African Journal of Ecology

Ficus sp. and *Musanga leo-errerae*: coexistent keystone fruits for chimpanzees in Kalinzu forest

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Abstract

The composition of *Ficus* sp. and *Musanga leo-errerae* in Chimpanzees' diet was investigated by faecal analysis and direct observation in the medium altitude forest of Kalinzu, along the albertine rift, south-western Uganda. The fruit availability of *Ficus* species showed significant variations while that of *Musanga leo-errerae* was consistent and significantly higher than that of *Ficus* ($P = 0.053$; $t = -2.034$) all year round. Their consumption was not opportunistic as no correlation existed between their fruit abundance and their occurrence in chimpanzee faecal samples/diet (*Musanga leo-errerae*: $r = 0.153$, $P = 0.456$; *Ficus* sp.: $r = 0.039$, $P = 0.848$). Results showed that *Musanga leo-errerae* and *Ficus* species seeds occurred in 80.2% and 67.2% respectively of the total 2635 chimpanzee faecal samples analyzed. Although there was no significant difference between chimpanzees party size that fed on *Musanga leo-errerae* and *Ficus* tree species, the rate of consumption was significantly different in the low ($t = 3.835$; $P = 0.031$) than the high fruiting season ($t = 2.379$; $P = 0.063$). *Ficus* sp. and *Musanga leo-errerae* genera function as coexistent keystone fruits for chimpanzees because they perfectly complement each other in terms of chimpanzees' sustenance. This information has significant implications in the management of tropical forests like Kibale, Budongo, Bwindi Impenetrable, Gombe and Mahale inhabited by primate populations especially the endangered ones like the chimpanzee.

Key words: chimpanzees, *Ficus* sp., fruit, keystone, *Musanga leo-errerae*

Résumé

La composition du régime alimentaire des chimpanzés en *Ficus* sp. et en *Musanga leo-errerae* fut étudiée par analyse des excréments et par observation directe dans la forêt de moyenne altitude de Kalinzu, dans le Rift albertin, au sud-ouest de l'Ouganda. La disponibilité des fruits des figuiers présentait d'importantes variations alors que celle des *Musanga leo-errerae* était constante et significativement plus élevée que celle des *Ficus* ($P = 0{,}053$; $t = -2{,}034$) tout au long de l'année. Leur consommation n'était pas opportuniste parce qu'il n'y avait pas de corrélation entre l'abondance des fruits et leur présence dans les échantillons fécaux/le régime des chimpanzés (*Musanga leo-errerae :* $r = 0{,}153$, $P = 0{,}456$; *Ficus* sp *:* $r = 0{,}039$, $P = 0{,}848$). Les résultats montraient que les semences de *Musanga leo-errerae* et des différentes espèces de *Ficus* se trouvaient respectivement dans 80,2% et 67,2% du total des 2 635 échantillons fécaux analysés. Bien qu'il n'y ait pas de différence significative entre la taille des groupes de chimpanzés qui se nourrissaient de *Musanga leo-errerae* et des différentes espèces de *Ficus,* le taux de consommation était significativement différent en basse saison de fructification ($t = 3{,}835$; $P = 0{,}031$) et en haute saison ($t = 2{,}379$; $P = 0{,}063$). Les genres *Ficus* sp. et *Musanga leo-errerae* sont tous deux des fruits essentiels pour les chimpanzés parce qu'ils se complètent parfaitement dans le régime alimentaire. Cette information a des implications importantes pour la gestion de forêts tropicales telles que celles de Kibale, de Budongo, de la Forêt Impénétrable de Bwindi, de Gombe et de Mahale, habitées par des populations de primates en danger comme le chimpanzé.

Introduction

Research on chimpanzees in Uganda dates back from 1962, starting with Budongo forest followed by Kibale forest in which the keystone fruits for chimpanzees have been recorded to be *Ficus* species: Budongo (Tweheyo &

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Lye, 2003) and Kibale (Isabirye-Basuta, 1990; Wrangham, Conklin & Hunt, 1991; Wrangham, Clark & Isabirye-Basuta, 1992; Wrangham *et al.*, 1993, 1996). Similar chimpanzee studies in Kalinzu forest have documented *Musanga* to be the keystone fruit (Hashimoto, Furuichi & Tashiro, 2001), although various *Ficus* species also occur. Kalinzu Forest Reserve (700–1845 m above sea level) (0°17′S and 30°07′E) borders Maramaganbo forest and the two form one continuous forest ecosystem with Kalinzu forming a pocket on the rift valley escarpment and Maramagambo on the rift valley floor. Maramagambo Forest reserve forms part of the Queen Elizabeth National Park (Howard, 1991). There are two rainy seasons (April–May, September through December) and two dry seasons (January through March, June through August). Total mean annual rainfall is 1584 mm (Hashimoto, Furuichi & Tashiro, 2001). Kalinzu is inhabited by six primate species namely *Pan troglodytes, Papio anubis, Colobus guereza, Cercopithecus ascanius, Cercopithecus l'hoesti* and *Cercopithecus mitis*.

The genus *Ficus* belongs to family *Moraceae* and contains about 750 species and occurs in all tropical regions. All *Ficus* species produce edible figs (fruit or synconia) (Janzen, 1979; Berg, 1989). The phenology of *Ficus* is different from other tropical trees in that it depends on specific short-lived symbiots (the aganoid wasps) for pollination, and the genus has evolved to produce fruits at short interval cycles (Kameyama, Harrison & Yamamura, 1999). Features have evolved that favour the continuous development of these symbiots throughout the year (Janzen, 1979).

Diverse mammals and birds eat figs and some species rely heavily on them when nonfig fruits are scarce for example, Sumatran orangutans, *Pongo pygmaeus* (Sugardijito, te Boekhorst & van Hoof, 1987) and Ugandan chimpanzees, *Pan troglodytes* in Budongo (Newton-Fisher, 1999; Tweheyo & Obua, 2001; Tweheyo & Lye, 2003). The combination of large fruit crops and asynchronous intrapopulation fruiting characteristics makes fig trees important keystone resources for many frugivores in the tropics (Leighton & Leighton, 1983; Korine, Kalko & Herre, 2000). In Kibale National Park, figs were found to be the most important fallback foods owing to their high fruit availability all year round (Wrangham, Conklin & Hunt, 1991; Wrangham *et al.*, 1993, 1996).

The length and severity of fruit scarcity influence the role of keystone foods and differ in sites and years (Tutin *et al.*, 1997; Chapman *et al.*, 1999); thus, keystone foods may also vary. *Ficus* sp. have been recorded as key food for chimpanzees in various habitats across Africa like in Senegal (McGrew, Baldwin & Tutin, 1988), Tanzania (Goodall, 1986) Guinea (Sugiyama, Komman & Sow, 1988), Budongo in Uganda (Newton-Fisher, 1999), Gabon (Tutin & Fernandez, 1993), Congo Brazzaville (Kuroda *et al.*, 1996) and in Kibale forest (Malenky, Wrangham & Chapman, 1994; Wrangham *et al.*, 1996). Keystone foods are food items that these species depend on during the periods of general food scarcity. *Musanga leo-errerae* has been recorded to be an important diet component of primates in areas where the fruiting pattern of *Ficus* species becomes unpredictable, e.g. in Gabon (Gauter-Hion & Michauloud, 1989). *Ficus* sp. were also reported as being less preferred than nonfigs and were eaten by chimpanzees when nonfigs were in short supply (Conklin & Wrangham, 1994; Kuroda *et al.*, 1996; Wrangham *et al.*, 1996). Another species of *Musanga* genus, *Musanga cecropioides,* functions as a fall back food in Bossou, Guinea (Yamakoshi, 1998) and D.R. Congo (Thomas (1991). *Musanga leo-errerae* is the one that occurs in Kalinzu forest. Like *Ficus, Musanga* genus is also restricted to logged humid tropical forests in Africa.

Materials and methods

The determination of tree density

Ten parallel transects of 5 km long and 5 m wide running east to west were used to collect data. Distances between the transects were 500 m. Each of these transects was divided into ten 500-m sections totalling to 100 plots. A tree census was carried out after which the natural occurrence of all trees of *Ficus* sp. and *Musanga leo-errerae* above 10 cm in diameter at breast height within 5 m of each side of the transect (Alder & Synnot, 1992) was teased out. The perpendicular distance for each sited *Ficus* or *Musanga* tree species to the middle of the transect was also recorded. Species name (identity determined at the herbarium of Makerere University) and *dbh* of each tree were recorded. The number of trees of each species in 5×500 m block was used as a variable for the analysis.

Fruit census, monitoring and diet composition

From October 2002 to November 2004, a fruit census was conducted on each of the transects, every 15 days. On each transect, fallen fruit was counted, and fallen fruit

from one tree 2 m of each side of the transect was considered as one fruit cluster. The numbers of fruit in each cluster was grouped as 1–4, 5–9 or >10 and assigned a frequency score of 1, 3 or 9, respectively. A fruit abundance index was determined from the total number of scores per hectare (Furuichi, Hashimoto & Tashiro, 2001). To examine the relationship between number of fruit in the tree and number of fallen fruit, 90 monitor trees were randomly chosen on the transects, to monitor the fruiting pattern for each of the *Ficus* species and *Musanga leo-errerae*. These included 30 *Musanga leo-errerae* and 10 of each of the *Ficus* species.

A faecal analysis method was used to determine composition of *Musanga* and *Ficus* genera in the diet of chimpanzees. Fresh chimpanzee faecal samples were collected but those that were scattered on the ground or among branches were ignored because of the difficulty in picking a representative sample of such. After a day's collection, the faecal samples were preserved in plastic bags with 100% ethanol, and the date of collection, collection location, time of collection and the visible contents of the faecal sample by majority constituent were noted. Once a month, the accumulated faecal samples were placed in a metal sieve with 1-mm mesh and washed in running water. Once the soluble solution had gone, the seeds of *Musanga leo-errerae* and *Ficus* sp. were sorted out and the per cent occurrence of the two genera per sample recorded. *Ficus* seeds were treated as one 'species group' belonging to one genus as it was difficult to identify them to species level.

To quantify the number of *Musanga leo-errerae* and *Ficus* sp. fruit eaten by the chimpanzees, the average volume of seeds found in each fruit for the two genera was first determined. For *Ficus* sp., the volume of seeds each belonging to a different species eaten by chimpanzees in Kalinzu forest was added and averaged. This was because *Ficus* seeds could be differentiated to species level as they appear the same in faeces. The volume of seeds found in the faecal samples was then divided by the average volume of one seed to determine the number of fruits consumed by chimpanzees.

Faecal analysis was supplemented by direct observations of feeding patterns. Fruit consumption was recorded daily between 07.00 and 19.00 h at 15-min intervals using instantaneous scan sampling. The party size of chimpanzees (Chapman, Wrangham & Chapman, 1995) that fed on a *Ficus* sp. and *Musanga leo-errerae* tree species and the frequency of consumption were also recorded.

Data analysis

Spearman's correlation coefficient was used to find the correlation between fruit abundance and consumption of the two genera. The *t*-test was used to test the difference between fruit abundance of *Musanga leo-errerae* and *Ficus* species, difference between frequency of consumption of *Musanga leo-errerae* and *Ficus* fruit and chimpanzees' party size found feeding on the two species.

Results

One species *Musanga leo-erarae* and fourteen *Ficus* species were counted along the ten transects. The occurrence and the distribution of these species indicated a concentration in the middle of the study area along transects 400–600 which then spread out in a descending order on either side (Fig. 1). The distribution of the two genera is also very similar (Figs 2 and 3). The total density of the two species shows that *Musanga leo-errerae* has a higher density of 536.4 tree stands per hectare compared with 411.4 *Ficus* species' tree stands per hectare. Fourteen identified *Ficus* species do occur in Kalinzu Forest Reserve. These include *Ficus sur, F. dawei, F. thoningii, F. natalensis, F. denstipulata, F. artocarpoides, F. vallis-choudea, F. otttonifolia, F. sansibarica, F. lingua,*

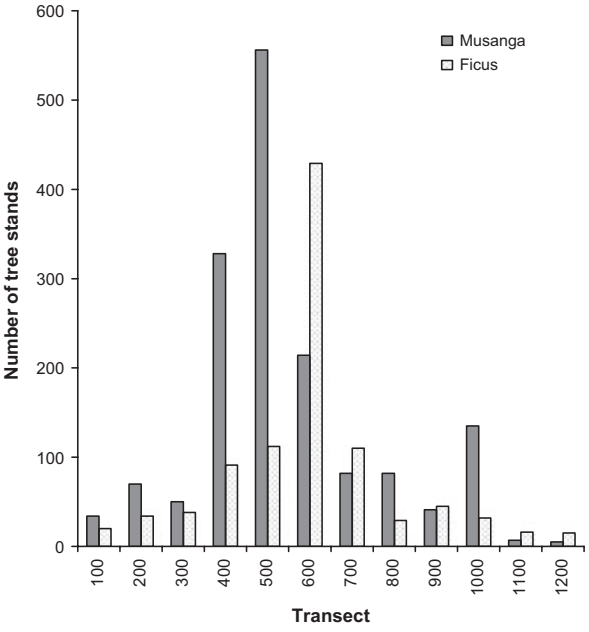

Fig 1 Occurrence of *Musanga* and *Ficus* genera along study transects

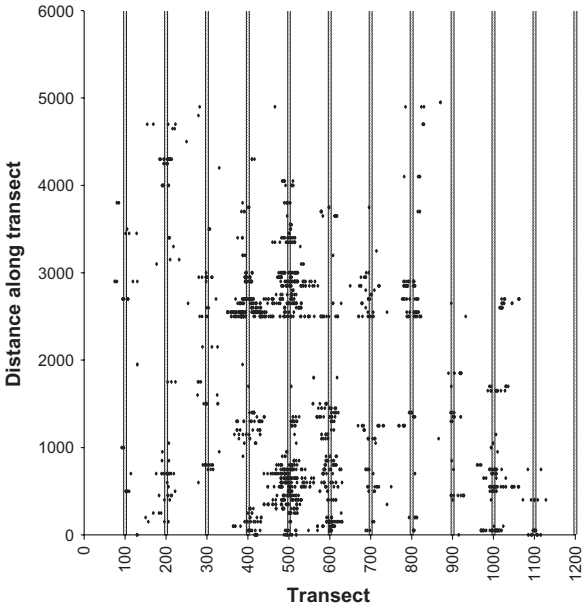

Fig 2 Distribution of *Musanga leo-errerae* along transects in Kalinzu forest

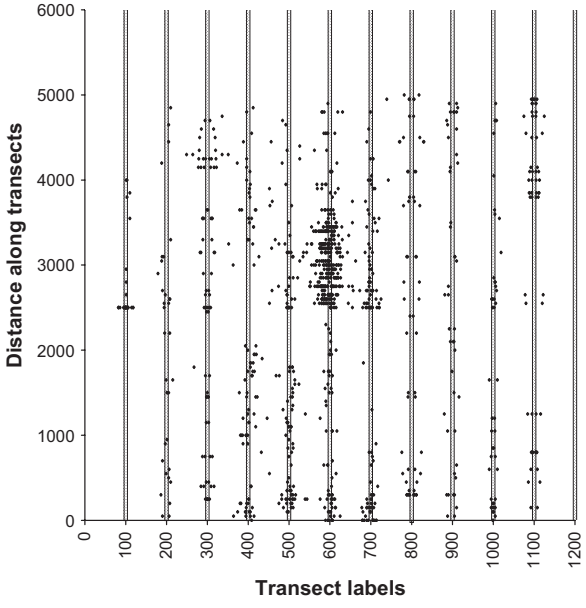

Fig 3 Distribution of *Ficus* sp. along transects in Kalinzu forest

F. trichopoda, F. barteri, F. bubu and F. cyanthostipulata in descending order of tree stand density. Considering fruit production, the major figs included *F. thoningii* with a fruit availability index of almost 40 doubling the next four namely *F. natalensis, F. sur, F. dawei and F. denstipulata* and *F. vallis-choudea* as the last in the top six. The rest of the figs had an index of five and below, *F. barteri* coming last with 0.1.

Fruit phenology indicated that *Musanga leo-erarae* produced fruit all year round with peaks around the rainfall peaks. The fruit availability index was almost constant throughout the study period but increased greatly towards the low fruiting season of January to March and August to October. The young unripe fruits were always superabundant than the ripe mature fruit, suggesting that chimpanzees do not feed on raw *Musanga.*

Ficus fruit production showed significant variations (asynchronous) among species, and fruit ripening was species specific. Fruits of *F. sansibarica* and *F. vallis-choudea* took more than 5 weeks to ripen. Seasonal variation in fruit production was also species specific, and although *Ficus* fruit production varied within species, it was little affected by either dry or wet season. Chimpanzees were seen to feed on fruit of *F. sur* more than other figs. *F. sur* was available for most of the year. In general, most fig trees have a fruiting interval of one or two crops a year. For *F. sur*, the average duration of fruiting interval is short, and one individual tree can produce fruits up to five times a year, but on average, it produces fruit three times a year (Tweheyo & Lye, 2003). Fig trees in Kalinzu shed a fairly substantial part of their leaves during the dry season with new leaf coming up immediately after the dry season.

Fruit abundance (Fruit Availability Index) indicated that *Musanga leo-errerae* fruit was higher than that of *Ficus* sp. all year round, and the crop of the two species was higher in the first year than in the second year. Although present all year round, the fruit of the two genera also increased with rainfall, their abundance being lowest during the dry month of July (Fig. 4). The fruit abundance of *Musanga leo-errerae* was found to be marginally higher than that of *Ficus* ($P = 0.053$; $t = -2.034$). There was no correlation between the abundance of the two fruit and their occurrence in faecal samples (*Musanga*; $r = 0.153$, $P = 0.456$; *Ficus*; $r = 0.039$, $P = 0.848$). This indicates that these two species were not only eaten, because they were available, but also selected by the chimpanzees.

Of the 2635 faecal samples analysed, 80.2% contained *Musanga leo-errerae* seeds and 67.2% contained *Ficus* sp. seeds. In terms of quantity contribution to chimpanzee diet, fruit contributed 75% to the total diet. Of this, *Musanga leo-errerae* contributed 37.2% and *Ficus* sp. contributed 26% leaving only 11.8% as contribution by other

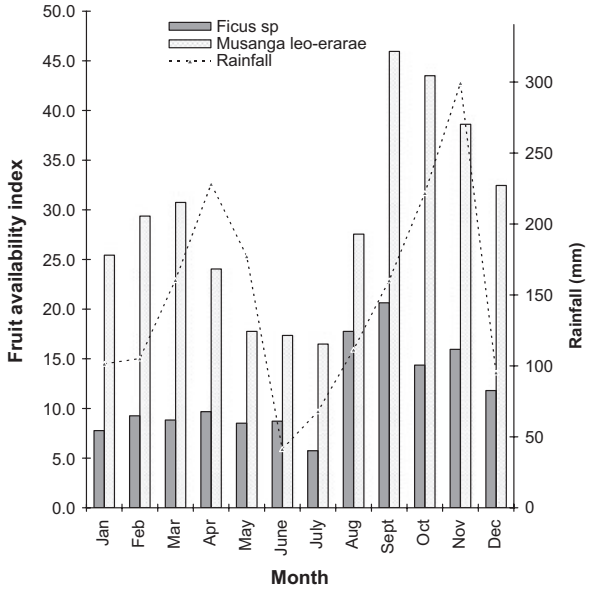

Fig 4 Monthly total fruit availability index of *Musanga* and *Ficus* species in relation to total monthly rainfall

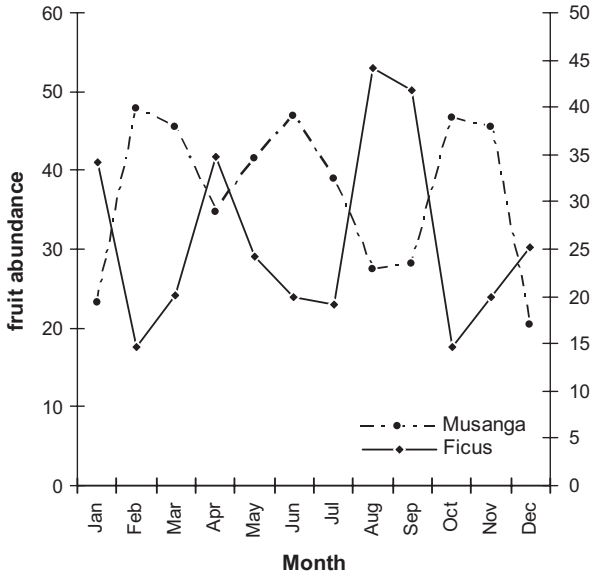

Fig 5 Average monthly contribution of *Musanga* and *Ficus* sp. fibre to chimpanzee diet

fruit species. The frequency of occurrence of fruit seed of *Musanga leo-errerae* and *Ficus* sp. species in faecal samples varied seasonally.

The occurrence of *Musanga leo-errerae* fruit in chimpanzee diet was higher than that of *Ficus* sp. except for the months of August–September, January and April. The difference in occurrence between *Musanga leo-errerae* and *Ficus* sp.' fruit seed in chimpanzee faeces was highest in February, July and October. There was, however, no significant difference between the occurrence of the two in chimpanzee diet ($P = 0.232$; $t = 1.225$). Although *Musanga* consumption was much higher than that of *Ficus*, the two genera were complementary food items for chimpanzees in Kalinzu Forest Reserve (Fig. 5). When the two fruits were equally consumed in April, there was no significant difference in consumption of both genera in this month ($P = 0.77$, $t = 0.293$, df = 93).

Similarly, the number of *Musanga leo-errerae* fruits consumed was consistently higher than that of *Ficus* sp. throughout the study except for the months of January and September of the first year and November of the second year of study. The mean number of chimpanzees (party size) found feeding on a tree species with mature fruit was higher in *Ficus* genus than in *Musanga.* There was, however, no significant difference between the numbers of chimpanzees (party size) found feeding on

Table 1 Relationship between chimpanzees party size found feeding on *Musanga leo-errerae* and *Ficus* fruit trees species

Season	Species	Mean	SD	SE	Sign. *t*	*P*
Annual	*Musanga*	6.88	0.9	0.26	−1.476	0.168
	Ficus	7.67	2.03	0.59		
	Paired *t*-test	−0.78	1.84	0.53		
Rainy season	*Musanga*	6.8	0.52	0.21	−1.332	0.24
	Ficus	7.1	1.26	0.51		
	Paired *t*-test	−0.72	1.32	0.54		
Dry season	*Musanga*	7.5	1	0.5	−1.699	0.188
	Ficus	9.1	2.58	1.29		
	Paired *t*-test	−1.6	1.88	0.94		

Musanga leo-errerae and *Ficus* sp. tree species over the annual cycle covering the dry and wet seasons (Table 1). There was, on the other hand, a significant difference in the frequency of feeding on *Musanga leo-errerae* and *Ficus* species ($t = 3.672$; $P = 0.04$) but more so in the dry season ($t = 3.835$; $P = 0.031$) than in the wet season ($t = 2.379$; $P = 0.063$).

Discussion

Ficus fruits have been recorded as staple food for chimpanzees in various habitats across Africa ranging from savannah – dominated areas in Senegal (McGrew, Bald-

win & Tutin, 1988) – to mosaic woodland forests in western Tanzania (Goodall, 1986; Nishida, 2000) and Guinea (Sugiyama, Komman & Sow, 1988), moist semi-decidous forest in Uganda (Wrangham, Conklin & Hunt, 1991; Wrangham *et al.*, 1993; Newton-Fisher, 1999), tropical rain forest in equatorial Guinea, Gabon (Tutin & Fernandez, 1993) and Congo Brazzaville (Kuroda *et al.*, 1996). Figs were also reported as being less preferred than nonfigs and were eaten by chimpanzees when nonfigs were in short supply (Kuroda *et al.*, 1996; Wrangham *et al.*, 1996). Studies in Kibale forest, where vegetation is similar to Kalinzu (Howard, 1991) but where *Musanga* species are not abundant, showed that figs and terrestrial herbaceous vegetation, terrestrial herbaceous vegetation (THV), functioned as fallback foods during periods of fruit scarcity (Wrangham, Conklin & Hunt, 1991; Wrangham *et al.*, 1993, 1996; Malenky, Wrangham & Chapman, 1994).

Correlation between *Musanga* and *Ficus* consumption and their fruit availability was negative; therefore, they were not only eaten because they were available but chimpanzees also sought for them especially when other fruits were scarce, *Musanga* more than *Ficus*. This is in line with Hashimoto, Furuichi & Tashiro (2001), who suggested that *Musanga leo-errerae* fruit attracted chimpanzees in Kalinzu especially when other fruits were scarce. The number of *Musanga* fruits eaten as per faecal analysis was higher than *Ficus* fruit. Fruiting and consumption by chimpanzee may vary between years as results showed consumption variation between the first and second years of study. Both *Ficus* and *Musanga* had the same trend of occurrence in chimpanzee diet being lowest in October. This was because October was the onset of fruiting of other pulpy, juicy and sugary fruits that were liked by chimpanzees like *Myrianthus holstii, Pseudospondius microcarpa, Drypetes bipidensis* and *Bielschmiedia ugandensis.*

Many researchers have examined the factors influencing the size of chimpanzee parties (Goodall, 1986; Boesch, 1991, 1996; Wrangham, Clark & Isabirye-Basuta, 1992; Tutin & Fernandez, 1993; Chapman, White & Wrangham, 1994; Sakura, 1994; Chapman, Wrangham & Chapman, 1995; Doran, 1997; Matsumoto-Oda *et al.*, 1998; Matsumoto-Oda, 1999; Wrangham, 2000). They revealed that fruit availability has a positive effect on party size. When the availability of fruit increases, chimpanzees tend to form larger parties (Boesch, 1991, 1996; Wrangham, Clark & Isabirye-Basuta, 1992; Chapman, Wrangham & Chapman, 1995; Wrangham, 1997, 2000; Matsumoto-Oda *et al.*, 1998; Matsumoto-Oda, 1999).

Fruits of diverse *Ficus* species were abundant and always available; though, the amount varied between months compared to *Musanga leo-errerae* that continuously produced evenly distributed fruits all over the canopy. The different fruiting and fruit availability did not limit party size in this case. Hashimoto, Furuichi & Tashiro (2001) evaluated the oestrus females as the possible factor that may influence party size, but further studies were needed on the actual movement of both male and female joining and leaving parties. As *Ficus* trees with large crowns have been documented as important for chimpanzee social interactions (Tweheyo & Obua, 2001), crown size in conjunction with fruit crop may affect chimpanzees' party size. As most figs and *Musanga have* big tree crowns, both may affect party size in an almost similar way.

Second, various definitions of party have been used: the number of individuals observed in single scanning samples (Wrangham, Clark & Isabirye-Basuta, 1992), the number of individuals observed in a given hour (Chapman, Wrangham & Chapman, 1995; Doran, 1997), and the total number on individuals observed in 1 day (Boesch, 1991, 1996; Sakura, 1994; Matsumoto-Oda *et al.*, 1998; Matsumoto-Oda, 1999). Chapman, White & Wrangham (1994) showed that different methodologies or definitions of 'party' may yield different results for the analysis of party size.

Results from faecal analysis indicated no significant difference between the occurrence of *Musanga* and *Ficus* in chimpanzee diet. Similarly, there was no significant difference between the frequencies of consumption of the fruit genera of *Musanga* and *Ficus* as per direct observation. There was, however, a significance difference in the consumption of the two fruits in the dry season. Although it is *Musanga leo-errerae* that occurs in Kalinzu forest, another species *Musanga cecropioides* has been recorded to function as a fallback food in Bossou, Guinea (Yamakoshi, 1998). Thomas (1991) also reported that, in Ituri forest, Democratic Republic of Congo, the density of *Cercopithecus* monkeys was high in secondary forest in response to continuous fruiting of *Musanga cecropioides*. As the phenology of *Musanga* trees in Kalinzu was not synchronized, chimpanzees depended more on *Musanga* during the dry season but *Ficus* species also played a major role in chimpanzee diet. Biochemical analysis shows that *Ficus* species' fruits contain more sugars than *Musanga*. If chimpanzees' fruit choice depended on

how sweet the fruit is (Nishida, 2000), like the tendency is in man, then *Ficus* fruit would have been eaten in greater quantities. *Musanga* contains glycogen, a remarkable principal storage product, and a carbohydrate that is extremely rare in plants (Kubitzki, Rohwer & Bittrich, 1993). As *Musanga* fruit contains average lipid and sugar levels, the importance of *Musanga* species must be explained by the continuous providing availability of its fruit and figs in their species diversity that results in one species fruiting after another, hence continuous fruit availability. Whereas *Ficus* genus and/or THV has been documented as key fruit for chimpanzees across most tropical forests, despite their occurrence in Kalinzu, neither of them two acts as key stone foods. *Musanga leo-errerae* takes over the role of key food in Kalinzu. Therefore, it is in Kalinzu Forest Reserve that two keystone fruit genera important to chimpanzees coexist, a rare opportunity in conservation and sustenance of this endangered species.

Acknowledgements

This field work was facilitated by ground work done by Assistant Professor Chie Hashimoto, the Ugandan staff of NFA and the Kalinzu forest project especially Muhairwe Gracious. This research was financed by Deutscher Akademischer Austausch Dienst (DAAD) awarded to the author (No. A/03/15191), to them we are very grateful. We also thank the Uganda National council for Science for the permission to work in Kalinzu forest.

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(*Manuscript accepted 20 May 2008*)

doi: 10.1111/j.1365-2028.2011.01292.x