

A Preliminary Study of Food Selection by the Orangutan in Relation to Plant Quality

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ABSTRACT. We observed the foraging behavior of orangutans in Central Indonesian Borneo during October, November, and December 1980, and analyzed food and nonfood items for water content, neutral detergent fiber, crude protein, available crude protein, and protein: fiber ratio and the presence of alkaloids and tannins. The diet of the orangutan during this season was unusual because it consisted predominantly of seeds and unripe, rather than ripe, fruits. Also, the major diet item, the seeds of *Irvingia malayana*, had been ignored in previous years when it had fruited. In leaves, protein content was more closely associated with food choice than either neutral detergent fiber or the protein: fiber ratio. Flowers had the highest protein content and protein: fiber ratio of any food item. Tannins were found in most food items, but the presence of alkaloids was found in only one.

Key Words: Orangutans; *Pongo pygmaeus*; Diet; Protein; Fiber; Tannins; Alkaloids.

INTRODUCTION

Orangutans (*Pongo pygmaeus*) are found only in the tropical rain forests of Borneo and northern Sumatra. They, like other primates, are selective in the foods they eat. In GALDIKAS' long-term study of orangutan biology at the Tanjung Puting Reserve (now a National Park) in Central Indonesian Borneo, ripe fruit was the preferred food item in the orangutan's diet from 1971–1975, accounting for 61% of its feeding time; however, less than 1% of the stems (≥ 0.1 m in diameter) bore fruit which was edible by orangutans at any one time (GALDIKAS, 1978, 1988). Also during this time period, the orangutans ate the leaves of over 45 plant species but just 2 species accounted for 43% of all leaf-eating bouts (GALDIKAS, 1978, 1988). The major hypotheses used to explain food selectivity in primates are: 1) selection to increase the intake of essential nutrients, e.g. protein, nonstructural carbohydrates, and minerals; 2) selection to reduce the consumption of relatively indigestible plant components, such as cellulose and lignin; and 3) selection to reduce the intake of plant secondary compounds which may be toxic, such as alkaloids, or interfere with digestion, such as tannins (MILTON, 1979; MCKEY et al., 1981; WATERMAN et al., 1983; WRANGHAM & WATERMAN, 1983; CALVERT, 1985; see review by GLANDER, 1982). In this study, we analyzed plant parts eaten versus parts ignored by the orangutan for the following dietary components: neutral detergent fiber, crude protein, available crude protein, protein: fiber ratio, water, and the presence of tannins and alkaloids.

A knowledge of the nutritional ecology of the orangutan provides for a better understanding of the factors affecting its foraging behavior, home range size, and population density, which are important to orangutan conservation. It may also help explain the

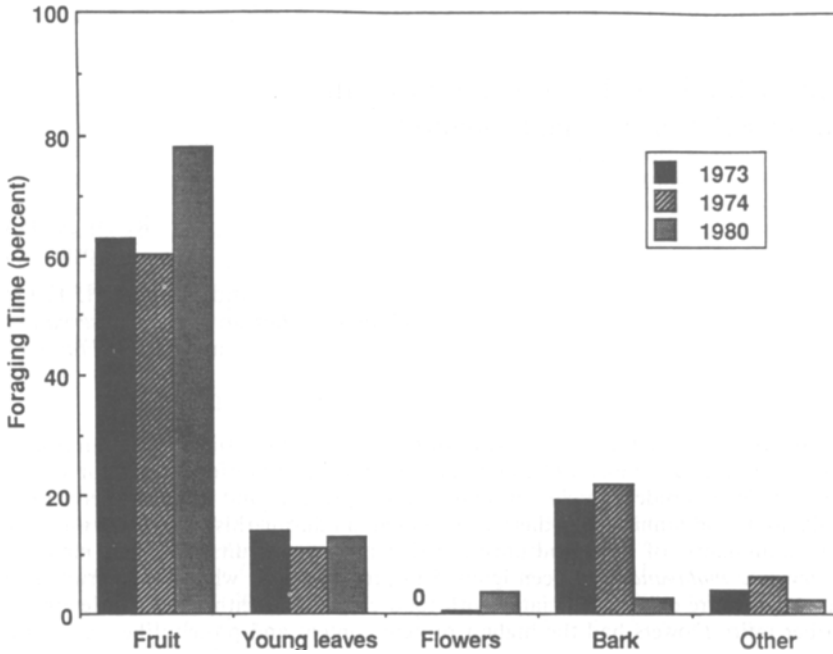


Fig. 1. Percent of foraging time orangutans spent in each food category from October through December. 1973 data based on 195 hr 21 min of observation, 1974 on 352 hr 50 min, and 1980 on 110 hr 52 min. 1973 and 1974 data adapted from GALDIKAS (1978).

orangutan's large body size and sexual dimorphism, which would provide insight into orangutan evolution. To our knowledge, there are no published data on the nutritional aspects of the orangutan diet. This is a preliminary study for further research into this area of orangutan biology.

METHODS

This study was conducted at the 40 km² Orangutan Research and Conservation Project study area in the Tanjung Puting Reserve/National Park in Central Indonesian Borneo (Kalimantan Tengah) during the beginning of the wet season in October, November, and December 1980. The study area, located approximately 30 km from the Java Sea, contains mostly mature kerangas forest with some dipterocarps (68%), peat swamp forest (27%), and young secondary forest, shallow lakes and grassland (5%).

Orangutans were observed for 176 hr 14 min over 19 days. This included 13 days of observation of orangutans from the time they left their nest in the morning until they made their nest in the late afternoon. Overall, the orangutans spent 110 hr 52 min foraging (63% of their time awake). Foraging was defined as the time during which an orangutan reached for, prepared, extracted, handled, chewed, and swallowed food at one food source. Movement within a food source to obtain food items was also included. Adult males were observed for ten days, subadult males for three days, and adult females for six days. All observations were made in dry ground kerangas forest. Data collected included: 1) species of plant eaten; 2) plant part eaten; and 3) length of time spent feeding at each food type.

A nutritional analysis was performed on food and nonfood items the orangutans encountered during foraging. In this study, nonfood items were plant parts that were ignored when an orangutan had entered a tree and had fed on something in that tree. For example, orangutans would eat the fruits of *Cantleya corniculata* but always ignored the young leaves present. These young leaves were classified as a nonfood item. Since orangutans fed at trees in which nonfood items were collected, we considered that these nonfood items would not require the additional expenditure of energy by orangutans to obtain them, thus reducing the possibility of non-nutritional factors (e.g. traveling time) explaining food selection.

Food samples were collected from fruit, leaves, or branches which the orangutan had dropped or were picked from a tree by Dayak field assistants after the orangutan had left. Whenever possible, samples of young leaves, mature leaves, unripe fruit, ripe fruit, and flowers were taken at each food source regardless of what was eaten. Leaves were classified as "young" on the basis of small size, color, and terminal position on the branch. All samples were stored in plastic bags until they could be dried in a camp drying room kept at approximately 45 to 55°C. Water content was determined by dividing a sample's weight loss after drying by its fresh weight. The samples were ground in a Wiley mill before laboratory analyses. One individual was randomly chosen from each plant species for nutritional analysis, provided there was sufficient quantity of dried material (2 g for each plant part) to run the various nutritional analyses.

A qualitative evaluation of hydrolyzable and condensed tannins was made using paper chromatography, following the methods of BATE-SMITH and METCALF (1957). Plant material was extracted with boiling HCl. The filtrate was then extracted with ethyl acetate and iso-amyl alcohol which were spotted onto chromatography paper and run in Forestal's solvent. Hydrolyzable tannins were detected by the presence of ellagic acid or gallic acid spots on the chromatogram while condensed tannins were detected by pink, red, or orange anthocyanidin spots. The presence of alkaloids was detected following the procedure described by SMOLENSKI et al. (1972). The plant material was extracted with ethanol and filtered. The filtrate was evaporated to dryness, HCl was added to the residue, and this was tested for the presence of alkaloids by using Mayer's, Wagner's, Dragendorff's, and Hager's reagents. A precipitate signified a positive test for alkaloids.

Crude protein (CP) was determined by multiplying the total nitrogen content of each sample by 6.25. Total nitrogen was determined by the kjeldahl procedure using Na₂SO₄ and CuSO₄ in the digestion mix and collecting the distillate in a boric acid solution. Unavailable nitrogen was estimated by treating a new sample with pepsin, a protease, following the pepsin method of GOERING and VAN SOEST (1970). The solution was then neutralized with sodium hydroxide and treated with neutral detergent using the neutral detergent fiber method described in ROBERTSON and VAN SOEST (1981) to obtain the neutral detergent fiber (NDF). The kjeldahl procedure was performed on the NDF to obtain the neutral detergent fiber nitrogen. This value was multiplied by 6.25 to obtain the neutral detergent fiber crude protein (NDF-CP). The NDF-CP represents unavailable crude protein. Available crude protein (ACP) is estimated by the subtraction of NDF-CP from CP. Available crude protein is an estimate of the amount of protein not bound by tannins (REED et al., 1982). This calculation of ACP probably underestimates the true ACP but can be used to find a relative index of ACP between plant samples. Neutral detergent fiber measures the cell wall constituents (hemicellulose, cellulose, lignin, and cutin) of plant material and represents the total fiber present. All samples were run in duplicate and averaged to obtain the final value. In all cases variation between the two estimates was <2%.

Crude protein, NDF, NDF-CP, and ACP were recorded as percentages of dry matter. Dry matter was based on hot weighing air dry samples from a 100°C oven. All percentage data were first transformed to $\arcsin(\sqrt{y})$ before performing statistical analyses.

During the 19 days of observation, the orangutans used over 45 plant species as food sources. Species that accounted for $\geq 1\%$ of foraging time are listed in Table 1. The seeds of *Irvingia malayana* and the fruits of *Gironniera nervosa* accounted for over 54% of the foraging time. Twelve species (including 12 food items and 15 nonfood items) were examined for nutritional components.

Table 1. Food plant species ranked by foraging time for foods representing $\geq 1\%$ of foraging time.

Species and family	Plant part eaten	% foraging time
<i>Irvingia malayana</i> (Simaroubaceae)	S	29.3
<i>Gironniera nervosa</i> (Ulmaceae)	FR	25.0
<i>Xanthophyllum</i> sp. 1 (Polygalaceae)	YL	6.4
<i>Sarcotheca diversifolia</i> (Oxalidaceae)	FR	6.3
<i>Eugenia lineata</i> (Myrtaceae)	FR	6.1
<i>Eugenia</i> sp. 1 (Myrtaceae)	FR	5.5
Insects		2.3
<i>Xanthophyllum</i> sp. 2 (Polygalaceae)	YL	2.3
Unidentified sp.	BRK	2.1
<i>Dillenia</i> sp. (Dilleniaceae)	FL	1.4
<i>Cantleya corniculata</i> (Icacinaeae)	FR/S	1.4
Vine sp. 1	FR	1.3
<i>Xanthophyllum</i> sp. 1 (Polygalaceae)	FL	1.3

FR: Fruit; S: seed; FL: flower; YL: young leaves; BRK: bark cambium.

YOUNG LEAVES AND MATURE LEAVES

Twelve species of trees and vines were used as young leaf food sources but one species, *Xanthophyllum* sp. 1, accounted for nearly half the foraging time on young leaves. The young leaves of this species had the highest ACP but also were the only ones examined which contained alkaloids. Tables 3 and 4 summarize *t*-test analyses comparing nutritional components between young leaves which were eaten and young leaves which were ignored and between young and mature leaves of the same species. Young leaves which were eaten had significantly higher CP and ACP than young leaves which were ignored; however, there were no significant differences in water content or NDF. Two of the five young leaf species eaten contained condensed tannins, while all four of the young leaf species ignored contained them. The protein:fiber ratios (both CP:NDF and ACP:NDF) were higher in the young leaves eaten than those ignored, although the results were not significantly different.

Mature leaves were never eaten. In a paired *t*-test comparison of young and mature leaves of the same species ($N=5$), young leaves had significantly higher water content and CP, but there was no significant difference in NDF. With the exception of *G. nervosa*, the relative difference between young and mature leaves within a species was similar. In two cases, young leaves had a higher NDF than mature leaves on the same tree. Qualitatively, young and old leaves were similar with respect to the occurrence of tannins and alkaloids. In all but one case, protein:fiber ratios (both CP:NDF and ACP:NDF) were higher in young leaves than mature ones.

Table 2. Water content, neutral detergent fiber (NDF), crude protein (CP), available crude protein (ACP), protein: fiber ratios (CP:NDF and ACP:NDF), and occurrence of hydrolyzable tannins, condensed tannins, and alkaloids in food and nonfood items of the orangutan.

Species name	Plant part	Eaten	Water	NDF	CP	ACP	CP:NDF	ACP:NDF	Hyd. Tan.	Cond. Tan.	Alk.
<i>Artocarpus</i> sp.	YL	+	73.2	45.8	13.2	6.2	0.29	0.14	-	-	-
<i>Baccaurea sumatrana</i>	YL	+	82.0	28.7	12.5	11.1	0.44	0.39	-	-	-
<i>Dialium</i> sp.	YL	+	83.0	54.9	15.9	9.4	0.29	0.17	-	-	-
<i>Gironniera nervosa</i>	YL	+	70.8	83.7	17.6	3.7	0.21	0.04	-	+	-
<i>Xanthophyllum</i> sp.	YL	+	60.1	68.7	16.6	12.4	0.24	0.18	-	-	+
x ± SD			73.8 ± 9.3	56.4 ± 21.1	15.2 ± 2.2	8.6 ± 3.6	0.29 ± 0.09	0.18 ± 0.13			
<i>Canitleya corniculata</i>	YL	-	59.0	23.3	8.4	7.6	0.36	0.33	-	+	-
<i>Dillenia</i> sp.	YL	-	76.2	80.4	18.1	1.4	0.23	0.02	+	+	n.d.
<i>Eugenia lineata</i>	YL	-	44.1	47.9	5.6	0.9	0.12	0.02	+	+	-
<i>Sarcothea diversifolia</i>	YL	-	62.7	80.4	9.3	3.1	0.12	0.04	-	+	n.d.
x ± SD			60.5 ± 13.2	58.0 ± 27.8	10.4 ± 5.4	3.3 ± 3.0	0.20 ± 0.12	0.10 ± 0.15			
<i>Artocarpus</i> sp.	ML	-	59.4	43.1	11.2	5.7	0.26	0.13	+	-	n.d.
<i>Baccaurea sumatrana</i>	ML	-	67.0	42.8	10.5	8.8	0.25	0.21	-	-	-
<i>Dialium</i> sp.	ML	-	56.1	62.2	9.5	5.0	0.15	0.08	-	+	-
<i>Gironniera nervosa</i>	ML	-	58.8	79.9	14.8	5.3	0.19	0.07	-	+	-
<i>Xanthophyllum</i> sp.	ML	-	53.5	69.7	15.6	11.4	0.22	0.16	-	-	+
x ± SD			59.0 ± 5.1	59.5 ± 16.4	12.3 ± 2.7	7.2 ± 2.8	0.21 ± 0.04	0.13 ± 0.06			
<i>Eugenia lineata</i>	FR peel	+	75.3	20.3	4.2	2.6	0.21	0.13	+	-	-
<i>Eugenia</i> sp.	FR peel	+	61.3	86.4	3.6	0.4	0.04	0.005	+	+	-
<i>Gironniera nervosa</i>	FR (entire)	+	83.0	77.0	12.7	5.1	0.16	0.07	+	+	n.d.
<i>Sarcothea diversifolia</i>	FR (entire)	+	91.0	28.5	7.1	4.6	0.25	0.16	+	+	-
Vine sp. 2	FR peel	+	71.4	31.4	14.4	12.7	0.46	0.40	-	+	-
x ± SD			76.4 ± 11.3	48.7 ± 30.6	8.4 ± 4.9	5.1 ± 4.6	0.22 ± 0.15	0.15 ± 0.15			
<i>Eugenia lineata</i>	S	-	43.2	36.4	2.9	0.0	0.08	0.00	+	+	-
<i>Eugenia</i> sp.	S	-	47.7	70.5	2.3	0.0	0.03	0.00	+	+	-
<i>Irvingia malayana</i>	FR flesh	-	78.6	22.2	5.9	5.0	0.27	0.23	+	-	-
Vine sp. 2	S	-	51.4	29.4	13.5	10.3	0.46	0.35	-	-	-
x ± SD			55.2 ± 15.9	39.6 ± 21.4	6.2 ± 5.1	3.8 ± 4.9	0.21 ± 0.19	0.14 ± 0.17			
<i>Dillenia</i> sp.	FL	+	79.7	48.0	25.2	16.6	0.53	0.35	+	+	-
<i>Xanthophyllum</i> sp.	FL	+	74.1	50.3	22.2	18.7	0.44	0.37	-	-	n.d.
<i>Dillenia</i> sp.	FL bud cover	-	85.3	80.1	12.9	0.1	0.16	0.001	+	+	n.d.

Values as % dry matter, except for water content (% fresh water) and ratios. YL: Young leaves; ML: mature leaves; FR: fruit; S: seed; FL: flower; +: yes/present; -: no/absent; n.d.: not done.

Table 3. *T*-test comparisons of plant quality components between young leaves eaten vs ignored.

Plant quality component	<i>t</i>	<i>p</i>	<i>df</i>
Water	1.783	0.118	7
NDF	-0.104	0.920	7
CP	1.942	0.093 [†]	7
ACP	2.478	0.042*	7
CP:NDF	1.417	0.199	7
ACP:NDF	1.198	0.270	7

[†]Significant at $p \leq .10$; *significant at $p \leq .05$.

Table 4. Paired *t*-test comparisons of plant quality components between young leaves eaten vs mature leaves of same species, not eaten.

Plant quality component	<i>t</i>	<i>p</i>	<i>df</i>
Water	4.225	0.013*	4
NDF	-0.871	0.433	4
CP	2.945	0.042*	4
ACP	1.102	0.332	4
CP:NDF	2.338	0.080 [†]	4
ACP:NDF	1.384	0.239	4

[†]Significant at $p \leq .10$; *significant at $p \leq .05$.

FLOWERS

The flowers that were eaten from two tree species (*Dillenia* sp. and *Xanthophyllum* sp. 1) had the highest ACP (16.6% and 18.6%) of all food items analyzed in this study. They also had the highest protein:fiber ratios. In eating flowers of *Dillenia* sp. the orangutans carefully peeled off the flower bud cover to consume the flower (4 mm in diameter). These bud covers contained almost no ACP.

FRUIT

Unripe fruits of the following species were eaten: *Eugenia* sp. 1, *Eugenia* sp. 2, *Eugenia lineata*, *Gironniera nervosa*, *Cantleya corniculata*, *Tetramerista glabra* (F. Tetrameristaceae), *Bouea burmanica* (F. Anacardiaceae), and *Sarcotheca diversifolia*. In October, the clusters of small fruits (<1 cm in diameter) of *Gironniera nervosa* were light green with soft, immature seeds. With time, these fruits changed in color turning yellow and then orange, and the seeds became hard. The light green oblong fruits (≤ 3 cm long) of *Sarcotheca diversifolia* were also observed to ripen during the study period. The orangutans ate these fruits from October to December. In October, the sucrose content of these fruits (measured by a refractometer) averaged 3.5%. By December, the sucrose content increased to 9.2%.

During this study, orangutans spent the longest amount of time foraging on immature seeds of *Irvingia malayana*. This fruit was about 5 cm long and 3.5 cm wide. Orangutans bit off one end of the fruit and, using their molars, squeezed the gelatin-like contents of the seed into their mouth. The firm resinous flesh of this fruit was discarded. An orangutan was able to exhaust the fruit supply at these trees; one individual orangutan consumed 2,545 fruits at a single tree in one foraging bout. Since only a few, if any, fruits were left in a tree, we were unable to collect enough seeds for chemical analyses.

Generally fruits were low in CP and ACP with the exception of vine sp. 2 (F. Leguminosae). The fruit of this species was small (1.5 cm long) and contained a hard seed surrounded by what felt like sharp sclereids. Orangutans consumed the skin of this fruit (2–3 mm thick) by scraping it off the seed with their teeth and then discarding the seed. Similar behavior was observed when the orangutans ate the fruits of *Eugenia* sp. 1 (round, 3 cm diameter), and *Eugenia lineata* (peanut shaped, 3 cm long); seeds of these species were discarded after the orangutans had scraped off the outer green peel with their teeth. Both of these latter seeds had no ACP and were very astringent tasting when sampled by the authors. Most fruits consumed by the orangutans contained both hydrolyzable and condensed tannins.

DISCUSSION

An unusual aspect of this season was the high amount of unripe fruit and seeds consumed. Normally the orangutans in this area eat predominantly ripe fruits (GALDIKAS, 1978, 1988). Seeds of *Irvingia malayana*, (which accounted for 29% of foraging time) were ignored in some other years when this tree fruited (GALDIKAS, 1978). Although this study only spanned three months, it does represent a natural unit of time where two predominant species of food plant, *Gironniera nervosa* and *Irvingia malayana*, began and ended fruiting.

Orangutans were selective in the plant species and food parts they ate during this study, as shown by the predominance of only a few species in their diet, their preference for young versus mature leaves, and the careful way they separated and consumed one part of a fruit or flower and discarded the remainder. Based on the variables examined in this study, protein content (CP and ACP) was most closely associated with leaf choice in young leaves. Among young leaves eaten, the species they spent the most time foraging on, *Xanthophyllum* sp. 1, had the highest ACP and lacked tannins. The leaves of *G. nervosa* were unusual in that they had the highest CP (17.6%) but the lowest ACP (3.7%) of any young leaves eaten. Since the fruit of this species accounted for such a large proportion of the orangutans' foraging time, they may have eaten these leaves due to their proximity. It is also interesting to note that the leaves of *Artocarpus* sp. which are eaten had a CP of 13.2%, an ACP of 6.2%, but no detectable tannins. Some condensed tannins are insoluble in normal tannin solvents (e.g. Forestal) but their presence may be indirectly detected in the pepsin-insoluble NDF-CP (REED et al., 1982).

Several investigators have examined the basis for the preference of young over mature leaves in primates. MILTON (1979), OATES et al. (1980), and MCKEY et al. (1981) compared young and mature leaves of several species and found that young leaves had higher protein content and lower fiber content. However, both MILTON (1979) and MCKEY et al. (1981) described cases in which some young leaves had the opposite characteristics and yet were still preferred by primates. MILTON (1979) attributes the higher protein:fiber ratio as a major factor in the preference of howler monkeys for young versus mature leaves. This is due to constraints put upon the herbivore limiting their food intake, which is related (at least in ruminants) to the fiber content of the food, interacting with a preference for protein in order to maintain a nitrogen balance. In this study, young leaves generally tended to have higher water content, CP, ACP, and protein:fiber ratios (CP:NDF and ACP:NDF), although mature leaves did not have significantly higher NDF than young leaves.

Flowers were notable for their high ACP and protein:fiber ratios. In one species the bud

cover, which was discarded, contained almost no ACP. Fruit was generally low in ACP. However, the fruit *Gironniera nervosa*, which made up 25% of the orangutans' foraging time, had an ACP of 5.1% which was higher than that of the young leaves of this species that were eaten. Fruit may provide a significant protein contribution to the orangutans' diet due to the large volume of fruit consumed. Protein content and the presence of tannins may have been factors in the orangutans avoiding the seeds of two *Eugenia* species; these seeds had no ACP. A third seed that was avoided contained sharp sclereids. Fiber in fruits did not appear to be a factor in determining food choice since NDF was lower in the fruit parts discarded than in those which were eaten. An examination of other factors, such as caloric value, lipid content, and micronutrients, may better explain fruit and seed selection.

Orangutans are large herbivores. Adult female orangutans from Borneo weigh approximately 37 kg while adult males average 73 kg (ECKHARDT, 1975). Orangutans have a solitary or semisolitary lifestyle. To explain this unusual attribute in primates, GALDIKAS (1978) on the basis of WRANGHAM (1979) proposed that the major orangutan food source, the flesh of ripe fruits, has few or no toxins, allowing orangutans to maximize the quantity eaten of specific fruits. This, in combination with their large size, allows individual orangutans to deplete all the ripe fruit at one source. Thus, there would be direct competition for food between orangutans (particularly the large adult males) if they foraged together. The basis for GALDIKAS' assumption that the flesh of tropical fruits is low in toxins is that tropical plants use orangutans and other mammals as seed dispersal agents (GALDIKAS, 1982). While feeding on fruits, orangutans usually do not destroy all the seeds but either spit them out or digest the fruits and then eliminate the seeds away from the parent plant (GALDIKAS, 1982). Thus, in order to be attractive to herbivores, the flesh of ripe fruits should not contain toxins or other compounds to inhibit herbivory (while the seeds themselves should do so). The absence of alkaloids in fruits examined in this study support this hypothesis, although one might expect immature fruits to possess some type of herbivore deterrent.

Orangutans have a digestive tract similar to humans (STRAUS, 1936). WHEATLEY (1982) hypothesized that the large size of the orangutan, with its high amount of fat reserves, enabled it to survive on unpredictable seasonal foods (such as fruits and flowers) because fat provided energy reserves to sustain it through times of poor food quality. Also, fiber may be a less critical diet component for the orangutan than for smaller primates since large size (and thus longer food retention time) aids in the fermentation of cellulose and other partially digestible components of fiber (DEMMENT & VAN SOEST, 1983). In seasons in which food is of poorer quality than usual, these factors may make protein content a more important factor than fiber content, caloric content, or protein:fiber ratio. The large sexual dimorphism in body size between male and female orangutans may allow the sexes to partition food resources differently, allowing males eating food items with higher fiber contents.

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