

RESEARCH ARTICLE

Diurnal Variation in Nutrients and Chimpanzee Foraging Behavior

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Primate feeding behavior varies over long (e.g., weekly, seasonally, yearly) and short (e.g., hourly) scales of time due to changes in resource availability and the nutritional composition of foods. While the factors that affect long-term changes in feeding behavior have received considerable attention, few data exist regarding what drives variability in feeding behavior over the course of a single day. To address this problem, we investigated diurnal variation in chimpanzee feeding on the leaves of two species of saplings, *Pterygota mildbraedii* and *Celtis africana*, at Ngogo, Kibale National Park, Uganda. Specifically, we related short-term changes in chimpanzee feeding behavior on these leaves to diurnal variation in their nutritional composition. Results showed that chimpanzees fed on the leaves of both saplings more in the evening than they did in the morning. The nutritional quality of leaves also improved over the course of the day. Concentrations of cellulose and lignin were lower and total non-structural carbohydrates (including sugars and starch) were higher in the evening for *P. mildbraedii*, and sugars were higher in the evening for *C. africana*. These data suggest that chimpanzees consume these resources when their quality is highest, and consequently, may track the nutrient composition of their foods over very short periods that span only a few hours. In the future, foods collected for analyses must control for time of sampling to ensure biologically meaningful assays of nutrient composition. *Am. J. Primatol.* 75:342–349, 2013. © 2013 Wiley Periodicals, Inc.

Key words: chimpanzee; *Pan troglodytes*; feeding; foraging; nutritional ecology

INTRODUCTION

Primates display diurnal variation in feeding behavior, with individuals frequently eating leaves or other resources late in the day [Chapman & Chapman, 1991; Domingo-Roura & Yamagiwa, 1999; Heymann & Smith, 1999; Raemaekers, 1978]. For example, Costa Rica spider monkeys (*Ateles geoffroyi*) eat leaves in the early evening, late morning, and before resting [Chapman & Chapman, 1991]. Japanese macaques (*Macaca fuscata yakui*) consume leaves more often in the afternoon and evenings than they do other times of the day [Domingo-Roura & Yamagiwa, 1999]. Similarly, gibbons (*Hylobates lar*) and siamangs (*Symphalangus syndactylus*) typically eat fruit in the morning and leaves in the afternoon [Raemaekers, 1978].

Processes of photosynthesis, translocation, and storage result in nutrient cycling associated with light and dark periods [Hodges, 1967; Kokubun & Shimada, 1994; Kramer & Kozlowski, 1979]. As products of photosynthesis, the concentration of carbohydrates within leaves and phloem sap fluctuate diurnally in association with light intensity [Huber, 1981]. The translocation of nitrogen from roots to leaves occurs within the xylem sap and is depen-

dent on leaf transpiration rate. Nitrate concentration within xylem sap has been shown to reach a peak around midday [Siebrecht et al., 2003], which implies that protein concentration within the leaves may vary diurnally.

Despite this evidence suggesting diurnal variation in carbon and nitrogen accumulation and transportation, few studies have specifically addressed whether such variation influences primate food choice [Ganzhorn & Wright, 1994]. The feeding behavior of primates changes over both short (e.g., hourly) and long (e.g., yearly) scales of time [Chapman et al., 2002]. From year to year, the availability and abundance of any given resource may increase

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or decrease as a result of variation in biotic and abiotic factors, including competition with sympatric species, precipitation, and solar radiation. Significant intraspecific variation in nutrient composition [Chapman et al., 2003; Rothman et al., 2012; Worman & Chapman, 2005] and resource breadth and abundance [Watts et al., 2012b] may vary from season to season and year to year.

Additional factors influence primate food selection over shorter periods of time. Frugivorous primates often use color, texture, and taste to determine the ripeness of fruits [Dominy et al., 2001], and preferentially consume them when they are highest in easily digestible energy [Garber, 1987; Lambert, 1998; Reynolds et al., 1998]. In these cases, primates presumably use the developmental stage of plants, comparing mature leaves to immature leaves and unripe fruits with ripe fruits, to assess nutritional quality over the course of days and weeks. Theoretically, these sensory mechanisms should also permit primates to evaluate the nutritional quality of plants over even shorter time periods (e.g., hourly) if such variation exists.

Like other primates, chimpanzees eat fruit early in the day and consume leaves later in the afternoon [Wrangham, 1977]. While fruit pulp provides a readily digestible source of energy, leaves typically have more protein and less digestible energy. Therefore, when ripe fruit is less abundant chimpanzees may obtain most dietary protein from leaves [Conklin-Brittain et al., 1999]. Whether diurnal variation in the nutritional quality of leaves affects their selection, however, is unknown. In this article, we investigate this issue. We begin by establishing the time of day chimpanzees consume the young leaves of two saplings at Ngogo, Kibale National Park, Uganda. We then conduct assays to determine whether the young leaves from these two species vary in their nutritional composition over the course of the day. Finally, we combine these data to examine whether diurnal variation in leaf chemistry influences chimpanzee feeding behavior.

METHODS

The Ngogo chimpanzees reside in Kibale National Park, Uganda, near the Western Great Rift Valley about 24 km east of the Rwenzori Mountains. Kibale includes a mosaic of forest types, including moist evergreen forest, woodlands, and colonizing scrub [Struhsaker, 1997, p 16]. The Ngogo study site is covered by closed canopy forest, with open grasslands of *Pennisetum purpureum* that the chimpanzees occasionally cross to exploit additional resources, patrol their territorial borders, and hunt. The Ngogo chimpanzee community is the largest observed in equatorial Africa currently numbering 187 individuals [Mitani, unpublished data]. Chimpanzees there have been under observation since

1995 and are easily followed as they are well habituated to human presence [Mitani, 2009].

For the analyses presented here, we recorded observations of feeding behavior over 10 years from 2002 to 2011, primarily during the dry season months between June and August. Observations were made of 41 adult male chimpanzees (mean = 26.9/year, SD = 1.6), which were followed for 5,461 hrs (mean = 546 hrs/year, SD = 188). During 1-hr focal animal sampling sessions, we recorded feeding observations every 10 mins. We tallied observed *Pterygota mildbraedii* and *Celtis africana* sapling feeding events into three periods of consumption: morning, 7:00–11:00 a.m.; midday, 11:00 a.m. to 3:00 p.m., and late afternoon, 3:00–7:00 p.m. We examined heterogeneity in consumption over time with a chi-square test. Because these tests revealed that there was significant variation in feeding on *P. mildbraedii* and *C. africana* saplings across the three periods, we subsequently used chi-square tests to investigate differences in feeding between specific pairs of times.

To assess potential nutrient variation across the day, young leaves were collected from five saplings of *P. mildbraedii* and *C. africana* at dawn, midday, and dusk toward the end of the dry season in late July and early August 2011. These are two of the most frequently consumed and most widely distributed species of leaves within the Ngogo chimpanzee dietary niche, together constituting approximately 11.7% of overall feeding time [Watts et al., 2012a]. *Pterygota mildbraedii* saplings have very large leaves up to 30 × 18 cm and grow in thin patches, with each tree possessing only a few branches. Any given sapling contains only a small number of young leaves for chimpanzee consumption, and thus a feeding bout often includes leaves from multiple neighboring saplings. We accordingly collected samples from the same patch of saplings at each time point over a single day. No two samples, however, originated from the same sapling. *Pterygota* leaves were collected from closed canopy forest, with a relatively open understory and moderate light passing to the ground. The sky was overcast or partly cloudy throughout the day, with light rain from 12:30 p.m.–2:00 p.m.

Celtis africana, saplings often grow as isolated trees with many thin branches and many small leaves varying in size from 2 × 1 cm to 4 × 7 cm across. Chimpanzees usually eat from a single sapling before moving on to another food or activity. Five *Celtis* saplings were sampled at each of the three time points under sunny conditions in a forest margin with a relatively low canopy, thick undergrowth, and patchy sunlight exposure on the forest floor. Leaves from each sapling were selected across all branches, so that each sample (morning, midday, evening) would have similarly aged and positioned leaves. Younger and smaller leaves were

preferentially selected at each time point in keeping with chimpanzee preference.

All samples were immediately returned to camp and oven-dried at 65°C for approximately 200 min. To control for cross-contamination, samples were separated within the drying oven by an aluminum foil partition and labeled accordingly.

Nutrient analyses were conducted at the Primate Nutritional Ecology Laboratory at Hunter College of the City University of New York. Samples were milled using a Wiley Mill and a 1 mm screen. Neutral detergent fiber (NDF), acid detergent fiber (ADF), lignin, crude protein, simple sugars (water soluble carbohydrates), fat, and ash were selected for analysis, while hemicellulose, cellulose, and total nonstructural carbohydrate were calculated by subtraction from those values.

Water soluble carbohydrates (hereafter labeled sugars for convenience) were extracted from samples using boiling water, and determined after acid hydrolysis with sulfuric acid and colorimetric reaction with potassium ferricyanide following Hall et al. [1999]. Methods for analyzing NDF, ADF, and lignin followed Van Soest et al. [1991]. We used combustion methods for crude protein [Association of Official Analytical Chemistry (AOAC), 1991]. Hemicellulose was calculated by subtracting ADF from NDF. Cellulose was calculated by subtracting lignin from ADF. Total nonstructural carbohydrate was calculated by subtracting NDF, protein, fat, and ash from 100. All results are reported on a dry matter basis. We employed analysis of variance to assess variation in nutrient content attributable to time of sampling, and the Scheffe test for pairwise comparisons between periods. In addition, we calculated Spearman correlation coefficients (r) to examine trends across the day.

All research was done in compliance with the authors Institutional Animal Care Committee, the American Society of Primatologists Principles for the Ethical Treatment of Non Human Primates, and adhered to legal obligations from the Ugandan authorities.

RESULTS

Field observations indicated that chimpanzees did not feed on the saplings of either tree species uniformly across the day (Fig. 1). There was heterogeneity in feeding activity on each species among the three periods (*P. mildbraedii*: chi-square = 64.15, $P < 0.001$, $df = 2$; *C. africana*: chi-square = 22.92, $P < 0.001$, $df = 2$). Additional analyses revealed that the chimpanzees fed on *P. mildbraedii* more often at midday and late afternoon than they did during the morning (chi-square: $P < 0.001$, $df = 1$ for both comparisons; Fig. 1). In contrast, there was no difference in the amount of feeding on *Pterygota* saplings between midday and late afternoon (chi-square =

1.20, $P > 0.20$, $df = 1$; Fig. 1). A similar set of analyses showed differences in feeding on *C. africana* saplings between morning and midday, morning and late afternoon, and midday and late afternoon, with increased feeding in each later period (chi-square: $P < 0.05$, $df = 1$ for all three comparisons; Fig. 1).

Leaves of *P. mildbraedii* exhibited compositional variation in hemicellulose, cellulose, and lignin as a function of time (hemicellulose: $F_{2,12} = 8.48$, $P < 0.01$; cellulose: $F_{2,12} = 6.81$, $P < 0.05$; lignin: $F_{2,12} = 11.03$, $P < 0.005$). All three fiber fractions were significantly correlated with time of collection. Concentrations of hemicellulose increased, while cellulose and lignin decreased over the course of the day (Fig. 2A). Total nonstructural carbohydrates were also positively correlated with time of day (Spearman $r = 0.65$, $P < 0.05$); analysis of variance, however, did not reveal heterogeneity in total nonstructural carbohydrates among time periods ($F_{2,9} = 3.22$, $P = 0.088$). Protein, fat, and sugar composition within leaves of *P. mildbraedii* exhibited no variation or correlation with time of day.

These shifts are nutritionally important for primates as the overall trend indicates increasing digestibility later in the day. Cellulose and lignin are largely indigestible, and decreased between 10 and 33% from morning to evening. The more digestible fractions, hemicellulose and total nonstructural carbohydrates, increased between 15 and 100%, respectively, from morning to evening.

Among *C. africana* saplings, there were no significant differences between time periods in fiber fractions, protein, or sugars (Fig. 2B). Analysis of variance, likewise, revealed no relationship between nutrient composition and time of day in *Celtis* leaves, although variation in cellulose approached significance ($F_{2,12} = 3.51$, $P = 0.0632$). There was, however, a significant correlation between sugars and time of day (Spearman $r = 0.63$, $P < 0.05$). Late afternoon concentrations approximately doubled those in the early morning (Fig. 2B). This is significant as sugars are both detectable on the palate and an easily digested source of calories for all primates.

DISCUSSION

The nutritional composition of both species of saplings changed across the day. In *C. africana*, sugars became increasingly concentrated as the day progressed, while most fiber fractions (hemicellulose and lignin) and crude protein remained unchanged. Among *P. mildbraedii* leaves, the concentration of all fiber fractions decreased throughout the day, while total nonstructural carbohydrates increased. Increasing concentration of total nonstructural carbohydrate has been previously reported through the day [Orr et al., 1997; Pelletier et al., 2010] and is likely responsible for the decline in percent dry

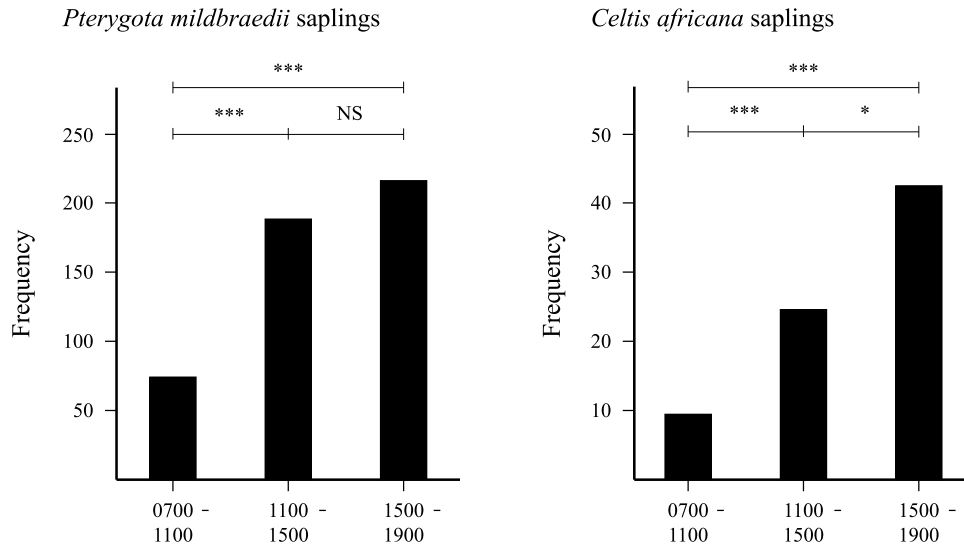


Fig. 1. Observed feeding bouts on two species of saplings at various times of the day. Observations were made on adult male chimpanzees over 10 years from 2002 to 2011. NS, not significant, $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

mass of structural carbohydrates (fiber) observed in *P. mildbraedii*.

These results add to our understanding of primate dietary ecology and chimpanzee feeding behavior in two important ways. First, they show that the nutritional composition of at least some dietary resources varies not only over days or weeks, but also over very short intervals spanning hours. Second, primates, such as chimpanzees, may track the nutritional quality of their foods over these short periods and adjust their feeding behavior accordingly.

Diurnal Variation in Nutrient Composition

Previous studies have demonstrated that nutrient composition changes as dietary resources develop or mature [Azevedo-Meleiro & Rodriguez-Amaya, 2005; Boldingh et al., 2000; Ferland & Sadowski, 1992; Jimenez et al., 2002; Smith et al., 1992; Tharanathan et al., 2006]. This recognition has led to sampling resources for nutritional analysis at the stage of maturity and ripeness consistent with consumption. For example, the most appropriate sampling protocol for chimpanzees targets ripe fruits, as they prefer them to unripe figs and other fruits. Sampling ripe fruits, however, is inappropriate for assessing nutrient intake during fallback periods where the consumption of unripe fruit may increase. To eliminate potential sources of sampling error, one ideally assays what the primates actually eat at the time of ingestion. Sampling foods from observed feeding bouts, however, dramatically extends the amount of time one must spend in the field, which may not always be possible due to practical constraints.

In primate ecology, it has been generally assumed that nutrient composition is static through-

out the day with negligible hourly differences due to the maturation of leaves or fruit. As a result, the time of day primates consume their foods is not typically controlled when plants have been sampled for nutritional analysis. Nevertheless, the results presented here suggest that the nutritional quality of two species of young leaves is higher later in the day. As most photosynthesis occurs within a plant's leaves, these dietary resources may be most sensitive to diurnal nutrient cycling.

Other plant parts aside from leaves probably vary in their nutritional composition across the day. The pith of herbaceous vegetation, for example, consists of channels containing sugars and other nutrients transported throughout the plant. One might expect diurnal variation in these resources as metabolism and nutrient concentration are affected by photosynthetic activity and transpiration [Huck et al., 1962; Wertin & Teskey, 2008]. As resource sinks, fruits, seeds, and underground storage organs may show some diurnal variation in nutritional composition as well [Klages et al., 2001]. Given the quantity of nutrients already stored relative to those accumulated over the course of any given day, however, such diurnal variation may fall below practical relevance.

In sum, our results suggest that the nutrient composition of some foods is not static throughout the day. In cases where it is not known when primates actually consume foods, a prudent strategy would be to report the time of day foods were sampled for nutritional analysis so that this potential source of variation can be evaluated. In situations where foods are eaten across all times of the day, the most effective strategy would be to sample plants at the times primates most frequently consume them.

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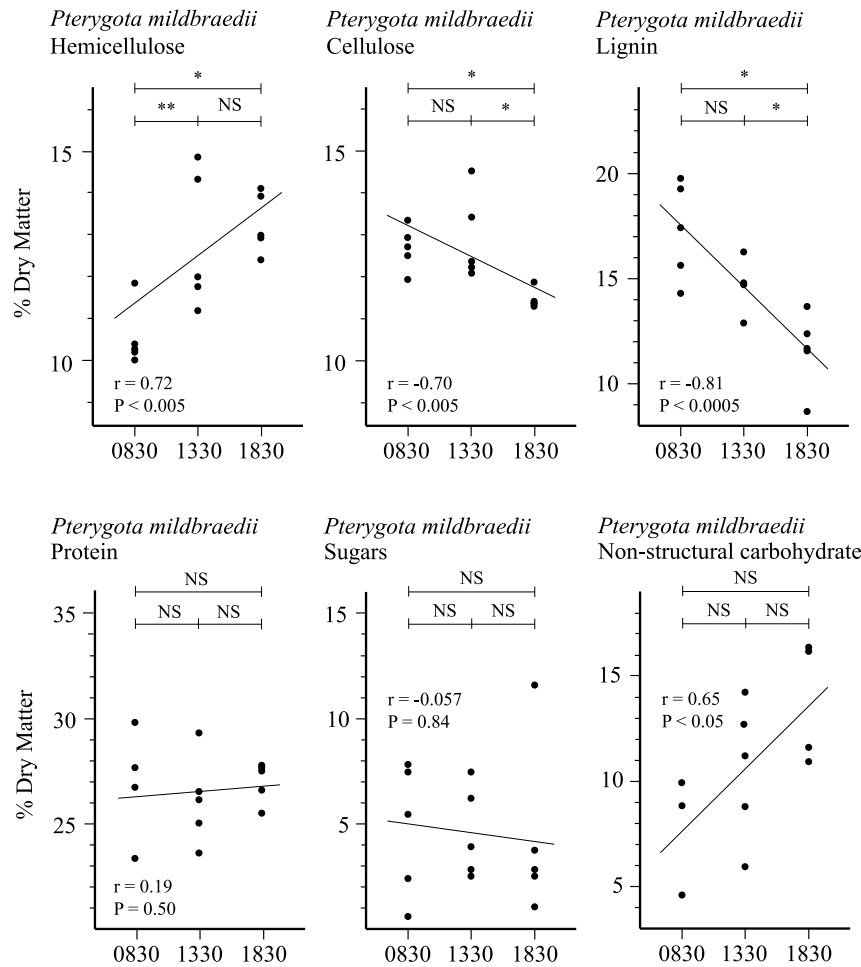


Fig. 2. Diurnal variation in the nutrient composition of two species of leaves commonly consumed by chimpanzees at Ngogo. Samples were collected from (A) *Pterygota mildbraedii* and (B) *Celtis africana* just after sunrise, at midday, and shortly before sunset. Lab analyses assessed concentrations of neutral detergent fiber, acid detergent fiber, acid detergent lignin, protein, sugars, fat, and ash. Hemicellulose, cellulose, and total nonstructural carbohydrate were calculated by subtraction. Results of Spearman correlation tests and ANOVA are shown. For ANOVA: * $P < 0.05$; ** $P < 0.01$; NS, not significant.

Feeding Behavior Associated with Nutritional Quality

Our findings also demonstrate that chimpanzees consume the young leaves of *Pterygota* and *Celtis* nonrandomly across the day, ingesting them more often in late afternoon when nutritional quality is higher. Previous research has shown that primates typically prefer foods high in protein and sugar, and low in fiber [Chapman & Chapman, 2002; Doran-Sheehy et al., 2009; Malenky & Stiles, 1991; Milton, 1979]. They employ several sensory mechanisms, including vision, texture, taste, and smell, to detect these properties as fruits ripen and leaves mature [Dominy et al., 2001]. Chimpanzees, in particular, prefer ripe fruits, and as fruits ripen within individual trees increase the amount of time spent feeding on them. Thus, chimpanzees alter their feeding be-

havior over the course of days and weeks as they select for ripeness and abundance.

The results presented here suggest that chimpanzees may also employ mechanisms to track nutrients as they change over the course of the day. Studies in crop and animal sciences have previously demonstrated that forage quality varies diurnally in nonstructural carbohydrate content, including sugar and/or starch [Holt & Hilst, 1969; Miller, 1924; Morin et al., 2011]. In addition, domestic animals adjust their feeding behavior to preferentially select the forage with higher nonstructural carbohydrates [Fisher et al., 1999; Orr et al., 1997]. For example, sheep, cattle, and goats preferred tall fescue hays that were harvested in the afternoon compared with those that were cut in the morning [Fisher et al., 1999]. This preference was associated with a diurnal

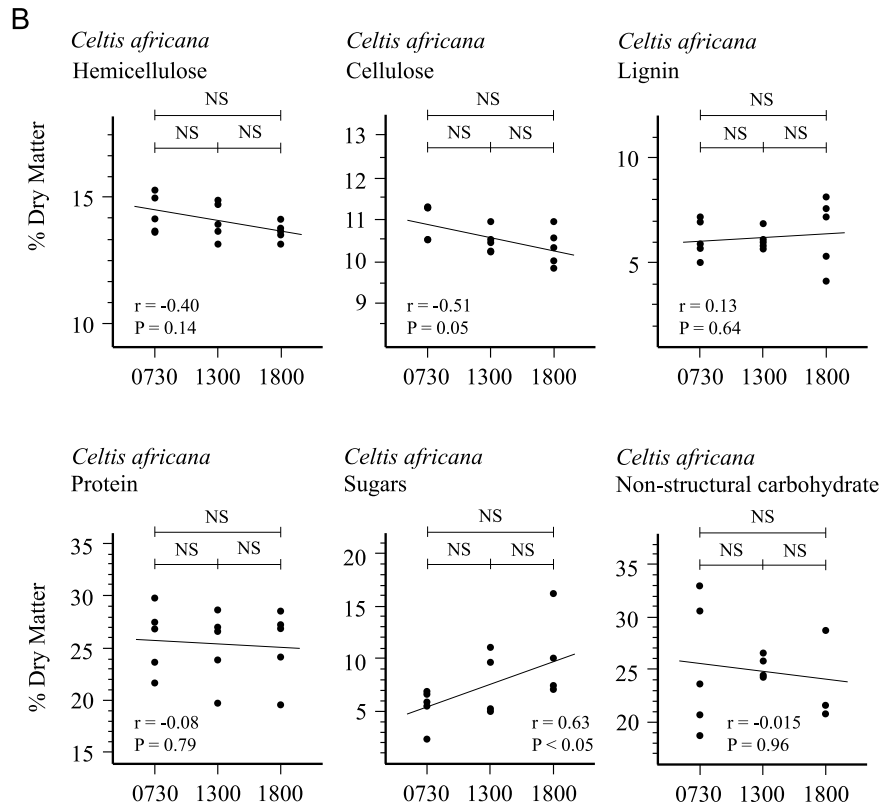


Fig. 2. Continued

decline in fiber concentrations and concomitant increase in nonstructural carbohydrate concentrations [Fisher et al., 1999]. In an experimental study, sheep provided with alfalfa harvested in the morning or afternoon preferred the afternoon alfalfa; however, after sugar was added to the morning alfalfa samples they began to prefer the morning samples [Burritt et al., 2005], demonstrating that sugar was driving food selection.

Our study demonstrates that chimpanzees consume the leaves of saplings when nonstructural carbohydrates are highest and supports the hypothesis that primates are able to track resources according to the times when they are most profitable [Ganzhorn & Wright, 1994]. Several other, nonmutually exclusive hypotheses, however, have been proposed to account for diurnal variation in primate feeding behavior [Chapman & Chapman, 1991; Clutton-Brock & Harvey, 1977; Ganzhorn & Wright, 1994]. First, it is possible that primates eat leaves later in the afternoon to fill their guts before resting [Chapman & Chapman, 1991; Janson & Chapman, 1999]. Because leaves are typically higher in fiber than fruit pulp, they fill the gut and require more time for digestion [Milton, 1979, 1981]. Since gut motility is reduced during sleep or rest [Bassotti et al., 1993], eating fibrous foods at these times might enhance digestibility. Second, fruits provide little available

protein [Janson & Chapman, 1999; Rothman et al., 2008], so primates may consume leaves with high protein later in the day after their energy needs are met. Third, frugivorous primates may preferentially consume leaves in the afternoon as a result of taste fatigue after hours of feeding on fruit, their preferred resource. Dietary variety has been documented to reduce satiety and increase consumption in humans [Rolls, 1985; Wisniewski et al., 1992]. Assuming similar taste bud physiology between human and nonhuman primates this phenomenon may play a similar role in variety-seeking feeding behavior in primates.

The Ngogo chimpanzees spend a considerable amount of time in the early morning through mid-day hours in large fruit trees [Mitani, unpublished data]. Consumption of fruit in the early hours of the day may be related to the need to obtain energy and satisfy other nutritional demands. Gathering at fruit trees leads to several chimpanzees congregating, permitting them to reestablish and maintain social bonds [Mitani, 2009]. In contrast, the consumption of saplings occurs mostly in the afternoon when individuals come out of the trees and disperse individually or form small foraging groups. In this way, both social dynamics and nutritional demands may help to explain the differential timing of resource consumption, with fruit eaten in the morning and the leaves of saplings consumed in the afternoon.

Additional research will be necessary to evaluate whether and how nutritional, social, and physiological factors influence diurnal variation in the feeding behavior of chimpanzees and other primates.

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