Available online at www.sciencedirect.com
SCIENCE DIRECT®
Forest Ecology and Management 188 (2004) 267–278
Forest Ecology and Management
www.elsevier.com/locate/foreco

Chimpanzee diet and habitat selection in the Budongo Forest Reserve, Uganda

Mnason Tweheyo[a,b,*,1], Kåre A. Lye[b], Robert B. Weladji[c,2]

[a]Department of Forest Biology and Ecosystems Management, Faculty of Forestry and Nature Conservation, Makerere University, P.O. Box 7062 Kampala, Uganda
[b]Department of Biology and Nature Conservation, Agricultural University of Norway, P.O. Box 5014, N-1432 Ås, Norway
[c]Department of Animal Sciences, Agricultural University of Norway, P.O. Box 5025, N-1432 Ås, Norway

Received 9 August 2002; received in revised form 20 May 2003; accepted 16 July 2003

Abstract

Between June 2000 and August 2001 observations were made on food types, plant species and parts consumed by chimpanzee in relation to various habitats in the Budongo Forest Reserve (BFR), Uganda. Factors influencing their occurrence as well as their activity patterns were also assessed. The chimpanzees of the BFR spent 80% of their daytime feeding and their diet comprised 56 plants species of which 94% were trees. Chimpanzees spent most of their feeding time on *B. papyrifera*, *Ficus sur*, *Ficus mucuso*, *Ficus exasperata* and *Ficus variifolia*. Chimpanzees fed mostly on fruits (71%), favouring ripe ones, and young leaves (16%). Factors positively influencing occurrence of chimpanzees included habitat types (logged area and forest edge), plant types (trees), food types (fruits), fruit maturity (ripe fruits), and fruit quantity. Logged area and forest edge provided 76% of the chimpanzee food but are also the habitats with the highest human interference, e.g. logging and agriculture encroachment. Past forest management plans did not consider chimpanzee food trees; most were considered weeds and killed with aboricides. We conclude that the long-term survival of chimpanzees of the BFR requires implementation of management plans based on conservation of food tree species.

Keywords: Chimpanzees (*Pan troglodytes*); Feeding habits; Budongo Forest Reserve; Human disturbance; Uganda

1. Introduction

Ecological changes occur whenever after disturbance, and in tropical forests, activities such as logging, mining and other forms of exploitation affect the availability and quality of wildlife (Whitmore and Sayer, 1992). The challenge to tropical forest wildlife is to adapt to these changes. Uganda has several species diverse rain forests supporting large populations of wildlife (Butynski, 1984; Banana and Tweheyo, 2001) and among these is the Budongo Forest Reserve, which is well known for its chimpanzee (*Pan troglodytes*) populations (Howard, 1991). However, the combined effects of logging activities and increasing encroachment with agriculture are threatening the reserve and its population of chimpanzee (Reynolds, 1992).

* Corresponding author. Tel.: +476-49-48-494; fax: +476-49-48-502.
E-mail addresses: tweheyo.mnason@ibn.nlh.no, tweheyo@forest.mak.ac.ug (M. Tweheyo).
[1] Tel.: +256-41543647; fax: +256-41533574.
[2] Permanent address: Department of Wildlife and Protected Areas, Ministry of Environment and Forestry, Yaoundé, Cameroon.

0378-1127/$ – see front matter © 2003 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2003.07.028

Factors influencing chimpanzee behaviour have received considerable attention in Budongo (e.g. Reynolds and Reynolds, 1965; Suzuki, 1971) and elsewhere (e.g. Kibale Forest National Park in Uganda: Wrangham et al., 1991; and Gombe and Mahale Forest National Parks in Tanzania: Hladik, 1977; Goodall, 1986; Nishida and Hosaka, 1996). Although Budongo has one of the longest (dating to 1910) research records in Africa (Eggeling, 1947; Paterson, 1991) and has included some studies of chimpanzee feeding habits (Newton-Fisher, 1999; Tweheyo and Obua, 2001) more information is needed on chimpanzee diet and habitat preference to maintain chimpanzee habitats that are being threatened by increasing timber demands and human encroachment.

Eggeling (1947) described the vegetation structure of Budongo and most tree species that appear in each vegetation type, but his classification focused on timber species production and did not address of her vegetation that supports chimpanzees. Our study determined food types, plant species and plant parts eaten by chimpanzees in relation to habitat occurrence in Budongo as well as chimpanzee activity patterns and habitat preferences in order to fill in this gap. Our results have implications for the management of Budongo Forest, in particular, and other tropical forest, in general, and may help forest managers understand of how wildlife can be maintained in areas managed for timber.

2. Methods

2.1. Study area

This study was conducted with the chimpanzees of the Sonso community in the Sonso region (Fig. 1). The Budongo Forest Reserve is an outlier of the great Ituri forest of the Democratic Republic of Congo and resembles in many respects rain forests of West Africa (Eggeling, 1947). It covers an area of 825 km^2 that comprises Uganda's largest forest reserve (Howard, 1991). In the reserve, 437 km^2 (53%) is continuous moist semi-deciduous tropical forest and the remainder is grassland communities thought to be capable of supporting forest (Howard et al., 1997). Eggeling (1947) described Budongo as a lowland moist semi-deciduous forest with varying vegetation characteristics, such as early successional, forests; mixed forest, *Cynometra* forest, swamp forest, shrubland, and grassland.

Budongo was gazetted as a forest reserve in 1932 and is the largest and most valuable timber forest in Uganda (Howard, 1991). Timber has been selectively extracted from the forest since 1910. Detailed management records of each compartment and the research carried out there are available (Philip, 1964; Plumptre, 1996). Due to overexploitation, enrichment planting of mahogany (*Khaya* and *Entandrophragma*) was carried out to encourage regeneration. Also during the 1950s and 1960s, arboricide treatment (e.g. 2,4,5-T and 2,4-D) was applied to various ''weed'' species of trees, i.e. trees with no marketable value including figs, an important component of most frugivore diets in the forest, including chimpanzees (Plumptre et al., 1994; Tweheyo and Obua, 2001). This treatment stopped in the 1970s, when government departments lost management control of the forest. Selective mechanical logging was followed by pit-sawing and the problem of illegal pit-sawing persists today. Pit-sawing is the manual harvesting and sawing of logs in which a pit is used as a platform for the log being sawn. The process of sawing usually involves two men who by force drive the saw into the log to produce the planks.

Budongo Forest Reserve is of high importance for global biodiversity, ranking third in overall importance of Ugandan forests (Howard et al., 1997). It contains about 465 species of trees and shrubs (Eggeling, 1947; Howard, 1991). In addition, there are five species of diurnal primates including chimpanzees (with a population of about 700), black and white colobus monkeys (*Colobus guereza occidentalis*), baboons (*Papio anubis*), red tailed monkeys (*Cercopithecus ascanius schmidti*), and blue monkeys (*Cercopithecus mitis stuhlmanii*). The chimpanzees of the Sonso community, which was our study group, used the forest management compartments referred to as N1, N2, N3, N4, N15, and W21 (Fig. 1).

Compartment N1 was mechanically logged in 1945, N2 in 1945 through 1947, N3 in 1947 through 1952, N4 in 1952 through 1954, while N15 remained unlogged (nature reserve with permanent sample plots). All these compartments, apart from N3 and N15, were selectively logged again by pit-sawing between 1990 and 2000 (Babweteera et al., 2000).

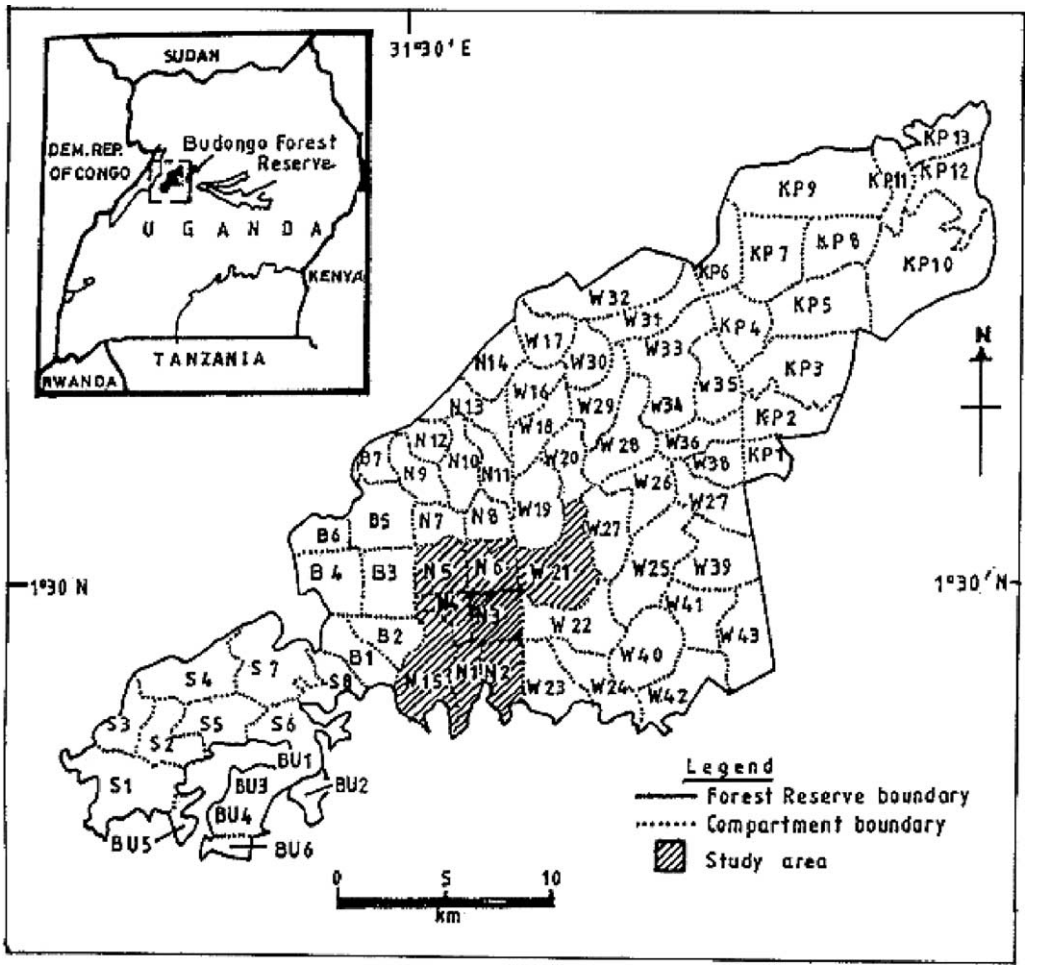

Fig. 1. Map of forested portion of Budongo Forest Reserve showing the study area. The five main blocks of the forest from which the compartments take their letter codes are—S: Siba, B: Biiso, N: Nyakafunjo, W: Waibira, K: Kaniyo. The inside borders show different compartments.

The study area is situated at an altitude between 1000 and 1200 m.

2.2. Data collection

2.2.1. Scan sampling

Scan sampling method was used to record chimpanzee diet, activities and habitats. Binoculars were occasionally used to improve visibility and clarity. Chimpanzee groups were followed from dawn to dusk between June 2000 and August 2001 except in situations when chimpanzees were lost. During this period, we followed chimpanzees for 3 days in a week and in total we had 176 days of scan observations and a total of 2641 scans were recorded. A scan was conducted after every 30 min recording the activities of individual chimpanzees on the food trees. Only one individual was observed from a group when more than one chimpanzee was in a feeding tree. The specific individual was observed for 5 min. Thereafter, a different chimpanzee was chosen from the same group after another 30 min and the process repeated until the animal(s) left the plant or until darkness fell. Choice of the individual animal was dependant on the most visible chimpanzees in a group. Our scan records included only adults and juveniles.

Data were collected once we had identified all individuals within a group. Scan sampling enabled feeding data to be collected that was evenly representative across all individuals. When animals were not feeding, we recorded other activities, such as resting, travelling, grooming, or mating.

2.2.2. Data recording

2.2.2.1. Chimpanzee focal activity. Chimpanzee activities included feeding (F), resting (R) and other activities (P). Feeding was defined as active consumption of plant parts (e.g. fruits, leaves) as well as soil and prey, while resting was time spent other than feeding, socialising, travelling or grooming. Other activities were those that did not include feeding, but were socially active, such as travelling, grooming or mating.

2.2.2.2. Habitat types. Since chimpanzees occupy different parts of the forest, we recorded the habitats they used. Our study area was thus divided into seven habitats, namely: logged area (LA), forest edge (FE), nature reserve (NR), forest gap (FG), inter-canopy (IC), cleared patches (CP) and riverine or riparian forest (R). Logged areas are those parts of the forest that were at one time cut down either by clear cutting or selective logging. Forest edge is that part of the forest where the forest reserve borders open land. We considered forest edge to extend 150 m into the forest from the border and 50 m outside the border equalling a total of 200 m following Struhsaker (1997). We did include up to 150 m outside the forest edge, because this would have included some open land and farms. The nature reserve is that part of the forest that had never been logged. Forest gaps are small openings inside the forest with sizes ranging between 86 and 1845 m^2 according to Babweteera et al. (2000). Inter-canopy is a semi-open habitat between areas of forest with closed canopies and is mostly covered by shrubs and young trees. Inter-canopy occurs in the forest either due to gaps which are closing up or due to some sites in the forest that have poor soils that do not support big trees that form canopy. Cleared patches are areas inside or outside the forest significantly disturbed by human activities. Riverine/riparian forest is swampy or marshy area in the forest. In our study area we estimated logged areas to about 52%, forest edge 9%, inter-canopy 10%, riverine 12%, nature reserve 14%, forest gaps 2%, and cleared patches 1%. These percentages represent the proportion of each habitat type relative to the total study area. We marked specific habitats with flagging tapes so that none of the habitat was recorded twice. Our study area has a well-marked grid system and estimating sizes for individual habitats was made possible. We marked habitats basing on chimpanzee utilisation while past studies have marked habitats in Budongo basing on timber utilisation (Eggeling, 1947). We assumed that if our findings are considered together with past studies, then management of the Budongo Forest would be able to integrate conservation and utilisation.

2.2.2.3. Diet selection, food types and fruit maturity. In the process of scan sampling, all types of food eaten by chimpanzees were recorded: flowers (FW), insects (IS), buds (B), fruits (F), leaves (L), pith (PI), bark (BK), seeds (SE), prey (PE), nuts (NT), soil (SO), wood (W). The development stages of both leaves and fruits were additionally recorded as: young leaves (YL), mature leaves (ML), emerging fruits (EF), young fruits (YF), sub-mature fruits (SMF), and ripe fruits (RF). Stages in fruit maturity were recorded according to fruit size changes with time from the day of emerging to sub-mature fruits, but ripe fruits stage was identified by colour changes from green to either yellow, orange or red.

2.2.2.4. Food species and plant types. All plant species that provided food to chimpanzees were recorded and identified immediately or later. The labelling of most trees by the Uganda Forest Department made immediate identification of most trees possible. Otherwise, samples were collected and later identified either at the Makerere University herbarium or at the Agricultural University of Norway (Department of Biology and Nature Conservation). Plant species were given a unique code to each plant group and were recorded as: herb (Hb), climber (Cl), epiphytes (Ep), trees (T), shrubs (S), grasses (G) and those not identified were recorded as Unk = unknown with corresponding numbers e.g. Unk1, Unk2, etc.

2.2.2.5. Fruit quantity. During scan sampling, fruit quantity was estimated using the method of Plumptre et al. (1994). Fruit quantity on a given tree was

classified according to its cover of branches into five classes as follow: ≤10% cover, i.e. a tree with fruits that cover less than 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.

2.3. Data analysis

Prior to analysis, data were cross-tabulated with contingency tables using SPSS 8.0 for windows (SPSS, 1997). In order to assess factors affecting the occurrence of the chimpanzees in different feeding habitats, we fitted four different models to the following predictor variables or combination of variables: (1) habitat type and food type, (2) habitat type and plant type, (3) habitat type and fruit quantity, and (4) habitat type and fruit maturity. The data were analysed with a generalised linear model (McCullagh and Nelder, 1989) using the GENMOD procedure in SAS (SAS, 1998). Since the response was count data (i.e. values are positive integers), a Poisson distribution of error with a log link function was used in the analysis. The significance of the explanatory variables was assessed by their likelihood ratio statistics (χ^2 distributed). In case of overdispersion, an empirical scale parameter was adjusted using the scale option in the GENMOD procedure (SAS, 1999). Pairwise comparisons for means of chimpanzee occurrence by each of the predictor variables were carried out by *t*-test. We assessed habitat preference using a ''habitat preference index'' (HPI) calculated by the following formula:

$$\mathrm{HPI} = \log 10\left[\frac{\%\,\text{occurrence}}{\%\,\text{habitat}}\right]$$

where % occurrence is the proportion of occurrence in one habitat relative to the total number of feeding instances; and % habitat is the proportion in size of one habitat relative to the total habitat size. All statistical analyses were performed by SAS (1998) and the 5% level of significance was used.

3. Results

3.1. Plant eaten, part eaten and common habitat

A total of 2641 occasion records of feeding, resting and other activities were collected during the study period and we spent 1321 h while observing chimpanzees of which 1150 h were spent while recording feeding. A total of 56 plant species were recorded as eaten by chimpanzees (Table 1). The most commonly eaten species were from three families: Moraceae, Marantaceae and Ulmaceae. These taxa accounted for 34, 11 and 9% of the feeding records, respectively. Chimpanzees fed on many different parts of the plant including fruits, leaves, bark, flowers, seeds, wood, and pith (Table 1). Feeding frequency was higher for tree species (94%) than climbers (2%), shrubs (1%), grass (1%), herbs (1%) and epiphytes (1%). Furthermore, records seemed to occur more frequently in the logged area (52%) and forest edge (24%) as compared to other habitat types (Table 1). In this period, chimpanzees also fed on soil, preyed on a monkey and fed on ants. However, chimpanzees spent 71% of their feeding time on fruits and 16% on young leaves, but 78% of the total fruit feeding time was on ripe fruits, which was 56% of the total feeding time.

Twenty-one plant species accounted for at least 1% of the feeding time and chimpanzees spent 46% of the feeding time on only five species (Table 2). These species belong to the Moraceae family and most of them were figs. Chimpanzees were only observed eating the flowers of *Milicia excelsa* and *Broussonetia papyrifera*. *Ficus sur* is mostly found in logged area, although it also appears in forest edges, but *B. papyrifera* is a forest edge species.

3.2. Factors influencing chimpanzee occurrence

Chimpanzee occurrence differed significantly among habitats ($\chi^2 = 709.8$, $P < 0.001$, $n = 7$); logged areas and forest edge were the habitats where they spent most of their feeding time. Least square means differences confirmed that logged area and forest edge were significantly more used than the other habitats (Fig. 2; $P < 0.05$); chimpanzee occurrence was significantly greater in logged areas than in forest edges ($P < 0.001$). It is important to note that logged areas made up a proportionally larger area than other habitats. Accordingly, forest edge, cleared patches and forest gaps were more preferred than other habitats when we adjusted for the habitat size using the habitat preference index (Fig. 3). There was a dependency between chimpanzee occurrence and the type of plant they were feeding on ($\chi^2 = 330.4$, $P < 0.001$, $n = 6$),

Table 1
Plant species eaten by chimpanzees by part eaten, common habitat and growth habit recorded in Budongo during June 2000 to August 2001[a]

Species	Family	Part eaten	Common habitat	Growth habit
Acalypha neptunica Muell.Arg.	Euphorbiaceae	YL	IC	S
Adenia tricostata de Wilde	Passifloraceae	YL	FG, LA	CL
Alafia sp.	Apocynaceae	MF, RF	LA, FG	CL
Antiaris toxicaria Leschen.	Moraceae	RF	LA	T
B. papyrifera (L.) Vent.	Moraceae	YL, FW, MF, MF, RF	EC, CP	T
Celtis gomphophylla Bak.	Ulmaceae	YL, RF	EC, R	T
C. mildbraedii Engl.	Ulmaceae	YL	LA, FG	T
Celtis phillipensis Blanco	Ulmaceae	YL, RF	LA, FG	T
Celtis zenkeri Engl.	Ulmaceae	RF	LA	T
C. albidum G. Don	Sapotaceae	RF	LA, FG	T
Chrysophyllum gorungosanum Engl.	Sapotaceae	RF	LA, FG	T
Cleistopholis patens (Benth.) Engl.	Annonaceae	WD, BK	LA, R	T
C. millenii Bak.	Boraginaceae	MF, RF	EC, LA	T
C. alexandri Wright.	Fabaceae × Caesalpinioïdeae	SD, BK, YL	LA, NR	T
Desmodium sp.	Fabaceae	YL	FE, CP	S
Desplatzia dewevrei (De Wild & Th. Dur.) Burret	Tiliaceae	RF	LA, R	T
Entandrophragma angolense Welw.	Meliaceae	RF	LA, NR	T
Ficus asperifolia Miq.	Moracea	RF	LA, IC	T
Ficus barteri Sprague	Moracea	RF	LA, R	T
Ficus exasperata Vahl	Moracea	YL, BK, SMF, RF	LA, EC	T
Ficus lingua De wild.	Moracea	RF	LA, EC	T
Ficus mucuso Ficalho	Moracea	YL, EF, YF, SMF, RF	EC, LA	T
Ficus natalensis Hochst	Moracea	RF	EC, LA, R	T
Ficus ottoniifolia (Miq.) Miq.	Moracea	YL	LA	T
Ficus polita Vahl.	Moracea	RF, SMF	LA, EC	T
Ficus sansibarica Warb.	Moracea	RF	LA, EC	T
Ficus saussureana DC.	Moracea	RF, SMF	LA, R	T
F. sur Forssk	Moracea	EF, YF, SMF, RF	LA, EC, R	T
Ficus thonningii Bl.	Moracea	RF	LA, EC	T
Ficus vallis-choudae Del.	Moracea	RF	LA, R	T
Ficus variifolia Warb.	Moracea	YL, BK, EF, YF, RF	LA, EC	T
Gynura scandens O. Hoffm.	Asteraceae	YL,	FG, EC	CL/HB
Klainedoxa gabonensis Pierre ex Engl.	Simarubaceae	RF	R	T
Lannea welwitschii (Heirn) Engl.	Anacardiaceae	RF, WD	LA, EC	T
Lasiodiscus mildbraedii Engl.	Rhamnaceae	YL	FG, EC	T
Leptaspis zeylanica Steud.	Poaceae	PI	IC	G/HB
Maesopsis eminii Engl.	Rhamnaceae	RF	LA, EC	T
Marantochloa leucantha R. Schum.	Marantaceaa	PI	LA, FG	G/HB
Marantochloa purpurea Ridl.	Marantaceaa	MF, PI	IC	G/HB
M. excelsum Harms	Fabaceae × Caesalpinioïdeae	RF	EC	T
M. excelsa (Welw) C. Berg	Moraceae	FW, RF	R, IC	T
Mimusopsis bagshawei S. Moore	Sapotaceae	RF	R, IC	T
M. mesozygia Stapf	Moraceae	YL, RF	LA	T
Myrianthus holstii Engl.	Moraceae	RF	LA	T
Platycerium elephantotis Schweinf.	Polypodiaceae	YL	LA, NR	EP
Pseudospondias microcarpa (A. Rich) Engl.	Anacardiaceae	RF	R, NR	T
Raphia farinifera (Gaertn.) Hyl.	Arecaceae (Palmae)	WD	R	T
Sarcophrynium schweinfurthianum O. Ktze	Marantaceae	PI	FG, EC	HB
Setaria megaphylla (Steud.) Th. Dur. & Schinz.	Poaceae	PI	EC, FG	G/HB
Solanecio angulatus (Vahl) C. Jeffrey	Asteraceae	YL	FG, CP	CL
Strychnos mitis S. Moore	Loganiaceae	RF	LA, FG	T
Syzygium guineense (Willd.) DC.	Myrtaceae	RF	LA, CP	T

Table 1 (*Continued*)

Species	Family	Part eaten	Common habitat	Growth habit
Tectaria gemmifera (Fee) Alston	Dryopteridaceae	PI	FG	HB
Trachyphrynium braunianum (K. Schum.) Bak.	Marantaceae	PI	NR, LA	EP
Treculia africana Decne.	Moraceae	RF	LA	T
Whitefieldia elongata Beaur.	Acanthaceae	YL	LA, IC	S

[a] YL: young leaves, EF: emerging fruits, YF: young fruits, MF: mature fruits, RF: ripe fruits, BK: bark, FW: flowers, WD: wood, PI: pith, LA: logged area, EC: forest edge, R: riverine, IC: inter-canopy, NR: nature reserve, FG: forest gap, CP: cleared patches, T: tree, CL: climbers, HB: herbs, G: grasses, Ep: epiphytes, S: shrub.

with trees providing the largest component of the food and significantly more than other plant types (Fig. 2; $P < 0.001$ for all pairwise comparisons with trees). Based on the amount of variability being explained by each habitat or plant types, it seemed that chimpanzee occurrence depended more on food plant types than habitat type, i.e. trees were of high importance independently of the habitat type. Indeed, after we accounted for the effect of habitat, food type still affected the occurrence of chimpanzees ($\chi^2 = 453.4$, $P < 0.001$, $n = 9$). Detailed observation of the least square differences revealed that chimpanzee occurrence was more determined by the presence of fruit (significantly higher than all other food types; $P < 0.05$; Fig. 4), followed by leaves (significantly higher than all other food type except fruit; $P < 0.05$; Fig. 4) and flowers (significantly higher than all other food type except fruit and leaves; $P < 0.05$; Fig. 4). These dominant food types appeared to be highest in both logged area and forest edge (Fig. 4).

Table 2
Plant species accounting for at least 1% of the chimpanzees feeding time in Budongo during June 2000 and August 2001

Species	Time spent on each species by chimpanzees (%)
B. papyrifera	15.4
F. sur	15.0
F. mucuso	7.2
F. exasperata	4.3
F. variifolia	4.2
C. alexandri	2.2
F. thonningii	2.2
C. mildbraedii	2.0
C. millenii	2.0
F. saussureana	2.0
C. albidum	1.7
F. vallis-choudae	1.7
F. barteri	1.3
M. excelsa	1.3
F. natalensis	1.2
Desplatsia dewevrei	1.1
F. sansibarica	1.1
M. mesozygia	1.1
S. guineense	1.1
F. polita	1.0
M. excelsum	1.0

Chimpanzee occurrence differed significantly among levels of fruit quantity ($\chi^2 = 100.5$, $P < 0.001$, $n = 5$), after accounting for habitat type. Logged areas and forest edge accounted for more fruits eaten by chimpanzees than any other habitat in our study area (Table 3). Furthermore, within each habitat, chimpanzee occurrence depended on the available fruit quantity (Table 3). Out of 2219 feeding scan counts, 1578 (71%) were on fruits among which 990 were from logged areas. Of 990 counts of fruit trees in logged areas at full maturity before fruit ripening, 619 counts were on trees with more than 75% fruit cover in the fruit production zone. High fruit quantities are important to chimpanzees because they move in groups. This suggests that trees in logged areas produce more chimpanzee food than trees in other habitats.

Fruit maturity significantly affected chimpanzee feeding distribution ($\chi^2 = 523.5$, $P < 0.001$, $n = 12$). Our sampling counts showed that chimpanzee preferred ripe fruits in all habitats, which provided 55% of the total diet of chimpanzees in Budongo (Fig. 5), followed by young leaves (16%) and sub-mature fruits (11.3%).

3.3. Chimpanzee activities

Chimpanzees spent 80% of their time feeding, followed by resting (18%) and other activities, mainly playing, for the rest of the time. Apart from

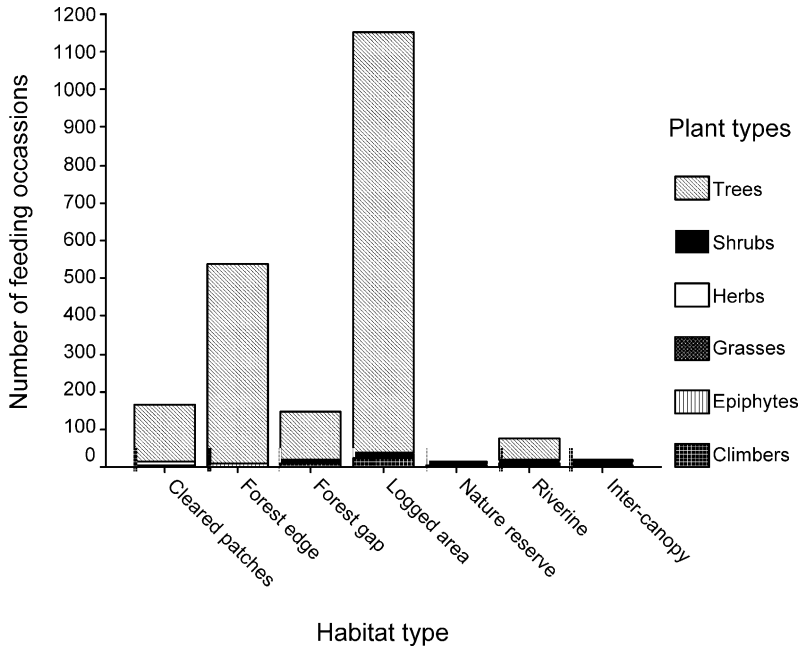

Fig. 2. Different plant types used by chimpanzees in Budongo Forest Reserve Uganda and their corresponding habitats.

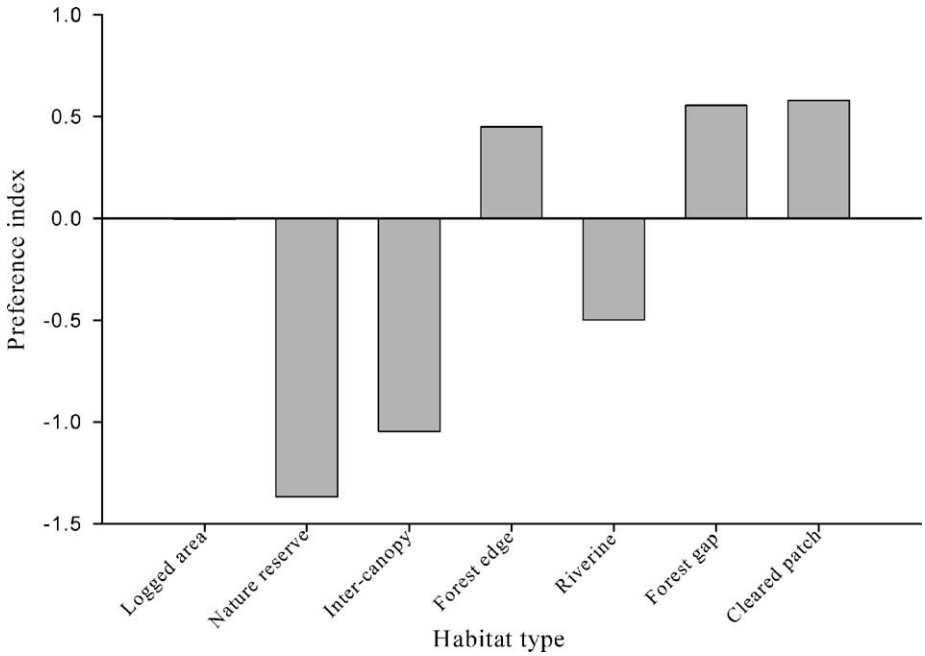

Fig. 3. Graph showing the relative use of each habitat in our study area. Preference index is the ratio to $\log_{10}$ of number of chimpanzee feeding instances recorded in each habitat to size of that habitat.

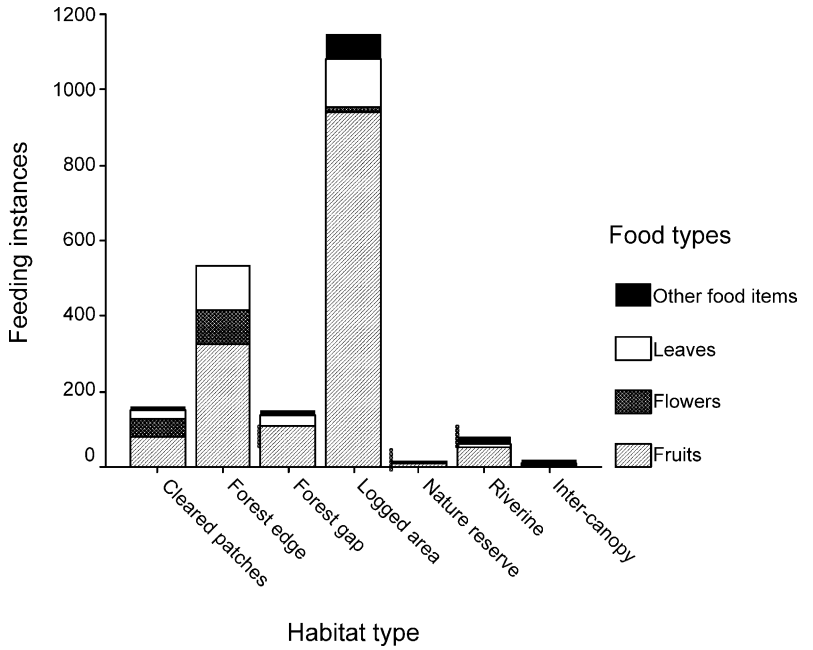

Fig. 4. Chimpanzee feeding instances in different habitat types in Budongo Forest Reserve, Uganda.

inter-canopy habitats, this pattern was similar in all other habitat types, i.e. chimpanzees spent most of their time feeding in all habitats. In inter-canopy habitat, chimpanzees spent more time resting (86%) than feeding (13%) and playing.

4. Discussion

This study shows that the chimpanzees of Sonso community exploit a relatively large variety of plant species. This is consistent with past studies reporting chimpanzees to have a broad diet (Wrangham, 1977; Tutin et al., 1991; Newton-Fisher, 1999). The chimpanzees of Budongo fed largely on trees, mainly figs, which have been reported to be important food resources to primates (Janzen, 1979; Leighton and Leighton, 1983; Tweheyo and Obua, 2001). Moreover, fruits dominated their diet, concurring with previous findings that chimpanzees are primarily frugivores in Budongo (e.g. Newton-Fisher, 1999) and elsewhere (Hladik, 1977; Struhsaker, 1997). We found that

Table 3
Occurrence of chimpanzees in Budongo habitats in relation to different categories of fruit quantity ($n = 1578$)

	Fruit quantity					χ^2	P value
	≤10%	≥10 and <25%	≥25 and <50%	≥50 and <75%	≥75%		
Cleared patches	0	13	32	23	15	47.61	<0.001
Forest edge	4	53	68	104	101	138.91	<0.001
Forest gap	2	9	37	22	33	48.70	<0.001
Logged area	33	88	226	206	437	507.04	<0.001
Nature reserve	2	1	0	0	5	[a]	
Riverine	13	5	8	0	28	48.70	<0.001
Inter-canopy	0	2	4	4	0	[a]	

[a] Data not appropriate for statistical test.

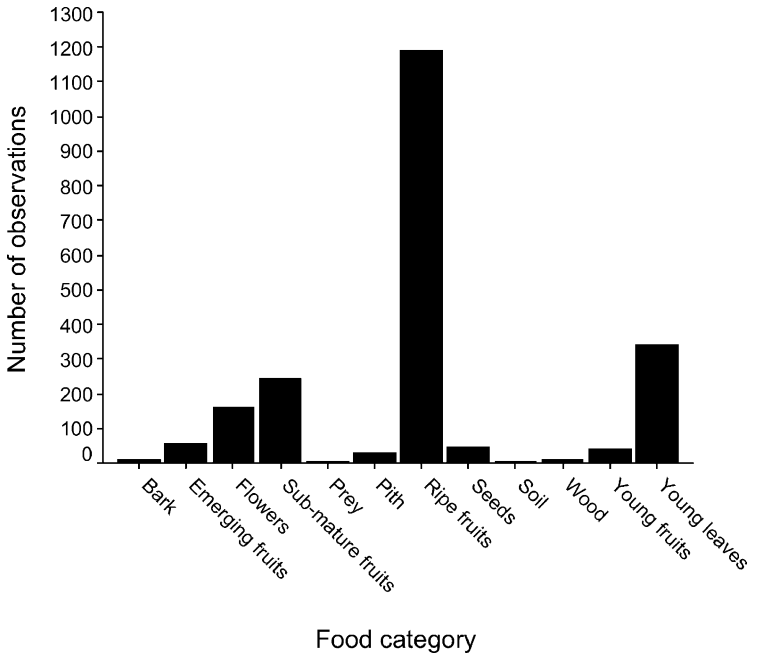

Fig. 5. Different chimpanzee foods in Budongo Forest Reserve, Uganda.

chimpanzees preferred ripe fruits. Reynolds and Reynolds (1965) reported that chimpanzee movement and distribution are affected by the ripening of fruit trees at different times and in different places. Of the 21 plant species on which chimpanzee spent at least 1% of the feeding time (Table 2), seven (*Cynometra alexandri*, *Celtis mildbraedii*, *Cordia millenii*, *Chrysophyllum albidum*, *M. excelsa*, *Morus mesozygia*, and *Mildbraediodendron excelsum*) are considered important timber species (Philip, 1964).

Furthermore, tree species that are used both for timber and as food by chimpanzees are common in logged areas where chimpanzees spend most of their time feeding. This is an important consideration for management in this forest reserve. For the conservation of chimpanzees, plants that provide food, but do not have timber value, need to be considered. They will decline in abundance if management plans continue to be based on economic returns of timber. In the 1950s and 1960s, tree species graded by Uganda Forestry Department to be of low timber value in Budongo were killed by poisoning with aboricides in order to promote regeneration of timber species (Philip, 1964). These species, especially figs, provide most food for chimpanzees.

The formerly logged area of Budongo was an important food habitat as described earlier by Plumptre et al. (1997), as was forest edge. This observation is important because Budongo Forest is under multiple-use programmes and timber harvesting has high priority. Logged area and forest edge, which appeared to have the highest number of tree species that support chimpanzee food plants, are the same habitats that are utilised by both local people and the Forestry Department. Forest edge habitat in the reserve borders private land. This habitat, though important for chimpanzee food, is also a multiple-use zone for community harvesting of firewood, medicinal plants, poles, etc. It is also through this interface habitat of forest edge that chimpanzees go out of the forest to raid agricultural crops.

Logged habitat, as the name suggests, is an area under actual and/or past timber harvesting. Past studies have also shown that chimpanzees move in groups (Reynolds, 1992; Plumptre and Reynolds, 1996) and that large fruit quantities attract chimpanzees more than small quantities of fruits scattered among small trees and shrubs (Tweheyo and Obua, 2001). Our study supports these findings and we further show that such trees mainly occurred in logged areas. Plumptre et al.

(1997) reported that prevention of mechanical logging and high disturbances in Budongo since 1970 have favoured the growth of trees that are fed on by chimpanzees.

The potential conflict is not management of logged areas per se, but about which species to manage and how. We found that 82% of the trees providing food to chimpanzees in Budongo are not considered to be important timber species. Different studies (Newton-Fisher, 1999; Tweheyo and Obua, 2001) have reported that figs are important food resources to chimpanzees. We found that of the 20 trees that provided 65% of total food to chimpanzee, 75% of these are not regarded important to timber species.

5. Conclusions

The chimpanzees of Budongo are primarily frugivores and feed mainly on ripe fruits. This study clearly shows that two habitats provide the greatest number of plant trees for the Sonso community chimpanzee food, viz. logged areas and forest edges and that both are areas mostly exposed to and close to human activity. Although some of the species fed on by chimpanzees are important timber trees, most of them are not yet considered to be valuable. Prohibition of mechanical logging since 1970s apparently stimulated the growth of trees that provide food to chimpanzees, thereby supporting the intermediate disturbance hypothesis (Connell, 1978) if we consider that the intensity of logging were going extreme then. We therefore suggest that if logging had continued, or if the ongoing logging is accentuated, such intense disturbances may be harmful to the population dynamics of chimpanzee and perhaps other animals in the Budongo Forest Reserve. This is useful information for forest managers who are to compare the conservation value of chimpanzees and exploitation of timber. Since many trees of low timber value have high conservation value to chimpanzees, alternative, but non-degrading, sources of income like ecotourism based on chimpanzee viewing should be promoted, while considering their effect on chimpanzee behaviour. Indeed this study has also identified factors influencing chimpanzee occurrence, such as plant types (e.g. trees), food type (e.g. fruit), fruit maturity (e.g. ripe fruit), and fruit quantity (higher occurrence on habitat with higher amount of fruit). One could then use this information to find the chimpanzees within the Budongo for viewing. Furthermore there is a need to provide sufficient information on the feeding patterns of other chimpanzee communities in the Budongo in order to have a clearer understanding of their movements and hence their management. Studying other communities of chimpanzees is important since it may provide more information on habitat selection as the forest landscape and management vary in different blocks. Failure to combine conservation and utilisation in the management of the Budongo Forest may lead to a reduction of food resources for chimpanzees, and this may have effect on the entire ecosystem. Indeed, chimpanzees are frugivores, move long distances and therefore can be of great value to forest regeneration and maintenance through seed dispersal (Cordeiro and Howe, 2001; Poulsen et al., 2001). A good understanding of chimpanzee food and habitats is essential for making informed decisions about the conservation of the species and associated food trees and habitats especially in natural forests under human pressure like Budongo.

Acknowledgements

NORAD and NUFU project 63/2003 funded this research through Faculty of Forestry and Nature Conservation, Makerere University and Department of Biology and Nature Conservation, Agricultural University of Norway. We are grateful to Dr. J.R.S. Kaboggoza of Makerere University, F. Babweteera of Budongo Forest Project and Professor V. Reynolds of Oxford University. We thank the anonymous reviewers together with Professor J. Swenson and Dr. A.J. Plumptre for critically reading and commenting on the manuscript. We also thank the Budongo Forest Project staff especially M.G. Mbotella for his assistance in the field.

References

Babweteera, F., Plumptre, A.J., Obua, J., 2000. Effect of gap size and age on climber abundance and diversity in Budongo forest reserve, Uganda. Afr. J. Ecol. 38, 230–237.

Banana, A.Y., Tweheyo, M., 2001. The ecological changes of Echuya afromontane forest, Uganda. Afr. J. Ecol. 39, 366–373.

Butynski, T.M., 1984. Primates and their conservation in Uganda. Primate Conserv. 6, 68–72.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.

Cordeiro, N.J., Howe, H.F., 2001. Low recruitment of trees dispersed by animals in forest fragments. Conserv. Biol. 15, 1733–1741.

Eggeling, W.J., 1947. Observations on the ecology of the Budongo rain forest, Uganda. J. Ecol. 34, 20–87.

Goodall, J., 1986. The Chimpanzees of Gombe: Patterns of Behaviour. The Belknap Press of Harvard University Press, Cambridge, MA.

Hladik, C.M., 1977. Chimpanzees of Gombe and the chimpanzees of Gabon: some comparative data on the diet. In: Clutton-Brock, T.H. (Ed.), Primate Ecology. Academic Press, New York, pp. 481–501.

Howard, P.C., 1991. Nature Conservation in Uganda's Tropical Forest Reserves. IUCN, Gland, Switzerland.

Howard, P.C., Davenport, T., Kigenyi, F., 1997. Planning conservation areas in Uganda's natural forests. Oryx 31, 253–264.

Janzen, D.H., 1979. How to be a fig. Ann. Rev. Ecol. Syst. 10, 13–51.

Leighton, M., Leighton, D.R., 1983. Vertebrate response to fruiting and seasonality with a Bornean rain forest. In: Sutton, S.L., Whitmore, T.C., Chadwick, A.C. (Eds.), Tropical Rain Forest: Ecology and Management. Blackwell Science Publications, Oxford, pp. 181–196.

McCullagh, P., Nelder, J.A., 1989. Generalized Linear Models, 2nd ed. Chapman & Hall, London.

Newton-Fisher, N.E., 1999. The diet of chimpanzees in the Budongo forest reserve, Uganda. Afr. J. Ecol. 37, 344–354.

Nishida, T., Hosaka, K., 1996. Coalition strategies among adult male chimpanzees of the Mahale mountains, Tanzania. In: Macgrew, W.C., Marchant, L.F., Nishida, T. (Eds.), Great Ape Societies. Cambridge University Press, Cambridge, UK, pp. 114–135.

Paterson, J.D., 1991. The ecology and history of Uganda's Budongo forest. For. Conserv. Hist. 34, 179–187.

Philip, M.S., 1964. Working Plan for Budongo Central Forest Reserve. Government Printer, Entebbe, Uganda.

Plumptre, A.J., 1996. Changes following sixty years of selective timber harvesting in the Budongo forest reserve, Uganda. For. Ecol. Manage. 89, 101–113.

Plumptre, A.J., Reynolds, V., 1996. Censusing chimpanzees in the Budongo forest. Int. J. Primates 17, 85–99.

Plumptre, A.J., Reynolds, V., Bakuneeta, C., 1994. The contribution of fruit eating primates to seed dispersal and natural regeneration after selective logging. ODA Project Report R4738.

Plumptre A.J., Reynolds, V., Bakuneeta, C., 1997. The effects of selective logging in monodominant tropical forest on biodiversity. Overseas Development Administration Project Report R6057, UK.

Poulsen, J.R., Clark, C.J., Smith, T.B., 2001. Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. J. Trop. Ecol. 17, 787–808.

Reynolds, V., 1992. Chimpanzees in the Budongo forest, Uganda. J. Zool. (London) 228, 695–699.

Reynolds, V., Reynolds, F., 1965. Chimpanzees of the Budongo forest. In: Devore, I. (Ed.), Field Studies of Monkeys and Apes. Holt, Reinhart & Winston, New York, pp. 368–419.

SAS, 1998. The SAS System for Windows, Release 6.12. SAS Institute, Cary, NC.

SAS, 1999. SAS OnlineDoc®, Version 8. SAS Institute, Cary, NC.

SPSS, 1997. SPSS for Windows Releases 8.0. SPSS Inc.

Struhsaker, T.T., 1997. Ecology of an African Rain Forest: Logging in Kibale and Conflict between Conservation and Exploitation. University of Florida, Gainesville, USA.

Suzuki, A., 1971. Carnivory and cannibalism of chimpanzees observed among forest-living chimpanzees in Budongo forest, Uganda. J. Anthropol. Soc. Jpn. 79, 30–48.

Tutin, C.E.G., Fernandez, M., Rogers, M.E., Williamson, E., MacGrew, W.C. Phil. Trans. Roy. Soc. London, Ser. B 334, , 179–186.

Tweheyo, M., Obua, J., 2001. Feeding habits of chimpanzees (*Pan troglodytes*), red-tailed monkeys (*Cercopithecus ascanius schmiditi*), and blue monkeys (*Cercopethecus mitis stuhlmanii*) on figs in Budongo forest reserve, Uganda. Afr. J. Ecol. 39, 133–139.

Whitmore, T.C., Sayer, J.A., 1992. Tropical Forest Deforestation and Species Extinction. Chapman & Hall, London.

Wrangham, R., 1977. Feeding behaviour of chimpanzees in Gombe National park, Tanzania. In: Clutton-Brock, T.H. (Ed.), Primate Ecology. London Academic Press, UK, pp. 503–538.

Wrangham, R.W., Conklin, N.L., Chapman, C.A., Hunt, K.A., 1991. The significance of fibrous foods for Kibale Forest chimpanzees. Phil. Trans. Roy. Soc. 334, 171–178.