Plate 7.3.). When road-crossing, the risk associated with crossing the large road and leaving forest for open areas was reflected in increased waiting time. The presence of people and vehicles was probably the crucial factor in the apes' assessment of each road-crossing event. However, the reduction in waiting time at the large road in Study 2 highlights the possible influence of neophobia (defined as caution towards novel features of the environment) on the chimpanzees' perception of risk: over time the chimpanzees got used to the new condition.

Plate 7.3. Chimpanzee progression into orchard.

The road-crossings took place at times of the day when pedestrian numbers were both high and low, so the chimpanzees did not always time crossings to avoid confrontation with people. As party size increased, waiting time on both roads also increased. Although this may simply be a case of larger parties taking more time to get organised, an alternative explanation is that as the number of vulnerable individuals present increased, the party as a whole became more cautious. Party waiting time on the large road was further influenced by the direction of travel: when initially leaving the protection of a forested area to move into a more open area, the chimpanzees were more cautious, indicated by longer waiting times. The larger field of observation available to the chimpanzees when crossing the large road did not reduce waiting times, which reinforces the idea that the chimpanzees were influenced by the inherent degree of risk in this environment.

7.4.2 First or last?

During dangerous excursions certain positions may be more advantageous than others, depending upon age and sex. In the cases of crop-raiding and road-crossing, the first individual to scan the road or field/orchard checks for potential danger, but could also be caught unaware, while the individual leading the progression might have to face unnoticed dangers. Additionally, during road-crossings the last individual may also be exposed to risk, or get left behind. In contrast, the individuals in the middle occupy the safer positions.

Adult males, less fearful and more physically imposing than other group members, took up forward and rearward positions. The location of adult females and young within the progressions is of course as important as male positioning, and throughout this study they continually occupied the more protected middle positions. Overall, these results are generally congruent with findings on road-crossing progressions in the Bossou chimpanzees in earlier years (Matsuzawa and Sakura, 1988) and progression orders in other primates; namely terrestrial baboons (Rhine and Westlund, 1981; Rhine at al., 1985), Sulawesi macaques (Priston, 2005), arboreal gray-cheeked mangabeys (Waser, 1985) and arboreal black-and-gold howler monkeys (Bicca-Marques and Calegaro-Marques, 1997).

From data collected after the large road was widened (Study 1), comparisons of small and large road-crossings showed that the second- and third-ranking Bossou males were often first to scan and to cross at both roads. Although the first individual to scan was usually the first individual to cross, this happened less frequently on the large road than the small road. This may be due to greater uncertainty or risk when crossing the large road, resulting in the first individual continuing to survey the surrounding area more thoroughly. This could explain the decreased frequency of the second-ranking male being first to cross but not first to scan at the large road, and the consequent increase in the elderly, third male and alpha female leading the large-road progressions.

The alpha male was more rearward during large road crossings, where the risk of crossing was higher, whereas the elderly, alpha female showed a dramatic reduction in frequency of being last when crossing the large road compared to the small road. This female may have brought up the rear more frequently than expected on the small road as she was physically slower than other members of the group. When the perceived threat increased on the large road however, she took up a more frontward position.

During Study 2, the alpha male showed a dramatic reduction in his rearward positioning during both large and small road progressions, and increased his frontward positioning particularly on the large road. In contrast to Study 1, the second- and third-ranking males increased their rearward positioning, meaning that across both studies, adult males were rearward in a similar percentage of progressions. The alpha female again showed a decrease in her rearward presence when crossing the large compared to the small road. One can speculate that this old female makes a special effort not to get left behind when crossing the large road.

Guarding behaviour, predominantly by the alpha male, appeared to be a response to people presence on both the roads, although did not occur every time that people were present. On occasion juvenile males were observed joining the adult males in exhibiting guarding behaviours. Although more detailed studies are required, it supports the idea that younger members of the group are learning in a ‘master-apprentice’ fashion (Matsuzawa, 2006) and cultural behaviours when road-crossing are being passed down through generations. It would be interesting to examine whether the occurrence of guarding behaviour varies according to the nature of the human presence e.g. age- and sex-class of the people present, and their behaviour.

All three adult males increased their frontward presence when crop-raiding compared to when feeding on low-risk, abandoned cultivars. Similarly to road-crossing, when only the alpha- and second-ranking males were present during raids (compared to all three males) the alpha male showed behavioural flexibility by increasing his leadership. The alpha male was also more frontward when raiding in mixed compared to male-only parties. This raises the possibility that when females and juveniles were present the alpha male increased his protective role in the group; and may have used crop-raiding as an opportunity to 'show-off' his boldness (Teleki, 1973).

7.4.3 Anti-predator behaviour?

Miller and Treves (2006) suggested that primates may have developed specialised behaviours for avoiding human predators, but relevant data are lacking. The Bossou adult male chimpanzees increased their forward tendency during risky ventures, and showed several similarities in their spatial organisation when road-crossing and crop-raiding. Modern Bossou chimpanzees encounter predators infrequently (Sugiyama, 2004), and although humans themselves are not 'predators' of these chimpanzees, they may harass them. Road-crossing and crop-raiding (both human-created challenges) present new situations that call for flexibility of responses by chimpanzees to variations in perceived risk.

The Bossou chimpanzees employ a phylogenetically-old mechanism which involves an ancient male tendency to stand up to predators, to adapt to more recent and current dangerous situations. However, the positioning of dominant and bolder individuals changed depending on both the degree of risk and number of adult males present. As hypothesised, dominant individuals do act cooperatively with a high level of flexibility to maximise party protection. To this aim they display a degree of collective intention, suggesting knowledge of party composition, relative vulnerability of members, and physical capabilities (McGrew, 2004). At a proximate level each individual may have preferred and recognised positions; however, it remains unknown whether positioning is individual- or rank-specific. A long-term study on progression orders in relation to changes in rank would be informative in this regard.

Behavioural adaptations do not fossilize so it is unknown how hominoids travelled in risky habitats. Data on progression orders of other great ape populations are required to help shape hypotheses about emergence of this hitherto neglected aspect of hominoid social organisation.

Chapter 8

Scratching the Surface of Coexistence

Scratching the Surface of Coexistence

8.1 Introduction

Self-maintenance behaviours such as self-grooming are common across the animal kingdom, functioning proximately to remove ectoparasites and maintain the condition of the fur or feathers. However, self-directed behaviours (SDBs) which include scratching and grooming are often characterised by their apparent irrelevance to the situation in which they appear (Maestripieri et al., 1992). Behavioural and pharmacological evidence indicates that primates engage in more SDBs in situations of stress, arousal, or during periods of conflicting emotions (Pavani et al., 1991; Maestripieri et al., 1992; Schino et al., 1996). SDBs can therefore provide us with non-invasive behavioural indicators of emotional states (Maestripieri et al., 1992).

Scratching is amongst the most commonly reported SDB in non-human primates and has primarily been reported as occurring in social contexts (Maestripieri et al., 1992; Baker and Aureli, 1997). Past research has shown that scratching is differentially displayed in monkeys as a function of dominance rank. Diezinger and Anderson (1986) showed that in rhesus monkeys, intermediate-ranking individuals are the ones which become most anxious and scratch themselves most when in competitive feeding situations. The dominants can monopolise the food and the subordinates simply stay clear of the feeding area, but the intermediates are often caught in ‘no-man’s land’. Further evidence of a relationship between rank and scratching in monkeys comes from long-tailed macaques: an individual’s scratching rate increased when in proximity to high-ranking males (Troisi and Schino, 1987; Pavani et al., 1991). Scratching in male baboons has also been associated with tension levels and dominance status in the group (Easley et al., 1987). Additional research has shown that scratching in female olive baboons increases when an individual is spatially distant from near neighbours, possibly because of a feeling of increased risk (Castles et al., 1999). However, scratching found to relate to anxiety in one taxon may not necessarily be the same in another, and inter-species differences are important when discussing how different primates assess both social relationships and their environment (Pavani et al., 1991; Baker and Aureli, 1997; Aureli and Schaffner, 2002).

It is important to remember that SDB has a self-maintenance function, and thus should not be seen as a ‘pure’ measure of anxiety (Maestripieri et al., 1992; Castles et al., 1999; Kutsukake, 2003). Troisi and Schino (1991) demonstrate that scratching in long-tailed macaques is also influenced by proximate climatic factors which might affect the condition of the pelage, however other data are lacking.

Past studies have shown increased SDBs in various social situations by both humans and chimpanzees. In the latter, SDB has been described as a robust and methodologically practical tool for investigating emotional states (Baker and Aureli, 1997). Humans presenting with high anxiety levels also exhibit high levels of SDB including scratching (Fairbanks et al., 1982; Troisi et al., 1998). In chimpanzees, rough self-scratching (RSS), when the scratching action includes large movements of the arm, was associated with uncertainty when the difficulty of match-to-sample tasks was manipulated (Leavens et al., 2001). Among captive group-housed chimpanzees, RSS levels were greater in crowded compared to less dense housing conditions (Aureli and de Waal, 1997).

From field observations, RSS has been linked with conflict, frustration and anxiety in chimpanzees (van-Lawick-Goodall, 1972). In contrast to past data showing that high-ranking chimpanzees tended to RSS more frequently than low-ranking ones (te Boekhorst et al., 1991), Kutsukake (2003) found that the male RSS rate in Kibale was inversely correlated with dominance rank. Kutsukake also found that RSS rate by chimpanzees differed across individual activities, being rare during foraging or moving, but frequent during resting. An additional point to consider is that anxiety-inducing situations may differ between male and female chimpanzees as a result of different selective pressures (Kutsukake, 2003).

Previous work has indicated that RSS was differentially associated with regions of the body. Diezinger and Anderson (1986) showed that the vast majority of RSS episodes in rhesus monkeys were directed towards the legs, back and sides, not necessarily matching preferred sites for self-grooming. In captive chimpanzees, RSS has been found to be mostly directed towards the body, whereas rubs tend to be directed more towards the face (Leavens et al., 1997, 2001). Goodall (1986) showed that the majority of RSS in chimpanzees at Gombe were directed towards the upper torso and arm.

It is possible that SDB has an adaptive function, especially when considering the amount of time and energy invested in this activity. Maestripieri et al. (1992, p.976) stated that SDB “may function as a means of limiting the costs related to an internal conflict and act as re-regulating activities that in some way keep the animal within optimal psychological limits”. Another possible function of SDB is communication. Performing SDB may convey information about an individual’s motivational state and be relevant in several social situations in which the assessment of the other’s intentions is critical. For example, Kummer (1968) noted high rates of scratching in male hamadryas baboons during the initial phases of group coordination for movement. He suggested that the males scratch frequently before finally shifting position due to conflicting impulses while choosing a travel direction. Increased levels of scratching in rhesus monkeys were also associated with a change in behaviour, and were interpreted as moderate indecision on behalf of the performer (Diezinger and Anderson, 1986). Goodall (1986) stated that the chimpanzees of Gombe used RSS in the context of group travelling: RSS by the male leader is a clear-cut signal that he is about to go. Goodall (1986) further noted that adult females may also use RSS to signal to an infant her intention to move.

The communicative function of scratching has also been highlighted by Pika and Mitani (2005), who recently provided the first quantitative evidence that wild male chimpanzees in Kibale may use ‘directed scratching’ as a referential gesture to request grooming of specific body areas. The authors concluded that the recipient of the signal has an understanding of the intended meaning of the gesture, and consequently that some form of mental state attribution characterised these social interactions.

Most earlier research has focussed on the social contexts of SDB. However, many aspects of the complex environments of primates may be considered as tension-producing. No data exist on the effect of ‘environmental risk’ on RSS levels in wild chimpanzee populations. RSS represents a quantifiable means to reveal and evaluate differences between individuals in how they react to stressful or risky situations, including for the purpose of this study, the extent to which they are able to cope with a predominantly human-dominated environment. It may allow us to further understand the individual’s environmental perceptions and the potential threats therein, and the different behavioural strategies adopted in response.

8.1.2 Hypotheses

(a) RSS level will be affected by climatic variables such as rainfall

(b) RSS level will vary according to activity state and sex class, with males exhibiting greater levels than females.

(c) Higher levels of RSS will be exhibited in risky situations.

8.2 Methods and analyses

Rough self-scratching behaviour (RSS) was defined in accordance with Baker and Aureli (1997, p.1036) as “Rak[ing] one’s own hair or skin with fingernails, including large movements”. RSS is distinguished from gentle scratching by the movement of the shoulder joint (Leavens et al., 2001).

Data on RSS were recorded over an 11-month period, from June 2005 to December 2006. Observations made during May 2005 were used to ensure that RSS was accurately distinguished from gentle scratching. All occurrences of RSS were noted, including the individual, area of body scratched (head, arm, leg, back, stomach), and behavioural context (Activity A). Any behavioural change of the individual performing RSS within 5 seconds after the RSS (Activity B; see the Chapter 3 for behavioural classifications) was recorded. The food name and type, guard level and any contextual factors were recorded if RSS occurred in feeding or raiding contexts (see Chapter 3). RSS bouts were defined by occurrences lasting more than 5 seconds (Baker and Aureli, 1997).

8.3 Results

8.3.1 Precipitation

A total of 888 RSS events were recorded over the 11-month study period. Chimpanzees RSS throughout the day during both the dry and wet seasons (see Figure 8.1 (a)). To reduce the effects of 'time-class' observational biases, RSS rates for the dry and wet seasons were calculated: the frequency of RSS during each time class and during both the wet and dry seasons was divided by the total focal observation time throughout each time class in both the dry and wet seasons. A wet day was classed as one with 30 minutes or more of continuous rainfall (Priston, 2005).

To establish whether rain increased RSS rates, wet season days when it rained were compared to wet season days when it did not rain. There were 17 'rainy' days and 66 'non-rainy' days on which data on RSS were recorded. Interestingly, RSS rates throughout days when it rained were significantly lower than days when it did not rain (Mann-Whitney test, $Z=-2.08$, $n=12$, $p<0.05$). Additionally, RSS rates on rainy days did not correlate with the likelihood of rain falling throughout the day (Figure 8.1 (b); $r_s=-0.09$, $n=12$, ns); in fact most RSS occurred towards the end of the day, two hours after the rainfall peak.

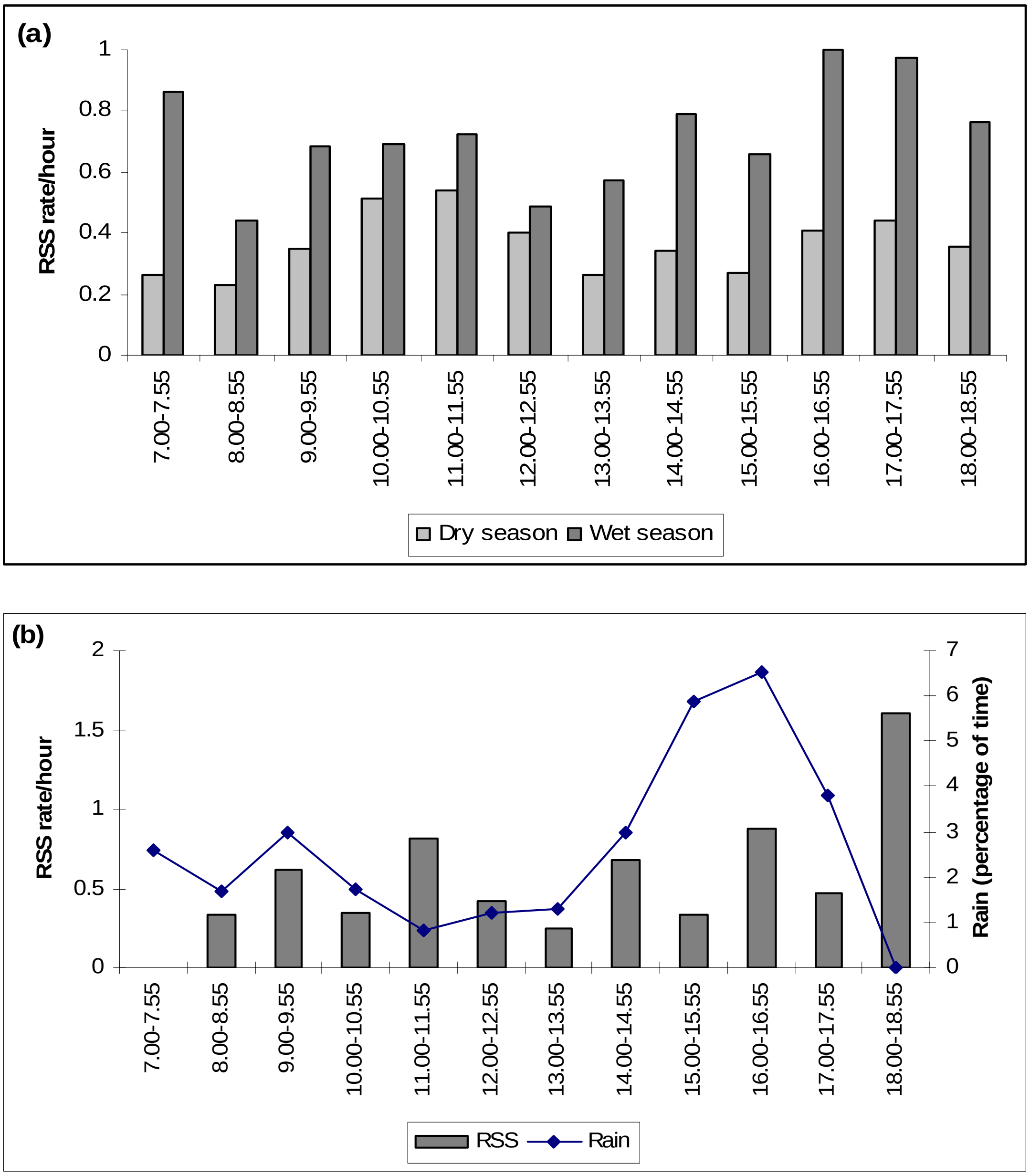


Figure 8.1. RSS rates throughout the day during the (a) dry and wet seasons and (b) days when it rained during the wet season plotted against percentage of focal time raining throughout the day.

8.3.2 Behavioural activity

Considerable inter-individual and sex differences were observed in RSS total frequency and rate (see Table 8.1). Adult males exhibited RSS significantly more frequently than adult females (759 out of 888 events; binomial, p<0.01). One adult male in particular, the second-ranking male showed RSS rates more than twice as high as other males.

Table 8.1. Inter-individual RSS frequency and rate (frequency/scan observation time).

Chimpanzee	Sex	RSS frequency	RSS rate
YL	M	180	0.21
FF	M	428	0.47
TA	M	151	0.21
Yo	F	34	0.04
Jr	F	28	0.04
Pm	F	18	0.03
Fn	F	29	0.04
Vl	F	20	0.04

Initially, the four main activity categories were analysed for the occurrence of RSS: feed, move, rest and social. A total of 313 RSS events occurred when the chimpanzees did not change activity (Activity A only), and 575 RSS events occurred before a change of activity was observed (Activity A to Activity B).

Figure 8.2 shows the RSS corrected frequencies associated with each activity when no change in activity was observed. The chimpanzees clearly exhibited a higher RSS corrected frequencies when resting than when engaged in other activities.

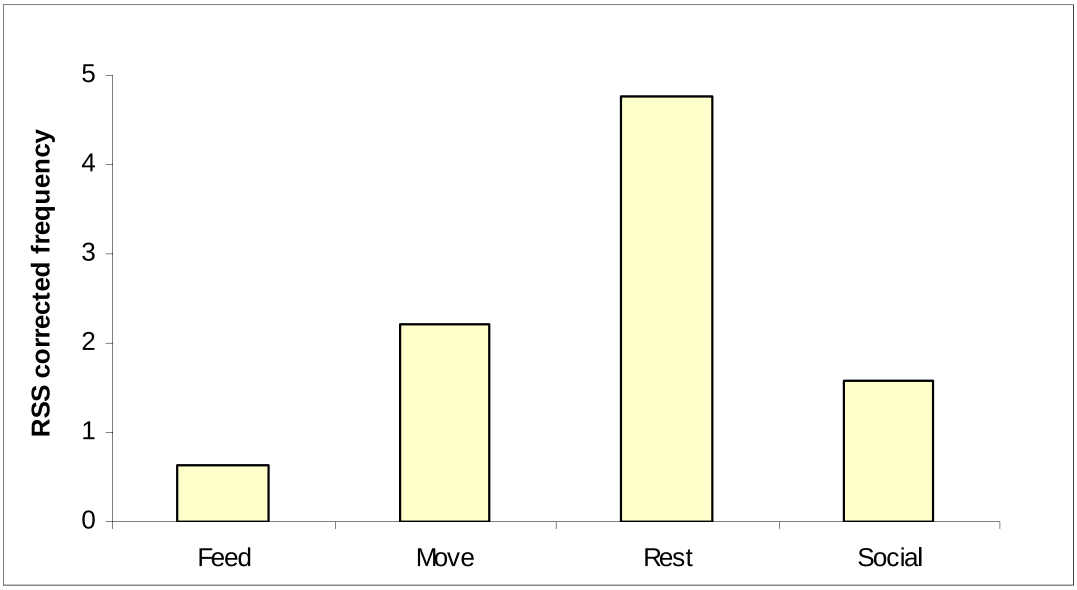


Figure 8.2. RSS corrected frequencies (RSS frequency/proportion of day engaged in activity) when engaged in different activities.

As the majority of RSS events occurred when an individual changed behaviour, the question arises whether scratching can be used to predict a change in activity state (as suggested by Goodall, 1986). However, as I do not have exact frequencies of activity changes within a 5-second time frame at other times, it is not possible to test observed against expected frequencies. Therefore the following analysis assumes that changes between activities occur equally often. There were highly significant differences between the RSS frequencies within each activity class and change (see Table 8.2; $X^2(9) = 168.9$, $p<0.001$), with rest accounting for 82.4% (777 out of 888 events) of 'Activity A'. Focusing on events with a change of activity, RSS frequencies were noticeably high (67.5%; 388 out of 575 events) when changing from rest to move. A change from rest to move accounted for around half of RSS events by females when a change of activity was observed (48.8%; 39 out of 80 events).

Within the social category, 74.0% of RSS events occurred in the context of male display (85 out of 115 events); 77.6% of those display-related RSS events (66 out of 85 events) occurred when the scratching individual changed from rest to social display. Additionally, a total of 18 RSS events by adult males were recorded during courtship display, where males would shake branches or heel-tap to encourage a swollen female to come closer.

Table 8.2. Activity when RSS occurs (Activity A) and the activity change within 5 seconds of ending the RSS (Activity B). The grey boxes illustrate when no activity change occurred.

		Activity B			
		Feeding	Moving	Resting	Social
Activity A	Feeding	14	12	6	1
	Moving	8	43	42	6
	Resting	14	388	246	84
	Social	0	5	9	10

8.3.3 Body Part

Variations existed in the parts of the body to which the RSS was directed. The front torso and arm were scratched more frequently (36.8% and 33.4% respectively) than the back torso and leg (15.2% and 13.2% respectively), with the head being rarely scratched (1.4%).

The RSS body part did not vary depending on sex ($X^2(4) = 6.90$, ns) or whether there was an activity change or not ($X^2(4) = 5.93$, ns). Data were further analysed to establish if RSS body region varied with activity. Figure 8.3 illustrates that RSS is predominantly directed to the front torso and arm. However, a greater percentage of RSS events were directed to the front torso during move than rest activities, with more RSS directed to the back torso during rest.

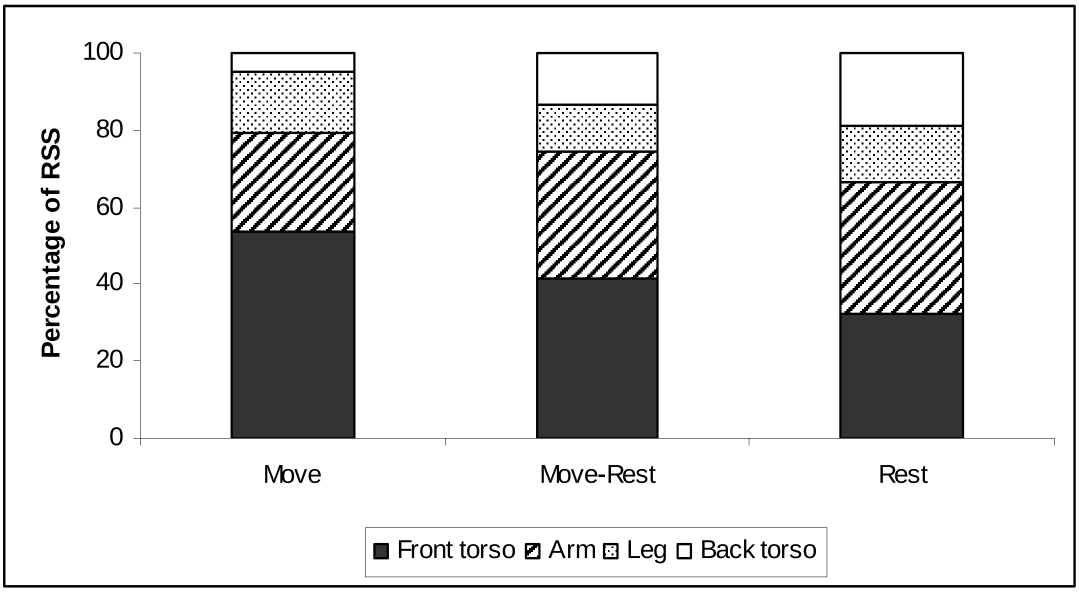


Figure 8.3. Percentage of RSS episodes directed to different body regions during move (n=43), an activity change from rest to move (n=381), and rest (n=219).

8.3.4 High-risk activities: crop-raiding

To examine RSS frequencies during crop-raids compared to feeding on abandoned cultivars and feeding on wild foods, feeding and searching behaviours were combined as both are likely to affect anxiety levels. RSS frequencies were substantially higher when engaged in raiding behaviours compared to when feeding on wild or abandoned food sources (see Figure 8.4).

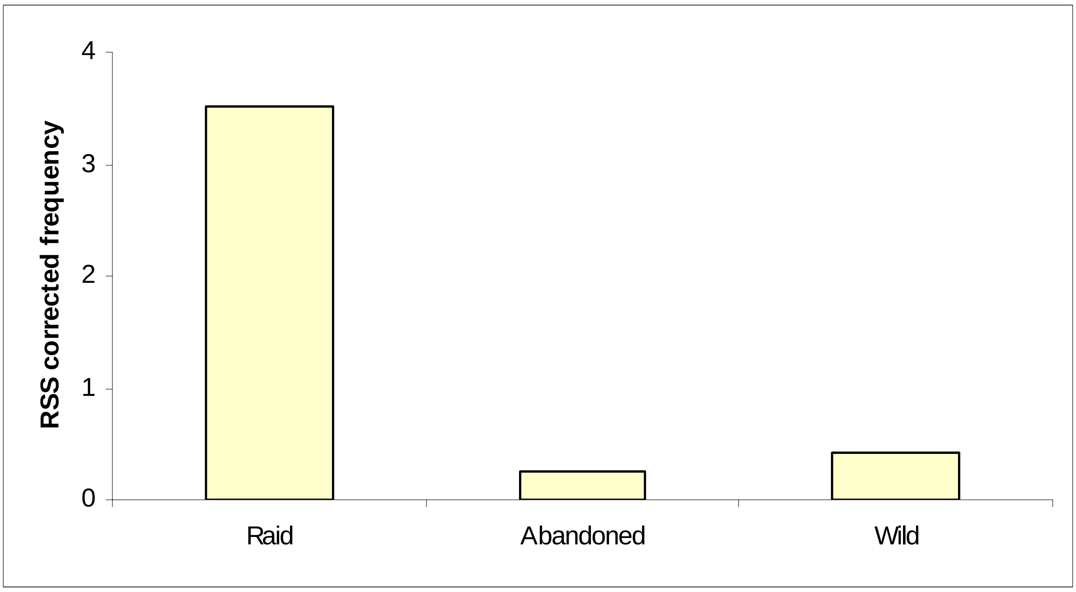


Figure 8.4. RSS corrected frequency (RSS frequency/proportion of total feeding time) when feeding on different sources.

During crop-raids, the majority of RSS (27 out of 32 events) occurred whilst raiding simple-sugar (SS) fruits. These raids were therefore compared with SS-raids where no RSS occurred. RSS was recorded during only 11% of SS-raiding bouts (14 out of a total of 128 bouts), and the RSS frequency during a raiding bout ranged from 1 to 5 (mean: 1.9; S.D ± 1.4). During SS-raids, only adult males showed RSS. However, the individual leading the crop-raid did not always perform RSS; the leader did so in 6 out of the 14 raids. The chimpanzees were significantly more likely to RSS in the presence rather than absence of people ($X^2(1) = 4.1$, $p<0.05$), but no effect of location ($X^2(1) = 0.8$, ns) or guard level was observed ($X^2(1) = 1.2$, ns). Although, chimpanzees were more likely to RSS when raiding further from the forest edge (means: 12.2m vs 15.4m), this difference failed to reach significance (Mann-Whitney U-test; Z = -1.43, p=0.151). Interestingly, vocalisations were more likely to be associated with RSS events than not ($X^2(1) = 4.8$, $p<0.05$).

A one-way ANOVA was used to determine the effects of party size during SS-raids on RSS occurrence. As can be seen by Figure 8.5, the group size when RSS occurred was significantly larger than when RSS did not occur ($F_{1,126} = 7.06$, $p<0.01$), even though there was no significant difference between the number of males present during SS-raids with and without RSS ($X^2(2) = 2.10$, ns). Party compositions also tended to vary when RSS occurred compared to when RSS did not occur, but this just failed to reach statistical significance ($X^2(3) = 7.06$, $p=0.07$). More specifically, RSS was significantly less likely during male-only raids (even though they are associated with more risk) compared to when males were present with other age- and sex-classes ($X^2(1) = 4.86$, $p<0.05$).

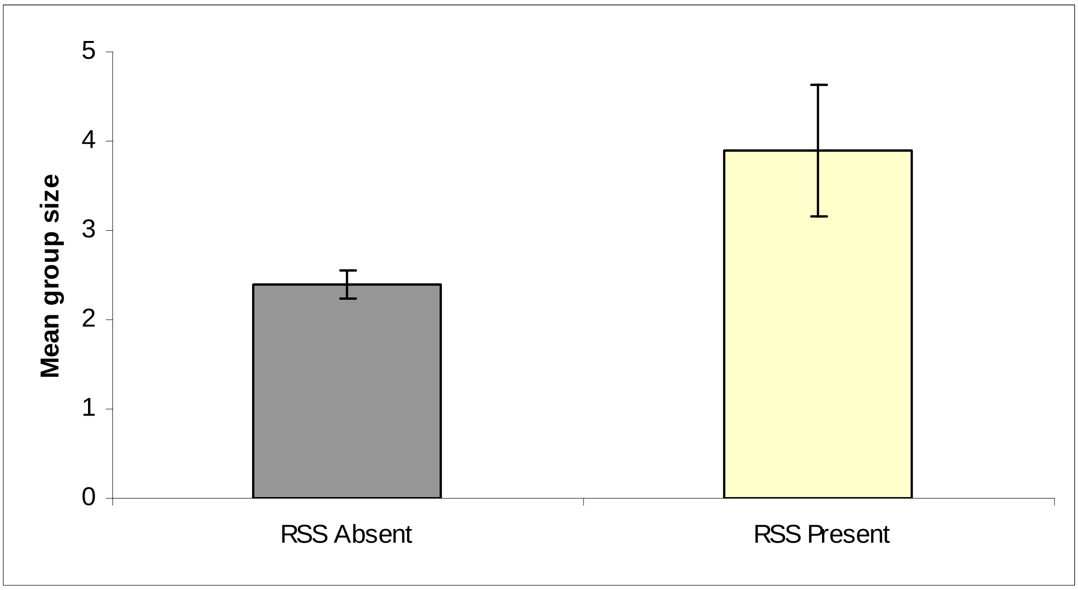


Figure 8.5. Mean group size during SS-raids when RSS was absent and present.

8.3.5 High-risk activities: road-crossing

RSS frequencies were also calculated when the chimpanzees were road-crossing and moving within the forest (see Figure 8.6). RSS frequencies when road-crossing should not be directly compared with RSS frequencies during crop-raids, as crop-raid frequencies were calculated using total feeding time, and the associated risks were reduced on occasions when food was transported back to the forest.

As can be seen from Figure 8.6, RSS frequencies were about 8 times higher during road-crossing episodes than when chimpanzees were moving through the forest. The majority of RSS was performed by adult males (85%), the remaining 15% being performed by females.

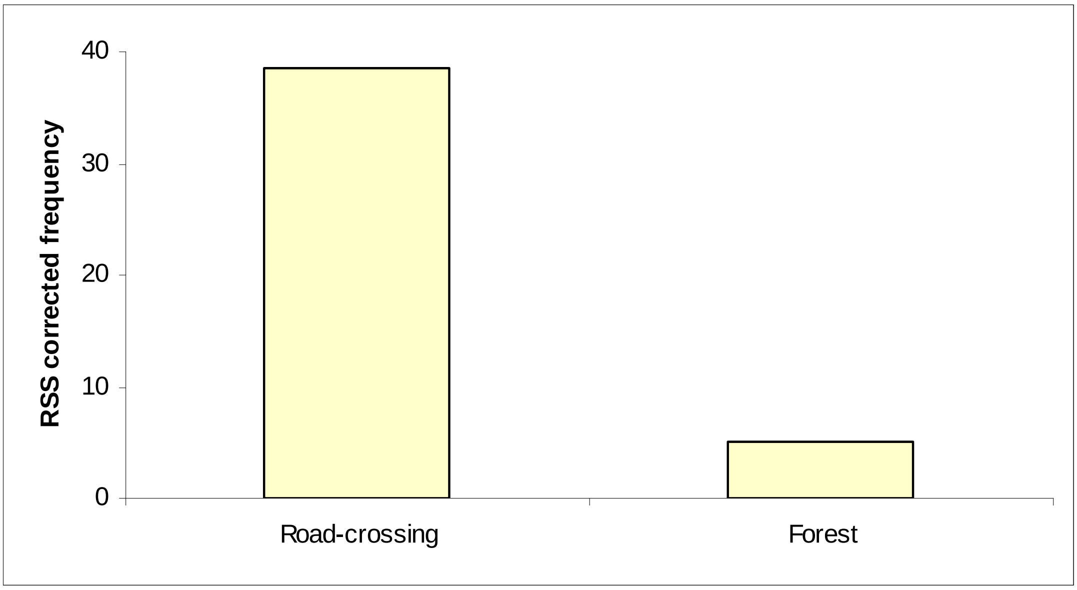


Figure 8.6. RSS corrected frequency (RSS frequency/proportion of total moving time) when road-crossing and moving within the forest.

During all road-crossings (all party compositions included), progressions when RSS occurred (n=14) were compared to those where RSS did not occur (n=141). The chimpanzees were significantly more likely to RSS when crossing the large road than the small road (12 out of 14 events; X^2 (1) = 6.40, $p<0.05$). A one-way ANOVA was used to test the effect of party size on RSS for all large road progressions. Party sizes were significantly larger when RSS occurred (absent vs present: 4.4 vs 9.5 individuals; $F_{1,81}$ = 25.53, $p<0.001$), and all RSS events occurred during mixed-party progressions.

For consistency with analyses presented in Chapter 7, mixed-party progressions containing all three adult males (n=53) when RSS occurred (n=12) were compared with those where RSS did not occur (n=41). RSS was again significantly more likely to occur when crossing the large road than the small road (see Figure 8.7; X^2 (1) = 9.06, $p<0.01$). The mean waiting time on large road-crossings was less when no RSS occurred than when it did (absent vs present: 82s (SD ± 21.6) vs 188s (SD ± 57.0)), however, this difference failed to reach significance (Mann-Whitney U test: Z = -1.47, n = 24, ns). This was probably due to the high variability in waiting times when RSS was present. A one-way ANOVA was used to test the effect of party size on RSS in mixed party compositions when all three adult males were present: RSS occurrence did not vary with party size on large road crossings (absent vs present: 9.1 vs 9.4 individuals; $F_{1,122}$= 0.067, ns). Furthermore, there was no significant difference between the likelihood of RSS during road-crossing in Study 1 when the large road was newly widened and the follow up period in Study 2 (X^2 (1) = 0.8, ns).

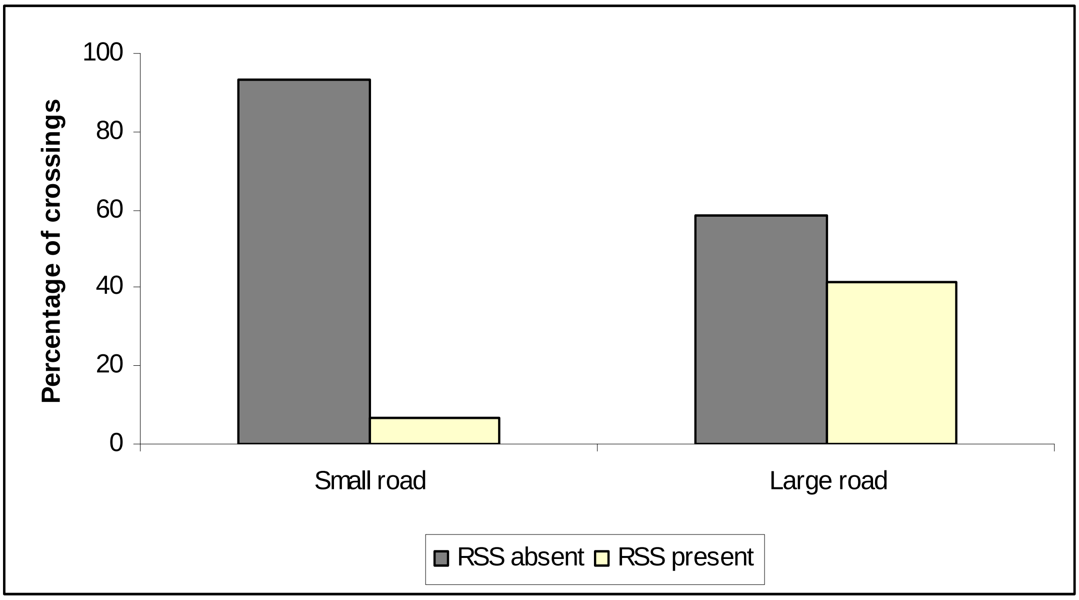


Figure 8.7. The percentage of mixed party composition crossings on the small (n=29) and large (n=24) roads in which RSS was absent or present.

8.3.6 Other risks

RSS was also observed on two occasions when the chimpanzees encountered a viper - a highly venomous snake. During both episodes, the chimpanzees vocalised (a vocalisation that the guides and myself recognise as being specific to snake encounters) and all individuals present showed RSS continuously until they moved away. Also, the adult males showed high levels of RSS when a gun was fired in a field 200m from where they were resting in the forest. In total 13 RSS episodes were recorded within 8-minutes, and RSS was accompanied by pant-hoot vocalisations.

8.4 Discussion

As SDB has a self-maintenance function, it should not be seen as a ‘pure’ measure of anxiety (Maestripieri et al., 1992; Castles et al., 1999; Kutsukake, 2003), and therefore RSS rates were correlated with rainfall over the course of this study. Even though higher RSS rates occurred throughout the wet season than the dry season, in contrast to previous research on macaques (Pavani et al., 1991), RSS frequency did not appear to be influenced by proximate climatic factors. On days when it rained there was actually a reduction in chimpanzee RSS rate; chimpanzees do not RSS due to the wet condition of the hair. However, chimpanzee RSS rates did increase two hours following peak afternoon rainfall levels which may be related to a ‘drying out’ phenomenon.

8.4.1 Sex-differences

Strong sex differences were observed in RSS rates, with adult males showing a much greater propensity to RSS than adult females. Males and females may perceive situations differently and certainly do not engage equally in high-risk behaviours; dominant males engage in more risky behaviours and also take-up protective roles within the group. However, such strong RSS variations between the sexes are unlikely to be explained simply by dichotomies in overall anxiety. The second-ranking male exhibited much higher RSS rates than the two other adult males, though it is not possible to say whether this is a function of his rank or his individual temperament. He may show more RSS than the other chimpanzees as a result of greater internal anxiety. Maestripieri et al. (1992, p.976) note that “a particularly strict relationship between emotions and behaviour may be argued for primates whose social life entails a high degree of cognitive capabilities”. As primates may have evolved functional characteristics aimed at reducing anxiety associated with social interactions, an interesting line of enquiry would be to explore the relationship between ‘personality’ and SDB in chimpanzees and other great apes (Weiss et al., 2006).

8.4.2 Behavioural change

RSS predominantly occurred before behavioural changes, especially when chimpanzees switched from resting to moving. Recently there have been considerable advances in our understanding of the complexities of social communication in non-human primates, including gestural signalling (Slocombe and Zuberbuhler, 2005; Pika and Mitani, 2005; Arnold and Zuberbuhler, 2006). From the data presented in this chapter alone it is not possible to conclude whether RSS was used particularly by males, as an auditory and visual communicative gesture signalling a move, or simply as a sign of anxiety prior to movement. Although more detailed observations are required to examine the communicative hypothesis, consistencies between Gombe in East Africa and Bossou in West Africa supports the distinct possibility that RSS may be a widespread form of gestural communication in chimpanzees.

Previous work has indicated that RSS was differentially associated with regions of the body. Like the chimpanzees of Gombe (Goodall, 1986), the chimpanzees of Bossou predominantly directed RSS to the arm and front torso, and rarely the head. RSS was directed to similar body regions in both sexes, whether there was a change in activity or not. However, data comparing the body region targeted during move, rest and a change from rest to move show that RSS may have been directed to the most accessible and convenient body region. Also, if the auditory aspect of the RSS is important, it may be worth assessing the hair quality in different regions of the body.

8.4.3 Environmental and social stress

Many aspects of the complex social and physical environment of the Bossou chimpanzees can be considered as tension-producing. The lowest overall RSS frequency during all activities was observed during feeding. Of course the expression of RSS may be constrained when hands are being used for purposes other than RSS, for example food processing (Kutsukake, 2003), but feeding may also be a ‘relaxed’ time for chimpanzees.

As expected, RSS was exhibited by chimpanzees when engaged in anxiety-related social behaviours such as aggressive displays.

The chimpanzees also exhibited variations in RSS frequencies according to the degree of risk posed by their environment. RSS frequencies were greater when engaged in raiding than when feeding on abandoned or wild foods, highlighting elevated anxiety levels during raids. Looking more specifically at SS-raiding, adult males were the only age-sex class to RSS. Adult males showed a higher tendency to RSS when raiding in larger groups and when more vulnerable individuals were present in the raiding party; notably they only rarely showed RSS when in male-only parties. Additionally, the presence of humans during raids increased RSS tendencies, further emphasising the influence of human presence on the perceived degree of risk when raiding. The chimpanzees did exhibit more behavioural signs of anxiety with increasing distance from the forest edge; however the effect was dampened by high variance. An interesting point to note is that the first individual to crop-raid was not the only party member to RSS; anxiety was also displayed by the other adult males present in the raiding party.

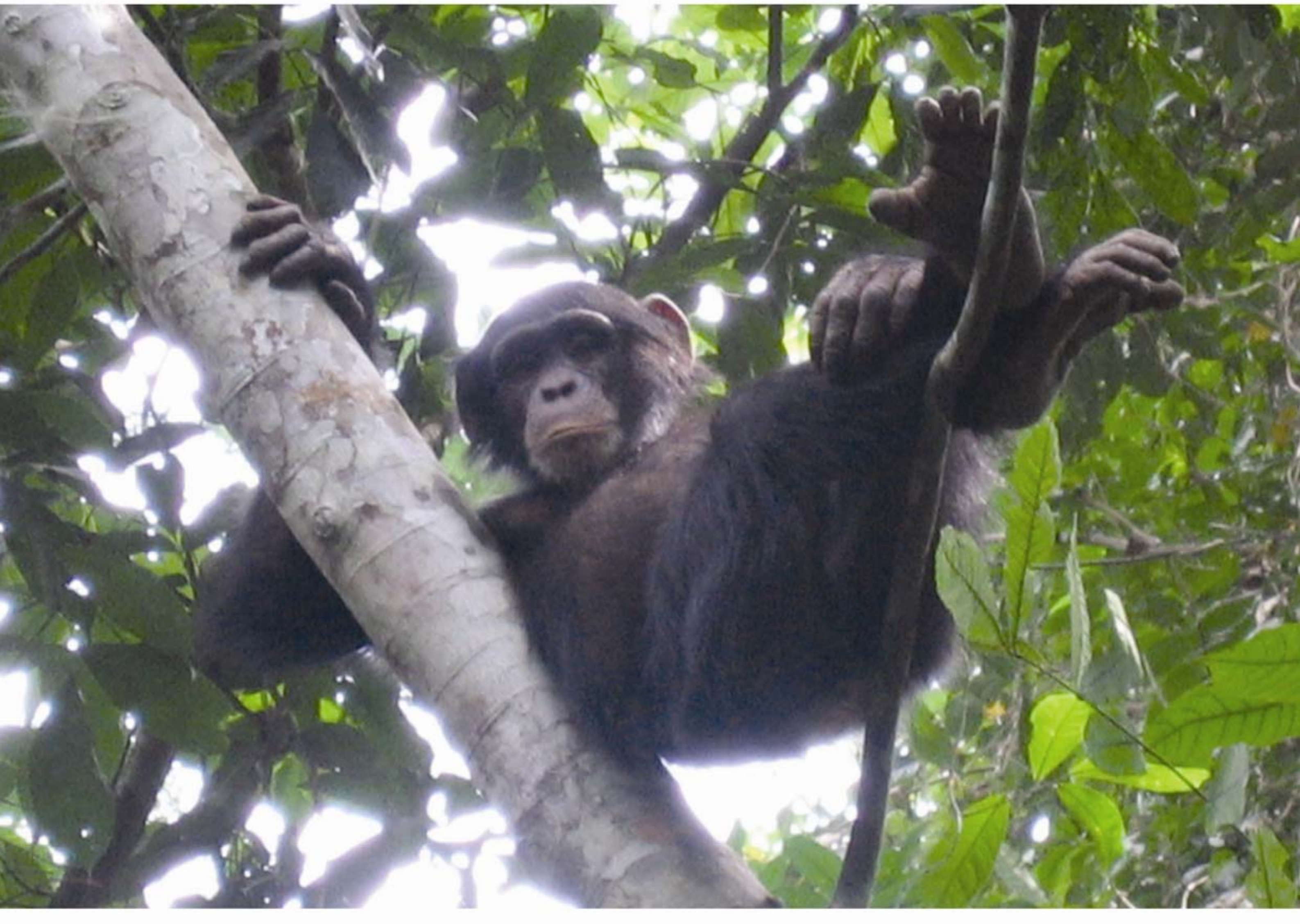
When the chimpanzees encountered a hunter with a gun, RSS was accompanied with vocalisations. Furthermore during crop-raids, vocalisations again accompanied RSS significantly more frequently than when no RSS behaviour occurred. Vocalising while crop-raiding requires an explanation as it might be expected that by their suppression, chimpanzees can avoid human confrontation (also see Chapter 6 (Section 6.3.4)). Vocalisations may indicate high levels of arousal, explaining why a ‘keep-quiet’ strategy was not always adopted in risky situations.

The chimpanzees also exhibited higher RSS frequencies when road-crossing than when moving within the forest. Over all recorded road-crossing progressions and those of only mixed composition, the chimpanzees were more likely to RSS on the large road than the small road. This indicates heightened anxiety levels when crossing the large road. During all progressions, individuals were more likely to RSS when party size was larger; this effect was not observed during mixed-party progressions because party sizes were consistently high. Mean waiting time at the large road when RSS occurred was approximately double that of when RSS did not occur. This pattern is consistent with RSS levels being higher when perceived risk is greater.

RSS appears to be an expression of anxiety and may also function as a signalling gesture to move in the Bossou chimpanzees. In this sense, it is likely that RSS originated as a signal of stress and subsequently evolved a communicative function to influence the attention, arousal and behaviour of others. This study reinforces the value of looking at RSS as a non-invasive measure of stress in wild chimpanzees.

Chapter 9

Summary, Conclusions and Future Directions



Summary, Conclusions and Future Directions

This thesis has taken an essentially chimpanzee-centred *(Pan troglodytes verus)* approach to the range of adaptations and behavioural flexibility by a community of chimpanzees living in the increasingly human-influenced environment in Bossou. My research focused on the chimpanzees' perspective of their environment, the risks and opportunities presented by a human-dominated landscape, and detailed their day-to-day coexistence with humans.

The major findings can be summarised as follows: Chapter 4 identifies seasonal variations in the availability of both wild and cultivated food at Bossou, and highlights potential wild fallback foods for the chimpanzees. Chapter 5 shows that cultivars are fully integrated into the Bossou chimpanzees' dietary repertoire, and the usage patterns of wild and cultivated foods are inextricably connected. Chapter 6 (Part One) demonstrates that cultivars have a pervasive influence on the chimpanzees' activity budgets. Crop-raiding also impacts upon party composition, with adult males being more likely than other age-sex classes to raid in exposed environments. After adult males acquire these risky-to-obtain cultivars, Chapter 6 (Part Two) shows how they share them with reproductively valuable females. Chapter 7 details how the Bossou chimpanzees exhibit high levels of socio-spatial flexibility and cooperation when dealing with anthropogenic aspects of their environment such as road-crossing and crop-raiding. Chapter 8 used rough self-scratching (a behavioural indicator of stress) to quantify elevated levels of anxiety that the chimpanzees of Bossou experience when dealing many aspects of a human-dominated environment.

9.1 Living with humans

The Bossou chimpanzees consume a wide range of cultivated foods which are found extensively throughout their small, fragmented home range. There is significant variation in the importance of various cultivars in the chimpanzees' diet; certain cultivars are mostly fallback foods, while others are preferred food-items and taken according to their availability. In general, simple-sugar fruits are taken in response to wild fruit scarcity. This finding has potential future management implications for conserving and encouraging certain species, such as the Umbrella tree (*Musanga cecropioides),* which provide natural fallback foods for the chimpanzees and which are not consumed by humans. Although the conservation of primary forest is paramount, species such as the Umbrella tree are quick-growing and thrive in secondary forest, thus making them a potentially 'rapid' means of alleviating crop-raiding during periods of low wild fruit availability. In contrast to simple-sugar fruits, other crops such as maize and rice pith are also taken by chimpanzees as a function of their availability in time and space; such crops are therefore considered to be at most risk from being raided. In agreement with Naughton-Treves et al. (1998, p.604) "to avoid heavy losses, highly palatable seasonal crops such as maize, should not be planted on the forest edge", or in the case of Bossou, also within the forest itself.

Although the Bossou chimpanzees do crop-raid, and throughout this thesis future management strategies are proposed, it would be wrong to assume that the phenomenon presents a problem that 'needs to be solved'. Priston (2005, p.335) emphasises that "by using the term conflict, and initiating management strategies and plans we could be elevating people's perceptions to a state of increased conflict". We need to be very careful when considering such issues. Although relatively little conflict exists now at Bossou, the potential for increasing human-ape conflict throughout Africa is huge. There is a need for management strategies to be designed, and to this aim the results of this thesis are important.

This study has shown that adult male chimpanzees are more likely than other group members to raid cultivars, especially in risky and exposed environments that present increased likelihood of human confrontation. In many situations (including tool-use) chimpanzees learn through a ‘master-apprenticeship’ effect (Matsuzawa, 2006), and thus when the younger members of the group observe the confident and successful raiding behaviours of adult male group members, the chances increase that they will in turn exhibit similar behaviours. In chimpanzee communities that do not frequently engage in raiding, or that are yet to discover the palatability or nutritional value of certain crops, younger group members may be more exploratory towards novel food items and thus introduce new crops into the dietary repertoire of their community (Lee, 2003). Takashi (1983) reported that within the Mahale chimpanzee community, it was a juvenile male chimpanzee who was first to consume mango fruit, after which the behaviour quickly propagated to other group members. Thus, adult males at Bossou influence the raiding behaviours of the community in two main ways: firstly, vulnerable group members are more likely to accept the risks associated with raiding while in the presence of adult males; secondly, this produces an inter-generational transmission effect by which raiding behaviours are maintained in the repertoire of a community. Understanding the range of subsistence behaviours of adult males is critical for determining the extent to which a community raids and will continue to raid cultivated foods. This also has interesting implications for studies of chimpanzee cultural transmission, in which subsistence and other behaviours are usually passed from adults to younger group members.

The exploitation of human cultivars affects the socio-sexual behaviour of the Bossou chimpanzees. Chimpanzees share the fruits of their risky labours (crop-raiding) as a food-for-sex strategy, by which adult males advertise prowess and enhance affiliative relationships with reproductively valuable females (Hockings et al., under review). The cognitive implications of sophisticated behaviours such as food sharing invite us to speculate about how and when such changes may have occurred in our own evolutionary history. Stanford (2001, p.117) notes that "males and females in both human and non-human primate societies have a strong vested interest in obtaining key foods, but both the means and the goal of obtaining the food differ between the sexes. Studying these differences leads us to many of the most interesting features of our humanity and of the origins of human cognition". The present data suggest that obtaining risky or difficult-to-obtain plant food items may have played a role as important as meat-sharing in the advancement of complex food sharing behaviours in hominoids.

Figure 9.1 presents one way of illustrating the intricate web of factors operating in a chimpanzee's decision to crop-raid at Bossou (inspired by Stanford, 2001, p.103). Although there may be overlap between chimpanzee communities in the factors that influence choices about whether to raid, each community may be faced with different combinations of social, ecological and cultural factors to those found at Bossou. Crop-raiding is definitely not tolerated throughout Africa to such an extent as Bossou (in many areas a potential cost to crop-raiding is death), and thus chimpanzees will have to evaluate a localised set of costs and benefits when deciding whether or not to crop-raid.

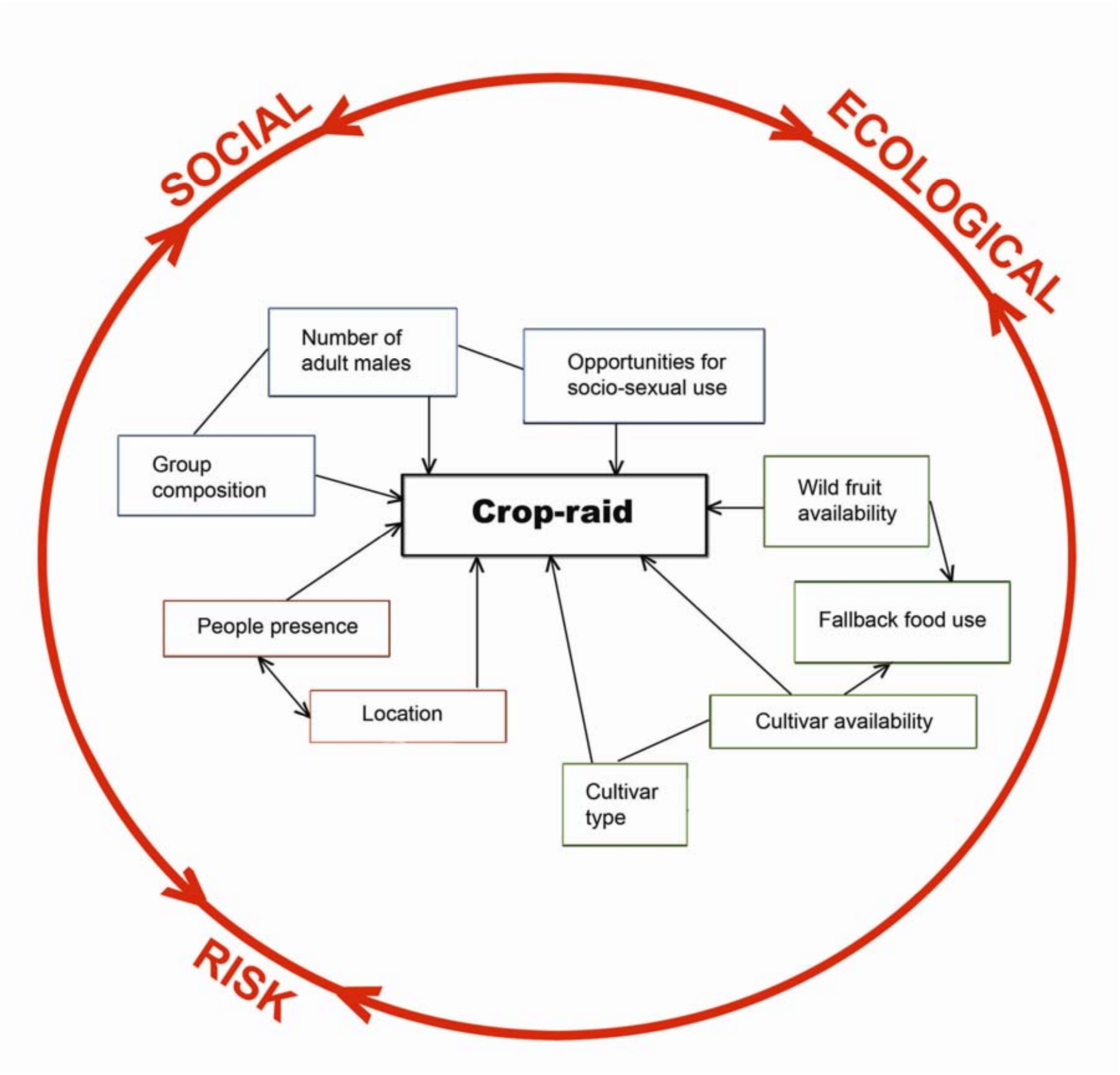


Figure 9.1. Factors influencing a Bossou chimpanzee's decision to crop-raid. The direction of arrows shows direction of influence, and the lines without arrows represent a link but with no direct influence. The length of the arrow is unrelated to the factors' degree of influence. Factors in the top left of the diagram illustrate social influences, factors in the right show ecological influences and factors in the bottom left show the influences of potential risk.

In response to other high-risk situations such as road-crossing, the chimpanzees' behaviour was modified through flexible socio-spatial organisation and cooperation (Hockings et al., 2006). Risks were differentially assumed by individuals in ways that maximised group protection, with the dominant and bolder individuals tending either to be first to enter risky environments, or protective of others when they perceived possible hazards. In agreement with previous studies (for review see Maestripieri et al., 1992), rough-scratching (a self-directed behavioural pattern) was identified as a reliable means to quantitatively evaluate the chimpanzees' levels of anxiety when confronted with some of the challenges posed by their physical and social environment. The potential communicative function of rough-scratching in chimpanzees was also highlighted, supporting other lines of evidence for this behaviour functioning as a communicative gesture (Diezinger and Anderson, 1986; Goodall, 1986; Pika and Mitani, 2005).

In contrast to previous findings reported in captive chimpanzees (Silk et al., 2005), data from this thesis indicate that chimpanzees are not indifferent to the welfare of other group members. Darwin (1871, p.77) proposed that "Many animals certainly sympathise with each other's distress or danger"; the chimpanzees of Bossou appear to have an understanding of other group members' vulnerability and they take action in response to this knowledge. The present research shows that greater insights may be obtained through studying the cognitive capacities of primates in the wild. Although contrived laboratory tasks may be useful for revealing hitherto unknown abilities (such as numeric memory span in chimpanzees, see Matsuzawa 2006, p.30), it should be remembered that cognitive potential has evolved for dealing with situations in the wild.

9.2 Costs and benefits of coexistence

The next stage to this research will be to detail both human and chimpanzee perspectives, focussing on how rural people throughout Africa perceive and value chimpanzees, and how this in turn affects chimpanzee behaviour and capacity to survive in increasingly human-dominated landscapes. The advent of agriculture marked a critical transition in the relationship between human and non-human primates. Although it seems likely that both would have previously competed over natural resources to some extent, agriculture undoubtedly altered the nature and the cost-benefit ratios of coexistence. Furthermore, the increasing rate of human population growth has expanded the human-primate interface, with more conversion of natural primate habitat to agricultural land.

Elevated levels of crop-raiding by primates are a by-product of natural resources becoming less available, and the nutritional riches of agricultural production becoming increasingly known to the primates. It is in this framework that complex human social and ethical issues become increasingly important when discussing primate conservation. Whether rural people value, fear or consume chimpanzees is a function of culture and context. Although the competition between the two species may not be even, both humans and chimpanzees exhibit adaptations or behavioural strategies that can only be properly understood when both are included in analyses. These human-ape interactions and the human perceptions of our nearest living relatives are important because the behaviour and choices of rural people who live in daily contact with wildlife ultimately will play a crucial role in its survival (Kiss, 1990).

Although the chimpanzees of Bossou are fortunate enough to be afforded a degree of protection and tolerance by local Manon people (Plate 9.2), other chimpanzee communities throughout Africa are not so privileged. The habituated community at Bossou provides us with a template for studying other chimpanzee communities living in small and heavily fragmented forests. For example, rather than exploiting cultivars, other chimpanzee communities overlap substantially with humans in their use of forest resources. Even though research conducted by Yamakoshi (2005) has confirmed that cultivated fields have been present on Mont Gban for over 30-years, the Bossou example illustrates a chimpanzee community that has already undergone a shift from natural resource competition to cultivar competition. Other chimpanzee communities may provide transitional examples of how this change in relations emerges and evolves. Competition between humans and chimpanzees can be considered as dynamic, involving a balance of natural and cultivated resources. Analysing these interactions in terms of costs and benefits to both parties will lead to a useful comparative predictor of the long-term outlook for chimpanzees.

Plate 9.2. The Bossou villagers making a sacrifice to the chimpanzees at the annual celebrations of Mont Gban.

Although the local people's perceptions of chimpanzee crop-raiding at Bossou were not systematically detailed through questionnaires, personal observations show that these varied depending upon crop type. Most crops at Bossou are not grown to sell, but are primarily for consumption. In the case of papaya, the fruit is considered mainly 'child food', and therefore the fact that it is raided is often not considered problematic. However, the presence of papaya trees brings chimpanzees into close proximity to people's houses, and this is perceived to increase the likelihood of chimpanzee attacks on humans, especially children. This has resulted in some people cutting down papaya trees located near the forest edge in an attempt to reduce human-chimpanzee contact. In contrast, pineapple is mostly grown for commercial reasons: one large pineapple can fetch a substantial amount of money, often the equivalent to half a day's salary. Therefore pineapple raiding is rarely tolerated, and humans heavily guard these cultivated areas with the use of dogs. However, in Bossou, pineapples are rarely cultivated in close proximity to the forest; whether this is a direct response to the high likelihood of chimpanzee raiding is unknown. Establishing the local importance of specific subsistence and cash crops in future studies of primate crop-raiding is paramount.

Cost-benefit analyses of economics, interactions, risks and rewards to each party can help tease out the significant ecological and cultural dimensions to human-chimpanzee relations. For example, if farmers perceive direct benefits from chimpanzee conservation, they are more likely to accept crop damage. Much money from KUPRI (Kyoto University Primate Research Institute in Japan) has been invested in improving the health and education facilities at Bossou, which probably contributes to a 'social pressure' to accept a certain degree of crop-raiding by the chimpanzees. We need detailed knowledge of social issues and pressures, as well as of chimpanzee ecology and ethology, at this interface of human-chimpanzee subsistence.

Communities of people who maintain positive attitudes will be those where conservation efforts have the greatest chance of being successful (Lee and Priston, 2005). In Western society, by highlighting the strong genetic, behavioural and physical similarities between humans and our ‘closest living relatives’ we assume that humans will be less inclined to exploit them; however, this may not apply to traditional cultures. For example, in communities where apes and other non-human primates are considered mythological, education may increase knowledge and decrease fear, and consequently apes may become de-mythologized, making them more vulnerable to direct exploitation. This further highlights the importance of understanding the beliefs of local people when establishing conservation education programmes.

We need to understand the workings of such fragile and contingent relations between humans and chimpanzees if we are to hope for the continued survival of this endangered great ape species. Wild chimpanzees have declined by more than 66% over the last 30-years, to a mere 200,000 individuals (Butynski, 2001). Chimpanzees and other non-human primates are threatened by an intricate web of factors including deforestation and fragmentation, poaching, disease, and capture for the pet trade, all of which are exacerbated by massive rates of human population growth. These are human problems, the solutions to which will benefit both people and chimpanzees.

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Appendix A

Crop-raiding species of primates, location, human perception and conflict context (adapted from Lee and Priston, 2005).

Common name	Scientific species name	Location	References	Human perceptions	Conflict context
Coquerel's sifaka	***Propithecus verreauxi coquereli***	Madagascar	(Ganzhorn and Abraham, 1991)	Protected or sacred in some areas.	Raid cashew fruit, mango, tamarinds.
Lemur	***Eulemur fulvus***	Madagascar	(Ganzhorn and Abraham, 1991)		Raid cashew fruit, mango, tamarinds.
Mongoose lemur	***Eulemur mongoz***	Comoros	(Tattersall, 1998)	This negative perception is relatively new. Farmers are now considering the use of poison to discourage perceived lemur depredations, and there is also widespread use of slingshots by children.	Raid breadfruit, jackfruit and coconut.
Edward's sportive lemur	***Lepilemur mustelinus edwardsi***	Madagascar	(Ganzhorn and Abraham, 1991)		Raid cashew fruit, mango, tamarinds.
Western woolly lemur	***Avahi laniger occidentalis***	Madagascar	(Ganzhorn and Abraham, 1991)		Raid cashew fruit, mango, tamarinds.
Aye-Aye	***Daubentonia madagascariensis***	Madagascar	(Fitter, 1974; Mittermeier *et al*., 1994; Oryx, 1964)	Local superstitions surrounding this species often mean it is killed if it passes through a village.	Raid coconut and lychee plantations.
Potto	***Perodicticus potto***	Cameroon	(Pimley, pers .comm: Priston)	No negative impact on perceptions. Losses are not great and are attributed to other animals as they raid at night.	Raids gardens for fruit.
Allen's squirrel galago	***Galago alleni***	Cameroon	(Pimley, pers. comm: Priston)	Few negative perceptions reported.	Nocturnal garden raider.
Common marmoset	***Callithrix jacchus***	Brazil	(Moura, pers. comm: Priston)		Raids fruit plantations.
Brown capuchin	***Cebus apella***	Brazil, Northern and Central America	(Freese and Oppenheimer, 1981; Lynch and Rimoli, 2000; Moura, pers. comm: Priston)	The use of a dead monkey hung at the edge of a field has limited success, but depends on the alarm call of an approaching troop. Kept as pets and also hunted.	Prolific crop raider. Raids maize and sugar cane. Increased manual dexterity makes this species particularly troublesome.
White-fronted capuchin	***Cebus albifrons***	Brazil, Northern and Central America	(Freese and Oppenheimer, 1981;		Raids agricultural crops, particularly maize.
White-faced capuchin	***Cebus capuchinus***	Costa Rica	(Gonzalez-Kirchner and Sainz de la Maza, 1998; Baker and Schutt, 2005)	Considered by many farmers to be the most destructive raider. However, in some parts considered to have pruning effect.	Raids agricultural crops, particularly maize and bananas.
Weeping capuchin	***Cebus olivaceus***	Venezuela	(Kinsey and Norconk, 1988)		Raids agricultural crops
Central American squirrel monkey	***Cebus oerstedii***	Costa Rica	(Gonzalez-Kirchner and Sainz de la Maza, 1998)		Occasional raider of plantations
Mantled howler monkey	***Alouatta palliata***	Costa Rica	(Gonzalez-Kirchner and Sainz de la Maza, 1998)		Occasional raider of plantations
Rhesus macaque	***Macaca mulatta***	India, Nepal, Pakistan, China	(Chalise, 2000; Goldstein and Richard, 1989;	Weed species.	Raid wheat and rice fields and edible crops.

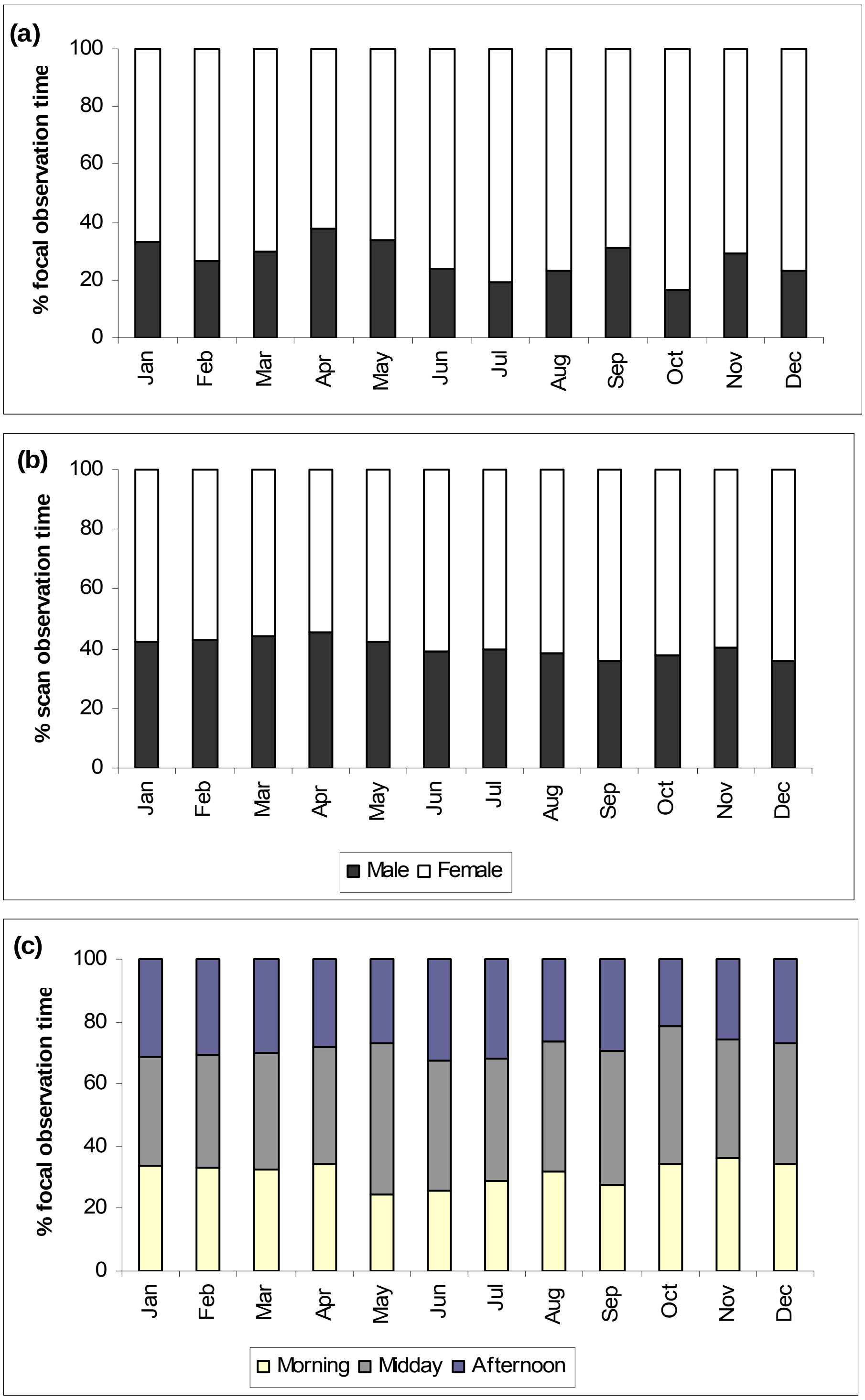
			Lindburg, 1976; Makwana, 1978; Malik and Johnson, 1994; Mukherjee, 1972; Neville, 1968; Pirta *et al.*, 1997; Richard and Goldstein, 1981; Southwick and Lindburg, 1986; Southwick and Siddiqi, 1994; Wang and Quan, 1986; Zang *et al.,*1989)		
Bonnet macaque	***Macaca radiata***	India	(Caldecott, 1986; Crockett and Wilson, 1980; Eudey, 1986; Malik and Johnson, 1994; Richard and Goldstein, 1981; Richard *et al.*, 1989; Southwick and Lindburg, 1986)	Weed species.	
Long-tailed macaque	***Macaca fascicularis***	Borneo, Malaysia, Mauritius, Sumatra, Thailand	(Caldecott, 1986; Crockett and Wilson, 1980; Eudey, 1986; Richard and Goldstein, 1981; Richard *et al.*, 1989; Salafsky, 1993)	Weed species. Major pest where introduced.	Damages sugar cane, vegetables and fruit.
Barbary macaque	***Macaca sylvanus***	Gibraltar, North Africa	(Eudey, 1994; Richard and Goldstein, 1981; Richard *et al.*, 1989; Tappen, 1960)	Tourist attraction; provisioned and poses health problems through contact. Forestry pest in High Atlas.	Population expansion due to provisioning on Gibraltar.
Buton macaque	***Macaca ochreata***	Sulawesi	Priston, 2005; Lee and Priston, 2005.	Crop-raiding is tolerated	Raids variety of cultivars cassava, papaya, sweet potato, maize.
Assam macaque	***Macaca assamensis***	Nepal, Thailand	(Chalise, 2000; Eudey, 1986, 1994; Richard and Goldstein, 1981; Richard *et al.*, 1989; Wheatley and Harya Putra, 1994)		Edible crops.
Japanese macaque	***Macaca fuscata***	Japan	(Asquith ,1989; Knight, 1999; Richard and Goldstein, 1981; Richard *et al.*, 1989)	Tourist attraction.	Crop raider in past; provisioned at feeding sites.
Pigtail macaque	***Macaca nemestrina***	Indonesia, Malaysia, Thailand	(Crocket and Wilson, 1980; Richard and Goldstein, 1981; Richard *et al.*, 1989; Salafsky, 1993)	Used for harvesting coconuts.	Plantation pest.
Taiwan macaque	***Macaca cyclopis***	Taiwan	(Richard and Goldstein, 1981; Richard *et al.*, 1989)	Tourist attraction. Provisioned in some places.	Edible crop pest.
Toque macaque	***Macaca sinica***	Sri Lanka	(Richard and Goldstein,1981; Richard *et al.*, 1989)	Weed species.	
Liontail macaque	***Macaca silenus***	India	(Richard *et al.*,1989)	Little evidence that they are serious crop pests, but they are shot by farmers in the belief they damage the cardamom crop.	
Celebes crested macaque	***Macaca nigra***	Sulawesi	(O'Brien and Kinnaird, 1997; Whitten *et al.*, 1988)	Pest with some incorporation into traditional belief systems. Hunted.	Garden raider.
Moor macaque	***Macaca maura***	Sulawesi	(Richard *et al.*,1989)		Raids agricultural crops infrequently.

Stump-tailed macaque	***Macaca arctoides***	China, India, Thailand	(Richard and Goldstein,1981; Richard *et al.*, 1989)	Considered a pest	Raids agricultural crops.
Anubis and yellow baboon	***Papio anubis & P. cynocephalus***	Kenya, Uganda, Nigeria	(Harding, 1973; Hill, 2000; Maples, 1969; Maples *et al.*, 1976; Musau and Strum, 1984; Naughton Treves, 1998a, b; Oyaro and Strum, 1984; Strum, 1984, 1987, 1994; Tappen, 1960; Ross and Warren, 2006; Reynolds, 2005)	Considered serious crop pests. Viewed as malicious, cunning and dangerous.	Raid maize, banana, cassava and cashew crop as well as fruit. Raids garbage houses and lodges. Use of 'deceptive' tactics demonstrated.
Hamadryas baboon	***Papio hamadryas***	Saudi Arabia	(Biquand *et al.*, 1992; Dunbar, 1977; Tappen, 1960	Considered sacred, but also dangerous pest species.	Raids garbage and crops.
Chacma baboon	***Papio ursinus***	Botswana	(Balakrishnan and Ndhlovu, 1992; Parry and Campbell, 1992)		Raids rubbish, lodges and crops.
Gelada baboon	***Theropithecus gelada***	Ethiopa	(Dunbar 1977)	Shot for manes in traditional dress.	Rare raider of wheat farms.
Mandrill	***Mandrillus sphinx***	Gabon, Cameroon	(Lahm, 1996; Tappen, 1960)	Intensely hunted and valued for meat.	Raids cassava.
Drill	***Mandrillus leucophaeus***	Nigeria, Cameroon	(Lee *et al.*, 1988; Morgan, pers. Comm: Priston)	Intensely hunted and valued for meat.	
Hanuman langur	***Semnopithecus entellus***	India	(Chalise, 2000; Malik and Johnson, 1994; Mohnot, 1971; Pirta *et al.*, 1997; Southwick and Lindburg, 1986)	Sacred primate to Hindus.	Raids mainly large fruit trees.
Western purple-faced langur	***Semnopithecus vetulus nestor***	Sri Lanka	(Mittermeier et al., 2006)		Raid cultivated fruits.
Maroon langur	***Presbytis rubicunda***	Borneo	(Salafsky, 1993)	Perceived to be destructive.	Often raids gardens.
Angolan colobus	***Colobus angolensis***	Angola	(Wakuluzu, 1999)		Raid agricultural areas.
Guereza colobus	***Colobus guereza***	Uganda	(Hill, 2000; Oates, 1977)		Raids fruit plantations and cashews.
Eastern colobus	***Colobus abyssinicus***	Africa	(Tappen, 1960)		Infrequent raider.
Black colobus	***Colobus satanus***	Gabon	(Lahm, 1996)		Reported to raid agricultural crops infrequently.
Zanzibar red colobus	***Procolobus kirkii***	Zanzibar	(Siex and Struhsaker, 1999, 2005)	Raiding may actually increase harvest despite farmers' opinions to the contrary.	Raids coconuts and other plantations.
Talapoin monkey	***Miopithecus talapoin***	Gabon	(Lahm, 1996)		Reported to raid agricultural crops.
Red-capped mangabey	***Cercocebus torquatus***	Congo, Nigeria, Cameroon, Guinea, Gabon	(Lahm, 1996; Tappen, 1960)		Garden raider, peanut crops.
Smoky mangabey	***Cercocebus albigena***	Gabon	(Lahm, 1996)		Reported to raid agricultural crops infrequently.
Sooty mangabey	***Cercocebus atys***	Ghana, Guinea, Ivory Coast, Sierra Leone, Liberia	(Tappen, 1960)		Cacao plantation and garden raider.
Agile mangabey	***Cercocebus galeritus agilis***	Central African Republic, Cameroon, Gabon, Congo, DRC, Uganda, Tanzania, Kenya	(Kamisse and Turkalo, 2002; Tappen, 1960)		Rice farm raider. Also raids maize, cassava, papaya, peanuts and will steal cassava being soaked for consumption.
Sclater's guenon	***Cercopithecus sclateri***	Nigeria	(Oates *et al.*, 1992)	Heavily hunted.	Raids gardens.
Moustached monkey	***Cercopithecus cephus***	Gabon, Cameroon, DRC	(Lahm, 1996; Tappen, 1960)		Regular raider.
Patas monkey	***Erythrocebus patas***	East Africa	(Tappen, 1960)		Occasional farm raider.

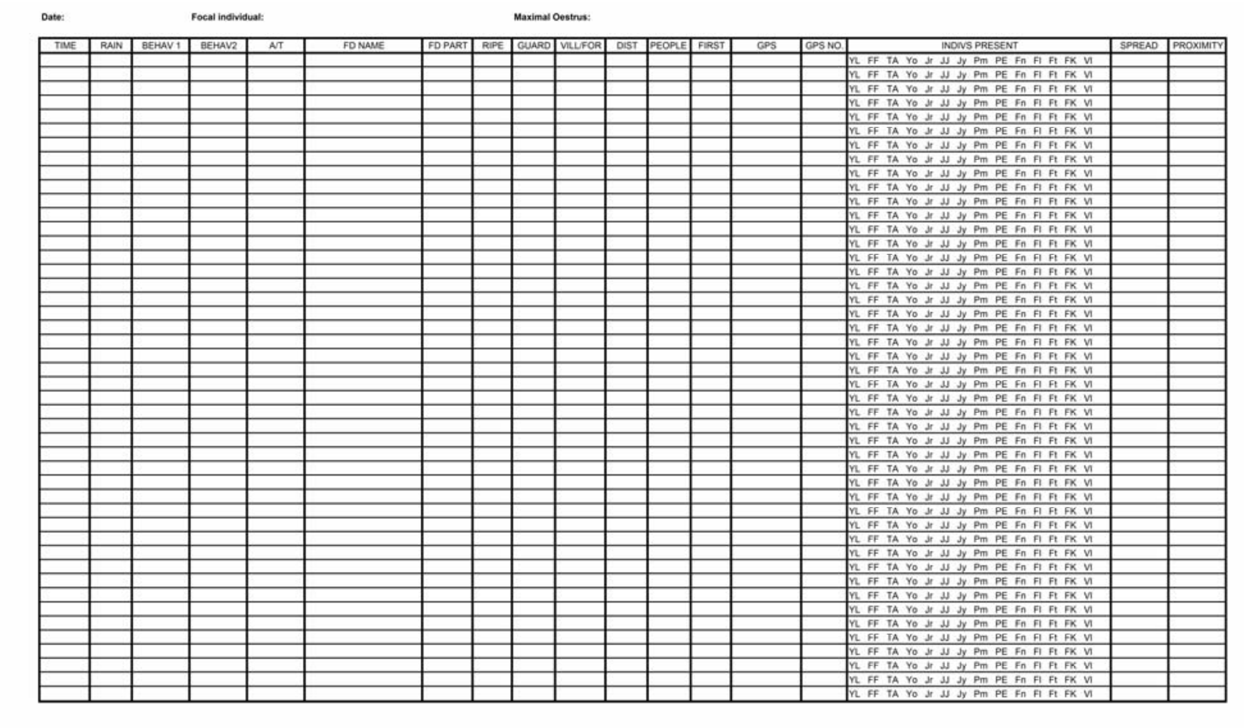
Vervet monkey	***Cercopithecus aethiops***	Barbadoss, Cameroon, Kenya, Malawi, St Kitts	(Balakrishnan and Ndhlovu, 1992; Boulton *et al.*, 1996; Eley and Else, 1984; Gillingham and Lee, 1999; Hill, 2000; Kavannagh, 1978; King and Lee, 1987; Lee *et al.*, 1986; Naughton Treves, 19978a, b: Parry and Campbell, 1992; Struhsaker, 1967; Tappen, 1960)	Often resident on farms. Considered 'vermin' and a major weed species.	Raids maize, banana and cassava.
Red-tail monkey	***Cercopithecus ascanius***	Uganda	(Hill, 2000; Naughton Treves, 1998a, b)		Raids maize, banana and cassava mainly.
Blue monkey	***Cercopithecus mitis***	Kenya, Uganda, Zanzibar, South Africa	(Bell, 1984; Hill, 2000; Oates, 1977; Siex and Struhsaker, 1999)	Tourist lodge pest. Considered major pest species.	Crop and plantation raider.
Greater spot-nosed guenon	***Cercopithecus nictitans***	Gabon	(Lahm, 1996)		Reported to raid agricultural crops infrequently.
L'hoest monkey	***Cercopithecus l'hoesti***	Uganda	(Biryahwaho, 2002; Naughton Treves, 1998a, b)		Infrequent garden raiders.
Sun-tailed guenon	***Cercopithecus solatus***	Gabon	(Lahm, 1996)		Reported to raid agricultural crops infrequently.
Agile gibbon	***Hylobates agilis***	Borneo	(Salafsky, 1993)	Often present in forest garden-buffer zones.	Occasionally raids crops.
Western lowland gorilla	***Gorilla gorilla gorilla***	Gabon	(Lahm, 1996)		Reported to raid agricultural crops such as cassava.
Mountain gorilla	***Gorilla gorilla berengei***	Uganda	(Biryahwaho, 2002; Andama, E. pers. comm: Priston)	Increased due to loss of fear of humans through habituation. Considered quiet animals, generally afraid of humans. Valuation in context of eco-tourism.	Raid field crops.
Eastern chimpanzee	***Pan troglodytes schweinfurthii***	Uganda, Tanzania	(Biryahwaho, 2002; Hill, 2000; Reynolds, 2005; Naughton Treves, 1998a, b)	Considered human-like yet dangerous.	Raid maize, banana, cassava, mango and sugar plantations. Use cultivars as fallback foods.
Central chimpanzee	***Pan troglodytes troglodytes***	Gabon	(Lahm, 1996)		Raid cultivars.
Western chimpanzee	***Pan troglodytes verus***	Guinea, Senegal.	(Dunnet, 1970; Takemoto, 2000; Pruetz, 2002; Humle, 2003 a,b; Yamakoshi, 2005)	Considered sacred, and are not hunted in some parts due to cultural taboo. Overlap between human and chimpanzee in use of forest and cultivated resources.	Extensive crop-raiders of orange, grapefruit, papaya, cassava and rice. Use cultivars as fallback foods.
Bornean orangutan	***Pongo pygmaeus***	Borneo	(Salafsky, 1993; Siregar, pers. comm: Priston; Anne Russen, pers. comm.)		Reported to damage oil palm plantations. Use cultivars as fallback foods.
Sumatran orangutan	***Pongo abelii***	Sumatra	(SOCP, 2002)	Often killed when found raiding.	Reported to damage fruit tree crops and palm oil plantations. Use cultivars as fallback foods.

Appendix B

Appendix B1. Monthly observational biases showing the percentage of (a) focal and (b) scan observation time between the sexes [scan samples (min: 16.6, max: 37.7, SD 3.1) showed less temporal variability than focal samples (min: 36, max: 45.8, SD 6.3)] and (c) focal observation time at different periods of the day [midday had the longest observation time; morning: 0700-1059 (min: 24.6, max: 36.3, mean: 31.5, SD: 3.8), midday: 1100-1459, (min: 35.1, max: 48.3, mean: 40.1, SD: 3.8) and afternoon: 1500-1859 (min: 21.4, max: 32.3, mean: 28.5, SD: 3.1)].



Appendix B2. Front and back of check sheet used in data collection (reduced in size).



Date: **Focal individual:** **Maximal Oestrus:**

TIME	RAIN	BEHAV 1	BEHAV2	A/T	FD NAME	FD PART	RIPE	GUARD	VILL/FOR	DIST	PEOPLE	FIRST	GPS	GPS NO.	INDIVS PRESENT	SPREAD	PROXIMITY
															YL FF TA Yo Jr JJ Jy Pm PE Fn Fl Ft FK Vl		
															YL FF TA Yo Jr JJ Jy Pm PE Fn Fl Ft FK Vl		
															YL FF TA Yo Jr JJ Jy Pm PE Fn Fl Ft FK Vl		
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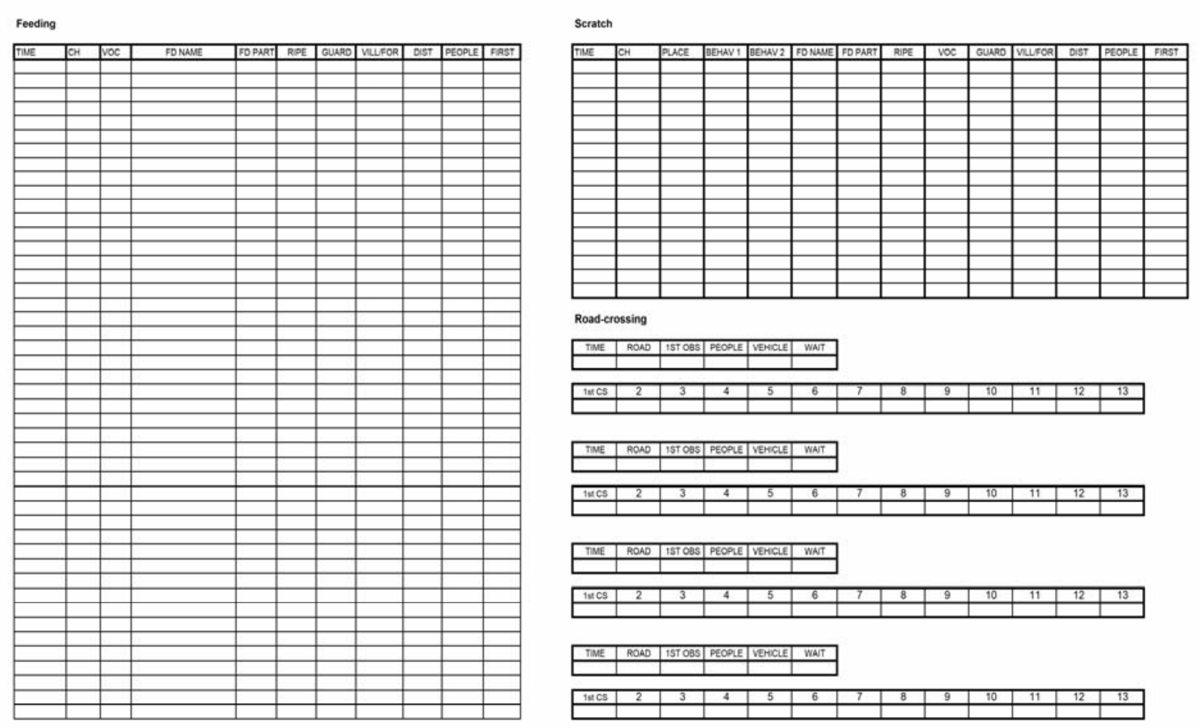


Feeding

TIME	CH	VOC	FD NAME	FD PART	RIPE	GUARD	VILL/FOR	DIST	PEOPLE	FIRST

Scratch

TIME	CH	PLACE	BEHAV 1	BEHAV 2	FD NAME	FD PART	RIPE	VOC	GUARD	VILL/FOR	DIST	PEOPLE	FIRST

Road-crossing

TIME	ROAD	1ST OBS	PEOPLE	VEHICLE	WAIT

1st CS	2	3	4	5	6	7	8	9	10	11	12	13

TIME	ROAD	1ST OBS	PEOPLE	VEHICLE	WAIT

1st CS	2	3	4	5	6	7	8	9	10	11	12	13

TIME	ROAD	1ST OBS	PEOPLE	VEHICLE	WAIT

1st CS	2	3	4	5	6	7	8	9	10	11	12	13

TIME	ROAD	1ST OBS	PEOPLE	VEHICLE	WAIT

1st CS	2	3	4	5	6	7	8	9	10	11	12	13

Appendix B3. Ethogram used during focal animal samples.

Code	Behaviour 1	Description	Code	Behaviour 2	Description
FE	Feeding	The direct gathering, processing and ingestion of food	**AD**	Ant-dipping	Insertion and withdrawal of a fishing probe to obtain ants
			ALD	Algae-dipping	Insertion and withdrawal of a fishing probe to obtain algae
			BG	Begging for food	Begging for food from the possessor
			DK	Drinking	Drinking of water or other liquids
			FG	Foraging	Any foraging behaviours
			LS	Leaf sponging	Using a sponge made of leaves to drink water
			MV	moving	Moving whilst feeding
			NC	Nut-cracking	Use of stone tools to crack open nuts
			PE	Peeling	The peeling of a food item
			PK	Picking	Picking of a food item
			PL	Pull	The pulling of an object to obtain food item
			PP	Pestle pounding	The pounding of oil-palm with tool to obtain the pith
			RP	Riping	The ripping of a food item
			SC	Scraps	Feeding on food discarded by other individuals
			SH	Sharing	Allowing another individual to take food controlled by owner
			WD	Wadge	The chewing of fibrous foods before ingestion
MV	Moving	Any travel on the ground or trees	**CS**	Cross road	Crossing the small or large road
			FD	Food transport	Transporting food
			S	Searching	Deliberate food searching behaviours
RE	Resting	Inactivity or relax behaviours: Ground, tree or nest.	**AS**	Sitting or lying down	Sitting or lying down on the ground or in a tree
			LC	Leaf-clipping	Pull a leaf repeatedly between lips or teeth with one hand
			NE	Nesting	Construct a platform for resting or sleeping
			ST	Standing	Standing without moving quadrapedially
			SG	Self-grooming	Any self-directed grooming behaviour
SC	Social	Aggressive, affiliative or communicative interactions	**BS**	Branch shaking	The shaking of a branch to get attention
			CP	Copulation	Intromission and pelvic thrusting between male and female
			DP	Displaced	Any displacement caused by another individual
			DS	Display	Any display behaviour
			FT	Fight	Physical aggressiveness between individuals
			GR	Grooming	Any grooming behaviour involving another individual
			HT	Heel tapping	Tapping of heel to get attention
			LC	Leaf-clipping	Pull a leaf repeatedly between lips or teeth with one hand
			PA	Play	Play behaviour, usually involving infants

Appendix B4 **Distance estimation tests performed on author KH during the study. Distances measured and estimated to the nearest metre. During all three periods, there were no significant differences between actual and estimated distances (Paired samples t-test; May 2004: $t_{19} = 1.00$, p=0.33; January 2005: $t_{19} = 0.24$, p=0.815; November 2005: $t_{19} = 1.00$, p=0.33).**

			May 2004		January 2005		November 2005	
Trial			**Actual (m)**	**Estimate (m)**	**Actual (m)**	**Estimate (m)**	**Actual (m)**	**Estimate (m)**
1	**Arboreal**	**Forest**	21	20	16	19	20	20
2			15	15	21	20	46	45
3			41	41	55	50	6	6
4			7	7	17	18	22	22
5			12	13	7	5	5	5
6		**Open**	24	23	15	16	12	11
7			4	5	4	4	7	7
8			8	8	16	16	18	17
9			55	54	7	7	4	4
10			9	10	43	45	33	30
11	**Terrestrial**	**Forest**	29	29	17	17	12	13
12			33	31	9	10	53	50
13			12	12	49	50	23	25
14			5	6	4	4	6	6
15			25	24	11	13	18	19
16		**Open**	3	3	8	8	15	15
17			22	20	3	3	7	6
18			15	15	20	20	8	8
19			32	32	7	6	25	23
20			6	5	52	48	51	53

Appendix C

Appendix C1. All plant species present on the transect, including scientific name and family, the local manon name, the plant type (L: liana, PA: small trees of less than 10m or petite arbre, A: medium size tree of 10-20m or arbre, GA: large tree of more than 20m or grande arbre), the number of individuals of that species present on the transect, and whether the fruit of that species is fed on by chimpanzees (0: no, 1: yes).

Scientific name	Family	Manon name	Type	Pres	Ch fed
Acacia pennata	Mimosaceae	DAN / GO-DAN	L	3	0
Albizia adianthifolia	Mimosaceae	KPANFORO	A	16	0
Albizia ferruginea	Mimosaceae	KPANFORO	A	41	0
Albizia lebbeck	Mimosaceae	SAFOUKLE	A	24	0
Albizia zygia	Mimosaceae	KPANTI	A	137	0
Alchornea cordifolia	Euphorbiaceae	FANALE	PA	117	0
Allophyllus africanus	Sapindaceae	WEILAZANA	PA	15	0
Amphimas ptericarpioides	Caesalpiniaceae	GBIEOUNDOYIRI	GA	42	0
Aningueria altissima	Sapotaceae	YARA	GA	55	1
Anthocleista djalonensis	Loganiaceae	GONYIRI	A	1	0
Anthocleista sp	Loganiaceae	LOU ROU	PA	1	0
Anthonotha macrophylla	Caesalpiniaceae	GBEKETOA	PA	186	0
Antiaris africana	Moraceae	KPO	GA	77	1
Baphia nitida	Papilionceae	DORO	PA	3	0
Belschiemeidia mannii	Lauraceae	KWE	PA	4	0
Blighia sapida	Sapindaceae	GLEINPOUROU	GA	1	1
Blighia welwitschii	Sapindaceae	GLEIN	GA	26	1
Bombax buonopozense	Bombacaceae	GUEE / GUEDERE	GA	3	0
Bosquea angolensis	Moraceae	PAA	A	74	0
Bridelia micrantha	Euphorbiaceae	LUUGUAN	PA	11	1
Canarium schweinfurthii	Burseraceae	BIIN	A	35	1
Canthium horizontale	Rubiaceae	NI-INWELEYIRI	PA	7	1
Carapa procera	Meliaceae	GBON	PA	113	0
Cassia sieberiana	Caesalpiniaceae	SEKEYEIN	L	13	0
Cassipourrea lescotiana	Rhizophoraceae	BOMALE	PA	21	0
Ceiba pentandra	Bombacaceae	GUE	GA	38	0
Celtis adolfi-frederici	Ulmaceae	KOSINGWAN	A	11	1
Chlorophora excelsa	Moraceae	GUEI	GA	74	0
Chlorophora regia	Moraceae	GUEI LEI SENA SANA	GA	2	0
Cissus aralioides	Vitaceae	KANSO / KIE LIE DENE	L	2	1
Citropsis articulata	Rutaceae	TOFONGHENE	PA	15	1
Clerodendron speciosissimum	Verbenace	GUENEZOROGUAN	L	1	0
Cnestis ferruginea	Connaraceae	N	PA	1	0
Cola cordifolia	Sterculiaceae	BOBA	A	6	1
Cola reticulata	Sterculiaceae	GUELAPURUYIRI	PA	14	1
Cratispernum laurinum	Rubiaceae	GBEKE	PA	122	0
Cratispernum caudatum	Rubiaceae	YIELAGBEKE	PA	1	0
Crossonophelis adamii	Sapindaceae	YIRI WANGA BLE WANGA		3	1
Crossonophelis africanus	Sapindaceae	WUISON-YIRI / BIE SOON YIRI	L	21	1
Crossonophelis sp	Sapindaceae	GLAH	L	1	0
Cuviera macroura	Rubiaceae	LOUCAFELETII	PA	1	0
Dalbergia albiflora	Papilionceae	TUNULAGUAN	L	1	0
Daniella thurifera	Caesalpiniaceae	BHELIN / GBAAN	A	7	0
Dialium dinklagei	Caesalpiniaceae	KPEI	A	2	1
Dracaena perrotetii	Agavaceae	SIILADENE	PA	163	0
Dycrostachys glomerata	Mimosaceae	TENE	PA	12	0

Elaeis guineensis	Palmae	TOUN	A	64	1
Entada pursaetha	Mimosaceae	DIE	L	1	0
Entandrophragma sp	Meliaceae	KPITIRI	A	1	0
Erythrina senegalensis	Papilionceae	GUEIYIRI	PA	1	0
Fagara leprieurii	Rutaceae	MENEYIRI	PA	1	0
Ficus exasperata	Moraceae	NYANALE	A	41	1
Ficus macrosperma	Moraceae	GORO	A	1	1
Ficus mucuso	Moraceae	SOROBLO	GA	18	1
Ficus sur	Moraceae	BLO	A	70	1
Ficus umbellata	Moraceae	GORO	A	9	1
Ficus vogelli	MORACEAE	GORO	A	1	1
Funtumia elastica	Apocynaceae	SEKELE	PA	25	0
Gambeya gigantia	Sapotaceae	WEINGBEINLE / BOMO	A	6	1
Gambeya perpulchra	Sapotaceae	WEINGBEINLEGUAN	GA	1	1
Gambeya taiense	Sapotaceae	BOMOGWAN	A	1	0
Grewia barombiensis	Tiliaceae	DIETII	PA	1	0
Grewia pubescens	Tiliaceae	LUU ZAN	PA	2	1
Hannoa klaineana	Siimaroubaceae	FAA	PA	3	0
Harrisonia abyssinica	Simaroubaceae	KAABA	PA	11	0
Harungana madagascariensis	Hypericeae	LORO	PA	7	1
Hippocratea paniculata	Celastraceae	KPANE / KAPANE TII	L	1	0
Holarrhena floribunda	Apocynaceae	MINASEKELE	A	3	0
Omalium aubrevillei	Samydaceae	BARAKELEZEYIRI	A	16	1
Omalium mole	Samydaceae	WENITII	A	3	0
Itridendron bequaertii	Sapotaceae	LOUGIN / LOUGEI	A	6	1
Khaya grandifolia	Meliaceae	KPITIRILEBOBOI	GA	14	1
Khaya ivoriensis	Meliaceae	KPITIRIZORO	GA	4	1
Kigelia africana	Bignoniaceae	DEII / BONN	A	5	0
Landolphia inserta	Apocynaceae	DEKPOLO / BLEKPOLO	L	3	1
Landolphia owariensis	Apocynaceae	SENEDE	L	3	1
Lasciodiscus marmoratus	Rhamnaceae	LOUBONBON	PA	4	0
Lecaniodiscus cupanoides	Sapindaceae	GLEINKABA	PA	60	1
Leptoderris brachyptera	Papilionceae	TOUBLEGWAN	L	2	0
Leptoderris fasciculata	Papilionceae	TOUBLE	L	2	0
Lindackeria dentata	Flacourtiaceae	KOOYIRI	PA	3	0
Lophira alata	Ochnaceae	FLII	GA	1	0
Macarange barteri	Euphorbiaceae	BEGHOU	PA	2	1
Macaranga heterophylla	Euphorbiaceae	GBINLAGO	PA	48	0
Macaranga huritifolia	Euphorbiaceae	GHOUPOUROU	PA	17	0
Mangifera indica	Anacardiaceae	MANGOLO	A	5	1
Manihot utilissima	Euphorbiaceae	ZIKIZAKA	H	2	0
Mareya micrantha	Euphorbiaceae	WANA	PA	49	0
Mezoneuron benthamianum	Caesalpiniaceae	KPONKPON	A	1	0
Milletia dincklagei	Papilionceae	KPETUAN LEEKENE	PA	3	0
Milletia lanepoolei	Papilionceae	BIELAMAYIRI	PA	23	0
Milletia zechiana	Papilionceae	KPETUAN	PA	110	1
Mitragyna stipulosa	Rubiaceae	BOON	A	2	0
Monodora tenuifolia	Annonaceae	KPANAYIRI	A	17	1
Morinda germinata	Rubiaceae	ZOROBON	PA	39	0
Morus mesozygia	Moraceae	GHANGBE	GA	16	1
Musanga cecropioides	Moraceae	WOLO	A	29	1
Myrianthus arboreus	Moraceae	GBALE	PA	42	1
Myrianthus libericus	Moraceae	GBALO	PA	194	1
Myrianthus serratus	Moraceae	GBALOGWAN	PA	1	0

Napoleona leonensis	Lecythidaceae	NIMO / DIPAADO-YIRI	PA	7	1
Napoleona vogelli	Lecythidaceae	DOLE / DEYI / DEI	PA	11	1
Nauclea diderichii	Rubiaceae	WEINYIRI	PA	1	1
Nauclea latifolia	Rubiaceae	YEILAWEINYIRI / YEILA ZOROGBON	PA	5	1
Newbouldis laevis	Bignoniaceae	DIAN	PA	56	0
Octoknema borealis	Octoknemataceae	NEINNINYIRI / NEINEI YIRI	A	1	0
Ongokea gore	Olacaceae	KOSING	A	1	0
Oxyanthus abyssinica	Rubiaceae	LUKAFE LEE TU	PA	1	0
Oxyanthus formosus	Rubiaceae	WOLO-YIRI	PA	3	0
Parkia bicolor	Mimosaceae	KOMI	GA	40	1
Pentaclethra macrophylla	Mimosaceae	KPAKELEGUAN	GA	1	0
Phyllanthus discoideus	Euphorbiaceae	TIE	PA	62	0
Piptadenia africana	Mimosaceae	BERA	GA	14	0
Premna hispida	Verbenaceae	NEGBOSOROYIRI	PA	20	0
Pseudospondias microcarpa	Anacardiaceae	PONI	A	114	1
Pycnanthus angolensis	Myristicaceae	DINI	A	29	1
Rauvolfia vomitoria	Apocynaceae	MON-YAYIRI	PA	19	0
Rhaphiostylis beninensis	Icacinaceae	PLOPLO	PA	6	1
Ricinodendron heudelotti	Euphorbiaceae	KOO	GA	15	0
Rinorea oblongiflora	Violaceae	GBAYIRI	PA	1	0
Rothmania hispida	Rubiaceae	LUA SONI	PA	9	1
Rothmania longiflora	Rubiaceae	LOUKPILALE	PA	1	1
Rothmania withfieldii	Rubiaceae	BONOLEKENIN	PA	1	1
Samanea africana	Mimosaceae	SEINBERA	N	8	0
Samanea dinklagei	Mimosaceae	SINBERA	N	7	0
Santiria trimera	Burseraceae	GOO	PA	15	0
Solanum verbascifolium	Solanaceae	NAWAN	PA	24	0
Spathodea campanulata	Bignoniaceae	BOLOTANYIRI	PA	34	0
Spondias cytera	Anacardiaceae	GUEIBUNA	PA	47	0
Spondias mombin	Anacardiaceae	BUNA	PA	31	1
Sterculia tragacantha	Sterculiaceae	TOU	A	229	1
Terminalia glautescens	Combretaceae	BEIBAN	A	2	0
Terminalia ivoriensis	Combretaceae	BEI	GA	28	0
Terminalia superba	Combretaceae	BEIBAN	A	7	0
Tetracera potatoria	Dilleniaceae	ZOBLE	L	1	0
Tertrochidium didymostemon	Euphorbiaceae	LONGLO	PA	63	0
Tremna guineensis	Ulmaceae	WAMA / BIE LA WAMA	PA	9	0
Tricalysia bracteata	Rubiaceae	LUUKAFE	PA	3	0
Trichilia emitica	Meliaceae	WAAGWAN	A	1	0
Trichilia heudelotti	Meliaceae	WAA	A	72	1
Triplochiton scleroxylon	Sterculiaceae	ZOKULO	A	25	0
Turreanthus africanus	Meliaceae	SOUNG	A	1	0
Uapaca heudelotti	Euphorbiaceae	SONA	A	6	1
Uvariopsis guineensis	Annonaceae	BLAYIBHONO / GBLEINGPOUROU	PA	4	1
Visimia guineensis	Hypericaceae	GBALALORO	PA	4	0
Vitex doniana	Verbenaceae	BOUYIRI / BOM	A	2	1
Vitex micrantha	Verbenaceae	BOUYIRI	A	1	1
Voacanga africana	Apocynaceae	TOKLOUA	PA	49	0
Xylopia aethiopica	Annonaceae	GBAN	PA	4	0
Xylopia paravifolia	Annonaceae	GBANZORO	PA	1	0

Appendix C2. The length (metres), number of trees, and mean tree DBH (cm) on each section of the transect.

		Length	Number of trees	Mean DBH
Gban	North	380	239	17.8
	South	260	207	18.7
	Seiba	470	365	12.7
	East	436	360	14.6
	West	540	432	13.8
Guein	North	210	163	18.1
	South	660	367	14.7
	East	210	214	10.6
	West	690	508	14.8
Gboton	North	115	99	12.6
	South	309	215	13.2
	East	320	305	11.3
	West	139	137	12.4
Total		**4739**	**3611**	

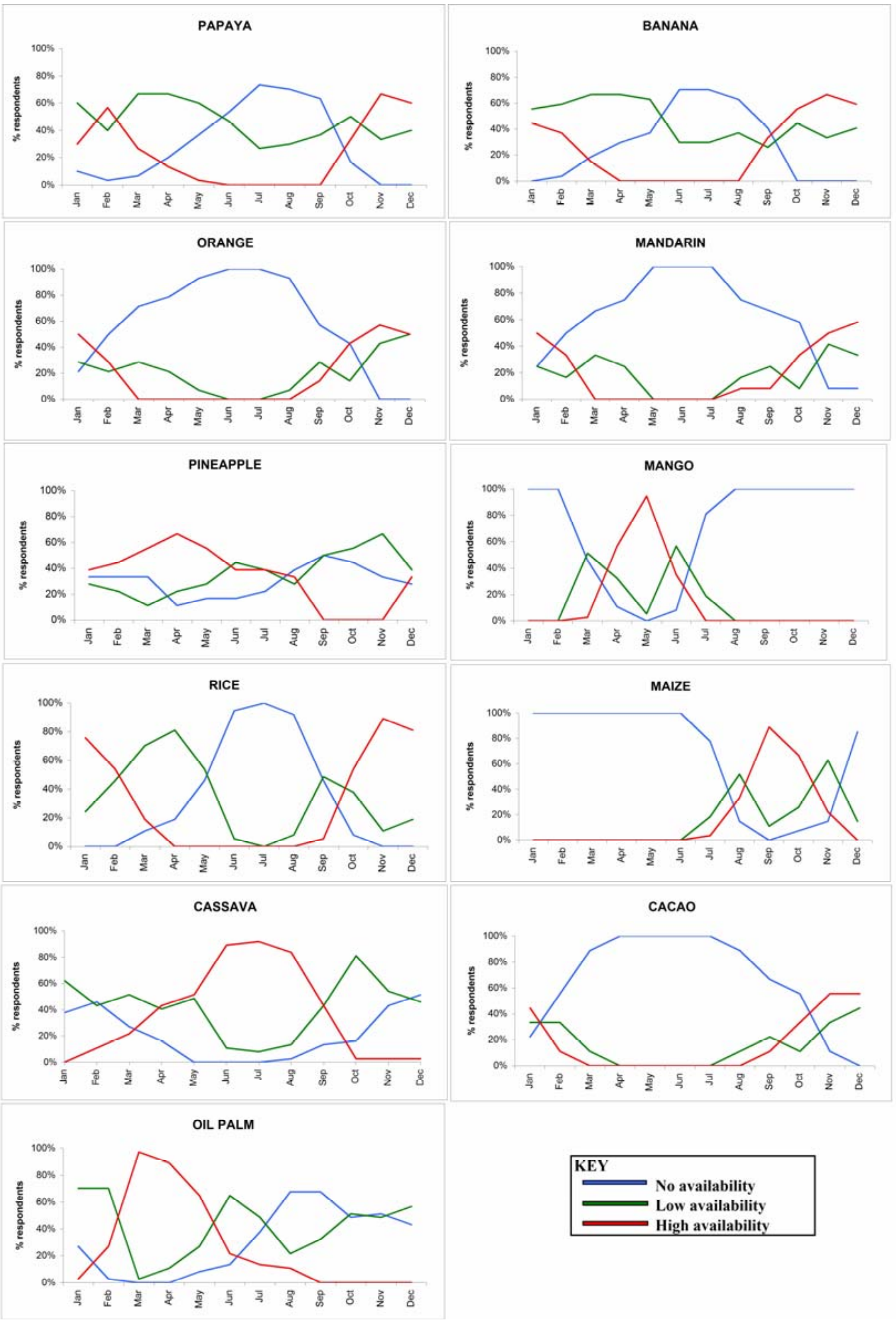
Appendix C3. All trees that were cut or died on the transect during the study period, including tree location, scientific name and family, the plant type (PA: small trees of less than 10m or petite arbre, A: medium size tree of 10-20m or arbre), the DBH of the tree and whether that species is fed on by chimpanzees (0: no, 1: yes).

Location	Scientific plant name	Family	Type	DBH (cm)	Ch fed
Gboton E	Macaranga huritifolia	Euphorbiaceae	PA	28.6	0
	Sterculia tragacantha	Sterculiaceae	A	44.2	1
	Solanum verbascifolium	Solanaceae	PA	18.1	0
	Phyllanthus discoideus	Euphorbiaceae	PA	28.8	0
	Allophyllus africanus	Sapindaceae	PA	22.8	0
	Macaranga heterophylla	Euphorbiaceae	PA	17.6	0
Gboton W	Sterculia tragacantha	Sterculiaceae	A	26	1
	Anthonotha macrophylla	Caesalpiniaceae	PA	23.3	0
	Macaranga heterophylla	Euphorbiaceae	PA	32	0
	Ficus exasperata	Moraceae	A	30.1	1
Gboton N	Musanga cecropioides	Moraceae	A	41.2	1
	Milletia zechiana	Papilionaceae	PA	17.4	1
	Solanum verbascifolium	Solanaceae	PA	26	0
	Solanum verbascifolium	Solanaceae	PA	31	0
Gboton S	Bridelia micrantha	Euphorbiaceae	PA	18.9	1
Gban E	Carapa procera	Meliaceae	PA	18.5	0
	Rauvolfia vomitoria	Apocynaceae	PA	29.5	0
	Alchornea cordifolia	Euphorbiaceae	PA	20.2	0
Gban W	Morinda germinata	Rubiaceae	PA	27	0
	Dracaena perrotetii	Agavaceae	PA	25.8	0
	Premna hispida	Verbenace	PA	19.6	0
Gban N	Spondias cytera	Anacardiaceae	PA	47.5	0
	Cratispermun laurinum	Rubiaceae	PA	26.4	0
	Harungana madagascariensis	Hypericaceae	PA	36	1
Seiba	Alchornea cordifolia	Euphorbiaceae	PA	19	0
Guein E	Spondias mombin	Anacardiaceae	PA	26.5	1
Guein W	Sterculia tragacantha	Sterculiaceae	A	27.3	1
	Voacanga africana	Apocynaceae	PA	22.1	0
	Milletia zechiana	Papilionaceae	PA	30.3	1
	Santira trimera	Burseraceae	PA	45	0
Guein S	Sterculia tragacantha	Sterculiaceae	A	24.7	1

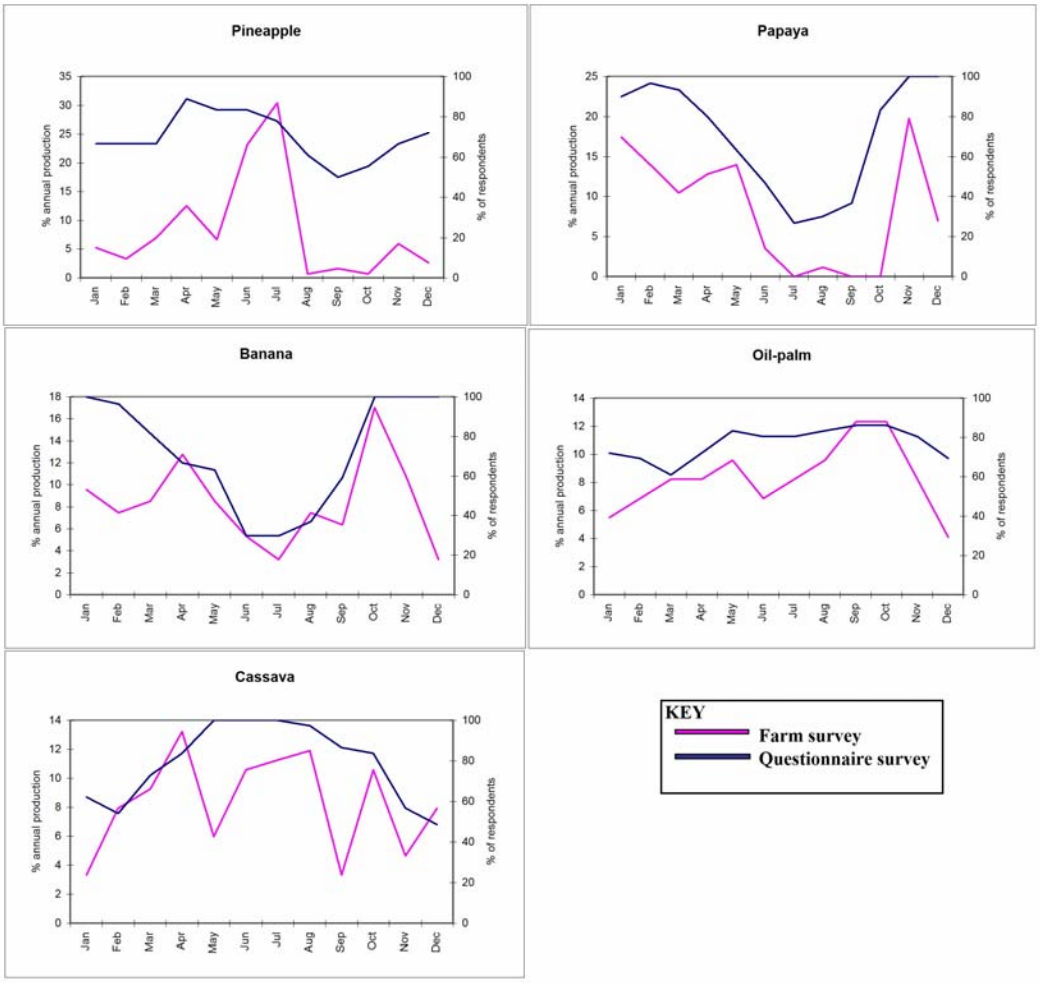
Appendix C4. **All results (including coefficients, test statistics and significance values) of linear regressions predicting the percentage availability of individual cultivars in relation to community wide species (CW) and chimpanzee food species (Ch Fd) ripe fruit availability, rainfall, rainfall (including 1-hour lag) and mean, maximum and minimum temperatures.**

		Constant	FA Index CW	FA Index Ch Fd	Rainfall	Rain lag	Mean temp	Min temp	Max temp	R²
Papaya	coeff	53.943	15.731	—	-0.059	—	—	—	—	**0.793**
	test stat	4.323	3.66	-1.151	-3.3	-1.143	0.059	0.117	-0.481	
	signif	**0.002**	**0.005**	**0.283**	**0.009**	**0.286**	**0.955**	**0.910**	**0.644**	
Banana		57.646	15.202	—	-0.064	—	—	—	—	**0.820**
		4.962	3.799	-2.218	-3.802	0.378	-1.714	1.319	-0.385	
		0.001	**0.004**	**0.057**	**0.004**	**0.715**	**0.125**	**0.224**	**0.710**	
Orange		68.989	—	—	-0.097	—	—	—	—	0.382
		5.293	1.690	0.999	-2.793	-0.356	0.146	-0.035	0.100	
		0	**0.125**	**0.344**	**0.019**	**0.730**	**0.887**	**0.973**	**0.923**	
Mandarin		-1.679	18.994	—	—	—	—	—	—	**0.361**
		-0.089	2.376	-0.662	-1.789	-0.388	-1.155	0.898	-0.424	
		0.931	**0.039**	**0.524**	**0.107**	**0.707**	**0.278**	**0.392**	**0.681**	
Pineapple		173.4	-13.398	2.717	-0.008	-0.007	2.739	-3.435	-2.827	**0.621**
		0.789	-1.526	0.682	-0.347	-0.351	0.602	-1.000	-0.589	
		0.474	**0.202**	**0.533**	**0.746**	**0.744**	**0.580**	**0.374**	**0.587**	
Mango		-2228.7	-50.118	11.582	-0.018	0.012	17.37	-2.301	-2.831	**0.372**
		-0.224	-1.231	0.627	-0.168	0.125	0.824	-0.144	-0.127	
		0.834	**0.286**	**0.565**	**0.875**	**0.90**	**0.456**	**0.892**	**0.905**	
Rice		36.876	24.208	—	-0.082	—	—	—	—	**0.843**
		2.383	4.543	-1.908	-3.674	0.829	-1.108	0.891	-0.181	
		0.041	**0.001**	**0.093**	**0.005**	**0.431**	**0.300**	**0.399**	**0.861**	
Maize		-158.6	—	—	—	—	—	11.23	—	**0.48**
		-2.483	1.234	-0.154	-0.092	1.086	-0.684	3.038	**0.858**	
		0.032	**0.248**	**0.881**	**0.929**	**0.306**	**0.511**	**0.013**	**0.413**	
Cassava		108.31	-13.79	—	—	—	—	—	—	**0.563**
		11.94	-3.59	0.83	2.249	1.274	-0.134	-0.049	-0.329	
		0.00	**0.005**	**0.428**	**0.051**	**0.235**	**0.896**	**0.962**	**0.75**	
Cacao		61.273	—	—	-0.0905	—	—	—	**-**	**0.407**
		4.540	1.242	0.875	-2.620	-0.421	-0.006	0.062	-0.129	
		0.001	**0.246**	**0.404**	**0.026**	**0.683**	**0.995**	**0.952**	**0.900**	
Oil-palm		175.386	-	-	-	-	-	-6.210	**-**	**0.417**
		4.376	-0.788	-0.550	-0.142	-0.824	0.953	-2.677	-0.055	
		0.001	**0.451**	**0.596**	**0.890**	**0.431**	**0.365**	**0.023**	**0.957**	

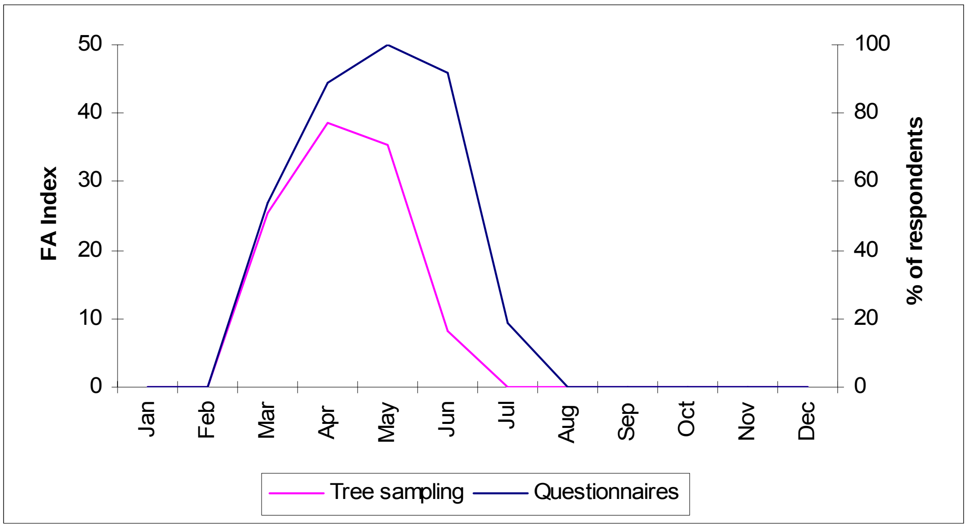
Appendix C5. **The monthly availability of cultivars rated by questionnaire respondents.**



Appendix C6. **The monthly availability of cultivars from the farm survey (% of annual production) plotted against corresponding availability rated by questionnaire respondents (% of respondents). Total number of monitored plants/trees on the farm: 225 pineapple plants, 10 papaya trees, 13 banana plants, 15 oil-palm trees, 80 cassava plants.**



Appendix C7. **The monthly availability of mango fruits from tree sampling (FA Index) plotted against corresponding availability rated by questionnaire respondents (% of respondents). Total number of monitored trees: 7 in the village and 7 in the forest.**



Appendix D

Appendix D1. Frequency that each plant (including species and family names) and part were consumed by the Bossou chimpanzees throughout the study period.

KEY

FT: fruit
LF: leaf
PI: pith
GM: gum
FL: flower
NT: nut
TB: tuber
BK: bark
WT: woody tissue

SPECIES	FAMILY									
		FT	LF	PI	GM	FL	NT	TB	BK	WT
Abrus stictosperma	Papilionceae		27							
Acacia pennata	Mimosaceae		5							
Aframomum sp	Zingiberaceae	4	4	479						
Albizia adianthifolia	Mimosaceae				1					
Albizia ferruginea	Mimosaceae				12					
Albizia lebbeck	Mimosaceae				1					
Albizia zygia	Mimosaceae				145					
Ampelocissus macrocirrha	Ampelidaceae	11								
Ancistrophyllum secundiflorum	Arecaceae		1							
Aningueria altissima	Sapotaceae	76								
Antiaris africana	Moraceae	40	67							
Artabotrys jollyanus	Annonaceae		2							
Baphia nitida	Papilionceae		9							
Bosquea angolensis	Moraceae		30						2	
Bridelia micrantha	Euphorbiaceae	8	2							
Canarium schweinfurthii	Burseraceae	18								
Canthium horizontale	Rubiaceae	4								
Ceiba pentandra	Bombacaceae		37							
Celtis adolfi-frederici	Ulmaceae	5	7							
Celtis brownii	Ulmaceae		3							
Chlorophora excelsa	Moraceae	1	15	1		8				
Chrysophyllum perpulchrum*	Sapotaceae	2								
Cissus aralioides	Vitaceae	2								
Cnestis ferruginea	Connaraceae		5							
Cola cordifolia	Sterculiaceae	2								
Cola reticulata	Sterculiaceae	2								
Costus afer	Zingiberaceae	1	1	7						
Cratispernum laurinum	Rubiaceae		1							
Dacroydes sp	Burseraceae		1							
Dalbergia albiflora	Papilionceae		12							

		FT	LF	PI	GM	FL	NT	TB	BK	WT
Dialium dinklagei	**Caesalpiniaceae**	14								
Dioscorea alata	**Dioscoreaceae**		21							
Dioscoreophyllum cumminsii	**Menispermaceae**	17	12						1	
Elaeis guineensis	**Palmae**	101		194		4	13		2	12
Erythrina senegalensis	**Papilionceae**		6							
Fagara macrophylla	**Rutaceae**		9							
Ficus annomani	**Moraceae**	60	3							
Ficus barteri	**Moraceae**	4	1							
Ficus bignonifolia	**Moraceae**	32	2							
Ficus capensis	**Moraceae**	3								
Ficus eriobotrioides	**Moraceae**	5								
Ficus exasperata	**Moraceae**	7	172							
Ficus macrosperma	**Moraceae**	2								
Ficus mucuso	**Moraceae**	84	5							
Ficus ovata	**Moraceae**	4								
Ficus polita	**Moraceae**	12								
Ficus sur	**Moraceae**	136	1							
Ficus thonningii	**Moraceae**	2	3							
Ficus umbellata	**Moraceae**	163	33							
Ficus valle chouda	**Moraceae**	16	1							
Ficus variifolia	**Moraceae**	64	76							
Ficus vogelli	**Moraceae**	14								
Ficus sp	**Moraceae**	4	4							
Funtumia elastica	**Apocynaceae**			3					1	
Gambeya perpulchra	**Sapotaceae**	2								
Glyphaea brevis	**Tiliaceae**		8							
Gongronema latifolium	**Asclepiadaceae**	14	25	6					17	
Grewia bicolor	**Tiliaceae**	8								
Grewia pubescens	**Tiliaceae**	1								
Harungana madagascariensis	**Hypericeae**	15								
Hypselodelphis violaceae	**Marantaceae**	7	5	249		1				
Itridendron bequaertii	**Sapotaceae**	5								
Justicia sp	**Acanthaceae**		11							
Landolphia dulcis	**Apocynaceae**	24								
Landolphia hirsuta	**Apocynaceae**	22		1						
Landolphia inserta	**Apocynaceae**	11								
Landolphia owariensis	**Apocynaceae**	62							1	
Lasciodiscus marmoratus	**Rhamnaceae**	2								
Lecaniodiscus cupanoides	**Sapindaceae**	23								
Leptoderris fasciculata	**Papilionceae**		105	1					3	
Marantochloa macrophylla	**Marantaceae**			4						
Megaphrynium macrostachyum	**Marantaceae**	86		15						
Milletia zechiana	**Papilionceae**		2							
Momordica cabraei	**Curcurbitaceae**	7								
Monodora tenuifolia	**Annonaceae**	15								
Morus mesozygia	**Moraceae**	16	18							
Musanga cecropioides	**Moraceae**	577	13	6						
Myrianthus arboreus	**Moraceae**	39	26	8						
Myrianthus libericus	**Moraceae**	113	17	1						
Napoleona vogelli	**Lecythidaceae**	7								
Nauclea diderichii	**Rubiaceae**	4								
Nauclea latifolia	**Rubiaceae**	2								
Newbouldis laevis	**Bignoniaceae**		7							

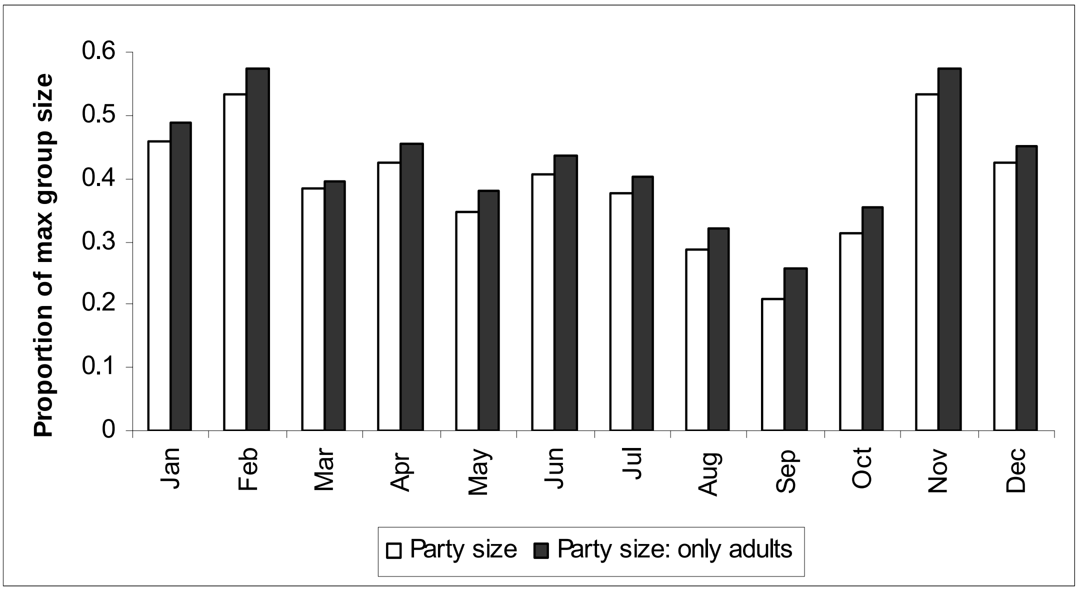
		FT	LF	PI	GM	FL	NT	TB	BK	WT
Okoubaka aubrevillei	**Octonemataceae**		2							
Palusota hirsuta	**Commelinaceae**	3		2		2				
Parkia bicolor	**Mimosaceae**	87			6					
Pennisetum purpureum	**Gramineae**			123						
Phyllanthus discoideus	**Euphorbiaceae**		1							
Piper guineense	**Piperaceae**		1	3						
Polycephalium capitatum	**Icacinaceae**	4								
Polypodium aureum	**Polypodiaceae**		15							
Pseudospondias microcarpa	**Anacardiaceae**	299	7	1						
Pycnanthus angolensis	**Myristicaceae**	6								
Pyrenacantha acuminata	**Icacinaceae**	7								
Rhaphiostylis beninensis	**Icacinaceae**	81								
Rhigiocarya racemifera	**Menispermaceae**	16								
Rothmania hispida	**Rubiaceae**	4								
Rothmania longiflora	**Rubiaceae**	11								
Rothmania withfieldii	**Rubiaceae**	8					1			
Salacia columna	**Celastraceae**	10								
Sarcophrynium prionogonium	**Marantaceae**	5								
Sherbournia calycina	**Rubiaceae**	1								
Smilax kraussiana	**Smilacaceae**		110	2						
Spondias cytera	**Anacardiaceae**								2	
Spondias mombin	**Anacardiaceae**	74		1						
Sterculia tragacantha	**Sterculiaceae**	11	3							
Strophanthus sarmantosus	**Apocynaceae**	7								
Tenniderm equidin			3	1						
Tetracera potatoria	**Dilleniaceae**		2							
Tetrapleura tetraptera	**Mimosaceae**		1							
Thaumatococus danielli	**Marantaceae**	3		213						
Treculia africana	**Moraceae**	3								
Tremna guineensis	**Ulmaceae**	3	1							
Trichilia heudelotti	**Meliaceae**	6								
Trichilia lanata	**Meliaceae**	1								
Triplochiton scleroxylon	**Sterculiaceae**		3							
Uapaca guineensis	**Euphorbiaceae**	50	1	4						
Uapaca heudelotti	**Euphorbiaceae**	34	3							
Uvaria afzelli	**Annonaceae**	31								
Uvariopsis guineensis	**Annonaceae**	1								
Vitex doniana	**Verbenaceae**		1							
Vitex micrantha	**Verbenaceae**	5								
UNIDENTIFIED		34	38	1	4	1				

Appendix D2. **Monthly wild fruit availability values, counts of species in the diet and the corresponding Shannon-Wiener Indices.**

	FA Index	No. spp	J'
Jan	6.6371779	65	0.8841983
Feb	3.055552	54	0.7798353
Mar	5.9864164	54	0.8204373
Apr	3.289926	50	0.8407629
May	1.393143	32	0.7808816
Jun	1.272052	57	0.840957
Jul	0.8567092	51	0.7921634
Aug	1.251534	40	0.8935331
Sep	1.4841237	46	0.8750245
Oct	2.2541993	52	0.8783105
Nov	0.7430315	61	0.8154624
Dec	5.1679638	56	0.8807663

Appendix E

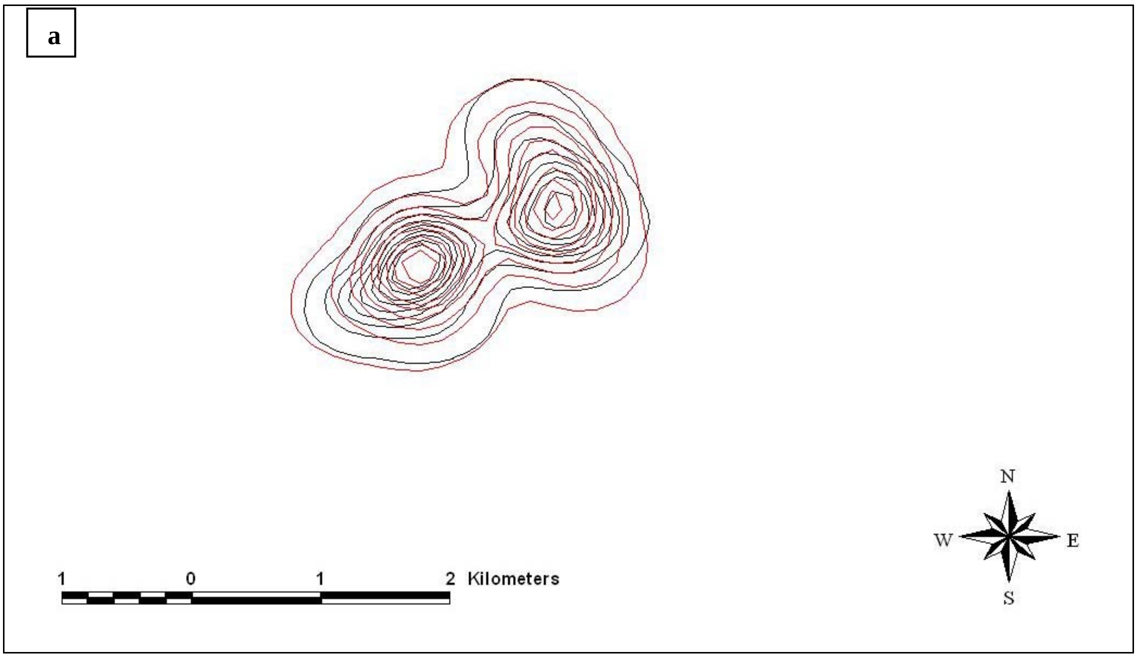
Appendix E1. Mean party size as a proportion of maximum group size, when juveniles and young were included (max: 12-14 individuals) and excluded (max: 8-9 individuals) from analyses. The two measures of party size are positively correlated (rs=0.984, n=12, p<0.001).



Appendix E2. 'Large fruit trees' selected for vocalisation analyses, using a combination of focal feeding duration (hours) and size (A: medium size tree of 10-20m or 'arbre', GA: large tree of more than 20m or 'grande arbre').

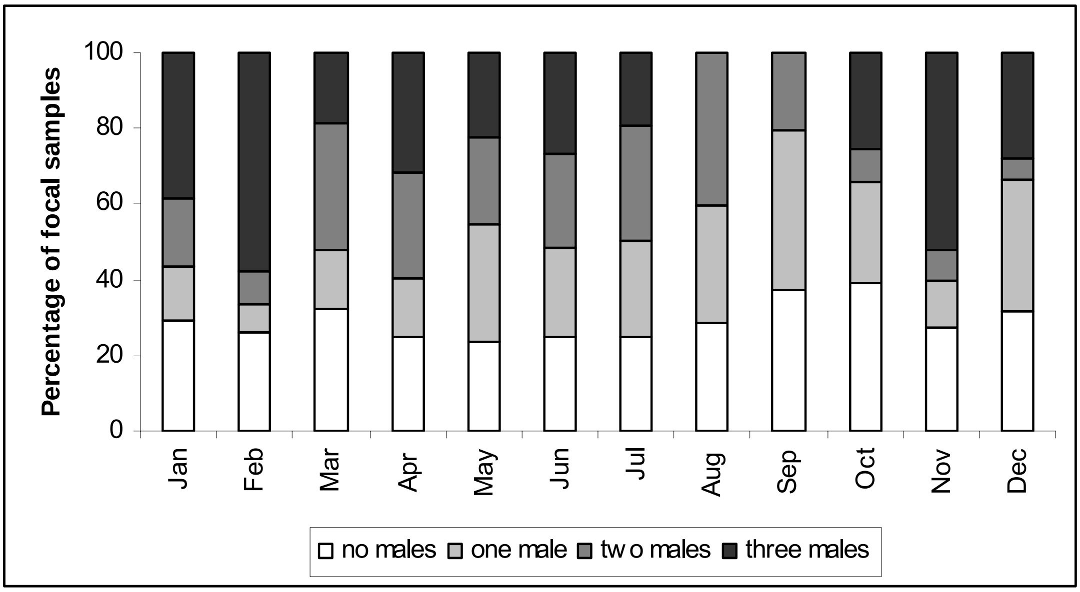
Tree species	Focal feeding (hours)	Size classification
Aningueria altissima	7.42	GA
Antiaris africana	4.92	GA
Ficus anomani	3.17	GA
Ficus mucuso	8.58	GA
Ficus umbellata	11.83	A
Ficus variifolia	9.08	GA
Musanga cecropioides	37.00	A
Parkia bicolor	8.42	GA
Pseudospondias microcarpa	20.17	A

Appendix E3. Kernel analyses (consists of placing a probability density over each observation point) of feeding locations (a) from 10-90% of area used during period of wild-fruit scarcity (red line) and wild-fruit abundance (black line). (b) 25%, 50% and 75% of core area used by chimpanzees (km). As the chimpanzees' core area is very small, very similar patterns of core area use are shown during periods of wild-fruit abundance and scarcity. Feeding activity is centred at both the summits of Gban and Guein (Worton, 1989; Seaman and Powell, 1996).



b)	**Core area use (km)**		
	25%	50%	75%
Low wild-fruit availability	0.022	0.043	0.059
High wild-fruit availability	0.023	0.040	0.056

Appendix E4. **The percentage of monthly focal samples containing from zero to three males.**



Appendix F

Hockings, K.J., Anderson, J.R., and Matsuzawa, T. (2006) Road-crossing in chimpanzees: A risky business. *Current Biology* **16,** 668-670.

the Y. Likewise, X chromosomes spend 2/3 of their time in females, and should be selected to produce female-biased sex ratios. Hamilton marshaled the evidence supporting biased sex ratios caused by genes on the sex chromosome. Because autosomes continue to favor a balanced sex ratio, the important implication is that individuals do not always have indivisible interests — instead there can be conflict between contending sets of selfish genes.

This particular bias will not occur in the haplodiploid Hymenoptera because sex is determined by ploidy rather than by special chromosomes, although maternally transmitted parasites can cause their preferred expected female biased sex ratios. But there is a spectacular example of a selfish sex ratio distorter in the parasitoid *Nasonia vitripennis* studied by Jack Werren. Called PSR for paternal sex ratio, it causes fathers to have excess sons, which ought to be puzzling because haploidiploid males cannot normally have sons (if the egg is fertilized, it becomes diploid and hence a daughter). It works because PSR is inherited on a B chromosome. B chromosomes are small inessential chromosomes that exist in one or more copies in some cells, They do not segregate neatly like autosomes (or A chromosomes) but copies do get transmitted in less regular fashion to offspring. When one or more copies of this B chromosome are transmitted via sperm, they cause the father's A chromosomes to condense into chromatin and be lost. What remains then, are the maternal autosomes, whose haploid state directs the development of a male, along with the successfully transmitted B chromosome. Models that incorporate the details of PSR's effects into sex ratio theory show that PSR can spread only when sex ratios are otherwise female-biased, but that it can spread at all is remarkable. It is an ultimate selfish element; in each generation, the B chromosome succeeds only by completely destroying its fellow traveler A chromosomes and joining a new set.

Conclusion

Düsing's basic insight into how sex ratios evolve has been developed into a wide-ranging and successful theory that predicts both the conventional 1:1 sex ratios and numerous extraordinary ones. A surprising amount of the evidence has come from haplodiploid Hymenopteran insects, though many of these effects can also be found in other organisms, even where chromosomal sex determination mechanisms would seem to lock them into 1:1 sex ratios. Most important, this seemingly arcane topic has played very prominent roles in the development of game theory, in the debate over group selection, in supporting kin selection and parent-offspring conflict, and in the field of within-organism conflict. Many biological advances will require high tech instrumentation and deeper probing into molecular mechanisms of model organisms. But there remains room for a good theory, for adroit choice of non-standard organisms, and even for simple counting.

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Road crossing in chimpanzees: A risky business

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During group movements, monkeys may cooperate to reduce the risk of predatory attacks through adaptive spatial patterning. For example, adult males move toward the front of the group when travelling towards potentially unsafe areas such as waterholes, and bring up the rear when retreating [1–4]. Comparable data on progression orders in moving groups of great apes are lacking.

We hypothesised that chimpanzees evaluate risk when crossing roads, and draw on a phylogenetically-old principle of protective socio-spatial organization to produce flexible, adaptive and cooperative responses to risk. Progression orders were studied in the small community of chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea, as they crossed two roads, one large and busy with traffic, the other smaller and frequented mostly by pedestrians. We found evidence that the degree of risk, estimated in terms of the width of roads and the amount and type of traffic they carried, influenced the waiting time before crossing the roads and the order in which the chimpanzees crossed.

The home range of the 12-strong chimpanzee community at Bossou (7' 39" N; 8' 30" W), covers about 15 km² of mixed forests surrounded by abandoned and cultivated fields. It is dissected by a narrow road (3 m wide) which is used by pedestrians, and a recently widened larger road (12 m wide at the crossing point), which carries trucks, cars, motorbikes and pedestrians. The Bossou chimpanzees have to cross

Figure 1. How do chimpanzees cross roads?

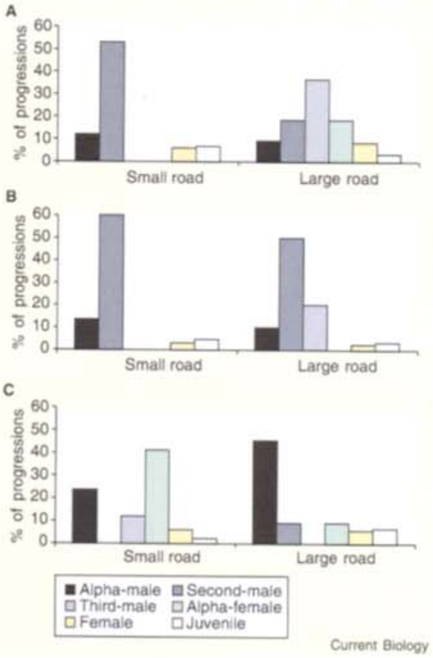
Dominant individuals act cooperatively with a high degree of flexibility to maximise group protection.

both roads regularly to reach foraging sites in their fragmented home-range and typically cross at specific points that the group has used for decades. There is forest up to the edge of the roads, the latter being separated by secondary forest and plantations. Two observers recorded progression orders in both directions (Figure 1 and Supplemental data); the first chimpanzee to scan the road was termed first individual to scan. The latency between arrival of the first individual to scan and the last group-member to cross the forest-road edge was termed the waiting time. During the study (January–April 2005), the group contained three adult males, five adult females, three juveniles and one infant [5]. The social rank of the Bossou males has varied over the years, but during this study the relative statuses of the alpha male (Yolo), the second male (Foaf) and the third male (Tua) were stable [5].

Waiting time was analysed for 19 combined road-crossings in which the same group members crossed the two roads. The analysis of road-crossing progressions used data from 28 mixed-group progressions (17 small and 11 large road crossings), with mean group size 10.6 individuals (SD 2.1). Chimpanzees waited longer before crossing the large road than the small road (means: 180 versus 24 seconds; Wilcoxon test: $T = 5$, $N = 19$, $p < 0.01$). Presence or absence (either auditory or visual) of people had no effect on waiting time on the small road (Mann-Whitney test: $Z = -0.168$, $N = 19$, $p = 0.905$), but people ($Z = -2.059$, $N = 19$, $p = 0.043$) and vehicles ($Z = -2.043$, $N = 19$, $p < 0.01$) increased waiting time on the large road. A significant effect of direction of travel emerged concerning the large road ($Z = -2.083$, $N = 19$, $p = 0.041$); the same effect for the small road approached significance ($Z = -1.915$, $N = 19$, $p = 0.062$): the chimpanzees took longer to move from forest to more open areas than vice-versa.

When all three adult males were present, one led more often than expected (18 of 28 progressions; binomial test: $p < 0.001$) and was more likely to scan the road prior to crossing (binomial: $p < 0.001$). In contrast, an adult male did not occupy the rearmost position more frequently than expected. As the second- and third-ranking males frequently led, the frequency of the alpha male being last was tested; this was highly significant (Bonferroni correction included; binomial: $p < 0.01$).

Figure 2 summarizes the progression order data. The



Current Biology

Figure 2. Summary of progression order data.

The percentages of progressions in which the three males, the alpha female and the average non-alpha female and juvenile were: (A) first to cross; (B) first to scan the road; and (C) last in the progression on the two roads (infant excluded from analysis).

first individual to scan was the first to cross the small road in 100% of cases, compared to 70% for the large road. On the large road the second-ranking male sometimes continued scanning while the elderly third male and alpha female took up the lead on the large-road progressions. The alpha male increased his rearward presence on the large road, whereas the alpha female showed a dramatic reduction in frequency of being last; in other words when the degree of risk increased she took up a more forward position. Additionally, when the alpha male was present in mixed-group progressions containing one other adult male ($N = 6$, mean group size: 6.7), he was first to scan and cross in 50% of large road-crossings and last in only 33%. This suggests that his rearward position at other times was not due to fear.

Modern Bossou chimpanzees encounter predators infrequently [6], and although humans themselves are not 'predators' of these chimpanzees, we propose that road-crossing, a human-created challenge, presents a new situation that calls for flexibility of responses by chimpanzees to variations in perceived risk.

Crossing the large road and leaving forest for open areas are potentially risky situations for chimpanzees, reflected in increased waiting time. During dangerous excursions certain positions may be more advantageous than others, depending upon age and sex [4]. Adult males, less fearful and more physically imposing than other group members, take up forward and rearward positions, with adult females and young occupying the more protected middle positions.

As hypothesised, the Bossou chimpanzees employ a phylogenetically-old mechanism to adapt to a more recent dangerous situation. However, the positioning of dominant and bolder individuals, in particular the alpha male, changed depending on both the degree of risk and number of adult males present; dominant individuals act cooperatively with a high level of flexibility to maximise group protection. At a proximate level each individual may have preferred and recognised positions; however, it is unknown whether positioning is individual- or rank-specific. Data on progression orders of other great ape populations are required, and would help shape hypotheses about emergence of this aspect of hominoid social organisation.

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Supplemental data
Supplemental data, with a video-clip of the Bossou chimpanzees crossing the large road, are available at http://www.current-biology.com/cgi/content/full/16/17/R668/DC1/

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Minimal plastid genome evolution in the *Paulinella* endosymbiont

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It is an enduring mystery how organelles were first established in eukaryotes. A key player in this saga is the thecate amoeba *Paulinella chromatophora* which over 100 years ago [1] showed naturalists that once free-living cells could exist as endosymbionts [2]. This species has the honor of being the only known case of an independent primary (cyanobacterial) plastid acquisition [3,4] and is a model for understanding plastid establishment. The *Paulinella* plastid, often referred to as the cyanelle, retains typical cyanobacterial features such as peptidoglycan and phycobilisomes, but is considered to be a *bona fide* endosymbiont because it is no longer bound by a vacuolar membrane but lies free in the cytoplasm, its number is regulated, suggesting genetic integration, and it cannot be cultured outside the host [5–7]. *Paulinella* is, however, difficult to culture, and so it has resisted detailed molecular biological investigation. Here we took advantage of a Lambda DASH II phage library made from limited amounts of *Paulinella* total genomic DNA to reconstruct the evolutionary history of its recently established plastid [3]. Our data show the *Paulinella* plastid genome to have characteristics typical of cyanobacterial, not plastid genomes.

The *Paulinella* library was screened with the highly conserved *psb*A, *psb*C and 16S rDNA plastid genes from the glaucophyte *Glaucocystis nostochinearum*. Two plastid inserts of 9.4 kb and 4.3 kb were obtained by this approach; a third, 5 kb fragment has already been described [3]. Because the *P. chromatophora* culture is not axenic (see [3]), we