Changes in Orangutan Caloric Intake, Energy Balance, and Ketones in Response to Fluctuating Fruit Availability

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I used novel quantitative measures to assess the impact of fruit seasonality on changes in diet and energy balance during 4918 hours of observation on >60 orangutans in Gunung Palung National Park, West Kalimantan, Indonesia, from September 1994 through September 1995. During this period a mast fruiting occurred, resulting in large fluctuations in fruit availability, measured by monitoring of 558 orangutan fruit trees. Orangutan diet varied tremendously in accordance with these fluctuations. During the month of highest fruit production, 100% of the orangutan diet was composed of fruit. In contrast, during the fruit-poor period as little as 21% of the diet was fruit, while 37% was bark. Nutritional analyses of 78 of the foods most commonly eaten during this study show that mast foods were significantly higher in caloric content than were nonmast foods, which translates into substantial changes in caloric intake. During the month of highest fruit consumption (January), males consumed an estimated 8422 kcal/day and females consumed 7404 kcal/day. During the month of lowest fruit consumption (May), males consumed 3824 kcal/day and females consumed 1793 kcal/day. These differences were significantly different between the 2 months for both males and females. In May, males ate significantly more kcal/day than females did. Time spent feeding did not differ between the two periods for either males or females. I assessed the impact of these changes in diet and caloric intake on orangutan physiological functioning by measuring ketones in 257 urine samples collected from adult males and females. Ketones—products of fat metabolism—were present in urine only during the fruit-poor period. These data suggest that orangutans are highly efficient at storing fat during fruit-rich periods and

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utilizing the reserves during times of fruit shortfall. This response may have important implications for orangutan survivorship, reproduction, and behavior.

INTRODUCTION

Primates live predominantly in the tropics, where seasonal changes in weather are minimal compared to the temperate zone (Whitmore, 1986). However, dramatic fluctuations in food availability in tropical rain forests occur and may have important consequences for primate behavior, physiological functioning, and evolution. Orangutans are an interesting species in which to study the effects of changing food availability because of the mast fruiting that can occur in the Southeast Asian rain forest where they live.

Mast fruiting is a phenomenon in which a large number of rain forest trees fruit in synchrony approximately every 2–10 years (Ashton *et al.*, 1988). During these periods, the dominant dipterocarp trees and up to 88% of all canopy species can produce fruit after years of reproductive inactivity (Medway, 1972; Appanah, 1981; van Schaik, 1986). At Gunung Palung, where I conducted this study, mast fruiting events have occurred in 1987, 1991, and 1995 (Curran *et al.*, 1998).

Thus, despite no seasonal change in temperature and little variation in rainfall, the Southeast Asian rain forest is characterized by substantial fluctuations in fruit production. In addition to supraannual mast-fruiting events, annual fruit peaks also occur. This seasonal change in fruit availability has been linked to significant vertebrate migrations (Leighton and Leighton, 1983) and to primate reproductive patterns (van Schaik and van Noordwijk, 1985). I will demonstrate how this variability in fruit production ultimately impacts orangutan energy balance through physiological measures of weight loss.

Measuring the physiological response of wild primates to changing food availability has only been accomplished by weighing captured or provisioned animals (Mori, 1979; Goodall, 1986; Altmann *et al.*, 1993). This is often not possible or desirable in studies of wild great apes. I present a new method to assess weight loss through the measurement of ketones in urine. Ketones are produced when the body metabolizes its own fat reserves to produce energy. The production of ketones in response to excessive fat metabolism is a widespread phenomenon amongst mammals (Robinson *et al.*, 1980), including humans (Fischbach, 1988; Watson and Jaffe, 1995). This method of measuring physiological indicators of weight loss provides

a noninvasive way to quantify negative energy balance in wild great apes through simple field collection and analysis of urine.

We know that orangutans may modify time spent feeding (Rodman, 1977; MacKinnon, 1974; Mitani, 1989), dietary composition (Galdikas, 1988) and food selectivity (Leighton 1993) in response to fluctuations in fruit availability. However, measurements of total caloric intake have not previously been attempted. I present the first data on seasonal changes in caloric intake for any wild great ape. Through combining data on calories consumed with records of time spent feeding and dietary composition we can more rigorously assess dietary adequacy; allowing us to measure the physiological impact of fruit seasonality on individual subjects.

The application of these new techniques allows us to quantify the level of physiological response to changes in fruit availability. Such fluctuations in fruit production are important because of the ultimate effect they may have on fitness through a variety of proximate mechanisms, such as weight loss, disease, and hormonal functioning. The magnitude of the differences in energy balance that I documented could have serious consequences for both survivorship and reproduction. Accordingly, I discuss the ultimate impact of fruit seasonality on orangutan evolution.

METHODS

Study Site

I conducted the study at the Cabang Panti Research Site in Gunung Palung National Park, West Kalimantan, Indonesia, on the island of Borneo (1°13'S, 110°7'E). The field site is located in primary tropical rain forest that is characterized by a rich mosaic of habitats. The core study area occupies approximately 2100 ha inside the larger 90,000 ha-national park. The average annual rainfall of 4300 mm is relatively evenly distributed throughout the year, with typically 1 drier month with <100 mm of rain between June and September. No formerly captive orangutans have been released into the park.

Fruit Availability

I assessed relative changes in fruit availability by monitoring 558 orangutan fruit trees. The sample represented 93% of the known fruit tree genera that orangutans fed on within the study period. The selection of trees was based on records of orangutan census observations collected between

1986 and 1993 by Mark Leighton and his assistants. I set up phenological transects based on their records, which included all trees in which orangutans had been observed feeding that were ≤25 m of the trail. The trees were distributed along 12 phenological routes, 2 in each of the following habitat zones found at Cabang Panti: peat swamp, freshwater swamp, alluvial terrace, lowland sandstone, lowland granite, and upland granite. Beginning in September 1994, my assistants and I monitored them monthly for the presence of buds, flowers, and immature, mature, and ripe fruit. Immature fruits are not yet full-sized. Mature fruits are full-sized, but at a stage before ripening. Ripe fruits evidence species-specific changes in color and fruit pulp softness.

Orangutan Study Population

This report encompasses the period from September 1994 through September 1995, during 4918 hr of observation. During the initial part of the study, subjects were habituated to human presence by myself and my team of field assistants. We individually recognized, named, and followed extensively a core of 31 subjects. Additionally, >30 other orangutans occasionally used the study area and were followed briefly. Once contacted, we followed focal subjects until they made a night-nest and then recontacted them upon our arrival at the nest before dawn the next morning. Normally we followed subjects continuously until they were either lost or left the study area. Follow durations during this period range from <1 day to 47 days, with the average follow of 3.16 days.

Feeding Observations and Processing of Food Samples

We recorded the time of initiation and termination of all feeding bouts on focal subjects. We collected data continuously on focal subjects throughout full or partial day follows. Using a stopwatch, we collected 1-min feeding rates every 3 min, until 10 feeding rates were obtained. After that, we took an additional feeding rate for 1 of every 5 min in order to monitor changes in feeding behavior. Feeding rates for fruits that took >1 min to eat were recorded by timing the period between picking one fruit and picking the next fruit. Thus, both measures included harvesting as well as processing time. We also noted the part of fruit eaten—seed, pulp, and/or husk—the percentage eaten of each respective part, and the maturation stage of the fruit: immature, mature, or ripe. In some cases, such as when subjects ate large durian or *Neesia* fruits, the total number of fruits eaten could be counted.

We collected samples of fruit either from the ground or by tree climbing. Fruits representative of those eaten by the orangutans were chosen based on observing the size and maturation stage of fruits the orangutans selected. Ripe fruits were often knocked down by orangutan movement through the tree, making this collection possible. Trees were climbed to obtain fruit or leaves if an appropriate sample could not be found on the ground.

We obtained ≥5 samples of each fruit type or species. At the research camp, my assistants and I divided them into component parts, e.g. seed, pulp, husk, and weighed them. Then we dried them in a kerosene drying oven averaging 40°C for approximately 2 weeks. We weighed the dry samples to estimate the average grams of dry weight for each fruit. We then sealed dried samples in plastic bags and I brought them back to Harvard University for nutritional analysis.

We obtained feeding rates for leaves in the same way as for fruits and recorded the maturation stage—young or mature—and the leaf part—blade or bud. Young leaves are typically found at the end of twigs and are different in color and softer in texture than mature leaves. We collected leaves as we did fruit. For each feeding bout, we combined all the collected sample leaves from that tree and weighed them. After drying, I divided the total dry weight by the number of leaves collected to determine the number of grams per leaf.

I estimated bark consumption by measuring the surface area of bark that had been extracted by the orangutan and then calculating the grams of edible material that were consumed. First, if possible, we collected all bark discarded by the orangutan after feeding. At the research camp, we measured the length and width of each piece of bark in order to calculate the total area of bark that was fed upon. We examined each piece of bark and estimated the percentage of bark actually eaten, usually the inner cambium. We removed the remaining portion of the cambium not eaten by the orangutan and weighed the sample. I calculated the total grams of bark consumed from each piece by dividing the weight of the sample by the percentage of edible material the sample represented. The total number of grams consumed during a feeding bout could then be determined by summing the grams consumed from each piece of bark. This also provided a measure of grams of edible cambium consumed per surface area of bark fed upon.

If all the bark could not be picked up, then I recorded the percentage of bark pieces collected by the observer. We measured all sample pieces of bark as above to provide the surface area of bark collected. This was divided by the estimated percentage of bark pieces collected to determine the total surface area of bark upon which the orangutan fed. I determined

the grams of bark for a given surface area from the pieces that were collected and multiplied this number by the total surface area of bark consumed to provide the total grams consumed during the bout.

If no bark could be collected, then we examined the tree to estimate the surface area of bark that was fed upon. I determined the grams consumed from the tree by dividing the estimated surface area of bark fed on by an average value of grams of cambium eaten per surface area (determined from other feeding bouts as described above). I matched samples that were used to obtain this average as closely as possible to feeding bouts on the same tree species, by the same orangutan, and within the same time period.

Orangutans fed on rotan, *Pandanus*, and other epiphytes and pithy plants by extracting the soft, pithy portions and then discarding the remaining part. We collected these leavings and estimated the amount of material that was missing, which I assume to have been consumed. First, we measured the width and length of each stalk. Then we collected uneaten plants of the same species, extracted and weighed the edible material, and measured the outer covering of the stalks. This provided an estimate of the grams of edible material per stalk of a given length from which grams eaten could be calculated.

Nutritional Analysis

All analyses were conducted at the Nutritional Chemistry Laboratory, Anthropology Department, Harvard University. Crude protein (CP) was determined using the Kjeldahl procedure for total nitrogen and multiplying by 6.25 (Pierce and Haenisch, 1947). The digestion mix contained Na_2SO_4 and $CuSO_4$. The distillate was collected in 4% boric acid and titrated with 0.1 N HCl. The detergent system of fiber analysis (Goering and van Soest, 1970) as modified by Robertson and van Soest (1980) was used to determine the neutral-detergent fiber (NDF) or total cell wall fraction. Lipid content was measured using petroleum ether extraction for 4 days at room temperature, a modification of the method of the Association of Official Analytical Chemists (AOAC, 1984). Dry matter (DM) was determined by drying a subsample at 100°C for 8 hr and hot weighing. Total ash was measured by ashing the above subsample at 520°C for 8 hr and then hot weighing at 100°C. Organic matter (OM) was calculated as 1 minus ash multiplied by DM. The remaining total nonstructural carbohydrates (TNC) were estimated by subtraction [100 − (NDF + CP + lipid + ash)]. An NDF coefficient of 54.3% was used to estimate the amount of fiber available as energy due to hindgut fermentation. This value of 54.3% was cal-

culated using chimpanzee feeding trials by Milton and Demment (1988). Such trials have not been done for orangutans. Female orangutans have a body size similar to that of adult chimpanzees and should be able to digest at least this much fiber at comparable levels. However, this may underestimate metabolizable energy available to adult male orangutans because their larger body size may lead to an increased capability for hindgut fermentation.

I calculated total calories based on the energetic value of the above nutrient fractions assuming the values of 9 kcal/g lipid, 4 kcal/g CP, and 4 kcal/g TNC, taken from values used for humans (National Research Council, 1980) and % NDF × 0.543. I multiplied the kilocalories of metabolizable energy per gram of each food item by the grams of that food item ingested per bout to obtain a measure of the kilocalories consumed during each feeding bout.

Urinalysis

We collected urine samples from each focal subject on a daily basis when possible. Disposable plastic pipettes were used to collect urine from clean plastic sheets placed beneath urinating animals or pipetted directly from vegetation (Knott, 1997). I used urinalysis strips (Boehringer Mannheim Chemstrip 10 with SG) made for human clinical analysis to test samples for the presence of disease and physiological status (Knott, 1996, 1997). These are plastic strips with various reagents on pads that produce a color reaction when urine is applied. The tests were conducted as soon after collection as possible, often while still in the field. The ketone test provides a semiquantitative measure of the degree of ketosis, which is the accumulation of ketone bodies resulting from the breakdown of fat for energy. Ketone values were scored on a 4-point scale as follows: negative, trace, positive, or double positive.

RESULTS

Food Availability

The forest at Cabang Panti experienced dramatic changes in fruit availability during the study period (Fig. 1). This was due to a mast fruiting event between September 1994 and February 1995 in which a large portion of trees flowered and then fruited in synchrony. Twice as many of the orangutan fruit trees being monitored bore fruit during the month of high-
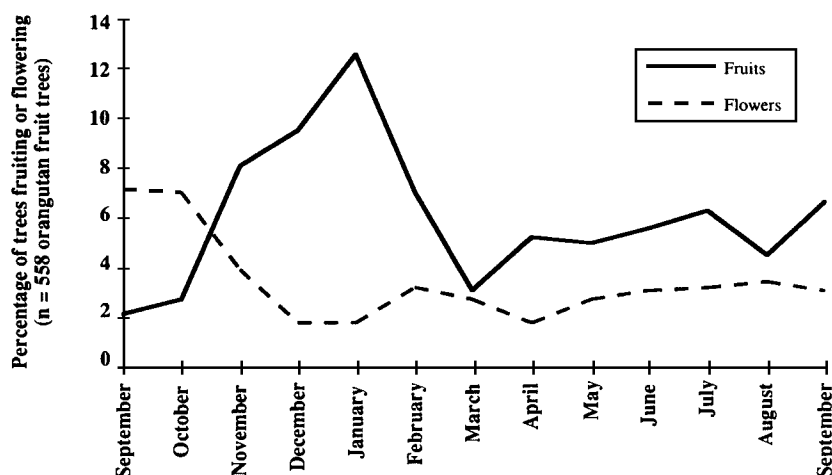
Fig. 1. Fluctuations in orangutan fruit and flower availability between September 1994 and September 1995. From November 1994 through February 1995 the forest at Gunung Palung experienced a mast fruiting when a substantial percentage of trees fruited in synchrony. Twice as many trees were fruiting during the peak mast month (January) compared to the middle of the nonmast period (May).

est orangutan fruit consumption—January—compared to May, the month of lowest fruit consumption. Furthermore, the actual amount of fruit available for orangutans during the mast may have been even greater than evident in this measure. Mast fruiting species were not well represented in the sampled orangutan fruit trees because only two masts occurred during the 8 year period during which census observations leading to the compilation of this tree list were conducted.

Dietary Composition

In accordance with changes in fruit availability, orangutan diets varied dramatically during the course of the study. Figure 2 shows data between September 1994 and May 1995, based on 3421 observation hours from >60 subjects. In September, flowers were extremely prevalent and became a major component of orangutan diet. Later, as fruits matured, orangutans fed almost entirely on seeds, whole fruit and pulp. In January, the diet was composed entirely of fruit. Leaves, pith, bark, insects, and flowers were completely missing from the diet. With the end of the mast fruiting in February, a period of severe fruit shortage began. Orangutans shifted to bark as their primary dietary component. In May, 37% of the diet was composed
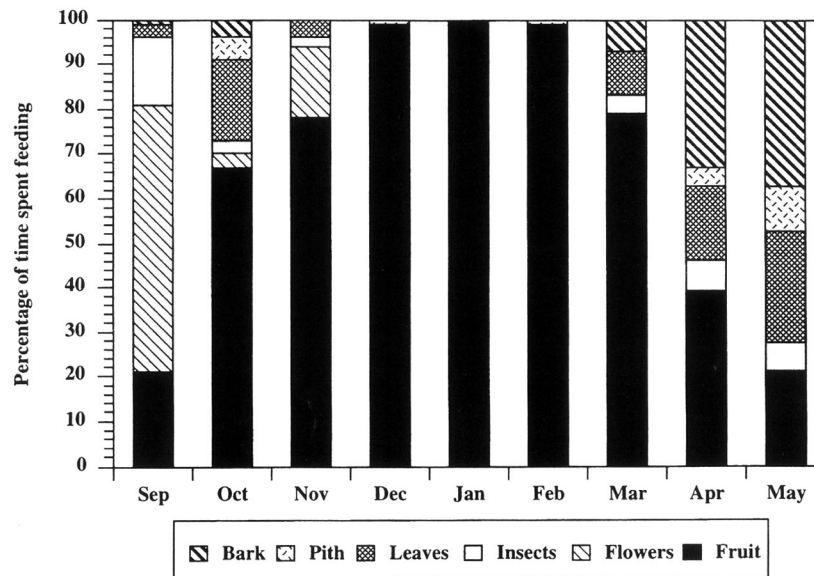
Fig. 2. Changes in orangutan dietary composition between September 1994 and May 1995 based on 3421 hr of follows from >60 individuals. Note the dramatic differences in percentage of fruit eaten throughout the year, with 100% of the diet composed of fruit in January, compared to 21% in May. No bark was consumed in November 1994 through February 1995. However, the diet was 37% bark during May of 1995 when fruit availability was low.

of bark. In addition, they ate a large number of leaves and insects as well as fruit when they encountered it.

Caloric Intake

Nutritional analyses were performed on 78 of the foods most commonly eaten by orangutans at Cabang Panti during periods of both high and low fruit availability. Fruit was not only more abundant during the mast, but mast foods were significantly higher in caloric content than were nonmast foods (t test, $n = 78$, $p < 0.005$). Table I compares the average caloric value of the 5 most commonly eaten foods during the mast period versus the 5 most commonly eaten foods during the nonmast period.

We conducted a total of 94 full or partial day follows in January and May. For the purpose of analyzing caloric intake, I include only follows from adult females and adult males—those with fully developed cheek pads. Thus, all subadult males and adolescent females are excluded from the analysis. Additionally, many new unhabituated animals were drawn into the study area

Table I. kcal/100 g of the 5 Most Commonly Eaten Mast Foods vs the 5 Most Commonly Eaten Nonmast Foods[a]

Food	Part eaten	% TNC	% Lipid	% crude protein	% NDF	Total kcal/100 g
Mast						
Baccaurea sp.	Seed	39.8	14.9	11.8	33.5	359
Castanopsis sp.	Seed	65.3	0	5.7	29.0	300
Diterocarpus sublamellatus	Seed	78.0	4.1	5.1	12.8	376
Durio sp.	Pulp/seed	40.2	2.0	16.2	41.6	266
Sindora sp.	Seed	59.1	6.7	7.4	26.8	341
Nonmast						
Average bark	—	12.3	3.4	10.0	74.3	176
Average leaves	—	18.5	2.1	11.9	67.5	177
Epiphyte leaves	—	22.6	2.2	4.0	71.2	165
Polyalthia sumatrana	Seed	2.0	3.0	6.8	88.2	110
Neesia sp.[b]	Seed	31.7	46.0	12.4	9.9	596

[a]Values are percentage weight of organic matter. TNC, total nonstructural carbohydrates; NDF, neutral-detergent fiber. Total kilocalories per gram were calculated assuming the values of 9 kcal/g lipid, 4 kcal/g CP, and 4 kcal/g TNC and an NDF coefficient of 54.3%.
[b]Neesia fruits were eaten predominantly by adult males during May.

during the period of high fruit availability and they are excluded from the analysis. Data are thus presented for the same adult male in both January and May and for 3 adult females, 2 of which are the same individual, in January and May.

I excluded all follows in which <75% of the diet had been analyzed from the sample. In the resulting data set, the average percentage of diet analyzed is 96%. In order to estimate total caloric intake, I extrapolated the remaining unanalyzed percentage of the diet based on the average caloric intake per minute for a given animal on a given day. I calculated rates based on the kilocalories consumed per hour of follow time to allow for the inclusion of both full- and partial-day follows. Follow time is the time between when the animal first got up, or was first contacted, to the time that it bedded down at night, or the follow was terminated. I performed Mann–Whitney U tests on the data due to lack of normality (Sokal and Rohlf, 1981). As inherent in great ape studies, the same individuals were repeatedly sampled, thus some samples are not independent.

The differences in the caloric content of the fruits available during the 2 months led to significant changes in orangutan caloric intake. The magnitude of these differences are substantial. Both adult males (1 individual, 18 follows) (Mann–Whitney U test, $n = 18$, $U = 0$, $p < 0.003$) and adult females (3 individuals, 29 follows) (Mann–Whitney U test, $n = 29$, $U = 0$, $p < 0.0001$) consumed significantly more calories per follow hour in January compared to May. On average, males ate 896 kcal/hr in January, compared to 338 kcal/hr in May. Females ate, on average, 707 kcal/hr in January, compared to only 162 kcal/hr in May.

Figure 3 presents data on the kilocalories consumed per day during January (the month of highest fruit consumption) compared to May (the month of lowest fruit consumption). Sampling only full-day follows from habituated, adult animals in which >75% of the diet had been analyzed, the average caloric consumption was 8422 kcal/day for males (5 follows, 1 individual) and 7404 kcal/day for females (10 follows, 1 individual) in January. In May, males (4 follows, 1 individual) ate 3824 kcal/day, compared to 1793 kcal/day for females (14 follows, 2 individuals). These full-day follows also indicate that females ate significantly more calories in January compared to May (Mann–Whitney U test, $n = 27$, $U = 7$, $p < 0.001$). The same finding exists for males (Mann–Whitney U test, $n = 9$, $U = 1$, $p < 0.02$).

Some sex differences are also apparent in caloric intake (Fig. 3). In the samples described above, during May males ate significantly more calories per day (Mann–Whitney U test, $n = 18$, $U = 3$, $p < 0.001$) and per hour ($n = 18$, $U = 4$, $p < 0.01$) than females did. In January there were no significant differences in either hourly ($n = 29$, $U = 69$, $p =$
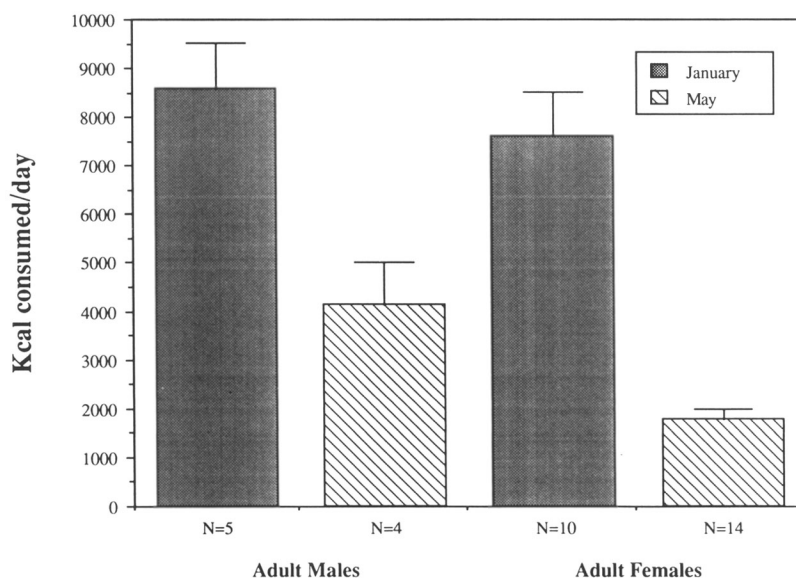
Fig. 3. Comparison of kilocalories consumed per day during January versus May for adult males and adult females. Standard errors of the data and number of follows are shown. The sample reflects all full-day follows from habituated adult animals in January or May in which >75% of the diet was analyzed. Differences between months are highly significant for both males (Mann–Whitney U test, $n = 9$, $U = 1$, $p < 0.02$) and females ($n = 27$, $U = 7$, $p < 0.001$). Kilocalories consumed per day are significantly greater in males than in females during May ($n = 18$, $U = 3$, $p < 0.001$) but not in January ($n = 29$, $U = 69$, $p = $ NS).

NS) or daily caloric intake between the sexes ($n = 15$, $U = 20$, $p = $ NS).

I examined time spent feeding by evaluating all full day follows from habituated, adult animals, regardless of the degree of dietary analysis. For both males (Mann–Whitney U test, $n = 10$, $U = 9$, $p = $ NS) and females ($n = 33$, $U = 99$, $p = $ NS), time spent feeding was remarkably similar (Fig. 4) between the 2 months. Mean time spent feeding per day for males was 346.7 min in January (5 follows, 1 individual), compared to 302.8 min in May (5 follows, 1 individual). Females spent 240.3 min feeding in January (10 follows, 1 individual), compared to 227.5 min in May (23 follows, 2 individuals). Sex differences were apparent in January when males spent significantly more time feeding than females did ($n = 15$, $U = 8$, $p < 0.05$), but the difference was not significant in May ($n = 28$, $U = 31$, $p = $ NS).
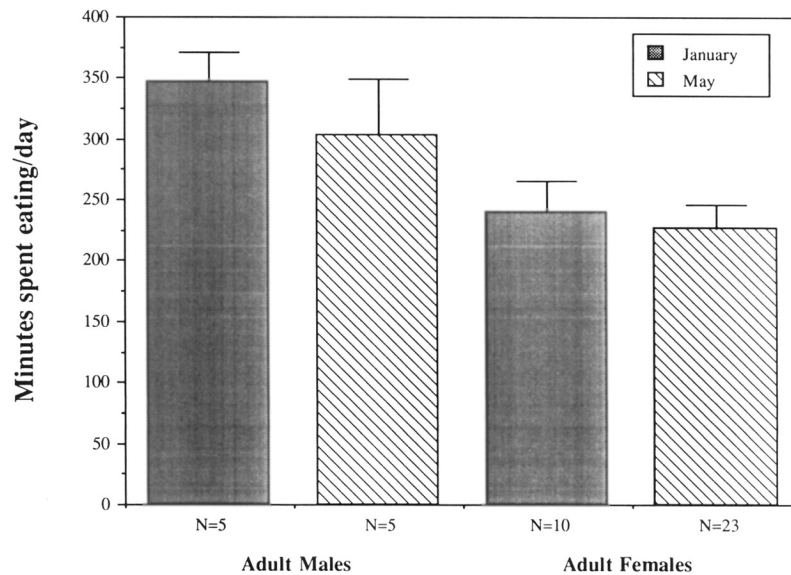
Fig. 4. Comparison of total time spent feeding for males and females during full-day follows in January and May. Standard errors of the data and number of full-day follows are shown. Time spent feeding did not differ between January and May for either males (Mann–Whitney U test, $n = 10$, $U = 9$, $p = $ NS) or females ($n = 33$, $U = 99$, $p = $ NS). Males spent significantly more time feeding than females did in January ($n = 15$, $U = 8$, $p < 0.05$), but not in May ($n = 28$, $U = 31$, $p = $ NS).

Energy Balance

Between September 1994 and September 1995, we collected a total of 336 urine samples, from which we tested 122 from 9 adult males and 135 from 13 adult females. Urinalysis revealed that ketones were present only during the period of severe fruit shortage (March 1994 through September 1995). Ketones were absent from orangutan urine during the mast months (September 1994 through February 1995). In order to reduce the problem of pseudoreplication and nonindependence of data, I determined the presence or absence of ketones on a weekly basis for each subject that was sampled. Figure 5 presents the distribution of weekly samples in which ketones were present.

Additionally, for each subject, I determined a daily ketone value by giving the ketone test result a numeric value as follows: no ketone present = 0, trace ketones = 1, positive ketones = 2, and double positive ketones = 3. From this, I calculated the average weekly ketone value for each orangutan in order to reduce the bias caused by repeated sampling of the
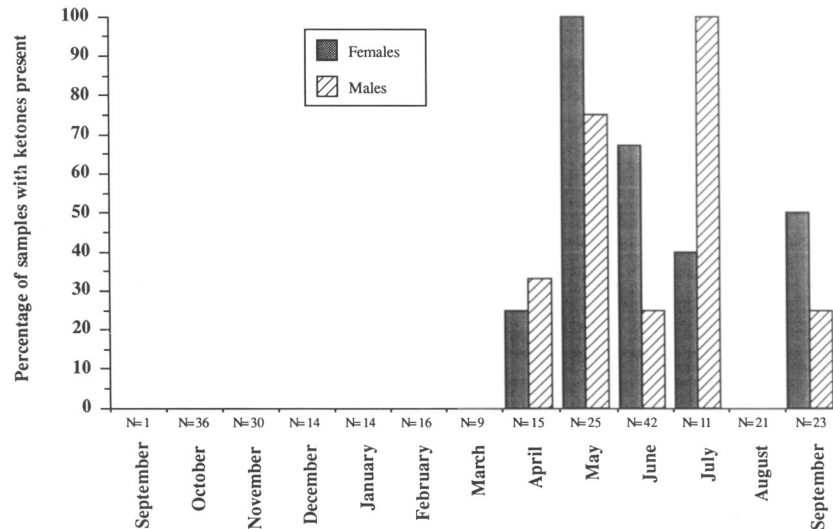
Fig. 5. Percentage of urine samples containing ketones based on weekly ketone values calculated from 257 urine samples collected from 13 adult females and 9 adult males from September 1994 through September 1995. Each individual's average weekly ketone value was used to minimize the problem of pseudoreplication. N represents the total number of urine samples collected during each month. Ketones were present in urine samples only during the period of low fruit availability between March 1995 and September 1995 (see Fig. 1). No ketones were present in urine during the high flower and fruit availability period between September 1994 and February 1995.

same individuals. Comparing males and females during the period of low fruit availability (March through September 1995) revealed that females had significantly higher levels of ketones in their urine than males did (T test, $n = 46$, $p < 0.05$).

DISCUSSION

Fluctuations in fruit availability have highly significant effects on orangutan nutritional intake, but what does this tell us about dietary adequacy? Orangutan nutritional requirements have not been directly measured, but a rough estimate can be made by applying standard tables used to calculate human energy needs based on body weight and activity level (ADA, 1992). These provide an estimate of 40 kcal/kg/day for a normal, active adult human. Applying this figure to orangutans and substituting body weights of 37.8 kg for wild adult females and 83.6 kg for wild adult males (Rodman, 1984) provides an estimated daily energy requirement of 1512 kcal/day for females and 3344 kcal/day for males. These figures are

similar to, but slightly lower than, the figure of 2333 kcal/day for a 55-kg orangutan calculated by Wheatley (1982) based on equations using basal metabolic energy expenditure and activity levels in laboratory and domestic animals. Rodman (1979) calculated total energy requirements as 2530 kcal/day for one adult male and an average of 1495 kcal/day for two adult females. None of these figures take account of additional energy requirements for pregnant or lactating females.

The caloric intake values during January, 8422 kcal/day for males and 7404 kcal/day for females, demonstrate that during periods of high fruit availability orangutans can greatly exceed their daily caloric intake requirements. Although weight gain could not be measured directly, these figures suggest that orangutans were gaining weight during this period. A caloric consumption of 7700 kcal/day over baseline energy requirements results in a 1-kg weight gain. Based on the above figures, orangutans may have been gaining as much as 0.66 kg per day. Thus, when fruit is abundant orangutans are able to take advantage of this period of plenty to put on additional fat stores.

Among the great apes, orangutans may be particularly adapted for fat storage because of the great supraannual fluctuations in fruit availability in the Southeast Asian rain forests. This idea is supported by the particular propensity toward obesity in captive orangutans compared to other great apes (MacKinnon, 1971). In captivity, orangutans tend to have higher rates of disease associated with obesity, such as diabetes, than do other great apes (Bond, National Orangutan Studbook Keeper, personal communication). As has been suggested by previous researchers (MacKinnon, 1974; Wheatley, 1982, 1987; Leighton, 1993), the ability of orangutans to store large amounts of energy as fat allows them to subsist on lower quality foods in an environment where fruiting is unpredictable.

During the period of low fruit availability, when orangutans were feeding predominantly on bark, the production of ketones indicates that orangutans were losing weight and were energetically stressed (Robinson et al., 1980). Thus, the daily caloric intake of 1793 kcal/day for females and 3824 kcal/day for males was probably insufficient. These values are slightly higher than predicted basal energy requirements based on human measures. However, orangutans may have higher levels of energy expenditure than calculated for humans or laboratory animals. The fact that they spent the same amount of time feeding in both January and May suggests that they were trying to maximize their caloric intake during both periods. Despite this, during the period of low fruit availability, food quality was poor and they were not able to maintain body weight. This was especially true for females.

Interestingly, in May males consumed significantly more calories than females did, but they did not do this by spending more time feeding. Instead, this appears to have been accomplished by the greater exploitation by males of lipid-rich *Neesia* seeds compared to that of adult females. The seeds contain 46% lipid and are thus extremely high in calories (Table I). *Neesia* are very large, hard fruits with irritating hairs surrounding the seeds. They are ripped open by orangutans at Cabang Panti, and thus the more extensive intake of *Neesia* seeds by males may be due to their greater ability to open the fruits. That *Neesia* may be difficult to extract is also evidenced by the observation of van Schaik and Fox (1996) that orangutans in Suaq Balimbing forest in Sumatra use tools to extract the seeds. Thus, extractive abilities during fruit-poor periods may give certain individuals a selective advantage during periods of scarcity.

Females were more severely impacted by the period of low fruit availability than males were, as shown by the higher percentage of female urine samples that tested positive for ketones. This sex difference is not surprising given that males were able to consume more calories than females were during May. Despite their smaller body size, some females may also have high metabolic costs due to the energetic costs of motherhood. In fact, the highest ketone values occurred in the only female in the study that had both a nursing infant and an accompanying older juvenile. This may reflect the additional costs of lactation, carrying an infant, and decreased foraging efficiency due to time spent waiting for a slower juvenile. The second highest ketone values were from a pregnant female.

What implications do these effects on physiological functioning have for understanding orangutan evolution? First, these data provide support for the proposition that orangutans have evolved the ability to exploit periods of high fruit abundance by storing excess energy as fat. This fat storage ability seems to enable orangutans to mobilize stored energy to survive periods of severe fruit shortage. It also provides the opportunity for orangutans to subsist in an environment in which fruit is patchily distributed in both space and time.

Second, if sustained, negative energy balance can lead to starvation and eventually death, periods of fruit shortage can serve as strong selective forces. Disease resistance may be compromised during periods of low fruit availability as more energy is needed to fight infection. For example, when calculating energy requirements, clinicians multiply the required kilocalories per day by an injury factor to reflect the greater energy needs of sick individuals. Injury factors due to infection range from 1.0 to 1.8 (ADA, 1992). Orangutans, particularly adult males, may at times experience high rates of infection due to injury (Knott, 1996). Thus, if injuries are sustained

during periods when caloric intake is marginal, it could severely compromise their survival ability.

Third, changes in energy balance may have a significant effect on orangutan reproductive functioning. Orangutans have an average 8-year interbirth interval (Galdikas and Wood, 1990). In humans, changes in energy balance have significant impact on hormonal functioning (Ellison et al., 1993). If similar mechanisms control reproduction in orangutans, such large fluctuations in fruit availability may have an effect on the wide birth spacing of orangutans. Prolonged periods of negative energy balance may compromise the ability of orangutans to conceive. I am currently investigating the effect of changes in energy balance on orangutan hormonal functioning.

Fourth, these fluctuations in fruit availability may be a critical factor in shaping orangutan behavior and social organization. For example, during periods of high fruit availability orangutans at Cabang Panti formed groups more often than during periods of food scarcity (Knott, 1998). The large dipterocarp trees that were fruiting during the mast allowed several orangutans to feed simultaneously. Thus, when fruit was abundant and occurred in large patches, orangutans readily formed groups. During periods of high fruit availability food competition was infrequent but occurred at rare, highly dispersed trees such as durian.

Ultimately, the phenomenon of mast fruiting in Southeast Asia that leads to extreme supraannual variability in fruit production can be seen as a strong force selecting for the ability of orangutans to maximize caloric intake during high fruit periods to sustain them during periods of severe fruit shortage. These periods of fruit shortage probably played a major role in shaping orangutan evolution through proximate physiological and behavioral adaptations. Such ecological factors should be a major factor to consider when seeking to understand orangutan evolution and behavior.

ACKNOWLEDGMENTS

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