KURENAI
Kyoto University Research Information Repository

KYOTO UNIVERSITY

Title	PHENOLOGY OF FRUITS CONSUMED BY A SYMPATRIC POPULATION OF GORILLAS AND CHIMPANZEES IN KAHUZIBIEGA NATIONAL PARK, DEMOCRATIC REPUBLIC OF CONGO
Author(s)	YAMAGIWA, Juichi; BASABOSE, Augustin Kanyunyi; KALEME, Kiswele Prince; YUMOTO, Takakazu
Citation	African Study Monographs. Supplementary Issue (2008), 39: 3-22
Issue Date	2008-04
URL	http://dx.doi.org/10.14989/66241
Right	
Type	Departmental Bulletin Paper
Textversion	publisher

Kyoto University

PHENOLOGY OF FRUITS CONSUMED BY A SYMPATRIC POPULATION OF GORILLAS AND CHIMPANZEES IN KAHUZI-BIEGA NATIONAL PARK, DEMOCRATIC REPUBLIC OF CONGO

Juichi YAMAGIWA
Laboratory of Human Evolution Studies, Graduate School of Science,
Kyoto University
Augustin Kanyunyi BASABOSE, Kiswele Prince KALEME
Centre de Recherche en Sciences Naturelles
Takakazu YUMOTO
Research Institute of Humanity and Nature

ABSTRACT Monthly fluctuations in the abundance of fruits eaten by a sympatric population of gorillas (*Gorilla beringei gaueri*) and chimpanzees (*Pan troglodytes schweinfurthii*) were estimated by a transect system and a fruit trail system in the montane forest of Kahuzi-Biega National Park, Democratic Republic of Congo. Fruit species eaten by gorillas and chimpanzees and their preferences were defined mainly by fecal analysis. Data were collected for 80 months from 1994 to 2002, with a period of forced inactivity due to the civil war in 1997. A belt transect 5,000 m long and 20 m wide was set up in the study area to pass through most of the vegetation types in which gorillas and chimpanzees range, and 2,033 trees, including shrubs and strangling figs, above 10 cm in diameter at breast height (DBH) of 49 species from 29 families were identified. Of these, fruits of 21 (6) species and 25 (12) species were eaten (preferred) by gorillas and chimpanzees, respectively. The fruit species preferred by gorillas were also preferred by chimpanzees. Monthly fruit index calculated from total basal area per ha and the proportion of the number of trees in fruit for each species shows a larger fluctuation in the abundance of fruits eaten by chimpanzees than that by gorillas. Unlike the phenology of fruits in the lowland tropical forests, monthly fluctuation in ripe fruit abundance negatively correlated with rainfall in some years. This tendency was more distinct for fruits preferred by gorillas in the primary forest. Fruit species preferred only by chimpanzees showed a distinct intra-specific synchrony in fruiting, while fruit species preferred by gorillas and chimpanzees did not. These differences in fruiting patterns may influence the foraging patterns of gorillas and chimpanzees. Gorillas tended to travel widely in a cohesive group and to increase their consumption of fruits in the primary forest during the dry season. By contrast, chimpanzees tended to continuously visit particular fruiting trees individually in a small home range throughout the entire year. Some tree species that have large basal areas and that bear fruits for a long period may be able to support the survival and sympatry of gorillas and chimpanzees.

RÉSUMÉ Les fluctuations mensuelles de l'abondance des fruits mangés par les populations sympatriques des gorilles et des chimpanzés étaient estimées par le système de transect et de piste le long duquel la phenologie des fruits est observée dans la forêt de montagne du Parc National de Kakuzi-Biega, République Démocratique du Congo. Les espèces de fruits consommés par les gorilles et les chimpanzés et leurs préférences étaient définies principalement par l'analyse des matières fécales. Les données étaient récoltées pendant 80 mois, de 1984 à 2002, avec une période d'inactivité due à la guerre civile de 1997. Un transect de 5.000 m de long et 20 m de largeur était installé dans le milieu d'étude passant dans les différents types de végétations que visitent les gorilles et les chimpanzés, et 2.030 arbres, comprenant les arbustes

et les figuiers, dont le diamètre au niveau de la poitrine (DBH) est supérieur à 10 cm de 49 espèces regroupées en 29 familles étaient identifiées. De ceci, les fruits de 21 (6) espèces et 25 (12) espèces étaient consommés (préférés) par les gorilles et les chimpanzés respectivement. Les espèces de fruits préférées par les gorilles l'étaient aussi par les chimpanzés. L'index de fructification mensuelle calculé à partir de la surface à la base totale par hectare et la proportion du nombre d'arbres portant des fruits pour chaque espèce, a montré une plus grande fluctuation de l'abondance de fruits consommés par les chimpanzés que celle des gorilles. Contrairement à la phénologie des fruits dans les forêts tropicales humides en basse altitude, la fluctuation mensuelle de l'abondance des fruits mûrs était négativement corrélée avec la précipitation pendant quelques années. Cette tendance était plus claire pour les fruits préférés par les gorilles dans la forêt primaire. Les espèces de fruits préférées uniquement par les chimpanzés ont clairement montré une synchronie intra-specifique en fructification, pendant que les fruits préférés aussi bien par les gorilles que par les chimpanzés n'ont pas montré cette tendance. Ces différences dans les modes de fructification peuvent influencer les modes de broutage des gorilles et des chimpanzés. Les gorilles avaient tendance à se promener en un groupe cohésif sur des grandes distances et d'augmenter leur consommation des fruits en forêt primaire pendant la saison sèche. Par contre, les chimpanzés avaient tendance à visiter continuellement des arbres particuliers portant des fruits, individuellement dans un espace réduit pendant toute l'année. Quelques espèces d'arbres avec des grandes surfaces basales et qui portent des fruits pendant une longue période seraient capables de supporter la survie et la sympatrie des gorilles et des chimpanzés.

Key Words: Fruit phenology; Synchrony in fruiting; Montane forest; Gorilla; Chimpanzee; Foraging strategy.

INTRODUCTION

Clumped fruiting is the general tendency for the majority of tree species in tropical forests (Daubenmire, 1972; Frankie *et al.*, 1974; Foster, 1982). Seasonality in rainfall is the major characteristic of the tropical climates and may influence seasonal fluctuations in fruit production (Lieberman, 1982), although various factors, such as temperature, irradiance, activities of pollinators or seed dispersers, and conditions of germination also influence fruiting patterns (Janzen, 1967; Rathke & Lacey, 1985; van Schaik, 1986). Seasonal changes in fruit availability play an important role in the survival of frugivorous primates in the dense tropical forests (Gautier-Hion, 1990; Leighton & Leighton, 1983; Terborgh, 1983).

In the earlier studies on the sympatric populations of gorillas and chimpanzees, dietary separation had been regarded as the main factor allowing their coexistence in the same habitat. Gorillas usually feed on herbaceous vegetation in wet valleys or in the secondary regenerative vegetation, while chimpanzees are consistent frugivores in the primary forest (Schaller, 1963; Jones & Sabater Pi, 1971). However, recent studies on western and eastern gorillas show their strong frugivory and extensive overlap in dietary composition with that of chimpanzees (Williamson *et al.*, 1990; Tutin & Fernandez, 1993; Kuroda *et al.*, 1996; Yamagiwa *et al.*, 1996a).

In spite of their remarkable similarity in morphological features related to diet, such as gut morphology and gut passage time (Chivers & Hladik, 1984; Milton,

1984), gorillas and chimpanzees show different foraging patterns. Gorillas usually form a cohesive group that contains one male and several females with immatures (Schaller, 1963; Yamagiwa, 1983; Parnell, 2002), while chimpanzees form a fluid group including plural males and females based on individual foraging (Goodall, 1968; Nishida, 1970; Wrangham, 1979). Gorillas increase consumption of vegetative food and decrease day journey length during periods of fruit scarcity (Tutin & Fernandez, 1993, Yamagiwa & Mwanza, 1994; Goldsmith, 1999), while chimpanzees use fig fruits as fallback food and tend to change party size according to fruit abundance (Chapman *et al.*, 1994; Conklin & Wrangham, 1994). These observations suggest that dietary constraints induced by fruit scarcity may differently influence their foraging strategies. However, the seasonal changes in fruit abundance and the phenology of fruits preferred by gorillas or chimpanzees have not yet been comprehensively reported. Knowledge of these differences is vital for understanding the sympatry of gorillas and chimpanzees and for taking appropriate measures for their conservation.

In this paper, we describe annual and monthly changes in abundance of fruits eaten by a sympatric population of gorillas and chimpanzees. Data were collected on fruits of trees above 10 cm in diameter at breast height (DBH) by monitoring them semi-monthly for 8 years in the montane forest of Kahuzi-Biega National Park, Democratic Republic of Congo. A transect was set to estimate tree density and basal area in each type of vegetation used by gorillas or chimpanzees. We used the fruit trail system, which monitors key species (Chapman *et al.*, 1994) to estimate fruit abundance in the secondary and primary forests. A group of gorillas and a unit-group of chimpanzees were habituated and followed daily to observe their feeding and to collect their fresh feces. Preferred fruits by gorillas and chimpanzees were determined by direct observations and fecal analysis. Seasonal changes in abundance of fruits and fruiting patterns of each species are discussed in relation to foraging strategies of gorillas and chimpanzees.

METHODS

I. Study Area

The Kahuzi-Biega National Park is located to the west of Lake Kivu and covers an area of 6,000 km^2 at an altitude of 600 to 3,308 m (Fig. 1). The Park consists of highland (600 km^2) and lowland (5,400 km^2) sectors, which are interconnected by a corridor of forest. The study area covers about 30 km^2 along the eastern border of the park at an altitude of 2,050–2,350 m, where four groups of gorillas (*Gorilla beringei graueri*) and a unit-group of chimpanzees (*Pan troglodytes schweinfurthii*) have ranged sympatrically (Yamagiwa *et al.*, 1996a). Forty-four species of larger mammals, including ten primate species, are found in the highland sector (Mankoto *et al.*, 1994).

The highland sector is made up of bamboo *Arundinaria alpina* forest, primary montane forest, secondary montane forest, *Cyperus latifolius* swamp and other vegetation, as described by Casimir (1975) and Yumoto *et al.* (1994). Meteoro-
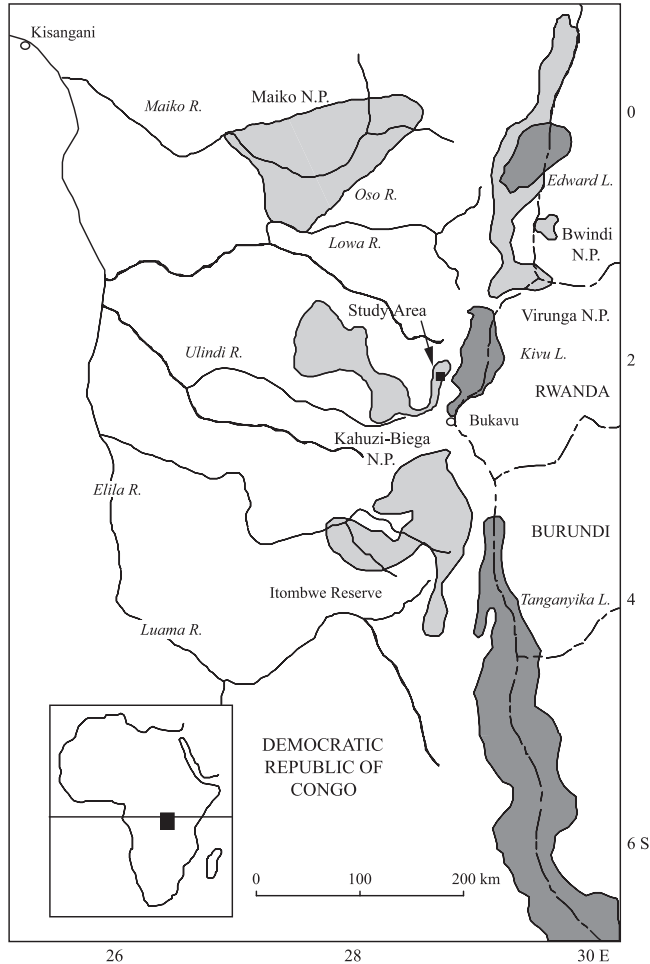
Fig. 1. Map of study area.

logical data are available from the Meteorological Station at the Centre de Recherches en Science Naturelles (CRSN) (1,600 m above sea level), which is located 4 km from the study area. The mean annual rainfall during the study period (1994–2002) was 1,660 mm (range: 1,409–2,180 mm) with a distinct dry season in June, July and August, in which the mean rainfall was below 50 mm (Fig. 2). The mean monthly temperature was 20.1°C (mean maximum: 26.5°C; mean minimum: 13.8°C).

II. Vegetation Survey

In order to estimate the diversity and density of woody species and to assess fruit availability, we made a vegetation survey by using a line transect. In August 1994, we set up a belt transect 5,000 m long and 20 m wide in the study area
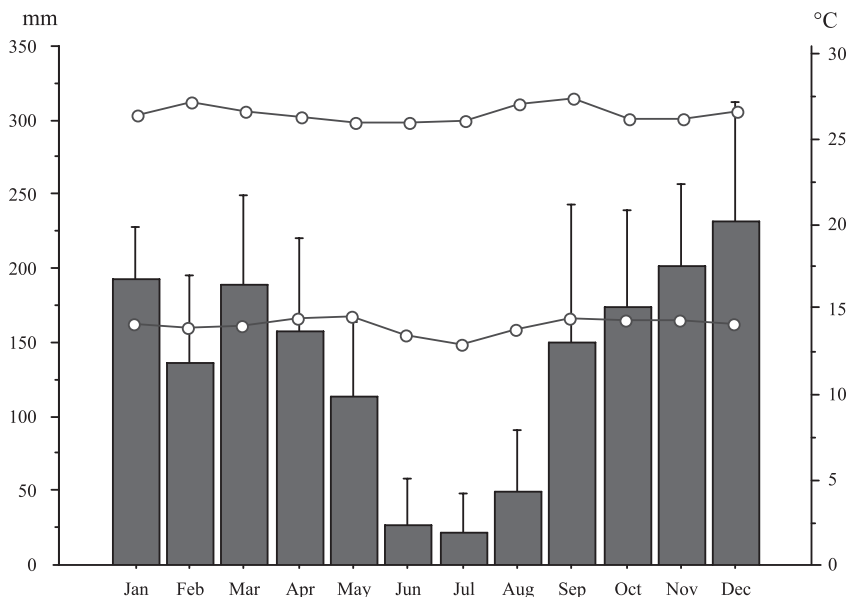
Fig. 2. Monthly changes in rainfall and temperature (maximum and minimum) at Kahuzi from 1994 to 2002.

to pass through most of the vegetation types in which gorillas and chimpanzees range. The length of the transect line corresponded to the area of each vegetation type. The bamboo forest, in which chimpanzees rarely ranged during the study period, was excluded from the analysis of this study. Every tree, shrub or strangling fig above 10 cm in diameter at breast height (DBH) was identified. The phenological data presented here are from two sets: set 1 from August 1994 to July 1996 and set 2 from February 1998 to December 2002. Data for set 1 involved 2,033 trees, including shrubs and strangling figs, above 10 cm in DBH of 49 species from 29 families and one unidentified species recorded along the transect (Appendix 1).

The density and basal area $[(1/2 \text{ DBH})^2 \times \pi]$ of each species were calculated. The top 10 species (basal area) in both secondary and primary forests were emergent trees of which the largest DBH was over 60 cm. One understory species (*Galiniera coffeoides*) was found among the top 20 species. *Macaranga kilimandscharica* was the most frequently represented (33%) species and was also ranked as having the largest basal area in the secondary forest. *Neoboutonia microcalyx* was the most frequently represented (14%) species, and *Parinari curatellifolia* was ranked as having the largest basal area in the primary forest. At least 31 species were classified as zoochory, 10 species as anemochory, and 5 as autochory according to the type of seed dispersal.

The presence of fruit was recorded for all identified trees and shrubs twice each month. Data for set 2 involved 28 species (24 species in which fruit is eaten by apes and 4 species in which fruit is not eaten by apes). For each species, fruits (ripe and unripe) of at least 10 (range: 10–13) reproductively mature trees were monitored twice each month.

The monthly datum on the presence of fruit was the average of the two records. To estimate fruit abundance (biomass and number) of tree species, we used DBH (Chapman *et al*., 1992). We calculated a monthly fruit index (F_m) as

$$F_m = \sum_{k=1}^{s} P_{km} B_k$$

where P_{km} denotes the proportion of the number of trees in fruit for species k in month m, and B_k denotes the total basal area per ha for species k. The fruit index was calculated in each month, and its seasonal fluctuation was compared between primary and secondary forests.

III. Data on Ape Diet

In 1991, we found four groups of gorillas and a single unit-group of chimpanzees in the study area. These groups had extensive overlapping ranging areas (Yamagiwa *et al*., 1996a; Yamagiwa *et al*., 1996b). Since then we have tried to habituate a group of gorillas and the unit-group of chimpanzees. Until 1994, both groups had been semi-habituated and occasionally tolerated the presence of human observers when we stayed at a distance of 20–50 m. The total numbers of individuals were 17–25 in the gorilla group and 22–23 in the unit-group of chimpanzees between 1994 and 2000.

The compositions of diet for gorillas and chimpanzees were estimated from direct observations, evaluation of feeding remains along fresh trails, and fecal analysis. Fresh (up to one day old) feces were collected mainly at nest sites, washed in 1-mm mesh sieves, dried in sunlight, and stored in plastic bags. The contents of each sample were examined macroscopically and listed as seeds, fruit skins, fiber, leaves, fragments of insects, and other matter. Fruit seeds and skin were identified at the species level macroscopically. Plant specimens were identified by T. Yumoto at the National Botanical Garden in Belgium (Yumoto *et al*., 1994) and at the herbarium of CRSN at Lwiro, where vouchers of all the specimens are kept.

Over 71 months from August 1994 to November 2000, 12,269 gorilla fecal samples were collected, averaging 173 fecal samples per month (range: 36–361). Over 78 months from January 1994 to December 2000, 7,212 chimpanzee fecal samples were collected, averaging 93 fecal samples per month (range: 17–427). Seeds or fruit skins of 21 species were found in gorilla's fecal samples, and those of 25 species were found in chimpanzee's fecal samples (Appendix 1.). The fruit preference by apes was determined from fecal analysis. The fruit species (fruit skin or seeds) found in more than 1% of the total fecal samples were defined as the preferred fruit by each ape species. Six species were preferred by gorillas and twelve species were preferred by chimpanzees. The fruit species preferred by gorillas were also preferred by chimpanzees.

RESULTS

I. Diversity of Woody Plant Species and Fruits Eaten by Apes

We found similar numbers of woody plant species above 10 cm DBH in the secondary (41 species) and primary forests (39 species) (Table 1). Only five species were found in the swamp. The mean density was higher in the secondary forest than in the primary forest, while the basal area per hectare was lower in the former. This means that larger trees are distributed more sparsely in the primary forest.

The woody plant species in which fruit was eaten by gorillas or chimpanzees accounted for a considerable proportion in density and basal area of the top five or ten species (Table 2). The top five species made up nearly half and the top ten species comprised about three-fourths of the total woody plants and basal area in both secondary and primary forest. The species in which fruit was eaten by apes were found at higher density in the secondary forest than in the primary forest, while the basal areas of these species were mostly similar between the forests. These results are largely attributed to *Macaranga kilimandscharica*, which was found at the highest density in the secondary forest and at the eighth highest density in the primary forest. *Macaranga Kilimandscharica* is a pioneer species that is frequently found in the secondary forest after deforestation. However, its fruit was not frequently eaten by gorillas or chimpanzees.

The fruit species preferred by gorillas and chimpanzees, which was found in the top five species for density, was *Bridelia bridelifolia* in the secondary forest

Table 1. Comparison of diversity, density and basal area of woody plant species above 10 cm DBH among different types of vegetation.

	Secondary forest	Primary forest	Swamp
Length of transect	3,170 m	1,212 m	618 m
Number of species	41	39	5
Mean density	6.0/ha	4.8/ha	1.6/ha
Basal area per ha	136,250 cm^2/ha	197,775 cm^2/ha	3,148 cm^2/ha

Table 2. Proportion of fruit species eaten by gorillas and chimpanzees in top five and ten species in terms of density and basal area (proportion of the preferred fruit indicated in the parenthesis).

|	Density	Basal area	Fruit eaten (preferred) by							
			Gorilla				Chimpanzee			
			Density		Basal area		Density		Basal area	
	%	%	# species	%	# species	%	# species	%	# species	%
Top 5 species/Total										
Secondary forest	63.3	45.0	2 (1)	41.5 (8.8)	2 (1)	22.8 (6.4)	3 (1)	50.0 (8.8)	2 (1)	22.8 (6.4)
Primary forest	50.7	56.7	2 (1)	17.9 (6.0)	2 (1)	22.3 (7.8)	3 (1)	31.8 (6.0)	2 (2)	22.3 (22.3)
Top 10 species/Total										
Secondary forest	81.2	69.1	5 (1)	50.1 (8.8)	6 (3)	41.0 (15.4)	7 (2)	63.3 (12.0)	6 (5)	41.0 (24.6)
Primary forest	68.2	78.4	5 (2)	28.5 (10.1)	6 (3)	38.0 (15.7)	7 (2)	46.2 (10.1)	7 (4)	44.0 (30.0)

and *Syzygium parvifolium* in the primary forest. For basal area, the top species was *Ficus oreadryadum* in the secondary forest and *Syzygium parvifolium* in the primary forest. *Newtonia buchananii* was also ranked in the top five as the preferred fruit by chimpanzees in the primary forest for basal area.

More preferred fruit species were included in the top ten species for basal area than for density. These results suggest that fruits of the large tree species (the large fruit patch) may be preferred by both apes. Adding to the top five species, *Ficus thonningii* and *Myrianthus holstii* were preferred both by gorillas and chimpanzees, and *Allophyllus* sp., *Ekebergia capensis*, and *Maesa lanceolata* were preferred by chimpanzees. The fruit species preferred by chimpanzees were found to have larger basal area than those by gorillas in both the secondary and primary forests. These suggest that chimpanzees tended to feed on fruits of larger tree species than gorillas.

II. Seasonal Change in Abundance of Fruits Eaten by Gorillas and Chimpanzees

Fruit index was calculated from fruit species preferred by at least gorillas or chimpanzees. Twelve species were preferred by chimpanzees (*Allophyllus* sp., *Bridelia bridelifolia*, *Cassipourea ruwenzoriensis*, *Diospyros honleana*, *Ekebergia capensis*, *Ficus oreadryadum*, *Ficus thonningii*, *Maesa lanceolata*, *Myrianthus holstii*, *Newtonia buchananii*, *Psychotria palustris*, and *Syzygium parvifolium*), and six out of these species (underlined species) were also preferred by gorillas.

Monthly change in fruit index calculated from the proportion of fruiting trees shows that the fruit index for chimpanzees fluctuates more than that for gorillas in both the secondary and primary forests (Fig. 3). Annual differences in the fruit
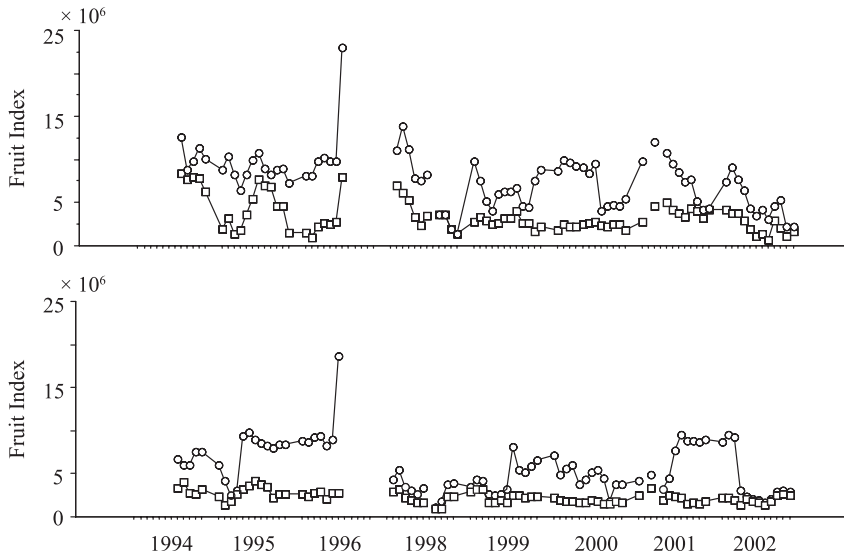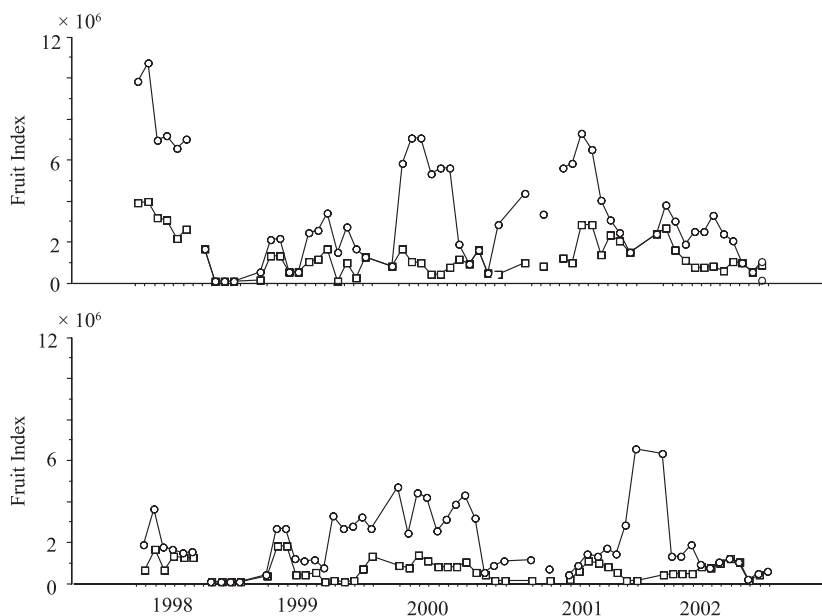

Fig. 3. Monthly change in fruit index for fruit species eaten by gorillas (square) and chimpanzees (circle) in the secondary forest (upper) and primary forest (lower) from 1994 to 2002.

index for chimpanzees are also larger than those for gorillas. Exceptionally, from 1994 to 1996 the fruit index for gorillas fluctuates more than that of chimpanzees in the secondary forest. Monthly changes in fruit index highly correlate positively between gorillas and chimpanzees in the secondary forest (Regression correlation, $R^2=0.357$, $p<0.0001$), while there is no significant correlation in the primary forest ($R^2=0.184$, $p=0.33$).

Monthly changes in fruit index do not correlate significantly with rainfall (gorillas: $R^2=0.001$ in the secondary forest and $R^2=0.001$ in the primary forest; chimpanzees: $R^2=0.009$ in the secondary forest and $R^2=0.001$ in the primary forest). Comparison within each year (1995, 1998, 1999, 2000, 2001, and 2002) shows that monthly changes in fruit index negatively correlate with rainfall for gorillas in the secondary forest in 2000 ($R^2=0.509$, $p<0.01$).

Monthly changes in ripe fruit index (1998–2002) calculated from the proportion of trees bearing ripe fruits also show that the fruit index for chimpanzees fluctuate more largely than that for gorillas (Fig. 4). Monthly changes in ripe fruit index positively correlate between gorillas and chimpanzees in the secondary forest ($R^2=0.121$, $p<0.01$), but not in the primary forest ($R^2=0.039$, $p=0.1427$).

Monthly changes in ripe fruit index negatively correlate with rainfall only for gorillas in the primary forest ($R^2=0.108$, $p<0.05$). Correlation with rainfall for gorillas in the secondary forest ($R^2=0.02$) and those for chimpanzees in both the secondary and primary forests ($R^2=0.042$, 0.005) were not significant. Comparison within each year shows that the ripe fruit index negatively correlates with rainfall in the primary forest for gorillas ($R^2=0.430$, $p<0.05$ in 2000; $R^2=0.660$,


Fig. 4. Monthly change in ripe fruit index for fruit species eaten by gorillas (square) and chimpanzees (circle) in the secondary forest (upper) and in the primary forest (lower) from 1998 to 2002.

p<0.01 in 2002) and for chimpanzees (R^2=0.334, p<0.05 in 2000).

III. Phenology of Fruit Species Eaten by Gorillas and Chimpanzees

Among the twelve species whose fruits were preferred by gorillas or chimpan-zees, four species show significant correlations of monthly changes in the pro-portion of trees bearing ripe fruits with rainfall (Fig. 5). *Ficus thonningii* shows positive correlations (R^2=0.105, p<0.05), and *Bridelia bridelifolia* (R^2=0.089,
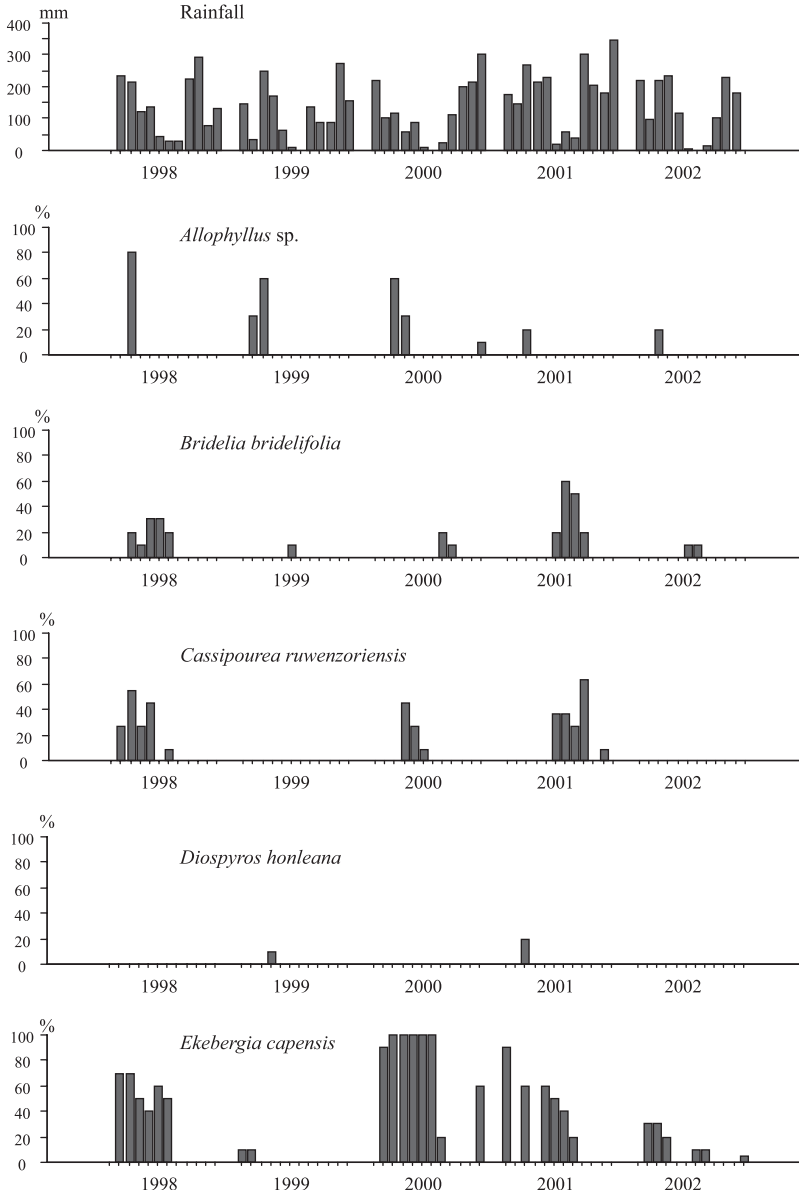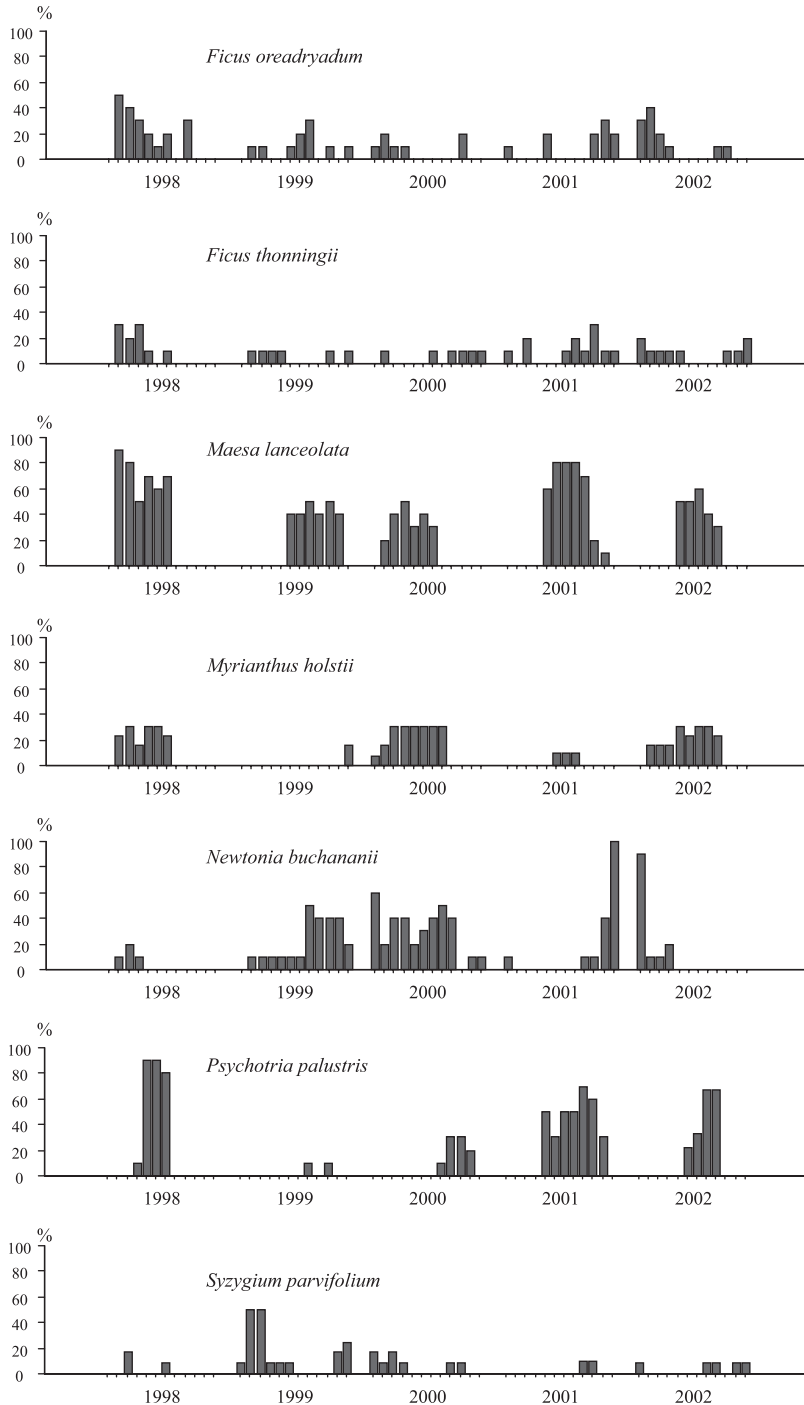
Fig. 5. Monthly changes in rainfall and the proportion of trees bearing ripe fruits for each tree species from 1998 to 2002.

Table 3. Correlation coefficients between each fruit species from the regression coefficient analysis on monthly changes in the proportion of trees bearing ripe fruits

	B. bridelifolia	C. ruwenzoriensis	D. honleana	E. capensis	F. oreadryadum
Allophyllus sp.	0.015	0.057	0.008	0.088*	0.035
Bridelia bridelifolia		0.308***	0.007	0.011	0.01
Cassipourea ruwenzoriensis			0.007	0.119**	0.025
Diospyros honleana				0.005	0.023
Ekebergia capensis					0.014
Ficus oreadryadum					
Ficus thonningii					
Maesa lanceolata					
Myrianthus holstii					
Newtonia buchananii					
Psychotria palustris					
Syzygium parvifolium					

	F. thonningi	M. lanceolata	M. holstii	N. Buchananii	P. palustris	S. parvifolium
Allophyllus sp.	0.011	0.005	0.039	0.003	0.045	0.318***
Bridelia bridelifolia	0.011	0.353***	0.06	0.044	0.330***	0.02
Cassipourea ruwenzoriensis	0.051	0.416***	0.094	0.008	0.098*	0.002
Diospyros honleana	0.039	0.029	0.023	0.012	0.013	0.003
Ekebergia capensis	0.003	0.113*	0.313***	0.00005	0.001	0.022
Ficus oreadryadum	0.168**	0.025	0.003	0.036	0.0001	0.000001
Ficus thonningii		0.002	0.013	0.0002	0.00002	0.005
Maesa lanceolata			0.227***	0.027	0.255***	0.037
Myrianthus holstii				0.001	0.062	0.015
Newtonia buchananii					0.093*	0.002
Psychotria palustris						0.013
Syzygium parvifolium						

* $p<0.05$, ** $p<0.01$, *** $p<0.001$: all significant correlations are positive

$p<0.05$), *Maesa laceolata* ($R^2=0.125$, $p<0.01$), and *Myrianthus holstii* ($R^2=0.220$, $p<0.001$) show negative correlations with rainfall.

Monthly changes in the proportion of trees bearing ripe fruits show similar patterns between several species (Table 3). All significant correlations are positive. *Bridelia bridelifolia*, *Cassipourea ruwenzoriensis*, *Ekebergia capensis*, *Maesa lanceolata*, *Myrianthus holstii*, and *Psychotria palustris* show significant positive correlations ($p<0.001$) with each other. A high proportion of *Ekeberigia capensis*, *Maesa lanceolata*, and *Psychotria palustris* trees tended to bear ripe fruits for prolonged periods continuously. *Ficus oreadryadum*, *Ficus thonningii*, and *Newtonia buchananii* also bore ripe fruits for prolonged periods (in more than 30 out of 56 months), although the proportion of fruiting trees was relatively low. These fruits available for long periods may constitute stable foods for the apes. Ripe fruits of *Allophyllus* sp., *Bridelia bridelifolia*, *Cassipourea ruwenzoriensis*, and *Diospyros honleana* were available within short limited periods.

Five out of six tree species preferred by gorillas tended to bear ripe fruit in a small proportion of the trees in any month. By contrast, five out of six tree species only preferred by chimpanzees tended to bear ripe fruits in a large proportion of trees within a month.

DISCUSSION

The diversity of tree species in the montane forest of Kahuzi-Biega National Park and that of fruit species eaten by gorillas and chimpanzees are low. We found only 49 species of trees above 10 cm in DBH in a transect of 20 m×5,000 m, in which 21 fruit species were eaten by gorillas and 25 fruit species were eaten by chimpanzees. In the lowland tropical forest at Lopé, Gabon, 345 tree species (above 10 cm in DBH) were counted on five transects of 5 m×5,000 m, and of these, 65 fruit species were eaten by gorillas and 87 fruit species were eaten by chimpanzees (Williamson *et al*., 1990; Tutin *et al*., 1994; Tutin & Fernandez, 1993). In the lowland extension of Kahuzi-Biega National Park (at an altitude of 650 m), about 150 tree species (above 10 cm in DBH) were counted on a transect of 10 m×8,000 m, and 46 and 35 fruit species were eaten by gorillas and chimpanzees, respectively (Yumoto *et al*., 1994; Yamagiwa *et al*., 2003). Furthermore, the top 5 species accounted for half of the total basal area in Kahuzi. The montane forest of Kahuzi is characterized by its low diversity of trees and the few dominant tree species representing the major basal area, as observed in other montane forests in Equatorial Africa (Hamilton, 1975; Sun *et al*., 1996). These results suggest that seasonal fluctuation in fruit abundance of these dominant tree species may have a great influence on the survival of gorillas and chimpanzees.

Among the top ten species in basal area, fruit species preferred by gorillas (*Bridelia bridelifolia*, *Ficus oreadryadum*, *Ficus thonningii*, and *Syzygium parvifolium*) did not show a marked intra-specific synchrony in fruiting. Five out of six tree species preferred by gorillas tended to bear ripe fruit in a small proportion of trees in any month. These fruit species were also preferred by chimpanzees. However, in the fruit species preferred only by chimpanzees, many species showed synchrony in fruiting. Among the top ten species in basal area, *Allophyllus* sp., *Ekebergia capensis*, and *Maesa lanceolata* showed marked synchrony. Five out of six species only preferred by chimpanzees showed clumped fruiting patterns. These differences in fruiting patterns may influence the foraging patterns of apes. Gorillas tend to travel widely and to visit fruiting trees opportunistically, while chimpanzees continuously visit particular fruiting trees for a prolonged period within a small area at Kahuzi (Yamagiwa *et al*., 1996b; Basabose & Yamagiwa, 2002).

Monthly fluctuation in abundance of fruits eaten by gorillas or chimpanzees did not correlate with rainfall. Although annual variations are large, monthly fluctuation in abundance of ripe fruits negatively correlated with rainfall in some years. These observations are inconsistent with other studies in the lowland tropical forests, where fruiting often peaks in the rainy season or during the wettest period (Hilty, 1980; Sabatier, 1985). In the lowland tropical forests that both gorillas and chimpanzees inhabit sympatrically, the dry season is regarded as a period of fruit scarcity (Tutin & Fernandez, 1993; Kuroda *et al*., 1996). The germination hypothesis predicts that more plants should time their fruiting to coincide with the start of the rainy season in seasonally dry forests (Garwood, 1983; van Schaik *et al*., 1993). In the Kibale Forest, Uganda (at an elevation of 1,500 m),

fruiting tended to peak at the end of the wet season and at the start of the dry season, probably because biannual rainfall may reduce water stress (Chapman *et al.*, 1999). However, this is not the case for Kahuzi, where only one dry season was common. In the montane forest of Nyungwe, Rwanda (almost the same altitude as Kahuzi), the peak of fruiting was extended from the major rainy season throughout the entire dry season (Sun *et al.*, 1996). White (1994) suggested that species fruiting during the dry season tended to produce fruit over a long period, perhaps because environmental conditions limited the amount of fruit that could ripen at any given time. At Kahuzi, most tree species having a peak in fruiting during the dry season tended to extend the peak into the first one or two months of the subsequent rainy season. This tendency may reflect the strategies of these tree species to avoid intra-specific competition for animal dispersers. Apparently gorillas and chimpanzees play an important role in seed dispersal of these fruit species at Kahuzi.

Negative correlations of monthly fruit index with rainfall were more distinct for fruits preferred by gorillas in the primary forest. The seasonality of fruiting may influence a gorilla's foraging patterns. At Kahuzi, gorillas tended to range in the primary forest and prominently increased consumption of fruits during the dry season (Yamagiwa *et al.*, 1996a; Yamagiwa *et al.*,1996b). By contrast, chimpanzees did not change ranging areas throughout the entire year, although they also increased consumption of fruits during the dry season. Monthly fluctuation in abundance of preferred fruit was larger for chimpanzees than for gorillas. Chimpanzees rely on more unstable fruit food resources than gorillas. Fission and fusion grouping patterns and individual foraging of chimpanzees may mitigate within-group feeding competition, which is variable with these unstable foods.

White (1994) pointed out that tree species fruiting over a long period, such as *Duboscia macrocarpa*, may constitute a keystone food for apes in the lowland tropical forest at Lopé. Fig fruits in Kibale Forest and fruits of *Musanga Leo-errerae* in Kalinzu Forest, Uganda, provide fallback food for chimpanzees due to their long availability, especially during periods of fruit scarcity (Wrangham *et al.*, 1996; Furuichi *et al.*, 2001). At Kahuzi, fruit species preferred by gorillas or chimpanzees tended to fruit for long periods. Among these, *Ficus* spp. *Myrianthus holstii*, and *Syzygium parvifolium* are ranked in the top ten species in basal area and were preferred by both apes. Adding to these species, *Maesa lanceolata* and *Newtonia Buchananii* are important for chimpanzees, representing a large basal area and bearing long lasting fruits.

In the montane forest of Kahuzi, gorillas inhabit the area at a higher density than do chimpanzees (0.43–0.47 gorillas/km^2 vs. 0.16 chimpanzees/km^2, Yamagiwa *et al*, 1992; Yamagiwa *et al*, 1993). This may reflect a smaller home range of chimpanzees and wide areas unused by chimpanzees within the park (Basabose & Yamagiwa, 2002). In other montane forests neighboring Kahuzi, gorillas and chimpanzees inhabit the Virunga Vocanoes allopatrically, and only chimpanzees inhabit the Nyungwe Forest. Although human disturbance in the past may have various influences on the present distribution of apes, seasonal availability of high-quality foods may be one of the factors causing such consequences. The availability of fruits is the most important factor for the survival of chimpanzees.

In the Kibale Forest, where only chimpanzees inhabit the area at high density ($1.5–2.5$ chimpanzees/km^2, Ghiglieri, 1984), fruiting is synchronous for 64% of the tree species (Chapman *et al.*, 1999). At Kahuzi, fruit species preferred only by chimpanzees were synchronous, while fruit species preferred by gorillas were not. The low density of chimpanzees at Kahuzi may be attributed to the small biomass of tree species with synchronous fruiting and the presence of gorillas showing seasonal frougivory. Our study suggests that fruiting patterns may influence the foraging strategies of gorillas and chimpanzees as well as their sympatric coexistence. Monitoring of the important fruit species and maintaining these fruit resources are crucial tasks for conservation of the gorillas and chimpanzees and for wise management of national parks.

REFERENCE

Basabose, A.K. & J. Yamagiwa 2002. Factors affecting nesting site choice in chimpanzees at Tshibati, Kahuzi-Biega National Park: Influence of sympatric gorillas. *International Journal of Primatology*, 23: 263-282.

Casimir, M.J. 1975. Feeding ecology and nutrition of an eastern gorilla group in the Mt. Kahuzi region (République du Zaire). *Folia Primatologica*, 24: 1-36.

Chapman, C.A., L.J. Chapman, R.W. Wrangham, K. Hunt, D. Gebo & L. Gardner 1992. Estimates of fruit abundance of tropical trees. *Biotropica*, 24: 527-531.

Chapman, C.A., R.W. Wrangham & L.J. Chapman 1994. Indices of habitat-wide fruit abundance in tropical forests. *Biotropica*, 26: 160-171.

Chapman, C.A., R.W. Wrangham, L.J. Chapman, D.K. Kennard & A.E. Zanne 1999. Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology*, 15: 189-211.

Chivers, D.J. & C.M. Hladik 1984. Diet and morphology in primates. In (D.J. Chivers, B.A. Wood & A. Bilsborough, eds.) *Food Acquisition and Processing*, pp. 213-230. Plenum Press, London.

Conklin, N.L. & R.W. Wrangham 1994. The value of figs to hind-gut fermenting frugivore: A nutritional analysis. *Biochemical Ecology & Systematics*, 22: 137-151.

Daubenmire, R. 1972. Phenology and other characteristics of tropical semi-deciduous forest in north-western Costa Rica. *Journal of Ecology*, 60: 147-170.

Foster, R.B. 1982. The seasonal rhythm of fruitfall on Barro Colorado Island. In (E.G. Leigh,

A.S. Rand & D.M. Windsor, eds.) *The Ecology of a Tropical Forest: Seasonal Rhythms and Longterm Changes*, pp. 151-172. Smithsonian Institution Press, Washington, D.C.

Frankie, G.W., H.G. Baker & P.A. Opler 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology*, 62: 881-919.

Furuichi, T., C. Hashimoto & Y. Tashiro 2001. Fruit availability and habitat use by chimpanzees in the Kalinzu Forest, Uganda: Examination of fallback foods. *International Journal of Primatology*, 22: 929-945,

Garwood, N.C. 1983. Seed germination in a seasonal tropical forest in Panama: A community study. *Ecological Monographs*, 53: 159-181.

Gautier-Hion, A. 1990. Interactions among fruit and vertebrate fruit-eaters in an African tropical rain forest. In (K.S. Bawa & M. Hadley, eds.) *Reproductive Ecology of Tropical Forest Plants*, pp. 219-230. UNESCO, Paris.

Ghiglieri, M.P. 1984. *The Chimpanzees of Kibale Forest: A Field Study of Ecology and Social Structure*. Columbia University Press, New York.

Goldsmith, M.L. 1999. Ecological constraints on the foraging effort of western gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. *International Journal of Primatology*, 20: 1-23.

Goodall, J. 1968. The behavior of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs*, 1: 161-331.

Hamilton, A.C. 1975. A quantitative analysis of altitudinal zonation in Uganda forests. *Vegetation*, 30: 99-106.

Hilty, S.L. 1980. Flowering and fruiting periodicity in a premontane rain forest in Pacific Colombia. *Biotropica*, 12: 292-306.

Janzen, D.H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. *Evolution*, 21: 620-637.

Jones, C. & J. Sabater Pi 1971. Comparative ecology of *Gorilla gorilla* (Savage and Wyman) and *Pan troglodytes* (Blumenbach) in Rio Muni, West Africa. *Bibliotheca Primatologica*, 13: 1-96.

Kuroda, S., T. Nishihara, S. Suzuki & R.A. Oko 1996. Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. In (W.C. McGrew, L.F. Marchant & T. Nishida, eds.) *Great Ape Societies*, pp. 71-81. Cambridge University Press, Cambridge.

Lieberman, D. 1982. Seasonality and phenology in a dry tropical forest in Ghana. *Journal of Ecology*, 70: 791-806.

Leighton, M. & D.R. Leighton 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. In (S.L. Sutton & T.C. Whitmore, eds.) *Tropical Rain forest: Ecology and Management*, pp. 181-196. Blackwell Science Publication, Oxford.

Mankoto, M.O., J. Yamagiwa, B-B. Steinhauer, N. Mwanza, T. Maruhashi & T. Yumoto 1994. Conservation of eastern lowland gorillas in the Kahuzi-Biega National Park, Zaire. In (B. Thierry, J.R. Anderson, J.J. Roeder & N. Herrenschmidt, eds.) *Current Primatology*, *Vol. I: Ecology and Evolution*, pp. 113-122. University of Louis Pasteur, Strasbourg.

Milton, K. 1984. The role of food-processing factors in primate food choice. In (P.S. Rodman & J.G.H. Cant, eds.) *Adaptations for Foraging in Nonhuman Primates*, pp. 249-279. Columbia University Press, New York.

Nishida, T. 1970. Social behavior and relationship among wild chimpanzees of the Mahale Mountains. *Primates*, 11: 47-87.

Parnell, R.J. 2002. Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. *American Journal of Primatology*, 56: 193-206.

Rathke, B. & E.P. Lacey 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics*, 16: 179-214.

Sabatier, D. 1985. Saisonalite et determinisme du pie de fructification en foret guyanaise. *Terre et Vie*, 40: 289-320.

Schaller, G.B. 1963. *The Mountain Gorilla: Ecology and Behavior*. University of Chicago Press, Chicago.

Sun, C., B.A. Kaplin, K.A. Kristensen, V. Munyaligoga, J. Mvukiyumwami, K.K. Kajongo & T.C. Moermond 1996. Tree phenology in a tropical montane forest in Rwanda. *Biotropica*, 26: 668-681.

Terborgh, J. 1983. *Five New World Primates: A Study in Comparative Ecology*. Princeton University Press, Princeton.

Tutin, C.E.G. & M. Fernandez 1993. Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé Reserve, Gabon. *American Journal of Primatology*, 30: 195-211.

Tutin, C.E.G., L.J.T. White, E.A. Williamson, M. Fernandez & G. McPherson 1994. List of plant species identified in the northern part of the Lopé Reserve, Gabon. *Tropics*, 3: 240-276.

van Schaik, C.P. 1986. Phenological changes in a Sumatran rain forest. *Journal of Tropical Ecology*, 2: 327-347.

van Schaik, C.P., J.W. Terborgh & S.J. Wright 1993. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, 24: 353-377.

White, L.J.T. 1994. Patterns of fruit-fall phenology in the Lopé Reserve, Gabon. *Journal of Tropical Ecology*, 10: 289-312.

Williamson, E.A., C.E.G. Tutin, M.E. Rogers & M. Fernandez 1990. Composition of the diet of lowland gorillas at Lopé in Gabon. *American Journal of Primatology*, 21: 265-277.

Wrangham, R.W. 1979. Sex differences in chimpanzee dispersion. In (D.A. Hamburg & E.R. McCown, eds.) *The Great Apes*, pp. 480-489. Benjamin/Cummings, Menlo Park.

Wrangham, R.W., C.A. Chapman, A.P. Clark-Arcadi & G. Isabirye-Basuta 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In (W.C. McGrew, L.F. Marchant & T. Nishida, eds.) *Great Ape Societies*, pp. 45-57. Cambridge University Press, Cambridge.

Yamagiwa, J. 1983. Diachronic changes in two eastern lowland gorilla groups (*Gorilla gorilla graueri*) in the Mt. Kahuzi region, Zaire. *Primates*, 24: 174-183.

Yamagiwa, J., N. Mwanza, A. Spangenberg, T. Maruhashi, T. Yumoto, A. Fischer, B-B. Steinhauer & J. Reyfisch 1992. Population density and ranging pattern of chimpanzees in Kahuzi-Biega National Park, Zaire: a comparison with a sympatric population of gorillas. *African Study Monographs*, 13: 217-230.

Yamagiwa, J., N. Mwanza, A. Spangenberg, T. Maruhashi, T. Yumoto, A. Fischer & B-B. Steinhauer 1993. A census of the eastern lowland gorillas *Gorilla gorilla graueri* in Kahuzi-Biega National Park with reference to mountain gorillas *G. g. beringei* in the Virunga region, Zaire. *Biological Conservation*, 64: 83-89.

Yamagiwa, J. & N. Mwanza 1994. Day-journey length and daily diet of solitary male gorillas in lowland and highland habitats. *International Journal of Primatology*, 15: 207-224.

Yamagiwa, J., T. Maruhashi, T. Yumoto & N. Mwanza 1996a. Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaire. In (W.C. McGrew, L.F. Marchant & T. Nishida, eds.) *Great Ape Societies*, pp. 82-98. Cambridge University Press, Cambridge.

Yamagiwa, J., K. Kaleme, M. Milynganyo & K. Basabose 1996b. Food density and ranging patterns of gorillas and chimpanzees in the Kahuzi-Biega National Park, Zaire. *Tropics*, 6: 65-77.

Yamagiwa, J., K. Basabose, K. Kaleme & Y. Yumoto 2003. Within-group feeding competition

and socioecological factors influencing social organization of gorillas in the Kahuzi-Biega National Park, Democratic Republic of Congo. In (A.B. Taylor & M.L. Goldsmith, eds.) *Gorilla Biology: A Multidisciplinary Perspective*, pp. 328-357. Cambridge University Press, Cambridge.

Yumoto, T., J. Yamagiwa, N. Mwanza & T. Maruhashi 1994. List of plant species identified in Kahuzi-Biega National Park, Zaire. *Tropics*, 3: 295-308.

Correspondence Author's Name and Address: Juichi YAMAGIWA, *Laboratory of Human Evolution Studies, Department of Zoology, Graduate School of Science, Kyoto University, Sakyo, Kyoto 606-8502, JAPAN.*
E-mail: yamagiwa@jinrui.zool.kyoto-u.ac.jp

Appendix 1. Density and basal area of each woody plant species and fruit eaten by gorillas or chimpanzees.

Scientific name	Family name	Secondary forest		Primary forest		Swamp		Fruit eaten by		Seed dispersal
		D No./ha	BA cm²	D No./ha	BA cm²	D No./ha	BA cm²	Gorilla	Chimp.	
Acanthus pubescens	ACANTHACEAE	0.2	379	1.2	1,226					Anem
Agauria salicifolia	ERICACEAE	19.6	62,241	0.4	4,976					Anem
○*Aidia micrantha*	RUBIACEAE	2.8	4,883	3.7	2,457					Zoo
○*Albizia gummifera*	MIMOSACEAE	1.6	35,249	3.3	29,068				*	Auto
Alchornea hirtella	EUPHORBIACEAE			1.2	414					?
○*Allophyllus sp.*	SAPINDACEAE	8.0	15,001	5.4	2,035			*	**	Zoo
Anthocleista sp.	LOGANIACEAE			0.4	496					?
Bersama ugandensis	MELIANTHACEAE	0.2	4,397							Auto
○*Bridelia bridelifolia*	EUPHORBIACEAE	21.8	40,000	7.4	12,552			**	**	Zoo
○*Cassipourea ruwenzoriensis*	RHIZOPHORACEAE	1.1	3,406	4.1	3,021			*	**	Anem
Conopharyngia durissima	APOCYNACEAE	11.4	55,127	12.8	29,330	0.8	1,825			?
○*Diospyros honleana*	EBENACEAE			1.2	6,974			*	**	Zoo
○*Dombeya goetzenii*	STERCULIACEAE	7.0	27,858	5.4	3,880			*	*	Zoo
○*Ekebergia capensis*	MELIACEAE	0.5	41,139	0.4	3,995			*	**	Zoo
Entandrophragma excelsum	MELIACEAE			0.4	2,249					Anem
Erica arborea	ERICACEAE	0.5	938							Anem
Erythrina tomentosa	PAPILIONACEAE	2.1	7,978							Auto
○*Ficus oreadryadum*	MORACEAE	0.5	55,568					**	**	Zoo
○*Ficus thoningii*	MORACEAE	0.8	37,273	0.8	10,272			**	**	Zoo
○*Galiniera coffeoides*	RUBIACEAE	4.7	3,692	21.9	7,363	0.8	115	*	*	Zoo
○*Gambeya gorungosana*	SAPOTACEAE			1.7	19,785			*	*	Zoo
○*Hagenia abyssinica*	ROSACEAE	6.8	52,145					*		Anem
Hypericum revolutum	GUTTIFERAE	2.4	2,277							Anem
Lindackeria bukombensis	FLACOURTIACEAE	3.3	3,952	4.5	1,504					Anem
○*Macaranga kilimandscharica*	EUPHORBIACEAE	81.1	141,604	6.6	11,845			*	*	Zoo
○*Maesa lanceolata*	MYRSINACEAE	5.7	38,061					*	**	Zoo
○*Maesopsis eminii*	RHAMNACEAE	0.2	2,717	7	6,721	0.8	617		*	Zoo
Manniophyton fulvum	EUPHORBIACEAE	0.3	9,833							Zoo
Massularia acuminata	RUBIACEAE			0.4	241					Zoo
Microdesmis pierlotiana	EUPHORBIACEAE	0.3	390	5.8	3,069					Zoo
○*Milletia dura*	FABACEAE	8.5	15,680					*	*	Auto

Scientific name	Family name	Secondary forest		Primary forest		Swamp		Fruit eaten by		Seed dispersal
		D No./ha	BA cm²	D No./ha	BA cm²	D No./ha	BA cm²	Gorilla	Chimp.	
Morinda sp.	RUBIACEAE			1.2	2,908					Zoo
○*Myrianthus holstii*	MORACEAE	0.8	10,269	5	25,100			**	**	Zoo
○*Neoboutonia microcalyx*	EUPHORBIACEAE	21.1	37,025	25.6	12,425	4.9	1,325		*	Zoo
○*Newtonia buchananii*	MIMOSACEAE			5	69,185			*	**	Auto
○*Nuxia congesta*	LOGONIACEAE	9.6	27,037	2.9	4,620				*	Zoo
○*Parinari curatellifolia*	CHRYSOBALANACEAE			1.7	80,012		*			Zoo
Polyscias fulva	ARALIACEAE	0.2	11,436							Zoo
○*Psychotria palustris*	RUBIACEAE	1.1	2,018	3.3	1,499			**	**	Zoo
Rytiginia sp.	RUBIACEAE	0.2	315	0.4	215					Zoo
Sapium ellipticum	EUPHORBIACEAE	12.6	73,943	21.9	55,367					Zoo
Senecio mannii	COMPOSITAE	0.2	97							Anem
○*Strombosiopsis tetranda*	OLACACEAE	2.7	13,905	2.5	17,641			*	*	Zoo
○*Symphonia globulifera*	GUTTIFERAE	0.3	9,912	0.8	5,714					Zoo
○*Syzygium parvifolium*	MYRTACEAE	0.9	8,010	11.1	37,405	0.8	562	**	**	Zoo
○*Tricalysia* sp.	RUBIACEAE	0.8	749	1.2	704			*	*	Zoo
Vernonia ampla	COMPOSITAE	1.3	2,439	0.4	258					Anem
Xylopia sp.	ANNONACEAE	0.2	249	0.4	81					Zoo
○*Xymalos monospora*	MONIMIACEAE	4.1	3,825	3.7	1,483			*	*	Zoo
Unidentified sp.	(MUZO)			0.8	526					?

○ monitored for data set 2
* eaten, ** preferred to eat (its seed was found in more than 1% of total fecal samples)
Seed dispersal: Zoo, Zoochory; Anem, Anemochory; Auto, Autochory