

RESEARCH ARTICLE

Diet of Chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 1. Diet Composition and DiversityDAVID P. WATTS^{1*}, KEVIN B. POTTS², JEREMIAH S. LWANGA³, AND JOHN C. MITANI⁴¹Department of Anthropology, Yale University, New Haven, Connecticut²Department of Biology, Augsburg College, Minneapolis, Minnesota³Makerere University Institute for the Environment and Natural Resources, Kampala, Uganda⁴Department of Anthropology, University of Michigan, Ann Arbor, Michigan

Chimpanzees (*Pan troglodytes*) are ecologically flexible omnivores with broad diets comprising many plant and animal foods, although they mostly eat fruit (including figs). Like other ecologically flexible nonhuman primates (e.g., baboons, *Papio* spp.) with broad diets, their diets vary across habitats. Much data on diets come from short studies that may not capture the range of variation, however, and data are scant on variation within habitats and populations. We present data on diet composition and diversity for chimpanzees at Ngogo, in Kibale National Park, Uganda, collected over a 15-year period, with a focus on the plant components of the diet. We compare Ngogo data to those on chimpanzees at the nearby Kibale site of Kanyawara, on other chimpanzee populations, and on some other frugivorous–omnivorous primates. Results support the argument that chimpanzees are ripe fruit specialists: Ngogo chimpanzees ate a broad, mostly fruit-based diet, feeding time devoted to fruit varied positively with fruit availability, and diet diversity varied inversely with fruit availability. Comparison of Ngogo and Kanyawara shows much similarity, but also pronounced within-population dietary variation. Chimpanzees fed much more on leaves, and much less on pith and stems, at Ngogo. Figs accounted for somewhat less feeding time at Ngogo, but those of *Ficus mucoso* were quantitatively the most important food. This species is essentially absent at Kanyawara; its abundance and high productivity at Ngogo, along with much higher abundance of several other important food species, help explain why chimpanzee community size and population density are over three times higher at Ngogo. High inter-annual variation at Ngogo highlights the value of long-term data for documenting the extent of ecological variation among chimpanzee populations and understanding how such variation might affect population biology and social dynamics. *Am. J. Primatol.* 74:114–129, 2012. © 2011 Wiley Periodicals, Inc.

Key words: chimpanzees; feeding ecology; diet variation; frugivory; figs

INTRODUCTION

Like nearly all nonhuman primates, chimpanzees (*Pan troglodytes*) are omnivores. Their ability to use many food types from multiple trophic levels and to engage in extractive foraging, sometimes with tools, allows them to occupy a broad range of habitats. But their diets are overwhelmingly plant-based, and they are often labeled “ripe fruit specialists” [e.g., Wrangham et al., 1998] because fruit typically is the main diet component and accounts for much of their foraging effort even when scarce [Basabose, 2002; Conklin-Brittain et al., 1998; Kuroda et al., 1996; Newton-Fisher, 1999; Preutz, 2006; Potts et al., 2009; Rogers et al., 2004; Stanford & Nkurunungi, 2003; Tweheyo & Lye, 2003; Wrangham et al., 1996, 1998]. Chimpanzees often concentrate on drupaceous fruit, but figs (*Ficus* spp.) are often major diet components also [e.g., Kanyawara: Wrangham et al., 1993; Sonso: Tweheyo & Lye, 2003].

Chimpanzees have a fission–fusion social system in which individuals belong to social communities, but community members do not forage cohesively, instead forming subgroups (parties) that vary in size, composition, and duration. Data from Kibale National Park, Uganda, suggest that chimpanzee community size varies with variation in the density and productivity of species that yield edible fruit and

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with temporal variation in productivity [Potts et al., 2009]. Gregariousness potentially entails costs due to feeding competition, and party size and stability presumably reflect a balance between these costs and potential benefits like access to mating opportunities and protection against predators and hostile conspecifics [Lehmann & Boesch, 2008; Wrangham, 1977]. Variation in fruit availability is an important source of variation in party size [Anderson et al., 2002; Mitani et al., 2002; Newton-Fisher et al., 2000; Stanford et al., 1994; Wrangham et al., 1996] and probably contributes to variation in chimpanzee gregariousness among and within habitats [Langergraber et al., 2009; Lehmann & Boesch, 2008; Wakefield, 2010]. Also, ecological effects on chimpanzee life histories should occur, as they do in other primates [e.g., *Presbytis entellus*: Borries et al., 2001]. For example, female reproductive success in some chimpanzee communities is positively correlated with rank, presumably largely because of differential access to food, especially fruit, in spatially and temporally varying habitats [e.g., Gombe: Pusey et al., 1997; Kanyawara: Emery-Thompson et al., 2007].

Considerable empirical information on chimpanzee foraging and diets exists. Studies that use indirect evidence from feces or food remains [e.g. Kuroda et al., 1996] provide valuable data on diet composition, the relative importance of different food types, and seasonality, but do not allow identification of all foods, and the relationship of proxy measures like the percent of fecal samples that contain seeds of a given species or “foliage scores” to feeding time or food intake is unknown [Tutin & Fernandez, 1993]. Surprisingly, few studies have comprehensively documented the diets of particular chimpanzee communities using direct observations, despite the importance of such data for explaining variation in chimpanzee behavioral ecology and demography. Most observational studies provide data only for single communities per population on timescales too short to give more than limited insight into responses to inter-annual and supra-annual variation in food availability. Kanyawara, in Kibale National Park, Uganda, is an exception: Wrangham et al. [1996] documented inter-annual variation in feeding time for major food categories over a three-year period; Conklin-Brittain et al. [1998] and Wrangham et al. [1998] documented inter-monthly variation in responses to fluctuations in fruit availability over an annual cycle, and Emery-Thompson and Wrangham [2008] summarized some aspects of feeding data collected over a 12-year period. Kanyawara researchers have also investigated use of fallback foods and many aspects of nutritional ecology [Conklin-Brittain et al., 1998, 2006; Wrangham et al., 1991, 1993, 1998]. Yet the only published data on the complete composition of the diet at Kanyawara covered only a single year [Potts et al.,

2011]. Moreover, important differences in vegetation and short-term diet profiles at Ngogo, a nearby site in Kibale, caution against taking data from Kanyawara as representative of all Kibale chimpanzees [Potts et al., 2009, 2011].

Here, we use data collected between 1995 and 2010 to describe the composition and diversity of the chimpanzee diet at Ngogo and use data collected over eight consecutive years during this interval to examine long-term dietary variation. We focus only on foods other than meat, because we have given considerable attention to meat eating elsewhere [e.g., Mitani & Watts, 1999; Watts & Mitani, 2002] and individual meat intake varies widely [Mitani & Watts, 1999]. These data complement data collected over shorter time periods by K. Potts on diet, foraging efficiency, and habitat use at Ngogo and Kanyawara [Hohmann et al., 2010; Potts et al., 2009, 2011] and by Wakefield [2010] on the diets of females at Ngogo. They strengthen the conclusion by Potts et al. [2009] that floristic differences between Ngogo and Kanyawara are major determinants of the remarkable differences in chimpanzee community size and population density between the two sites. We also provide a comparative overview of chimpanzee diets and compare the range of variation in these to dietary variation documented for several other highly frugivorous and/or ecologically flexible primate taxa, notably spider monkeys and baboons. In a companion paper [Watts et al., 2011], we examine year-to-year variation in the use of particular important foods, dietary seasonality, and use of fallback foods and consider the importance of variation in food availability as a further determinant of variation in chimpanzee population density.

METHODS

Study Site and Study Animals

Kibale National Park is in southwestern Uganda between 0°13 and 0°41 N and 30°19 and 30°32 E. The 795-km² park is mostly covered by moist evergreen or semi-deciduous forest transitional between lowland and montane forest [Struhsaker, 1997]. The Ngogo study area, in the center of Kibale, is mostly a mosaic of dry-ground forest at various stages of succession, 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 pubescens*, papyrus (*Cyperus papyrus*) swamp, and anthropogenic grassland [Lwanga et al., 2001]. Chimpanzees use all vegetation formations [Lwanga, 2003], but predominately use old-growth forest. They stay entirely within the Park; they do not reach the boundary and do not raid crops. Kibale follows north-south gradients of decreasing altitude and rainfall. The Ngogo study area lies between

1,400–1,470 m in altitude and receives about 1,479 mm of annual rainfall, mostly from March to May and September to December.

The Ngogo chimpanzee community has been observed continuously since mid-1995. It is the largest ever documented and has had between about 142 and 165 members, including 22–32 adult males and about 42–48 adult females [Langergraber et al., 2009]. Adult males and some adolescent males were well habituated by late 1995. Most other community members have since become well habituated, and all now tolerate observers at least when they are in parties with other chimpanzees. Consequently, data presented here come entirely from direct observations.

Sampling of Feeding Behavior

We used two data sets in our analyses. One includes focal data collected by D. Watts in 58 months of observation between 1995 and 2010. Watts identified, in so far as possible, all foods that focal individuals ingested and continuously recorded the amount of time that they spent eating each. A “food” was defined as a distinct plant part and species or a distinct type of nonplant food (e.g., honey). Most foods were classified based on the type of plant part (e.g., fruit, leaves); other categories included mushrooms, honey, soil, meat, and foods of invertebrate origin. Because the main goal of focal sampling was to record data on male social behavior, the data are biased toward adult and, to some extent, adolescent males, although they include some samples of females. More representative sampling of females might change some of our results, and we consider below the possibility that the bias toward males explains some of the differences between the long-term data set and the results of Potts’ [2008]; Potts et al. [2011] and Wakefield’s [2010] shorter studies. However, we also note that fission–fusion sociality, combined with differential home range use, means that different members of a chimpanzee community can eat completely different sets of food on any given day and that sampling difficulties beset any effort to encompass the total range of dietary variation and to construct a single, representative “diet.” Unlike data collected by Potts [2008] and Potts et al. [2011], samples sometimes included incomplete feeding bouts because they were rotated among the members of the parties under observation. The second data set comprises monthly summaries of scan samples collected by Ngogo Chimpanzee Field Assistants from January 1999 through November 2006, excluding months when Watts was at Ngogo ($N = 67$ months). During scans at 15-min intervals, observers identified the food that the majority of feeding chimpanzees in view were consuming. In combination, these two data sets

provide uninterrupted monthly coverage of eight consecutive years starting in October 1998.

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 , simply 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 total number of scans for the month, multiplied by 100.

Focal sampling provides durational data; scan sampling estimates the durations of the same events, although it includes multiple individuals, and the two should provide similar results [Altmann, 1974]. Using data from simultaneously conducted focal and scan sampling, Gilby et al. [2010] directly tested whether this was the case for the time that chimpanzees at Kanyawara spent feeding and for the proportion of feeding time devoted to non-fig fruit. Scan sampling consistently gave higher estimates of total feeding time than focal sampling for males, perhaps because males were often in large parties in which the probability that at least one individual was feeding per scan was relatively high. However, the two methods yielded similar results for estimates of female feeding time and, more importantly, for the proportional importance of non-fig fruit for both males and females. Given that our concern is with dietary proportions, this gives us confidence that we can combine data from our two methods. Still, Gilby et al. [2010] did not compare feeding proportions on an item by item basis, and scans might be less likely to include foods that the chimpanzees ate rarely and might underestimate intake of foods typically found in small patches and/or that the chimpanzees ingest in small quantities while moving between the sites of prolonged feeding bouts. Also, Field Assistants often did not stay with chimpanzees past 1600 hr; this might have biased the scan data if the chimpanzees routinely fed disproportionately heavily on particular foods or food types (e.g., leaves) late in the day. To determine whether such biases existed and led to systematic discrepancies between the data sets, we used Wilcoxon matched pairs, summed ranks tests to compare the percent of feeding time devoted to each food for a sample of 17 months during which both D. Watts and Field Assistants collected data. For these 17 months, we also calculated overlap in the monthly diets as estimated by the two methods. Overlap was given by:

$$\sum_{i=1}^n \text{minimum } [p_i(\text{focal}), p_i(\text{scan})],$$

where p_i (focal) was the percent of food i in the diet as estimated by focal sampling, p_i (scan) the percent estimated by scan sampling, and n the total number

of foods recorded by both methods combined. We did not expect overlap to approximate 100%, because observers were often in different places with different chimpanzees who encountered different arrays of food and because we expect inter-individual variation in diet, especially in association with known variation in habitat use [Langergraber et al., 2009; Mitani & Amstler, 2003].

Analysis of Overall Diet Composition

Observation time was not equal for all months in the sample, so compilation of the proportional contribution of each food to the overall diet should be based on average monthly contributions. We compiled the monthly data in several ways. First, we simply calculated the mean percent of monthly feeding time devoted to each food across all months in the sample ($N = 125$). However, individual months were not equally represented in the long-term data (for example, data were available for July in 15 years, but for November in 10 years and for January in only 8 years). To avoid biases that might have arisen if some tree species consistently fruited in the same months, either annually or supra-annually, we also calculated, for each month, the mean percent of feeding time devoted to each food, then calculated the average monthly value for each food. We refer to this measure of feeding time corrected for monthly variation as the “composite diet,” and used it as a basis to describe inter-monthly variation and for comparison with overall diet composition values from other sites. In practice, values averaged across all months were very similar to those corrected for variation among months. Finally, we also computed annual percent feeding time values for each food for each of the eight years in the consecutive year sample; results were quite similar to values in the composite diet and those calculated by averaging across all months.

We used arcsin-square root transformations of percentage data to investigate how monthly proportions of feeding time devoted to different food categories varied in relationship to fruit availability and to dietary diversity.

Dietary Diversity

We calculated dietary diversity in two ways. First, we calculated a diversity value for each month and for the composite diet using the Shannon–Weaver Diversity Index (H'):

$$H' = - \sum_{i=1}^n p_i \cdot \ln(p_i)$$

where p_i is the percentage of feeding time accounted for by the i th and $\ln(p_i)$ is the natural logarithm of this value. Following Newton-Fisher [1999], we also calculated a normalized diversity value (Hill’s [1973]

equitability index, or J') for each month and for the composite diet to control for variation in the number of foods; this is given by $J' = H'/n$.

Assessment of Fruit Availability

Field Assistants at Ngogo collect monthly phenology data on a sample of 20 stems each of 20 tree species from which the chimpanzees eat fruit. Fruit and seeds from these species accounted for 70.4% of total feeding time in the composite diet [Appendix A]. We used these data to calculate a monthly 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 fig species; because figs tend to be lower in readily-digestible carbohydrates and less seasonal than drupaceous fruit and are potential fallbacks when such fruit are scarce [Hohmann et al., 2010; Wrangham et al., 1993], we also calculated separate fruit availability scores for these species combined (“RFS_{fig}”). We refer to the corresponding combined scores for the 14 non-fig fruit species as “RFS_{nff}”, and to the combined scores for all 20 species as “RFS_{all}”. For some purposes, we also used the RFS for the fig *Ficus mucoso* (“RFS_{Fm}”) because this was quantitatively the most important food and its absence at Kanyawara clearly distinguishes between chimpanzee diets there and at Ngogo (below; cf. Potts, 2008; Potts et al., 2011).

All data were observational only and methods adhered to Ugandan legal requirements and the ASP principles for the ethical treatment of nonhuman primates.

RESULTS

Comparison of Scan and Focal Data

Scan data yielded higher estimates of time devoted to eating figs (mean = $29.3 \pm 5.5\%$; $N = 17$ months) than focal data (mean = $24.3 \pm 4.6\%$; Wilcoxon matched pairs summed ranks test, $T^+ = 121$, $N = 11$, 6; $P = 0.035$). Correspondingly, estimates of non-fig fruit feeding time were higher for focal data ($61.0 \pm 3.9\%$ vs. $53.6 \pm 4.6\%$; $T^+ = 9$, $N = 1$, 16; $P = 0.0005$). This might have resulted partly from a tendency of Field Assistants to stay longer with chimpanzees eating figs from *Ficus mucoso*, which were quantitatively the most important food (below; Appendix A). Mature stems of this species reach the upper canopy and have extremely broad crowns; they produce enormous fig crops that can attract extremely large parties (up to 50 individuals at Ngogo), and chimpanzees often visit

stems with large fig crops on a near daily basis for up to two weeks. Inclusion of much more late afternoon feeding in focal data might also have contributed to the differences. However, they also resulted from the fact that observers often sampled different parties; thus they reflect synchronic variation among individuals due partly to variation in habitat use. Estimates of feeding time devoted to leaves (focal data: $15.9 \pm 1.6\%$; scans: $15.3 \pm 2.1\%$) and to pith and stems (focal data: $2.0 \pm 0.4\%$; scans: $1.6 \pm 0.3\%$) were similar and did not differ significantly. Overlaps between the two data sets also attest to dietary variation. Mean monthly overlap was $86.8 \pm 6.6\%$ for non-fig fruit (range 74.9–96.1%), $87.7 \pm 8.2\%$ for figs (range 72.4–98.1%), $91.1 \pm 5.2\%$ for leaves (range = 82.8–97.3%), $98.2 \pm 1.3\%$ for pith and stems (range = 94.7–98.5%), but only $61.5 \pm 12.9\%$ for all foods combined (range = 41.5–81.9%). Because the two data sets capture real variation and absolute differences in the estimates for fig and non-fig fruit use were small, combining them is justified.

In contrast, focal data led to substantially higher estimates of the number of foods eaten per month (34.4 ± 5.2) than did scan data (21.6 ± 3.6 ; 2-sample *t*-test, $t = 12.04$, $df = 16$, $P < 0.0001$). This is partly a sample time effect (focal data covered more hours per day and more days per month). It is also one of the methodology: Field Assistants did not record items eaten in small quantities between scheduled scans, whereas these were included in focal data and accounted for most of the difference.

Diet Composition

Overall diet breadth was high: chimpanzees at Ngogo ate 167 identified plant foods, plus at least 24 unidentified plant foods that might have been distinct from these (Appendix A). They also ate mushrooms of one unidentified species, honey and honeycomb, and soil (Appendix A). The invertebrate component of the diet included pupae of an unidentified wasp species; at least one unidentified species of termite and one of caterpillar; and secretions made by an unidentified caterpillar species. We have seen chimpanzees use tools to try to extract what we suspect were larvae of stingless bees from dead branches. We have not seen them eat ants. They also prey on 10 vertebrate species, including all seven other diurnal primates at the site, although they mostly hunt red colobus monkeys (*Procolobus rufomitratus tephrosceles*; Watts & Mitani, 2002, unpublished data). Except for meat, the quantitative contribution of the nonplant part of the diet was trivial (Appendix A).

Identified plant foods represented 102 species from 78 genera in 38 families (Appendix A). Unidentified plant foods might have represented up to 24 additional species. Plant food types included figs; mesocarp and arils from non-fig fruits; leaves

and leaf buds; flowers and flower buds; seeds; pith from several herbs and from *Phoenix reclinata* palms, elephant grass (*Pennisetum purpureum*), a fern (*Pteryis* sp.), papyrus (*C. papyrus*), and terminal branches of *Pterygota mildbraedii* saplings; cambium; roots; and rotting wood. The chimpanzees made wadges of palm pith, elephant grass pith, papyrus pith, cambium of various species, wood from roots of *Neoboutonia macroclyx*, and figs from several species (including *Ficus mucoso*) that they discarded after chewing them to extract soluble material. They ingested all other plant foods. The chimpanzees mostly spat out large seeds (e.g., those of *Uvariopsis congensis* and of ripe *Pseudospondias microcarpa*) or swallowed them inadvertently, in which case they passed through the gut whole. However, they preyed on the wind-dispersed seeds of several species, notably *Pterygota mildbraedii* and *Illigera pentaphylla* (Appendix A). They also sometimes retrieved whole unripe fruit of *Pseudospondias microcarpa* from their feces after these had passed through the gut intact, re-ingested them, and apparently chewed the seeds.

The proportional representation of plant parts was highly skewed toward fruit and figs. The chimpanzees mostly ate mesocarp from non-fig fruits (42.3% of feeding time in the composite diet) and figs (28.4%). Leaves and leaf buds accounted for most of the remainder (19.6%), followed by seeds (3.95%), flowers (2.46%), pith and stems (2.2%), cambium (0.6%), and roots (0.4%). Other food types each accounted for less than 0.1%. Mean values from the consecutive years sample were nearly identical to composite diet totals, but show considerable inter-annual variation (Fig. 1). Ranges of annual feeding time values were 35.8–49.6% for non-fig fruit, 25.8–32.6% for figs, and 63.4–76.2% for all fruit combined; 16.3–22.3% for leaves; 1.2–7.2% for seeds; 0.3–4.8% for flowers; 1.0–2.4% for pith and stems;

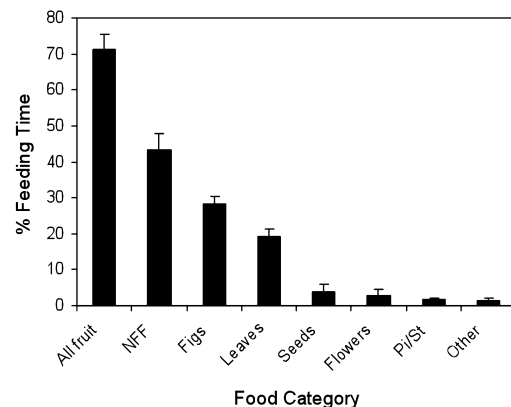


Fig. 1. Inter-annual variation in the percent of feeding time devoted to different food categories. Column height = mean of annual monthly values for eight consecutive years; error bars = 1 standard deviation. All fruit = figs plus non-fig fruit; NFF = non-fig fruit; Pi/St = pith and stems combined; Other = cambium, roots, honey, invertebrates, and soil.

TABLE I. Inter-Monthly Variation in the Percent of All Feeding Time Devoted to Different Major Food Categories (N = 125 months)

Food	Mean	SD	Minimum	Maximum
All fruit	72.1	12.5	36.2	94.1
Non-fig fruit	45.9	20.5	6.0	90.0
Figs	26.2	17.4	0.4	66.9
Leaves	19.4	9.2	1.4	48.8
Seeds	3.7	7.1	0	36.7
Flowers	2.65	4.9	0	30.7
Pith & Stems	2.5	3.7	0	26.0

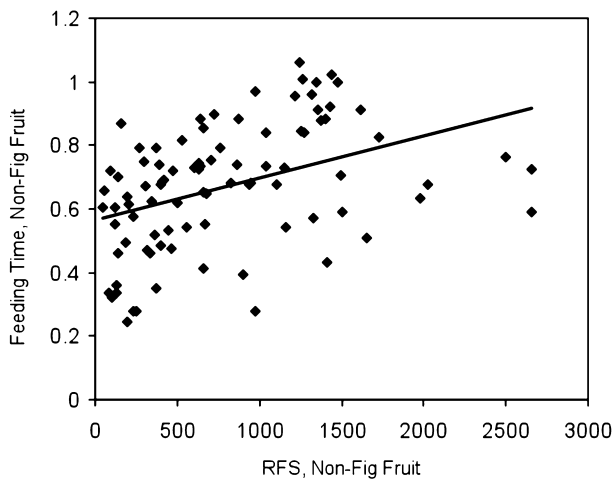


Fig. 2. Relationship between time feeding on non-fig fruit per month and availability of non-fig fruit, estimated by the monthly RFS. Feeding time values were arcsin-square root transformed from percentage data. $F = 17.46$, $df = 88$, $R^2_{adj} = 0.16$, $P < 0.0001$.

and 0.2–1.1% for cambium. Averaging across all months produced mean values quite similar to those from the sample of eight consecutive years, but inter-monthly variation greatly exceeded that among years (Table I). For example, non-fig fruit accounted for as little as 6.0% of monthly feeding time and as much 90.0%.

Monthly feeding time devoted to non-fig fruit was positively associated with the RFS_{nff} ($F = 17.46$, $df = 108$, $P < 0.0001$; Fig. 2). However, this relationship explained little of the variance in feeding time ($r^2_{adj} = 0.16$).

Figs from *Ficus mucuso* accounted for 18% of feeding time, by far the most of all foods (Fig. 3; Appendix A). Figs from *F. dawei*, *F. brachylepis*, and *F. natalensis* also contributed over 1% of feeding time. *Uvariopsis congensis* (10% of feeding time) was the most important non-fig fruit, and seven other fruit species also accounted for over 1% of feeding time (Fig. 3; Appendix A). Availability of fruit and figs is temporally restricted, and consideration of maximum monthly feeding time values further

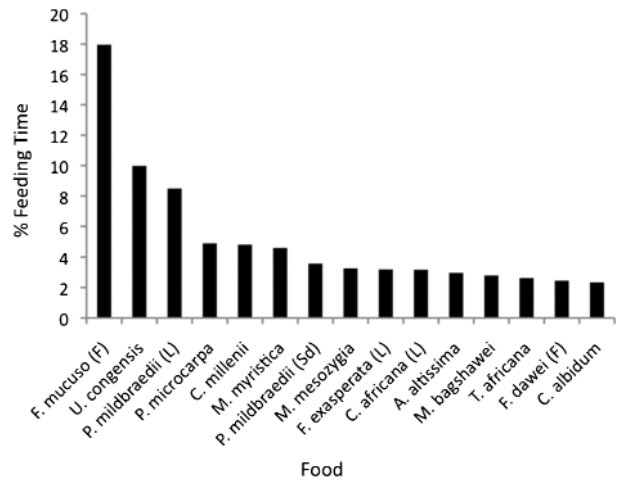


Fig. 3. Percent of total feeding time devoted to each of the top 15 foods in the composite diet. F = figs; L = leaves; Sd = seeds; other foods are non-fig fruit.

highlights their importance: all nine foods that sometimes accounted for over 50% of monthly feeding time were fruit or figs, and maximum values were routinely much higher than overall values for fruit and figs generally (Appendix A). The disparity was relatively low for *Ficus mucuso* despite the high maximum value for figs of this species, but this was because one or more stems bore figs during most months [Watts et al., 2011].

The most commonly eaten leaves were those of *Pterygota milbraedii* (Fig. 2, Appendix A). The chimpanzees ate seeds, seed wings, mesocarp, and cambium from mature trees of this species, which are common in old growth forest at Ngogo, and its seed wings and seeds are particularly important foods [Fig. 3, Appendix A; cf. Potts et al. 2009, 2011]. However, they rarely ate leaves from mature, canopy-level stems, but instead regularly stripped them from saplings, which occur at high densities in much of their home range. They also spent considerable time eating young leaves of *Ficus exasperata* and *Celtis durandii* (Fig. 3, Appendix A). They fed heavily on flowers of *Morus mesozygia* and on flowers, flower buds, and seeds of *Illigera pentaphylla* whenever these were available. Flowers and seeds from other species had minor importance (Appendix A).

Overlap Between Years

Mean dietary overlap between consecutive years in the eight-year sample was $67.9 \pm 3.4\%$ (range = 64.3–74.2%). Mean overlap between all pairs of years in the eight-year sample was similar ($68.6 \pm 4.8\%$; range = 54.2–77.3%). Despite the large number of different foods, only 21 were among the top ten per year in one or more years of the consecutive eight-year sample; most of these were

figs or non-fig fruit. Figs from *F. mucoso* were the top food every year, and fruit of *Uvariopsis congensis* and leaves of *Pterygota mildbraedii* were among the top ten foods every year.

Diet Diversity

Overall diversity was moderate ($H' = 3.282$). The top 15 foods accounted for 77.1% of feeding time in the composite diet (Fig. 3), and the top 20 accounted for 84.7%. Monthly diversity values varied from 1.184 to 3.078 (mean = 2.098 ± 0.392). Monthly J' values varied from 0.333 to 0.868 (mean = 0.650 ± 0.104). They varied inversely with the monthly availability of non-fig fruit, estimated by the $RFS_{\text{non-fig}}$, although this relationship accounted for little of the variance ($F = 7.58$, $R^2 \text{ adj} = 0.08$, $df = 88$, $P = 0.0072$; Fig. 4). J' values were independent of the monthly availability of figs, estimated by the RFS_{fig} ($F = 0.05$, $R^2 \text{ adj} = 0.001$, $df = 88$, $P = 0.8324$; Fig. 4). J' values decreased significantly as the proportion of feeding time devoted to non-fig fruit increased ($F = 42.98$, $r^2 \text{ adj} = 0.26$, $df = 120$, $P < 0.01$; Fig. 5). In contrast, adjusted diversity increased significantly with the percent of monthly feeding time devoted to figs, although this relationship explained little of the variance in J' ($F = 11.12$, $R^2 \text{ adj} = 0.08$, $df = 120$,

$P = 0.0011$; Fig. 5). It was also positively related to the amount of time spent eating leaves ($F = 74.20$, $r^2 \text{ adj} = 0.38$, $df = 120$, $P < 0.0001$; Fig. 5).

Analysis of the relationships of H' to RFSs and feeding time data (not shown) were similar. The number of items eaten per month (including months from the focal data set only) was independent of RFSs and of feeding percentages.

The importance of figs, plus that of leaves of *Ficus exasperata* and *F. varifolia* and fruit from several non-fig Moraceae species, meant that the Moraceae was by far the most prominent plant family in the diet (Fig. 6). Diversity of family use was low: the top five families accounted for over 80% of feeding time, with species of Annonaceae (14.62%) and Sterculiaceae (13.19%) most important after Moraceae, and the top 10 families accounted for almost 95% (Fig. 6).

DISCUSSION

Long-term data show that the chimpanzees at Ngogo have a broad diet that includes many food types, although relatively few foods and food species account for most feeding time, and confirm that they spend much more time eating fruit, including figs, than any other food type. Feeding time does not necessarily measure relative intake accurately, and a next step in data analysis will be to apply Potts' [2008] and Potts et al. [2011] estimates of intake rates to the long-term data and to compare the resulting nutritional profile to his shorter-term profiles for both Ngogo and Kanyawara. Still, Ngogo chimpanzees clearly devote most of their foraging effort to non-fig fruit and to figs, given that feeding is the major temporal component of foraging effort and that searching for fruit sources occupies much of the chimpanzees' travel time [Potts 2008; Potts et al., 2011]

Comparisons to Other Ngogo Studies

Two shorter term data sets on diet composition at Ngogo, both based on direct observation and compiled during periods encompassed within the long-term observations reported here, are available. Potts [2008] and Potts et al. [2011] collected data on adults and adolescents of both sexes using focal sampling; Wakefield [2010] did focal samples of adult and adolescent females only. Many of their observations were independent of those made by Field Assistants and by D. Watts when he was present because observers followed different chimpanzees. Potts' study subjects used *Ficus mucoso* especially heavily (34.1% of feeding time); thus figs in general (42.8% of feeding time) accounted for more feeding time than the long-term average (Table II). In the data set used here, *F. mucoso* accounted for 21.3% of feeding time during the months of Potts' study; this difference reflects sampling of different parties and

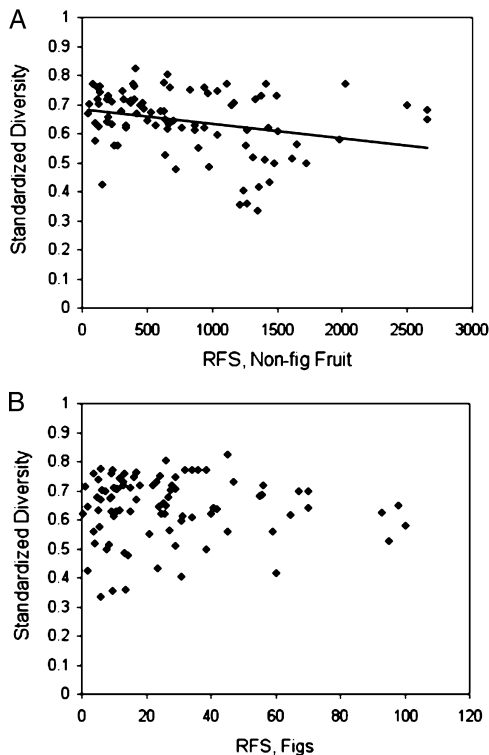


Fig. 4. Relationship of monthly standardized dietary diversity [J'] to (A) the monthly availability of non-fig fruit, estimated by the $RFS_{\text{non-fig}}$ [$F = 7.58$, $R^2 \text{ adj} = 0.08$, $df = 88$, $P = 0.0072$], and (B) the monthly availability of figs, estimated by the RFS_{fig} [$F = 0.05$, $R^2 \text{ adj} = 0.001$, $df = 88$, $P = 0.8324$].

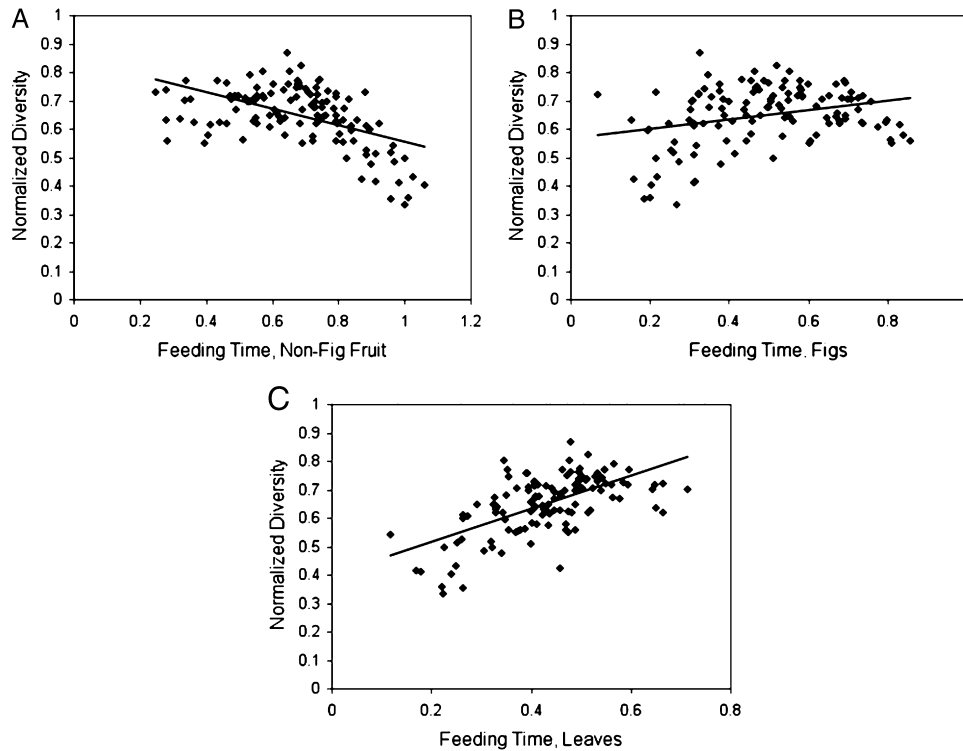


Fig. 5. Relationship of monthly standardized dietary diversity [J] to the proportions of monthly feeding time devoted to (A) non-fig fruit [$F = 42.98$, $R^2_{adj} = 0.26$, $df = 120$, $P < 0.0001$]; (B) figs [$F = 11.12$, $R^2_{adj} = 0.08$, $df = 120$, $P = 0.0011$]; and (C) leaves [$F = 74.20$, $R^2_{adj} = 0.38$, $df = 120$, $P < 0.0001$]. Percent feeding time values are arcsin-square root-transformed.

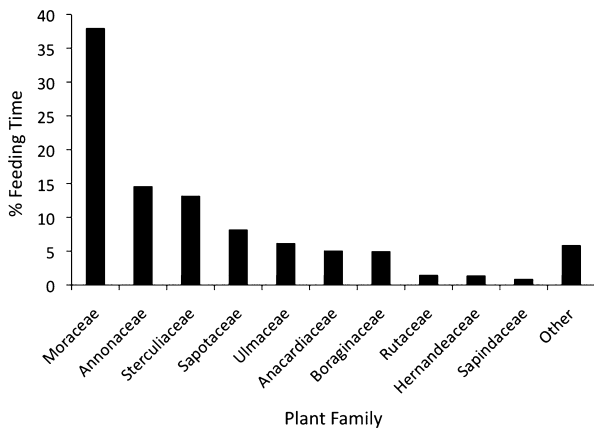


Fig. 6. Percent of total feeding time devoted to each of the top 10 plant families in the composite diet and to all other families combined.

different individuals and may also reflect under-sampling of feeding bouts by Field Assistants late in the day. The contribution of nonfig fruit (46.0%) was close to the long-term average, but the combined contribution of figs and non-fig fruit was higher (Table II). Another notable difference concerns *Chrysophyllum albidum* (9.8% of feeding time in Potts' data set vs. 2.3% in the long-term data; Appendix A). This is a mast-fruiting species that produces little or no fruit in most years [Watts et al.,

2011]. Potts' study period included a masting event. The chimpanzees fed much less on leaves than was typical over the long term (Table II). Seeds, pith, and flowers made contributions similar to or slightly lower than in the long-term data, and all other categories made very small contributions (Table II). Potts documented 68 foods, far less than the long-term total; his list did not include some species that did not fruit during his study period (e.g., *Aphania senegalensis*).

Wakefield's subjects also spent considerably more time eating fruit (85.6%) than typical of the long-term, mostly because they spent more time spent eating figs (47.3%), and less eating all other categories, especially leaves and pith (Table II). This reflects variation in food availability among years and in individual habitat use and food choice, but probably also reflects sex differences in feeding ecology. Bates and Bryne [2009] found that when chimpanzees at Sonso (Budongo) fed at trees with large fruit crops in the morning, females often revisited these in the afternoon, while males more often traveled away from them and used other food sources. Comparable data on movement patterns are not available for Ngogo, but our overwhelming impression is that the same difference exists, with females especially prone to rest in or near individual stems of *Ficus mucuso* and other trees with extremely large canopies (e.g., *Aningeria altissima*) after morning feeding sessions and more likely than males to feed in them again later.

TABLE II. Percent of Total Feeding Time Devoted to Different Plant Food Categories at Chimpanzee Research Sites for Which Direct Observational Data Are Available (All Fruit = Figs and Non-fig Fruit Combined)

Site	All fruit	Non-fig fruit	Figs	Leaves	Seeds	Flowers	Pith/stems	Other
Ngogo ^a	70.7	42.3	28.4	19.6	4.0	2.5	2.2	1.0
Ngogo ^b	87.0	45.1	41.9	3.6	6.0	0.8	1.4	1.2
Ngogo ^c	85.6	38.3	47.3	6.5	3.6	0.5	0.3	2.5
Budongo ^d	64.5	42	23	19.7	<i>nd</i>	8.8	3.2	3.8
Budongo ^e	70.1	<i>nd</i>	<i>nd</i>	27.0	<i>nd</i>	<i>nd</i>	<i>nd</i>	2.9
Budongo ^f	71	<i>nd</i>	<i>nd</i>	16.0	c. 2.0	c. 7	c. 1.0	c. 3.0
Fongoli ^g	65.8	<i>nd</i>	<i>nd</i>	16.8	0	11.6	3.2	2.5
Gombe ^h	59.4	<i>nd</i>	<i>nd</i>	21.2	<i>nd</i>	<i>nd</i>	<i>nd</i>	19.4
Goualago ⁱ	57.0	<i>nd</i>	<i>nd</i>	32.0	0	4.0	2.0	5.0
Mahale ^j	64.5	60.1	4.1	5.8	0.4	0	14.8	14.1
Kanyawara ^k	82.1	<i>nd</i>	<i>nd</i>	8	<i>nd</i>	<i>nd</i>	11.7	0.1
Kanyawara ^l	79.0 [74.5–84.5]	39.0	40.0 [32.7–44.5]	2.8 [1.1–5.3]	<i>nd</i>	<i>nd</i>	16.9 [12.3–19.9]	0.7 [0.1–1.1]
Tai ^m	78.0	<i>nd</i>						

^aSources: this study.

^bSources: Potts et al. [2011].

^cSources: Wakefield [2010].

^dNewton-Fisher [1999].

^eFawcett [2000].

^fTweheyo et al. [2003].

^gPreutz [2006].

^hWrangham [1977].

ⁱMorgan and Sanz [2006].

^jMatsumata-Oda & Hayashi [1997].

^kChapman et al. [1994].

^lWrangham et al. 1996 [annual means for a four year period; values in parentheses are ranges].

^mAnderson et al. 2002. *nd* = data not provided. Values for Fongoli and Mahale have been adjusted to exclude meat and invertebrates, which were included in published totals; those for Gombe include meat and invertebrates, thus are underestimates for the plant fraction of the diet.

Comparisons to Other Sites

Data on the percent of feeding time devoted to different types of plant food over a three-year period at Kanyawara [Wrangham et al., 1996; Table II] yield an estimated overlap of 73% in food types with Ngogo. A 12-year Kanyawara data set that included these three years gives an overlap of 69.5–73.3% [Emery Thompson & Wrangham, 2008; Table II]. Figs accounted for proportionately more feeding time in both Kanyawara data sets, and non-fig fruit for less, than in the long-term Ngogo data (Table II). Four of the top seven Kanyawara food species during a 3-year period were figs [Wrangham et al., 1996], and four of the top five fruit sources were figs in the longer data set [Emery Thompson & Wrangham, 2008]. However, the mean annual percent of feeding time devoted to figs there (Table II) was similar to values reported by Potts [2008], Potts et al. [2011] and Wakefield [2010] for shorter periods at Ngogo. Pith and stems were much more important at Kanyawara [Table II; cf. Chapman et al., 2004], while leaves were much more important at Ngogo and chimpanzees there ate more flowers and seeds (Table II). Leaves served as fallbacks at Ngogo, but not Kanyawara [Wrangham et al. 1996; Watts et al., 2011].

Detailed analysis of long-term overlap between Ngogo and Kanyawara is not yet possible, but important similarities and contrasts are evident. Several tree species are major food sources at both sites [Emery Thompson & Wrangham 2008; Potts

et al., 2011]. Fruit from *Mimusops bagshawei* (12.4%), *Uvariopsis congensis* (5.9%), and *Pseudospondias microcarpa* (2.9%) accounted for 21.2% of feeding time over 12 years at Kanyawara [Emery Thompson & Wrangham, 2008] and 16.7% at Ngogo, although *Mimusops* was considerably less important, and *Uvariopsis* considerably more so, there (Appendix A). Among figs present at both sites, those of *Ficus natalensis* were the top Kanyawara food in terms of feeding time (13.6% vs. 2.3% at Ngogo), those of *F. sansabarica* (= *F. brachylepis*) accounted for 11.5% at Kanyawara but only 1.6% at Ngogo, those of *F. exasperata* were much more important at Kanyawara (6.4% vs. 0.4%), and *F. saussureana* (= *F. dawei*) accounted for similar proportions of feeding time at both sites [Kanyawara = 3.5%, Ngogo = 2.5%; Emery Thompson & Wrangham, 2008; Appendix A]. The most striking contrasts involve species important at Ngogo but rare or absent at Kanyawara, including *Ficus mucoso* (absent) and *Pterygota mildbraedii*, the two species most important quantitatively at Ngogo. Such species, plus several others with minor importance at Ngogo, accounted for about 40% of feeding time in the composite Ngogo diet [cf. Potts et al., 2011]. *Ficus mucoso* stands out most notably: one or stems in the phenology sample bore fruit in over 70% of months and stems not included in the sample fruited in other months, and the diet included figs from this species in over 70% of months [Watts et al., 2011]. Other figs were also available in most

months. Figs generally, and *F. mucuso* in particular, were staples at Ngogo, and the relatively high density and high availability of *F. mucuso* at the site almost certainly helps to explain why chimpanzee population density is about three times higher than at Kanyawara [Potts et al., 2009, 2011; Watts et al., 2011].

Comparison to non-Kibale sites for which observational data on feeding times are available shows that the Ngogo composite diet most closely resembles that of the Sonso community in Budongo in terms of relative contributions by different food categories (Table II). Three studies there [Fawcett, 2000; Newton-Fisher, 1999; Tweheyo et al., 2003] yielded values for all fruit and leaves quite similar to those from Ngogo. Newton-Fisher's [1999] values for figs and non-fig fruit are the closest, although the composition of the fig component of the diet differed. *F. sur*, a minor food at Ngogo, was the most important fig species at Budongo [Newton-Fisher, 1999; Tweheyo & Lye, 2003; Tweheyo et al., 2003], and *F. mucuso*, while a major food at Sonso, contributes much less of the diet than at Ngogo (e.g., 9.8% of feeding time during Newton-Fisher's [1999] study). Leaves were the most important non-fruit food category at Budongo. Leaves have similar quantitative importance at Tai National Park, Ivory Coast, where the diet also mostly comprises fruit [Anderson et al., 2002; Table II], but unlike at Tai, nuts are unimportant at Ngogo. Values from Fongoli, Senegal, are also similar to those from Ngogo despite strong contrasts in climate and vegetation, but the Fongoli data come from a short study [Preutz, 2006] and may eventually be considerably revised. The high value for time eating flowers at Fongoli distinguishes it from all other sites except for one study at Budongo [Newton-Fisher, 1999] and may reflect short-term sampling bias. Similarly, published quantitative data from Mahale Mountains, Tanzania span only four months [Matsumata-Oda & Hayashi, 1997], although the diet at Mahale is clearly much broader than evident from this short term study [Nishida & Uehara, 1983], and those from the Goulougo Triangle, Republic of Congo [Morgan & Sanz, 2006] may change as sample time increases. As data from Ngogo [this study] and Kanyawara [Wrangham et al., 2006] demonstrate, diet composition at a given site can vary considerably from year to year, and single annual cycles have limited comparative value.

The high feeding time value for pith and stems at Mahale [Matsumata-Oda & Hayashi, 1997] may reflect short-term sampling bias, but such bias could not explain the consistent difference in consumption of pith and stems between Kanyawara and Ngogo [this study; Chapman et al., 2004; Potts, 2008; Potts et al., 2011; Wakefield, 2010; Wrangham et al., 1996]. Pith and stem from herbaceous vegetation have considerable nutritional importance at Kanyawara [Wrangham et al., 1991] and are "secondary" fallback foods there after figs [Wrangham et al., 1996], but they are much less important absolutely and in relation to

non-fig fruit availability at Ngogo, where they are not fallbacks [Potts et al., 2011; Watts et al., 2011].

Cross-site comparisons of diet breadth [number of items and species eaten] and diversity are problematical because of potential sampling biases; in particular, breadth probably increases asymptotically with study length. Diet breadth at Ngogo is lower than at Bossou, for which Sugiyama and Koman [1987] noted 205 different plant foods from 156 species and Hockings et al. [2009] subsequently reported 212 plant foods from 140 identified species, including 24 from 17 cultivated species, and at Mahale, for which Nishida and Uehara [1983] reported 271 plant foods. Both sites receive more rain than Ngogo, and Bossou is a lowland evergreen forest; this implies that plant species diversity is higher than at Ngogo, a moderately diverse, mid-altitude forest [Struhsaker, 1997]. But many important food species at Ngogo are abundant (e.g., *Uvariopsis congensis*), which may explain why the diet is not much broader there than in the montane forest at Kahuzi (156 plant items from 116 species, including 62 that were sources of fruit pulp, and 57 families [Basabose, 2002]), where plant species diversity is presumably lower.

Chimpanzees as Frugivores

Many primates show considerable dietary flexibility across habitats and across time within habitats [reviewed in Lambert, 2007]. Redtail monkeys (*Cercopithecus ascanius*) and blue monkeys (*C. mitis*) are notable examples. Redtails in Kibale are also highly frugivorous, but Chapman et al. [2002] reported that the percent of time that different groups ate fruit varied from 26 to 60% and that data from other East African populations extended the range to 13–61%. They also reported that blue monkeys in different populations spent 26–91% of their feeding time eating fruit and 3–47% eating leaves. In contrast, fruit (including figs) accounted for the majority of feeding time at all chimpanzee sites included in Table II. Similarly, limited observational data and analysis of fecal samples highlight the greater importance of fruit for chimpanzees than for gorillas in habitats where these two African apes are sympatric [Basabose, 2002; Kuroda et al., 1996; Stanford & Nkurunungi, 2003].

Comparing chimpanzee diet profiles with those of baboons (*Papio* spp.) and spider monkeys (*Ateles* spp.) is particularly worthwhile. Baboons have remarkably broad diets and are extremely flexible feeders; those in some populations mostly eat fruit (or fruit and seeds), but their ability to subsist on diets comprising mostly nonfruit plant parts highlights the importance of fruit to chimpanzees. Baboons are "eclectic" and "selective" omnivores that use many food plants, but selectively eat the best parts [Altmann, 1998; Hamilton et al., 1978]. Their diets vary greatly across populations and habitats in terms of plant categories and species

composition [Altmann, 1998]. Variation in the importance of fruit is much higher than for chimpanzees. Fruit (including seeds) accounts for most feeding time at some study sites, but for a mean of only 34% in 11 studies summarized by Whiten et al. [1991] and 39.6% (range = 3–73.5%) in 21 studies summarized by Altmann [1998; these included the studies in the Whiten et al. sample]. The coefficient of variation (CV) was 0.47 for Altmann's [1998] sample. Fruit accounted for a mean of 67.3% of feeding time in the chimpanzee sample summarized in Table II if the calculation is based on only one data point per site (including long-term Ngogo and Kanyawara values and a single value equal to the mean of the three Budongo studies); the CV was 0.11. Underground plant parts or leaves accounted for over 50% of feeding time in some baboon populations. Cross-site variation in the use of other plant parts by baboons was considerable, but not necessarily higher than variation across chimpanzee communities and habitats. For example, leaves accounted for as little as 7.3% of baboon feeding time and as much as 53% [Altmann, 1998; Whiten et al., 1991]; Altmann [1998] gives a mean of 18.3% (CV = 0.40). The chimpanzee mean was 17.0% (CV = 0.58; one data point per site). Similarly, the CV for underground plant parts, which accounted for a mean of 24.6% of baboon feeding time in Altmann's [1998] sample, was 0.64, while that for pith and stems for chimpanzee studies included in Table II was 1.02.

Spider monkeys also concentrate on ripe fruit and have a classic fission–fusion social system in which party size variation depends partly on variation in fruit patch availability [Di Fiore & Campbell, 2007; cf. Russo et al., 2005]. Fruit accounted for a mean of 81.4% of feeding time for *Ateles belzebuth* at six sites (range = 73.0–91.7%, CV = 0.09) and leaves for 15.5% (range = 7.0–15.5%, CV = 0.34; calculated from Table III in Di Fiore & Campbell [2007]). At seven sites, *A. geoffroyi* devoted a mean of 73.0% of feeding time to fruit (range = 60.0–83.7%, CV = 0.16) and 15.0% to leaves (range = 10.7–25.4%, CV = 0.33; values calculated from Table I in Gonzáles-Zamora et al. [2009], excluding populations in forest fragments and using means from multiple studies at single sites). Van Roosmalen [1985] gave values of 79.8% of feeding time devoted to fruit and 7.9% to leaves for an *A. paniscus* community in Surinam. These resemble chimpanzee values, although spider monkeys generally spend slightly more time eating fruit and less eating leaves, as expected given differences in body mass.

Are Ngogo Chimpanzees Ripe Fruit Specialists?

The positive relationship between feeding time on non-fig fruit and estimated fruit abundance at Ngogo agrees with Conklin-Brittain et al.'s [1998] finding for Kanyawara, despite large differences in

forest ecology and chimpanzee feeding between these sites (most notably, figs from *Ficus mucosa*) are often abundant at Ngogo when non-fig fruit is scarce, and the chimpanzees can concentrate on these instead of devoting more search effort to non-fig fruit; above [Potts et al., 2009, 2011; Watts et al., 2011]. In contrast, redtail monkeys, blue monkeys, and grey-cheeked mangabeys at Kanyawara all switched to heavy use of nonfruit items when fruit was scarce. The positive relationship between fruit feeding time and RFSs would probably be stronger except for error in calculation of RFSs. This includes unknown error associated with extrapolating from DBH to fruit crop size; this may be a particular problem for strangler figs, which make up much of the diet at Kanyawara. It also results from the fact that the chimpanzees have very large home ranges, and even extensive phenology samples cannot capture all the variation in fruiting by species abundant in large parts of this area, especially when fruiting is not tightly synchronized intra-specifically. For example, ripe *U. congensis* fruit is sometimes abundant in part of the Ngogo chimpanzees' home range and is the main food for many individuals at times when the species has either not yet ripened or has finished fruiting elsewhere; the location of trees in the phenology sample may miss this spatio-temporal variation. The small amount of variation in non-fig fruit feeding time explained by the RFS points to such error and to the need for more accurate fruit availability estimates. Nevertheless, the positive relationships between foraging effort devoted to non-fig fruit and its availability at both Kibale study sites reinforces the characterization of chimpanzees as ripe fruit specialists.

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Appendix A

Composition of the diet at Ngogo is given in Table AI.

TABLE AI. Composition of the Diet at Ngogo

Species	Family	Part	% Feeding Time
Ficus mucoso	Moraceae	fig	17.9650
Uvariopsis congensis	Annonaceae	fr	9.9800
Pterygota mildbraedii	Sterculiaceae	lv	8.4876
Pseudospondias microcarpa	Anacardiaceae	fr	4.9000
Cordia millenii	Boraginaceae	fr	4.8240
Monodora myristica	Annonaceae	fr	4.6001
Pterygota mildbraedii	Sterculiaceae	sd	3.5738
Morus mesozygia	Moraceae	fr	3.2566
Ficus exasperata	Moraceae	lv	3.1861
Celtis Africana	Ulmaceae	lv	3.1699
Aningeria altissima	Sapotaceae	fr	2.9600
Mimusops bagshawei	Sapotaceae	fr	2.7889
Treculia africana	Moraceae	fr	2.6200
Ficus dawei	Moraceae	fig	2.4496
Chrysophyllum albidum	Sapotaceae	fr	2.3433
Ficus natalensis	Moraceae	fig	2.2579
Celtis durandii	Ulmaceae	fr	1.5889
Ficus brachylepis	Moraceae	fig	1.5502
Teclea nobilis	Rutaceae	fr	1.2763
Morus mesozygia	Moraceae	fl	0.9183
Celtis mildbraedii	Ulmaceae	lv	0.7467
Illigera pentaphylla	Hernandiaceae	fl	0.7104
Aframomum mildbraedii	Zingiberaceae	pi	0.7004
Acanthus pubescens	Acanthaceae	pi	0.6100
Zanha golungensis	Sapindaceae	fr	0.6096
Morus mesozygia	Moraceae	lv	0.5591
Ficus variifolia	Moraceae	fig	0.5242
Illigera pentaphylla	Hernandiaceae	sd	0.5198
Chaetacme aristata	Ulmaceae	lv	0.5144
Warburgia ugandensis	Canellaceae	fr	0.4476
Cyperus papyrus	Cyperaceae	Pi	0.4201
Cola gigantean	Sterculiaceae	Fr	0.4168
Elaeodendron buchanii	Celastraceae	Fr	0.3833
Ficus exasperata	Moraceae	fig	0.3830
Pterygota mildbraedii	Sterculiaceae	flbd	0.3820
Neoboutonia macrocalyx	Euphorbiaceae	rt	0.3506
Ficus variifolia	Moraceae	lv	0.2906
Ficus sur	Moraceae	fig	0.2882
Ficus vallis-choudae	Moraceae	fig	0.2736
Ficus pseudomangifera	Moraceae	fig	0.2585
Unidentified climber		lv	0.2582
Bosqueia phoberos	Moraceae	fr	0.2505
Piper capense	Piperaceae	pi	0.2436
Pterygota mildbraedii	Sterculiaceae	ca	0.2409
Celtis durandii	Ulmaceae	lv	0.2320
Ficus congensis	Moraceae	fig	0.2047
Phytolacca dodecandra	Phytolaccaceae	fr	0.1926
Ficus cyathistipula	Moraceae	fig	0.1710
Trichelia dregeana	Meliaceae	lv	0.1672
Cordia millenii	Boraginaceae	fl	0.1507
Ipomea spathulata	Sapindaceae	lv	0.1466
Unidentified tree		ddwd	0.1272
Pennisetum purpureum	Rosaceae	pi	0.1248
Urera hypsilodendron	Urticaceae	lv	0.1230
Pseudospondias microcarpa	Anacardiaceae	sd	0.1145
Phoenix reclinata	Palmae	pi	0.1079
Aphania senegalensis	Sapindaceae	fr	0.1068
Ficus brachypoda	Moraceae	fig	0.1065
Antiaris toxicaria	Moraceae	fr	0.1041
Marantachloa leucantha	Sapotaceae	pi	0.0997

TABLE AI. Continued

Species	Family	Part	% Feeding Time
<i>Allophyllus abyssinicus</i>	Sapindaceae	fr	0.0962
<i>Pseudospondias microcarpa</i>	Anacardiaceae	lv	0.0951
<i>Ficus stipulifera</i>	Moraceae	fig	0.0861
<i>Celtis africana</i>	Ulmaceae	ca	0.0858
<i>Parinari excelsa</i>	Rosaceae	fr	0.0816
Unidentified climber		lv	0.0808
<i>Piper umbellatum</i>	Piperaceae	pi	0.0800
<i>Antiaris toxicaria</i>	Moraceae	lv	0.0759
Unidentified tree		flbd	0.0700
<i>Pterygota mildbraedii</i>	Sterculiaceae	fr	0.0663
<i>Discopodium penninervum</i>	Solanaceae	pi	0.0656
<i>Ficus</i> sp.	Moraceae	fig	0.0641
<i>Mitragena</i> sp.	Rubiaceae	ca	0.0628
<i>Phoenix reclinata</i>	Palmae	fr	0.0533
<i>Antiaris toxicaria</i>	Moraceae	fl	0.0512
<i>Tabernaemontana holstii</i>	Apocynaceae	fr	0.0509
<i>Neoboutonia macrocalyx</i>	Euphorbiaceae	ddwd	0.0503
Unidentified shrub		flbd	0.0500
Caterpillars		invert	0.0500
Unidentified tree		rt	0.0500
<i>Toddalia asiatica</i>	Rutaceae	fr	0.0498
<i>Ilygera pentaphylla</i>	Hernandiaceae	lv	0.0497
Unidentified sapling		lv	0.0463
<i>Ficus thoningii</i>	Moraceae	fig	0.0452
<i>Ficus dawei</i>	Moraceae	lv	0.0406
<i>Afrosersalisia cerasifera</i>	Sapotaceae	fr	0.0388
<i>Fluegea virosa</i>	Euphorbiaceae	fr	0.0379
<i>Hoslundia opposita</i>	Labiatae	fr	0.0347
<i>Markhamia platycalx</i>	Bignoniaceae	ca	0.0341
<i>Ficus cyathistipula</i>	Moraceae	lv	0.0319
<i>Mimulopsis arboreus</i>	Acanthaceae	sd	0.0306
<i>Celtis africana</i>	Ulmaceae	fl	0.0301
Honeycomb		comb	0.0300
<i>Aframomum zambesiacum</i>	Zingiberaceae	pi	0.0300
<i>Parkia filcoidea</i>	Leguminosae	fr	0.0296
<i>Ficus natalensis</i>	Moraceae	lv	0.0293
<i>Ficus natalensis</i>	Moraceae	ca	0.0288
<i>Bequaertiodendron</i> sp.	Sapotaceae	fr	0.0287
<i>Rubia cordifolia</i>	Rubiaceae	lv	0.0264
<i>Acalypha neptunica</i>	Euphorbiaceae	lv	0.0258
Unidentified tree		fr	0.0203
<i>Dovyalis macrocalyx</i>	Flacourtiaceae	lv	0.0203
<i>Ficus cyathistipula</i>	Moraceae	ca	0.0195
<i>Beilschmiedia ugandensis</i>	Lauraceae	fr	0.0195
<i>Monodora myristica</i>	Annonaceae	ca	0.0185
<i>Monodora myristica</i>	Annonaceae	lv	0.0175
Unidentified tree		fl	0.0171
<i>Aframomum mildbraedii</i>	Zingiberaceae	fr	0.0171
<i>Pteris</i> sp.	Pteridaceae	lv	0.0161
<i>Trichelia dregeana</i>	Meliaceae	flbd	0.0157
<i>Brillantaisia nitens</i>	Acanthaceae	fl	0.0155
Honey		honey	0.0148
<i>Brillantaisia nitens</i>	Acanthaceae	rt	0.0144
<i>Cola gigantea</i>	Sterculiaceae	ca	0.0138
<i>Ficus othoralis</i>	Moraceae	fig	0.0136
<i>Pteris</i> sp.	Pteridaceae	pi	0.0132
<i>Lovoa swynnertonii</i>	Meliaceae	fl	0.0130
<i>Pseudospondias microcarpa</i>	Anacardiaceae	ca	0.0128
<i>Neoboutonia macrocalyx</i>	Euphorbiaceae	fl	0.0124
<i>Fagaropsis angolensis</i>	Rutaceae	fr	0.0118
<i>Antiaris</i> sp.	Moraceae	fr	0.0117

TABLE AI. Continued

Species	Family	Part	% Feeding Time
<i>Pancovia turbinata</i>	Sapotaceae	fr	0.0116
<i>Dovyalis macrocalyx</i>	Flacourtiaceae	fr	0.0112
Unidentified tree		fl	0.0107
<i>Ficus polita</i>	Moraceae	fig	0.0106
<i>Celtis mildbraedii</i>	Ulmaceae	fr	0.0102
<i>Conopharyngia holstii</i>	Apocynaceae	fr	0.0102
<i>Teclea nobilis</i>	Rutaceae	lv	0.0097
<i>Ficus brachylepis</i>	Moraceae	ca	0.0095
<i>Ficus mucoso</i>	Moraceae	lv	0.0091
<i>Dasylepis eggelenii</i>	Flacourtiaceae	fr	0.0089
Unidentified tree		lv	0.0087
<i>Linociera johnsonii</i>	Oliaceae	ddwd	0.0084
<i>Chaetacme aristata</i>	Ulmaceae	fr	0.0084
<i>Ficus mucoso</i>	Moraceae	ca	0.0083
<i>Glyphaea brevis</i> [lateriflora]	Tillriaceae	lv	0.0073
<i>Pterygota mildbraedii</i>	Sterculiaceae	tbpi	0.0065
<i>Funtumia latifolia</i>	Apocynaceae	lv	0.0064
Unidentified climber		fl	0.0063
Unidentified shrub		lv	0.0062
Wasp pupae		invert	0.0062
<i>Trichelia</i> sp.	Meliaceae	fl	0.0056
<i>Cola gigantea</i>	Sterculiaceae	fl	0.0052
<i>Aframomum mildbraedii</i>	Zingiberaceae	lv	0.0051
<i>Bosqueia phoberos</i>	Moraceae	ca	0.0050
<i>Aframomum zambesiaccum</i>	Zingiberaceae	fr	0.0050
Soil		soil	0.0050
Caterpillar secretions		invert	0.0050
Termites		invert	0.0048
Unidentified herb	Zingiberaceae	fl	0.0047
<i>Morus mesozygia</i>	Moraceae	ca	0.0043
<i>Schrebera arborea</i>	Oleaceae	fl	0.0041
<i>Calyx</i> sp.		fr	0.0041
<i>Marantachloa leucantha</i>	Sapotaceae	fr	0.0038
<i>Ficus exasperata</i>	Moraceae	ca	0.0036
Unidentified tree		ca	0.0034
Acacia	Fabaceae	ca	0.0033
<i>Brillantaisia nitens</i>	Acanthaceae	pi	0.0033
<i>Urera hypsilodendron</i>	Urticaceae	fl	0.0032
<i>Ficus asperifolia</i>	Moraceae	lv	0.0032
<i>Premna angolensis</i>	Verbenaceae	ca	0.0031
Unidentified tree		ca	0.0031
Unidentified climber	Rubiaceae	lv	0.0031
Unidentified		mush	0.0031
<i>Euadenia eminens</i>	Capparidaceae	fr	0.0030
<i>Drypetes battiscombei</i>	Euphorbiaceae	fr	0.0028
<i>Formix</i> [?] sp.		fr	0.0027
<i>Chaetacme aristata</i>	Ulmaceae	ca	0.0026
<i>Markhamia platycalx</i>	Bignoniaceae	lv	0.0026
Unidentified herb		pi	0.0026
Unidentified herb		pi	0.0024
<i>Acanthopale</i> [?] sp.	Acanthaceae	fl	0.0023
<i>Rubus</i> sp.	Rubiaceae	fr	0.0023
Unidentified herb	Zingiberaceae	pi	0.0023
<i>Reissantia</i> sp.	Celastraceae	sd	0.0023
<i>Ficus variifolia</i>	Moraceae	ca	0.0021
<i>Dasylepis eggelenii</i>	Flacourtiaceae	fl	0.0020
<i>Celtis africana</i>	Ulmaceae	fr	0.0020
<i>Strombosia scheffleri</i>	Olacaceae	ca	0.0019
Unidentified tree		fl	0.0019
<i>Blighia unijugata</i>	Sapindaceae	fr	0.0019
<i>Trichelia dregeana</i>	Meliaceae	fr	0.0013

TABLE AI. Continued

Species	Family	Part	% Feeding Time
<i>Dombeya goetzenii</i>	Sterculiaceae	fr	0.0009
<i>Richeia albersii</i>	Capparidaceae	fr	0.0009
<i>Trichelia dregeana</i>	Meliaceae	ca	0.0008
Unidentified shrub		ca	0.0008
<i>Ficus</i> sp.	Oliaceae	fr	0.0007
<i>Ficus</i> sp ind yl	Moraceae	lv	0.0006
<i>Dasylepis eggelenii</i>	Flacourtiaceae	lv	0.0005
<i>Piper capense</i>	Piperaceae	fr	0.0004
<i>Ficus thoningii</i>	Moraceae	lv	0.0004
<i>Hibiscus</i> sp.	Malvaceae	lv	0.0004
<i>Cissus</i> sp.	Vitaceae	fr	0.0002
<i>Piper capense</i>	Piperaceae	lv	0.0002
<i>Trichelia dregeana</i>	Meliaceae	pi	0.0002
<i>Funtumia latifolia</i>	Apocynaceae	fr	0.0001
<i>Myrianthus holstii</i>	Moraceae	lv	0.0001
<i>Funtumia latifolia</i>	Apocynaceae	tbpi	0.0001

Foods are listed in descending order according to their mean contribution to monthly feeding time. Ca = cambium; ddwd = dead wood; fig = figs; fl = flowers; flbd = flower buds; fr = non-fig fruits; invert = invertebrates; lv = leaves; mush = mushrooms; pi = pith from herbs; rt = roots; sd = seeds; tbpi = pith from terminal tree branches. Items in boldface are included in the phenology sample used to calculate the ripe fruit score.

REFERENCES

- Altmann J. 1974. Observational methods in the study of behaviour. *Behaviour* 49:227–267.
- Altmann SA. 1998. Foraging for survival. Chicago: University of Chicago Press. 609p.
- Anderson D, Nordheim EV, Boesch C, Moermond TC. 2002. Factors influencing fission-fusion grouping in chimpanzees in the Taï National Park, Côte d'Ivoire. In: Boesch C, Hohmann G, Marchant L, editors. Behavioral diversity in chimpanzees and bonobos. Cambridge: Cambridge University Press. p 90–101.
- Basabose K. 2002. Diet composition of chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. *International Journal of Primatology* 23:1–21.
- Bates LA, Bryne R. 2009. Sex differences in the movement patterns of free-ranging chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology* 64:247–255.
- Borries C, Koenig A, Winkler P. 2001. Variation of life history traits and mating patterns in female langur monkeys (*Semnopithecus entellus*). *Behavioral Ecology and Sociobiology* 50:391–402.
- Chapman CA, Chapman LJ, Cords M, Gauthua M, Gautier-Hion A, Lambert JE, Rode KD, Tutin CEG, White LJT. 2002. Variation in the diets of cercopithecine species: differences within forests, among forests, and across species. In: Glenn M, Cords M, editors. The guenons: diversity and adaptation in African monkeys. New York: Plenum. p 319–344.
- Chapman CA, Chapman LJ, Struhsaker TT, Zanne AE, Clark CJ, Poulson JR. 2004. A long-term evaluation of fruiting phenology: importance of climate change. *Journal of Tropical Ecology* 21:31–45.
- Conklin-Brittain NL, Wrangham RW, Hunt KD. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance II: macronutrients. *International Journal of Primatology* 19:971–998.
- Conklin-Brittain NL, Knott CD, Wrangham RW. 2006. Energy intake by wild chimpanzees and orangutans: methodological considerations and a preliminary comparison. In: Hohmann G, Robbins M, Boesch C, editors. Feeding ecology in apes and other primates. Cambridge: Cambridge University Press. p 445–472.
- Di Fiore A, Campbell C. 2007. The atelines: variation in ecology, behavior, and social organization. In: Campbell CJ, Fuentes A, Mackinnon KC, Panger M, Bearder SK, editors. Primates in perspective. Oxford: Oxford University Press. p 155–185.
- Emery Thompson M, Kahlenberg SM, Gilby IC, Wrangham RW. 2007. Core area quality is associated with variance in reproductive success among female chimpanzees at Kanyawara, Kibale National Park. *Animal Behaviour* 73:501–512.
- Emery Thompson M, Wrangham RW. 2008. Diet and reproductive function in wild female chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National park, Uganda. *American Journal of Physical Anthropology* 135:171–181.
- Fawcett KA. 2000. Female relationships and food availability in a forest community of chimpanzees. Ph.D. thesis, University of Edinburgh.
- Gilby IC, Pokempner AA, Wrangham RW. 2010. A direct comparison of scan and focal sampling methods for measuring wild chimpanzee feeding behavior. *Folia Primatologica* 81:254–264.
- Gonzales-Zamora A, Arroyo-Rodriguez V, Chaves OM, Sanchez-Lopez S, Stoner KE, Riba-Hernandez P. 2009. Diet of spider monkeys (*Ateles geoffroyi*) in Mesoamerica: current knowledge and future directions. *American Journal of Primatology* 71:8–20.
- Hamilton WJ III, Buskirk RE, Buskirk WH. 1978. Omnivory and utilization of food resources by chacma baboons, *Papio ursinus*. *American Naturalist* 112:911–924.
- Hill MO. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54:427–432.
- Hockings K, Anderson JR, Matsuzawa T. 2009. Use of wild and cultivated food at Bossou, Republic of Guinea: feeding dynamics in a human influenced environment. *American Journal of Primatology* 71:636–646.
- Hohmann G, Potts KB, N'Guesson A, Fowler A, Mundry R, Ganzhorn JR, Ortmann S. 2010. Plant foods consumed by *Pan*: exploring the variation of nutritional ecology across Africa. *American Journal of Physical Anthropology* 141:476–485.
- Kuroda S, Nishihara T, Suzuki S, Oko RA. 1996. Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. In: McGrew WC, Marchant LF, Nishida T, editors.

- Great ape societies. Cambridge: Cambridge University Press, p. 71–81.
- Lambert JL. 2007. Primate nutritional ecology: feeding ecology and diet at ecological and evolutionary scales. In: Campbell CJ, Fuentes A, Mackinnon KC, Panger M, Bearder SK, editors. *Primates in perspective*. Oxford: Oxford University Press.
- Langergraber KG, Vigilant L, Mitani JC. 2009. Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology* 71:840–851.
- Lehmann J, Boesch C. 2008. Sex differences in chimpanzee sociability. *International Journal of Primatology* 29: 65–81.
- Lwanga JS. 2003. Forest succession in Kibale National Park, Uganda: implications for forest restoration and management. *African Journal of Ecology* 41:9–22.
- Lwanga JS, Butynski TM, Struhsaker TT. 2001. Tree population dynamics in Kibale National Park Uganda. *African Journal of Ecology* 238–247.
- Matsumata-Oda A, Hayashi Y. 1999. Nutritional aspects of fruit choice by chimpanzees. *Folia Primatologica* 70:154–162.
- Mitani JC, Amsler SJ. 2003. Social and spatial aspects of male subgrouping in a community of wild chimpanzees. *Behaviour* 140:869–884.
- Mitani JC, Watts DP. 1999. Demographic influences on the hunting behavior of chimpanzees. *American Journal of Physical Anthropology* 109:439–454.
- Mitani JC, Watts DP, Lwanga JS. 2002. Ecological and social correlates of chimpanzee party size and composition. In: Boesch C, Hohmann G, Marchant L, editors. *Behavioral diversity in chimpanzees and bonobos*. Cambridge: Cambridge University Press, p. 102–111.
- Morgan D, Sanz C. 2006. Chimpanzee feeding ecology and comparisons with sympatric gorillas in the Goulougo Triangle, Republic of Congo. In: Hohmann G, Robbins MM, Boesch C, editors. *Feeding ecology in apes and other primates*. Cambridge: Cambridge University Press, p. 97–122.
- Newton-Fisher NE. 1999. The diet of chimpanzees in the Budongo Forest. *African Journal of Ecology* 34: 344–354.
- Newton-Fisher NE, Reynolds V, Plumptre AJ. 2000. Food supply and chimpanzee (*Pan troglodytes schweinfurthii*) party size in the Budongo Forest, Uganda. *International Journal of Primatology* 21:613–628.
- Nishida T, Uehara S. 1983. Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): long-term records from the Mahale Mountains, Tanzania. *African Studies Monographs* 3:109–130.
- Potts KB. 2008. Habitat heterogeneity on multiple spatial scales in Kibale National Park, Uganda: implications for chimpanzee population ecology and grouping patterns. Ph.D. Thesis, Yale University.
- Potts KB, Chapman CA, Lwanga JS. 2009. Floristic heterogeneity between forested sites in Kibale National Park, Uganda: insights into the fine-scale determinants of density in a large-bodied frugivorous primate. *Journal of Animal Ecology* 78:1269–1277.
- Potts KB, Watts DP, Wrangham RW. 2011. Comparative feeding ecology of two communities of chimpanzees (*Pan troglodytes*) in Kibale National Park, Uganda. *International Journal of Primatology* 32:669–690.
- Preutz J. 2006. In: Hohmann G, Robbins MM, Boesch C, editors. *Feeding ecology in apes and other primates*. Cambridge: Cambridge University Press, p. 123–159.
- Pusey AE, Williams J, Goodall J. 1997. The influence of dominance rank on the reproductive success of female chimpanzees. *Science* 277:828–831.
- Rogers E, Abernethy K, Bermejo M, Cipoletta C, Doran D, McFarland K, Nishihara T, Remis M, Tutin CEG. 2004. Western gorilla diet: a synthesis from six sites. *American Journal of Primatology* 64:173–192.
- Russo SE, Campbell CJ, Dew JL, Stevenson PR, Suarez SA. 2005. A multi-forest comparison of dietary preferences and seed dispersal by *Ateles* spp. *International Journal of Primatology* 26:1017–1037.
- Stanford CB, Nkurunungi JB. 2003. Behavioral ecology of sympatric chimpanzees and gorillas in Bwindi Impenetrable National Park, Uganda: diet. *International Journal of Primatology* 24:901–918.
- Stanford CB, Wallis J, Mpongo E, Goodall J. 1994. Hunting decisions in wild chimpanzees. *Behaviour* 131:1–18.
- Struhsaker TT. 1997. *Ecology of an African rainforest*. Gainesville: University Presses of Florida.
- Sugiyama Y, Koman J. 1987. A preliminary list of chimpanzees' alimentation at Boussou, Guinea. *Primates* 28:133–147.
- Tutin CEG, Fernandez M. 1993. Fecal analysis as a method for describing diets of apes: examples from sympatric gorillas and chimpanzees at Lopé, Gabon. *Tropics* 2:189–198.
- Tweheyo M, Lye KA. 2003. Phenology of figs in Budongo Forest and its importance for the chimpanzee diet. *African Journal of Ecology* 41:306–316.
- Tweheyo M, Lye AK, Weladji BR. 2003. Chimpanzee diet and habitat selection in the Budongo Forest Reserve, Uganda. *Forest Ecology and Management* 188:267–278.
- van Roosmalen MGM. 1985. Habitat preferences, diet, feeding strategy, and social organization of the black spider monkey (*Ateles paniscus paniscus Linnaeus 1758*) in Surinam. *Acta Amazonica* 15:1–238.
- Wakefield ML. 2010. Socioecology of female chimpanzees (*Pan troglodytes*) in the Kibale National Park, Uganda: social relationships, association patterns, and costs and benefits of gregariousness in a fission-fusion Society. Ph.D. Thesis, Yale University.
- Watts DP, Mitani JC. 2002. Hunting by chimpanzees at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology* 23:1–29.
- Watts DP, Potts KB, Lwanga JS, Mitani JC. 2011. Diet of chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 2. Temporal variation and fallback foods. *American Journal of Primatology* 73:1–14.
- Whiten A, Byrne RW, Barton RA, Waterman PG, Henzi SP. 1991. *Dietary and foraging strategies of baboons*. Philosophical Transactions of the Royal Society, London, Series B 334:187–197.
- Wrangham RW. 1977. Feeding behavior of chimpanzees in Gombe National Park, Tanzania. In: Clutton-Brock TH, editor. *Primate ecology*. London: Academic Press, p. 503–538.
- Wrangham RW, Conklin NL, Chapman CA, Hunt KD. 1991. The significance of fibrous foods for Kibale Forest chimpanzees. *Philosophical Transactions of the Royal Society, London, Series B* 334:171–178.
- Wrangham RW, Conklin NL, Etot G, Obua J, Hunt KD, Hauser MD, Clark AP. 1993. The value of figs to chimpanzees. *International Journal of Primatology* 14: 243–256.
- Wrangham RW, Chapman CA, Clark-Arcadi AP, Isabirye-Basuta G. 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the cost of great ape groups. In: McGrew WC, Marchant LF, Nishida T, editors. *Great ape societies*. Cambridge: Cambridge University Press, p. 45–57.
- Wrangham RW, Conklin-Brittain NL, Hunt KD. 1998. Dietary responses of chimpanzees and cercopithecines to seasonal variation in fruit abundance I: antifeedants. *International Journal of Primatology* 19:949–970.