

## RESEARCH ARTICLE

Diet of Chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 2. Temporal Variation and Fallback FoodsDAVID P. WATTS<sup>1\*</sup>, KEVIN B. POTTS<sup>2</sup>, JEREMIAH S. LWANGA<sup>3</sup>, AND JOHN C. MITANI<sup>4</sup><sup>1</sup>Department of Anthropology, Yale University, New Haven, Connecticut<sup>2</sup>Department of Biology, Augsburg College, Minneapolis, Minnesota<sup>3</sup>Makerere University Institute for the Environment and Natural Resources, Kampala, Uganda<sup>4</sup>Department of Anthropology, University of Michigan, Ann Arbor, Michigan

Highly frugivorous primates like chimpanzees (*Pan troglodytes*) must contend with temporal variation in food abundance and quality by tracking fruit crops and relying more on alternative foods, some of them fallbacks, when fruit is scarce. We used behavioral data from 122 months between 1995 and 2009 plus 12 years of phenology records to investigate temporal dietary variation and use of fallback foods by chimpanzees at Ngogo, Kibale National Park, Uganda. Fruit, including figs, comprised most of the diet. Fruit and fig availability varied seasonally, but the exact timing of fruit production and the amount of fruit produced varied extensively from year to year, both overall and within and among species. Feeding time devoted to all major fruit and fig species was positively associated with availability, reinforcing the argument that chimpanzees are ripe fruit specialists. Feeding time devoted to figs—particularly *Ficus mucuso* (the top food)—varied inversely with the abundance of nonfig fruits and with foraging effort devoted to such fruit. However, figs contributed much of the diet for most of the year and are best seen as staples available most of the time and eaten in proportion to availability. Leaves also contributed much of the diet and served as fallbacks when nonfig fruits were scarce. In contrast to the nearby Kanyawara study site in Kibale, pith and stems contributed little of the diet and were not fallbacks. Fruit seasons (periods of at least 2 months when nonfig fruits account for at least 40% of feeding time; Gilby & Wrangham., Behavioral Ecology and Sociobiology 61:1771–1779, 2007) were more common at Ngogo than Kanyawara, consistent with an earlier report that fruit availability varies less at Ngogo [Chapman et al., African Journal of Ecology 35:287–302, 1997]. *F. mucuso* is absent at Kanyawara; its high density at Ngogo, combined with lower variation in fruit availability, probably helps to explain why chimpanzee population density is much higher at Ngogo. Am. J. Primatol. 74:130–144, 2012. © 2011 Wiley Periodicals, Inc.

**Key words:** chimpanzees; seasonality; frugivory; figs; fallback foods

## INTRODUCTION

Nonhuman primates face temporal variation in food abundance and quality that may or may not be seasonal, where seasonal events “occur with very high predictability from year to year in the same few calendar months” [Struhsaker, 1997, p 41]. This variation influences diet, habitat use, social structure, social relationships, and mating and life history strategies [reviewed in Campbell et al., 2007; Hemingway & Bynum, 2005]. Major seasonal changes in food abundance occur in some habitats, especially those with long, predictable dry seasons. Even when seasonal variation is less marked, how effective behavioral and physiological responses to changes in food supplies are can influence fitness, especially when food is scarce. For example, decreased fruit availability during long dry seasons in southwestern Madagascar underlies birth seasonality in lemurs and seasonal changes in physiology ranging from lowering basal metabolism and growth rates while

remaining active in ringtailed lemurs [*Lemur catta*; Pereira, 1993] to torpor and hibernation in cheirogaleids [Schülke & Ostner, 2007]. At the opposite extreme, mountain gorillas (*Gorilla gorilla beringei*) in the Virungas show no predictable seasonality in diet or habitat use unless their home ranges contain bamboo forest [Watts, 1998].

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Kibale National Park, Uganda, is home to eight diurnal primate species [Struhsaker, 1997], including eastern chimpanzees (*Pan troglodytes schweinfurthii*). Kibale typically has rainy seasons from March through early June and from September through November, separated by intervening dry periods, but considerable interannual variation in the amount and timing of rain exists [Chapman et al., 2004; Struhsaker, 1997]. Likewise, the exact timing of fruiting, flowering, and new leaf production and the degree of phenological synchrony varies within and among tree species, some of which fruit supraannually and many of which might bear some fruit at any time of year [Butynski, 1994; Chapman et al., 1997, 2004; Struhsaker, 1997]. Primates that rely heavily on fruit should respond to fruit scarcity by tracking available fruit supplies and/or devoting more foraging effort to alternative foods, such as flowers, nectar, nonreproductive plant parts, and invertebrates [Conklin-Brittain et al., 1998; Lambert, 2007; Marshall & Wrangham, 2007; Marshall et al., 2009; Terborgh, 1983; Wrangham et al., 1991, 1998]. For example, redtail monkeys (*Cercopithecus ascanius*) and blue monkeys (*Cercopithecus mitis*) at the Kanyawara study site in Kibale eat more leaves and forage for invertebrates more when drupaceous fruit is scarce [Conklin-Brittain et al., 1998; Lambert, 2002].

Flexibility in foraging often includes use of “fallback foods.” This term has been defined variously, but typically refers to relatively low-quality foods used in inverse proportion to the abundance of high-quality, preferred foods, hence used mostly or exclusively when these are scarce [Harrison & Marshall, 2011; Lambert, 2007; Marshall & Wrangham, 2007; Marshall & Leighton, 2006; Marshall et al., 2009; Wrangham et al., 1998]. “Quality” refers to ease of energy extraction; for plant parts, this not only depends partly on extraoral processing but also varies inversely with digestibility, thus with structural carbohydrate content. Leaves, pith, and other plant parts high in cellulose and hemicellulose are usually low-quality foods, whereas fruit usually [but see Rothman et al., 2004] is high quality. Some primate species can subsist better than others on foods high in structural carbohydrates because of morphological and/or physiological adaptations (e.g., specialized fermentation chambers in the gut) or simply because large size decreases their relative metabolic needs; they thus can use fallback foods toward the low end of the quality spectrum [Lambert, 2007; Marshall & Wrangham, 2007; Marshall et al., 2009]. Low-quality foods are usually more abundant than high-quality foods [Marshall & Wrangham, 2007]. Fallbacks also vary in the degree to which they enable individuals to meet physiological functions [Lambert, 2007], from “staples” that can meet all such functions and can contribute 100% of the diet when preferred

resources are scarce to “fillers” that cannot do so and never contribute 100% of intake for extended periods [Marshall & Wrangham, 2007; Marshall et al., 2009]. “Staple” and “filler” usually refer to food categories, not particular foods. For example, Marshall et al. [2009] characterize western gorillas (*Gorilla gorilla gorilla*) as using staple fallbacks when fruit is scarce, but the “staples” include pith, stems, and leaves from multiple species [Rogers et al., 2004]. Staples are usually more abundant and poorer quality than fillers, but overlap in quality can be considerable [Marshall et al., 2009].

Potential fallbacks can vary in availability (e.g., western gorilla staple fallbacks are perennially available), and the degree of within-species phenological synchrony can influence their use [Potts, 2008]. Figs (*Ficus* spp.) are important foods for many primate species in both the Old and New World tropics [e.g., Sumatran orangutans, *Pongo pygmaeus*: Wich et al., 2004, 2006]. Fruit production tends to be asynchronous within and among fig species, which makes figs good candidates for staple fallbacks where they are abundant, as is the case for white-bearded gibbons (*Hylobates albibarbis*) at Gunung Palung [Marshall & Leighton, 2006].

Chimpanzees are large-bodied, omnivorous primates that mostly consume fruit [reviewed in Harrison & Marshall, 2011; Watts et al., 2011]. Their propensity to pursue available fruit crops even when drupaceous fruit are scarce overall, coupled with their ability to reduce feeding competition by foraging solitarily or in small parties, leads some researchers to label them “ripe fruit specialists” [e.g., Wrangham et al., 1996]. Chimpanzees rely heavily on figs in many habitats [e.g., Budongo: Reynolds, 2006]. At Kanyawara, chimpanzees focused their foraging effort on drupaceous fruit over a 1-year period [Wrangham et al., 1998], but used figs as primary fallbacks and perennially available pith and stems of herbaceous plants as secondary fallbacks [cf. Wrangham et al., 1991, 1993, 1996, 1998]. Kanyawara chimpanzees also often concentrated on certain important fruit species during “seasons,” defined as periods of two or more months during which nonfig fruit accounts at least 40% of feeding time [Gilby & Wrangham, 2007].

In a companion article [Watts et al., 2011], we used long-term data to document diet composition and diversity for chimpanzees at Ngogo, a second Kibale site. Fruit was the largest diet component at Ngogo, and, like at Kanyawara [Wrangham et al., 1998], chimpanzees at Ngogo ate ripe fruit other than figs in proportion to its overall abundance. However, the most important food species at Ngogo was a fig, *Ficus mucoso*, which accounted for nearly 18% of total feeding time during a 122-month period that included eight consecutive years. Also, chimpanzees spent considerably more time in eating leaves and much less in eating pith and stems at

Ngogo than at Kanyawara. Earlier work indicated that fruit abundance varied less at Ngogo [Chapman et al., 1997], and in a 1-year study, Potts [2008] found that important food species that fruited synchronously when overall fruit abundance was low were more common at Ngogo. These findings raise the possibility that substantial differences in responses to fluctuations in fruit availability and in use of fallbacks exist between the two sites. Along with differences in overall food abundance, this could help to explain why the chimpanzee community at Ngogo is over three times as large as that at Kanyawara and population density is correspondingly higher.

Here, we use the same data on diet and long-term phenology data to examine how food abundance varies over time and how this influences diet composition at Ngogo. In particular, we ask whether the chimpanzees used fruit from particular species in proportion to its abundance; whether consistent seasonal variation occurred; and whether figs, leaves, and/or pith and stems served as fallback foods when nonfig fruits were scarce. We place the Ngogo data in the context of information on fallback foods at other chimpanzee study sites and on the general importance of figs in the diets of many nonhuman primate species. We also compare the frequency and length of fruit “seasons” [sensu Gilby & Wrangham, 2007] to data from Kanyawara. The data on the phenology of important fruit and fig food sources augment previous data from Ngogo [Chapman et al., 1997; Mitani et al., 2005; Potts et al., 2009, 2011].

## METHODS

### Study Site and Study Animals

Kibale National Park is in southwestern Uganda between 0°13'–0° 41' N and 30°19'–30° 32' E. Most of the 795-km<sup>2</sup> park is covered by moist evergreen or semideciduous forest transitional between lowland and montane forest [Struhsaker, 1997]. The Ngogo study area is in the center of Kibale, about 11 km SSE of the Kanyawara study area, and is mostly a mosaic of dry-ground forest at various successional stages, including large tracts of old growth stands adjacent to early- to mid-stage colonizing forests that were grasslands until 1955 or later [Lwanga, 2003]. It also includes areas of swamp forest, bush dominated by *Acanthus pubescans*, papyrus (*Cyperus papyrus*) swamp, and anthropogenic grasslands [Lwanga et al., 2000]. Ngogo chimpanzees use all vegetation formations [Lwanga, 2003], but predominately use old-growth forest. Their home range lies entirely within the forest; they do not raid crops. Kibale follows north–south gradients of decreasing altitude and rainfall. The Ngogo study area lies between about 1,400 and 1,470 m in altitude and receives about 1,479 mm of annual rainfall, mostly from March to May and from September to December.

The Ngogo chimpanzee community is the largest ever documented; it has been observed continuously since mid-1995, during which time it has had about 142–165 members, including 22–32 adult males and about 42–50 adult females [Langergraber et al., 2009]. As of August 2011, it had at least 165 members, including 31 adult and 17 adolescent males, at least 52 adult females (the status of two peripheral females was uncertain), 11 adolescent females, and at least 33 infants and 21 juveniles [Watts, personal observation]. Its home range is about 35 km<sup>2</sup>, including an area of recent range expansion [Mitani et al., 2010]. In contrast, the Kanyawara community, which has a similar-sized home range [c. 32 km<sup>2</sup>; Stumpf et al., 2009; Wilson, 2001], had 53 members in August 2011 and has averaged around 50 members during the history of research at the site [M. Muller, pers. comm. to D. Watts, August 29, 2011]. The Ngogo chimpanzees are well habituated, and all feeding data presented here come from direct observations.

### Sampling of Feeding Behavior

We used two data sets for the analyses presented below [cf. Watts et al., 2011]. One includes focal data collected by Watts in 55 months of observation between 1995 and 2009. During samples, Watts tried to identify all foods that focal individuals ingested and recorded the total amount of time that they spent in eating each. A “food” was a distinct plant part and species or a distinct type of nonplant food (e.g., honey). Most foods were classified by plant part; other categories included mushrooms, honey, soil, meat, and foods of invertebrate origin [Watts et al., 2011]. The main goal of focal sampling was to record data on male social behavior, so the data are biased toward adult and, to a lesser extent, adolescent males, although they include some samples of females. We discuss the possible implications of this bias elsewhere [Watts et al., 2011]. The second data set comprises monthly summaries of scan samples collected by Ngogo Chimpanzee Project Field Assistants from January 1999 through November 2006, excluding 67 months when Watts was at Ngogo. During scans at 15-min intervals, observers identified the predominant food that chimpanzees were eating. The two methods gave similar pictures of monthly diet composition, with most differences due to sampling of different individuals/parties in different areas by different observers on the same day; this justifies combining the two data sets [Watts et al., 2011]. Direct comparison of data collected simultaneously by the two methods at Kanyawara also gave similar pictures of general diet composition [Gilby et al., 2010].

For each data set, we estimated the total percent of feeding time devoted to each distinct food item on a monthly basis. For focal data, these values were,

for each food  $i$ , the number of minutes spent eating food  $i$  in a given month divided by the total number of minutes of feeding data for the month and then multiplied by 100. For scan data, the equivalent measures were the number of scans in which food  $i$  was recorded that month divided by the number of scans for the month, multiplied by 100. We also calculated the percentage of feeding time devoted to each food category per month. In assigning foods to categories, we distinguished figs from other (“non-fig”) fruits. We transformed percentage data to arcsine or square root values for linear regressions of monthly proportions of feeding time devoted to different food categories or to specific foods on the availability of those foods or of all nonfig fruits.

### Assessment of Fruit Availability

Field Assistants at Ngogo collect monthly phenology data on 20 stems each of 20 tree species from which the chimpanzees eat fruit (including figs). Together, fruit and seeds from these species together contributed 70.4% of the chimpanzees’ total feeding time; this included 98.0% of feeding time devoted to nonfig fruits, 90.3% of feeding time devoted to figs, and 98.6% of feeding time devote to seeds [Watts et al., 2011]. We used the phenology data for each month to calculate a ripe fruit score (RFS), given by Mitani et al. [2002]:

$$\text{RFS} = \sum_{i=1}^{20} p_i \cdot d_i \cdot s_i$$

where  $p_i$  is the percentage of the  $i$ th tree species possessing ripe fruit,  $d_i$  is the density of the  $i$ th tree species (stems per ha), and  $s_i$  is the mean DBH (cm) of the  $i$ th tree species. The sample includes six species of figs; below, we refer to the combined scores for these species only as “RFS<sub>fig</sub>,” to the combined scores for the 14 nonfig fruit species as “RFS<sub>nff</sub>,” and to the combined scores for all 20 species as “RFS<sub>all</sub>.” The resulting scores allow assessment of variation in overall fruit availability, fig availability, and availability of nonfig fruit among different calendar months, within the same month across years, and among years. They also allow calculation of RFSs for each of the individual species included in the sample, notably for *Ficus mucoso*; we refer to the scores for this species as RFS<sub>Fm</sub>. Phenology data extend from January 1998 through December 2009; this includes 109 months for which diet data were available (October 1998 through November 2006; June through August in 2007, 2008, and 2010; and June through October 2009). We used all 144 months to investigate monthly and annual variation in fruit production, and used the 109-month sample to analyze relationships between diet and phenology.

Potts et al. [2009] used a partial version of the same phenology data set (January 1999 through October 2005) to examine monthly variation in habitat-wide fruit production and to categorize important food species as those that fruited mostly when overall fruit availability was high vs. those that fruited mostly when it was low, with these further categorized as showing high or low fruiting synchrony. We used phenology scores to calculate five additional measures of fruiting periodicity and synchrony intended to provide comparative information on how often individual species produced fruit crops and how long these lasted. These included (1) the percent of all months during which one or more stems of a given species bore fruit; (2) the mean length of intervals (the number of consecutive months) during which at least one stem bore fruit; (3) the mean length of intervals during which no stems bore fruit; (4) the mean length of intervals between months in which the RFS fell in the top quartile of all scores for the species; and (5) the mean length of intervals during which the RFS fell into the top quartile of all scores for the species. We also performed time series analysis of monthly RFS<sub>all</sub>, RFS<sub>fig</sub>, RFS<sub>nff</sub>, and RFS<sub>Fm</sub> values, using the Decomposition procedure in Minitab 16, to examine the extent of seasonality in these variables. For each month, this procedure yields a seasonality index that is simply the difference between the respective RFS score for that month and the overall mean for all months. We used  $\chi^2$  tests to look for significant seasonal effects.

All data were observational only, and methods were adhered to Ugandan legal requirements and the ASP principles for the ethical treatment of nonhuman primates. This research was granted an exemption by the Yale University IACUC.

## RESULTS

### Variation in Fruit Availability

#### Overall variation

Fruit abundance varied considerably, and fruit production and fruiting schedules varied extensively among and within species. The RFS<sub>all</sub> was always greater than zero—that is, at least one stem in the phenology sample bore ripe fruit in all 144 sample months—but it varied by more than two orders of magnitude (mean =  $942.0 \pm 644.1$ , range = 15.3–2,755.0). On average, annual fruit production was lowest during January through March, typically a dry season and the start of a rainy season. It peaked in May to July, a period that typically included most of the second dry season, and a second, somewhat higher peak occurred in the September to December rainy season (Fig. 1A). This overall pattern mostly reflected RFS<sub>nff</sub> values, which accounted for most of the RFS<sub>all</sub> (Fig. 1B). Variation among years in the RFS<sub>all</sub> and RFS<sub>nff</sub> values for each

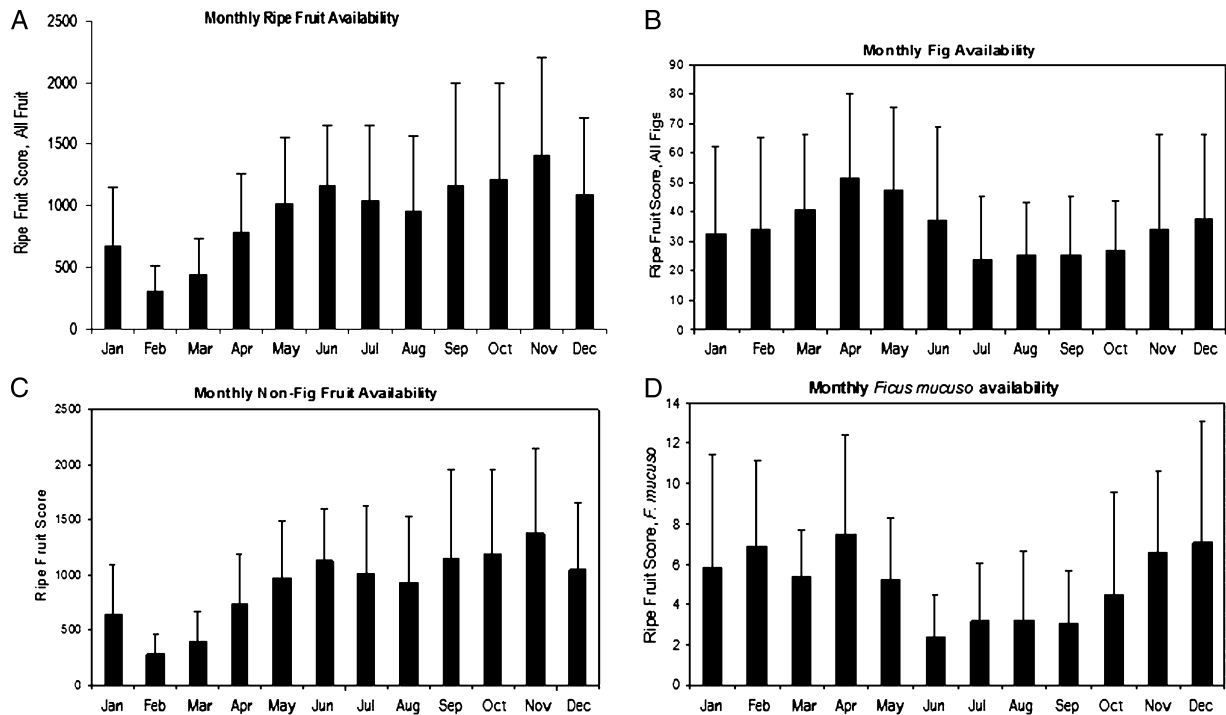


Fig. 1. Variation among and within months in fruit production by major chimpanzee food species at Ngogo. Column height indicates the mean RFS for a given month; bar indicates one SD (A) All fruit; (B) all nonfig fruits; (C) all figs; (D) *Ficus mucuso*. Note: Scale of Y-axis varies. RFS, ripe fruit score.

of the 12 calendar months was high for all months (Fig. 1A and B) and exceeded variation in mean values across months. The coefficient of variation (CV) for monthly mean  $RFS_{all}$  values was 0.41; CV values for individual months ranged from 0.43 to 0.93. Likewise, the CV among monthly mean  $RFS_{nff}$  scores was 0.40, whereas within-month coefficients of variation ranged from 0.43 to 1.27. Despite this within-month variation, time series analysis of the full data set showed significant seasonal components in overall fruit abundance ( $\chi^2 = 133.76$ ,  $df = 11$ ,  $P < 0.001$ ) and in the abundance of nonfig fruit ( $\chi^2 = 138.31$ ,  $df = 11$ ,  $P < 0.001$ ).

Mean  $RFS_{fig}$  values were also nonzero for all months; in contrast to nonfig fruits, values peaked in March to May and were relatively low in July through October (Fig. 1C). Mean  $RFS_{Fm}$  values were nonzero for all months, but within-month variation was high (Fig. 1D) and in some sample months, no stems in the phenology sample bore fruit. *F. mucuso* generally followed the overall fig pattern, although with a peak in February and a deeper trough in June through October (Fig. 1D). As for nonfig fruits, CVs for RFSs were higher within months for both all figs (range = 0.57–0.94) and for *F. mucuso* (range = 0.41–1.05) than they were across months (all figs: CV = 0.56; *F. mucuso*: CV = 0.37). Despite high within-month variation, time series analysis also showed significant seasonal components in the availability of all figs ( $\chi^2 = 85.22$ ,  $df = 11$ ,

$P < 0.001$ ) and the availability of *F. mucuso* ( $\chi^2 = 116.62$ ,  $df = 11$ ,  $P < 0.01$ ).

Fig availability was not consistently high when nonfig fruit was scarce. In fact,  $RFS_{fig}$  values were positively correlated with the  $RFS_{nff}$  ( $r = 0.28$ ,  $n = 144$ ,  $P < 0.001$ ).  $RFS_{Fm}$  values were also positively associated with those for nonfig fruit, but this relationship was nonsignificant ( $r = 0.09$ ,  $n = 144$ ,  $p = 0.26$ ). Across all months, fig availability varied more than that of nonfig fruit: the coefficients of variation for both the  $RFS_{fig}$  (0.77) and the  $RFS_{Fm}$  (0.81) were slightly higher than that for the  $RFS_{nff}$  (0.69). The mean monthly CV was significantly higher for figs ( $0.87 \pm 0.14$ ,  $n = 12$ ) than for nonfig fruits ( $0.77 \pm 0.06$ ; paired  $t$ -test, data square-root transformed,  $t = -3.03$ ,  $P < 0.05$ ).

#### Variation in fruiting phenology within and among species

At least one stem of the average species bore fruit in 42.7% of months, and most species produced some fruit in at least 30% of months [Table I; this table does not include *Ficus cyathistipula* and *F. exasperata*, figs of which each contributed less than 0.4% of feeding time Watts et al., 2011]. The highest values for the number of months during which some fruit was available belonged to figs: at least one stem of *Ficus natalensis* and one of *F. mucuso* bore fruit in 72.2% of all months, and

**TABLE I. Intervals Between Fruiting Events and Length of Fruiting Events for the Top Fruit and Fig Food Species in the Diet at Ngogo**

Species	% Months	Between fruiting	3rd quartile, between	Fruiting interval	3rd quartile, fruiting	3rd Quartile, RFS
<i>Aningeria altissima</i>	31.3	8.91 (3–23)	8.30	3.75 (1–8)	5.00	3.64 (1–8)
<i>Celtis durandii</i>	59.7	3.86 (1–21)	4.05	5.38 (1–15)	8.75	2.17 (1–4)
<i>Chrsyophyllum albidum</i>	31.3	5.29 (1–21)	6.92	3.46 (1–10)	7.5	3.23 (1–9)
<i>Cordia millennii</i>	69.4	3.07 (1–6)	7.14	6.67 (1–15)	10.00	2.86 (1–6)
<i>Ficus brachylepis</i>	58.3	3.00 (1–13)	4.00	4.67 (1–18)	5.00	2.65 (1–7)
<i>Ficus dawei</i>	43.1	1.89 (1–3)	4.86	3.88 (1–9)	5.75	2.00 (1–6)
<i>Ficus mucuso</i>	72.2	2.23 (1–13)	3.42	9.45 (1–40)	4.90	1.92 (1–5)
<i>Ficus natalensis</i>	72.2	1.64 (1–6)	5.65	4.52 (1–16)	6.00	2.29 (1–9)
<i>Mimusops bagshawei</i>	42.4	3.94 (1–14)	8.75	3.89 (1–9)	6.25	3.64 (1–7)
<i>Monodora myristica</i>	27.8	6.67 (1–19)	6.67	2.86 (1–8)	4.50	2.86 (1–8)
<i>Morus mesozygia</i>	17.4	6.63 (1–11)	6.33	1.32 (1–4)	1.00	1.32 (1–4)
<i>Pseudospondias microcarpa</i>	41.0	5.15 (1–17)	6.75	3.11 (1–11)	3.00	2.44 (1–8)
<i>Pterygota mildbraedii</i>	40.3	4.12 (1–19)	10.00	4.83 (1–8)	7.75	4.10 (1–8)
<i>Teclea nobilis</i>	29.2	6.25 (1–14)	6.25	2.63 (1–6)	4.75	2.63 (1–6)
<i>Treculia africana</i>	37.5	7.73 (1–33)	7.73	3.38 (1–16)	3.50	3.38 (1–16)
<i>Uvariopsis congensis</i>	34.0	6.71 (1–17)	8.00	3.77 (1–15)	4.50	2.85 (1–7)
<i>Warburgia ugandensis</i>	52.1	2.74 (1–12)	6.53	3.26 (1–11)	5.00	2.75 (1–8)
<i>Zanha golungensis</i>	9.0	12.89 (1–40)	12.89	1.63 (1–3)	2.75	1.63 (1–3)

Species listed here accounted for 67.7% of feeding time in long-term diet records (Watts et al., 2011). Data span 12 consecutive years of phenology records (1998–2009). % Months = percent of all sample months ( $n = 144$ ) in which at least one stem bore ripe fruit; Between fruiting = mean interval length (months) between periods of fruit/fig production (range in parentheses); 3rd Quartile, between fruiting = number of months that exceeded 75% of intervals with no fruit/figs; fruiting interval = mean length of fruit/fig production periods (number of consecutive months at least one stem bore ripe fruit; range in parentheses); 3rd quartile, fruiting = mean length of fruit/fig production (months) that exceeded 75% of all intervals; 3rd quartile, RFS = mean length (months) of intervals during which fruit/fig production (estimated by the ripe fruit score) was in the top 25% of values (range in parentheses).

the corresponding value for *F. brachylepis* was 58.3%. *Cordia abyssinica*, *Celtis durandii*, and *Warburgia ugandensis* also produced fruit in more than half of all months (Table I). At the other extreme, *Zanha golungensis* had fruit in only 9.0% of months. Fruit of *Morus mesozygia*, *Teclea nobilis*, and *Aningeria altissima* was also available relatively infrequently (Table I).

Only *Z. golungensis* had an average interval of  $\geq 1$  year with no fruit production (Table I). Otherwise, the mean length of intervals with no fruit varied from only 1.6 months (*F. natalensis*) to 8.9 months (*A. altissima*), and the overall mean among species was 5.2 months (Table I). Interspecific variation in the mean length of intervals without fruit was significant (Kruskal–Wallis one-way ANOVA:  $H_{\text{adj}} = 68.45$ ,  $df = 17$ ,  $P < 0.001$ ; Table I). *Monodora myristica*, *M. mesozygia*, and *U. congensis* also had relatively long mean intervals between fruit production, while mean intervals were short for *Ficus* spp., *Warburgia ugandensis*, *Celtis durandii*, and *Cordia millennii* (Table I). Intraspecific ranges in the lengths of intervals without fruit were large. For example, *A. altissima* failed to produce fruit during one 23-month interval, and several other species also went for close to or more than 2 years without producing fruit (Table I). *Treculia africana* was notable: no tree in the sample bore fruit during one 33-month interval, but at least one stem had fruit during another 16-month interval (Table I).

Although at least one *F. mucuso* bore ripe fruit in most months and the mean interval with no fruit production was only 2.2 months, no stems had fruit during one interval of 13 months (Table I).

The length of intervals during which at least one tree in the phenology sample bore fruit also varied significantly among species (Kruskal–Wallis one-way ANOVA,  $H_{\text{adj}} = 54.53$ ,  $df = 17$ ,  $P < 0.001$ ; Table I). Figs, especially *F. mucuso*, were generally available for extended periods, as were fruit of *C. durandii* and *C. millennii*; in contrast, *M. myristica* and *M. mesozygia* produced fruit for only 1–2 months, on average (Table I). Again, intraspecific variation was extensive. Seven species had at least one fruit-production interval that exceeded 1 year, and at least one *F. mucuso* fruited during each of 40 consecutive months from September 2006 through December 2009 and each of 20 consecutive months between October 2004 and May 2006. Only two species included in Table I (*M. mesozygia* and *Z. golungensis*) had maximum fruit-bearing intervals of less than 6 months.

Similar variation occurred in the duration of relatively long periods of fruit production (those in the highest 25% of interval lengths) and in the mean duration of periods of high fruit productivity (the number of months during which the RFS was in the highest quartile for a given species; Table I). For example, few fruit production intervals for *M. mesozygia*, *Pseudospondias microcarpa*, or

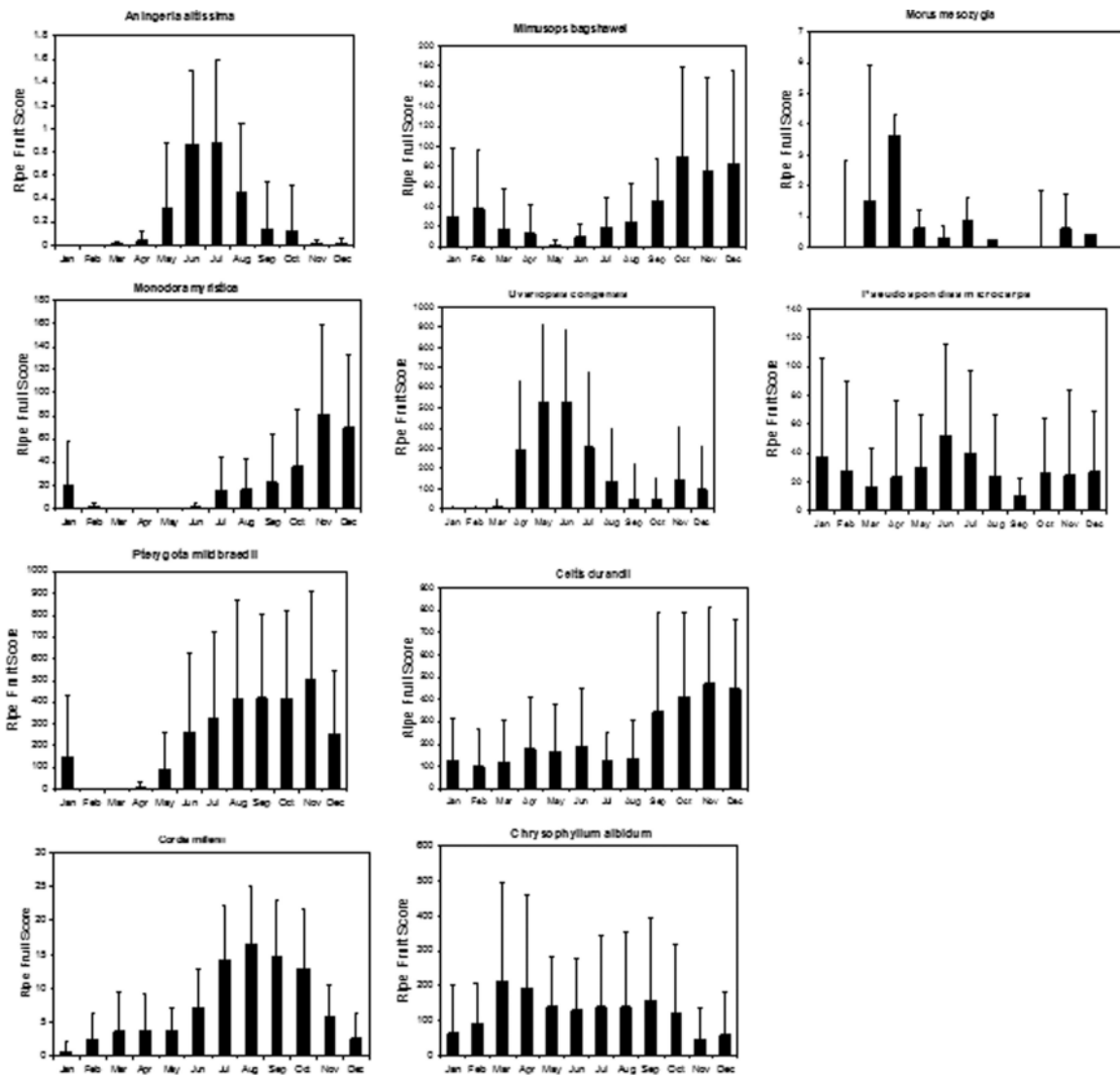


Fig. 2. Variation within and among months in ripe fruit production for ten species that were important sources of nonfig fruit at Ngogo. Note: Y-axis scale varies.

*Z. golungensis* exceeded 2 months, but 25% of those for *C. millennii* were 10 months or longer and those for figs also tended to be long.

The composite patterns in Figure 1 derived from several general patterns of intermonthly variation in RFSs for important nonfig species (Fig. 2), but these were not consistent among years. For example, *A. altissima* fruiting peaked in June to July, with moderately high fruit production in May and August and little to none in other months, but individual stems did not consistently fruit every year. *Mimusops bagshawei* and *M. myristica* showed overall October to December peaks; *M. myristica* produced little or no fruit from March through June, whereas *M. bagshawei* stems were more likely to fruit at any time. However, individual trees skipped years, and neither species consistently produced large October to December fruit crops every year. *U. congensis*

showed a marked peak in April to July (especially in May and June), but the exact timing of fruit production and the size of ripe fruit crops varied greatly. In 5 of 13 years (including 1995, when D. Watts collected feeding data but not phenology data), stems of this species fruited again in October to December, although only two of the five fruit crops were as large as the major April to July fruit crops. *C. millennii* fruiting was relatively high overall in July through October, but fruit production was usually concentrated in only about 2 months per year and was quite low in some years, and it could occur during any month.

*Chrysophyllum albidum*, which is highly abundant in the chimpanzee home range, deserves special mention. Fruiting could occur during any month, with somewhat of a trough in November through February. However, most stems produced little or no

fruit in most years, whereas masting events, during which virtually all trees produced large fruit crops and the fruit dominated the chimpanzee diet for several months, occurred in 2000, 2005, and 2010 (and 2011; data not included here: D. Watts, personal observation); each event started in July or August and continued for several months.

### Temporal Variation in Diet

#### Feeding time devoted to individual species

The proportion of feeding time that the Ngogo chimpanzees devoted to all ripe nonfig fruit varied positively with the  $RFS_{\text{nff}}$  [Watts et al., 2011]. The same result held for the individual major nonfig fruit foods in the diet. The species-specific RFS significantly predicted monthly feeding time for all 13 major nonfig fruit foods included in the phenology sample (Table II; we did not include *Pterygota mildbraedii* because the chimpanzees mostly eat seeds from unripe fruit of this species and leaves from saplings [Potts et al., 2011; Watts et al., 2011; below]. Species-specific RFSs also significantly predicted the proportion of feeding time devoted to the four major species of figs in the diet (Table II; we did not include *F. cyathistipula* or *F. exasperata*).

Relative foraging effort, defined as the extent to which the chimpanzees concentrated on a particular kind of fruit in relation to its abundance, depended partly on how long fruit were available, on the frequency of fruiting events, and on the extent of within-species fruiting synchrony. Overall, it was high for species that infrequently produced fruit crops available for short periods (e.g., *A. altissima*,

*M. mesozygia*; Table II), and lower on species that offered fruit more often, over longer periods (e.g., *F. mucoso* and *U. congensis*). The strength of correlation coefficients between proportional feeding time and RFSs varied inversely with the mean length of fruiting events ( $n = 17$ ;  $F = 7.76$ ,  $r^2_{\text{adj}} = 0.30$ ,  $P < 0.05$ ) and with the percent of all months during which the species bore fruit ( $n = 17$ ;  $F = 7.76$ ,  $r^2_{\text{adj}} = 0.63$ ,  $P = 0.01$ ).

*F. mucoso*, *C. millenii*, and *C. albidum* merit special mention. The RFS explained little of the variation in monthly *F. mucoso* feeding time (Table II), partly because enormous fig crops produced by stems not included in the phenology sample accounted for considerable feeding time in many months. However, the  $r^2$  value was higher than expected given the long fruiting events for this species. The relationship was also relatively strong for *C. millenii* (Table II), which was available during many months. In contrast, the  $r^2$  value for *C. albidum* was lower than expected given its common availability (Table II), because most fruiting events were small to moderate and attracted little attention, whereas *C. albidum* fruit assumed major dietary importance during infrequent massive fruiting events (above).

As the positive relationships between RFSs and relative feeding times imply, monthly variation in time devoted to particular kinds of fruit largely mirrored variation in fruit production (Figure 3). For example, feeding on *U. congensis* fruit tended to be seasonal and bimodal, although April to May fruit crops mostly aborted or failed to ripen in some years and October to December fruit crops were sporadic (above) and, in 3 years, were relatively small and led to low feeding time compared with typical April to July peaks. Feeding on *C. millenii* peaked in July to September, although in some years little fruit was available during these months, and feeding on *A. altissima* and *C. albidum* was also unimodally distributed, but fruit crops either did not occur or were small in some years during the overall peak months. The extreme interannual variation for *C. albidum* reflects the occurrence of masting events. Feeding time devoted to *F. mucoso* showed two broad peaks, but on average figs from this species accounted for over 5% of feeding time during all months.

#### Fallback and staple foods

Because monthly feeding time devoted to figs of particular *Ficus* species was positively related to their availability, monthly feeding time on all figs was significantly associated with the  $RFS_{\text{fig}}$ , although this relationship accounted for little of the variance in feeding time ( $F = 5.97$ ,  $N = 109$ ,  $r^2_{\text{adj}} = 0.04$ ,  $P < 0.05$ ). If figs were fallbacks, combined fig feeding time should have varied inversely with the overall availability of nonfig fruits, assessed by the  $RFS_{\text{nff}}$ .

**TABLE II. Relationships Between Ripe Fruit Scores for Individual Species Included in the Phenology Sample (Excluding *Pterygota mildbraedii*) and the Percent of Monthly Feeding Time Devoted to that Species**

Species	N months	F	$r^2_{\text{adj}}$	P
<i>Aningeria altissima</i>	40	21.32	0.343	<0.001
<i>Celtis durandii</i>	60	18.92	0.233	<0.001
<i>Chrysophyllum albidum</i>	47	5.91	0.097	0.019
<i>Cordia millenii</i>	73	59.29	0.447	<0.001
<i>Ficus brachylepis</i>	96	15.59	0.133	<0.001
<i>Ficus dawei</i>	86	27.72	0.239	<0.001
<i>Ficus mucoso</i>	100	10.22	0.085	0.002
<i>Ficus natalensis</i>	92	12.07	0.108	<0.001
<i>Mimusops bagshawei</i>	63	18.98	0.225	<0.001
<i>Monodora myristica</i>	57	60.02	0.513	<0.001
<i>Morus mesozygia</i>	44	116.62	0.729	<0.001
<i>Pseudospondias microcarpa</i>	69	35.75	0.338	<0.001
<i>Teclea nobilis</i>	17	21.71	0.564	<0.001
<i>Treculia africana</i>	77	41.39	0.347	<0.001
<i>Uvariopsis congensis</i>	60	73.33	0.551	<0.001
<i>Warburgia ugandensis</i>	70	20.87	0.224	<0.001
<i>Zanha golugensis</i>	36	57.83	0.619	<0.001

Percentage values were arcsine-transformed.



This was the case ( $F = 9.39$ ,  $N = 109$ ,  $P < 0.01$ ), although this relationship explained little of the variance in fig feeding time ( $r_{\text{adj}}^2 = 0.07$ ). Feeding time devoted to figs showed a strong inverse relationship to feeding time devoted to nonfig fruits ( $F = 196.80$ ,  $N = 109$ ,  $r_{\text{adj}}^2 = 0.62$ ,  $P < 0.001$ ; we removed values for *P. mildbraedii* from the  $\text{RFS}_{\text{all}}$  for this analysis). Feeding time for *F. mucoso* alone was inversely related to the  $\text{RFS}_{\text{nonfig}}$ , but this relationship was nonsignificant overall ( $F = 3.49$ ,  $N = 109$ ,  $r_{\text{adj}}^2 = 0.023$ ,  $P = 0.064$ ). The relationship between these variables was significant when the effects of variation in *F. mucoso* abundance were controlled: for those months in which *F. mucoso* was available, standardized residuals from the regression of *F. mucoso* feeding time on the  $\text{RFS}_{\text{Fm}}$  were significantly and inversely related to the  $\text{RFS}_{\text{nonfig}}$  ( $F = 5.58$ ,  $N = 100$ ,  $P < 0.05$ ). However, this relationship explained little of the variance in *F. mucoso* feeding time ( $r_{\text{adj}}^2 = 0.040$ ). Both absolute and residual *F. mucoso* feeding time values were also inversely and significantly related to time devoted to eating nonfig fruits; these relationships were stronger (absolute feeding time:  $F = 99.39$ ,  $N = 122$ ,  $r_{\text{adj}}^2 = 0.448$ ,  $P < 0.001$ ; residual feeding time:  $F = 67.94$ ,  $N = 100$ ,  $r_{\text{adj}}^2 = 0.383$ ,  $P < 0.001$ ).

Chimpanzees at Ngogo prey on the wind-dispersed seeds of *P. mildbraedii*, to which they gain access by opening unripe fruit. The seeds are an important diet component, accounting for 3.5% of feeding time in the Ngogo long-term data set [Watts et al., 2011; cf. Potts et al., 2011]. Partly because fruiting is not restricted to only a few months, they are sometimes abundant when other nonfig fruits is relatively scarce, and the chimpanzees then eat them in large quantities [Fig. 2; Potts et al., 2011]. This conveys the impression that they are filler fallbacks. However, although feeding time devoted to *P. mildbraedii* seeds during months when these were available was negatively associated with the  $\text{RFS}_{\text{nonfig}}$  (excluding *P. mildbraedii* fruit), this relationship was nonsignificant ( $F = 1.63$ ,  $N = 49$ ,  $r_{\text{adj}}^2 = 0.013$ ,  $P = 0.208$ ).

In contrast, feeding time devoted to leaves varied inversely with the abundance of nonfig fruits ( $F = 8.52$ ,  $N = 109$ ,  $P < 0.005$ ), although this relationship explained little of the variance in feeding time ( $r_{\text{adj}}^2 = 0.065$ ). The relationship between feeding time devoted to leaves and feeding time devoted to nonfig fruits, also significantly negative, was stronger ( $F = 62.36$ ,  $N = 122$ ,  $r_{\text{adj}}^2 = 0.336$ ,  $P = 0.004$ ). Leaves from *P. mildbraedii* saplings, which are highly abundant in much of the study area, accounted for 8.5% of total feeding time in the long-term data set [Watts et al., in press] and were especially important in January through March (Fig. 3), when the abundance of nonfig fruits tended to be low (Fig. 1). They also were relatively important during September through December (Fig. 3); nonfig fruit

was usually abundant during these months (Fig. 1B), but not in all years. Leaves of *Celtis africana* were also a major food, accounting for 3.2% of total feeding time [Watts et al., in press]; the chimpanzees ate these throughout the year, but particularly during March to April and September to October (Fig. 3).

Long-term data indicate that stems and pith accounted for only 1.6% of feeding time for the Ngogo chimpanzees [Watts et al., 2011]. Time devoted to these foods was independent of nonfig fruit availability ( $F = 0.92$ ,  $N = 109$ ,  $r_{\text{adj}}^2 = 0.01$ ,  $P = 0.341$ ) and of feeding time devoted to nonfig fruits ( $F = 1.137$ ,  $N = 122$ ,  $r_{\text{adj}}^2 = 0.03$ ,  $P = 0.240$ ). However, stem and pith feeding time was inversely related to feeding time devoted to *F. mucoso*, although the relationship had little explanatory power ( $F = 6.03$ ,  $N = 122$ ,  $r_{\text{adj}}^2 = 0.04$ ,  $P < 0.05$ ). Use of *Cyperus papyrus* pith appeared to have a seasonal component: at least once during 30 months, observers followed parties of chimpanzees to a papyrus swamp in the far northwest part of their home range, where they spent up to 6 hr chewing wadges of this pith to extract water and soluble carbohydrates. Nineteen of these 30 months were a June, July, or August; these are typically dry months. Other minor plant food categories (flowers, cambium, seeds other than those of *P. mildbraedii*, cambium, roots, rotting wood) each contributed at most 3% of feeding time (flowers) and typically much less [Watts et al., 2011].

#### Fruit “seasons”

Feeding data from Ngogo include 23 intervals of  $\geq 2$  months when nonfig fruits accounted for at least 40% of feeding time. Four intervals were open-ended (data were not available for the preceding or subsequent month). The lengths of the 19 completed intervals (mean =  $3.06 \pm 1.70$  months) did not differ significantly from those of 20 such intervals at Kanyawara [ $2.45 \pm 1.57$  months; two-sample *t*-test,  $t = -1.14$ ,  $df = 34$ ,  $P = 0.263$ ; Kanyawara data from Figure 2 in Gilby & Wrangham, 2007]. However, intervals between these fruit “seasons” were shorter at Ngogo and nonfig fruit abundance was high ( $>40\%$  of feeding time) in a larger proportion of months at Ngogo (61.2% of months) than at Kanyawara (31.3% of months; chi-square test;  $\chi^2 = 25.29$ ,  $P < 0.001$ ).

## DISCUSSION

Considerable variation in nonfig fruit availability occurred across months at Ngogo, and the fruiting schedules and fruit crop sizes of individual species important in the chimpanzees’ diet varied markedly across years. Fig availability also varied, and fig abundance was positively related to the abundance of nonfig fruit, but some figs were available in almost all months and time devoted to eating figs varied inversely with time devoted to

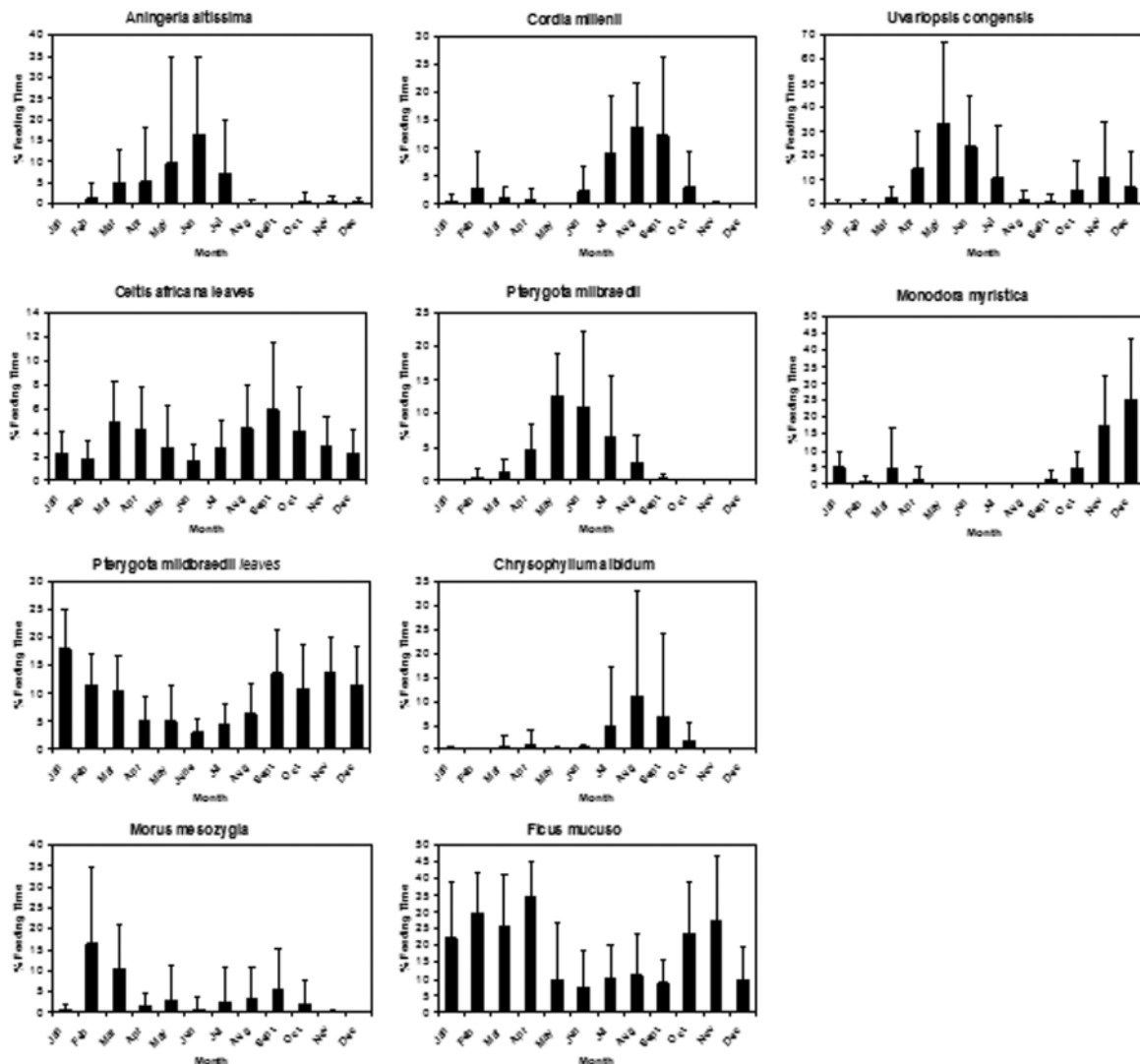


Fig. 3. Variation within and among months in feeding time that Ngogo chimpanzees devoted to fruit or figs from eight major sources of these foods and to leaves of *Celtis africana* and *Pterygota mildbraedii*. Note: Y-axis scale varies.

eating nonfig fruit. This was specifically true for figs of *Ficus mucoso* (quantitatively the top food). Figs as a class, and *F. mucoso* specifically, thus were fallback foods by Marshall & Wrangham's [2007] definition. However, as was the case for all major nonfig fruits in the diet, the amount of time that the chimpanzees spent eating figs varied positively with their abundance. Thus, figs may be better regarded as staples, although this depends on how one defines this term [Harrison & Marshall, 2011; below]. Leaves were an important class of fallback food: the chimpanzees devoted feeding time to leaves in inverse proportion to both the availability of nonfig fruits and the proportional contribution of such fruit to their feeding time budget. In contrast to Kanyawara [Wrangham et al., 1991, 1993], pith and stems from terrestrial vegetation were not fallbacks.

Phenology data presented here add to earlier reports [Chapman et al., 1997, 2010; Mitani et al.,

2002; Potts et al., 2009; Struhsaker, 1997] that fruit availability varies within and among months at Ngogo and elsewhere in Kibale. Combined monthly production of important fruit and fig foods showed significant seasonal components and was bimodally distributed, but variation was higher within than among months, and the amount and timing of fruit production varied considerably among years both overall and for individual species. At one end of a spectrum of variation were species like *A. altissima* that consistently produced fruit crops during certain months in those years when they fruited (although they did not necessarily fruit in all years) and that showed high within-species synchrony. At the other were species that fruited asynchronously and could fruit at any time of year (e.g., figs, especially *F. mucoso*).

The proportion of monthly feeding time that the chimpanzees devoted to fruit and figs from each of

the major food sources in the phenology sample was positively related to their abundance. This also seemed true for other, less common species from which the chimpanzees eat fruit in substantial amounts when it is available (e.g., *Aphania senegalensis*; *Elaeodendron guineense*). This finding reinforces the characterization of chimpanzees as ripe fruit specialists. Variation in RFSs accounted for most of the variation in feeding time in some cases (e.g., *U. congensis*, the most important nonfig fruit), but little in other cases (e.g., *F. mucuso*). The strength of the relationship between feeding time and relative abundance depended largely on variation in fruiting synchrony and fruit crop duration: it was generally weaker for species whose fruiting events were long and/or relatively evenly spread over time than for those with shorter, more temporally restricted events. Some of the unexplained variance resulted from the inability of the phenology sample to capture all the variation in such a large area. Importantly, the low synchrony of fig production means that figs of *F. mucuso* can be a major food in months when the associated RFS is zero, because the stems in use are not included in the phenology sample. Also, fruiting schedules sometimes vary spatially. Notably, *U. congensis* seems to ripen sequentially from southeast to northwest, and the phenology sample does not cover areas far to the northwest where fruit is still abundant when it is finished elsewhere. The fission–fusion social system of the chimpanzees introduces more error: chimpanzees foraging in different parts of the home range at the same time encounter different arrays of food, and neither observers nor the phenology sample captures all the resulting variation in diet composition.

Alberts et al. [2005] characterized yellow baboons in Amboseli as using underground plant parts as fallback foods when fruit and seeds from shrubs and trees was scarce, but also as following a “handoff” strategy by switching from one valuable, temporarily available food species or set of species to the next as availability waxed and waned. The “handoff” concept also makes sense for chimpanzees, which concentrate their foraging effort on ripe fruit, but, like baboons, are flexible generalists that eat highly varied diets from many food types. Chimpanzees at Ngogo tracked crops of both nonfig fruits and figs, sometimes eating fruit of a single species (e.g., *U. congensis*; *A. altissima*, *C. albidum*) almost exclusively for days or weeks and at other times combining large proportions of simultaneously available fruit crops (e.g., those of *C. albidum* and *M. mesozygia* in July and August, 2010). Figs were prominent in this strategy: the chimpanzees typically used them as they became available, and short intervals between fruiting, lack of within-species synchrony, and relatively nonseasonal fruit production meant that some figs were available at most times. Figs thus could potentially assume particular

importance when drupaceous fruit was scarce. This was particularly true for mature stems of *F. mucuso*, which have huge crowns that can produce enormous numbers of large figs, because the rate at which chimpanzees harvest calories from figs is positively related to fig size [Wrangham et al., 1993].

Figs are fallback candidates for chimpanzees at other sites (e.g. Kanyawara, Wrangham et al., [1998]; Bwindi, Uganda, Stanford & Nkurunungi, [2003], and Harrison and Marshall [2011]) characterize figs as the “major fallback” for chimpanzees generally, while emphasizing that chimpanzee feeding ecology varies. Figs are also presumed fallbacks for various other primates (e.g., black spider monkeys, *Ateles paniscus*, at Manu [Terborgh, 1983]; orangutans (*Pongo pygmaeus*) at Ketambe, Sumatra [Vogel et al., 2008]), and Marshall and Leighton [2006] found a significant inverse relationship between fig use by white-bearded gibbons at Gunung Palung and the availability of nonfig fruits and labeled figs filler fallbacks. By the criterion, figs were not fallbacks at Ngogo. However, figs generally, and *F. mucuso* in particular, met the primary criterion for fallbacks in that monthly proportion of feeding time spent eating figs and spent eating nonfig fruits were inversely related, although this relationship was weak for *F. mucuso*, which contributed most of the fig component of the diet.

But somewhat surprisingly, we found that fig availability had a significant seasonal component and was positively associated with nonfig fruit availability. More importantly, the positive associations between feeding time and availability for figs are unexpected for fallbacks. Long periods of fruit production by individual fig species and short intervals between these still meant that large fig crops often were available when nonfig fruits were scarce, but we think that figs, and *F. mucuso* in particular, should be considered “staples” because their availability varied little, they were eaten in proportion to availability, and they contributed much of the diet during most or all of the year, instead of fallbacks. This use of “staple” contrasts with Marshall and Wrangham’s [2007] definition of “staple fallbacks” as foods or food categories that seasonally comprise the entire diet, but is consistent with its application to chimpanzees at Sonso in Budongo [Newton-Fisher, 1999; cf. Tweheyo & Lye, 2003] and Kanyawara [Conklin & Wrangham, 1994] and to *Ateles chamekin* Bolivia [Felton et al., 2008]. In these cases, animals ate large quantities of figs throughout the year. Analysis of dung samples, combined with limited direct observation, showed that chimpanzees at Lopé [Tutin & Fernandez, 1993], the highland sector of Kahuzi-Biega [Basabose, 2002], and Nyungwe [Gross-Camp et al., 2009] also ate figs during most of the year, often in large quantities. The percentage of dung samples that contained fig seeds in Nyungwe was independent of

the percentage of fig trees in fruit and of the percentage of all major food species in fruit; this led Gross-Camp et al. [2009] to argue that they were not fallbacks, although their lack of extensive observational data prevented them from examining the relationship between feeding time devoted to figs and that devoted to nonfig fruits. Yamagiwa and Basabose [2009] characterized figs as “preferred” foods at Kahuzi-Biega, where nonfig fruit abundance is generally low. Some discrepancy about whether figs are seen as fallbacks for chimpanzees probably reflects real biological variation. For example, nonfig fruit production is strongly seasonal in the Montane forest of Bwindi [Stanford & Nkurunungi, 2003]; the lower synchrony of figs makes them correspondingly more important as alternatives than at Ngogo. However, Ngogo data show the importance of examining variation within and among fig species and caution against generalizations about their use as fallbacks.

At Budongo also, figs fruit during much of the year, intraspecific synchrony is low, and individual stems tend to fruit at short intervals [Tweheyo & Lye, 2003]. Figs of *F. sur* were the most important diet item at Sonso during both Tweheyo and Lye’s [2003] study and Newton-Fisher’s [1999] earlier one. Tweheyo and Lye [2003] contended that reliable availability of figs (especially *F. sur*) when nonfig fruit is scarce makes them essential for sustaining the Budongo chimpanzee population. This is plausible, because hindgut fermentation should increase the energy value of fig pulp and make figs good “maintenance” foods that provide relatively high and consistent amounts of metabolizable energy and moderate amounts of protein, despite generally low macronutrient content [Conklin & Wrangham, 1994; cf. Hohmann et al., 2010; Wrangham et al., 1993]. Figs are consistently prominent in long-term diets at both Kanyawara [Wrangham et al., 1996] and Ngogo [Watts et al., 2011], but the relatively high density of *F. mucuso* gives chimpanzees at Ngogo a particularly abundant and reliable maintenance food source that is probably a major reason why population density is so much higher at Ngogo [Potts et al., 2011; Watts et al., 2011]. Marshall [2004; cf. Marshall & Leighton, 2006] reported that fig abundance apparently limited the population density of white-bearded gibbons in different forest types on Borneo, and Wich et al. [2004] argued that orangutan population density on Sumatra depends on the abundance of strangler figs. The diversity of chimpanzee habitats and of chimpanzee foraging behavior is too great for any simple relationship between fig abundance and population density to apply across all populations. For example, the use of nut-cracking technology allows members of some western chimpanzee populations to use nutritionally valuable resources unavailable to chimpanzees in similar habitats who do not know how to use the technology

[Boesch & Boesch-Achermann, 2000], and fruit of *Musanga cecropioides* and pith from oil palms are fallbacks at Bossou, where several cultigens (especially fruit high in simple sugars) also have this role [Hockings et al., 2009]. However, positive relationships between fig density and population density may well hold within populations due to local habitat heterogeneity [Potts et al., 2009, 2011].

Potts et al. [2009] argued that, more broadly, species that fruit synchronously when overall fruit production is relatively low are crucially important for limiting population densities of tropical frugivores. On the basis of data from 7 of the 12 years in our phenology sample, they concluded that such species are more abundant at Ngogo than at Kanyawara and that this helps to explain the much higher chimpanzee population density there. Candidate species at Ngogo included *P. mildbraedii* (highly abundant at Ngogo, virtually absent as mature stems at Kanyawara), *M. bagshawei*, *M. myristica*, *M. mesozygia*, and *Teclea nobilis*. Further analysis of longer term data may revise this list. For one thing, despite the impression that Ngogo chimpanzees concentrate on *P. mildbraedii* seeds when these are available and fruit from other species is scarce, long-term feeding and phenology records show that they were not a fallback. An important reason why no significant inverse relationship between time feeding on these seeds and time devoted to fruit existed may be that *P. mildbraedii* seeds are not nutritional substitutes for fruit: they are high in protein [Potts, 2008], which could make them valuable complements to fruit pulp. Nevertheless, that chimpanzees at Ngogo used important fruit foods in proportion to their availability reinforces the argument that species that produce substantial high-quality fruit crops when habitat-wide fruit abundance is low have particularly high biological importance.

We would add that chimpanzees at Ngogo increased their reliance on leaves when fruit abundance is relatively low (Potts et al. were concerned only with frugivory) and leaves statistically qualified as “filler” fallbacks. Leaves from *P. mildbraedii* saplings were especially important; the density of saplings is extremely high in much of the home range and is higher than at Kanyawara. Leaves make up much more of the diet at Ngogo, and long-term Ngogo diet data show that *P. mildbraedii* leaves were the third most important food item in terms of feeding time after *F. mucuso* figs and *U. congensis* fruit [Watts et al., 2011]. Leaves are good protein sources, but, like fig pulp [Conklin & Wrangham, 1994], may also be valuable sources of metabolizable energy via hindgut fermentation. Leaves may often be fallbacks for chimpanzees, given that they are also major diet components at Sonso [Newton-Fisher, 1999; Tweheyo et al., 2003], Goualougo [Morgan & Sanz, 2006], Gombe [Wrangham, 1977], Tai [Anderson et al., 2006], and Boussou [Hockings et al., 2009],

but researchers at these sites have either not provided formal analyses of fallback food use or, for Boussou [Hockings et al., 2009], have suggested that leaves are fallbacks but not yet presented a thorough analysis of fallbacks other than cultigens. Morgan and Sanz [2006] noted that chimpanzees at Goulougo ate leaves of *Celtis mildbraedii* regularly throughout the year and considered these a “staple” food. *C. mildbraedii* is uncommon at Ngogo, but the chimpanzees regularly eat leaves when they encounter individual stems and sometimes seek these out [Watts et al., 2011]. Pith and stems make up much less of the diet at Ngogo than at Kanyawara [Potts et al., 2011; Wakefield, 2010; Watts et al., 2011; Wrangham et al., 1991, 1996] and were not fallbacks, in contrast to Kanyawara. But pith and stems are quantitatively important at several sites other than Kanyawara, including Goulougo [Morgan & Sanz, 2006], Kahuzi-Biega [Basabose, 2002], and Boussou, where oil palm pith is a fallback and pith from bananas might also have this role [Hockings et al., 2009]. In reviewing ape fallback strategies, Harrison and Marshall [2011] characterized leaves, stem, pith, and bark (cambium) as potential “filler” fallbacks for chimpanzees, but again noted that diets vary extensively among sites and that this may not be universally true. They had only Kanyawara data to represent Kibale; the contrasts between Ngogo and Kanyawara reinforce this point.

Finally, our findings that fruit seasons [*sensu* Gilby & Wrangham, 2007] were more common at Ngogo than at Kanyawara and that fruit contributed more than 40% of monthly feeding time more often at Ngogo also contribute to understanding why community size and population density differ so much between these two nearby sites. These are animal-centered measures of habitat quality [Gilby & Wrangham, 2007], and the comparison clearly shows that Ngogo is better habitat from the chimpanzee perspective.

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