



Flexible feeding on cultivated underground storage organs by rainforest-dwelling chimpanzees at Bossou, West Africa

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ABSTRACT

It has been proposed that exploitation of underground storage organs (USOs) played an important role in the evolution of the genus *Homo*, these items serving as 'fallback foods' during periods of low food availability. The use of USOs as food by wild chimpanzees is infrequent and seen mostly in populations inhabiting relatively arid environments, such as the savanna. Here, we specifically test the hypothesis that chimpanzees (*Pan troglodytes verus*) inhabiting tropical wet forest at Bossou (Republic of Guinea, West Africa) exploit USOs as a fallback food during periods of fruit scarcity. Chimpanzees were never observed feeding on wild USOs, that is, those that were never cultivated, and rarely on other underground plant parts. However, direct observations revealed regular consumption of the USOs of cultivated cassava (*Manihot esculenta*), a spatially abundant and continuously available plant, although the chimpanzees did not use tools when acquiring and feeding on cassava. In agreement with the fallback foods hypothesis, our results show that chimpanzees exploited cassava USOs more frequently when both wild and cultivated fruits were scarce, and consumption patterns of cassava paralleled those of wild fallback foods. These seasonal extractive USO foraging strategies by chimpanzees can strengthen attempts to construct a clearer picture of the importance of USO feeding in hominoid evolution.

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Introduction

The diet of wild chimpanzees (*Pan troglodytes*) is dominated by ripe fruit which, irrespective of the chimpanzees' environment, comprises 50 to 75% of overall feeding effort (Wrangham, 1977; Goodall, 1986; Tutin et al., 1997; Yamakoshi, 1998; Morgan and Sanz, 2006; Pruetz, 2006). Less commonly discussed, yet exploited by some communities of chimpanzees—particularly in more arid environments—are the subterranean parts of plants, including the underground storage organs (USOs; Kortlandt and Holzhaus, 1987; McGrew et al., 1988; Lanjouw, 2002; Laden and Wrangham, 2005; Hernandez-Aguilar et al., 2007). Savanna environments are drier and are generally considered to be more challenging habitats for chimpanzees to find fruit, requiring additional behavioural adaptations for survival, such as carbohydrate-rich USO consumption (McGrew et al., 1981; Moore, 1996). However, current data suggest that edible USO diversity and abundance are higher in savannas than in rainforests (Laden and Wrangham, 2005)—USOs are

probably a response to dry and unpredictable climates where plants need to store energy underground, offering an additional explanation for why USO consumption in chimpanzee communities inhabiting wet forest environments is so infrequent.

As most plant species exhibit periods of scarcity in fruit production, fruit specialists are often under considerable pressure to show dietary flexibility, often relying on specific fallback foods (Terborgh, 1986; Lambert, 2007). Fallback foods are typically non-preferred, indicated by the relationship between their availability and usage, but of high seasonal importance, although year-round use does not preclude a food item serving as a fallback food (Marshall and Wrangham, 2007). Laden and Wrangham (2005:13) 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."

Chimpanzees inhabiting savanna areas at Ugalla in Tanzania did not exploit USOs during periods of fruit scarcity (Hernandez-Aguilar et al., 2007). However, indirect data (such as knuckle-prints, faeces, and wadges of USO fibres) suggest that chimpanzees at this site dig up and eat seven species of USOs, sometimes with the use of tools during the wet season, which coincides with wild fruit abundance. The authors claim that their results contradict the

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'fallback foods' hypothesis but suggest that Ugalla chimpanzees might also exploit USOs to combat seasonal ailments, such as elevated parasite levels during the wet season (Huffman et al., 1997), as well as for nutritional gain. Intriguingly, chimpanzees at Tongo, Democratic Republic of Congo, inhabiting relatively dry forest, regularly dig deep holes (without the aid of tools) to reach water-rich tubers, especially during dry periods (Lanjouw, 2002); there is no evidence that tubers provided any calorific benefits.

Here, we test the hypothesis that cassava (*Manihot esculenta*) USOs (more specifically tuberous roots) act as fallback foods for wild chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea during periods of fruit scarcity (see Kortlandt and Holzhaus [1987] for a brief description). If cassava consumption is influenced by fluctuating availability of wild fruits (fruits that were never cultivated) and cultivated foods, and follows the same usage patterns as recognised wild fallback foods (e.g., Umbrella tree fruit, *Musanga cecropioides*, oil-palm pith, *Elaeis guineensis*; see Yamakoshi, 1998), then cassava USOs might be an important fallback food for the Bossou chimpanzees. Furthermore, if cassava is a fallback food for the chimpanzees, then they should not forego other available foods, such as leaves and pith, but should instead incorporate USOs into their broader ecological strategy. Alternatively, if cassava is a preferred food, it should be eaten consistently and frequently throughout the year because of palatability or nutritional benefits. Furthermore, we hypothesised that when wild fruits are relatively scarce, chimpanzees would increase cassava raiding even when local people are present and in highly guarded fields, despite the higher degree of risk—defined as potential negative impact that might arise from a future crop-raiding event (Hockings et al., 2009).

Materials and methods

Behavioural data were collected over 12 months (specifically, during every month of the year in three periods between May 2004 and December 2005), and phenological data were collected continually over the 20 months. The climate at Bossou is classified as tropical wet seasonal (Richards, 1996), with a clear wet season from March to October (397.7 mm average monthly rainfall in 2005) and a dry season from November to February (64.0 mm average monthly rainfall in 2005); this seasonality is consistent with past records (Yamakoshi, 1998; Takemoto, 2004). During 2005, the average annual temperature, monitored daily at 1700 h, was 26.9 °C (minimum of 12.3 °C, maximum of 36.9 °C).

Humans (*Homo sapiens*) and chimpanzees coexist at Bossou (7° 39' N; 8° 30' W), where the 15 km² home range (7 km² core area) of the chimpanzees' community is fragmented and surrounded by cultivated and abandoned fields, orchards, and farms (Hockings et al., 2006, 2007). Chimpanzees at Bossou regularly enter these cultivated areas to crop-raid and although the crops consumed seem to have varied over the years, reports suggest that cultivated foods have been present in their dietary repertoire since at least the 1960s (Kortlandt and Holzhaus, 1987; Sugiyama and Koman, 1987, 1992). Sugiyama and Koman (1987, 1992) reported that chimpanzees fed on 29 species of cultivated foods, although exact crop feeding levels are not available for that period. Large, guarded fields cultivated with sweet cassava are particularly abundant in Bossou (see Fig. 1). Cassava tuber has no known medicinal value and has high starch content that provides a staple carbohydrate source for the people in this region. Cassava varieties are often categorised as either 'sweet' or 'bitter,' signifying the absence or presence of toxic levels of cyanogenic glucosides; the sweet cassava can be eaten uncooked, whereas bitter cassava require cooking before consumption by humans (Kortlandt and Holzhaus, 1987; Aregheore and Agunbiade, 1991).

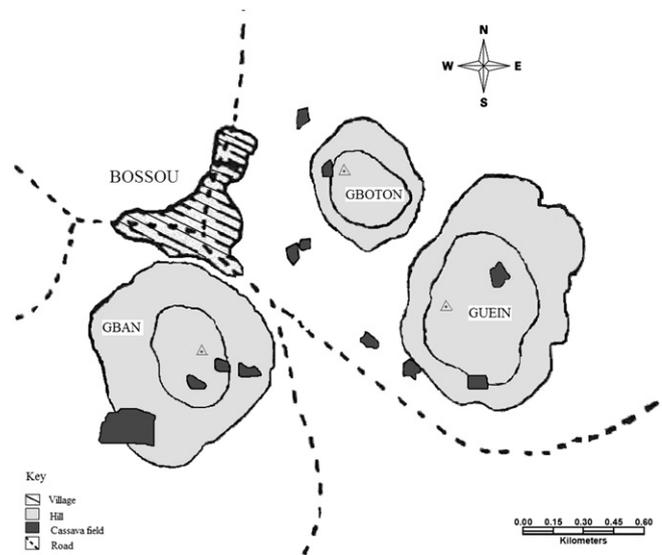


Fig. 1. A map of the field study site Bossou showing the village, the roads, and the three main hills (forest) of Gban, Guein, and Gboton. The presence of guarded cassava fields within and surrounding the Bossou chimpanzees' core area are highlighted in dark grey patches.

Phenological surveys

A total of six transect lines (total distance 4739 m) were set up to monitor all trees and lianas (total of 3611 trees/lianas) in the three principal hill forests of Bossou, namely Gban, Guein, and Gboton. 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 (north-to-south and east-to-west directions, respectively: *Gban*: 1110 m, 811 trees and lianas; 976 m, 792 trees and lianas; *Guein*: 870 m, 530 trees and lianas; 900 m, 722 trees and lianas; *Gboton*: 424 m, 314 trees and lianas; 459 m, 442 trees and lianas). Due to the restricted home range of the chimpanzees, this method was considered appropriate for maximising the area and number of trees and lianas sampled. Additionally, the transect lines passed through all the habitat types present in the Bossou home range, and the trees and lianas sampled are considered to be representative. Each transect line was 10 m wide and included every tree or liana greater than 5 cm in diameter at breast height (DBH). During every 2nd and 4th week of each month the transects were monitored, and each tree or liana 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 a circular cross-section of trunks (modified from Takemoto, 2004):

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

where P_i is the basal area of the tree (cm²), 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 KH during the study period (see below) and were used for subsequent calculations of wild fruit availability (using a total of 1596 trees from 59 species).

Cultivated food availability

To assess the spatial distribution of cassava within the chimpanzees' core area, cassava presence on the three main hills in the

home range and up to 50 m from the forest edge was recorded. To assess when cultivated foods were available for harvesting by humans and chimpanzees, 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 categorisation as 'harvested' or 'not harvested' was employed.

Behavioural observations

Community size varied from 12 to 14 individuals, with the same three adult males present throughout. Infants or juveniles less than 8 years old were classified as immature (Matsuzawa, 2006). A focal adult individual was randomly selected from a predetermined list each day prior to the observation session and followed from 0630 h to nest. Overall, 187 focal individual samples were collected (13–17 focal days/month; mean observation time: 8.95 h, S.D. \pm 2.37), totalling 1,673 h of focal observations. Scan samples were taken on the same 5-minute signal used during focal sampling to record the presence of all other individuals. Chimpanzee observation times from scans showed high inter-monthly variation (mean: 699 h/month; monthly range: 378–1161 h). Ad libitum sampling was used to record all observed occurrences of crop-raiding (see Fig. 2), feeding on abandoned cultivated foods and feeding on wild foods.

Some cultivated species were only consumed by chimpanzees in abandoned fields or orchards. As these areas were never guarded, acquiring these foods was not considered as crop-raiding. Crops were thus divided into two groups, namely abandoned: crops that are not guarded by humans; and guarded: crops that are at least periodically guarded by humans.

A crop-raiding 'event' was defined as any successful foray by an individual to obtain guarded cultivated food (Naughton-Treves et al., 1998). For both abandoned and guarded cultivated foods, the type and location of the crop, time of day, and human presence, defined as likely auditory or visual contact with the chimpanzees were noted. Guard level for guarded crops was also defined as either low (humans do not chase the chimpanzees away) or high (when humans are present they chase or throw stones to displace the chimpanzees). 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 (Hockings et al., 2009). This definition allows for multiple but independent daily raids that are not in immediate succession to one field to be counted as distinct crop-raiding 'bouts.' Similarly, during a wild feeding 'event,' if an individual started to feed again after a 10 min pause, a new event was recorded.

Crop-raiding rates were calculated by dividing the number of observed raiding events by the combined scan observation times for each individual per month to give crop-raiding rate per hour; this rate was then multiplied by 100. Crop feeding rates were compared with matched wild fruit availability values for exactly the same months.

All data were analysed using SPSS version 13, and, as data were not normally distributed, non-parametric tests were used. Two-tailed tests were employed throughout and the significance level was set at 5%.

Results

Wild fruit and cultivated food availability

There is marked seasonal variation in the availability of ripe fruit at Bossou. Consistent with past findings (Yamakoshi, 1998; Take-moto, 2004), months of high wild fruit availability are December through April, whereas low fruit availability months are May through November (FA Index values: mean \pm SE, high vs. low; 4.8 ± 0.6 vs. 1.4 ± 0.1). Over this study period, the 2004 December increase in ripe fruit availability is mirrored by a similar increase in December 2005.

Considerable variability in the temporal distribution of different cultivated foods exists (see Fig. 3). Some crops, such as mango, have a precise and relatively brief fruiting period, whereas others, including cassava, are available throughout the year. At the time of this study there were twelve guarded sweet cassava fields of varying size throughout the chimpanzees' core area (see Fig. 1; mean size of cassava fields: 9429 m²; range: 987–40587 m²; typical plant spacing is 1 m by 1 m). As a result of past cultivation, abandoned cassava plants were found scattered within thicket on the forest edge; abandoned cassava occurred at much lower densities than guarded cassava. Cassava planting took place between March and May. The period of cassava growth until maturity was between 10 and 17 months. Although it was harvested quite intensively throughout the year, cassava was harvested by all farmers during the wet season as a major carbohydrate source, in particular between the months of May and August, when other staple foods such as rice were relatively scarce. Cassava roots are very rich in starch and contain significant amounts of calcium, phosphorus, and vitamin C; however, they contain little protein and other nutrients (Okigbo, 1980). In addition to the foods indicated in Figure 3, small quantities of oil-palm (*Elaeis guineensis*) fruits and nuts were provided to the chimpanzees for nut-cracking experiments during the months of January and December (see Hockings et al. [2009] for detailed analyses of supplied oil-palm use by chimpanzees during the study period).

Chimpanzees' general use of cultivated foods

Throughout the study period the chimpanzees regularly visited cultivated areas, where they consumed a total of 17 species of crops (see Hockings et al. [2009] for further details). Overall, raided crops contributed to 8.8% of the chimpanzees' total feeding time (monthly range: 1.8–16.6%, SD \pm 4.8), and in total crops comprised 14% of feeding time (monthly range: 3.6–26.3%, SD \pm 6.9).



Fig. 2. Adult female, juvenile, and infant chimpanzees feeding on cassava tuber in a guarded field (photo provided by Etsuko Nogami).

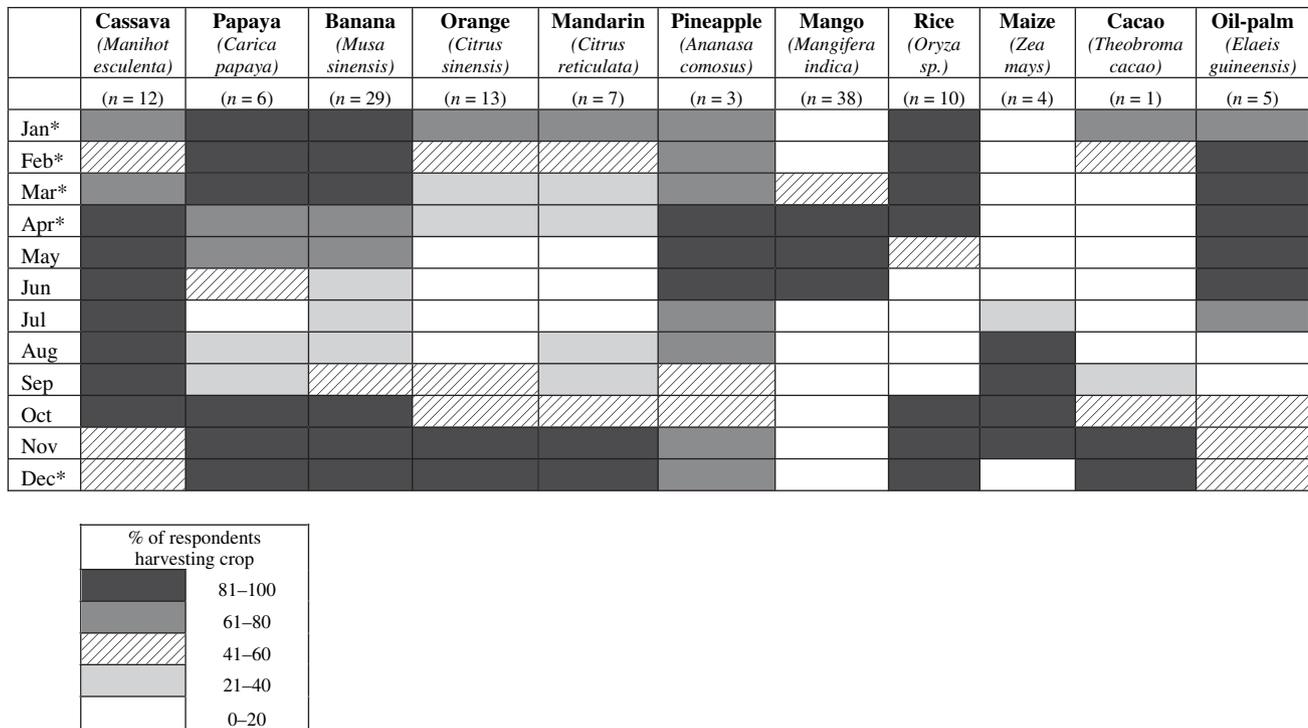


Fig. 3. The temporal availability of cultivated foods rated by questionnaire respondents (shown by coloured area), and the number of orchards, farms, or fields (plots) within the monitored areas containing each specific cultivated food (in brackets). Only foods frequently consumed by the chimpanzees were included. Months of highest wild fruit availability are highlighted (*).

Chimpanzees' use of USOs

Chimpanzees at Bossou were never observed feeding on wild USOs; however, observations confirmed that they occasionally feed on the rhizomes (horizontal stem of a plant that is usually found underground) of two plants, *Polypodium aureum* (fern species) and *Amorphophallus aphyllus* (herb). Each observation took place outside of the study period reported here (2nd and 10th October 2008, respectively) and in abandoned rice paddy fields. Cultivated yam tuber (*Dioscorea* sp.) was consumed only once, by an adult female (yam was cultivated in only one small field in the chimpanzees' core area). In contrast, there were 100 cassava tuber consumption events (33 bouts). The chimpanzees obtained the tubers by strenuously pulling on the above-ground plant stem until the tubers that were close to the soil surface were unearthed (see Supplementary Online Material [SOM] Movie1). They fed on cassava tubers during every month except May, which coincided with a marked increase in feeding on abandoned mango fruit—over 4 times higher than April (event rate per hour of scan observation \times 100: April: 4.19; May: 18.08; June: 0.96). On average, cassava was consumed 8 times per month, but this varied widely throughout the year (see Fig. 4; range: 0–23 events/month; $SD \pm 7.16$). Cassava tuber constituted only a relatively small portion of the total diet of the chimpanzees (see Table 1). Almost three quarters of cassava feeding events occurred during raids on guarded fields (74 out of 100 events), the remainder occurring in abandoned fields; both cases will be discussed.

Cassava-raiding rates and feeding durations failed to significantly correlate with wild fruit availability (raid event: Spearman rank correlation coefficient, $r_s = 0.06$, $n = 12$, ns; duration: $r_s = -0.03$, $n = 12$, ns), although the correlation between total cassava feeding rates (guarded and abandoned combined) and wild fruit availability approached statistical significance (total event: $r_s = -0.53$, $n = 12$, $p = 0.08$). As cassava was available all year round,

raided and total event frequencies were calculated for periods of low and high wild fruit availability. As the total scan observation time in months of high (4214 h: 50.3% of total time) and low wild fruit availability (4177 h: 49.7% of total time) were similar, they were directly compared. Although cassava-raiding events were more frequent during periods of low wild fruit availability, the difference was not significant (low: 43 events vs. high: 31 events; $X^2(1) = 1.95$, ns). However, the total cassava feeding score (guarded and abandoned combined) was higher during periods of low (59 events) compared to high wild fruit abundance (41 events): $X^2(1) = 4.65$, $p < 0.05$. Despite chimpanzees and local people both consuming cassava tuber, especially during the wet season, the percentage of respondents harvesting cassava did not correlate with the chimpanzees' use of cassava (see Fig. 5; event: $r_s = -0.02$, $n = 12$, ns; duration: $r_s = -0.01$, $n = 12$, ns).

To better understand the role of cassava tuber in the chimpanzees' diet, we analysed feeding behaviour in relation to raiding crops other than cassava. Cassava tuber showed the same usage patterns as other raided cultivated foods (event: $r_s = 0.818$, $n = 12$, $p < 0.01$; duration: $r_s = 0.893$, $n = 12$, $p < 0.01$). Furthermore, consumption of cassava showed statistically significant positive correlations with consumption of wild fallback foods (including umbrella tree fruit, *Musanga cecropioides*: event: $r_s = 0.629$, $n = 12$, $p < 0.05$; duration: $r_s = 0.580$, $n = 12$, $p < 0.05$; oil-palm pith, *Elaeis guineensis*, event: $r_s = 0.671$, $n = 12$, $p < 0.05$; duration: $r_s = 0.655$, $n = 12$, $p < 0.05$).

There were 19 observed cassava-raiding bouts (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. Chimpanzees were more likely to raid highly guarded fields ($X^2(2) = 19.69$, $p < 0.01$) and to raid when people were present ($X^2(1) = 5.83$, $p < 0.05$) during periods of wild fruit scarcity than during periods of wild fruit abundance. All 14 non-guarded cassava feeding bouts took place in the forest

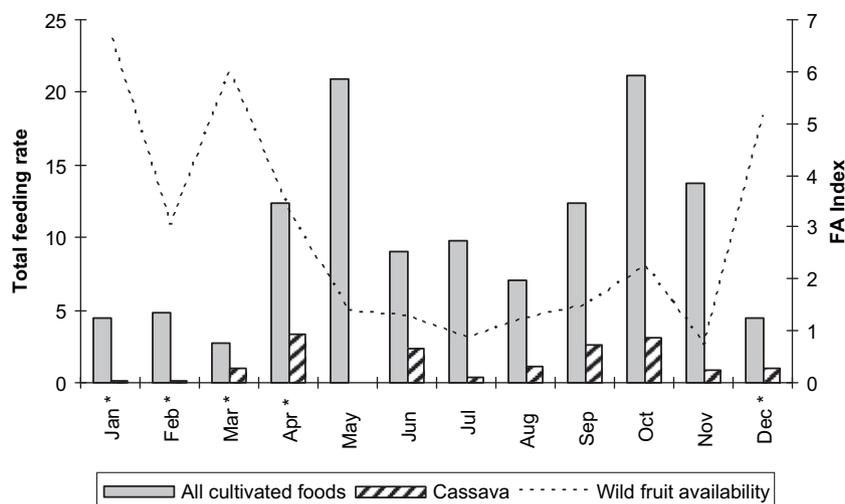


Fig. 4. Monthly feeding rates for other cultivated foods and cassava (abandoned and guarded combined), plotted against wild fruit availability; * indicates months with highest wild fruit availability.

where people were absent. Despite these differences, durations of feeding on abandoned and guarded cassava were similar (abandoned: average: 9.1 min, range: 2–28 min, $SD \pm 6.63$; guarded: average: 11.1 min, range: 1–25 min, $SD \pm 8.32$). The time of day was divided into three periods for analyses: morning (0700 h–1059 h), midday (1100 h–1459 h), and afternoon (1500 h–1859 h). Monthly focal observation times differed throughout the day (morning: min – 24.6, max – 36.3, mean – 31.5, $SD - 3.8$; midday: min – 48.3, mean – 40.1, $SD - 3.8$; afternoon: min – 21.4, max – 32.3, mean – 28.5, $SD - 3.1$). However, raids on sugar fruits, including papaya, orange, mandarin, pineapple, and banana showed no relationship with time of day ($X^2(2) = 4.62$, ns), whereas 82% of cassava feeding bouts occurred during the afternoon (abandoned: 11 out of 14 bouts, binomial [0.3], $p < 0.001$; guarded: 16 out of 19 bouts, binomial [0.3], $p < 0.001$).

Discussion

In agreement with past studies (Sugiyama and Koman, 1987, 1992), the Bossou chimpanzees never fed on wild USOs but very occasionally fed on horizontally growing plant rhizomes that were very easily unearthed. It is unknown whether the rhizomes were consumed for nutritional or medicinal use. From a summary table showing the diversity of USOs eaten by humans in relation to habitat type (presented by Laden and Wrangham, 2005:486–488),

Table 1

The monthly percentages of feeding events for fruit, pith, leaf, and USO that were consumed in abandoned, raided, and wild conditions combined.

(% events)	Fruit	Pith	Leaf	USO
Jan ^a	52.6	18.6	15.2	0.2
Feb ^a	49.9	27.9	16.2	0.5
Mar ^a	59.7	24.1	8.2	1.2
Apr ^a	52.6	23.1	14.1	3.8
May	60.3	16.4	21	0
Jun	46.1	23	17.6	3.1
Jul	45.7	22.2	22.9	0.5
Aug	53.8	11.8	22	1.3
Sep	48.3	21.3	18.1	2.1
Oct	50.6	24.3	14.6	2.9
Nov	54	25.2	13.1	1.3
Dec ^a	49.5	19.9	20	1.4
Mean ($\pm SD$)	51.9 (4.6)	21.5 (4.3)	16.9 (4.2)	1.5 (1.2)

^a indicates months with highest wild fruit availability.

five of the many documented USO species of plant are available at Bossou (*Dioscoreophyllum cumminsii*, *Smilax sp.*, *Dioscorea minutiflora*, *Dioscorea sagittifolia*, *Dioscorea bulbifera*). All of these must be cooked before consumption (K.H., unpublished data), which highlights the scarcity of edible USOs for the chimpanzees in the forest.

Cassava tuber is an important food to chimpanzees at Bossou, being eaten to different degrees throughout the year. Note that cassava feeding frequency may even be underrepresented due to restricted visibility, as mature cassava plants are generally taller than a chimpanzee and abandoned cassava fields were in areas of dense thicket. Chimpanzees at Bossou consumed cultivated cassava tubers for nutritional gain, although to a much lesser extent than other plant foods such as fruit, leaves, and pith. Fruits are perishable and need to be harvested quickly when ripe, whereas temporal and spatial availability of cassava is more stable. The month of April saw the highest levels of cassava consumption, which reflects low availability of wild fruit and other cultivated foods. In comparison, no cassava feeding was observed in May, when the chimpanzees fed frequently on mango fruit; access to other cultivated foods may therefore at least partly explain temporal variations in cassava consumption. Cassava was also eaten relatively infrequently during January and February, when wild fruits were abundant and oil-palm fruits and nuts were supplied to the chimpanzees. During the

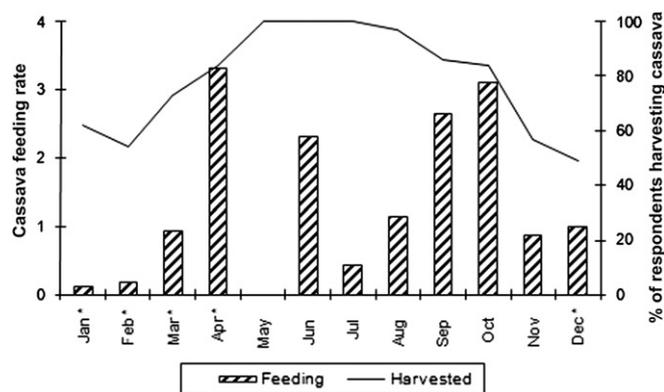


Fig. 5. Rate of feeding on cassava (abandoned and raided combined) plotted against the percentage of farmers at Bossou ($n = 36$) harvesting cassava during each month; * indicates months with highest wild fruit availability. The percentage of respondents harvesting cassava per month is used as a measure of the periods when cassava is harvested by local people.

dry season that coincides with the period of high wild fruit availability, local people report that cassava tubers are generally smaller and more bitter, possibly providing an additional reason for increased consumption during the wet season. In support of the fallback foods hypothesis (Laden and Wrangham, 2005), chimpanzees at Bossou consumed significantly more USOs during periods of wild fruit scarcity, using them much as they do wild fallback foods and other guarded cultivated foods. Cassava appears to constitute a ‘filler’ fallback food, never constituting the entire diet and not sufficient on its own to sustain chimpanzees at Bossou.

It is conceivable that cassava feeding diminishes during the dry season due to the difficulty of extracting the USOs from the harder ground (Laden and Wrangham, 2005). Although the Bossou chimpanzees habitually engage in tool use such as nut-cracking (Biro et al., 2003; Carvalho et al., 2008), pestle-pounding (Yamakoshi and Sugiyama, 1995), and ant-dipping (Humle and Matsuzawa, 2002), there was no evidence of tool use to dig for USOs. The absence of tool use in this context stands in contrast to that at Ugalla, Tanzania, and reflects a general lack of ‘ground-digging’ behaviour within the Bossou community, possibly meaning that the behaviour has yet to be innovated (Reader and Laland, 2001; Lee, 2003). In any case, for most of the year cultivated cassava tubers are relatively easy to unearth without tools due to their proximity to the soil surface. Additionally, tool use during dry spells when the ground is baked may be energy inefficient. It is possible that early hominins might have become more efficient harvesters of USOs by using tools to extract them.

Predicting foraging behaviour in biologically complex systems is difficult (Hockings and Humle, 2009); a chimpanzee’s decision to consume USOs, in particular those that are cultivated and guarded by humans, will be influenced by multiple factors. For example, when wild fruits were scarce, chimpanzees engaged in a greater-than-expected frequency of cassava raids when people were present and on highly guarded fields, indicating that chimpanzees are willing to take greater risks to obtain cultivated USOs during these limiting periods. A worthwhile line of future enquiry would be to compare USO and general food availability at Bossou and other chimpanzee sites to clarify whether large or nutritionally-rich USOs are absent from other sites or whether Bossou, like drier habitats, has a “scarce” food resource base. Kortlandt and Holzhaus (1987) have speculated that the chimpanzees’ adaptation to cassava feeding is due to lowered food availability.

We have demonstrated that chimpanzees at Bossou appear to use cassava as a fallback food during periods of food scarcity and that cassava is preferentially consumed later in the day when chimpanzees might possibly be less likely to encounter fruits (Laden and Wrangham, 2005; Marshall and Wrangham, 2007). USOs did not replace other fallback foods but were instead integrated into the chimpanzees’ overall fallback food strategy. We speculate that USO-feeding behaviour may have taken on greater importance in early hominins inhabiting more seasonal habitats, where knowledge of nonseasonal foods, such as USOs, would have become essential to survival.

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Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.jhevol.2009.11.004.

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