Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores

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Abstract: Seasonality in tropical forests can be more subtle than that of temperate forests but still affects the resources available to wildlife. Much work has been done describing changes in fruit availability and dietary composition but the nutritional quality of any particular food item is assumed to be relatively constant. We investigated seasonal changes in the quality of the ripe fruit of *Celtis durandii*, a common tree that produces fruit year-round and is important in the diets of many species. The lipid content of the ripe fruit was found to be highly variable (0.3–30.8% dry matter) among months and this variation was positively correlated with the summed daily rainfalls of the previous and concurrent months. The amount of this fruit in the diets of three frugivorous primate species (*Cercopithecus mitis*, *Cercopithecus ascanius* and *Lophocebus albigena*) was positively related to measured or estimated lipid levels in the fruit. Such predictable changes in the quality of a constantly available fruit have not been previously reported and suggest that the resources provided by tropical forests may be more seasonal than shown by common measures of fruit availability.

Key Words: *Celtis durandii*, *Cercopithecus ascanius*, *Cercopithecus mitis*, fruit, Kibale, lipids, *Lophocebus albigena*, nutritional ecology, Uganda

INTRODUCTION

Seasonality of climate and the corresponding temporally uneven distribution of resources place hardships on wildlife, which can limit population size and act as major forces in natural selection (Beeson 1989, Brown & Brown 2000, Brugiere *et al.* 2002, Fiksen 2000, Richardson 1991). Torpor, migration, and resource switching are some of the common solutions to predictable periods of resource scarcity (van Schaik *et al.* 1993); however, the effects of lean seasons can be exacerbated by climatic events (Hafner *et al.* 1994, Muri 1999) or human disturbance (Laurance & Williamson 2001).

While the effects of seasonality in temperate zones and dry tropical zones are obvious, the less distinct seasons of tropical moist forests and their impacts on vegetation have also long been recognized (Janzen 1967, Karr 1976) with much work describing the changing patterns of fruit availability (Chapman *et al.* 1999, De Walt *et al.* 2003, Larue *et al.* 2002, Schaefer & Schmidt 2002, Sun *et al.* 1996). Since the nutritional values of food items differ, the nutritional make-up and the availability patterns of each have been combined to indicate which seasons and/or nutrients are potentially limiting for frugivores (Conklin-Brittain *et al.* 1998, Rode *et al.* 2003). While there often appear to be periods of fruit or nutrient scarcity, previous studies have assumed that the nutritional value of any given type of food remains unchanged through time (Conklin-Brittain *et al.* 1998, Gupta & Chivers 1999). Therefore many months or years of phenology and diet data are combined with nutritional data from food items collected only once. This is, in fact, an assumption inherent to any study that ignores possible nutritional changes of dietary items over time, even those that do not include nutritional analyses. If this assumption of constant nutritional quality is not valid, the seasonality of tropical moist forests may be seriously underestimated and the dietary choices of wildlife may appear random or maladaptive, making the understanding of foraging strategies much more

difficult. When the foraging strategies of wildlife are poorly understood, critical dietary resources may be impossible to identify, which could frustrate attempts at conservation and management.

The objectives of this study were to explore the temporal variation in nutritional quality of a common fruit and investigate the relationships between frugivore consumption and the availability and quality of the ripe fruit. By focusing on the quality and consumption of a common fruiting species we show the value of incorporating the possibility of temporal variation of ripe fruit quality in ecological study designs.

METHODS

Phenological data and ripe fruit samples were collected each month from June to November 2002 and compared with rainfall (the main seasonally changing climatic variable) at the Kanyawara study site in Kibale National Park, Uganda ($0° 13' - 0° 41'$ N, $30° 19' - 30° 32'$ E). The forest is a mature, mid-altitude, moist, semi-deciduous and evergreen forest with a mean annual rainfall of 1712 mm (1990–2004), a mean daily minimum temperature of 15.5 °C, and a mean maximum daily temperature of 23.7 °C (Chapman *et al.* 2003). There are two rainy seasons: March–May and September–November, with the latter having the higher rainfall.

One of the more important fruit-bearing species in Kibale, in terms of both its abundance and contribution to the diets of frugivores, is *Celtis durandii* Engl. (Struhsaker 1997). The fruit is a small ovoid drupe (~ 0.8 cm) that changes from green to yellow with ripening and contains a single hard seed. *Celtis durandii* is an extremely common and prolific fruiter in many areas of Kibale (Barrett & Lowen 1998, Chapman *et al.* 1999, Struhsaker 1997). Its fruit is usually available to some extent in most, if not all, months of any given year (Struhsaker 1997) and was the only species that was constantly fruiting throughout the study (May–November 2002), making it a potentially important staple or fallback food in times of general fruit scarcity. The fruit is eaten by many birds (Struhsaker 1997) and is important in the diets of chimpanzees (*Pan troglodytes*) (Ghiglieri 1984), blue monkeys (*Cercopithecus mitis*) (Rudran 1978), redtail monkeys (*Cercopithecus ascanius*) (Stickler 2004), grey-cheeked mangabeys (*Lophocebus albigena*) (Olupot 1994), black-and-white colobus monkeys (*Colobus guereza*) (Struhsaker 1978), red colobus monkeys (*Piliocolobus tephrosceles*) (Struhsaker 1975) and probably many other animals.

Celtis durandii fruit was collected at the end of each month (June–November 2002). Ripe and unripe fruits were processed separately. A fruit was defined as ripe if it had changed from green to at least partially yellow. The fruit was peeled off the seed and dried in a dehydrator (35 °C), then stored in plastic bags for shipment to the University of Florida. The fruit was re-dried in a drying oven at 50 °C overnight before being ground in a Wiley mill. Samples were analysed for per cent lipids (detailed below), per cent total ethanol-soluble carbohydrates (TESC; detailed in Danish *et al.* in press), saponins, per cent acid detergent fibre, per cent total nitrogen, and alkaloids (the rest are detailed in Chapman *et al.* 2003). Our reporting of saponin levels differs from Chapman *et al.* (2003) in using the mean froth heights at 30, 60 and 300 s, as we found that heights at 1800 s are extremely variable within samples. All percentages are reported on a dry matter basis.

Since lipids showed the most dramatic change over time and the percentages of the other components either remained constant or decreased when lipid percentages increased, we focused on lipid levels as the most important ecologically and probably driving the changes in the other components. Other than lipids, only total nitrogen was correlated with rainfall (ripe fruit: r = -0.923, n = 5, P = 0.025; unripe fruit: r = -0.872, n = 6, P = 0.024). However when changing lipid levels were corrected for, the relationships were not significant (ripe: r = -0.839, n = 5, P = 0.076; unripe: r = -0.570, n = 6, P = 0.238).

The dry matter lipid content of the fruit was determined with a microwave-assisted extraction technique. The ground samples were re-dried, weighed, placed in petroleum ether in a closed vessel, and exposed to microwaves in a MARS 5^{TM} machine (Ferguson 2003) to subject the samples to extreme heat and pressure, allowing the lipids to be extracted quickly and efficiently. Matthaus & Bruhl (2001) show that methods utilizing microwaves, heat and pressure are comparable in results to the Soxhlet method but much quicker. The processed samples were rinsed in petroleum ether, dried and reweighed and the lipid content (per cent dry matter) was calculated from the difference. We found the results of this method to be highly reproducible and more reliable than the Soxhlet method when dealing with low sample weights. The data for the highest lipid percentages are probably underestimations as the more oily samples lost oil on the drying paper and sample labels during storage and processing.

The average lipid levels in each month were compared to the sum of the daily rainfalls of the concurrent and previous months (the best predictor months) using linear regression. To examine how changing lipid levels affected the amounts of the other nutritional components, t-tests were used to compare the amounts of alkaloids, fibre, lipids, nitrogen, saponins and TESC during lipid-poor months (June–July) and lipid-rich months (September–November) for ripe and unripe fruits separately (August fruits had intermediate levels of lipids).

To see if the lipid levels in the fruit affect the intake of *Celtis durandii* fruit by frugivores, monthly dietary information was gleaned from existing sources from the Kanyawara study area (one *Cercopithecus mitis*, one *Cercopithecus ascanius* and two *Lophocebus albigena* data sets were available). The *C. ascanius* data set (Stickler 2004 and C. Stickler, unpubl. data) was from the same specific location and time as this study and could be directly compared; however, the *C. mitis* data set was from 1973–4 (Rudran 1978) and the *L. albigena* data sets were from 1972–3 (Waser 1975) and 1992–3 (Olupot 1994) and could only be compared with lipid levels indirectly through the summed daily rainfall of the concurrent and previous months. Since 1973 and 1992 were very wet years, the resulting estimations of lipid content are probably unrealistically high. However, as correlations elucidate relative differences or ranks and not absolute amounts, this should not affect the conclusions.

Lwanga (1987) presented dietary data from the Ngogo study site, about 10 km to the south-east of Kanyawara, on one *Cercopithecus mitis* group and two *C. ascanius* groups from 1984–5. However, he reported that in 1985 a *Celtis durandii* fruit crop failure occurred in which fruit dropped before ripening. For example, none of the surveyed *Celtis durandii* trees produced ripe fruit in 1985, except during January and October (2 and 4% of the trees, respectively, had ripe fruit as calculated from Figure 3.2 in Lwanga (1987)). In comparison, much higher percentages of trees were reported as producing ripe fruit during the period of 1984 included in the study (October– December; 59, 64 and 18%, respectively). Unripe fruit, however, was reported as available throughout 1985. This unusual fruit failure lowers the usefulness of the data from that period but they have been incorporated to expand the current study to an otherwise unrepresented area of forest. Rainfall data from Ngogo were used when analysing data from Lwanga (1987).

Since the *Cercopithecus mitis* group was the focus of Lwanga (1987), the *C. ascanius* groups were observed for usually only one day or less per month resulting in data with potentially high sampling error. Because of this weakness, the *C. ascanius* data sets from Lwanga (1987) have not been analysed statistically. Instead they are presented graphically for general visual comparison with the overall pattern of the other data sets.

Rudran (1978), Waser (1975) and Olupot (1994) did not differentiate between ripe and unripe fruit, but that should not have a major effect on the results as the lipid content of the two fruit types by month is highly correlated (Pearson's r = 0.99, n = 6; P < 0.001). Lwanga (1987) likewise combined ripe and unripe fruit for the months when both were observed to be eaten and in his phenology (availability) data, so his partial distinction between ripe and unripe fruit has been ignored. The monthly percentages of *Celtis durandii* in the diet reported by Waser (1975) include both fruit and insects. However, the use of insects from *C. durandii* is negligible compared with fruit use. Additionally, Olupot (1994) only provided monthly dietary data from the top five foods. For five of nine months, *C. durandii* was not in the top five. Instead of assuming *C. durandii* fruit was not eaten at all, a more conservative tack was taken and it was assumed that *C. durandii* fruit was a close sixth in every such month (the percentage of the fifth rank minus 0.01%). This only reduced the r and increased the P-value slightly compared with the assumption of no consumption during months when *C. durandii* was not in the top five.

The availability index for *Celtis durandii* fruit from each study was compared with the importance of the fruit in each diet (except for Olupot (1994) because no availability index was provided in that case). Dietary data collected by C. Stickler (unpublished) were compared with the fruit availability of *Celtis durandii* ripe fruit as determined in Worman & Chapman (in press), but restricted to data from the area used by the *Cercopithecus ascanius* group. Data sets were analysed with Pearson's correlations except for that of Rudran (1987) which violated the assumption of normality and therefore was analysed using Spearman's ranked correlations. As we had predictions of directionality, one-tailed tests were used with the dietary data unless indicated.
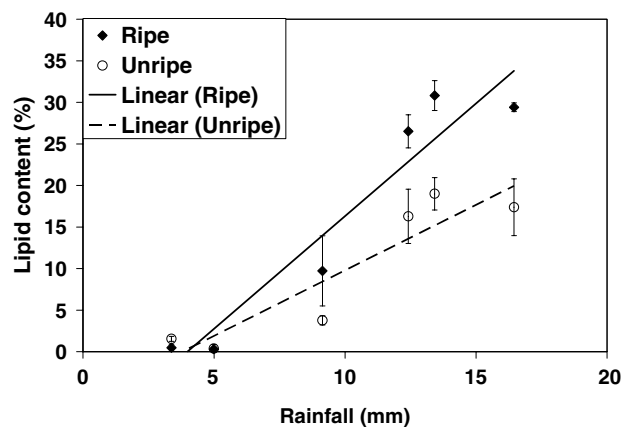
The true relationships between lipid content and rainfall, lipid content and consumption, and consumption and rainfall are probably best represented by logistic functions. However, the small sample sizes, especially at the higher end of the ranges, make fitting reasonable logistic curves questionable so the relationships were assumed to be linear for the purposes of analysis.

RESULTS

The dry matter lipid levels in *Celtis durandii* fruit varied over two orders of magnitude among months (ripe: 0.3%–30.8%; unripe: 0.4%–19.0%) and were predicted by the summed daily rainfall of the previous and concurrent months (ripe: $r^2 = 0.91$, n = 6, P = 0.003; unripe: $r^2 = 0.85$, n = 6, P = 0.009; Figure 1).

No differences were detected between lipid-poor and -rich seasons in levels of alkaloids, fibre or saponins. However, total nitrogen and TESC content were lower during high-lipid months for both ripe and unripe fruits (Table 1).

The relationship between monthly consumption by *Cercopithecus ascanius* (Stickler 2004 and C. Stickler, unpubl. data) of ripe *Celtis durandii* fruit and the lipid content of the fruit at the same time and place has a high correlation coefficient, but, given the sample size, this is not quite statistically significant when $\alpha = 0.05$ (r = 0.88, n = 4, P = 0.059; Figure 2a). The same is also

Figure 1. The relationship between the monthly dry matter lipid content of ripe and unripe *Celtis durandii* fruit and the summed daily rainfalls of the concurrent and previous months at Kibale National Park, Uganda for June 2002–November 2002 (ripe: $y = 0.0271x - 0.108, r^2 = 0.91$, $n = 6$, $P = 0.003$; unripe: $y = 0.0158x - 0.0596$, $r^2 = 0.85$, $n = 6$, $P = 0.009$). The error bars represent ± 1 SE.

true for the relationship between monthly consumption and rainfall ($r = 0.78$, $n = 5$, $P = 0.061$; Figure 2b).

The monthly percentage of *Celtis durandii* fruit in the diet of *Cercopithecus mitis* described by Rudran (1978) shows a significant positive correlation with rainfall ($r_s = 0.56$, $n = 16$, $P = 0.013$; Figure 2c). However, the intake of *Celtis durandii* fruit by the Ngogo *Cercopithecus mitis* group (Lwanga 1987) was not correlated with rainfall ($r = 0.13$, $n = 15$, $P = 0.320$).

The *Lophocebus albigena* data reported by Waser (1975) show a correlation between the monthly proportion of *Celtis durandii* fruit in the diet and rainfall ($r = 0.64$, $n = 13$, $P = 0.009$; Figure 2d), as do the data from Olupot (1994) ($r = 0.63$, $n = 9$, $P = 0.034$; Figure 2e).

The consumptions of *Celtis durandii* fruit by *Cercopithecus ascanius* (Stickler 2004 and unpubl. data) and *C. mitis* (Lwanga 1987, Rudran 1978) were not related to fruit availability ($r = -0.700$, $n = 4$, $P = 0.300$;

$r = 0.291$, $n = 15$, $P = 0.292$; $r = -0.319$, $n = 16$, $P = 0.229$; respectively, two-tailed tests). The *Lophocebus albigena* data from Waser (1975) show a negative correlation between availability and consumption ($r = -0.612$, $n = 12$, $P = 0.035$, two-tailed test; Figure 2f). All studies that report an index of fruit availability seem to show decreases in availability occurring at the same time as the peaks in consumption (Figure 3).

The two Ngogo *Cercopithecus ascanius* groups (Lwanga 1987) show similar gross patterns of intake to the other groups, with higher intakes in the major rainy season of September–November (if the transition month of August is also included) than in the rest of the year. Both groups also show smaller peaks of intake in the minor March–May rainy season not found in the other groups (Figure 3f, g).

DISCUSSION

While nutritional components of leaves and fruits are known to vary among species, location, position on the tree, stage of development, and/or time of day (Chapman *et al.* 2003, Fernandez-Escobar *et al.* 1999, Klages *et al.* 2001, Marquis *et al.* 1997, Nergiz & Engez 2000, Woodwell 1974), and yearly fruit production and quality have been shown to be dependent on environmental conditions of earlier months (temperature, rainfall, amount of sunlight, etc.; Sams 1999, Woolf & Ferguson 2000), to our knowledge this is the first time the nutritional quality of a continuously available ripe fruit has been shown to have predictable seasonal variation.

The range of lipid content in tropical fruits in general is quite large: from less than 0.1% (Matsumoto-Oda & Hayashi 1999) to 88.8% (Galetti *et al.* 2000), however the distribution is extremely skewed towards lower lipid levels. Jordano (2000) reports the mean lipid content in neotropical fruits as 18.5% and Stiles (1993) notes that only a quarter of fleshy fruits have a lipid content

Table 1. The major nutritional components of *Celtis durandii* fruit categorized by lipid season. The high, mean and low values for each component in each season are given for ripe and unripe fruit separately. Means that are statistically different between lipid-poor and -rich seasons (June–July and September–November, respectively) are indicated (* significant at $\alpha = 0.05$, ** significant at $\alpha = 0.001$). TESC = Total ethanol-soluble carbohydrates.

|	Alkaloids (0, 1, 2)		% Fibre		% Lipids		% Nitrogen		Saponins (mm)		% TESC	
	Poor	Rich	Poor	Rich	Poor	Rich	Poor	Rich	Poor	Rich	Poor	Rich
Ripe fruit												
High		1		18.5	0.7	33.9	4.7	3.0	9	11	12.8	9.3
Mean	N/A	0.8	N/A	16.2	0.4**	28.9**	4.5*	2.7*	9	7	11.6*	7.0*
Low		0		14.4	0.0	23.2	4.2	2.4	9	5	11.0	4.3
n		4		3	5	8	3	6	1	4	3	6
Unripe fruit												
High	1	1	14.5	16.6	1.9	21.9	4.4	3.4	21	6	18.2	14.4
Mean	1	1	13.5	14.4	0.9**	17.6**	4.0**	3.0**	12	5	14.8*	10.0*
Low	1	1	12.8	12.7	0.0	10.5	3.8	2.5	4	2	11.5	7.9
n	3	5	3	5	5	9	4	8	4	6	5	8
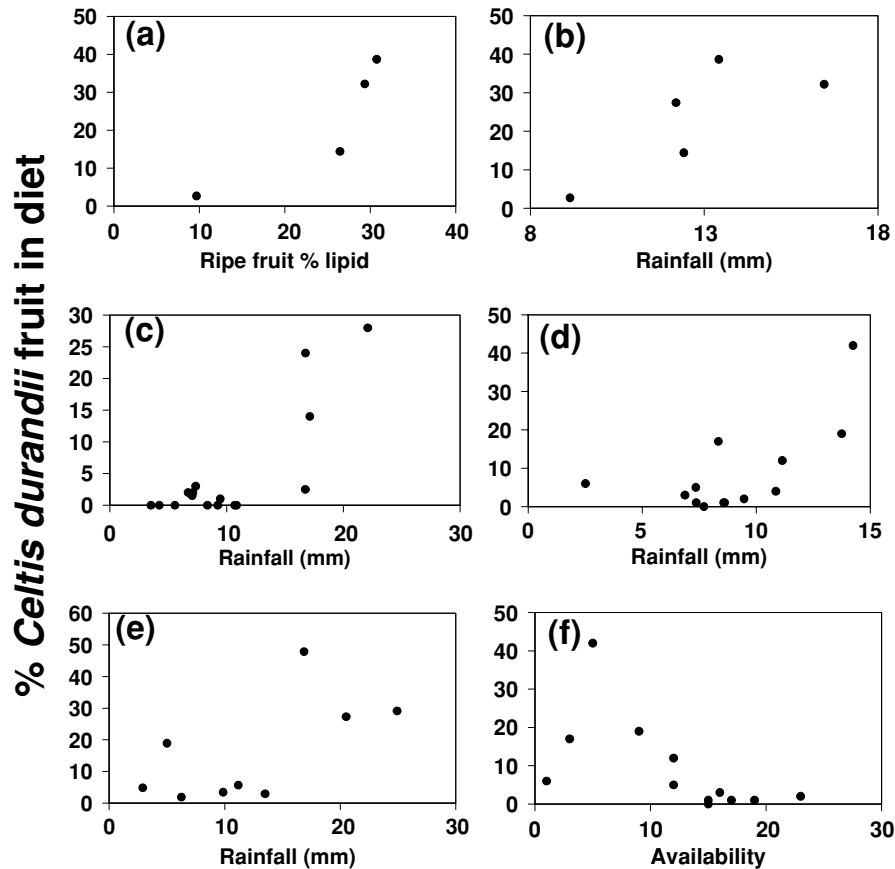
Figure 2. The relationships between reported dietary use of *Celtis durandii* fruit and lipid content of the fruit, daily rainfall of the previous and concurrent months (a predictor of lipid content) and fruit availability. All data sets are from Kibale National Park, Uganda. (a) The relationship between lipid content and *Cercopithecus ascanius* diet (C. Stickler, unpubl. data) for August 2002–November 2002 (r = 0.88, n = 4, P = 0.059). (b) The relationship between rainfall and *C. ascanius* diet (C. Stickler unpubl. data) from August 2002–December 2002 (r = 0.78, n = 5, P = 0.061). (c) the relationship between rainfall and *C. mitis* diet (Rudran 1978) from February 1973–May 1974 (r_s = 0.56, n = 16, P = 0.013). (d) The relationship between rainfall and *Lophocebus albigena* diet (Waser 1975) from May 1972–April 1973 (r = 0.64, n = 13, P = 0.009). (e) The relationship between rainfall and *L. albigena* diet (Olupot 1994) from October 1992–June 1993 (r = 0.63, n = 9, P = 0.034). (f) The relationship between fruit availability and *L. albigena* diet (Waser 1975) from May 1972–April 1973 (r = − 0.61, n = 12, P = 0.035, two-tailed test).

of > 10%. Compared with tropical fruits in general, the lipid levels of *Celtis durandii* fruit in June and July were extremely low while the levels in September through November fit comfortably within the range of lipid-rich fruits (Pannell & Kozioł 1987).

The fruit of none of the other eight species analysed (*Celtis africana, Diospyros abyssinica, Ficus brachylepis, Ficus natalensis, Mimusops bagshawei, Neoboutonia macrocalyx, Premna angolensis* and *Uvariopsis congensis*) showed significant relationships between nutrient composition and rainfall. During this study, other species fruited either synchronously or independently for 1–4 mo and those that fruited for more than 1 mo (*D. abyssinica* and *M. bagshawei*) tended to show slight increases in total ethanol-soluble carbohydrates (sugars) as the crops ripened (i.e. fruits collected as ripe when ripening began were not as ripe as the fruits collected at the end of the fruiting interval). However, this phenomenon was

not the case for *C. durandii* as (1) the trees did not fruit synchronously (fruit was constantly available due to different trees coming into and going out of fruit at different times), (2) fruits appear to ripen quickly (trees found with all unripe fruit generally had no fruit the month before and both ripe and unripe fruit a month later), (3) fruiting bouts of individual trees can last over 2 y (Struhsaker 1997), (4) ripe fruits probably do not stay on the tree for more than 1 mo (even without consumption by frugivores, each fruiting tree constantly drops ripe fruit), (5) the unripe fruit showed a similar increase in lipid levels with rainfall, and (6) the variation in lipid content of ripe fruit among months not only ranges over two orders of magnitude but is also greater than the largest difference between ripe and unripe fruits of the same month.

Resource availability estimates based solely on observed fruit loads and nutritional analyses of samples
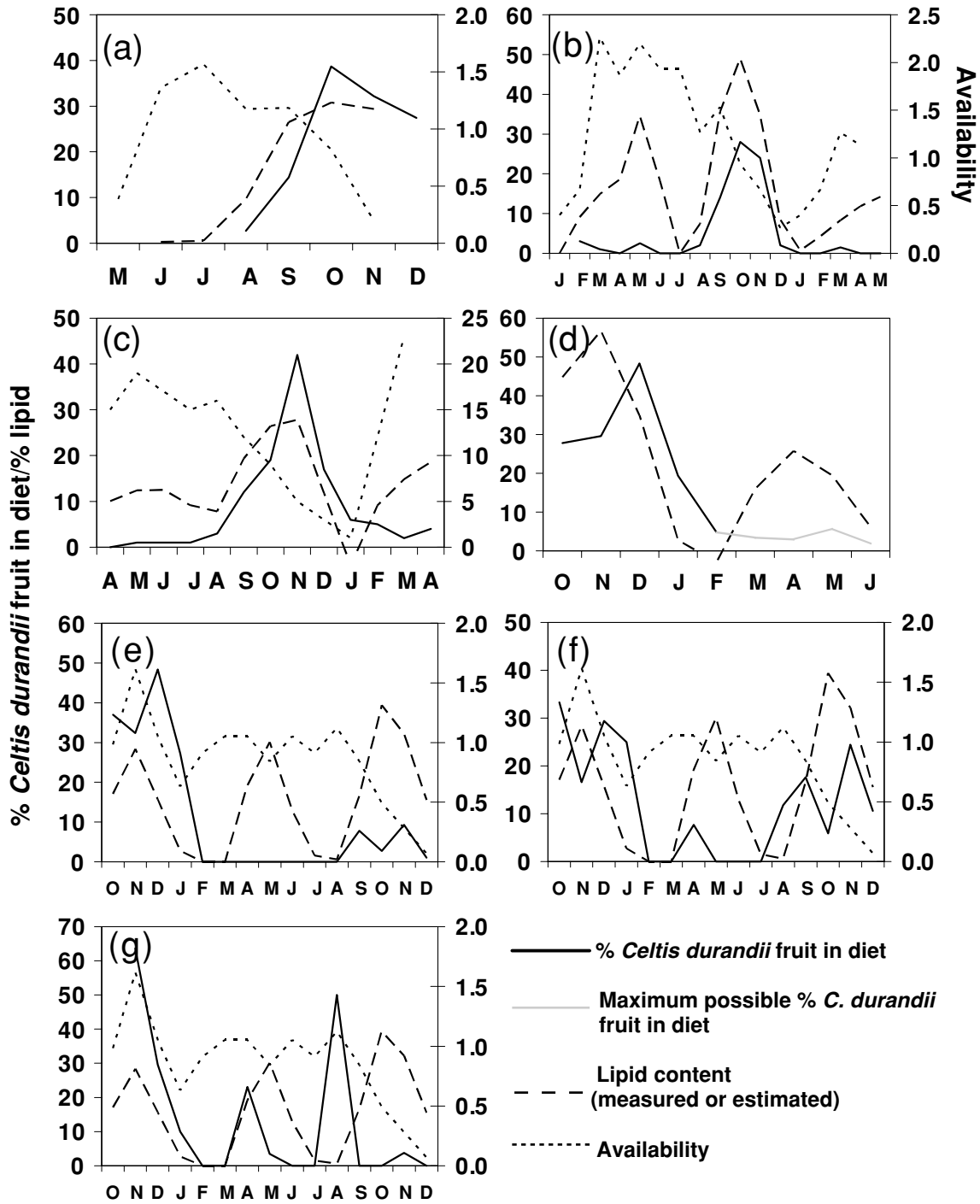
Figure 3. Changes in the percentage of *Celtis durandii* fruit in the diets of frugivores in relation to lipid content and fruit availability by month, Kibale National Park, Uganda. (a) *Cercopithecus ascanius* consumption of ripe fruit (C. Stickler unpubl. data) compared with measured lipid levels of ripe fruit and standardized fruiting intensity ($cm^2 m^{-2}$), May–December 2002. (b) *Cercopithecus mitis* consumption of fruit compared with availability on a scale of 0–4 (Rudran 1978) and fruit lipid content estimated from rainfall records, January 1973–May 1974. (c) *Lophocebus albigena* consumption of fruit compared with availability on a scale of 0–40 (Waser 1975) and fruit lipid content estimated from rainfall records, May 1972–April 1973. (d) *Lophocebus albigena* consumption of fruit (Olupot 1994) compared with lipid content estimated from rainfall records, October 1992–June 1993. Since only the top five foods were reported, the per cent of the fruit in the diet from February on was assumed to be the maximum possible (see text for full explanation). (e) *Cercopithecus mitis* consumption of fruit compared with availability on a scale of 0–4 (Lwanga 1987) and fruit lipid content estimated from rainfall records, September 1984–December 1985. (f) *Cercopithecus ascanius* SW group consumption of fruit compared with availability on a scale of 0–4 (Lwanga 1987) and fruit lipid content estimated from rainfall records, September 1984–December 1985. (g) *Cercopithecus ascanius* BTP group consumption of fruit compared with availability on a scale of 0–4 (Lwanga 1987) and fruit lipid content estimated from rainfall records, September 1984–December 1985. As 1973 and 1992 were very wet years, the lipid content of the fruit from those years is probably overestimated.

taken at one time may be misleading if seasonal changes in nutritional values commonly occur. The ripe fruits of *Celtis durandii* in the wet and dry seasons appear almost identical to human observers, only being plumper and juicier in the wet season. Despite this, the observed variation of lipid content is apparently important, as indicated by foraging effort, to at least three frugivorous species. During dry months when the lipid levels were negligible, *C. durandii* fruit was rarely eaten even when most abundant, but was heavily consumed when lipid levels increased. The fact that the data sets span four decades suggests that the pattern holds true over long periods of time. Rudran (1978) also notes that another of his *Cercopithecus mitis* groups (for which he did not present detailed data) had a similar pattern of *Celtis durandii* fruit consumption.

This study did not cover the minor rainy season in March–May. Lipid levels estimated with rainfall had two peaks a year, but consumption by the primates usually only showed one major peak (Figure 3b, c, d, e). The Ngogo *Cercopithecus ascanius* groups, however, appear also to have small peaks in consumption during the minor rainy season (Figure 3f, g). The minor rainy season peaks may simply be sampling error as these two groups were observed for very short periods of time each month or perhaps an alternative feeding strategy (e.g. seed predation). If consumption is a good indicator of lipid levels in general, it appears that lipid peaks may not be directly driven by moisture availability, but instead may occur only once a year during the September to November rains.

The lack of a correlation between diet and rainfall for the *Cercopithecus mitis* group from Ngogo (Lwanga 1987) is due to the confounding factors of a relatively wet minor rainy season in 1985 (assuming that lipid levels peak only during the major rainy season) and a general failure of *Celtis durandii* fruiting during 1985, which left very little fruit available during the September to November rainy season (Lwanga 1987). It is clear, however, that consumption of *Celtis durandii* fruit increased in the major rainy seasons of both 1984 and 1985 compared with other seasons (Figure 3e). This pattern also appears to be true for the Ngogo groups of *Cercopithecus ascanius* (Figure 3f, g). Therefore, it appears that the pattern of spikes in lipid content of *Celtis durandii* fruit during the major rainy season and corresponding increases in consumption by frugivores holds through space as well as time.

The changing lipid content of the fruit is probably also important to birds as they can distinguish as little as a 2% lipid difference, prefer foods higher in lipids in captivity (Schaefer *et al.* 2003), and are thought to focus on lipid-rich fruits in the wild, while primates, and mammals in general, are thought to focus on fruits rich in digestible carbohydrates (Debussche & Isenmann 1989, Jordano

1995, Pannell & Kozioł 1987). This has been interpreted as meaning that primates avoid lipids (Bollen *et al.* 2004) but Debussche & Isenmann (1989) actually state that the mammals in their study probably feed on lipid-poor fruits to avoid the noxious secondary compounds usually found in lipid-rich fruits. Also, preferring fruits rich in sugars is quite different from avoiding lipids: a fruit rich in both sugars and lipids would be eaten by a species preferring sugars but not by a species that avoids lipids. Additionally, it is important not to over-generalize: some primate species prefer lipids (*Ateles* spp., Di Fiore 2004; *Papio* spp., Whiten *et al.* 1991; *Pithecia pithecia*, Norconk & Conklin-Brittain 2004) or select for energy content in feeding trials regardless of the source nutrient (*Ateles geoffroyi*, Laska *et al.* 2000; *Cebus apella*, Visalberghi *et al.* 2003; *Saimiri sciureus*, Laska 2001). Though there is a scarcity of reported data regarding lipid discrimination abilities in primates, it is clear that they have multiple modes of nutrient perception (Dominy *et al.* 2001) with some studies indicating an importance of post-ingestion lipid detection (Visalberghi *et al.* 2003). These reasons led to our assumption that if increased lipid levels in fruit had an effect on consumption, it would be a positive one.

The negative correlation between fruit availability and monthly dietary importance from Waser (1975) and the observation that high usages occur in the same months as drops in availability (Figure 3) suggest that, barring extremes like the 1985 fruit failure, the availability of fruit may be restricted by consumption instead of consumption being limited by availability as is usually assumed. This may explain the observation by Chapman *et al.* (1999) that *Celtis durandii* has irregular flowering, but annual fruiting peaks. Because they used fruit load as a proxy for fruit production, it is impossible to distinguish between changes in production and changes in consumption. Instead of annual fruit production peaks, *C. durandii* may have annual consumer-driven lows in fruit load ultimately caused by seasonal lipid changes.

Why would a plant have a strategy of producing fruit year round but altering the value of the reward provided to seed dispersers? Perhaps (1) the most effective seed disperser in the wet season prefers the lipid-rich fruits and the most effective seed disperser in the dry season prefers the lipid-poor fruits, (2) the lipid-poor fruit is eaten and dispersed only as a last resort by desperate frugivores when little else is available, (3) the seeds are dispersed by seed predators or physical processes during the low-lipid season, or (4) the chances of seedling survival is low in drier seasons, thus the investment in more attractive fruits at a time when seed dispersal is most beneficial.

Whatever the underlying reasons for the seasonal change in lipid levels, it is clear that the abundance of this fruit is not related to its value as a food, and the nutritional value of the fruit has important impacts on the feeding

behaviour of its consumers. If this strategy of producing low-quality fruits during certain seasons or under certain conditions is shared by a number of tropical tree species, the seasonality of tropical moist forests could be more marked than previously thought and resource availability studies based on an assumption of constant quality in foods may be missing cryptic seasonality. Changes in the nutritional value of foods could go a long way towards explaining the sometimes shifting and enigmatic dietary preferences in frugivores and be an important consideration when evaluating habitat quality.

ACKNOWLEDGEMENTS

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