Patterns of frugivory of the Budongo Forest chimpanzees, Uganda

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Abstract

Frugivory patterns of the chimpanzees in the Budongo Forest Reserve, Uganda were studied between June 2000 and August 2001. Chimpanzee feeding habitats, movement, group size and food eaten were assessed using focal and scan sampling. It was found that fruits were scarce during the dry season, when chimpanzees appeared and moved in large groups over long distances and raided farms at the forest edge. Chimpanzee movement out of the forest to forage was influenced by seasonal fluctuations in availability of preferred foods as some cultivated crops are perennial. Presence of chimpanzees in a specific feeding habitat was related to the availability of edible fruits both within and between months, suggesting that the presence of food may influence chimpanzee movement patterns. Therefore, a good understanding of patterns of frugivory is essential for making informed decisions about conservation of chimpanzees and other frugivores like birds and monkeys in Budongo as different forest habitats are under varying human pressure because of logging and other forms of utilization.

Key words: chimpanzee group size, feeding habitats, movements, seasons

Résumé

La frugivorie des chimpanzés dans la Réserve forestière du Budongo en Ouganda fut étudiée entre juin 2000 et août 2001. Leur habitat d'alimentation, leur mouvement, la taille des groupes, et la sorte d'alimentation consommée furent enquêtés à travers l'échantillonnage directionnel ainsi que l'échantillonnage obtenu par balayage. Des fruits furent difficile à obtenir pendant la période sèche, lorsque les chimpanzés se révélaient et se déplaçaient en grands groupes sur des longues distances afin de faire des incursions sur les fermes au bord de la forêt. La migration des chimpanzés en dehors de la forêt afin de fourrager fut influencée par des fluctuations saisonnières dans la disponibilité de leurs aliments préférés car certaines cultures cultivées sont pérennes. La présence de chimpanzés dans un habitat d'alimentation spécifique fut liée à la disponibilité de fruits comestibles à la fois pendant et entre les mois, ce qui suggère que la présence de nourriture peut agir sur les habitudes de mouvement des chimpanzés. Ainsi, une bonne compréhension des habitudes frugivores s'avère essentielle pour les décisions bien informées sur la conservation des chimpanzés et d'autres frugivores comme des oiseaux et singes au Budongo, puisque différents habitats subissent un degré variable de pression de la part des humains à cause de l'abattage et d'autres formes d'utilisation.

Introduction

The current distribution of the chimpanzee extends into approximately 21 countries throughout equatorial Africa (Kingdon, 1971, 1997). Habitat loss, logging and hunting for bush-meat threaten chimpanzees, and the species is considered endangered by IUCN (Whitmore, 1990); even so, there is no unified conservation strategy to save chimpanzee populations. Chimpanzees are primarily frugivores (Tutin *et al.*, 1997; Lambert, 1998; Yamakoshi, 1998) inhabiting tropical forests, which are threatened by unsustainable exploitation of timber and agriculture encroachment. We examined patterns of frugivory in the Budongo chimpanzees in order to address the conservation of this species in particular and other species in general. Given that the Budongo Forest Reserve continues to be logged, and there is continuous human pressure to harvest nontimber products, it is important to understand how adaptive chimpanzees

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have been in their search for fruits. As such, there is a need to understand patterns in their frugivory to properly manage and sustain the tropical forests in which they inhabit. Studies like this are important because they consider factors pertinent to conservation and utilization, two important features in maintaining tropical forest biodiversity.

The Budongo Forest Reserve has undergone a process of timber harvesting in most of the compartments from 1900 (Eggeling, 1947) until the present (Plumptre, 1996; Tweheyo, Lye & Weladji, 2004). Previously some trees, considered to be of low timber value were poisoned in order to favour regeneration of high value timber species. However, the trees of low timber value, especially figs are important sources of chimpanzee foods (Tweheyo & Lye, 2003). This study is based on the assumption that a combination of human change of the landscape and natural seasonal changes between dry and wet have affected chimpanzee food availability and movement patterns in the Budongo forest. In Uganda's tropical forests, there are marked dry and wet seasons (Eggeling, 1947; Howard, 1991), causing the supply of food to vary.

Food supply has been suggested to regulate chimpanzee movements in tropical forests (Hladik, 1977; Conklin & Wrangham, 1994; Reynolds *et al.*, 1998). In this study we looked at strategies that chimpanzees adopt to cope with seasonal variation in food in the ecologically and economically important Budongo Forest Reserve. Given that chimpanzees raid cultivated crops of the surrounding areas (Tweheyo, Hill & Obua, in press), it is important to know how variation in food availability, particularly fruits, influences their movement patterns. We report the seasonal fruit production in the forest and relate it to chimpanzee movement patterns. We tested whether the seasonal variation of food influenced chimpanzee movements in and out of the forest. This knowledge of patterns of frugivory is necessary to understand food variations in the forest and the relationship between forest wildlife and surrounding communities.

Methods

Study area

This study was conducted from June 2000 to August 2001 in the Budongo Forest Reserve, Uganda. The forest is situated between 1° 35′ and 1°55′N and 31°8′ and 31°42′E, and has an average altitude of 1100 m. Budongo forest covers an area of 825 km^2 making it Uganda's largest forest reserve (Hamilton, 1984). Of this, 437 km^2 (53%) is a continuous moist semi-deciduous tropical forest and the remaining comprises grassland communities thought capable of supporting forest (Howard, Davenport & Kigenyi, 1997). The mean annual rainfall is 1780–1900 mm, with a dry season from December to March. On average, the annual minimum and maximum temperatures are 17–21°C and 27–29°C, respectively.

Eggeling (1947) described Budongo as a lowland moist semi-deciduous forest, with a tendency for *Cynometra alexandri* Wright to become monodominant. However, selective logging since the 1930s has altered the forest composition creating a mosaic of forest types, of which mixed forest is now the most common (Plumptre, 1996). Budongo forest is of high global biodiversity importance, ranking third in overall importance of Ugandan forests (Howard *et al.*, 1997). There are about 465 species of tree and shrub with *Celtis africana* Burn., *C. gomphophylla* Bak., *C. mildbraedii* Engl., *C. zenkeri* Engl., *Khaya anthotheca* DC. and *C. alexandri* being the most common species. There are five species of diurnal primates, namely chimpanzees (*Pan troglodytes schweinfurthii* Giglioli 1872), with a total population of about 700, black and white colobus monkeys (*Colobus guereza occidentalis* Ruppell 1835), baboons (*Papio anubis* Lesson 1827), blue monkeys (*Cercopithecus mitis stuhlmanii* Wolf 1822) and redtail monkeys (*Cercopithecus ascanius schmidtii* Matschie 1892).

Data were collected on the chimpanzees of the Sonso community. Sonso community chimpanzees occupy part of Budongo Forest Reserve located 'between' 1°44′N, 31°33′E. The Sonso community chimpanzees were chosen because they are habituated and could be observed at close range. Habituation of these chimpanzees was achieved without provisioning. At the time of the study the community had 54 individuals including adult males, females and infants. The system of trails allowing easy movement through the forest in this study site was set up and maintained by the Budongo Forest Project (Reynolds, 1992) based on earlier trails established by the Uganda Forest Department.

Using daily temperature and rainfall data recorded by the Budongo Forest Project field station from 1993 to 2001, we identified seasons in the Budongo Forest Reserve. Rainfall in Budongo exhibits a distinct bimodal pattern (Fig. 1) but the forest is generally wet. The average monthly rainfall is (±SD) 139 ± 67 mm and the average

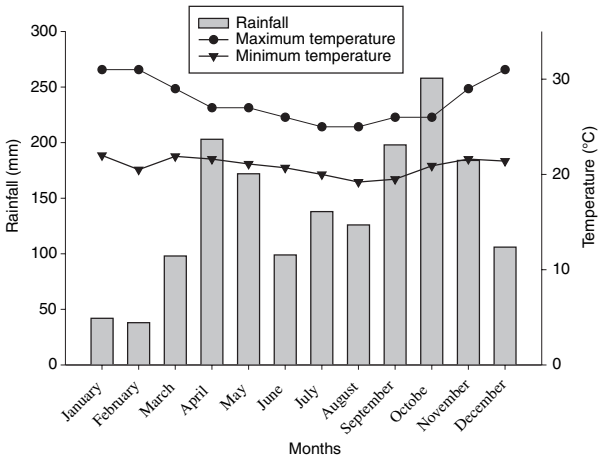

Fig 1 Mean values for monthly variation in rainfall and minimum and maximum temperatures in Budongo Forest Reserve. Based on monthly recordings between 1993 and 2000 by the Budongo Forest Project

minimum temperature is (±SD) 20.9 ± 1°C. There is a dry season between December and March (Fig. 1).

Food types, feeding habitats and movement patterns

Scan sampling and focal sampling methods were used to record chimpanzee food types, feeding habitats and movement patterns (Altmann, 1974).

Scan sampling

Scan sampling was used to determine the activities of chimpanzee at food sources. Binoculars were occasionally used to improve visibility and clarity. Chimpanzee groups were followed from dawn to dusk and all the foods consumed were recorded 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 made after every 30 min and the activities of individual chimpanzees on the food trees observed for 5 min. When there were several chimpanzees in a fruit tree, activities of only one individual were recorded from the group at each scan point. Then another chimpanzee was chosen 30 min later and the process repeated until the animal(s) left the tree or darkness fell. Choice of the individual animal was dependant on the most visible chimpanzees in a group. Our scan records were on adults and juveniles. Data were collected once we had identified all individuals within a group. Scan sampling enabled collection of feeding data that was evenly representative across all individuals.

All forms of food eaten by chimpanzees were recorded as: flowers (FL), insects (IS), buds (B), fruits (F), leaves (L), pith (PI), bark (BK), seeds (SE), prey (PE), nuts (NT), soil (SO) and wood (W). The developmental 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 they became visible to sub-mature fruits and ripe fruit was identified by change in colour from green to either yellow, orange or red.

Focal sampling

An individual male and female adult chimpanzee were observed for a whole day and their activities continuously recorded. Sampling was carried out for 2 days in a week, and in total our observation took 116 days. The choice of focal animal was determined prior to the day's observation. Reliable identification was possible because all chimpanzees in the Sonso community are individually known. Only focal sampling was used to gather ranging data, i.e. the distance covered and the trees visited by one animal during a whole day. Adult chimpanzees were followed an average of three times each during the focal sampling process.

Ranging by chimpanzees

Distances travelled by chimpanzees were recorded using a Garmin II plus GPS. GPS units were used to locate the position of the chimpanzee in the forest using 1951 Ordinance Survey maps of Uganda. The following information was recorded: (i) GPS location at start point in the morning, i.e. chimpanzee's nest of previous night, (ii) GPS location at the end point in the evening, i.e. chimpanzee's nest of that day's evening, (iii) in-between GPS locations in the day where chimpanzee travelled. In between distances were recorded after every 200 m to compute the total distance travelled in a day. From these, we calculated distance covered by a chimpanzee in a day. Where the forest canopy was closed and would not allow easy use of the GPS, distance was measured using a hipchain and rolls of biodegradable thread or a tape measure.

Species of food plants and fruit quantity

The plant species eaten by chimpanzees during this study has been documented by Tweheyo *et al.* (2004). The plant species were categorized on the basis of growth form as: herb (Hb), climber (Cl), epiphyte (Ep), tree (T), shrub (S), and grass (G). Fruit quantity on a given tree was classified according to Plumptre, Reynolds & Bakuneeta (1994) as follows: (i) ≤10% cover, i.e. a tree with fruits that cover <10% of the branches or any other fruit production zone; (ii) ≥10 and <25% cover; (iii) ≥25 and <50% cover; (iv) ≥50 and <75% cover and; (v) ≥75% cover.

Feeding habitat types

We divided our study area into seven feeding 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 mechanical logging or selective logging. Forest edge comprised of a zone 150 m into the forest from the forest edge strip and 50 m outside the forest from the forest edge strip, making it a total of 200 m (see Struhsaker, 1997). We did not consider 150 m outside the forest edge strip because this would have included some open land and farms. The nature reserve is part of the forest that has never been logged. Forest gaps are openings inside the forest ranging between 86 and 1845 m^2 (Babweteera, Plumptre & Obua, 2000). Inter-canopy is a semi-open habitat between closed canopies mostly covered by shrubs. Cleared patches are areas inside or outside the forest where there was evidence of human activities. Riverine/riparian forest is swampy or marshy area in the forest. Habitat types were identified and recorded during focal sampling according to Eggeling (1947). Habitat types were important in this study because they show where chimpanzees spent most of their feeding time and the corresponding time of the year. We estimated our study to comprise of about 52% logged area, 9% forest edge, 10% inter-canopy, 12% riverine, 14% nature reserve, 2% forest gaps, and 1% cleared patches. These are estimates based on area covered by chimpanzees while feeding and travelling.

Chimpanzee group size and seasonality in the Budongo

Group size was recorded only during scan sampling. It was the total number of individual chimpanzees within sight at one place at a particular time of observation. Group size was recorded only when a change occurred (i.e. if a group fed in a tree for 3 h, its size would be recorded once). The extent of seasonality and the timing of seasons were determined using rainfall and temperature data and seasons were recorded as dry (D) or wet (W).

Statistical analyses

Prior to analysis, data were cross-tabulated into contingency tables using SPSS 8.0 for windows (SPSS Inc., 1997). The tabulated data were reorganized for further statistical analyses. Custom and basic tables in SPSS version 8 were used to determine the variation in the distance travelled by chimpanzees with time of the year as factor (12 levels or 12 months: January to December). General linear models (GLM, procedures in SPSS version 8) were used to analyse the variation in the chimpanzees' group size with time of the year as factor (12 levels or 12 months: January to December). To control for the effects of group size, distance, and feeding habitats on the relationship between fruits and other food types GLM ANCOVA was used.

In order to assess whether the presence of the chimpanzees varied with month (i.e. time of the year); and with the abundance of fruits on trees (five quantity levels: ≤10, ≥10, ≥25, ≥50 and ≥75% cover); and habitat seven levels (i.e. seven habitats), a generalized linear model (McCullagh & Nelder, 1989) using the GENMOD procedure in SAS version 8 (SAS Institute Inc., 1999a) was applied. As 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 scale parameter being adjusted in case of overdispersion (McCullagh & Nelder, 1989; SAS Institute Inc., 1999b). The significance of the explanatory variables was assessed by their likelihood ratio statistics (chi-square distributed) and 5% level of significance was used throughout the analysis.

Results

Monthly variation in chimpanzees feeding habitats, movements, fruit quantity, food types and feeding group sizes

Chimpanzee presence differed significantly between feeding habitats ($\chi^2 = 985$, d.f. $= 6$, $P < 0.001$); logged area and forest edge being the habitat where they spent most of their feeding time (Fig. 2; $P < 0.05$); nature reserve and inter-canopy were least preferred feeding habitats. In the two

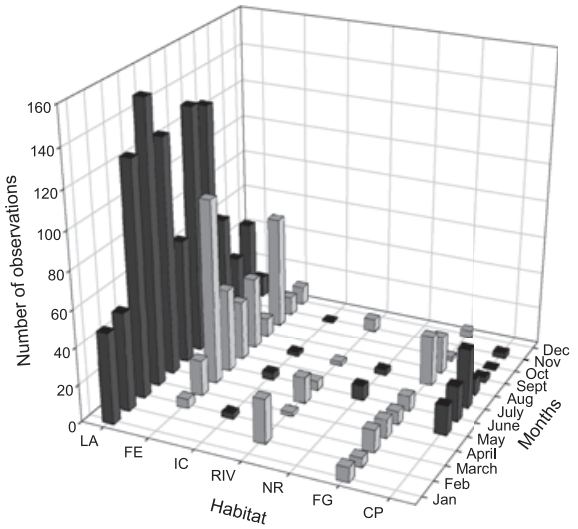

Fig 2 Frequency of chimpanzee feeding observations on food trees in different habitats of Budongo Forest Reserve with their corresponding months. The legend of black and white is only to improve clarity to the reader by avoiding any bar superimposing others but similar units were used for tabulating frequencies in all habitats. LA, logged area; FE, forest edge; IC, inter-canopy; RIV, riverine; NR, nature reserve; FG, forest gap; CP, cleared patches

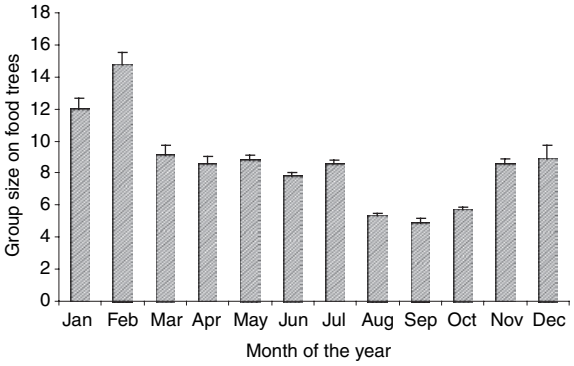

Fig 3 Monthly variation in average group size of chimpanzees counted on their food trees in Budongo between June 2000 and August 2001. Error bars represent confidence interval at $P < 0.05$

most preferred feeding habitats chimpanzee presence was significantly greater in logged areas than in forest edges ($P < 0.001$).

Chimpanzee group size on fruit trees varied significantly with the month of the year ($F_{11,2629} = 48.1$, $P < 0.001$). Between June 2000 and August 2001, chimpanzees formed large groups on food trees during the dry season (late November to early March) with the largest group size in February (Fig. 3), which is the dry season; and group size variation with seasons was significantly different ($\chi^2 = 304$, d.f. $= 32$, $P < 0.001$). Chimpanzee movement, measured by the distance travelled in the forest varied significantly with months ($F_{11,2629} = 138$, $P < 0.001$). We had 1308 h of chimpanzee movement recordings and chimpanzees moved longest distances in February and March (Table 1) and these are the months with low average monthly rainfall (Fig. 1) and are considered as a dry season. Slightly longer distances were also recorded in January, June, November and December (Table 1). Figure 2 shows that chimpanzees appear more common in forest edge habitat in May, June and October.

Fruit quantity on chimpanzee food trees varied significantly with seasons; $\chi^2 = 37$, d.f. $= 1$, $P < 0.001$ and also between months; $\chi^2 = 404$, d.f. $= 11$,$P < 0.001$. The dry season (November, December, January and February) had the lowest amount of chimpanzee fruits in the forest (Fig. 4). Chimpanzee feeding frequency varied significantly both with months ($\chi^2 = 49.6$, d.f. $= 11$, $P < 0.001$) and with fruit quantity ($\chi^2 = 71.3$, d.f. $= 4$, $P < 0.001$), indicating that chimpanzees in the Budongo forest are attracted to tree species with high numbers of fruits (>50%) in most months of the year. There were fewer trees with high number of fruits in the dry season.

Chimpanzees depended mostly on fruits in both the wet and dry seasons, (Fig. 5). When we controlled for

Table 1 Distance (m) travelled by chimpanzees (nest–nest day ranges) in Budongo by months of the year. Data were recorded from June 2000 to August 2001. Total number of focal observation days = 116

Months	Number of observation days	Distance travelled (m)			
		Minimum	Maximum	Mean	SE
January	8	700	2800	1300	283
February	8	500	4000	1763	434
March	8	400	4400	1225	477
April	8	400	1800	809	160
May	8	250	1800	544	186
June	16	400	3000	790	88
July	16	200	700	355	32
August	16	300	1600	530	81
September	8	400	1600	763	138
October	8	300	1600	650	140
November	8	500	3200	1166	359
December	4	600	2000	1250	352

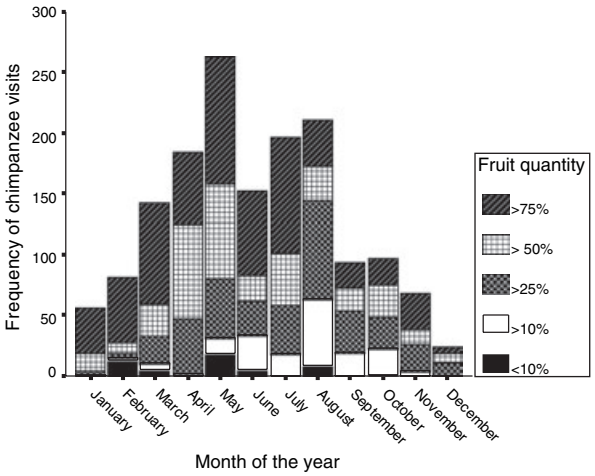

Fig 4 Monthly variation in fruit quantity frequencies on trees fed on by chimpanzees in Budongo between June 2000 and August 2001

group size, distance, and feeding habitats; within chimpanzee foods alone, fruits significantly differed from other food types at $P < 0.001$; (GLM ANCOVA). Other food types in Budongo were fed on at specific time periods depending on availability, e.g. flowers that were eaten by chimpanzees were available only in September, October, November and December (Fig. 5). In periods of high fruit quantity (April to August), chimpanzees basically fed on fruits supplemented by young leaves. During the dry season chimpanzees feed on a wider variety of food items including fruits, wood, pith, seeds, bark, buds and flowers (Fig. 5).

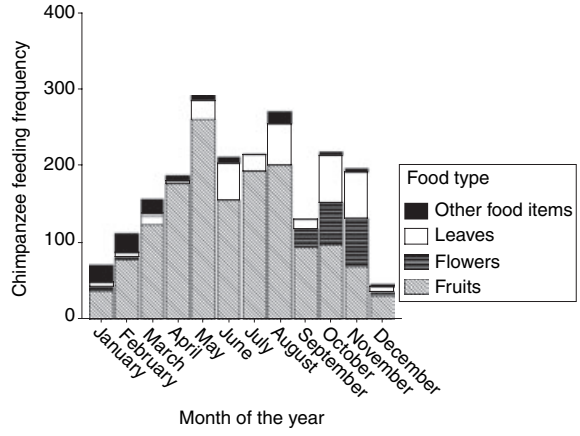

Fig 5 Frequencies of food types eaten by chimpanzees by month in Budongo between June 2000 and August 2001. Other food items include seeds, wood, soil, pith, prey nuts, buds, insects and bark

Discussion

Chimpanzees' feeding patterns

Chimpanzees' feeding mainly on fruits is not surprising as this is consistent with other findings (e.g. Newton-Fisher, 1999; Tweheyo & Obua, 2001). The significance of our findings is that chimpanzees followed specific patterns of frugivory including moving out of the forest in search for fruit. Chimpanzees moved long distances, fed on a variety of forest fruits and cultivated crops (Hill, 1997; Tweheyo *et al.*, in press), which are essential for their survival. The chimpanzees occupy a forest that is under pressure from logging and is surrounded by farmers who depend on subsistence agriculture and are threatening the forest by expanding their farms. Given the competing forest use, food distribution in feeding habitats and variations with seasons causes chimpanzee feeding and movement patterns to constantly change in this forest. The factor of increasing human use in and around the Budongo, affects chimpanzee feeding and movement patterns, an issue that is recorded in this study and needs to be addressed by forest managers and conservationists in order to protect this already endangered species.

Contrary to other findings (Chapman, Wrangham & Chapman, 1995), our observations on fruit quantity and movement patterns in the Budongo forest show that chimpanzees move long distances up to 4 km in periods of fruit scarcity and become a problem to farmers, especially sugarcane growers (Tweheyo *et al.*, in press). In the period of fruit scarcity, Budongo chimpanzees raid crops, which make them similar to the chimpanzees of Kibale (Naughton-Treves *et al.*, 1998). Food on farmlands attract chimpanzees to move out of the forest when forest foods are scarce.

Local people in the Budongo area reported that chimpanzees raided crops mostly between November and February and late May to early July (Tweheyo *et al.*, in press). Our results also show that chimpanzees appear more common in forest edge habitat in May, June and October, which are the main months for crop raiding (Hill, 1997; Tweheyo *et al.*, in press). The forest edge habitat forms the interface between the forest and farmers fields. Sugarcane stem (*Saccharum officinale* L.), mango fruits (*Mangifera indica* L.) and pawpaw fruits (*Carica papaya* L.) were raided

by chimpanzees (Tweheyo *et al.*, in press). Apart from *S. officinale* which is available year round, *M. indica* and *C. papaya* are available in March, late May, June and July and in small amounts from late October to December (Tweheyo *et al.*, in press).

Seasonal variation in fruit quantity, movement, feeding group sizes and chimpanzees' diet

The Sonso community chimpanzees move fairly long distances up to more than 4 km day^{-1}, aggregate more on food trees and had a broad diet during the dry season mostly because there are few trees producing large quantities of fruits, and any fruit tree which has a lot of fruits attracts many animals. Usually the first chimpanzee to reach a fruit tree makes loud calls and the rest respond in large numbers. In this case the Budongo chimpanzees differ from the Kibale Chimpanzees (Chapman *et al.*, 1995), which occur in small groups during periods of fruit scarcity. Compared with the wet season when there are many trees with a lot of fruits in the Budongo, presence of a tree with high fruit quantities during the dry season attracts more chimpanzees to come together. Considering feeding group size variation with seasons, the Sonso community chimpanzees were similar to those of Gombe in Tanzania (Wallis, 1995) and Kalinzu in Uganda (Hashimoto, Furuichi & Tashiro, 2001).

Studies have shown that during periods of food scarcity, wild animals extend ranging patterns (Leighton & Leighton, 1983) or maintain usual range areas and shift diet to other foods (Terborgh, 1983) and this is true for chimpanzees of the Budongo Forest Reserve. Accordingly, chimpanzee movement in and out of the forest may be considered typical. Indeed, the Sonso chimpanzees eat fewer fruits in the dry season than wet, and their dietary diversity increase in the dry period as they fed on leaves, flowers, pith and seeds. Seeds of *C. alexandri* provide a significant portion of the diet in January, February and early March as also reported by Reynolds & Reynolds (1965). In the dry season, chimpanzees chew the pith of many grasses and herbs. Consumption of these alternative foods and movement out of the forest (Tweheyo *et al.*, in press), may be an indicator of shortage of preferred fruits during the dry season. Our findings suggest that the combined effects of few trees with high fruit quantities and movement over long distances make chimpanzees congregate more in the dry season. Terborgh (1983) noted that individual animals travel further and spend more energy if they are in large groups than if they are in small groups. When chimpanzees move out of the forest to raid crops, farmers in turn put snares in the forest and as a result, about 20% of the chimpanzees in the Sonso community have injured limbs (Quiatt, Reynolds & Stokes, 2002). Generally, the problem of snaring is threatening chimpanzee conservation in their distribution range in Africa.

The combination of findings on forest fruits and feeding habitats with findings on cultivated crops (Hill, 1997; Tweheyo *et al.*, in press) reveals important food sources and frugivory patterns for the Budongo chimpanzees. Thus this study has identified a future need for a unified conservation approach involving local people and forest managers to conserve the forest. Among the cultivated crops, Tweheyo *et al.*, (in press) found that sugarcane was particularly important food for chimpanzees mostly during the dry season when forest fruits were few. This causes conflict with the farmers. In the short term, the conflict between farmers and chimpanzees may be bearable, but if economic development continues at the current rate, the conflict level may rise because the acreage of sugarcane plantations will probably increase and be located closer to the forest edge than before. In many tropical forests, economic resource utilization has encroached into forest reserves (Whitmore & Sayer, 1992) and the future of the chimpanzees in tropical forest will depend on sustainable management of their habitats.

It is important to understand chimpanzee patterns of frugivory because chimpanzees may reflect the health of a forest. For example, Wrangham, Chapman & Chapman (1994) reported that chimpanzee act as seed dispersers and are essential in forest regeneration, a factor that is important in ecosystem sustainability. Our study has added more information about the Budongo landscape, which in the past has been managed mainly for timber utilization. Therefore, a good understanding of patterns of frugivory is essential for making informed decisions about conservation of chimpanzees and other frugivores like birds and monkeys in natural forests under intense human pressure such as the Budongo Forest Reserve.

Acknowledgements

NORAD and NUFU project 63/2003 funded this research through the Faculty of Forestry and Nature Conservation, Makerere University and Department of Biology and Nature Conservation, Agricultural University of Norway.

We are also grateful to Dr J. R. S. Kaboggoza and Mr F. Babweteera. We thank Professor J. Swenson, Professor M. Ohlson, Dr S. R. Moe, Dr R. Weladji, Dr J. Obua, Dr P. Nyeko and Professor V. Reynolds for critically reading and commenting on the manuscript. We also thank M. G. Mbotella for his assistance in the field.

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(Manuscript accepted 9 March 2005)