RESEARCH ARTICLE

Use of Wild and Cultivated Foods by Chimpanzees at Bossou, Republic of Guinea: Feeding Dynamics in a Human-Influenced Environment

KIMBERLEY J. HOCKINGS[1−3*], JAMES R. ANDERSON[3], AND TETSURO MATSUZAWA[4]
[1]Department of Anthropology, New University of Lisbon, Lisbon, Portugal
[2]Centre for Research in Anthropology (CRIA), Lisbon, Portugal
[3]Department of Psychology, University of Stirling, Stirling, Scotland
[4]Primate Research Institute, Kyoto University, Inuyama, Aichi, Japan

Increased human population growth and more conversions of natural habitat to agricultural land have resulted in greater proximity between humans and nonhuman primate species. Consequent increases in resource competition including crop-raiding are a by-product of both natural resources becoming less available and the nutritional benefits of cultivated foods becoming more known to the nonhuman primates. Chimpanzees at Bossou in the Republic of Guinea, West Africa, consume 17 different types of cultivated foods that are grown extensively throughout their small, fragmented home range. Direct observations of feeding behavior conducted over an 18-month period revealed that during specific months crops account for up to one quarter of chimpanzee feeding time, with higher overall crop-raiding levels throughout the periods of wild fruit scarcity. Some cultivated foods, especially sugar fruits, are mostly fallback foods, whereas others, such as rice pith (*Oryza* sp.) and maize (*Zea mays*), are consumed according to their availability even when wild foods are abundant. These findings highlight the importance of both crop choice by farmers and a thorough understanding of the ecology of resident primate species when establishing land management techniques for alleviating human–primate conflict. Am. J. Primatol. 71:636–646, 2009.   © 2009 Wiley-Liss, Inc.

Key words: crop-raiding; chimpanzees; cultivated food availability; wild food availability; conflict mitigation

INTRODUCTION

As agricultural fields, plantations and orchards increasingly border and dissect natural forests, the geographical ranges of many nonhuman species shrink and fragment, resulting in more direct contact between humans and nonhumans and competition over resources. Consequently, crop-raiding by wildlife—venturing into cultivated areas to consume foods that humans see as belonging to them—is an adaptation by wildlife to a loss of both natural habitat and wild foods, and increased availability of alternative food resources. Cultivated foods are often energy-rich, clumped and offer increased foraging efficiency, lower toxicity and greater digestibility over natural foods [Strum, 1994].

Many species are reported to crop-raid and frequently come into conflict with people, large mammals such as elephants being an illustrative example [see Hoare, 2001]. In some areas nonhuman primates (hereafter, ''primates'') also pose severe problems as crop-raiders, owing to their ecological flexibility and behavioral plasticity, along with the large quantity of crops that they may damage and consume [Hill, 1997; Siex & Struhsaker, 1999]. For example, around certain reserves in Africa and Asia, primates are considered to be responsible for over 70% of damaging events to fields and 50% of the area damaged [Hill, 2000; Naughton-Treves, 1998]. Throughout the agriculture–wildlife interface, crop guarding by farmers [e.g. chasing wildlife away, throwing stones and shouting—for an overview of crop guarding practices, see Hockings & Humle, 2009] is a common practice to limit damage by wildlife. Despite such measures taken by farmers, nearly all families of primates include crops in their feeding repertoire, with the genera *Macaca* in Asia and *Papio* and *Chlorocebus* in Africa considered as particularly problematic.

Numerous studies indicate that primates select specific foods to meet their nutritional requirements and metabolic demands. For example, fruits are generally rich in sugars but deficient in proteins and fats; leaves serve as an important protein source; piths contain variable levels of sugars, protein and fermentable fiber; and nuts are high in protein, minerals and fats [Doran et al., 2002; Reynolds et al., 1998; Rode et al., 2003; Rogers et al., 1990; Wrangham et al., 1991]. Less commonly discussed, yet exploited by some primates are the subterranean parts of plants, including tubers, which provide an alternative energy source in the form of carbohydrates [Byrne et al., 1993; Hockings et al., 2009; Laden & Wrangham, 2005].

In addition to variations in the nutritional composition of foods, extrinsic factors such as effect of season or habitat can influence the value of food to primates by affecting its spatial and temporal availability [Lambert, 2007]. As most plant species are periodically scarce, fruit specialists are often under pressure to show dietary flexibility to survive fruit bottlenecks [Terborgh, 1986; Yamakoshi, 1998]. Fallback foods perform a vital role in sustaining primates through such limiting environmental periods. Lambert [2007] places fallback foods into two broad categories each relating to different consumption strategies: first, fallback foods of low nutritional density (e.g. leaves, bark, pith), which are often more abundant but also require more processing time, and, second, fallback foods of higher nutritional density (e.g. fruits and seeds), which are sometimes mechanically protected (e.g. nuts) and difficult to find. From the latter type of fallback food, behavioral innovation might also arise, such as nut-cracking by chimpanzees [Yamakoshi, 1998]. Although these foods are of high seasonal importance, year-round use does not exclude a food item serving as a fallback food [Marshall & Wrangham, 2007].

Wild chimpanzees are omnivorous but prefer foods with high sugar levels. Their diet is dominated by ripe fruit, which accounts for 50–75% of feeding effort [Goodall, 1986; Morgan & Sanz, 2006; Pruetz, 2006; Tutin et al., 1997; Wrangham, 1977; Wrangham et al., 1991]. Depending upon the habitat and subsistence traditions of the community, chimpanzees feed on other wild foods, especially during periods of wild fruit scarcity, namely leaves, bark, terrestrial herbaceous vegetation, pith and oil-palm (*Elaeis guineensis*) nut and fruit [Humle & Matsuzawa, 2004; McGrew, 1992; Nishida, 1976; Tutin et al., 1997; Wrangham et al., 1991, 1998; Yamakoshi, 1998]. However, crop-raiding by chimpanzees and other primates is on the increase [for an overview of crop-raiding by all nonhuman great ape species, see Hockings & Humle, 2009], but many studies of primate feeding ecology do not fully consider the importance of crop-raiding in providing primates with a range of high-quality foods during periods of wild food scarcity [Linkie et al., 2007; Naughton-Treves et al., 1998; Richard et al., 1989].

Throughout Africa different chimpanzee communities appear to display distinct crop-raiding behaviors depending upon factors including habitat quality and size, proximity to cultivated resources, type of cultivated resources available, temporal and spatial availability of wild and cultivated resources and the degree of risk (defined as potential negative impact that might arise from a future crop-raiding event) involved in crop-raiding [Humle, 2003; Reynolds, 2005]. Although quantitative data are lacking [for the exception, see Naughton-Treves et al., 1998], some crops might become important for the chimpanzees during periods of wild fruit scarcity, whereas others might be exploited simply because they are more tasty or nutritious than wild foods.

Data that bring together aspects of wild feeding and crop-raiding by chimpanzees, in addition to availability patterns of both cultivated and wild foods, are essential for answering questions on chimpanzees' feeding strategies in human-influenced environments. This study aims to test the following specific predictions on patterns of use of wild and cultivated foods:

(i) Wild fruit and crop availability will show variations throughout the year, and wild fallback foods will be available during periods of low wild fruit availability.
(ii) There will be seasonal variations in utilization of different wild food types (e.g. fruit, leaf and pith) and crops.
(iii) During periods of wild fruit scarcity, levels of crop-raiding for sugar fruits will increase owing to chimpanzees' high dependence on fruit.
(iv) Other crops high in complex carbohydrates, proteins or lipids will show different patterns of raiding according to crop type and availability.

METHODS

Study Site and Population

The village of Bossou is situated in the forest region in south-eastern Republic of Guinea, West Africa (latitude 7°38′71.7′N and longitude 8°29′38.9′W), approximately 6 km from the Nimba Mountain range. The climate at Bossou is classified as tropical wet seasonal, and the small hills (70–150 m high) that constitute the chimpanzees' 15 km^2 home range (7 km^2 core area) are covered in primary and secondary forest, cultivated and abandoned fields and orchards. Primary forest accounts for 1 km^2 and is predominantly located at the summit of the largest of three hills in the area, Gban. The main body of forest is mostly secondary and scrub

forest, with a noticeable occurrence of certain tree species including the umbrella tree (*Musanga cecropioides*) and the oil-palm tree (*E. guineensis*). Terrestrial herbaceous vegetation of the families Marantaceae and Zingiberaceae occurs throughout.

The village of Bossou is home to the Manon people who hold the neighboring chimpanzees sacred as the reincarnation of their ancestors, and believe that their ancestors' souls rest on the sacred hill of Gban [Kortlandt, 1986]. Owing to the local people's strong cultural beliefs, humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes verus*) have been able to coexist in such close proximity over many generations [Hockings et al., 2006]. Although Bossou has been informally declared as a reserve area, some farmers have previously and currently practice swidden (or "slash and burn") agriculture within the Bossou forests. Such practices have resulted in a mosaic of cultivated fields and orchards, both abandoned and guarded, within and bordering the reserve. The research complies with protocols approved by the Stirling University institutional animal care committee and adheres to the legal requirements of the country in which the research was conducted.

Behavioral Observations

Throughout the duration of this study, chimpanzee community size varied from 12 to 14 individuals, with 8–9 adults and the same 3 adult males present throughout. Infants and juveniles less than 8 years old were classified as immature [Matsuzawa, 2006]. Data were collected over 12 months, specifically during every month of the year in three periods between May 2004 and December 2005. A focal adult individual was randomly selected from a predetermined list each day prior to the observation session and followed from 06:30 hr to nest. Every 5-min instantaneous point sampling was used to record the ongoing behavior of the focal individual. 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), and a total of 187 focal-individual samples of adult chimpanzees were collected (13–17 focal days/month; mean observation time: 8.95 hr, SD ± 2.37), totaling 1,673 hr of observations. From the 187 focal samples, days of 5 or more hours of observation time were selected for focal analysis (termed "focal level" recordings/analysis; $n = 169$, mean: 9.6 hr, SD ± 1.46). While following the focal individual, ad libitum sampling was also employed (termed "party level" recordings/analysis) to record all observed occurrences of crop-raiding, feeding on abandoned cultivated foods and feeding on supplied foods. "Party level" recordings of adults feeding on "wild" foods, that is, foods that were never cultivated, were also taken. While following the focal individual, 5-min scan samples (exactly after focal

instantaneous point sampling was conducted) were employed to record the presence of all other individuals. For both abandoned and guarded crops, the crop type and location (village or forest), time of day (divided into three periods: morning (07:00–10:59 h), midday (11:00–14:59 h) and afternoon (15:00–18:59 h)), local people's presence (likely auditory and visual contact with chimpanzees combined) and guard level (low: humans do not chase the chimpanzees away; high: humans chase the chimpanzees away) were noted.

Some cultivated species, such as mango fruit (*Mangifera indica*), were only consumed by chimpanzees in abandoned orchards or fields. As these areas were never guarded by farmers, acquiring these foods was not considered as crop-raiding. Crops were thus divided into three groups, namely abandoned: crops that are not guarded by humans; guarded: crops that are at least periodically guarded by humans; and supplied: crops supplied by other researchers during nut-cracking experiments (only oil-palm, fruits and nuts and coula, *Coula edulis*, nuts were supplied).

As chimpanzees either fed within the field or orchard, or transported crops back to the forest to feed, a crop-raiding "event" is defined as any successful foray by an individual to obtain guarded cultivated food [Naughton-Treves et al., 1998]. A crop-raiding "bout" refers to all events (including time from exit of natural vegetation to the end of crop consumption) occurring within 10 min of each other. A bout was considered terminated when the interval before the next event exceeded 10 min. This "party level" definition allows for multiple but independent daily raids, which are not in immediate succession, to one field or orchard to be counted as distinct crop-raiding "bouts."

Phenological Surveys

A total of six transect lines (total distance 4,739 m) were set up to monitor trees in the three principal hill forests of Bossou. Each transect line was 10 m wide, and included every tree greater than 5 cm in diameter at breast height (DBH); lianas were also included [Chapman et al., 1992, 1994]. During every second and fourth week of each month the transects were monitored, and each tree was scored for ripe fruit availability as follows: 0: absent; 1: 1–25% of canopy cover; 2: 26–50% cover; 3: 51–75% cover; 4: 76–100% cover. The following formula was used to calculate the fruit availability index (FA Index), which assumes circular cross-section of trunks [modified from Takemoto, 2004]:

$$\text{FA Index} = \left[\sum (P_i \times F_i)\right] \bigg/ \left[\sum (P_i \times 4)\right] \times 100$$

where P_i is the basal area of the tree (cm^2) and F_i is the fruiting score of the tree (0–4). "Chimpanzee

food species'' are defined as those fruit species that chimpanzees were observed consuming by K. H. during the study period, and were used for subsequent calculations of wild fruit availability. Monthly FA Index values of food availability were calculated by taking the mean of the FA Index values for the two surveys.

Harvest and Distribution of Crops

To index the spatial distribution of cultivated foods within the chimpanzees' core area, their presence on the three main hills in the home range and up to 50 m from the forest edge was recorded. Villagers who owned farmland or orchards within or around Bossou ($n = 39$) completed verbally presented questionnaires at the end of the study period (December 2005) on the planting patterns and monthly harvest of the foods they produced for the preceding year (2005). To deal with the problem of obtaining accurate estimates of crop yield when crops are sold in variable units, harvested opportunistically and consumed as needed, a simple categorization as ''harvested'' or ''not harvested'' was employed; thus, percentage harvest of ''cultivated food A'' refers to the percentage of respondents who harvested ''cultivated food A'' in any particular month.

Systematic recordings of crops were also conducted on a large farm in Bossou—monthly harvest levels of certain crops, including pineapple (*Ananasa comosus*), papaya (*Carica papaya*), banana (*Musa* sp.), oil-palm fruit and cassava (*Manihot esculenta*) were monitored by K. H. and the farm owner for 1 year. Additionally, mango availability in both the village and the forest was recorded using the method outlined for transect recordings.

Data Analyses

Crop-raiding rates were calculated by dividing the number of observed raiding events or bouts by the combined ''party level'' ad libitum observation times for each individual per month, to give ''party level'' crop-raiding rate per hour; this rate was then multiplied by 100. As wild food feeding durations were not measured during ''party level'' ad libitum samples, ''focal level'' observation times were used when calculating the duration of feeding on wild foods.

All measures of crop-raiding were tested against wild fruit availability values (FA Index of chimpanzee food species) for exactly the same months. It was assumed that no interannual monthly variation existed in crop availability. When monthly crop availabilities were clumped, the mean of the availability values was calculated. All data were analyzed using SPSS version 13, and were tested for normality. Multivariate tests could not be used when monthly raiding events did not have a normal distribution or could not be transformed or there were not sufficient data. One-tailed or two-tailed tests were employed in accordance with the original hypotheses; one-tailed tests are indicated in the text.

RESULTS
Wild Fruit Availability and Crop Harvest

Wild fruit availability varied throughout the year for chimpanzee food species ($n = 1,596$ trees from 59 species). The period of ripe fruit ''abundance'' was from December to April; during the rest of the year (May to November) ripe fruit availability was consistently low (FA Index values: mean $\pm$ SE, *high* vs. *low*; 4.8 ± 0.6 vs. 1.4 ± 0.1). 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 1 month between the November reductions in rainfall and the December increases in ripe fruit availability. Both the oil-palm 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, highlighting their potential value as fallback resources (FA Index values: mean $\pm$ SE, *oil-palm* 3.1 ± 0.4, range $= 0.5$–5.9; *umbrella tree* 11.7 ± 0.9, range $= 5.5$–19.3).

There was also considerable variability in the temporal harvesting practices of different crops by farmers and the spatial availability of crops consumed by the chimpanzees; nevertheless overall crop availability remained relatively stable (see Fig. 1). Estimates of crop availability derived from questionnaires and monitoring were highly correlated for all crops except cassava tuber; unlike fruits on the farm survey, the latter was only unearthed by farmers when needed, which would account for the observed discrepancies.

Overview of the Nutritional Value of Crops

Sugar fruits, including papaya, banana, orange (*Citrus sinensis*), mandarin (*C. reticulata*) and pineapple, all contain greater than 5 g of sugar per 100 g (mean $\pm$ SE: 9.7 ± 1.05, range $= 5.9$–12.2), with varying levels of simple sugars, but consistently low levels of complex carbohydrate, protein and lipid. Likewise, mango fruit contains 14.8 g of sugar per 100 g and low levels of carbohydrate, protein and lipid. Other crops vary in their nutritional composition. For example, cassava tuber is a ready source of calories with high levels of complex carbohydrate (38 g per 100 g), but low levels of sugar, protein and fat. Maize contains some protein (3.2 g per 100 g) and is high in complex carbohydrates (19 g per 100 g) but low in sugars (3 g per 100 g). Cacao (*Theobroma cacao*) seeds contain high levels of lipid (between 40 and 50%). Oil-palm fruits are also high in lipids although the figure varies between 35 and 60%, whereas oil-palm nuts contain significant levels of

	Papaya	Banana	Orange	Mandarin	Pineapple	Mango	Rice	Maize	Cacao	Cassava	Oil-palm	Total
n	(n=26,6)	(n=28,29)	(n=14,13)	(n=12,7)	(n=10,3)	(n=34,38)	(n=37,10)	(n=17,4)	(n=9,1)	(n=37,12)	(n=12,5)	
r_s	0.65 *	0.86 **			0.80 **	0.89 **				0.36	0.80 **	
Jan >												
Feb>												
Mar>												
Apr>												
May												
Jun												
Jul												
Aug												
Sep												
Oct												
Nov												
Dec>												

% availability
81-100
61-80
41-60
21-40
0-20

Fig. 1. The temporal availability of cultivated foods (questionnaire data) represented by shading (number of respondents for each crop shown as first number in brackets), and the number of orchards, farms or fields within the monitored areas containing specific crops (second number in brackets). For all monitoring–questionnaire data correlations, $n = 12$, *$P < 0.05$, **$P < 0.01$. Months of highest wild fruit availability are highlighted ($>$).

protein. Papaya leaf contains 7 g of protein per 100 g, a figure that is relatively high compared with most other crops. Pith is generally energy-rich and a good source of fiber, although the specific nutritional values of banana and rice pith were not obtained. Although not discussed, crops vary in their levels of minerals and vitamins (nutritional information obtained from the National Nutrient Database: http://www.nal.usda.gov/fnic/foodcomp/search/).

Utilization of Wild Foods and Crops

The chimpanzees fed on a total of 140 identified plant species (party level), including 123 wild and 17 cultivated species (monthly median including crops = 53 sp., range = 32–65). This comprised 212 plant parts, including 188 wild and 24 cultivated plant parts [see Table I; for complete lists of wild foods, see Hockings, 2007; Matsuzawa & Sugiyama, 2009].

The chimpanzees ate fruit in over half of total feeding time (focal level) and recorded feeding events (party level) including crop-raiding showing that, despite fluctuations in the availability of wild ripe fruit, chimpanzees maintain a high proportion of ripe fruit in the diet (duration (focal level): mean: 60.3%, range: 46.4–75.6, SD ± 8.0; event (party level): mean: 51.9%, range: 45.7–60.3, SD ± 4.6). Leaves were also frequently consumed (duration: mean: 17.2%, range: 6.5–25.2, SD ± 5.1; event: mean: 16.9%, range: 8.2–16.9, SD ± 4.2) as was pith (duration:

mean: 15.2%, range: 10.8–24.6, SD ± 4.7; event: mean: 21.5%, range: 11.8–27.9, SD ± 4.3).

From focal follows of 5 hr or more, the Bossou chimpanzees were engaged in feeding behaviors for 22.5% of the day, on average for 129 min (SD ± 40.3 min). Of that daily feeding time, chimpanzees spent an average of 15 min per day feeding on crops from raided, abandoned and supplied sources (range: 0–105 min, SE ± 1.7 min). Overall, raided crops contributed to 8.8% of the chimpanzees' feeding time (monthly range (focal level): 1.8–16.6%, SD ± 4.8) and, in total, crops from all sources combined comprised 14% of feeding time (monthly range: 3.6–26.3%, SD ± 6.9). Fruit, leaf and pith, the majority of the diet, contributed to 6.0, 1.0 and 0.7%, respectively, of raided crop feeding time, and 9.6, 1.0 and 0.8% of crop feeding time from all sources combined. On days when crops were consumed (100 out of 167 focal days), there was also a significant negative correlation between hours of wild feeding time and crop feeding time (linear regression: $r^2 = 0.047$, $n = 100$, $P < 0.05$). Adult males spent significantly longer than females feeding on crops (one-way analysis of variance (ANOVA); $F_{1,167} = 24.0$, $P < 0.001$). Males spent on average 25.6 min per day feeding on crops (range: 0–105 min, SE ± 3.7 min), whereas females spent only 9.5 min per day (range: 0–55 min, SE ± 1.4 min).

In spite of year-round availability, wild fallback feeding rates on umbrella tree fruit showed the same

TABLE I. Crop-Raiding and Nonraiding Event Frequencies for Each Cultivated Food and Part (FT: Fruit, LF: Leaf, PI: Pith, TB: Tuber, SD: Seed, NT: Nut, FL: Flower, GM: Gum)

Cultivated food		Events		
Common name	Scientific name	Part	Raid	Nonraid
Papaya	*Carica papaya*	FT	126 (4)[+]	0
		LF	69[+]	0
Banana (sweet)	*Musa* sp.	FT	62 (3)[+]	23 (2)*
		PI	63[+]	26*
Orange	*Citrus sinensis*	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 (sweet)	*Manihot esculenta*	TB	74	26
Cacao	*Theobroma cacao*	SD	34	0
Oil-palm	*Elaeis guineensis*	FT	57 (1)[+]	24 (14)*
		SD/NT	8	53*
		FL	1	0
		PI	0[+]	0
	Coula edulis	NT	0	5
Okra	*Hibiscus esculentus*	LF/FT/FL	19	0
Raphia-palm	*Raphia gracilis*	GM	10	0
Sugarcane	*Saccharum officinarum*	PI	1	0
Avocado	*Persea americana*	LF	0	2
Yam	*Dioscorea* sp.	TB	0	1
Grapefruit	*Citrus grandis*	FT	0	1

Numbers in brackets indicate the frequency of consumption of more than one part of the specified cultivated food in a single event and [+] (raided), * (nonraided) indicate the parts. In addition to the results presented, there were seven events where multiple cultivated foods were raided. Okra leaf, fruit and flower were fed on quite often but very small quantities were taken. Sugarcane was grown on only one farm, and yam was only taken on one occasion. Two grapefruit trees were present within the Bossou forest, one abandoned and one owned by villagers, but during the study period the trees produced very few fruits. Also, for chimpanzees to feed on raphia-palm gum or "palm-wine," a person must have set up the specialized equipment to drain the gum from the tree; therefore, consumption of palm-wine by chimpanzees was infrequent.
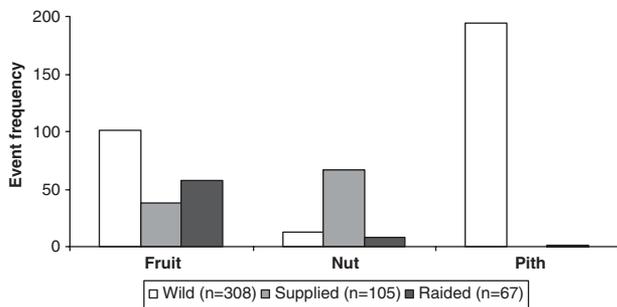
Fig. 2. The total frequency of all oil-palm fruit, nut and pith feeding events from wild, supplied and raided sources during the study period. When chimpanzees fed on harvested oil-palm fruits that had been cut down by villagers, covered by palm leaves for protection, and left for later collection, this was considered as crop-raiding as local people did not tolerate this behavior.

monthly usage pattern as raided crops (party level: *event*: $r_s = 0.629$, $n = 12$, $P < 0.05$). Looking more specifically at oil-palm usage, the chimpanzees obtained different oil-palm parts from different sources (see Fig. 2). Wild fallback feeding rates on oil-palm pith exhibited the same patterns as raided crops (party level: *event*: $r_s = 0.671$, $n = 12$, $P < 0.05$), but no significant correlations were found between wild fruit availability and event rates for wild, supplied and raided oil-palm fruit (Bonferroni corrections included: $r_s = -0.44^{wild}$, $0.59^{supplied}$, 0.13^{raided}, $n = 12$, ns). The correlation between combined wild and raided oil-palm fruit use and combined crop-raiding rates (oil-palm fruits excluded) was positive, but not significant (*event*: $r_s = 0.385$, $n = 12$, ns). However, combined consumption of wild and raided oil-palm fruits was significantly higher during periods of wild fruit scarcity than abundance ($\chi^2 = 8.61$, $df = 1$, $P < 0.01$). Nuts were consumed at consistently low levels unless obtained from supplied sources and therefore are not discussed.

In total, 1,118 crop feeding events, including 786 crop-raiding events, were observed during the 12-month study period (party level); certain crops will not be discussed as they were fed on infrequently or in very small quantities (see Table I). During months of wild fruit scarcity, chimpanzees spent a higher percentage of time feeding on guarded crops than those from abandoned and supplied sources (party level; see Fig. 3a). When comparing periods of high and low wild fruit availabilities, crop-raid and all crop feeding events were significantly higher
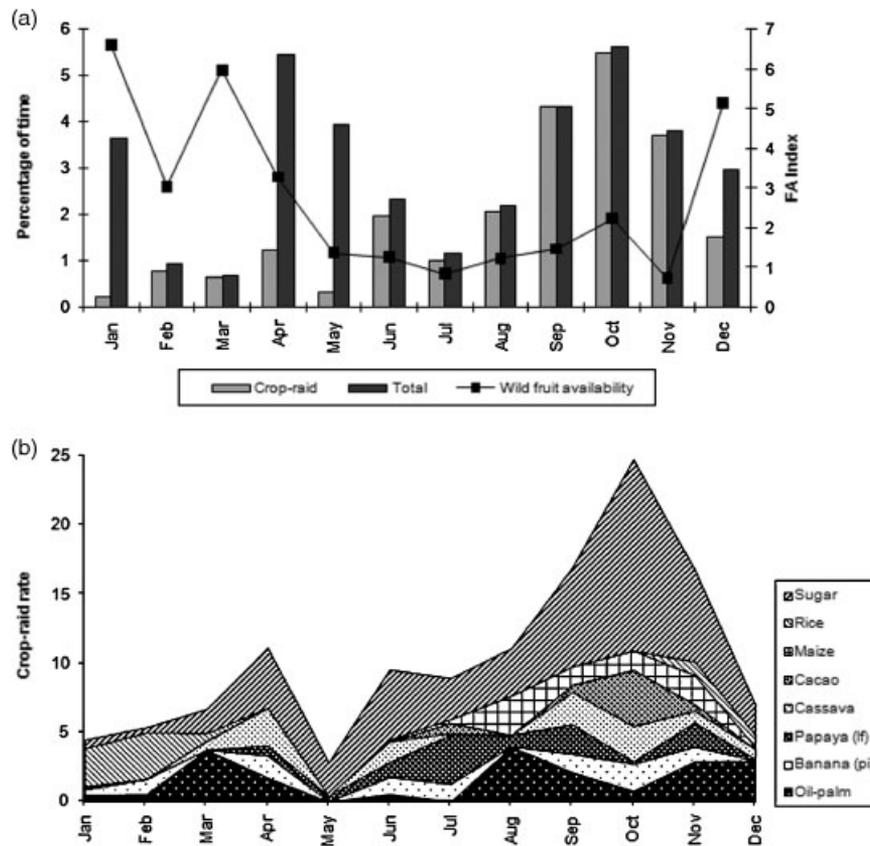
Fig. 3. (**a**) Percentage of monthly observation time spent crop-raiding and feeding on all crops in relation to wild fruit availability and (**b**) monthly raid event rates of different crops.

when wild fruits were scarce (party level: *crop-raid*: $\chi^2 = 80.92$, df = 1, $P < 0.01$; *total*: $\chi^2 = 32.43$, df = 1, $P < 0.01$). High monthly variations in raiding rates of different crops were observed (see Fig. 3b). As analyses of crop-raiding bouts and durations show the same statistical patterns as crop-raiding events, only analyses using events are presented from here on.

Sugar fruits were taken in 40.7% of all crop-raiding events (320 out of 786 events). They were available especially from October to April; the rest of the year abundance was relatively low (mean $\pm$ SE: 75 (± 5.5) and 34 (± 3.4)). Although the spatial availability of individual sugar fruits varied, overall they were abundant within the chimpanzees' home range.

Temporal variations in sugar fruit-raiding were observed (Fig. 4a; one-tailed: $r_s = -0.53$, $n = 12$, $P < 0.05$): when forest fruits were scarce raiding was more frequent. The availability of sugar fruits did not significantly influence the rate of raiding (Fig. 4b; one-tailed: $r_s = -0.15$, $n = 12$, ns), thus chimpanzees were not feeding on fruit crops simply because they were temporally abundant. Overall crop-raiding rates were highest from September to November, peaking in October; during these periods, forest fruit availability was low and cultivated fruit

availability had started to increase. From June to August, sugar fruit availability was substantially lower, possibly limiting crop-raiding levels. The observed variations in the frequency of crop-raiding during periods of low and high wild fruit availability could not be explained by differences in local people presence ($\chi^2 = 2.03$, df = 1, ns), location ($\chi^2 = 2.25$, df = 1, ns), time of day ($\chi^2 = 0.49$, df = 2, ns) or guard levels ($\chi^2 = 4.53$, df = 1, $P = 0.05$) in the field or orchard (Bonferroni corrections are included).

The only mango the chimpanzees ate was from the plentiful abandoned trees in the forest, and people were never present. Mango feeding has no associated risks and is comparable to feeding on wild foods. Forest fruit availability was not correlated with mango feeding (see Fig. 4a; $r_s = -0.07$, $n = 12$, ns), although it was consumed especially in May when wild food was scarce. However, the highly seasonal availability of mango significantly affected the rates of feeding on it (see Fig. 4b; *events*: $r_s = 0.84$, $n = 12$, $P < 0.01$).

Other crops were consumed by chimpanzees at different times of the year, showing variations in patterns of raiding; some were raided in particular during periods of wild fruit scarcity and others directly when they were available (see Table II).
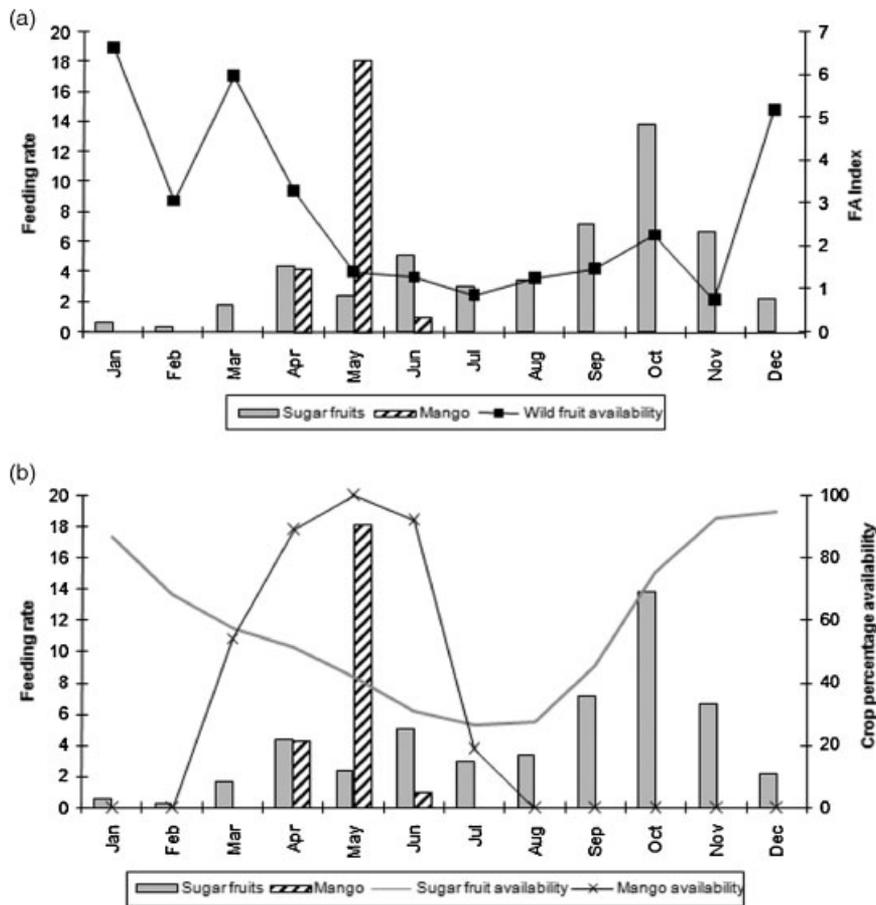
Fig. 4. Monthly crop-raiding event rates for sugar fruits and feeding event rates for mangoes plotted against (**a**) wild fruit availability and (**b**) sugar fruit and mango availability.

TABLE II. Spearman Rank Correlations Between Crop-Raiding Rates and Monthly Wild Fruit Availability (FA Index) and that Crop's Availability ($n = 12$ in all Cases, *$P < 0.05$, **$P < 0.01$)

| | Wild fruit availability | Cultivar availability |
Crop	Events	Events
Rice	0.41	**0.84****
Maize	**−0.70****	**0.87****
Cacao	−0.28	0.22
Cassava	0.06	−0.02
Papaya leaf	**−0.82****	–
Banana pith	−0.12	–

DISCUSSION

Like other chimpanzee sites, there is marked seasonal variation in the availability of wild foods at Bossou and the chimpanzees have a broad diet dominated by fruit. Unlike other communities, Bossou chimpanzees consume a wide and nutritionally varied range of crops that differ considerably in their spatial and temporal availability. Although crops at Bossou are generally available to the chimpanzees throughout the year, some have a relatively brief fruiting period, whereas others are available every month, meaning that these species may be potential fallback foods for chimpanzees.

Crops were obtained by the chimpanzees from different sources; some were guarded, some were abandoned, others were supplied. Overall rates of crop-raiding and all crop feeding were higher during periods of wild fruit scarcity, highlighting the general fallback nature of crops to the chimpanzees. Chimpanzees fed on higher levels of raided foods during months of wild fruit scarcity than during periods of high wild fruit availability, when they showed higher feeding rates from abandoned and supplied sources. A sex difference in crop feeding behaviors was also observed, with adult male chimpanzees relying more on crops than females.

The Bossou chimpanzees' exploitation of crops is inextricably connected with wild fruit availability and their use of wild foods. Other previously recognized wild fallback foods, including umbrella tree fruit and oil-palm pith, were exploited like raided crops, highlighting the role of both kinds of fallback foods in the chimpanzees' diets. Lipid-rich

oil-palm fruit did not emerge as a clear fallback food during this study, although feeding rates (excluding fruits from supplied sources) were higher during periods of wild fruit scarcity [also see Humle & Matsuzawa, 2004; Yamakoshi, 1998]. Efforts should be made to conserve these secondary forest species, as they almost certainly buffer crop-raiding rates during periods of wild fruit scarcity. Although cassava tuber-raiding was not related to wild fruit availability, as with wild fallback foods, patterns of use of energy-rich cassava were similar to those of other raided crops [for further details, see Hockings et al., 2009]. Cassava farming contributes heavily to deforestation in Bossou, but whereas other destructive crops such as coffee are not consumed, the chimpanzees are able to exploit the tubers from guarded and abandoned sources during critical periods. Although for most primates the negative impact of deforestation clearly outweighs new foraging opportunities arising from cultivation, the complete feeding ecology of primates should be of foremost importance when considering long-term land-use management practices such as the removal of introduced crop species [Nishida, 2008].

Certain crops were raided in strong association with wild fruit scarcity, whereas others were raided when available. As predicted, forest fruit scarcity was associated with more sugar fruit crop-raiding, showing the sugar fruits' role as fallback foods for the chimpanzees; however, the low availability of these crops from June to August co-occurred with decreased crop-raiding during this period. Chimpanzees also strongly preferred sugar-rich mango fruits when available compared with other crops, reflecting a preference to forage for low-risk and spatially abundant foods. The high rate of mango consumption during the month of May recalls a high wild fruit availability month.

Rice pith-raiding by chimpanzees correlated with rice availability, and fully grown plants were raided at around the time when the grain was ready for harvesting, which coincided with high wild fruit availability. In parallel, maize-raiding was tightly linked to availability, and increased with wild fruit scarcity. The chimpanzees' strong preferences for rice pith and carbohydrate- and protein-rich maize conform to the widespread view that crops are raided for their high nutritional value [Bell, 1984; Maples et al., 1976; Naughton-Treves et al., 1998]. It is therefore particularly risky for farmers to grow such crops, especially people's staple carbohydrate sources, near or within forest, as they will be sought out by wildlife.

Despite year-round availability within the forest, banana pith was consumed preferentially from April to December, and was most frequently taken during the months of July and November. As with cassava, the chimpanzees did not eat spatially abundant banana pith during May or August when mango and maize were plentiful. This is consistent with patterns of banana pith consumption by the Kibale chimpanzees [Naughton-Treves et al., 1998]. Like protein-rich papaya leaf that shows year-round availability yet was only exploited when forest fruit was scarce, high-fiber banana pith may function as a fallback food, although not always taken in preference to alternative cultivated foods. Cacao, a good source of lipids, was only available from one small forest plantation in the forest that was frequently visited by the chimpanzees. This might explain why crop-raiding on cacao was not correlated with wild fruit availability or its availability.

Even though the chimpanzees at Bossou are totemic to local people and are fortunate not to be killed when crop-raiding, they are often chased away by angry or scared farmers, sometimes with the use of stones and noise. Despite overlap in human factors that are likely to affect chimpanzee crop-raiding (e.g. location, guarding practices, people presence), each community will be faced with a different combination of social, ecological and cultural factors to those found at Bossou. Other chimpanzees living in larger and less disturbed forests might also exhibit preferences for particular crops when available, despite wild fruit abundance. Farmers will show varying tolerance levels to such raiding depending upon factors including crop type, invested time and effort in crop production, and commercial value of the crop, as well as local social and cultural practices [Priston, 2005; Webber et al., 2007]. It is not known how long communities of chimpanzees living in fragmented and anthropogenic habitats in Africa will be able to survive alongside their human neighbors [McLennan, 2008]. However, with tolerance from local people and protection from hunting, the situation at Bossou highlights that chimpanzees are able, if given a chance, to adapt ecologically to the various costs and benefits of living in a heavily human-influenced environment.

In conclusion, predicting foraging behavior in biologically complex systems is difficult, especially when a chimpanzee's motivation to crop-raid might be influenced by social factors, such as gaining prestige and access to mates, as well as simply gaining the highest return rate with the least energy expended [Hockings et al., 2007]. Although relatively little conflict exists now at Bossou, the potential for increasing human–ape conflict throughout Africa is huge [see Hockings & Humle, 2009]. It is crucial to gain a better understanding of the ecological determinants of primate crop-raiding. Investigations should incorporate more detailed nutritional analyses of both wild and cultivated foods consumed at different times of the year, and patterns and changes over longer periods of time, in order to design effective management strategies that will facilitate human–nonhuman primate coexistence.

ACKNOWLEDGMENTS

REFERENCES

Bell RHV. 1984. The man–animal interface: an assessment of crop damage and wildlife control. In: Bell RHV, McShane-Caluzi E, editors. Conservation and wildlife management in Africa. Proceedings of a US Peace Corps workshop, Malawi. p 387–416.

Byrne RW, Whiten A, Henzi SP, McCulloch FM. 1993. Nutritional constraints on mountain baboons (*Papio ursinus*): implications for baboon socioecology. Behav Ecol Sociobiol 33:233–246.

Chapman CA, Chapman LJ, Wrangham R, Hunt K, Gebo D, Gardner L. 1992. Estimators of fruit abundance of tropical trees. Biotropica 24:527–531.

Chapman CA, Wrangham R, Chapman LJ. 1994. Indices of habitat-wide fruit abundance in tropical forest. Biotropica 26:160–171.

Doran DM, McNeilage A, Greer D, Bocian C, Mehlman P, Shah N. 2002. Western lowland gorilla diet and resource availability: new evidence, cross-site comparisons and reflections on indirect sampling methods. Am J Primatol 58:91–116.

Goodall J. 1986. The chimpanzees of Gombe: patterns of behaviour. Cambridge, MA: Harvard University Press.

Hill CM. 1997. Crop-raiding by wild vertebrates: the farmer's perspective in an agricultural community in western Uganda. Int J Pest Manag 43:77–84.

Hill CM. 2000. Conflict of interest between people and baboons: crop raiding in Uganda. Int J Primatol 21:299–315.

Hoare R. 2001. A decision support system (DSS) for managing human–elephant conflict situations in Africa. Nairobi: AfESG (IUCN Elephant Specialist Group).

Hockings KJ. 2007. Human–chimpanzee coexistence at Bossou, the Republic of Guinea: a chimpanzee perspective. Dissertation. UK: University of Stirling.

Hockings KJ, Humle T. 2009. Best practice guidelines for the prevention and mitigation of conflict between humans and great apes. Gland, Switzerland: IUCN/SSC Primate Specialist Group (PSG). 40p.

Hockings KJ, Anderson JR, Matsuzawa T. 2006. Road-crossing in chimpanzees: a risky business. Curr Biol 16:668–670.

Hockings KJ, Humle T, Anderson JR, Biro D, Sousa C, Ohashi G, Matsuzawa T. 2007. Chimpanzees share forbidden fruit. PLoS ONE 2:e88.

Hockings KJ, Anderson JR, Matsuzawa T. 2009. Flexible feeding on cultivated underground storage organs by rainforest-dwelling chimpanzees at Bossou, West Africa, under review.

Humle T. 2003. Chimpanzees and crop raiding in West Africa. In: Kormos R, Boesch C, Bakarr MI, Butynski TM, editors. West African chimpanzees. Status survey and conservation action plan. Gland, Switzerland, Cambridge, UK: IUCN/SSC Primate Specialist Group, IUCN. p 147–155.

Humle T, Matsuzawa T. 2004. Oil palm use by adjacent communities of chimpanzees at Bossou and Nimba Mountains, West Africa. Int J Primatol 25:551–581.

Kortlandt A. 1986. The use of stone tools by wild-living chimpanzees and earliest hominids. J Hum Evol 15:77–132.

Laden G, Wrangham R. 2005. The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopith origins. J Hum Evol 49:482–498.

Lambert JE. 2007. Seasonality, fallback strategies, and natural selection: a chimpanzee versus cercopithecoid model for interpreting the evolution of hominin diet. In: Ungar P, editor. Evolution of human diet: the known, the unknown, and the unknowable. Oxford: University of Oxford Press. p 324–343.

Linkie M, Dinata Y, Nofrianto A, Leader-Williams N. 2007. Patterns and perceptions of wildlife crop raiding in and around Kerinci Seblat National Park, Sumatra. Anim Conserv 10:127–135.

Maples WR, Maples MK, Greenhood WF, Walek ML. 1976. Adaptations of crop-raiding baboons in Kenya. Am J Phys Anthropol 45:309–316.

Marshall AJ, Wrangham RW. 2007. Evolutionary consequences of fallback foods. Int J Primatol 28:1219–1235.

Matsuzawa T. 2006. Sociocognitive development in chimpanzees: a synthesis of laboratory work and fieldwork. In: Matsuzawa T, Tomonaga M, Tanaka M, editors. Cognitive development in chimpanzees. Tokyo: Springer. p 3–33.

Matsuzawa T, Sugiyama Y. 2009. The chimpanzees of Bossou and Nimba: a cultural primatology. Tokyo: Springer.

McGrew WC. 1992. Chimpanzee material culture: implications for human evolution. Cambridge: Cambridge University Press.

McLennan MR. 2008. Beleaguered chimpanzees in the agricultural district of Hoima, Western Uganda. Primate Conserv 23:45–54.

Morgan D, Sanz C. 2006. Chimpanzee feeding ecology and comparisons with sympatric gorillas in the Goualougo Triangle, Republic of Congo. In: Hohmann G, Robbins M, Boesch C, editors. Feeding ecology in apes and other primates. Cambridge: Cambridge University Press. p 97–122.

Naughton-Treves L. 1998. Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. Conserv Biol 12:156–168.

Naughton-Treves L, Treves A, Chapman C, Wrangham R. 1998. Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. J Appl Ecol 35:596–606.

Nishida T. 1976. The bark-eating habits in primates, with special reference to their status in the diet of wild chimpanzees. Folia Primatol 25:277–287.

Nishida T. 2008. Why were guava trees cut down in Mahale Park? The question of exterminating all introduced plants. Pan Afr News 15:12–14.

Priston N. 2005. Crop-raiding by *Macaca ochreata brunnescens* in Sulawesi: reality, perceptions and outcomes for conservation. Dissertation. UK: University of Cambridge.

Pruetz JD. 2006. Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. In: Hohmann G, Robbins M, Boesch C, editors. Feeding ecology in apes and other primates. Cambridge: Cambridge University Press. p 326–364.

Reynolds V. 2005. The chimpanzees of the Budongo Forest: ecology, behaviour, and conservation. Oxford: Oxford University Press.

Reynolds V, Plumptre AJ, Greenham J, Harborne J. 1998. Condensed tannins and sugars in the diet of chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. Oecologia 115:331–336.

Richard AF, Goldstein SJ, Dewar RE. 1989. Weed macaques: the evolutionary implications of macaque feeding ecology. Int J Primatol 10:569–594.

Rode KD, Chapman CA, Chapman LJ, McDowell LR. 2003. Mineral resource availability and consumption by colobus in Kibale National Park, Uganda. Int J Primatol 24:541–573.

Rogers ME, Maisels F, Williamson EA, Fernandez M, Tutin CEG. 1990. Gorilla diet in the Lope Reserve, Gabon: a nutritional analysis. Oecologia 84:326–339.

Siex KS, Struhsaker TT. 1999. Colobus monkeys and coconuts: a study of perceived human–wildlife conflicts. J Appl Ecol 36:1009–1020.

Strum SC. 1994. Prospects for management of primate pests. Rev Ecol—Terre Vie 49:295–306.

Takemoto H. 2004. Seasonal change in terrestriality of chimpanzees in relation to microclimate in the tropical forest. Am J Phys Anthropol 124:81–92.

Terborgh JT. 1986. Keystone plant resources in the tropical forest. In: Soule ME, editor. Conservation biology: the science of scarcity and diversity. Massachusetts: Sinauer Associates. p 330–344.

Tutin CEG, Ham RM, White LJT, Harrison MJS. 1997. The primate community of the Lope Reserve, Gabon: diets, responses to fruit scarcity and effects on biomass. Am J Primatol 42:1–24.

Webber AD, Hill CM, Reynolds V. 2007. Assessing the failure of a community-based human–wildlife conflict mitigation project in Budongo Forest Reserve, Uganda. Oryx 41: 177–184.

Wrangham RW. 1977. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: Clutton-Brock TH, editor. Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes. London: London Academic Press. p 504–538.

Wrangham RW, Conklin NL, Chapman CA, Hunt KA. 1991. The significance of fibrous foods for the Kibale forest chimpanzees. Philos Trans R Soc B 334: 171–178.

Wrangham RW, Conklin-Brittain NL, Hunt KD. 1998. Dietary response of chimpanzees and Cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. Int J Primatol 19:949–970.

Yamakoshi G. 1998. Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for ecological importance of tool use. Am J Phys Anthropol 106:283–295.