

FRUIT PHENOLOGY OF THE GREAT APE HABITAT IN THE MOUKALABA-DOUDOU NATIONAL PARK, GABON

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ABSTRACT Fruit phenology of the Moukalaba-Doudou National Park (MDNP), Gabon is monitored as basic information on the fluctuation of food production for great ape populations. During the period from January 2003 to February 2007, we conducted a census on fallen fruits by the line transect method twice a month, in the process counting fallen fruit clusters and identifying fallen fruit species. We recorded 117 fallen fruit species during the study period. The majority of fruits came from trees. The number of fallen fruit clusters obtained in each census session correlated with the number of fallen fruit species found in the sessions. There was a marked seasonal pattern to fruit production, whereas the number of fallen fruit clusters as well as the number of species tended to be larger in the rainy season than in the dry season. Of the 31 major fallen fruit species, 15 species showed a fruiting peak in the rainy season, and five species peaked in the dry season, while 11 species showed no difference in fruiting abundance between the rainy and dry seasons. Candidates of keystone fruit species were identified from species that fruit during the dry season. Five species of fruit, including the woody liana *Cissus dinklagei*, were constantly abundant, occurring in more than 70% of all census sessions. Four of them are important fruit food resources for the great apes. Several species including *Klainedoxa gabonensis* exhibited super-annual fluctuation in their fruiting pattern. The existence of constantly abundant fruit species may have supported the high density of great apes in the MDNP.

RÉSUMÉ La phénologie des ressources fruitières du Parc National de Moukalaba-Doudou (PNMB), Gabon a été contrôlée de manière à connaître les variations mensuelles de la ressource « fruit », une nourriture importante pour les populations de grands singes. De Janvier 2003 à Février 2007, nous avons recensé tous les 15 jours le nombre de fruits tombés au sol selon la méthode dite des transects en ligne en comptant les amas sous les arbres et en identifiant les espèces. Nous avons ainsi dénombré des fruits provenant de 117 espèces végétales, des arbres pour la plupart. Il est apparu que le nombre d'amas de fruits était corrélé avec le nombre d'espèces dont les fruits étaient tombés au sol sur la période de l'étude. Par ailleurs, la variation de la production fruitière des espèces végétales du PNMB était saisonnièrement marquée et le nombre de fruits comme le nombre d'espèces fruitières recensées étaient les plus importants en saison des pluies. Des 31 espèces végétales produisant le plus grand nombre de fruits, 15 avaient une production maximale en saison des pluies et 5 en saison sèche. Pour 11 espèces, nous n'avons mesuré aucune différence saisonnière. Les espèces végétales produisant des fruits en saison sèche ont été défini comme espèce « clé ». De plus, 5 espèces (dont une liane, *Cissus dinklagei*) ont produit en abondance constante des fruits, quelque soit la période de l'étude considérée. Ces fruits représentaient plus de 70% des fruits dénombrés. Parmi ces 5 espèces, 4 étaient des ressources fruitières importantes pour les grands singes. Par ailleurs, plusieurs espèces végétales, incluant *Klainedoxa gabonensis*, ont montré une fluctuation super-annuelle du nombre de fruits produits. L'existence d'une abondance en fruit constante

d'une saison sur l'autre explique certainement les importantes densités de grands singes calculées dans le PNMB.

Key Words: Fruit phenology; Chimpanzee; Gorilla; Diet; Moukalaba; Keystone fruit.

INTRODUCTION

Knowing the dynamics of fruit production in the African forest is important for understanding great ape ecology, as fruit provides a large amount of nutritious resources for most of the primate species, including the great apes in central African regions (chimpanzees, gorillas, and bonobos). Species composition, density, distribution and temporal fluctuation affect their ecological features such as diet (Furuichi *et al.*, 2001; Kuroda *et al.*, 1996; Remis, 1997a; Tutin *et al.*, 1997; Basabose, 2002), ranging (Remis, 1997b; Basabose, 2005; Yamagiwa & Basabose, 2006), group size (Hashimoto *et al.*, 2003; Basabose, 2004), reproductive parameters (Anderson *et al.*, 2006), patterns of social interaction (Itoh & Nishida, 2007) and tool-using behavior (Yamakoshi, 1998).

Comparison of fruit phenology is also important to understand the ecological differences in great apes among different study sites. The foraging strategy taken by western lowland gorillas in the Ndoki forest (Congo) and Lopé NP (Gabon) is described as generalized, opportunistic frugivory (Tutin *et al.*, 1991; Kuroda *et al.*, 1996), while gorillas in Bai-Hokou (CAR) make more effort to pursue several preferred fruit species (Remis, 1997a). Hashimoto *et al.* (2003) showed patterns of fluctuation in party size of chimpanzees are different among four chimpanzee study sites and suggested the differences in dynamics of fruit production among the sites as a cause. More detailed information on fruit phenology at each great ape study site is needed for further comparison.

The previous studies of great ape study sites showed that the patterns of fruit production vary among sites. As Terborgh (1986) pointed out, annual and seasonal fluctuations in fruit production are distinct, and a period of fruit scarcity exists at all study sites. Fruits are more abundant in the rainy season than in the dry season in Central Africa. In Lopé N.P. (Gabon), fruit abundance peaks in the early rainy season and fruits are scarce during the long dry seasons (Tutin *et al.*, 1991). Super-annual fluctuation of fruit production is also distinct (Tutin *et al.*, 1997). In Bai-Hokou, Mondika (CAR), and the Ndoki (Congo), temporal fruit abundance is correlated with available fruit species. Fruit abundance peaks during the mid-rainy season and there is scarcity during the dry season (Kuroda *et al.*, 1996; Doran *et al.*, 2002; Remis, 1997b). In East Africa, climatic factors influencing fruit phenology are varied among sites. In Mahale Mountains NP (Tanzania), the number of plant species in fruiting declines in December, January and February during the rainy season (Turner, 2006). In Kibale Forest (Uganda) and Kahuzi-Biega N.P. (DRC), fruit abundance is negatively correlated with monthly rainfall, and more fruits are available during the dry season (Chapman *et al.*, 1999; Yamagiwa & Basabose, 2006). In contrast, in Budongo and Kalinzu, peaks in fruit abundance occur during the rainy season (Furuichi *et al.*, 2001; Tweheyo

& Badweteera, 2007). In the two sites of West Africa, Taï N.P. (Côte d'Ivoire) and Bossou (Guinea), fruits tend to be abundant during the dry season (Anderson *et al.*, 2005; Yamakoshi, 1998).

Even in the same habitat, patterns of fruit production differ among species, life forms of plants, and vegetation types. Frugivorous animals respond to periods of fruit scarcity by changing their dietary composition and/or ranging patterns (Leighton & Leighton, 1983; Terborgh, 1986; Remis, 1997b; Yamagiwa & Basabose, 2006). Keystone fruits, such as fruit species that constitute a dependable resource during the period of fruit scarcity, play a vital role in the ecosystem of tropical forests (Gautier-Hion & Michaloud, 1989; Terborgh, 1986; Tutin *et al.*, 1991; White, 1994). Although fig fruit usually fulfills this role in tropical forests across continents, keystone species vary among areas even for the great apes (van Schaik *et al.*, 1993). In the Lopé Forest (Gabon), fruit species with prolonged availability, especially those available during the period of low fruit availability, such as *Duboscia macrocarpa* and *Elaeis guineensis*, are important for chimpanzees (White, 1994). On Rubondo Island (Tanzania), while fruits of tree plants are scarce in the dry season, lianas are constantly available (Moscovice *et al.*, 2007). In Kalinzu, while fruit abundance in the primary vegetation tends to fluctuate in correlation with rainfall, that of secondary forests is rather constant, and several species specific to secondary forest, such as *Musanga leo-errerae*, are available throughout the year (Furuichi *et al.*, 2001). It is important to identify these keystone species specific to the habitats for promoting an appropriate measure of efforts made for great ape conservation.

The purpose of this paper is to examine and describe the patterns of fruit phenology in the Moukalaba-Doudou National Park, Gabon, where we have been conducting a long-term research project of sympatric gorillas and chimpanzees. We monitored the patterns of fruit production by counting the number of freshly fallen fruits on line transects. The overall tendency of fruit abundance and the patterns of fruiting of 31 major species are analyzed in relation to climatic changes. Data presented in this paper provide basic information to examine the ecological data on gorillas and chimpanzees that we are collecting in our ongoing project.

METHODS

I. Study Site

Field study was conducted in the Moukalaba-Doudou National Park, Gabon (Fig. 1). The Park covers an area of 5,028 km², which consists of a mosaic of forest, savanna, and swamp. The Park faces the Atlantic Ocean on its south-western boundary. The Doudou Mountain Range, at altitudes up to 900 m, runs north and south. The vegetation is a complex mosaic of savanna and forest. Savanna dominates in the southern area, and the proportion of forests increases going north.

The study site (approximately 30 km²) is located in the southeastern part of the park. The vegetation of the study site is divided into mixed-species primary forest that had been selectively logged, secondary forest, *Musanga cecropioides*

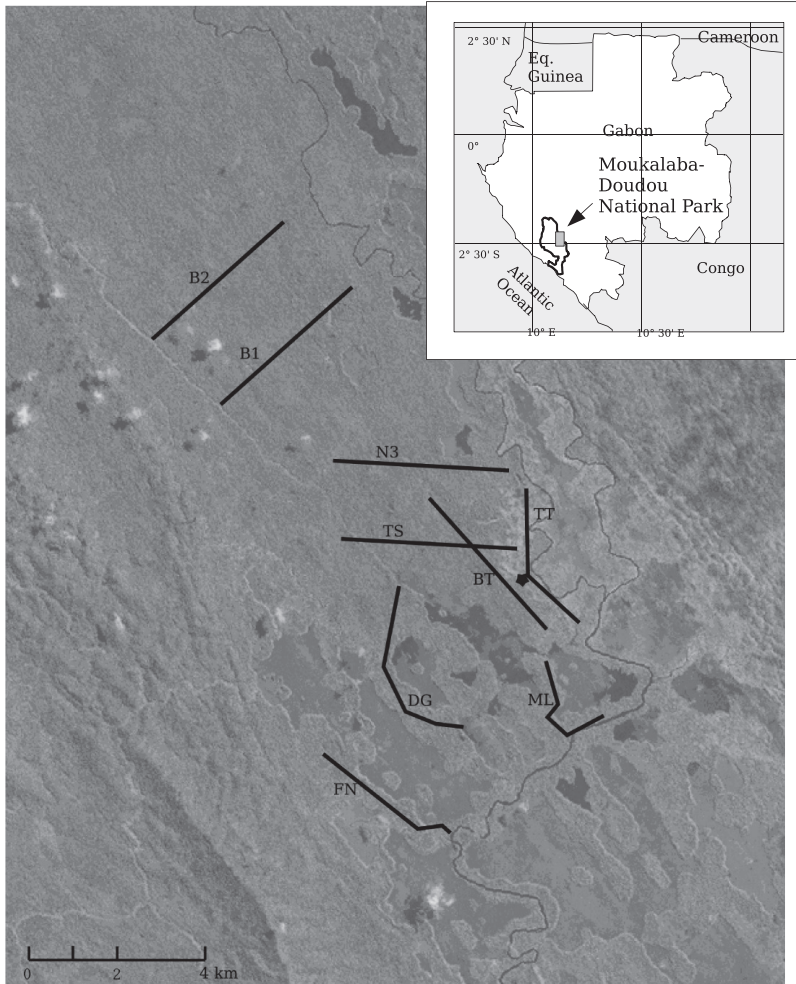


Fig. 1. Study site and phenology transects.

dominated forest regenerated from old plantations, temporarily inundated forest, and savanna.

II. Climate Data

We installed a rain gauge and a maximum-minimum thermometer at our field camp. We have measured daily accumulated rainfall since June 2001 and daily maximum/minimum temperatures since March 2005.

III. Fruit Phenology

We began monitoring fruit phenology from January 2003 and have continued to the present. In this paper, we use data obtained from the beginning of our

census activities until February 2007. We used a fallen fruit census based on line transects. We followed the method applied by Furuichi *et al.* (2001) in Kalinzu Forest, with a slight modification to adjust to the research conditions of our project. We installed several line transects in the study area and censused each transect twice a month at fixed intervals. In each census session, a group of two local assistants walked on all transects to record fallen fruit clusters.

Following Furuichi's method, a fruit cluster is an aggregation extending 1 m on each side of a transect that includes fruit fallen from a single tree. When there was a large contiguous cluster of fruit that came from several trees of the same species, we divided the cluster by the number of fruiting trees. Thus, the number of clusters matched the number of fruiting plants that dropped fruit within the census belt. We recorded the tree species, the number of fruit in each cluster, and whether the majority of fruits were ripe or unripe.

Although we grouped numbers of fruit in a cluster as 1–4, 5–9, or 10– as indicators of relative fruit abundance of each fruiting plant, we did not use this information in the following analysis. We used the number of fruit clusters as an index of fruit abundance. In each session, after a fruit cluster was recorded, the fallen fruits in the belt were removed in order to avoid recording those fruits in the next session.

We installed nine transects (Fig. 1). The length of one transect (DG) is 6.699 km and that of each of the other eight transects is 4 km. Five transects were cut in an entirely linear manner, while three had one or two nodes of changing direction (FN, TT and ML) in order to avoid savanna or large rivers. One transect (DG) takes a winding path, since we used elephant trails.

In the beginning, we used five transects: FN, DG, BT, B1, and B2. However,

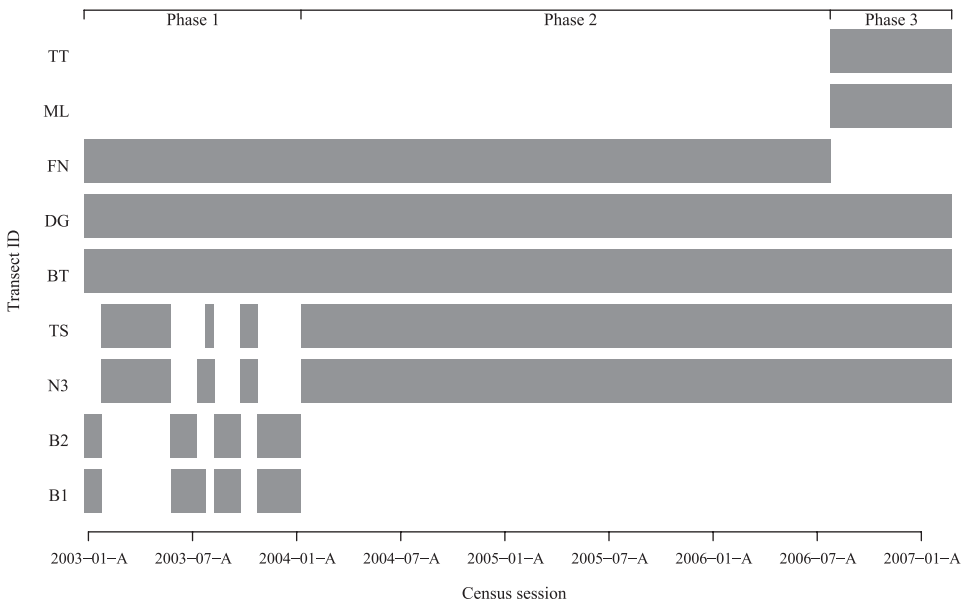


Fig. 2. Implementation of census for each transect.

it was sometimes difficult to reach B1 and B2 for logistical reasons. At such times, we used N3 and TS as alternative transects. Since February 2004, we settled on a census of FN, DG, BT, N3 and TS to maintain consistency of the transects used. Later, when it was found that FN was out of the home range of the gorilla study group (and probably out of the chimpanzee target group's range), we stopped using FN, and we added ML and TT in August 2006. Accordingly, we designate "Phase 1" as the period from the beginning to January 2004, "Phase 2" as that from February 2004 to July 2006, and "Phase 3" as that from August 2006 to February 2007. Implementation of the census for each transect is shown in Fig. 2.

IV. Statistics

For data processing and statistical tests, we used GNU R (version 2.6.1), an open source software program for statistical analysis (R Development Core Team, 2007).

RESULTS

I. Climate

Mean annual rainfall of five entire years (2002–2006) was 1,776.8 mm, with a range of 1,583–2,163 mm. Mean monthly rainfall during 69 months was 137.6 mm, ranging from 0 to 377 mm. Fluctuation of monthly rainfall and monthly mean maximum/minimum temperatures are shown in Fig. 3.

Mean monthly rainfall always dropped below 100 mm in June, July, August, and September throughout the study period and in May in most years. In general, two seasons are distinct: the dry season from May to September and the rainy season from October to April. These periods are typical, although there is variation in duration and timing of the dry season across years. Local people say that a short dry season occurs in the middle of the rainy season, but this is not always distinct. During the study period, rainfall in February 2003 and January 2007 fell below 100 mm.

In the following analysis, based on actual rainfall, we designate the dry season as the period lasting from April through October, when monthly rainfall was below 100 mm, and the rainy season as the other months. The two short dry months are included in the rainy season. Both monthly mean maximum and minimum temperatures tend to be higher in the rainy season than in the dry season. But no correlation between maximum and minimum temperature was statistically significant.

II. Fruit Phenology

1. *Fruit Diversity*

We recognized 117 fruit species throughout the census. As the cumulative number of fallen species is nearly saturated, most of the fruiting plants commonly

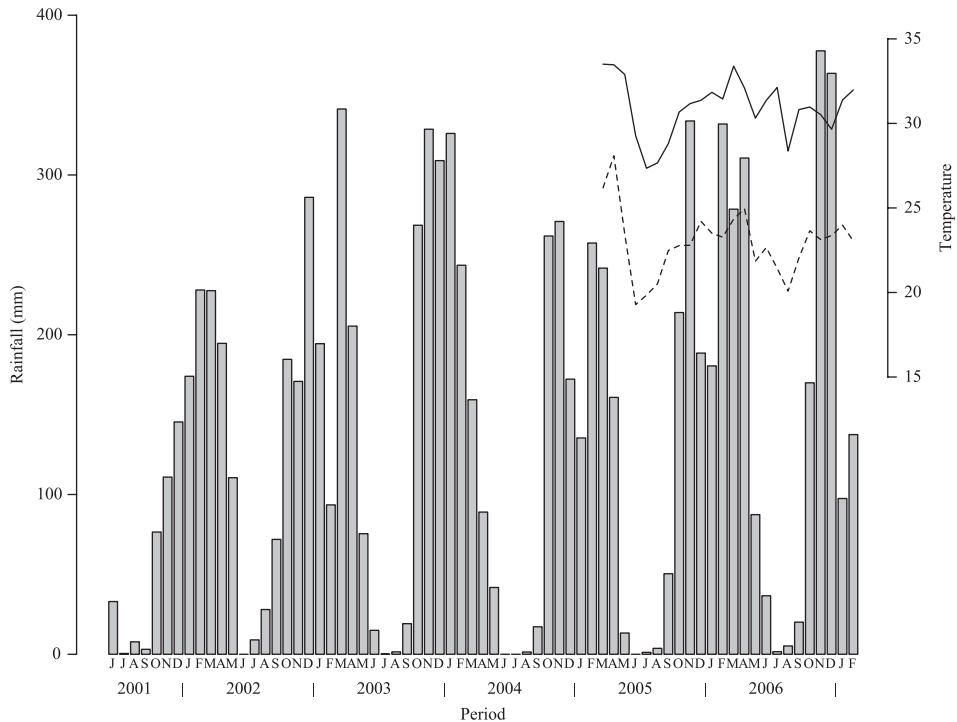


Fig. 3. Monthly rainfall and maximum/minimum temperature.

Table 1. Cumulative number of fallen fruit species recorded in each transects.

Transect ID	TT	ML	FN	DG	BT	TS	N3	B2	B1	ALL Transects
Cum N Spp.	38	44	76	83 (79)	81	78	79	42	43	117

Value in parentheses for DG indicates the cumulative number of fruit species of first 4 km sector.

grow and drop fruits in the study area were recorded. However, it must be noted that those species that commonly grow but do not drop fruits on the ground were not recorded.

The cumulative number of fruit species recorded in each transect is shown in Table 1. This number is positively correlated with the number of sessions implemented. In addition, the pattern of the cumulative curve of recorded species for each transect showed similarity with the patterns of the other transects. These results indicate no difference in diversity of fallen fruit species between transects. On the other hand, even in the transects implemented in more than 80 sessions, only up to 70% of fruit species of all recognized species were recorded. This suggests that species composition differs between transects.

The number of fallen fruit species per session showed a roughly annual cycle (Fig. 4). More fruit species occurred in the rainy season than in the dry season (analysis of variance, $F=14.592$, $p<0.001$). In particular, during the two years of Phase 2, a marked contrast is found between the rainy season and the dry season.

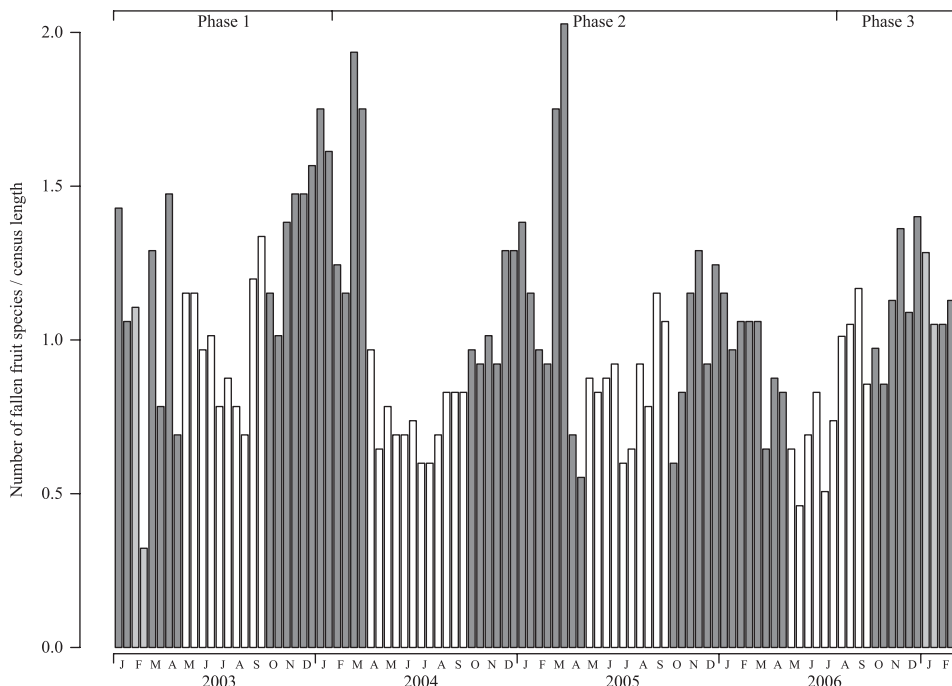


Fig. 4. Fluctuation in the number of fallen fruit species. In order to adjust the differences in total census length between sessions, the number of recorded species is divided by the census length. White column indicates the number in the dry season, black column in the rainy season, and gray column in the short dry season.

On the other hand, super-annual fluctuation is also suggested. For example, the number of fruit species during the 2003 dry season is similar or slightly larger than those in the 2005–2006 rainy season, though this may be caused artificially by the differences between the transects implemented in Phase 1 and those in Phase 2.

2. Fruit Abundance

Fluctuation in the total number of fallen fruit clusters per session showed a similar pattern to that of the number of fruit species. It is larger in the rainy season than in the dry season (Fig. 5). The number of fallen fruit clusters per session is positively correlated with the number of fallen fruit species (Fig. 6, analysis of variance, $F=88.4$, $p<0.001$). This means that higher fruit abundance is caused by an increasing number of fruiting species, rather than by an increasing number of fruiting plants of a particular fruit species.

3. Major Species

Among the 117 recognized species, we designated “major fruit species” as those that match at least one of the following two conditions: 1) gross number of clusters is 100 or more; 2) maximum number of clusters per session is 10 or more. Thirty-one species fulfilled one of those conditions, with 21 species matching both conditions (Table 2).

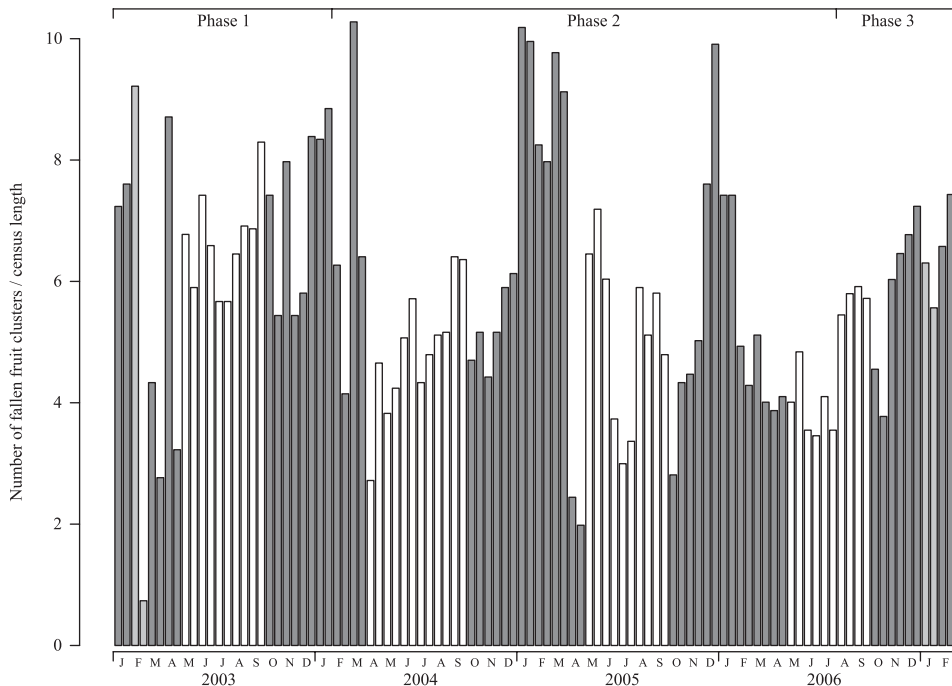


Fig. 5. Fluctuation in the number of fallen fruit clusters. In order to adjust the differences in total census length between sessions, the number of cluster is divided by the census length. White column indicates the number in the dry season, black column in the rainy season, and gray column in the short dry season.

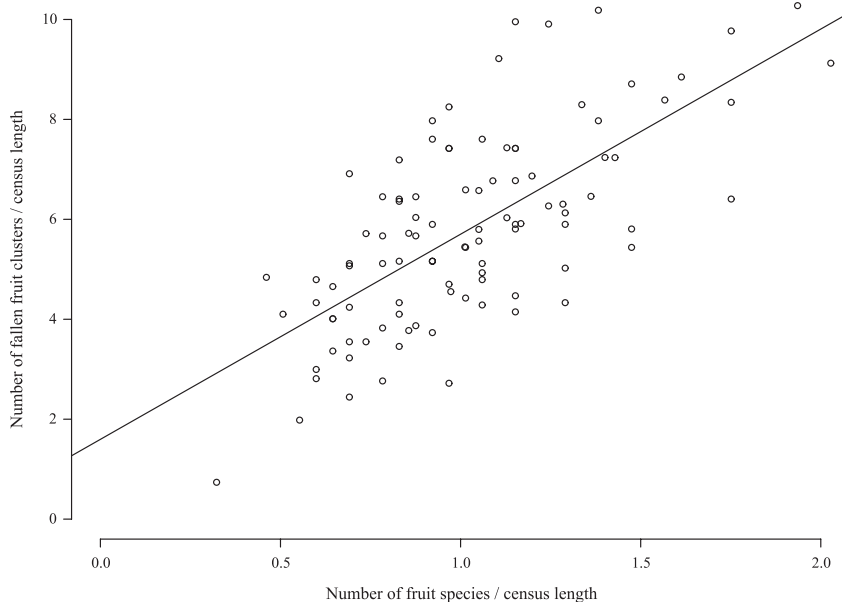


Fig. 6. Relation between number of species and number of fruit clusters.

Table 2. Major fallen fruit species.

Family	Species	Number of sessions occurred	Total number of fallen fruit clusters	Maximum number of fallen fruit clusters	Fruiting season
Verbenaceae	<i>Cissus dinklagei</i>	99	1822	56	dry>rain
Irvingiaceae	<i>Klainedoxa gabonensis</i>	70	1383	63	n.s.
Sterculiaceae	<i>Cola</i> sp.(fudi)	33	997	115	rain>dry
Myristicaceae	<i>Staudtia gabonensis</i>	81	847	33	dry>rain
Ebenaceae	<i>Diospyros</i> sp.(mufinzi)	49	785	56	n.s.
Myristicaceae	<i>Pycnanthus angolensis</i>	56	439	33	dry>rain
Annonaceae	<i>Xylopia guintassii</i>	52	418	29	dry>rain
Ebenaceae	<i>Diospyros</i> spp.(nemba)	34	415	64	rain>dry
–	(ilalaba)	48	372	26	n.s.
Annonaceae	<i>Meiocarpidium lepidotum</i>	58	358	17	rain>dry
Tiliaceae	<i>Duboscia macrocarpa</i>	82	306	13	n.s.
Meliaceae	<i>Trichilia prieureana</i>	20	274	47	dry>rain
Anacardiaceae	<i>Lannea welwitschii</i>	45	259	14	rain>dry
Euphorbiaceae	<i>Ricinodendron heudelotii</i>	51	242	19	rain>dry
Pandaceae	<i>Panda oleosa</i>	77	228	8	n.s.
Flacourtiaceae	<i>Caloncoba welwitschii</i>	47	207	14	rain>dry
Olacaceae	<i>Coula edulis</i>	31	188	25	rain>dry
Irvingiaceae	<i>Irvingia gabonensis</i>	31	186	19	rain>dry
Moraceae	<i>Myrianthus arboreus</i>	65	171	9	rain>dry
–	(dibimbi)	44	138	12	rain>dry
Annonaceae	<i>Hexalobus crispiflorus</i>	35	135	11	rain>dry
Humiriaceae	<i>Sacoglottis gabonensis</i>	48	133	12	n.s.
Olacaceae	<i>Diogoia zenkeri</i>	29	122	16	rain>dry
Euphorbiaceae	<i>Uapaca guineensis</i>	49	114	9	n.s.
Sapotaceae	(igamba gesi)	45	113	8	n.s.
Ebenaceae	<i>Diospyros mannii</i>	31	100	13	rain>dry
Sterculiaceae	<i>Octobotolis</i> sp.(grand fudi)	9	80	23	n.s.
Euphorbiaceae	<i>Dichostemma glaucescens</i>	16	75	14	rain>dry
Sapindaceae	<i>Eriocoelum macrocarpum</i>	17	1	11	rain>dry
–	(dibotsa)	17	68	12	rain>dry
Sapotaceae	<i>Synsepalum dulcificum</i>	5	39	14	rain>dry

Species are ordered by the total number of fallen fruit clusters.

Literals in parantheses are local names.

Cissus dinklagei, a woody liana, is the most abundant fruit in terms of total number of fallen fruit clusters. This fruit is highly preferred by both gorillas and chimpanzees. It occurred in 99 of 100 census sessions at high frequency, i.e. it is constantly available throughout the year, although it is less abundant in the rainy season (Fig. 7a).

The next-most abundant species is *Klainedoxa gabonensis*. Its fruiting period encompasses the dry season and the early rainy season. However, this species showed marked inter-annual fluctuation. Almost no fruits was available in 2006 (Fig. 7b).

Inter-annual fluctuation and lean years are also distinct in *Irvingia gabonensis* and *Diospyros* sp. (locally called “mufinzi”). The inter-annual fluctuation pattern

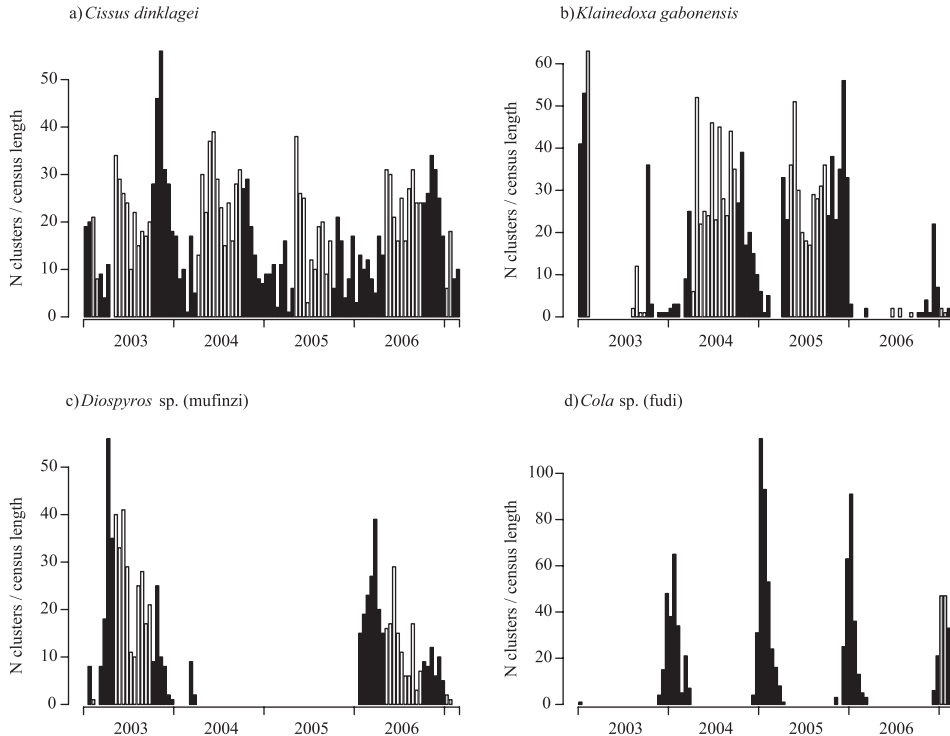


Fig. 7. Fluctuation in number of fallen fruit clusters for a) *Cissus dinklagei*, b) *Klainedoxa gabonensis*, c) *Diospyros* sp. (mufinzi) and d) *Cola* sp. (fudi). White column indicates the number in the dry season, black column in the rainy season, and gray column in the short dry season.

of *Klainedoxa* and that of *Diospyros* seem to be reversed, but this may be a coincidental phenomenon (Fig. 7c).

Cissus dinklagei, *Duboscia macrocarpa*, *Staudtia gabonensis*, *Klainedoxa gabonensis*, and *Panda oleosa* occurred in more than 70% of the census sessions. None of these species exhibits fruiting peaks in the rainy season. Four of them (other than *Panda oleosa*) are major foods for gorillas and chimpanzees.

Many species such as *Cola* sp., *Diospyros* spp., *Caloncoba welwitschii*, *Lannea welwitschii*, *Coula edulis*, and *Meiocarpidium lepidotum* have their fruiting peak in the rainy season and are rarely available during the dry season. These are predictable resources due to less inter-annual fluctuation (Fig. 7d).

Two Myristicaceae species, *Pycnanthus angolensis* and *Staudtia gabonensis* drop fruits during the dry season, at slightly different timings of fruiting peak. They can also be predicted to have less inter-annual fluctuation. These two species are strongly preferred by chimpanzees when they are available.

For each major species, we compared the abundance of fallen fruit clusters between the rainy and dry seasons. The number of fallen fruit clusters is larger in the rainy season for 15 species (Rainy season fruit), larger in the dry season for five species (Dry season fruit), and without any significant difference between the rainy and dry seasons for eleven species (Table 2).

In general, Dry season fruit species exhibited longer fruiting periods than Rainy season fruit species. The number of sessions in which the fruits appear is longer for Dry season fruit species than for Rainy season fruit species. The total and the maximum number of fruit clusters were also larger for Dry season fruit species than for Rainy season fruit species. However, these differences are not significant due to the small sample size.

DISCUSSION

The present study shows a low overlap of species found to be fruiting between transects. This reflects the high plant species diversity of the tropical forest at Moukalaba-Doudou National Park. General characteristics of fruit phenology in the Moukalaba-Doudou National Park can be summarized as 1) Overall fruit abundance at one time correlating with fruit diversity, i.e. the number of fruiting species; 2) Fruit abundance and diversity being larger in the rainy season than in the dry season.

When compared with other great apes study sites, fruit phenology in Moukalaba-Doudou is similar to those in the central African region. Ripe fruits are more abundant and diverse during the rainy season at Lopé in Gabon (Tutin *et al.*, 1991, Tutin *et al.*, 1997), Bai-Hokou in CAR (Remis, 1997a), and Ndoki in Congo (Kuroda *et al.*, 1996). The hot, wet and sunny conditions are likely to be suitable for fruit ripening. Many plants may adjust the time of fruiting for germinating seedlings during the wet season (Garwood, 1983). Species fruiting in the wet season are generally highly synchronized in order to swamp seed predators (Janzen, 1969) or encourage large bodied seed dispersers to concentrate their foraging time on those species (White, 1994). Large mammals that take the role of seed dispersal, such as elephants, large antelopes, and the great apes, are common in the tropical rain forests of Central Africa. Such similarities of animal-plant relationships may contribute to large fruit abundance and diversity in the rainy season as a standard pattern of fruit phenology in Central African forest.

Fruit phenology at Moukalaba is particularly similar to those of northeastern Gabon, probably due to the similar climatic patterns (Hladik, 1978; Gautier-Hion *et al.*, 1985; Feer, 1989). White (1994) found a total 195 species of fruit by counting the numbers of freshly fallen fruits on five 5-km line transects during a 1-year census at Lopé (compared to 117 species in our census). The dry months are defined as our study period, which is between June and September at Lopé. Although the majority of fruit species ripened during the rainy season, several species fruiting in the dry season were regarded as potential keystone foods for frugivores. The fruit species fruiting in the dry season at Moukalaba were extended fruiters, as indicated at Lopé. Such species are constantly available regardless of the season, with a slight bias of fruiting to the dry season. In addition, the larger number of plants bearing fruits are available simultaneously on the transects for such species. In particular, *Cissus dinklagei*, a Verberanaceae woody liana, provides constant fruit resources for great apes. Its fruits have been available constantly at high density during the 4 years of the study period. By contrast, the fruit of

Cissus dinklagei was only recorded in two months during the dry season at Lopé. This suggests differences in phenology for some plants between Moukalaba and Lopé, and such differences may affect the density of the great apes.

The previous studies reported the high density of the great apes at Moukalaba. In the nationwide census on gorillas and chimpanzees conducted by Tutin & Fernandez (1984) in the early 1980s, their densities were highest in Gabon (referred to as “Moabi” sector in the literature). In the 2000 census, the density of great ape nests in Moukalaba-Doudou was highest in Gabon (Walsh *et al.* 2003). The lower hunting pressure caused by the long distance from large cities may be a major reason for the high great ape density in Moukalaba-Doudou. Adding to this, the constant supply of fruit resources may be another important factor. *Cissus dinklagei*, *Duboscia macrocarpa*, *Staudtia gabonensis*, *Klainedoxa gabonensis*, and *Panda oleosa*, which fruit in more than 70% of the census sessions and have no fruiting peak in the rainy season, may fulfill the role of keystone fruits for the great apes. These species provide a large amount of fruits simultaneously, and the first four species are the major foods of the great apes; therefore, the availability of these species may support the high density at Moukalaba. *Klainedoxa gabonensis* and *Panda oleosa* are adapted for dispersal by elephants (White *et al.*, 1993). Fruits of *Duboscia macrocarpa* and *Klainedoxa gabonensis* are also available constantly in Bai Hokou and Mondika, Central Africa (Remis, 1997a; Doran *et al.*, 2002). *Duboscia macrocarpa* constitutes keystone fruit resources for both gorillas and chimpanzees at Lopé (Tutin *et al.*, 1991). Western lowland gorillas generally rely on fruit foods (Rogers *et al.*, 2004). Gorillas at Moukalaba also show a strong frugivorous diet and occasionally reuse the previous nest sites when they consume a large amount of fruits (Iwata & Ando, 2007). The keystone fruits with constant availability may enhance such frugivorous feeding and ranging strategies.

However, several species showed super-annual fluctuation, which prevents us from identifying keystone species with confidence. Although patterns of fluctuation did not synchronize between species, and a “lean fruit year” is not distinct at least during the study period, long-term monitoring of fruit phenology is needed to analyze the effects of keystone foods on densities of the great apes at Moukalaba.

Unlike tropical forests in Central Africa, habitats of eastern gorillas and chimpanzees show different fruit phenology. Fruits are more abundant in the dry season than in the rainy season in the montane forests of Kahuzi and Nyungwe, and in the tropical forests of Kibale and Mahale (Sun *et al.*, 1996; Chapman *et al.*, 1999; Yamagiwa & Basabose, 2006; Turner, 2006). Fig fruits show prolonged availability and constitute keystone foods for chimpanzees at Kibale and Kahuzi (Conklin & Wrangham, 1994; Basabose, 2002; Yamagiwa *et al.*, 2005). Fruit species taking a role of keystone foods are *Myrianthus holstii* for gorillas and chimpanzees at Kahuzi (Basabose, 2002; Yamagiwa *et al.*, 2005), *Saba florida*, a woody liana, for chimpanzees at Mahale, and *Musanga leo-errerae* for chimpanzees at Kalinzu (Furuichi *et al.*, 2001). By contrast, figs are uncommon and are thus not important keystone resources for the great apes in Gabon (Gautier-Hion & Michaloud, 1989; White, 1994). Fig fruits are not constantly available and are infrequently consumed by gorillas and chimpanzees at Moukalaba. These observations suggest different fruit phenology and keystone fruit species between western and

eastern habitats of the great apes. These differences may influence ecological and social features, such as ranging (Robbins & McNailage, 2003; Yamagiwa & Basabose, 2006; Turner, 2006) and grouping patterns (Watts, 1996; Yamagiwa *et al.*, 2003; Itoh & Nishida, 2007). We should take such differences into consideration for constructing wise conservation plans.

The fallen fruit census conducted in the present study is a conventional method to monitor fruit phenology that has two main advantages: 1) it enables us to calculate overall food density in the focused area, and 2) logically, the target is all of the plant species that drop fruits. On the other hand, it has three main disadvantages: 1) it underestimates or misses the rare species, 2) those species that do not drop fruits on the ground are ignored, and 3) fruiting patterns at the individual level cannot be examined. For example, most of the fruits of *Musanga cecropioides*, abundant in Moukalaba-Doudou, are eaten by the great apes in trees. The fallen fruits of this species are rarely found on the ground. For fruits of *Dialium*, as well as many Leguminosae species, their capsules split open on the tree when they are ripe. Fruits of these two species constitute important foods of gorillas and chimpanzees. A combination of this fallen fruits census and the tagged tree census applied in other study sites is required to resolve these problems and to permit inter-site comparison.

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REFERENCES

- Anderson, D.P., E.V. Nordheim, T.C. Moermond, Z.B. Gone Bi & C. Boesch 2005. Factors influencing tree phenology in Tai National Park, Côte d'Ivoire. *Biotropica*, 37: 631-640.
- Anderson, D.P., E.V. Nordheim & C. Boesch 2006. Environmental factors influencing the seasonality of estrus in chimpanzees. *Primates*, 47: 43-50.
- Basabose, A.K. 2002. Diet composition of chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. *American Journal of Primatology*, 58: 1-21.
- 2004. Fruit availability and chimpanzee party size at Kahuzi montane forest, Demo-

- cratic Republic of Congo. *Primates*, 45: 211-219.
- . 2005. Ranging patterns of chimpanzees in a montane forest of Kahuzi, Democratic Republic of Congo. *International Journal of Primatology*, 26: 33-54.
- 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.
- 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.
- Doran, D.M., A. McNeillage, D. Greer, C. Bocian, P. Mehlman & N. Shah 2002. Western lowland gorilla diet and resource availability: New evidence, cross-site comparisons, and reactions on indirect sampling methods. *American Journal of Primatology*, 58: 91-116.
- Feer, F. 1989. Comparaison des régimes alimentaires de *Cephalophus callipygus* et *C. dorsalis*, Bovidés sympatriques de la forêt sempervirente africaine. *Mammalia*, 53: 563-604.
- 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. & G. Michaloud 1989. Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. *Ecology*, 70: 1826-1833.
- Gautier-Hion, A., J-M. Duplantier, F. Quris, F. Feer, C. Sourd, J-P. Decoux, G. Dubost, L. Emmons, C. Erard, P. Hecketsweiler, A. Mounqazi, C. Roussilhon & J-M. Thiollay 1985. Fruit characteristics as a basis for fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia*, 65: 324-337.
- Hashimoto, C., S. Suzuki, Y. Takenoshita, J. Yamagiwa, A.K. Basabose & T. Furuichi 2003. How fruit abundance affects the chimpanzee party size: A comparison between four study sites. *Primates*, 44: 77-81.
- Hladik, A. 1978. Phenology and leaf production in rain forest of Gabon: Distribution and composition of food for arboreal folivores. In (G.G. Montgomery, ed.) *The Ecology of Arboreal Folivores*, pp. 51-71. Smithsonian Institution Press, Washington, D.C.
- Itoh, N. & T. Nishida 2007. Chimpanzee grouping patterns and food availability in Mahale Mountains National Park, Tanzania. *Primates*, 48: 87-96.
- Iwata, Y. & C. Ando 2007. Bed and bed-site reuse by western lowland gorillas (*Gorilla g. gorilla*) in Moukalaba-Doudou National Park, Gabon. *Primates*, 48: 77-80.
- Janzen, D.H. 1969. Seed eaters versus seed size, number, toxicity and dispersal. *Evolution*, 23: 201-228.
- Kuroda, S., T. Nishihara, S. Suzuki & R.A. Oko 1996. Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. In (W. McGrew, L. Marchant & T. Nishida, eds.) *Great Ape Societies*, pp. 71-81. Cambridge University Press, Cambridge.
- Leighton, M. & D.R. Leighton 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. In (S.T.C. Whitmore & A.C. Chadwick, eds.) *Tropical Rain Forest: Ecology and Management*, Vol. 2, pp. 181-196. Blackwell Scientific Publications, Palo Alto.
- Moscovice, L.R., M.H. Issa, K.J. Petrzalkova, N.S. Keuler, C.T. Snowdon & M.A. Huffman, 2007. Fruit availability, chimpanzee diet, and grouping patterns on Rubondo island, Tanzania. *American Journal of Primatology*, 69: 487-502.
- R Development Core Team 2007. *R: A Language and Environment for Statistical Computing*. Online. <http://www.r-project.org/> (Accessed December 1, 2007).
- Remis, M.J. 1997a. Ranging and grouping patterns of a western lowland gorilla group at Bai Hokou, Central African Republic. *American Journal of Primatology*, 43: 111-133.

- 1997b. Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: Use of variable resources. *American Journal of Primatology*, 43: 87-109.
- Robbins, M.M. & A. McNailage 2003. Home range and frugivory patterns of mountain gorillas in Bwindi Impenetrable national Park, Uganda. *International Journal of Primatology*, 24: 467-491.
- Rogers, M.E., K. Abernethy, M. Bermejo, C. Cipolletta, D. Doran, K. McFarland, T. Nishihara, M.J. Remis & C.E.G. Tutin 2004. Western gorilla diet: A synthesis from six sites. *American Journal of Primatology*, 64: 173-192.
- Sun, C., B.A. Kaplan & K.A. Kristensen 1996. Tree phenology in a tropical montane forest in Rwanda. *Biotropica*, 28: 668-681.
- Terborgh, J. 1986. Keystone plant resources in the tropical forest. In (I. Soulé & E. Michael, eds.) *Conservation Biology*, pp. 330-344. Sinauer, Sunderland.
- Turner, L.A. 2006. Vegetation and chimpanzee ranging in the Mahale Mountains National Park, Tanzania. *Memories of the Faculty of Science, Kyoto University*, 18: 45-82.
- Tutin, C.G.E. & M. Fernandez 1984. Nationwide census of gorilla (*gorilla g. gorilla*) and chimpanzee (*Pan t. troglodytes*) populations in Gabon. *American Journal of Primatology*, 6: 313-336.
- Tutin, C.E.G., M. Fernandez, M.E. Rogers, E.A. Williamson & W.C. McGrew 1991. Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lopé Reserve, Gabon. *Philosophical Transactions of The Royal Society of London Series B*, 334: 179-186.
- Tutin, C.E.G., R.M. Ham, L.J.T. White & M.J.S. Harrison 1997. The primate community of the Lopé reserve, Gabon: Diets, responses to fruit scarcity, and effects on biomass. *American Journal of Primatology*, 42: 1-24.
- Tweheyo, M. & F. Babweteera 2007. Production, seasonality and management of chimpanzee food trees in Budongo Forest, Uganda. *African Journal of Ecology*, 45: 535-544.
- 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.
- Walsh, P.D., R.A. Abernethy, M. Bermejo, R. Beyers, P. De Wachter, M.E. Akou, B. Huijbregts, D.I. Mambounga, A.K. Toham, A.M. Kilbourn, S.A. Lahm, S. Latour, F. Maisels, C. Mbina, Y. Mihindou, S.N. Obiang, E.N. Effa, M.P. Starkey, P. Teffer, M. Thibault, C.E.G. Tutin, L.J.T. White & D.S. Wilkie 2003. Catastrophic ape decline in western equatorial Africa. *Nature*, 422: 611-614.
- Watts, D.P. 1996. Comparative socio-ecology of gorillas. In (W. McGrew, L. Marchant & T. Nishida, eds.) *Great Ape Societies*, pp. 16-28. Cambridge University Press, Cambridge.
- White, L.J.T. 1994. Patterns of fruit-fall phenology in the Lopé Reserve, Gabon. *Journal of Tropical Ecology*, 10: 289-312.
- White, L.J.T., C.E.G. Tutin & M. Fernandez 1993. Group composition and diet of forest elephants, *Loxodonta africana cyclotis* Matschie 1900, in the Lopé Reserve, Gabon. *African Journal of Ecology*, 31: 181-189.
- Yamagiwa, J., J. Kahakwa & A.K. Basabose 2003. Intra-specific variation in social organization of gorillas: Implication for their social evolution. *Primates*, 44: 359-369.
- Yamagiwa, J., A.K. Basabose, K. Kaleme & T. Yumoto 2005. Diet of Grauer's gorillas in the montane forest of Kahuzi, Democratic Republic of Congo. *International Journal of Primatology*, 26: 1345-1373.
- Yamagiwa, J. & A.K. Basabose 2006. Diet and seasonal changes in sympatric gorillas and chimpanzees at Kahuzi-Biega National Park. *Primates*, 47: 74-90.
- Yamakoshi, G. 1998. Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. *American Journal of Physical Anthropology*, 106: 283-295.

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