Production, seasonality and management of chimpanzee food trees in Budongo Forest, Uganda

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Abstract

This study monitored the phenology of fruit and leaf of 575 chimpanzee food trees (40 species belonging to fifteen families) in the Budongo Forest Reserve (Uganda) from June 1999 to June 2006. We also monitored the phenology of all fig species in the study area. Fruit quantity varied significantly between species and seasons, with peak during wet season (April–June). The number of tree species in fruit correlated positively with rainfall and was higher during rainy season than dry season. *Ficus* species had exceptionally high fruit quantities ranging from 400 to 650,000 fruits per tree in a single production period. Leaf flushing peaked during late dry season and early wet season (February–April). Mature leaves were available at all seasons, even when young leaves were emerging. Only *Ficus sur*, *Broussonetia papyrifera* and *Celtis gomphophylla* had fruits throughout the year, and six species did not produce fruits during the study period. Of the twelve species that fruited between 40 and 58 months, three are very important timber species and seven were once killed with arboricides. We conclude that the long-term survival of chimpanzees in tropical forests requires conservation of their food trees.

Key words: Budongo, chimpanzee food, conservation, human disturbances

Résumé

Cette étude a suivi, de juin 1999 à juin 2006, la phénologie des fruits et des feuilles de 575 arbres qui servent de nourriture aux chimpanzés (40 espèces appartenant à 15 familles) dans la Réserve Forestière de Budongo (Ouganda). Nous avons aussi suivi la phénologie de toutes les espèces de figuiers présentes dans l'aire étudiée. La quantité de fruits variait significativement selon les espèces et les saisons, avec un pic pendant la saison des pluies (avril - juin). Le nombre d'arbres en fructification était positivement corrélé avec les chutes de pluies et était plus élevé pendant la saison des pluies qu'en saison sèche. Les *Ficus* avaient des quantités exceptionnelles de fruits, allant de 400 à 650.000 fruits par arbre en une seule saison de production. La production de feuilles était au maximum en fin de saison sèche et début de saison des pluies (février – avril). Des feuilles mâtures étaient disponibles en toutes saisons, même lors de la parution de nouvelles feuilles. Seuls *Ficus sur*, *Broussonetia papyfera* et *Celtis gomphophylla* portaient des fruits toute l'année, et six espèces n'ont pas produit de fruits du tout pendant toute la durée de l'étude. Des douze espèces qui ont fructifié pendant 40 à 58 mois, trois sont très importantes pour leur bois et sept ont été tuées par des 'arboricidesg'. Nous concluons que la survie à long terme des chimpanzés dans les forêts tropicales requiert la conservation des arbres qui leur servent de nourriture.

Introduction

The tropical forests of Africa are one of the most diverse terrestrial ecosystems on the earth (Whitmore, 1984) but these forests are undergoing severe ecological disturbances (Ashton, 1993). Indeed, in tropical forests, activities such as logging, mining and other forms of exploitation have affected the availability and quality of wildlife. Although diverse, some tree species providing high value timber are given much attention by management at the expense of other plants and animals that combine to form this complex ecosystem. Such selective activities are important in shaping the dynamics of the rain forests and our knowledge of the functioning of these neglected plant species due to human selection is scarce. In Uganda, recent decades have

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seen tropical rain forests being reduced to small and more isolated patches through increasing human population, agricultural intensification and logging (Howard, 1991; Tweheyo, Hill & Obua, 2005). The survival of the remaining tropical forest biodiversity will depend on the extent to which the neglected plant and animal species are incorporated into the management plans.

We investigated the phenology of trees species mainly neglected to draw some implications for the maintenance of biodiversity. We examined leaf and fruit phenology, and fruit productivity of chimpanzee food trees in Budongo Forest Reserve, Uganda. Forty-tree species comprising approximately 65% of the tree species known to be fed on by chimpanzees were studied. We sampled all fig species because figs are known to be the most important food of chimpanzees in this forest (Tweheyo & Obua, 2001; Tweheyo & Lye, 2003). Figs depend on wasp (Agaonidae, Chalcioidea, Hymenoptera) for pollination which have short-lived span (Kjellberg, Doumesche & Bronstein, 1988); thus to maintain their pollinators, figs must fruit continuously (Kameyama, Harrison & Yamamura, 1999). The continuous availability of fig fruits, when other seasonal fruits are scarce makes figs valuable for vertebrate seed dispersers (Tan, Zubaid & Kunz, 1998). This importance of figs in forest secession together with their value to maintain seed dispersers through food provision has lead figs to be regarded as a keystone component of tropical forests (Corner, 1988; Lambert & Marshall, 1991). Figs are keystone resources for chimpanzees and monkeys in other tropical forests in Uganda (Conklin & Wrangham, 1994; Hashimoto, Furuichi & Tashiro, 2001) and Cameroon (Tutin *et al.*, 1997). And yet, figs are among the tree species that were killed with arboricides in Budongo (Philip, 1964).

The process of arboricide treatment went through two stages viz: (i) pre-exploitation refining; (ii) postharvesting liberation of desirable trees. It involved poisoning plant species of two strata, i.e. overstorey trees that obstructed light needed for the desirable seedlings to establish and understorey shrubs that acted as 'weeds'. Both past and present forest management policies do not highlight the functional role of trees that provide food to wildlife without being necessarily important for timber.

The aim of this study was to describe the pattern of variations of fruit and leaf phenology of chimpanzee food trees. It was assumed that chimpanzee food trees vary with seasons (within and between years) in fruit and leaf production. Analyzing such an investigation is essential for the survival of the chimpanzees. Chimpanzee food trees were chosen because: (i) chimpanzees are an important and endangered species of primates that feed primarily on fruits; (ii) information on phenological patterns will assist conservationists in designing management strategies that ascertain food tree regeneration and survival; and (iii) there is a need to understand how chimpanzees will be affected by disturbances especially those associated with logging. Our results have implications for the management of Budongo Forest, in particular, and other tropical forests, in general, and may help forest managers understand how wildlife can be maintained in areas managed for timber by understanding the important food trees for frugivores.

Methods

Study area

Budongo Forest Reserve is situated between 1°35′ and 1°55′N and 31°8′ and 31°42′E. It is the largest tropical forest reserve in Uganda covering 825 km^2 of which 53% is a continuous tropical forest and the remaining comprises grassland communities (Hamilton, 1984). It has an average altitude of 1100 m. The monthly average (±SD) rainfall is 138.5 ± 66.74 mm, and has a relatively constant minimum temperature with a monthly average (±SD) of 20.86 ± 0.92°C. It is generally a wet forest with the dry season from December to February.

Budongo is of high global biodiversity importance, ranking third among the protected areas in species richness and overall importance in Uganda (Howard, Davenport & Kigenyi, 1997). The forest has about 465 species of trees and shrubs, five species of diurnal primates (including chimpanzees with a population of about 700 individuals), 159 species of forest birds and 42 species of forest swallowtail and *Charaxes* butterfly (Howard, 1991). Our research site was located in the Sonso region (1°44′N, 31°33′E) of the Budongo Forest.

Sampling procedures

Transect and specific figs sampling. One hundred sixty circular sampling plots (radius 20 m) were established systematically along eight line transects set at a distance 600 m apart and each was 2 km long. The sample plots were laid along each transect at an interval of 100 m. To include food trees that may not have occurred in systematic sample plots in case of similar vegetation gradient along a transect, four sample plots were laid out in a stratified random manner and positioned 500 m on either side of each line transect. This gave a total of 32 stratified random sample plots. Taken together but excluding selected figs species, 192 sample plots were surveyed giving a total of 521 individual trees representing 29 species belonging to fifteen families (Table 1). We sampled about 2.3% of the ranging area of the Sonso community chimpanzees excluding the area in which fig phenology was monitored.

Eleven species of figs (Table 1), which never appeared in the sampling plots, were selected for their phenology. Each of the eleven *Ficus* species was to be represented by eight individual trees and we attempted to monitor two individual trees per species in each of the four forest compartments in the study area. However, some of the *Ficus* species were represented by less than eight individuals in the whole ranging area, thus a total of 54 trees were monitored. In all we monitored 575 individual trees representing 40 species belonging to fifteen families (Table 1).

Basic considerations during phenology monitoring. Chimpanzee food trees were selected based on records from the Budongo Forest Project and results of previous studies (e.g. Synnot, 1985). We sampled trees with 10 or more centimetres of diameter at d.b.h. (diameter at breast height) following Onderdonk & Chapman (2000). An exception was *Ficus asperifolia* whose minimum trunk diameter was 4 cm. The phenology of *F. asperifolia* was monitored although its d.b.h. was <10 cm because the tree accomplishes all its physiological requirement below this size (Tweheyo, Lye & Weladji, 2003). For strangler figs, we measured and computed crown diameter (CD) instead of d.b.h. using the equation $D = (d_1 + d_2)/2$ where $D =$ mean diameter and $d =$ diameter of the two longest axes of the crown. Axes were measured by stretching a distance tape measure across the axis at the base of the tree. We decided to monitor phenology of trees with CD above 15 m because this was among the largest sizes in the forest which we assumed correlates with age and maturity.

Data recording

Fruit and leaf growth stages. Phenology data were recorded twice a month for 73 months (June 1999 to June 2006). In each month we spent 8 days monitoring phenology; 4 days in the middle of the month and 4 days towards the end of the month. The development stages of both leaves and fruits were recorded as: no fruits (f0), emerging fruits (f1), young fruits (f2), sub-mature fruits (f3) and ripe fruits (f4). Leaf status was recorded as no leaves (l0), young leaves (l1), mature leaves (l2). Stages in fruit maturity were recorded according to changes in fruit size from the day of emerging to becoming sub-mature fruits. Ripe fruit stages were identified by colour changes from green to yellow, purple, orange and red. In addition, we recorded the season either as wet season (w) or dry season (d) according to precipitation.

Fruit quantity. The quantity of fruits on each tree was estimated by visual counts. By counting the number of fruits on a branch and then multiplying it by the number of branches following the methods developed by Chapman *et al.* (1992). Larger fruits e.g. from *Desplatzia dewevrei* were individually counted. For *F. sur*, a tree that bears fruits in clusters, the number of fruits in a cluster were counted and multiplied by the total number of clusters. The total number of fruits on a tree were counted and recorded only during the sub-mature stage, which is a second last stage in the fruit development period. The sub-mature stage was selected because it was considered a time when fruits were much more visible than the emerging and young fruit period and less damaged by frugivores as is often the case when fruits are ripe. At the sub-mature stage, most fruits that survive abortion, which usually occurs at the emerging and young stages, are still attached to the mother tree.

Fruit and leaf growth proportion phases. All fruit and leaf growth stages were recorded in each month but the most dominant stage was recorded as the one with >75% growth stage of fruits and leaves during each monitoring period based on Plumptre, Reynolds & Bakuneeta (1994). For example, if we estimated that a tree had 75% or more young fruits in its production zone/s, it was recorded to be in the young phase of fruit development. Fruit growth phases were recorded in terms of percentage cover rather than numbers. For example, fruit phase on a given tree was classified according to its percentage cover of branches or any other production zone as follows: ≤10% cover, i.e. a tree with fruits that cover <10% of the branches or any other fruit production zone, ≥10% and <25% cover, ≥25% and <50% cover, ≥50% and <75% cover and ≥75% cover.

Table 1 Tree species surveyed for phenology in Budongo from June 1999 to June 2006

Code	Species	Family	Number observed in area sampled
Ant	*Antiaris toxicaria* Leschen.	Moraceae	19
Bp	*Trilepisium madagascariense* Baill.	Moraceae	15
Bpy	*Broussonetia papyrifera* (L.) Vent.	Moraceae	30
Cls	*Caloncoba crepiniana* (De Wild & Th.Dur.)	Flacourtaceae	5
Cdu	*Celtis gomphophylla* Bak.	Ulmaceae	68
Cmi	*Celtis mildbraedii* Engl.	Ulmaceae	110
Cze	*Celtis zenkeri* Engl.	Ulmaceae	34
Cal	*Chrysophyllum albidum* G. Don.	Sapotaceae	8
Clp	*Cleistopholis patens* (Benth.) Engl.	Annonaceae	6
Cmc	*Croton macrostachyus* Del.	Euphorbiaceae	26
Cog	*Cola gigantea* A. Chev.	Sterculiaceae	6
Com	*Cordia millenii* Bak.	Boraginaceae	13
Csy	*Croton sylvaticus* Krauss	Euphorbiaceae	7
Cya	*Cynometra alexandri* Wright	Fabaceae* Caesalpinioïdeae	11
Dd	*Desplatzia dewevrei* (De Wild & Th. Dur.)	Tiliaceae	21
Ena	*Entandrophragma angolense* Welw.	Meliaceae	4
Enc	*Entandrophragma cylindricum* Sprague	Meliaceae	2
Fe	*Ficus exasperata* Vahl	Moraceae	10
Fm	*Ficus mucuso* Ficalho	Moraceae	13
Fsu	*Ficus sur* Forssk.	Moraceae	22
Fvr	*Ficus variifolia* Warb.	Moraceae	14
Ka	*Khaya antotheca* Welw.	Meliaceae	6
Kia	*Kigelia africana* (Lam.) Benth.	Bignoniaceae	3
Lm	*Lasiodiscus mildbraedii* Engl.	Rhamnaceae	8
Me	*Maesopsis eminii* Engl.	Rhamnaceae	13
Mex	*Milicia excelsa* (Welw) C. Berg	Moraceae	21
Myh	*Myrianthus holstii* Engl.	Moraceae	13
Psm	*Pseudospondias microcarpa* (A. Rich.) Engl.	Anacardiaceae	9
Psg	*Psidium guajava* L.	Myrtaceae	4
	Selected figs		
Fa	*Ficus asperifolia* Miq.	Moraceae	8
Fb	*Ficus barteri* Sprague[a]	Moraceae	2
Fl	*Ficus lingua* De Wild[a]	Moraceae	4
Fn	*Ficus natalensis* Hochst.[a]	Moraceae	5
Fo	*Ficus ottoniifolia* (Miq) Miq.[a]	Moraceae	4
Fpo	*Ficus polita* Vahl.	Moraceae	6
Fsa	*Ficus sansibarica* Warb.[a]	Moraceae	8
Fss	*Ficus saussureana* DC.[a]	Moraceae	5
Fth	*Ficus thonningii* Bl.[a]	Moraceae	2
Ftr	*Ficus trichopoda* Bak.	Moraceae	2
Fvl	*Ficus vallis-choudae* Del.	Moraceae	8

Code represents the identification symbol used by Budongo Forest Project and Uganda Forestry Department to mark different tree species.

[a] Fig trees that are stranglers. The rest are freestanding.

Data analysis

In order to assess the factors affecting fruit quantities, we fitted models to the following predictor variables: month, year, season and tree species. We used general linear model (GLM) repeated measures ANOVA (GLM rmANOVA) to analyse pair-wise differences and reference contrast.

Data were analysed using SPSS (1997). Least square mean values of the factors were subjected to pair-wise comparisons using Tukey and accepted at $P < 0.05$. In order to assess variations in frequency of different fruit and leaf growth stages among months, generalized linear model (McCullagh & Nelder, 1989) using the GENMOD procedure in SAS (1999a) was conducted. We fitted regression models to analyse the relationship between rainfall and the number of fruiting species. The significance of the explanatory variables was assessed by their likelihood ratio statistics (chi-square distributed) using SAS (1999b), and accepted at $P < 0.05$.

Results

Tree species and seasonal production changes

Ficus sur, *Broussonetia papyrifera* and *Celtis gomphophylla* had fruits throughout the study. *Ficus exasperata*, *F. asperifolia*, *F. polita*, *F. natalensis*, *F. sansibarica*, *F. vallis-choudae*, *C. zenkeri*, *Maesopsis eminii* and *Lasiodiscus mildbraedii* had fruits in periods ranging between 40 and 58 months. Of these, *C. gomphophylla*, *C. zenkeri* and *M. eminii* were considered desirable timber species by the Uganda Forestry Department (Philip, 1964). Six of the species monitored did not produce fruits in the study period while three species had fruits in <10 months. Two of these species (*C. gomphophylla* and *M. eminii*) were among the top seven species in the diet of the Sonso chimpanzees between 1994 and 1995 (Newton-Fisher, 1999).

Fruit production did not depend on the number of individual trees (Tables 1 and 2). For example, *F. sur*, which had fruits throughout had 22 individual trees while *C. mildbraedii*, which had 110 trees fruited only in 36 months. Though *B. papyrifera* and *C. gomphophylla* had fruits throughout, the fruits were fewer than *F. sur* fruits. Fruit quantity varied significantly between the seven years ($F_{6,505} = 8.28$, $P < 0.01$, GLM rmANOVA) and the interaction between fruit quantities and tree was also significant ($F_{31,505} = 4.38$, $P < 0.\ 001$). In general *Ficus* trees had more fruits than other trees (Table 2). In the seven years, total fruit quantity did not vary significantly by month at $P < 0.05$ but varied significantly at $P < 0.1$. However, some months especially December, January and February showed a strong variation in mean fruit quantities (Fig. 1) in the two years; and there were significant interactions between months and species ($F_{713,3682} = 1.16$, $P < 0.005$, GLM rmANOVA). Fruit quantities varied significantly between species; ($F_{31,184} = 1.71$, $P < 0.01$) and species–season interaction was significant ($F_{31,505} = 3.04$, $P < 0.001$, GLM rmANOVA).

During the 7 years of study, fruit quantity varied with rainfall (Fig. 2). Although the mean fruit quantities seemed higher during the dry season, i.e. months with low rainfall, the number of trees with fruit were much lower (Fig. 3). There was a strong linear relationship between rainfall and the number of trees in fruit per month, $R^2 = 0.5379$ (Fig. 2).

Variations in fruit and leaf growth stages

Emerging fruits, young fruits and sub-mature fruits were more frequent than ripe fruits (Fig. 4) apparently because chimpanzees and other primates and birds ate ripe fruits. In total, both fruits and tree species in fruit were the most abundant in the wet season. The dry season (December to February) had few fruits and mainly figs had fruits. Fruit growth stage (emerging, young, sub-mature and ripe) varied between month ($\chi^2 = 914$, d.f. = 44, $P < 0.001$); and years of study ($\chi^2 = 227$, d.f. = 8, $P < 0.001$).

Leaf growth on chimpanzee food trees showed significant seasonal patterns that varied with months. Presence of mature leaves, young leaves and trees without leaves varied significantly with month; $\chi^2 = 1787$, d.f. = 22, $P < 0.001$. When we eliminated trees without leaves from the model, the frequencies of mature leaves and young leaves still varied significantly with month ($\chi^2 = 987$, d.f. = 11, $P < 0.001$). Trees with young leaves were less common during the wet season, increased slightly in the dry season and were the most abundant at the beginning of the wet season. Most trees had mature leaves even when young leaves were emerging.

Tree death

During the 7 years, we lost eight trees because of natural death and of these six were *F. sur* trees. Between January 2005 and June 2006, there was a massive death of *F. sur* in Budongo and almost all *F. sur* species with CD >15 cm died. Such massive death of a single tree specie in tropical forests is rare. We observed the death of *F. sur* not only in our plots but also else where in the forest. Apart from *F. sur*, there is little tree death in Budongo.

Table 2 Number of fruits produced (maximum and minimum) and recorded on different chimpanzee food trees in Budongo from June 1999 to June 2006

	Number of fruits per tree		
Tree species	Maximum	Minimum	Mean
Antiaris toxicaria	5000	5000	5000
Trilepisium madagascariense	10,000	10,000	10,000
Broussonetia papyrifera	35,000	3	4224
Caloncoba crepiniana	1000	2	59
Celtis gomphophylla	150,000	50	17,621
Celtis mildbraedii	30,000	40	9608
Celtis zenkeri	60,000	10	6632
Chrysophyllum albidum	10,000	500	7538
Cleistopholis patens	5000	50	879
Croton macrostachyus	30,000	500	4109
Cola gigantea	60	60	60
Cordia millenii	5000	500	2500
Croton sylvaticus	20,000	2000	8000
Cynometra alexandri	80,000	100	13,715
Desplatzia dewevrei	60	2	16
Entandrophragma angolense	–	–	–
Entandrophragma cylindricum	–	–	–
Ficus exasperate	500,000	500	121,359
Ficus mucuso	–	–	–
Ficus sur	650,000	400	69,488
Ficus variifolia	120000	666	50,067
Khaya antotheca	20,000	10	1610
Kigelia africana	–	–	–
Lasiodiscus mildbraedii	5000	5	832
Maesopsis eminii	300,000	20	16,163
Milicia excelsa	–	–	–
Myrianthus holstii	520	3	16
Pseudospondias microcarpa	–	–	–
Psidium guajava	–	–	–
Selected fig species			
Ficus asperifolia	700	100	280
Ficus barteri	–	–	–
Ficus lingua	500,000	15,000	206,670
Ficus natalensis	150,000	60,000	102,500
Ficus ottoniifolia	–	–	–
Ficus polita	40,000	200	6530
Ficus sansibarica	200,000	30,000	91,250
Ficus saussureana	40,000	20,000	30,000
Ficus thonningii	160,000	160,000	160,000
Ficus trichopoda	–	–	–
Ficus vallis-choudae	30,000	500	3030

–, Represents trees that never had fruits during our study period.

Discussion

Seasonality and productivity

The significant differences among species in fruit production are not surprising, as species may well have different physiologies that result in different phenologies. Our results demonstrate that the availability of chimpanzee food changes between years and months, and depended on the rainfall levels, implying that the chimpanzees have to adjust their diet to tree phonologies. Inter-annual and

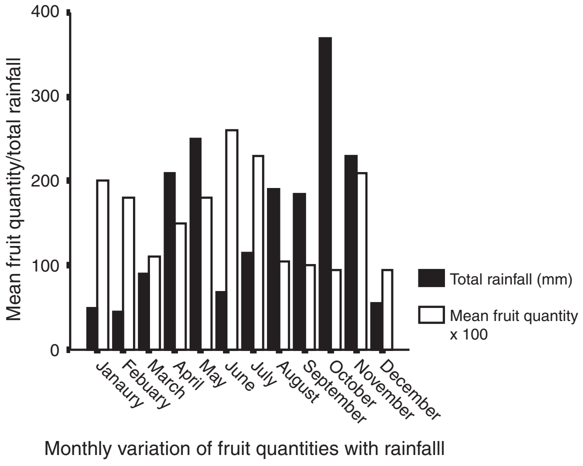

Fig 1 Variation in monthly rainfall with mean fruit quantities on chimpanzee food trees in Budongo from June 1999 to June 2006

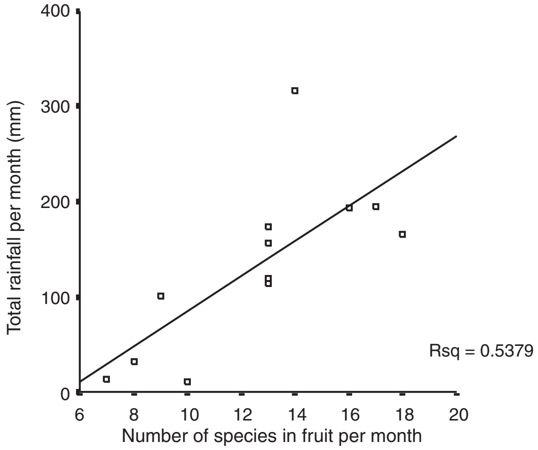

Fig 2 Relationship between total rainfall per month and number of chimpanzee food trees species in fruit in Budongo Rorest Reserve from June 1999 to June 2006

seasonal variation in species production in fruits and leaves have been reported in other tropical forest phenology studies (e.g. Sun *et al.*, 1996; Chapman *et al.*, 1999). Fruiting patterns of chimpanzee food trees are not synchronized and some trees take 2 years to produce fruits and some even longer (White, 1994; Wrangham, Chapman & Chapman, 1994). *Ficus* species, especially *F. sur*, produced a reliable fruit supply for the chimpanzees of Sonso community. In addition, *B. papyrifera* and *C. gomphophylla* also had a regular fruit supply, but they are fewer than fruits of *F. sur*, *F. exasperata* and *F. variifolia*.

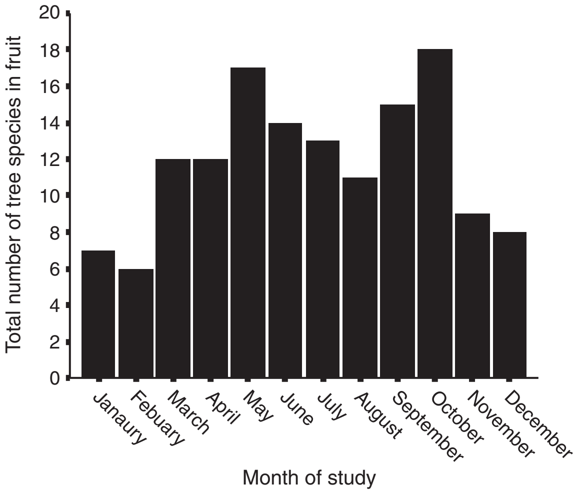

Fig 3 Variations in the average numbers of chimpanzees' food trees species in fruit per month from June 1999 to June 2006

Few trees had fruits in the dry season, which is also considered a period of chimpanzee food scarcity in the Budongo Forest Reserve (Newton-Fisher, 1999). Therefore, *Ficus* species together with *B. papyrifera* and *C. gomphophylla* are important food trees to chimpanzees as these species provided food throughout the study period. However, to ascertain more variations, it is important to observe these tree species over a longer-term period. Flowers were not recorded in this study because of difficulty in counting. While recording diet, Tweheyo *et al.* (2003) reported that chimpanzees feed on flowers of *B. papyrifera*. This may account for the low quantities of recorded fruits on *B. papyrifera* in this study. If we eliminated all other trees from the sample, the phenology of figs alone shows that chimpanzees' survival, and possibly the survival of other frugivores in Budongo, would depend on how well their food trees are managed. Survival here means chimpanzees and other frugivores maintaining their population through normal population recruitment and reducing conflict with local farmers through crop raiding. Management strategy for chimpanzee survival in this forest therefore should consider sustaining their food in the wild while reducing conflict with local communities.

We also found that young fruits, sub-mature fruits, and ripe fruits are common in the wet season. Elsewhere in the tropics, Lieberman (1982) and van Schaik, Terborgh & Wright (1993) found that phenological patterns in tropical forests have marked seasonal differences in fruit and leaf production. In Budongo, like other tropical regions, e.g. in

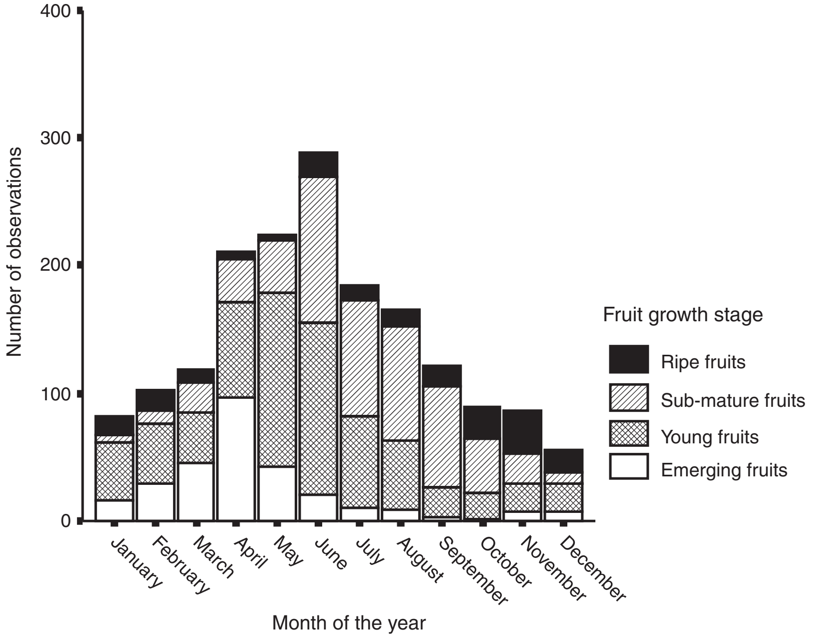

Fig 4 Seasonal variation in fruit growth stages in chimpanzee food trees in Budongo. The above figure groups together all different fruit stages from all trees that were recorded between 1999 and 2006

Borneo (Harrison, 2001) and Panama, (Nason, Herre & Hamrick, 1996, 1998) daily temperatures often exceed the yearly variations in mean temperatures, and it is the amount of rainfall and especially the length of the dry period that dictate forest seasonality. However, our findings indicate that even the short dry periods that occur in the seemingly non-seasonal Budongo have an important influence on phenology. The dry season in the Budongo Forest Reserve was associated with periods of reduced production of leaves and fruits. Similar kind of leaf and fruit production that correlates with rainfall peaks has also been reported in the tropical forests of Malaysia (Medway, 1972).

Compared to other studies in Africa, our findings correlated with results from tropical forests of Gabon (White, 1994) and Cameroon (Newbery, Songwe & Chuyong, 1998) where high fruit production in the wet season has been reported. In Budongo, changes in fruit production due to dry and wet season affect chimpanzee-feeding patterns by expanding their food choices, which include crop raiding. Thus conservation of trees that provide food to chimpanzees and those that provide food during periods of fruit scarcity should be among the management objectives.

At a landscape level, plant phenology affects the availability of plant resources for pollinators, seed predators and herbivores and hence influences the ecology of the forest. For plant species, given the duration of dry period compared to their life span, the impact of dry period on phenology may have a marginal effect on the chimpanzee food trees' fitness. However, changes in tree phenology on herbivores, pollinators and seed dispersers' can have substantial influence on the population of these animals in particular and ecology of the forest in general.

Management

Of the three species (*F. sur*, *C. gomphophylla* and *B. papyrifera*) that had fruits in 58 months, only *C. gomphophylla* is considered an important timber species by the National Forestry Authority (NFA). The Uganda Forestry sector has a focus on managing important timber species. As logging has been and is still prevalent in the Budongo Forest Reserve, understanding production of chimpanzee food trees may help in their conservation. Management of Budongo should consider trees in the family Moraceae as important foods for frugivores.

Human disturbances, especially logging, have changed the structure of the Budongo Forest and management options, both past and present, consider utilization in favour of a multifunctional ecosystem. The management tendency to favour few plant species will leave Budongo a natural forest biased towards a selected set of species and miss out on many ecological functions that depend on otherwise neglected tree species. Arboricide treatment favoured fewer tree species and should not be repeated as a management option. Postlogging management like enrichment planting is not ecologically beneficial because seedlings that are planted are of selected timber tree species.

Due to general economic failure in Uganda during the 1970s, there was reduced mechanical logging in the Budongo Forest, which led to overall recovery of trees. Plumptre *et al.* (1994), Plumptre, Reynolds & Bakuneeta (1997) reported that such recovery increased food trees for frugivores. Prohibition of mechanical logging in the 1970s apparently stimulated the growth of trees that provided food to chimpanzees. This is because we consider that intensity of logging was going extreme then. We therefore imply that if logging had continued, or if the ongoing logging is accentuated, such intense disturbances may be harmful to the population dynamics of chimpanzees and perhaps other animals in the Budongo Forest Reserve. This information is useful for forest managers who need to compare the conservation value of chimpanzees and exploitation of timber. Failure to combine conservation and utilization in the management of the Budongo Forest may lead to reduction in food resources for chimpanzees, and this may have negative effects on the entire ecosystem. Elsewhere, logging has been reported to affect the structure and composition of the tropical forests of Sabah in Malaysia (Woods, 1989) and similar situation may occur in the Budongo Forest.

Chimpanzees move long distances and therefore can be of great value to forest regeneration and maintenance through seed dispersal (Cordeiro & Howe, 2001; Poulsen, Clark & Smith, 2001). Yearly variations in chimpanzee food trees require continued long-term phenological studies so that clear management decisions can be made for the conservation of chimpanzees and other species like birds and monkeys that also depend on fruits. Understanding the phenology of chimpanzee food trees is therefore essential for making informed decisions about the conservation of the species and the associated food trees in the Budongo Forest Reserve and other natural tropical forests experiencing similar human pressure.

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