

RESEARCH ARTICLE

Fruit Availability, Chimpanzee Diet, and Grouping Patterns on Rubondo Island, Tanzania

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We examined seasonal patterns of fruit availability, dietary quality, and group size in the descendants of an introduced chimpanzee population on Rubondo Island, Tanzania. The site has supported a free-ranging population without provisioning for 40 years. Our goals were to determine whether Rubondo chimpanzees experience periods of fruit shortage, and whether they respond to changes in fruit availability similarly to chimpanzees at endemic sites. We indexed the fruit availability of tree and liana species on transects stratified across three chimpanzee ranging areas. We used fecal analyses to evaluate seasonal changes in diet, and used data on party size and nesting group size to examine seasonal patterns of grouping. Tree fruit availability was positively correlated with rainfall, with a period of relative tree fruit scarcity corresponding with the long dry season. Liana fruit availability was not related to rainfall, and lianas exhibited less variable fruiting patterns across seasons. Fruits made up the majority of the chimpanzee diet, with lianas accounting for 35% of dietary fruit species. Fruits of the liana *Saba comorensis* were available during all months of phenological monitoring, but they were consumed more when tree fruit was scarce, suggesting that *Saba comorensis* fruits may be a fallback food for Rubondo chimpanzees. There were no increases in consumption of lower-quality plant parts between seasons, and there were no changes in group size between seasons. These results contrast with evidence from several endemic chimpanzee study sites, and indicate that Rubondo chimpanzees

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may have access to abundant and high-quality foods year round. *Am. J. Primatol.* 69:487–502, 2007. © 2007 Wiley-Liss, Inc.

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INTRODUCTION

Studies of primate food supply in tropical forests indicate spatial and temporal limitations in resources [van Schaik & Brockman, 2005]. High-quality foods, characterized by low levels of secondary compounds and high levels of readily available energy [e.g., Wrangham et al., 1998], include plant parts such as ripe fruits and young leaves that are produced at low rates and are patchily distributed within tropical forests [Hemingway & Bynum, 2005]. Changes in climate and rainfall influence patterns of fruit, leaf, and insect availability, often resulting in seasonal periods of food scarcity [Hemingway & Bynum, 2005]. The length and severity of food scarcity periods, as well as the types of alternative resources available when preferred foods are scarce, may have important consequences for primate species [Furuichi et al., 2001b]. In habitats with severe seasonality in food availability, primates may suffer weight loss and reductions in caloric intake during food scarcity periods (e.g., orangutans (*Pongo pygmaeus*) [Knott, 1998]) and may exhibit innovative behaviors, such as tool use, to access embedded food sources (e.g., capuchin monkeys (*Cebus apella libidinosus*) [Moura & Lee, 2004]).

Seasonal fluctuations in tree fruit availability have been documented at the majority of chimpanzee (*Pan troglodytes*) study sites with published phenological surveys (e.g., Kahuzi, DRC [Basabose, 2002]; Kalinzu Forest, Uganda [Furuichi et al., 2001b]; Lope Reserve, Gabon [Tutin & Fernandez, 1993]; and Bossou, Guinea [Yamakoshi, 1998]). Based on their strong dietary preference for ripe fruits, and greater absolute body size relative to other frugivorous primate species, chimpanzees are expected to experience intragroup feeding competition over discrete fruit feeding sites [Wrangham, 2000]. Periods of habitat-wide fruit scarcity are likely to increase intragroup feeding competition in chimpanzees and/or increase energetic costs associated with visiting a greater number of fruit feeding sites.

Chimpanzees exhibit a range of behavioral modifications during seasonal periods of fruit scarcity, including changes in dietary diversity, activity budgets, and monthly ranges [reviewed in Yamagiwa, 2004]. Often there is increased consumption of fallback foods, relatively stable resources that are relied upon during periods of habitat-wide fruit scarcity [Furuichi et al., 2001b; Wrangham et al., 1998]. The available fallback foods are typically lower-quality plant parts that are more difficult to digest, such as terrestrial herbaceous vegetation (THV) [Wrangham et al., 1991] and leaf material [Basabose, 2002; Tutin & Fernandez, 1993]. *Ficus* species may exhibit asynchronous fruiting patterns, and thus *Ficus* fruits are often available when other fruits are scarce, and serve as important fallback foods at some sites [Tutin & Fernandez, 1993].

Changes in grouping patterns are another common response to seasonal periods of fruit scarcity [reviewed in Wrangham, 2000]. Chimpanzees vary the size of fluctuating subgroups or parties in response to ecological changes that occur over short time frames and spatial scales, resulting in a flexible fission-fusion social structure [Goodall, 1986]. At several sites, chimpanzees reduce party size during habitat-wide fruit scarcity (Kibale, Uganda [Chapman et al., 1995];

Gombe, Tanzania [Goodall, 1986]; and Mahale, Tanzania [Matsumoto-Oda et al., 1998]). This response is thought to reduce feeding competition and travel costs, since smaller parties should satisfy foraging requirements by visiting a smaller number of discrete fruit feeding sites [Wrangham, 2000].

Although chimpanzees at most study sites experience seasonal fluctuations in fruit availability, in some locations high-quality foods are consistently available across seasons. At Budongo Forest and Bwindi Impenetrable National Park in Uganda, important chimpanzee fruit foods are available across all months, with no distinct periods of habitat-wide fruit scarcity [Newton-Fisher, 1999; Newton-Fisher et al., 2000; Stanford & Nkurunungi, 2003]. At two other sites, high-quality fruits or nuts are available during seasonal periods of fruit scarcity [Kalinzu Forest, Uganda: Furuichi et al., 2001b; Bossou, Guinea: Yamakoshi, 1998]. At all of these sites, chimpanzees do not exhibit seasonal increases in consumption of lower-quality plant foods, such as THV or leaf fragments [Furuichi et al., 2001b; Newton-Fisher, 1999; Stanford & Nkurunungi, 2003; Yamakoshi, 1998]. Furthermore, at Budongo Forest and Kalinzu Forest, no relationship was found between monthly party size and fruit availability [Hashimoto et al., 2001; Newton-Fisher et al., 2000]. This combined evidence suggests that in environments with less seasonality in fruit availability, or with high-quality fallback foods available, chimpanzees may experience low levels of food competition and maintain a high-quality diet year round.

We examined fruit availability in relation to chimpanzee diet and grouping patterns at Rubondo Island National Park, a 237-km² island in Lake Victoria, Tanzania [Borner, 1985]. In 1966–1969, the Frankfurt Zoological Society (FZS) released 17 chimpanzees to the island, in the first documented introduction of chimpanzees from captivity to the wild [Grzimek, 1970]. The chimpanzees were wild-born in several West African countries and had been housed in captive facilities for various periods of time (from several months to several years) prior to their release [Borner, 1985]. By 2 months post-release, the chimpanzees were exhibiting a range of natural foraging behaviors and provisioning was terminated [Borner, 1985]. In 1997 the FZS initiated a habituation project in collaboration with Tanzania National Parks (TANAPA). The current size of the semihabituated population is estimated at 27–35 individuals, based on limited direct observations and nest counts (Liza R. Moscovice, unpublished results).

The patterns of food availability and chimpanzee behavior observed on Rubondo Island have some important implications. The ability of the original founders to initiate natural foraging after their release without training or extensive provisioning is surprising, considering the emphasis placed on pre-release training in foraging in other chimpanzee release efforts [Tutin et al., 2001]. Specific ecological factors, such as the presence of reliable and high-quality fallback foods, may result in a relatively consistent food supply across seasons. This may have aided in the rapid transition to natural foraging and the long-term survival of chimpanzees on the island. Considering the small number of founders originally released, it is also likely that the current population has not reached carrying capacity and may experience low levels of food competition as a result. Either situation implies the possibility of examining chimpanzee behavior in an environment of relative resource abundance, which occurs rarely at endemic study sites.

We had two main goals for this study: 1) to determine temporal and spatial patterns of potential food availability for chimpanzees, emphasizing sources of succulent fruits, which are likely to be more preferred; and 2) to evaluate chimpanzee dietary selection and grouping patterns across months. If there are

periods of seasonal fruit scarcity, we expected to find corresponding periods of increased reliance on lower-quality foods and/or reductions in group size. Alternatively, if high-quality foods are relatively abundant across seasons, Rubondo chimpanzees may exhibit little fluctuation in dietary quality and grouping patterns across months.

MATERIALS AND METHODS

Study Site

Rubondo Island is located in the southwestern portion of Lake Victoria (2° 18' S, 31° 50' E) at an altitudinal range of 1,100–1,500 m a.s.l. Total rainfall in 2003 was 1,461 mm, and there was a bimodal distribution of rainfall with peaks in March–May and October–December, and a dry season in June–August. The habitat is dominated by mixed evergreen and semideciduous forest, with common species including *Croton sylvaticus*, *Drypetes gerrardii*, and *Lecaniodiscus fraxinifolius*, and often with a dense understory of lianas, or woody vines. Common native fauna include the vervet monkey (*Chlorocebus aethiops*), sitatunga (*Tragelaphus spekei*), and bushbuck (*T. scriptus*). In addition to chimpanzees, there are 12 other introduced species on the island, including elephants (*Loxodonta africana*), giraffes (*Giraffa camelopardalis*), and black and white colobus (*Colobus abyssinicus*) [Borner, 1985]. This study was conducted over 19 months, from October 2002 to April 2004. Phenological monitoring was conducted in February–December 2003, and the results are based primarily on data collected during that period.

Phenological Monitoring

During a pilot study we identified three areas of predominantly semideciduous forest habitat where the majority of chimpanzee evidence was concentrated. The areas are separated from each other by 4–16 km, and are associated with ridges reaching 1,200–1,400 m a.s.l. [Moscovice & Huffman, 2001]. We distinguish these areas of high chimpanzee presence as the northern, central, and southern regions, based on their location along the longitudinal gradient of the island. We established nine transects, 300–500 × 10 m, in a stratified random procedure across the three regions. Transects were located perpendicular to ridges and were separated by ≥ 1 km within regions and ≥ 5 km between regions. We determined tree density and composition in 86 25 × 10 m quadrats, placed at 25-m intervals along transects. Trees with ≥ 10 cm diameter measured at 1.3 m above ground (diameter at breast height (DBH)) were tagged, the DBH was recorded, and the trees were identified to the species level. Plants were identified by Frank Mbago based on on-site classifications and vouchers analyzed at the University of Dar es Salaam Herbarium.

We randomly selected a subset of six quadrats per transect (n = 54 total) for phenological monitoring, with the stipulation that an equal number occurred at high and low elevations along transects. We monitored fruit availability of all tagged trees producing fleshy fruits and with more than three individuals present within the survey area. Several species of lianas also produced fruits and occurred at high densities within survey areas [Moscovice et al., 2004]. We also monitored the fruit availability of lianas > 1 cm DBH that produced fleshy fruits and were supported by tagged trees within the phenological survey quadrats. Lianas were considered to be supported by a tree if they came in direct contact with either the trunk or branches of the tree and reached a height of > 1.3 m above ground.

The total phenological monitoring area was 1.35 ha and included 600 trees, representing 21 species, and 839 lianas, representing 13 species.

One of four researchers (L.M., M.I., G. Graziani, or A. Gallestroni) monitored phenological activity within the first 10 days of each month. Observers periodically monitored transects together to ensure a high degree of interobserver reliability. Researchers recorded the number of tree fruit patches defined as a tagged tree with ripe or unripe tree fruit present in the canopy. In previous studies tree fruit patches were similarly defined to represent discrete areas where chimpanzees are able to collect food continuously [Chapman et al., 1995; White & Wrangham, 1988]. We also recorded the number of liana fruit patches defined as a tagged tree with ripe or unripe liana fruit present in the canopy. Lianas use trees as structural supports to ascend the canopy [Gentry, 1991], and liana fruit crops are generally found in the canopies of the supporting trees, so the tree is an appropriate unit by which to distinguish discrete liana feeding sites. We measured both ripe and unripe fruit, since it was difficult to distinguish between different maturation stages for some species.

Chimpanzee Diet

We relied primarily on fecal analyses, supported by direct observations, to determine chimpanzee dietary selection across months. A confirmed chimpanzee food occurred in more than one fecal sample and/or was confirmed to be consumed during direct observations of chimpanzees. Chimpanzees process fruits primarily by swallowing seeds, rather than spitting or destroying them [Lambert, 1999], and as a result seeds are typically intact in the feces and can be identified to the species level [Tutin & Fernandez, 1993].

From October 2002 to April 2004 we collected fresh fecal samples, which were found either below fresh nests or during direct observations of chimpanzees, and stored them in plastic bags. We limited the sample collection to one fecal sample from each chimpanzee per day during direct observations. At the nest sites we collected one fecal sample from below each fresh nest. On the same day as collection, each sample was weighed to the nearest gram. We rated the amount of plant vegetative material, *Ficus* seeds, and insect remains present in each fecal sample on a 0–4 abundance scale representing the following categories: none, scarce, present, common, or abundant. Similar abundance scales have been used to indicate seasonal changes in consumption of lower-quality plant parts at other sites (Bwindi, Uganda [Stanford & Nkurunungi, 2003]; and Lope, Gabon [Tutin & Fernandez, 1993]).

The samples were washed in 1-mm mesh sieves, and clean fruit seeds were identified to the species level and counted. Seeds were identified through comparisons with samples collected from known fruits and preserved in ethanol. The total number of seeds of a given fruit species in each fecal sample was divided by the wet weight of the fecal sample and multiplied by 100 to obtain a standardized measure of the relative amount of seeds consumed per fruit species per fecal sample. Similar methods have been used to compare differences in utilization of a fruit species between gorillas and chimpanzees [Tutin & Fernandez, 1994], but these methods have not been used to compare seasonal changes in consumption of specific fruit species by chimpanzees. We do not expect that the number of seeds in feces reflects the absolute amount of fruit consumed, since chimpanzees do to a lesser extent process fruit by methods other than seed-swallowing, such as seed-spitting and wadging [Lambert, 1999]. Rather, we consider seeds that are lost to alternative methods of processing to be a constant

source of error across months, and focus on monthly changes in the relative amounts of seeds of a given species in feces as an indicator of changes in relative consumption of that species.

We identified important fruit foods based on their percentage of occurrence in >10% of fecal samples, and determined fruit preferences using Jacobs' [1974] food preference index. We calculated a preference index (D_{ri}) for each fruit species using the formula $D_{ri} = (r_i - p_i) / (r_i + p_i - 2p_i r_i)$, where r is the proportion of fruit i in the diet, estimated by the proportion of fecal samples with species i present, and p is the relative production of that fruit in the forest, estimated as the proportion of total fruit patches containing species i . The index ranges from -1 (strong rejection) to 1 (strong preference).

Group Size

To examine grouping patterns over months and seasons, we ran two analyses: one based on party size from a limited number of direct observations with good visibility, and one using nesting group size. All chimpanzees other than dependent young make their own nest nightly, and one can determine nesting group size by counting the number of fresh nests within a 30–50 m radius [Fruth & Hohmann, 1994]. Nesting group size may reflect late-afternoon and early-morning foraging party sizes [Anderson et al., 2002] and at some study sites nesting group size changes between seasons [Baldwin et al., 1981; Furuichi et al., 2001a]. We collected data from fresh nests, which were estimated to be 0–4 days old based on the abundance of fresh leaves in the nest and fresh traces of chimpanzees in the area. When we found a fresh nest, we surveyed the area within a 40-m radius of the nest, and other fresh nests found within that area were considered part of the same nesting group. To facilitate comparison between our two measures of group size, we excluded dependent young from party size estimates based on direct observations.

Analysis

We compared patterns of seasonality in tree and liana fruit availability using Pearson correlation coefficients and repeated-measures analysis of variance (ANOVA). Because of the uneven monthly sample sizes and violations of normality, we used nonparametric tests to evaluate seasonality in dietary patterns and group size. We used Kruskal-Wallis tests and Mann-Whitney post-hoc tests to compare dietary selection and grouping patterns between months and seasons. We used Spearman rank order correlations to examine whether dietary selection or grouping patterns were correlated with fruit availability. All tests were two-tailed. When making multiple comparisons between groups, we used the Bonferroni correction to control for familywise error rate. We designate these tests by $\alpha^* = \alpha/c$, where α equals 0.05, and c equals the number of comparisons performed. For all other tests, $\alpha = 0.05$. Analyses were performed with SPSS© v13. Results from parametric tests are presented as $X \pm SE$, and results from nonparametric tests are presented as the median and range.

RESULTS

Fruit Availability Across Chimpanzee Ranging Areas

Patterns of tree fruit availability were similar on transects across regions, and higher in months with more rainfall (Pearson, $n = 11$, $r = 0.734$, $P = 0.01$).

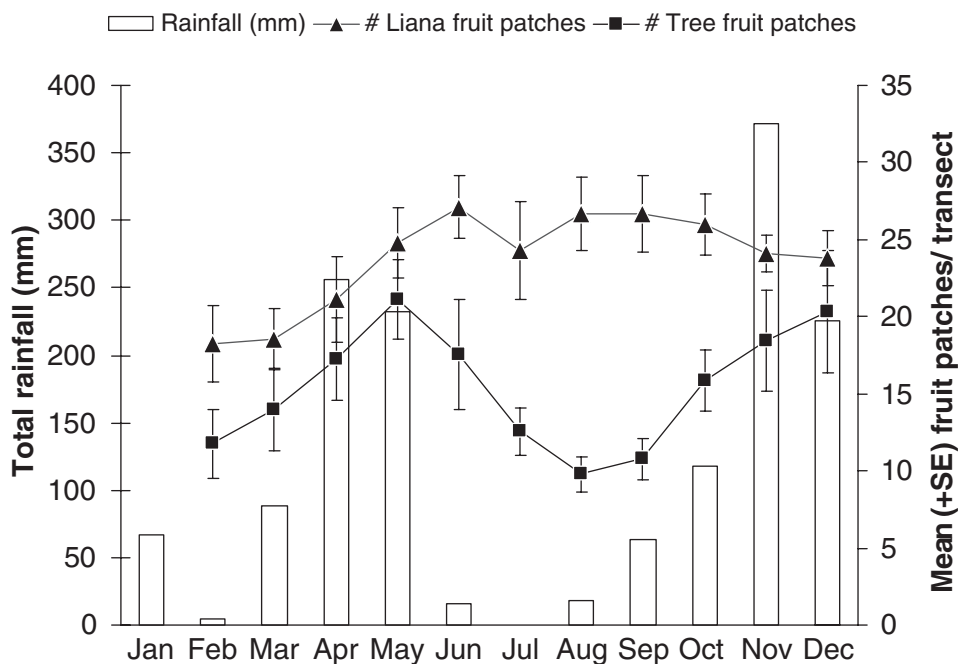


Fig. 1. Mean (\pm SE) transect density of tree and liana fruit patches in relation to rainfall. The monthly density of tree fruit patches is significantly correlated with monthly rainfall (Pearson, $P = 0.01$).

Patterns of liana fruit availability were also similar on transects across regions, but did not correlate with monthly patterns of tree fruit availability (Pearson, $n = 11$, $r = 0.052$, $P = 0.879$) or with monthly rainfall (Pearson, $n = 11$, $r = -0.059$, $P = 0.863$; Fig. 1). The density of tree fruit patches was lowest during a 3-month period in July–September, roughly coinciding with the dry season. We compared tree fruit availability in July–September with the corresponding 3-month periods occurring immediately before and after. The mean density of tree fruit patches differed significantly among the three periods ($F_{2,16} = 7.41$, $P = 0.005$), with a significant decrease in tree fruit patches in July–September compared to April–June and October–December (post-hoc, Bonferroni correction, $P < 0.014$, $\alpha^* = 0.017$). In comparison, liana fruit availability varied less across months, and the mean density of liana fruit patches did not differ among the three seasons of varying tree fruit availability ($F_{2,16} = 0.557$, $P = 0.584$).

Dietary Composition and Seasonality

From October 2002 to April 2004 we collected 147 fecal samples. We collected a median of seven samples per month (range = 0–27), from a median of four distinct locations (range = 0–8). The median number of samples collected per location was 1.5 (range = 1–6). We confirmed 46 plant food items in the diet, based on direct observation or occurrence in more than one fecal sample (Table I). Fruits accounted for 93.5% ($n = 43$) of plant food items. Of the fruit species, 35.7% ($n = 15$) were liana species, and the most common fruit in chimpanzee diet based on fecal samples was the liana *Saba comorensis* var. 1, which occurred in 66% ($n = 97$) of fecal samples. The mature fruits of *Saba comorensis* var. 1 weigh

TABLE I. Chimpanzee Plant Food List, October 2002–April 2004*

Family	Species	Life form	Part consumed	Evidence
Leguminosae	<i>Albizia gummifera</i>	Tree	Gum	O
Annonaceae	<i>Annona senegalensis</i>	Tree	Fruit	F
Moraceae	<i>Antiaris toxicaria</i>	Tree	Fruit	O/F
Rubiaceae	<i>Canthium lactescens</i>	Tree	Fruit	F
Capparidaceae	<i>Capparis erythocarpos</i>	Liana	Fruit	F
Capparidaceae	<i>Capparis tomentosa</i>	Liana	Fruit	F
Polygalaceae	<i>Carpolobia conradsiana</i>	Tree	Fruit	O
Ulmaceae	<i>Chaetacme aristata</i>	Tree	Fruit	O
Vitaceae	<i>Cissus quadrangularis</i>	Liana	Fruit	O
Rutaceae	<i>Citrus limon</i>	Tree	Fruit	F
Rubiaceae	<i>Coffea eugenioides</i>	Tree	Fruit	F
Combretaceae	<i>Combretum molle</i>	Tree	Leaf	O
Euphorbiaceae	<i>Croton sylvaticus</i>	Tree	Fruit	O/F
Sapindaceae	<i>Deinbollia fulvo-tomentella</i>	Liana	Fruit	F
Euphorbiaceae	<i>Drypetes gerrardii</i>	Tree	Fruit	O/F
Moraceae	<i>Ficus sansibarica</i>	Tree	Leaf	O
Moraceae	<i>Ficus</i> sp.	Tree	Fruit	O/F
Flacourtiaceae	<i>Flacourtia indica</i>	Tree	Fruit	F
Guttiferae	<i>Garcinia huillensis</i>	Tree	Fruit	O/F
Tiliaceae	<i>Grewia bicolor</i>	Tree	Fruit	F
Tiliaceae	<i>Grewia flavescens</i>	Liana/Shrub	Fruit	F
Sapindaceae	<i>Haplocoelum foliolosum</i>	Tree	Fruit	F
Rubiaceae	<i>Keetia venosa</i>	Liana/Shrub	Fruit	F
Anacardiaceae	<i>Lannea fulva</i>	Tree	Fruit	F
Sapindaceae	<i>Lecaniodiscus fraxinifolius</i>	Tree	Fruit	F
Rhamnaceae	<i>Maesopsis eminii</i>	Tree	Fruit	O
Sapotaceae	<i>Mimusops kummel</i>	Tree	Fruit	F
Moraceae	<i>Morus mesozygia</i>	Tree	Fruit	F
Sapindaceae	<i>Pancovia turbinata</i>	Tree	Fruit	O/F
Dichapetalaceae	<i>Parinari curatellifolia</i>	Tree	Fruit	O
Palmae	<i>Phoenix reclinata</i>	Tree	Fruit	F
Anacardiaceae	<i>Pseudospondias microcarpa</i>	Tree	Fruit	O/F
Icacinaceae	<i>Pyrenacantha sylvestris</i>	Liana	Fruit	O/F
Apocynaceae	<i>Saba comorensis</i> , var. 1 and var. 2	Liana	Fruit	O/F
Celastraceae	<i>Salacia erecta</i>	Liana	Fruit	O/F
Celastraceae	<i>Salacia leptoclada</i>	Liana	Fruit	O/F
Loganiaceae	<i>Strychnos lucens</i>	Liana	Fruit	O/F
Sapotaceae	<i>Synsepalum brevipes</i>	Tree	Fruit	O/F
Rutaceae	<i>Teclea nobilis</i>	Tree	Fruit	O/F
Menispermaceae	<i>Tinospora caffra</i>	Liana	Fruit	F
Annonaceae	<i>Uvaria angolensis</i>	Liana	Fruit	O/F
Annonaceae	<i>Uvaria</i> sp. A of FTEA	Liana	Fruit	O/F
Annonaceae	<i>Uvaria welwetschii</i>	Liana	Fruit	O/F
Verbenaceae	<i>Vitex doniana</i>	Tree	Fruit	O/F
Sapindaceae	<i>Zahna golungensis</i>	Tree	Fruit	O/F

*Scientific nomenclature follows Beentje [1994; 2002]

F, present in >1 fecal sample; O, observation of consumption.

167.8 g (± 34.5) and are among the largest fleshy fruits on the island. A second variety of *Saba comorensis* with much smaller fruits occurred in 25.9% (n = 38) of fecal samples. Fruits of an additional eight species constituted an important

TABLE II. Availability and Utilization of Important Chimpanzee Fruit Foods

Species	Growth form	% Feces containing seeds	Mean (\pm SE) monthly density fruit patches	Preference index ^a
<i>Garcinia huillensis</i>	Tree	46.9	9.8 (\pm 2.1)	0.91
<i>Antiaris toxicaria</i>	Tree	19.7	1.2 (\pm 0.26)	0.87
<i>Drypetes gerrardii</i>	Tree	21.8	5.5 (\pm 2.7)	0.75
<i>Saba comorensis</i> var. 2	Liana	25.9	23.5 (\pm 5.2)	0.60
<i>Teclea nobilis</i>	Tree	17.0	22.8 (\pm 3.3)	0.49
<i>Saba comorensis</i> var. 1	Liana	66.0	145.7 (\pm 7.6)	0.46
<i>Uvaria</i> sp.	Liana	12.2	17.2 (\pm 4.9)	0.06
<i>Strychnos lucens</i>	Liana	15.0	47.4 (\pm 4.6)	-0.03
<i>Pseudospondias microcarpa</i> ^b	Tree	12.2	NA	NA
<i>Phoenix reclinata</i> ^b	Tree	10.9	NA	NA

Scientific nomenclature follows Beentje [1994; 2002].

^aScores based on Jacobs' [1974] food preference index (+1, strongly preferred; -1, strongly rejected).

^bPhenology not monitored due to <3 individuals present in regions.

portion of chimpanzee diet, based on occurrence in >10% of fecal samples (Table II). Ficus seeds were present in 57.8% (n = 85) of samples, and fibrous leaf or pith material was present in 35.4% (n = 52) of samples. We also confirmed several nonplant foods in the diet, including termites (*Microtermes* and *Odontotermes* sp.), ants (*Polyrachis* sp.), and grasshoppers (*Homorocoryphus nitidulus vicinus*). We once observed chimpanzees killing and eating an immature sitatunga (*Tragelaphus spekei*).

Of the confirmed chimpanzee fruit foods, 53.8% (n = 14) of tree species and 73.3% (n = 11) of liana species were monitored on transects. The other species were not present in sufficient densities in the survey areas to be monitored. These included two species, *Phoenix reclinata* and *Pseudospondias microcarpa*, that constituted an important portion of chimpanzee diet based on occurrence in >10% of fecal samples. We determined food preferences for the eight important fruit foods that were monitored on transects. The most preferred foods were the tree species *Garcinia huillensis*, *Antiaris toxicaria*, and *Drypetes gerrardii*. Several other fruit species had scores near 0, indicating that they were eaten opportunistically (see Table II).

Because of the small monthly sample sizes, we compared fecal dietary contents among the three tree fruit availability seasons: the April–June high tree fruit availability season (n = 11 samples), the July–September low tree fruit availability season (n = 43 samples), and the October–December high tree fruit availability season (n = 30 samples). All fecal samples (n = 84) contained seeds of fruit, with a median of three fruit species per fecal sample (range = 1–6). The number of fruit species per sample remained constant across seasons (Kruskal-Wallis test, $\chi^2 = 0.256$, df = 2, $P = 0.88$).

During the low tree fruit availability season, chimpanzees consumed 16 different fruit species, although most occurred in only a small number of fecal samples. However, two species (the tree *Garcinia huillensis* and the liana *Saba comorensis* var. 1) were relied on heavily during this season. Seeds from *Garcinia huillensis* occurred in 69.8% (n = 30) of fecal samples, and seeds from the liana *Saba comorensis* var. 1 occurred in 100% (n = 43) of fecal samples in the

dry season. Consumption of *Garcinia huillensis* differed among seasons (Kruskal-Wallis test, $\chi^2 = 20.43$, $df = 2$, $P < 0.001$), with more *Garcinia* seeds in feces in the low tree fruit availability season than in either April–June (Mann-Whitney test, $U = 71.5$, $n_1 = 43$, $n_2 = 11$, $\alpha^* = 0.017$, $P < 0.001$) or October–December (Mann-Whitney test, $U = 375.0$, $n_1 = 43$, $n_2 = 30$, $\alpha^* = 0.017$, $P = 0.002$). There were also significantly more *Garcinia* seeds in the feces in October–December than in April–June (Mann-Whitney test, $U = 99.0$, $n_1 = 30$, $n_2 = 11$, $\alpha^* = 0.017$, $P = 0.016$; Fig. 2a). The main *Garcinia* fruiting period occurred from August–October, and the monthly median *Garcinia* seed score in feces was significantly correlated with the monthly median number of *Garcinia* fruit patches on transects (Spearman, $n = 10$, $r = 0.643$, $P = 0.045$), suggesting that consumption of *Garcinia* closely tracked its availability.

Consumption of *Saba comorensis* var. 1 also differed significantly between tree fruit availability seasons (Kruskal-Wallis test, $\chi^2 = 13.98$, $df = 2$, $P = 0.001$), with significantly more *Saba* seeds in feces in the low tree fruit availability season than in either April–June (Mann-Whitney test, $U = 87.5$, $n_1 = 43$, $n_2 = 11$, $\alpha^* = 0.017$, $P = 0.001$) or October–December (Mann-Whitney test, $U = 395.0$, $n_1 = 43$, $n_2 = 30$, $\alpha^* = 0.017$, $P = 0.005$). *Saba* seed scores did not differ between the high tree fruit availability seasons (Mann-Whitney test, $U = 130.5$, $P = 0.308$; Fig. 2b). Fruit of *Saba comorensis* var. 1 was available during all 11 months of phenological monitoring. There was no relationship between the monthly median *Saba* seed score in feces and the monthly median number of *Saba* fruit patches (Spearman, $n = 10$, $r = 0.447$, $P = 0.195$).

Ficus seed abundance scores did not differ significantly among seasons (Kruskal-Wallis test, $\chi^2 = 3.92$, $df = 2$, $P = 0.141$). The leaf and pith abundance score differed among seasons (Kruskal-Wallis test, $\chi^2 = 6.59$, $df = 2$, $P = 0.037$), with higher scores in October–December compared to April–June (Mann-Whitney test, $U = 82.5$, $n_1 = 30$, $n_2 = 11$, $\alpha^* = 0.017$, $P = 0.011$). However, the leaf and pith abundance score did not increase significantly in the July–September low tree fruit availability season compared to the other seasons (Mann-Whitney tests, $U = 195.0$ – 492.0 , $\alpha^* = 0.017$, $P = 0.093$ – 0.258 ; Fig. 3).

Grouping Patterns

We collected data on party size from 56 direct observations, with a median of 2.5 (range = 1–10) observations per month, and from 138 fresh nest sites, with a median of four nest sites surveyed each month (range = 1–26). The mean nesting group size was 3.42 (± 0.29), and median nesting group size was 2 (range = 1–19). These values are similar to party size estimates from direct sightings (mean party size = 3.29 (± 0.24); median party size = 3 (range = 1–9)). However, monthly nesting group size did not correlate with monthly party size (Spearman, $n = 18$, $r = -0.183$, $P = 0.467$). Nesting group size and party size did not change across months (Kruskal-Wallis, $\chi^2 = 17.40$ – 24.05 , $df = 18$, $P = 0.118$ – 0.496 ; Fig. 4), or across the three tree fruit availability seasons (Kruskal-Wallis, $\chi^2 = 0.346$ – 0.656 , $df = 2$, $P = 0.720$ – 0.841). Nesting group size tended to increase in months with the lowest density of tree fruit patches, although this relationship did not reach significance (Spearman, $n = 11$, $r = -0.567$, $P = 0.07$). Nesting group size was unrelated to monthly density of liana fruit patches, or to monthly density of combined fruit patches from trees and lianas (Spearman, $r = -0.097$ – 0.164 , $P = 0.776$ – 0.630). Monthly party size from direct observations was not related to measures of fruit availability (Spearman, $n = 11$, $r = -0.224$ – 0.310 , $P = 0.508$ – 0.946).

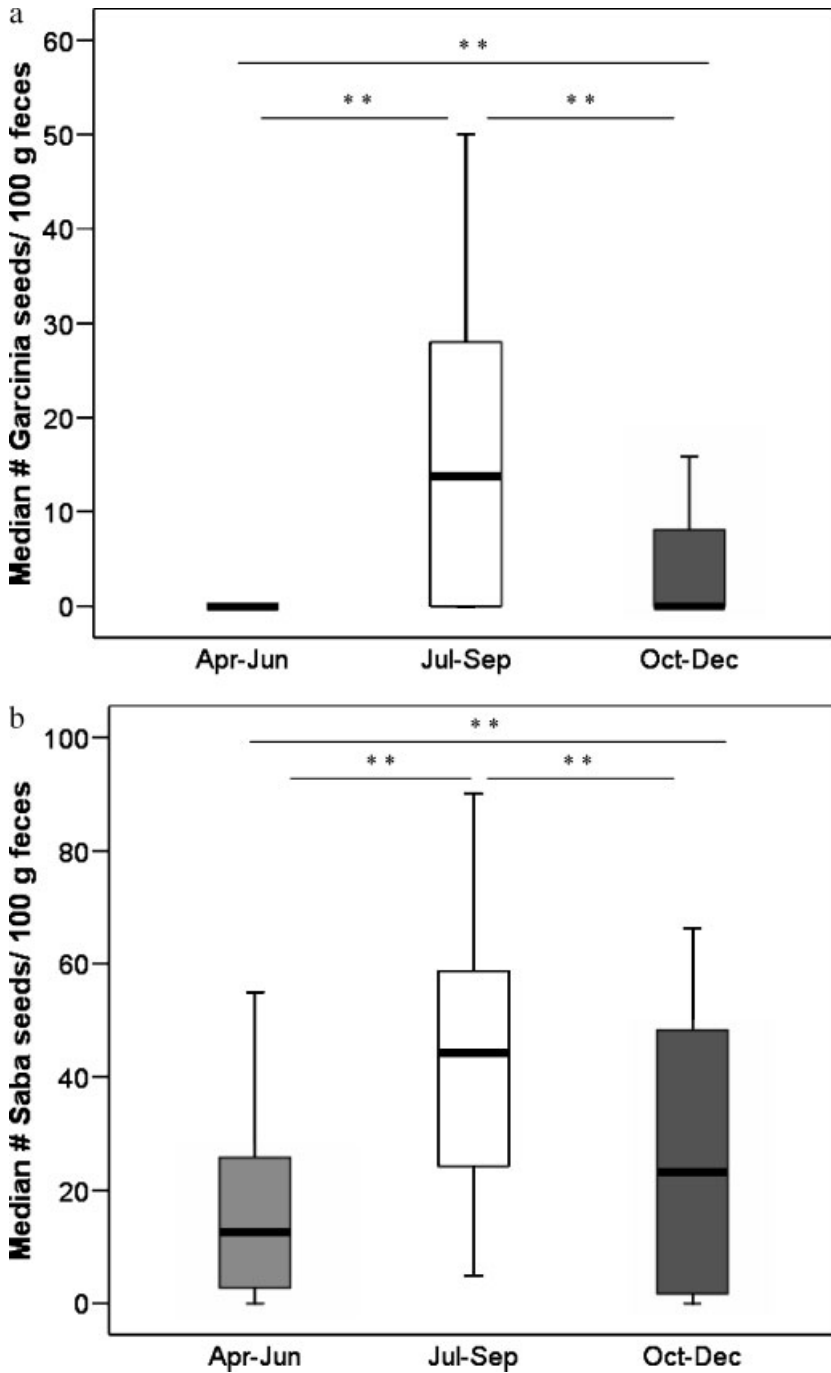


Fig. 2. **a:** Median fecal seed score of *Garcinia huillensis* across seasons. **b:** Median fecal seed score of *Saba comorensis* var. 1 across seasons. Boxes represent the interquartile range containing 50% of the values. The line across the box represents the median value. The whiskers extend to the smallest and largest values. ** $P < 0.01$.

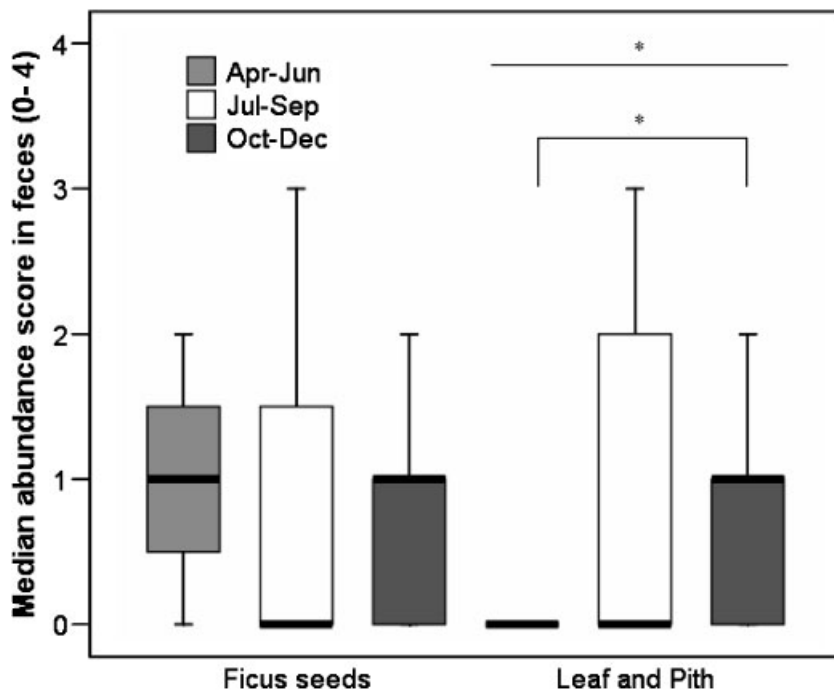


Fig. 3. Median fecal abundance score of *Ficus* sp. and leaf and pith material across seasons. Boxes represent the interquartile range containing 50% of the values. The line across the box represents the median value. The whiskers extend to the smallest and largest values. * $P < 0.05$.

DISCUSSION

We surveyed fruit availability on transects distributed widely across three regions of heavy chimpanzee utilization. Our results indicate similar patterns of fruit availability across the three regions. Peaks in tree fruit availability corresponded with the wettest periods of the year, and a period of relative tree fruit scarcity occurred across all transects beginning 1 month after the onset of the dry season. Similar dry season periods of habitat-wide tree fruit scarcity occur at other chimpanzee study sites as well [e.g., Furuichi et al., 2001b; Tutin & Fernandez, 1993].

In contrast to patterns of tree fruit availability, liana fruit availability was less variable across seasons, suggesting that liana fruit may play an important role in mitigating periods of tree fruit scarcity. This is consistent with evidence from several neotropical study sites, where liana fruiting patterns are more aseasonal compared to tree fruiting patterns [Opler et al., 1991; Putz & Windsor, 1987]. Lianas have several adaptations for accessing and storing water, including a deep root structure and efficient vascular system [Gentry, 1991], which may explain why lianas exhibit aseasonal fruit production and thrive in habitats with seasonal moisture stress [Perez-Salicrup et al., 2001].

Because of the relatively short length of this study and the semihabituated state of the chimpanzees, our data on dietary composition are not comprehensive. However, the fecal analyses were an effective, indirect method for identifying important fruit foods in chimpanzee diet, as has been found elsewhere [Basabose, 2002; Tutin & Fernandez, 1993]. The preference indices suggest that Rubondo

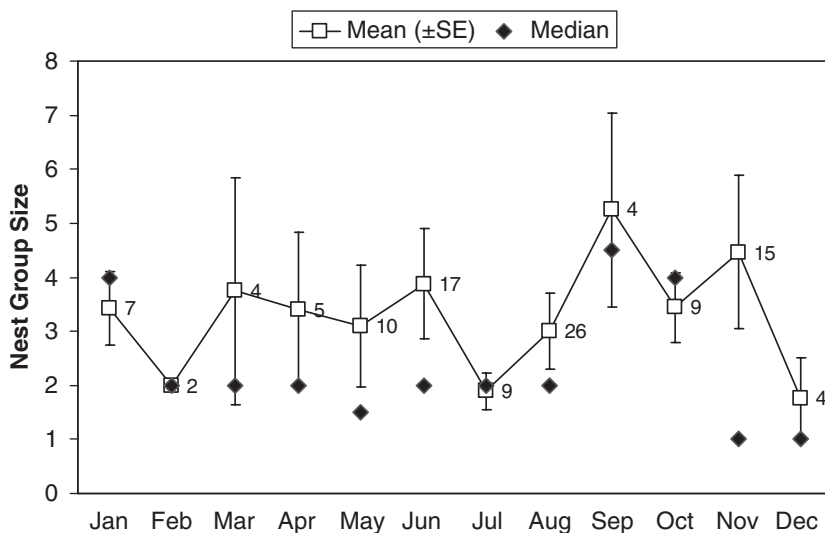


Fig. 4. Mean (\pm SE) and median nesting group size across months. The number of independent nest sites sampled in each month is indicated.

chimpanzees are selective in fruit consumption, utilizing the fruits of some tree species, including *Garcinia huillensis* and *Antiaris toxicaria*, disproportionately to their overall availability in the habitat. Further studies should determine fruit availability for other confirmed chimpanzee foods, including the two species of important foods that were not present in the transect areas. We suspect that the fruiting patterns of these species will coincide with broader wet-season tree fruiting peaks, since consumption of these species occurred primarily during the wet seasons (Liza R. Moscovice, unpublished results).

During the low tree fruiting season, the chimpanzees relied primarily on the fruits of the tree *Garcinia huillensis* and the liana *Saba comorensis* var. 1. *Garcinia huillensis* is not a stable fruit resource, but exhibits a fruiting peak late in the dry season when other tree fruit is scarce. Our results suggest that chimpanzees closely track *Garcinia* fruit availability and seek out fruit of this preferred species. In contrast, the liana *Saba comorensis* var. 1 fits the characteristics of a fallback food (i.e., a relatively stable resource that is utilized more during periods of habitat-wide tree fruit scarcity). *Saba* fruits may be eaten opportunistically because of their widespread availability across ranging areas [Moscovice et al., 2004]. Liana densities on Rubondo Island are extremely high relative to the few other chimpanzee study sites with data on liana densities [e.g., Eilu, 2000], which may explain the important role of liana fruits in chimpanzee diet at Rubondo. Several ecological factors associated with liana proliferation at other study sites, including a relatively dry climate [Perez-Salicrup et al., 2001] and high levels of tree-fall gaps within the forest [Schnitzer & Carson, 2001], also occur on Rubondo Island and may help to explain the high liana densities.

If Rubondo chimpanzees experience seasonal fruit shortages, we would expect corresponding increases in the use of lower-quality fallback foods, including pith and leaf material and possibly *Ficus* fruits. Based on the relatively low frequency of *Ficus* presence in fecal samples, and the lack of seasonal changes in *Ficus* consumption, *Ficus* may be a less important food source for chimpanzees on Rubondo Island compared with other endemic chimpanzee sites

[e.g., Basabose, 2002; Stanford & Nkurunungi, 2003]. The median abundance values of pith and leaf material in the feces remained low across seasons despite greater variance in abundance scores in the low tree fruit availability season. The majority of vegetative plant parts remaining in feces were undigested leaf fragments, with little evidence for pith from THV. Two common families of THV utilized at other chimpanzee study sites, *Zingiberaceae* and *Marantaceae* [Wrangham et al., 1996], were not found on Rubondo Island during preliminary vegetation surveys (Frank Mbago, unpublished report). Our data indicating that 35% of feces contain leaf fragments correspond to those from several other study sites where leaf remains were found in 18–56% of fecal samples (Lope, Gabon [Tutin & Fernandez, 1993]; and Kibale, Uganda [Wrangham et al., 1991]). However, the Rubondo site may differ in terms of the negligible role of THV in the diet compared to other sites.

The lack of significant variation in observed party size or nesting group size across months and seasons provides preliminary evidence that chimpanzee grouping patterns on Rubondo Island may not be strongly influenced by fruit availability. In contrast, at Kalinzu Forest, Uganda, nesting group size was significantly smaller in the dry season of low fruit availability [Furuichi et al., 2001a]. Additional data on day party size are needed to confirm these results.

Canopy trees dominate the fruiting rhythm in tropical forests because of their greater biomass and larger fruit crops relative to other plant types [Foster, 1982]. The strong preferences of Rubondo chimpanzees for fruits of several tree species show that tree fruiting patterns have an important influence on behavior. However, the diet and grouping patterns of the Rubondo chimpanzees are best understood by considering the role of a liana species in providing a fruit fallback food during periods of relative tree fruit scarcity. It is likely that more consistent fruit availability across seasons, resulting in part from the high density and aseasonal fruiting patterns of lianas, is an important factor in sustaining the introduced chimpanzee population on Rubondo Island.

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