

Seed-Eating by Red Leaf Monkeys (*Presbytis rubicunda*) in Dipterocarp Forest of Northern Borneo

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Received October 23, 1989; revised August 27, 1990

*Data are presented on the feeding behavior of *Presbytis rubicunda* at Sepilok, north Borneo. Emphasis is given to describing the fruit-eating behavior of this small colobine monkey, which specializes in eating seeds from large, dull-colored, and fleshless fruits. The seed predation is conspicuously different from the seed dispersal effected by sympatric monogastric primates and is characteristic of colobine frugivory at other forest sites. Most seed-eating occurred during the period of maximum fruit production and fewer small-seeded, animal-dispersed fruits were eaten at other times.*

KEY WORDS: *Presbytis rubicunda*; fruit structure; seed predation; fruiting synchrony.

INTRODUCTION

The colobine monkeys of Asia, despite being diverse in size, structure and taxonomic relationships, are linked by two characteristics of the sub-family Colobinae: a reduced thumb and an enlarged and sacculated forestomach (Napier, 1985). The forestomach contains a suspension of bacteria that breaks down foodstuffs through anaerobic fermentation (Bauchop and Martucci, 1968; Kay *et al.*, 1976). This can allow the digestion of plant cell wall molecules, such as cellulose, and much has been made of the potential for colobine monkeys to exploit foliage as a food source.

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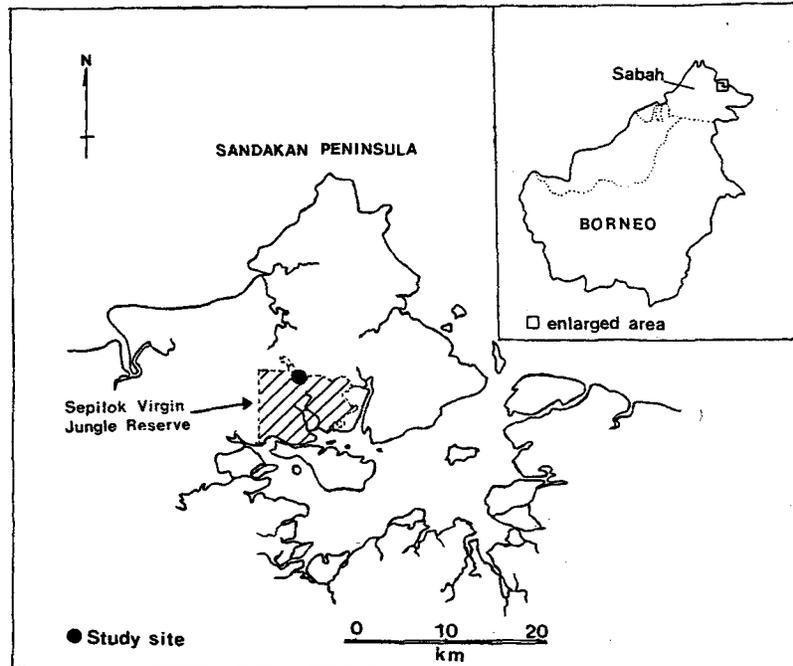


Fig. 1. Map showing location of Sepilok study area in northeast Borneo.

Until recently there was insufficient information on the diets of Asian colobines to judge whether foliage made up a major portion of the diet. Some species obtain over half of their annual diet from leaf parts: *Presbytis senex* (Hladik, 1977), *P. johnii* (Oates *et al.*, 1980), *P. obscura* (Curtin, 1980), and *P. cristata* (Kool, 1986; personal communication). However, there are other Asian colobines which do not depend on foliage to such an extent: *P. entellus* (Hladik, 1977) and both *P. meloalophos* and *P. rubicunda* (Davies *et al.*, 1988). These species eat substantial quantities of fruit parts, which account for just under half of the diet of the latter two species.

Colobine frugivory has been described and discussed for West Africa (McKey, 1978; Harrison, 1986), but it has not been dealt with in detail for Asian colobines. The intention in this paper is to describe the fruit-eating behavior of *P. rubicunda*, relating this to patterns of fruit production by rain forest trees and drawing distinctions between the frugivory of this colobine compared with monogastric primates living in the same forests.

Table I. Ten Most Common Tree Species at Sepilok^a

Flat plot (0.92 ha)			Ridge plot (0.64 ha)		
Species	Stems	B.A.	Species	Stems	B.A.
<i>S. leptoclados</i>	24	140,205	<i>S. macroptera</i>	17	6,429
<i>H. woodii</i>	22	13,518	<i>P. tomentella</i>	13	42,411
<i>P. tomentella</i>	16	31,637	<i>S. xanthophylla</i>	11	3,820
<i>E. zwageri</i>	15	31,500	<i>T. glabrum</i>	9	2,019
<i>D. caesia</i>	13	8,952	<i>G. kingiana</i>	8	947
<i>P. laxiflora</i>	12	7,167	<i>H. woodii</i>	7	2,653
<i>S. xanthophylla</i>	12	2,660	<i>S. smithiana</i>	5	2,316
<i>A. ebenaceum</i>	12	4,186	<i>D. lanceolata</i>	5	1,819
<i>H. borneensis</i>	9	2,130	<i>G. sabahaa</i>	5	1,304
<i>G. sabahna</i>	9	1,556	<i>M. Wallichii</i>	4	2,171
<i>N</i>	413	409,358	<i>N</i>	214	187,265

^aSpecies: *Alangium ebenaceum*, *Dehaasia caesia*, *Dryobalanops lanceolata*, *Eusideroxylon zwageri*, *Ganua kingiana*, *Gluta sabahna*, *Hydnocarpus borneensis*, *Hydnocarpus woodii*, *Melanorrhoea wallichii*, *Parashorea tomentella* || *Pentace laxiflora*, *Shorea leptoclados*, *Shorea macroptera*, *Shorea smithiana*, *Shorea xanthophylla*, *Teijsmanniodendron glabrum*. Stems: number of stems >30 cm in girth at breast height. B.A.: basal area (cm²).

STUDY SITE AND *P. Rubicunda*

This study was carried out in the Sepilok Virgin Jungle Reserve (05°05'N, 118°04'E), between April 1980 and August 1981. The main study area was on the northern edge of the Reserve, bordered by young forest, dominated by *Macaranga* trees, which had grown up in 5 years since the forest was cut and burned (Fig. 1). The 85-ha study area can be conveniently divided into two roughly equal parts: the low-lying western area, which is flooded by streams in the wettest months, and the eastern area, which was dominated by steep-sided sandstone ridges cut by streams that are dry for 6 months of the year.

Two botanical plots covering 1.56 ha were established, one in the flat zone (0.92 ha) and one in the ridge zone (0.64 ha). Enumeration of the 627 trees in the plots, which had girths at breast height >30 cm, indicated that over 60% of the stem basal area was accounted for by big trees from the family Dipterocarpaceae, of which there were 14 species (Waterman *et al.*, 1988). The Lauraceae contributed the next greatest biomass, almost entirely because of the abundance of the large and common Bornean ironwood (*Eusideroxylon zwageri*). Other tree families, even if they had many individuals, contributed relatively little to the tree biomass because they tended to be small (Table I).

A total of 171 species was identified among the 627 trees sampled. This was an underestimate of species richness in the forest because some

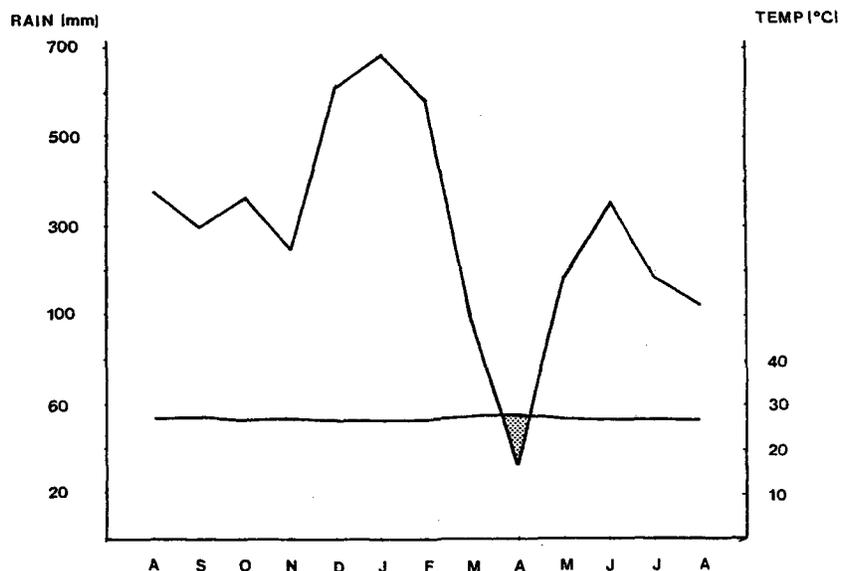


Fig. 2. Klimograph showing rainfall (upper line) and temperature (lower line) during the study period.

trees were identified only to genus and the area sampled was small. Nonetheless, the high species richness of the dipterocarp forest at Sepilok is apparent, conforming with generalizations elsewhere in Southeast Asia (Whitmore, 1975; Ashton, 1982). This abundance of plant species means that arboreal primates at Sepilok had a wide range of plant species from which to select foods.

Annual precipitation (approx. 3000 mm) was unevenly distributed through the year, peaking during the two monsoon seasons. Over 45% of the annual total fell between November and February, followed by a dry month in April. Therefore a short, unpredictable secondary wet season occurred between June and September. The mean daily temperature (around 27°C) was equable throughout the year (Fig. 2).

As a result of the seasonality in rainfall, plant part production varied, and this affected food availability for primates. Once a month, with the exception of January 1981, when the plots were flooded, the 627 sample trees were monitored to record the presence of young leaves, flowers, and fruits (Fig. 3).

There were two periods when young leaf production was low: during the wettest months and during the fruiting season, as has been recorded in West Malaysia (Raemaekers *et al.*, 1980). Flowering was relatively poor,

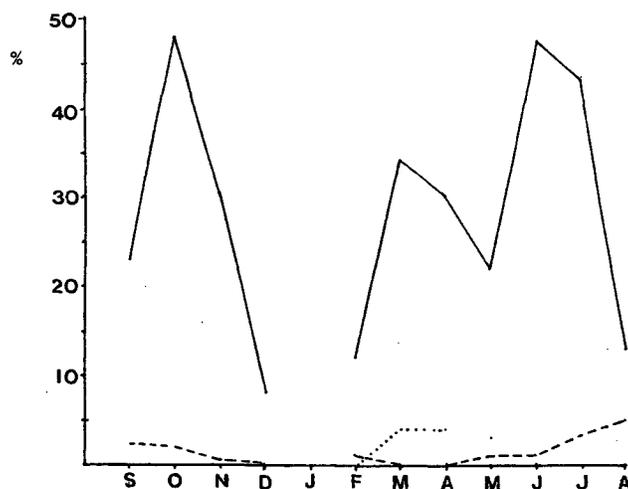


Fig. 3. Monthly variation in the production of young leaves (—), fruits (---), and flowers (···) in a sample of 627 trees (>30-cm girth at breast height), monitored between September 1980 and August 1981. No records for January, when plots were flooded.

peaking at 5% of the trees in March, compared with mass flowering, once every 9–15 years in Sabah (Wood, 1956), when a much greater proportion of the trees produces floral parts (Cockburn, 1975).

Fruit production followed the flowering season, with a maximum of only 5% of the sampled trees bearing fruit during the peak period, compared with 58% of large trees in mass fruiting years (Wood, 1956). Although the phenology sample showed a small peak of fruit production during this study, it was apparent to the observer that many more fruits were available in the forest at this time of year compared with other months. There were approximately 20 fruiting trees/ha, which tallies well with 20–40 ripe tree or liane fruit sources recorded at Kutai (also eastern Borneo), during peaks of fruit production (Leighton and Leighton, 1983).

Furthermore, lianes, which were not included in the Sepilok sample, produced most fruits in the same season, which substantially increased the number of fruit sources available to primates. Thus, fruiting was synchronized, as has been reported in previous years by foresters (*op. cit.*) and primatologists (MacKinnon, 1974) working in Sabah, but not gregarious.

In addition to the synchronized period of maximum fruit production, a scattering of fruits was available in the forest at other times. This applied

particularly to *Anthocephalus chinensis* and *Hydnocarpus borneensis*, as well as the asynchronous *Ficus* species.

In terms of food availability for primates at Sepilok, there was a period when many tree and liane fruits were available followed by a scarcity, in January 1981, when seeds and young leaves were simultaneously uncommon.

Presbytis rubicunda is a member of the *Presbytis* subgenus, which is found in inland forests throughout insular Southeast Asia (Napier, 1985). The species in this subgenus are indistinguishable from each other on the basis of skeletons (Medway, 1970; Napier, 1985), so *P. rubicunda* is endemic to Borneo and the adjacent Karimata Islands (Medway, 1977) but is closely related to several other *Presbytis* species in Southeast Asia.

P. rubicunda is small-bodied and gracile: adult males weigh 6.2 kg, and adult females weight 6 kg (Davis, 1962). The species lives in small unimale groups of 3 to 10 independent animals (Davies, 1987). The Sepilok study group of six independent animals occupied a home range of 70–84 ha. There was about 10% overlap with neighboring groups' home ranges, so population density and biomass were very low.

METHODS

The study group was habituated to an observer for 4 months. Systematic observations of feeding behavior were collected between August 1980 and August 1981. The group was followed from dawn until dusk on 15 consecutive days each month, and scan-sample records (Altmann, 1974) were collected at 10-min intervals from the time the first animal was seen to move in the morning until the last animal settled down to sleep in the evening. During each scan, the age/sex and activity of all animals within view were recorded. A feeding record was scored if the subject was handling food, putting it into its mouth, or chewing. The plant part and species were identified; 52% of feeding records were attributed to a plant species and over 95% to a plant part. The contribution of each item was calculated as a percentage of *all* feeding records, including both identified and unidentified items.

These methods follow precedent set in other colobine studies (Struhsaker, 1975; Oates, 1977), which allows comparison of time spent feeding on different items. One shortcoming with the scan-sample method is that there can be considerable differences in the weight of food ingested compared with time spent feeding (Hladik, 1977). Unfortunately this problem could not be overcome in this study because poor visibility prevented observation of a large sample of feeding rates.

The chemical analyses carried out on food items have been described in detail elsewhere (Waterman *et al.*, 1988; Davies *et al.*, 1988) and follow

precedent set in previous studies of colobine food selection (Gartlan *et al.*, 1980; Oates *et al.*, 1980). Nitrogen was estimated by the normal micro-Kjeldahl method and has been converted to protein by multiplying by 6.25 (Maynard and Loosli, 1969). Acid detergent fiber, which represents the least digestible plant cell wall polysaccharides, was measured using the method of van Soest (1963), and condensed tannins were measured using a modified butanol-HCl method (Gartlan *et al.*, 1980). *In vitro* digestibility was determined using pepsin and cellulase enzymes (after Choo *et al.*, 1981).

OVERALL DIET

The annual diet of *P. rubicunda* at Sepilok (Davies *et al.*, 1988) is characterized by a high intake of young leaves (36%), one-third of which come from lianes. Seeds were the second most commonly eaten item (30%), again with about one-third coming from lianes. The remaining 34% of the annual diet comprised flowers (11%), with trees and lianes contributing roughly equally, and whole fruits (pulp with seeds and, very rarely, pericarp), few of which came from lianes.

Minor items in the diet included mature leaf parts (1.1%), with petioles commonly being eaten and the lamina dropped (e.g., *Omphalia bracteata*). Mature leaves were superabundant throughout the year in this evergreen forest, but they are very seldom eaten, probably owing to their low digestibility (Waterman *et al.*, 1988). Pith, often from climbing bamboos, was eaten in very small quantities in most months. Soil from termite mounds was eaten on 13 occasions, for one or more reasons, including to supplement mineral intake, to buffer forestomach pH, and to adsorb toxins (Davies and Baillie, 1988). Termites were consumed six times, and the monkeys drank water 13 times in the driest months.

The yearly average figures obscure marked monthly variation (Table II), which correspond with seasonal variations in food supply. Mature leaves were eaten most in January (7%), when few young leaves or fruits were present in the forest, but they usually contributed less than 2%. The intake of young leaves reached a peak in June (71%), when there was a flush of succulent young leaves on many forest trees. But intake fell within 2 months to only 7%, at a time when seeds dominated the diet. Maximum seed-eating (87% in August) coincided with the period of maximum fruiting. However, whole fruit eating occurred later in the year, when fewer trees or lianes were producing fruits.

In general, seeds dominated the diet when most abundant in the forest, almost to the exclusion of everything else. Young leaves are eaten most when seeds did not predominate in the diet, but the high young leaf intake

Table II. Annual Diet (August 1980–July 1981)

	Percentage		
	average annual	maximum monthly	minimum monthly
Mature leaf parts	1.1	7	0
Young leaf parts	36.5	71	7
Seeds (excl. flesh and rind)	30.1	87	1
Fruit parts (incl. seed)	19.2	40	2
Floral parts	11.1	30	1

in June, when seeds were available in moderate quantities, indicates that succulent, very young leaves were selected more often than seeds. This is easy to appreciate when considering that some young leaves can have up to 30% protein (dry weight) and be 70% digestible (Waterman *et al.*, 1988).

The leaf monkeys were highly selective in their diet, and their foods were generally rare in the forest. Just over half the annual diet was contributed by 103 plant species. However, the most common trees in the forest, accounting for 51% of the tree biomass, contributed only 4% of the diet (Davies *et al.*, 1988).

FRUIT-EATING

The study animals ate seeds from 48 species of trees and liane and whole fruits from 24 plant species. But many fruit parts were exploited for only brief periods, contributing less than 0.1% of the annual diet (Tables III and AI). In an effort to extrapolate characteristic features of the fruits from this range of plant species, five parameters were considered: color, protection of fruit pulp (i.e., pericarp thickness), type of pulp, protection of seed, and whether the seed was destroyed or dispersed when eaten (Table IV). The categories used for each parameter follow those used in a study of mammalian frugivory in Gabon (Gautier-Hion *et al.*, 1985), except that the features recorded in the present study refer to the time when the fruit part was eaten (i.e., often unripe).

Fruit Structure

The red leaf monkeys seldom ate brightly colored fruits; only 10% were red, yellow, or orange, and one was buff-white. The bulk of the sample

Table III. Top Ten Fruit/Seed Items in the Diet^a

	T/L	Part	Diet	
			Annual	Top month
<i>A. chinensis</i> (RUBI) ^b	MT	Fruit	4.7	26.3
<i>P. nitium</i> (SAPIN)	UT	Seed	3.0	20.7
<i>C. borneensis</i> (RHIZ)	MT	Fruit	2.7	15.3
<i>C. beccariana</i> (MEL)	UT	Seed	2.5	12.2
<i>I. Palembangica</i> (LEG)	MT	Seed	1.8	12.4
<i>Z. horsfieldiana</i> (RHAM)	L	Seed	1.6	9.8
<i>D. parviflora</i> (LEG)	L	Seed	1.4	8.6
<i>P. excelsa</i> (LEG)	L	Seed	1.2	17.7
<i>L. grandis</i> (LAUR)	MT	Fruit	1.2	3.8
<i>X. intermedium</i> (SAPIN)	MT	Seed	1.2	13.9

^aSpecies: *Anthocephalus chinensis*, *Paranephelium nitidum*, *Carallia Borneensis*, *Chisocheton beccariana*, *Intsia Palembangica*, *Zizyphus horsfieldiana*, *Dalbergia parviflora*, *Phanera excelsa*, *Litsea grandis*, and *Xerospermum intermedium*. UT, understory tree; MT, midcanopy tree; L, liane.

^bFamily given in parentheses. For abbreviations, see Table AI, footnote a.

Table IV. Anatomical Features of All Fruits Exploited (N Refers to Each Different Species)^a

Color						
White	Yellow	Red	Orange	Violet	Brown	Green
1	3	—	2	—	22	21
Flesh						
None	Juicy/soft	Juicy/fibrous		dry/soft	dry/fibrous	
29	5	12		4	2	
Protection						
Skin			Seed			
Thin	Thick	Minimal	Tough testa	Stone		
14	37	24	24	2		
Seed size		Seeds destroyed/dispersed				
Small (<1 cm)	Large (>1 cm)	Destroyed			?Dispersed	
10	44	54			2	

^aColor, color of pericarp when consumed; Protection — thin skin, cherry-like; thick skin, orange-like or thicker; tough testa, apple-pip thickness; ?Dispersed, possible passage of seeds through alimentary tract, but unconfirmed.

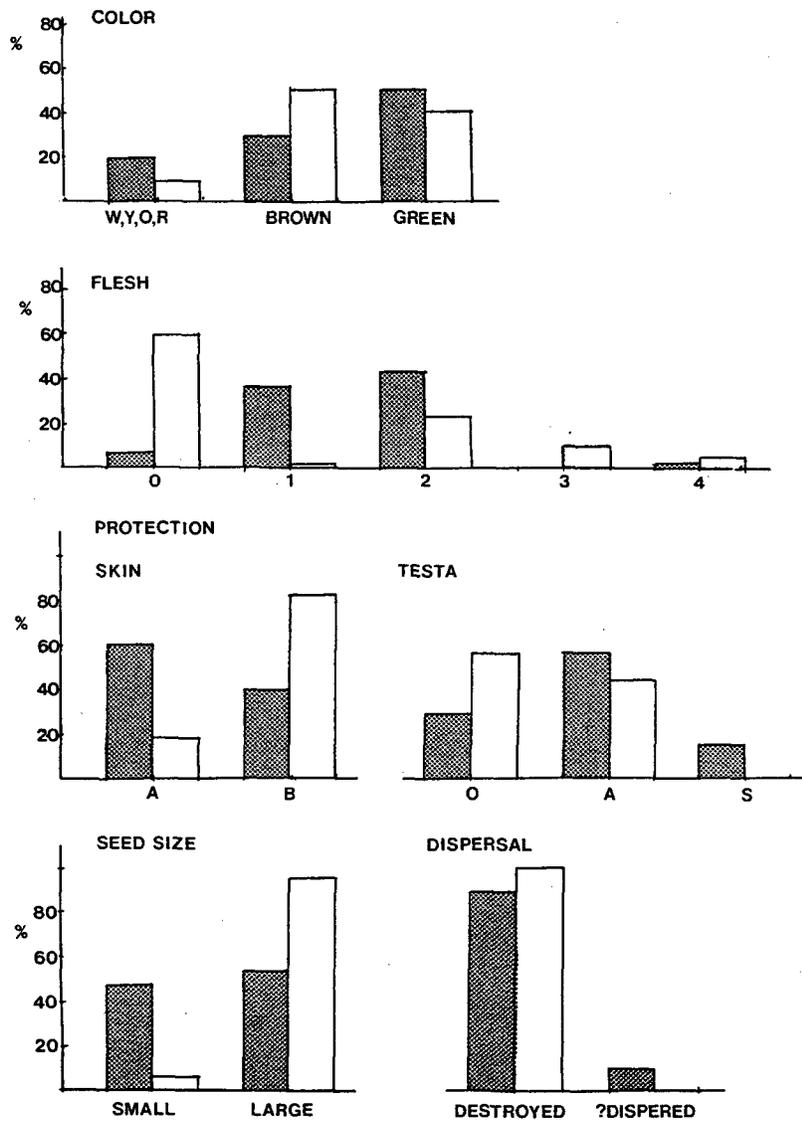


Fig. 4. Histograms showing fruit characters for whole fruit (shaded; $n = 14-19$) and seed (unshaded; $n = 38-42$) consumption by *P. rubicunda* (categories as in Table IV).

(86%) had dull green or brown pericarps, some of which were very dark. The thickness of the pericarp was variable and ranged from a cherry-like skin (e.g., *Carallia borneensis*) to a tough, leathery pod (*Dalbergia parviflora*). But the majority of fruits (72%) had thick pericarps, like orange peel in thickness and texture. In just over half of the fruits the pericarp enclosed no flesh, only seeds; and, the remaining half of the sample had fibrous flesh, either dry or juicy. Only two species had a seed enclosed in a stone: *Eusideroxylon zwageri* and *Chionanthus elaeocarpus*. These were exploited only in their earliest stages of development, before the stone was fully lignified. The remaining seeds which offered minimal protection against the monkeys.

There were conspicuous differences in the anatomy of species from which only seeds are ingested and those that provided both flesh and seeds (Fig. 4). Brightly colored fruits (white, yellow, orange, or red) tended to be exploited more when whole fruits were eaten and *P. rubicunda* selected seeds from fleshless fruits which had large seeds.

To account for different species' contribution to the diet, fruits were separated into two categories: large-seeded (>1-cm diameter at the widest point) and small-seeded (<1 cm). Fruits were further subdivided according to whether or not they had fleshy pulp (Table V).

The largest category, accounting for 59% of feeding records, comprised fruits with large seeds and no pulpy flesh. For convenience, these can be subdivided into legumes and other fruits. The legumes (four species of tree and eight species of liane) ranged in size and structure from the single or two-seeded pods of *Milletia* sp. 1, with each seed weighing 50 g or more, to the strap-like pods of *Intsia palembanica*, with 20-g seeds, or the single-seeded winged-fruits of *Spatholobus latistipulus* (seeds weighing <10 g). All legumes were dull green or dark brown when eaten, had no flesh, and had dry, nonfibrous seeds. The cotyledons and germ cells were eaten; occasionally the testa was seen to be discarded, but usually it was not clear whether or not the testa was eaten. The nonlegume, fleshless fruits (from 13 trees and 2 lianas) are exemplified by *Paranephelium nitidum* and *Chisocheton beccariana*. Both have large spherical seeds (>15 g), which are enclosed in a leathery pericarp.

The large-seeded fruits with juicy, fibrous flesh (10 trees, 2 lianas) were also largely exploited for their seeds. The juicy fibrous arils of *Xerospermum intermedium* and *Wallucharia wallichii*, as well as the waxy, lipid-rich arils of *Knema laterica*, were chiseled off the seeds and dropped to the forest floor, while the seed was chewed and swallowed. Sometimes flesh was ingested. In the case of *Xerospermum intermedium*, about half the feeding records included flesh with seeds, but the seed was still the main food ingested since it had the greater biomass.

Table V. Contribution of Different Types of Fruit to the Total Fruit Diet

	% annual fruit diet
Large seeds (>1 cm at widest point):	
(a) Lacking pulpy flesh	
Leguminosae	28
Nonlegumes (<i>Chisocheton beccariana</i>)	31
(b) Fibrous or waxy arils (<i>Xerosperum intermedium</i>)	10
(c) Fibrous flesh (<i>Litsea</i> sp)	8
Small seeds (<1 cm at widest point)	
(a) Lacking pulpy flesh (<i>Pentace laxiflora</i>)	1
(b) Fibrous/dry (<i>Anthocephalus chinensis</i>)	13
(c) Fibrous/juicy (<i>Carallia borneensis</i>)	8
(d) Figs	1

Table VI. Chemistry of Seeds, Whole Fruits, and Arils (After Davies *et al.*, 1988)

	Percentage dry weight			
	Condensed tannin	Acid detergent fiber	C/P ^a digestibility	Protein
Ripe seeds				
Eaten (<i>n</i> = 20)	4.4	15.8	62.8	9.6
Uneaten (<i>n</i> = 6)	3.8	25.0	71.7	8.4
Ripe fruits				
Eaten (<i>n</i> = 8)	8.4	39.8	52	8.2
Uneaten (<i>n</i> = 3)	21.9	29.6	52.9	8.0
Arils				
Uneaten (<i>n</i> = 7)	4.1	30.2	64.3	6.2

^aCellulase/pepsin.

Other fleshy, large seeded fruits (e.g., *Litsea* spp.) were eaten when unripe and the whole fruit was chewed. Occasionally the pericarp and mesocarp were discarded, but more often both were eaten with the developing seed.

The small-seeded fruit-eating (23% fruit-eating records) was completely dominated by just two species: *Anthocephalus chinensis* (13%) and *Carallia borneensis* (7%). *A. chinensis* is a spherical fruit (approx. 5-cm diameter) with narrow corolla tubes, the texture of dry wall-flower petals, densely packed on a central medulla. The seeds, of which there are over 100 per fruit, are tiny and lie at the bottom of each corolla tube. The monkeys ate the dense medulla, with the dry corolla tubes and tiny seeds contributing relatively little. *C. borneensis* is a simple berry, brightly colored with

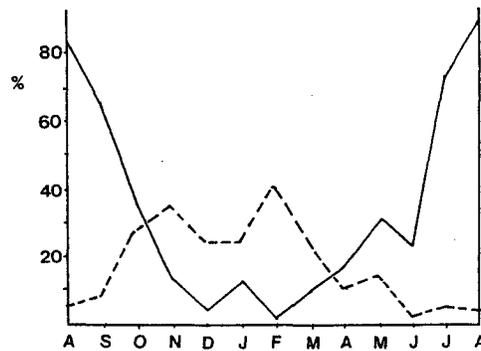


Fig. 5. Percentage of monthly diet contributed by seeds (solid line) and fruits (dashed line).

thin skin surrounding a juicy flesh with a pip (grape-seed sized) in the middle. The whole fruit was ingested.

Fruit Chemistry

In addition to the anatomical distinctions described above, there are obvious chemical differences between seeds and whole fruits (Table VI). Seeds had very low levels of condensed tannins and low acid detergent fiber levels, with correspondingly high digestibility. Protein levels in both seeds and whole fruits were low, especially compared with young leaves, which had twice as much protein on average (Waterman *et al.*, 1988). But the levels of tannins and acid detergent fiber in whole fruits were considerably higher than in seeds, making whole fruit much less digestible. A small sample of uneaten arils confirmed that this type of fruit flesh has high levels of fiber, low levels of protein, and moderate digestibility.

Seeds are most likely exploited for the readily digestible storage carbohydrates they contain, but the nutritional contribution of whole fruits is more difficult to assess since they have both high fiber and low protein levels. Arillate flesh is apparently low in nutritional value for leaf monkeys. Presumably low-quality items are eaten because they are the best available in certain months.

In addition to common compounds such as protein, tannins, and fiber, there is circumstantial evidence to indicate that toxins influence food selection. In particular, bacteriocidal resins in fruit pericarps (e.g., *Gonystilus keithii* and *Dipterocarpus* spp.) may have an adverse affect on colobine forestomach microbes. Seeds of *Ervatamia malacensis*, which contain high

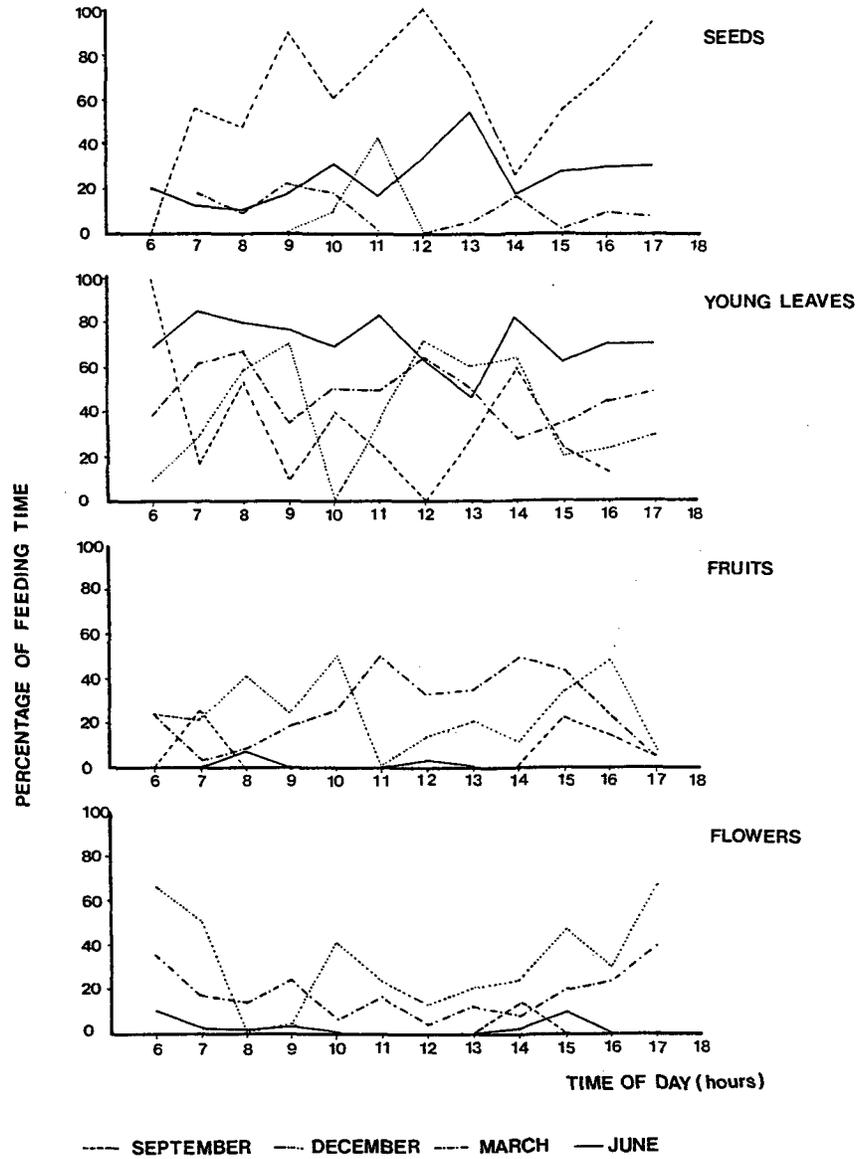


Fig. 6. Hourly diet percentages for the four main food items in four different months.

concentrations of alkaloids (Hegnauer, 1964), were also ignored by the study animals, indicating that alkaloids may have a negative influence on food selection. However, there is evidence from other sites that colobine monkey forestomach microbes have some capacity to tolerate or break-down alkaloids [e.g., *P. entellus* (Hladik, 1977), *C. satanas* (McKey, 1978)].

Temporal Variation

As noted above, seed-eating reached a peak in the middle of the period of maximum fruit production (Fig. 5). But the whole fruit eating occurred outside this period, between December and February, and there is a negative correlation between fruit availability and consumption of whole fruits ($r = -0.69$, $n = 11$, $P < 0.1$). Overall, therefore, small-seeded fleshy fruits were exploited in the nonfruiting season, commonly with foliage, while dry, large-seeded fruits were eaten in the main fruiting season.

Fruit eating has been reported as more common in the morning than the afternoon for some monogastric primates, *Pan troglodytes* (Wrangham, 1977) and *Hylobates syndactylus* (Chivers, 1974), leading to suggestions that high-energy fruits are eaten early in the day to offset energy deficits built up overnight (Clutton-Brock, 1977). To test this for *P. rubicunda*, the diet in every hour was calculated for September, December, March, and June (Fig. 6). Then, using paired-sample *t* tests, the diet between 0600 and 0900 hr was compared with the diet between 1200 and 1500 hr. No significant differences were discovered.

A similar lack of preference for fruits early in the day has been described for other colobines: *C. guereza* (Oates, 1977) and *P. melalophos* (Bennett, 1983). Fermentation digestion may account for this distinction between primates with simple stomachs and those with sacculated stomachs.

Fermentation of foodstuffs can produce energy at a constant rate for up to 10 hr [*P. cristata* (Bauchop and Martucci, 1968)], so energy deficits are less likely to build up overnight in colobine monkeys, and high-energy foods need not be sought first thing in the morning. Furthermore, succulent young leaves are as good a substrate for energy production through fermentation as many fruit parts (data of Waterman *et al.*, 1988; Davies *et al.*, 1988).

Seed Predation

Whether large-seeded or small-seeded fruits were exploited, the seeds were invariably ingested. Large seeds were bitten, chewed, swallowed, and digested, leaving no chance for survival. Some seeds were spilled beneath

feeding sites when large pods were opened, but this was poor dispersal compared with the explosive dehiscence or wind dispersal experienced by seeds from undamaged fruits. Only in the case of *A. chinensis* and *C. borneensis*, both of which have tiny seeds, was there a small possibility that seeds could pass undamaged through the gut.

Therefore, *P. rubicunda* can be considered predominantly a seed predator (*sensu* Janzen, 1969). Seeds are unlikely to survive chewing followed by fermentation digestion. This distinguishes *P. rubicunda* from the monogastric forest primates, which disperse seeds that pass undamaged through the gut or fall from cheek-pouches that are often emptied some distance from a food tree (Gautier-Hion *et al.*, 1985).

DISCUSSION

Frugivory Among Asian Colobines

P. rubicunda, both at Sepilok and in southern Borneo (Supriatna *et al.*, 1986), is not an obligate folivore whose diet is predetermined by the possession of a forestomach fermentation digestive system. On the contrary, its diet is an example of the wide range of foods and foraging strategies exhibited by Asian colobines, though some *Presbytis* subgenera have fewer adaptations to folivory than others.

Comparative studies of the dentition and alimentary tract anatomy indicate that *P. rubicunda* is poorly adapted for a folivorous diet: (a) Kay and Hylander (1978) pointed out that the shearing crests of the premolars are not highly developed for cutting through foliage, unlike those of folivorous colobines; (b) studies of dental microwear patterns further support the impression that *P. rubicunda* does not eat much fibrous material, since there are very few striations compared with more folivorous species (Teaford, 1982, 1983, personal communication); and (c) Chivers and Hladik (1980) showed that *P. rubicunda* has only 2.6% of its body weight comprising forestomach, a relatively low volume for fermentation digestion of folivorous material.

This lack of specialization for a folivory also applies to other species in the subgenus *Presbytis* (Medway, 1970; Chivers and Hladik, 1980; Napier, 1985), so it is not surprising to find that they, too, include a large portion of fruit parts in the diet. For example, *P. melalophos* has 49% fruit in its diet (Bennett, 1983); and *P. hosei* has been recorded eating substantial quantities of seeds in Kutai, east Borneo, although there are no figures for their annual diet (Leighton and Leighton, 1983).

Species in the subgenus *Trachypithecus* have greater molar shearing quotients for folivory (Kay and Hylander, 1978) and enlarged fermentation chambers in the alimentary tract (Chivers and Hladik, 1980). Not surprisingly, available field data show that species in this subgenus consume a greater quantity of foliage: *P. obscura* have 58% foliage in the annual diet (Curtin, 1980), and *P. cristata* in Thailand (Fooden, 1971) and Java (Kool, 1986, personal communication) have a high foliage intake. The subgenus *Kasi* has a close taxonomic affinity with the subgenus *Trachypithecus* (Napier, 1985), and both *P. senex* (Hladik, 1977) and *P. johnii* (Oates *et al.*, 1980) are highly folivorous — 56 and 60%, respectively.

The monospecific subgenus *Semnopithecus* comprises the Hanuman langurs (*P. entellus*) of South Asia, which are unlike other colobines in their terrestrial habits and aversion to closed-canopy evergreen forests. The diet of this species is very varied, but some populations include large portions of fruit parts: *P. e. thersites* in semievergreen forests of Polonnaruwa (Hladik, 1977) and *P. e. ajax* in the Himalayas, which relies heavily on conifer fruits at certain times of the year (Sugiyama, 1976).

In addition to anatomy and physiology, environmental factors such as plant chemistry will also influence colobine food selection (McKey, 1978; Waterman *et al.*, 1988).

Seed-Eating: A Colobine Specialty?

Seed predation by *P. rubicunda* is better appreciated when compared with sympatric macaque, gibbon, and orangutan frugivory in Borneo (Leighton and Leighton, 1983). These monogastric primates prefer fruit characterized by “inedible, but indehiscent rind or husk, yellow to orange or brown, with sugar-rich flesh and enclosed seeds [that are] swallowed.” They also eat the “green flesh of typical ‘bat-fruits,’ “sugar-rich bird berries,” and many figs, the latter contributing only 1% of the *P. rubicunda* diet.

This dichotomy in a primate community, between seed-predatory colobines and seed-dispersing monogastric primates, is widespread in Asian and African forests alike: Kutai, east Borneo (Rodman, 1978; Leighton and Leighton, 1983); Kuala Lompat, West Malaysia (Chivers, 1974, Gittins and Raemaekers, 1980; Bennett, 1983); Polonnaruwa, Sri Lanka (Hladik and Hladik, 1969; Dittus, 1977); Tana River, Kenya (Marsh, 1978; Homewood, 1978); and Kibale, Uganda (Oates, 1977; Waser, 1977; Struhsaker, 1978).

There is every likelihood that the different digestive systems of these two subfamilies, at least in part, account for different strategies of frugivory

and the following factors are likely to play an important role in fruit selection."

- (a) The colobine forestomach fluid is finely buffered and any decrease in pH, either through rapid production of volatile fatty acids during fermentation or ingestion of acidic fruit pulp, can cause forestomach disorders that may be lethal (Goltenboth, 1976);
- (b) The forestomach microbes can tolerate, and probably break down, some plant chemical defenses (e.g., alkaloids), but equally they will be susceptible to antibacterial compounds;
- (c) Fleshy fruit pulp eaten by simple-stomached primates tends to be fibrous and relatively indigestible; but the animals may get sufficient nutrients by passing the indigestible fiber rapidly through the gut, gleaning readily absorbed sugars [e.g., the food passage rate for captive spider monkeys is 4 hr (Milton, 1980)]. The colobine fermentation digestion is unlikely to allow such rapid food passage, so they would fill up with fiber for relatively few nutrients.

It is inappropriate to overgeneralize about colobine seed-eating, since succulent whole fruits are eaten by colobine monkeys [e.g., *P. entellus* at Polonnaruwa (Hladik, 1977), and even the highly semivorous *P. rubicunda* ate fleshy fruits at certain times of year. It is also worth noting that, unlike forest cercopithecines (Gauthier-Hion *et al.*, 1985), savanna-dwelling *Cercopithecus aethiops* specialize in seed-eating in certain seasons (Wrangham and Waterman, 1981).

Patterns of Fruit Production

In response to seed predation there are a number of evolutionary defense strategies open to plants, ranging from mechanical and chemical protection to specialized systems of flowering and fruiting (Janzen, 1969). Tree species that do not rely on frugivores to disperse their seeds can reduce seed losses by having dull-colored and well-protected fruits, lacking flesh and produced in a single, synchronized pulse over a short period to satiate seed predators. Conversely, plants with animal-dispersed seeds can fruit asynchronously to minimize competition between trees for seed dispersers (Snow, 1965; Smythe, 1970; McKey, 1975; Smith, 1975; Payne, 1980).

Inevitably, fruits with large seeds that rely on animal seed dispersal are prone to seed predation by one set of frugivores (e.g., colobines) but need to attract another set for seed dispersal (e.g., cercopithecines). In these circumstances opposing fruiting patterns will be favored. Further complications arise if effective chemical or mechanical protection evolves, which allows large-seeded fruit production throughout the year since strategies other than synchronized fruiting are employed to reduce seed losses.

With the myriad microbial, insect, avian, and mammalian seed predators of the rain forest all influencing fruit production patterns, it is unlikely that fruiting patterns of *P. rubicunda* food plants are reacting to feeding pressure from this species alone. However, seeds were eaten in the main fruiting season and whole fruits at other times, indicating that plants may be responding to pressures exerted by seed predators/dispersers, which in turn can influence food selection by *P. rubicunda*.

At Sepilok, fruits which lacked flesh were all eaten in the same 4 months (July–October), with four exceptions. Three lianes fruited early or late in the season and the understory tree *Chisocheiton micrantha* fruited in February but was eaten only once, probably because stiff hairs made it difficult to get at the seed. The production of unprotected fleshless fruit in a synchronized fruiting season, especially those with large seeds, is consistent with the predator satiation hypothesis.

The animal-dispersed fruits, which ranged from the very large *Eusideroxylon zwageri* seeds cached by the porcupine *Trichys lepidurus* (J. B. Payne, personal communication) to *Knema* spp./*Horsfieldia* spp./*Litsea* spp. dispersed by large frugivorous birds, such as hornbills (Payne, 1981; Leighton and Leighton, 1983), and *Anthocephalus chinensis*/*Carallia bormenis*, dispersed by bats, small birds, and primates (personal observation), were all eaten outside the main fruiting season. Thus, *P. rubicunda* feeds on fruits produced asynchronously by zoochoric plants but destroys the seeds instead of dispersing them.

ACKNOWLEDGMENTS

This research was sponsored by World Wildlife Fund Malaysia and was carried out with the permission of Mr. P. M. Andau (Wildlife Division, Sabah Forestry Department). The Sabah Forestry Department (Herbarium Section) collected plant materials, and chemical analyses were carried out by Jane Ross in the laboratories of Dr. Peter Waterman (Strathclyde, U.K.). Constructive comments were made by Dr. David Chivers and Dr. Tom Struhsaker when reviewing the original manuscript. I gratefully acknowledge all these contributions.

APPENDIX

Table AI.

	Family ^a	Part ^b	Diet ^c	T/L ^d	Color ^e	Skin ^f	Testa ^g	Flesh ^h	Seed size ⁱ	Dispersal ^j	Months ^k
<i>Antiocephalus chinensis</i>	RUB	frt	4.7	MT	Y/W	A	A	4	D	?D	F, JN, AG, O, N, D
<i>Paranephetium nitidum</i>	SAPI	sd	3.0	UT	W	B	O	0	L	P	AG, S, O
<i>Carallia borneensis</i>	RHIZ	frt	2.7	MT	O/R	A	A	1	S	?D	F, MR
<i>Chisocheon beccariana</i>	MEL	sd	2.5	UT	G(R)	B	O	0	L	P	AG, S, O
<i>Intsia palembanica</i>	LEG	sd	1.8	MT	B	B	A	0	L	P	JL, S, O
<i>Zizyphus horsfieldiana</i>	RHAM	sd	1.6	L	Y	B	O	0	L	P	MR, AP
<i>Dalbergia parviflora</i>	LEG	sd	1.4	L	B	B	A	0	L	P	O, N
<i>Plianera excelsa</i>	LEG	sd	1.2	L	B	B	O	0	L	P	AP, MY, JL, AG
<i>Litsea grandis</i>	LAUR	sd	1.2	MT	G	A	O	2	L	P	MR, AP, D
<i>Xerospermum intermedium</i>	SAPI	sd	1.2	MT	Y	B	A	1	L	P	MY
<i>Spatholobus</i> sp. 3	LEG	sd	1	L	G	B	O	0	L	P	AG
<i>Xerospermum intermedium</i>	SAPI	frt	0.9	MT	-	-	-	-	-	-	-
<i>Dalbergia</i> sp. 1	LEG	sd	0.7	L	B	B	A	0	L	P	O, N
<i>Litsea grandis</i>	LAUR	frt	0.7	MT	-	-	-	-	-	-	MR, AP, O, D
<i>Spatho' latistipulus</i>	LEG	sd	0.7	L	G	B	O	0	L	P	AG
<i>Chionanthus elaeocarpus</i>	ELEO	frt	0.6	MT	B	B	S	-	L	P	JA, F, MR
<i>Nesocortechinia</i> sp. 1	EUPH	sd	0.4	UT	G	A	O	3	L	P	AG
<i>Dioscorea</i> sp.	DIOS	frt	0.4	L	G	A	A	-	S	P	AP
<i>Cleistanthus paxii</i>	EUPH	sd	0.4	UT	G	B	A	0	S	P	JL, AG
<i>Neocort' forbesii</i>	EUPH	sd	0.4	UT	G	A	O	3	L	P	JN, JL
<i>Litsea ochracea</i>	LAUR	frt	0.4	MT	G/Y	A	O	2	L	P	JA, F, MR

<i>Spatholobus</i> sp. 4	LEG	sd	0.4	L	G	B	O	0	L	P	JL
<i>Horsfieldia fragillima</i>	MYRS	sd	0.35	MT	B	B	A	3	L	P	MR, JN
<i>Nilletia</i> sp. 1	LEG	sd	0.3	L	B	B	O	0	L	P	AG, S
<i>Dehaasia caesia</i>	LAUR	sd	0.3	UT	B	-	-	2	L	P	AP, JL
	PIP	frt	0.3	L	G	A	O	2	S	P	AP
<i>Ficus</i> sp.	MOR	frt	0.3	MT	G	A	O	2	S	P	MR
<i>Alangium ebenaceum</i>	ALAN	sd	0.2	T	-	B	-	-	L	P	JN
<i>Wallucharia wallichii</i>	MEL	sd	0.2	T	-	B	A	2	L	P	JL
<i>Nephetium mutabile</i>	SAPI	sd	0.2	UT	G	-	A	A	L	P	JL, AG
<i>Wallucharia wallichii</i>	MEL	frt	0.2	T	-	B	A	-	L	P	JL
<i>Spatholobus</i> sp. 2	LEG	sd	0.2	L	G	-	O	0	L	P	AG, S
<i>Zizyphus</i> sp. 1	RHAM	sd	0.15	L	B	B	A	0	L	P	JN
<i>Ardenia cordifolia</i>	PASS	frt	0.1	UT	-	-	-	-	-	-	F
<i>Pithecolobium ellipticum</i>	LEG	sd	0.1	MT	B	B	A	0	L	P	JN
<i>Drypetes</i> spp.	EUPH	sd	0.1	UT	-	-	-	-	-	-	JN
<i>Knema laterica</i>	MYRS	sd	0.1	UT	B	B	A	2	L	P	JN
<i>Knema emeritii</i>	MYRS	sd	0.1	UT	B	B	A	2	L	P	MY
<i>Chisocheton micrantha</i>	MEL	sd	+	UT	B	B	O	0	L	P	F
<i>Carallia brachitata</i>	RHIZ	frt	+	UT	-	A	A	1	S	P	JA
<i>Knema ?laterica</i>	MYRS	sd	+	UT	B	B	A	2	L	P	JA
<i>Fordia</i> sp.	LEG	sd	+	UT	G	B	A	0	L	P	JN
<i>Shorea xanthiophylla</i>	DIPT	sd	+	UT	B	B	O	0	L	P	AG, S
<i>Shorea leptoclados</i>	DIPT	sd	+	E	B	B	O	0	L	P	AG

<i>Neoscotechinia sumatrana</i>	EUPH	sd	+	-	-	-	-	-	-	JL
<i>Macranga giganteifolia</i>	EUPH	sd	+	UT	G	B	O	0	L	P AG
<i>Aporosa nitida</i>	EUPH	sd	+	UT	O	A	A	2	S	P JL
<i>Pithecolobium</i> sp.	LEG	sd	+	T	G	B	-	0	L	P JN
<i>Diosyloft</i> sp.	MEL	frt	+	T	-	-	-	0	L	P MY

^aALAN, Alangaceae; APO, Apocynaceae; DIOS, Dioscoreaceae; DIPT, Dipteroocarpaceae; EUPH, Euphorbiaceae; ELEG, Elaeocarpaceae; FAG, Fagaceae; FLAC, Flacoutiaceae; LAUR, Lauraceae; LECY, Lecythidaceae; LEG, Leguminosae; MAGN, Magnoliaceae; MEL, Meliaceae; MOR, Moraceae; MYRS, Myristicaceae; PASS, Passifloraceae; PIP, Piperaceae; RHAM, Rhamnaceae; RHIZ, Rhizophoraceae; RUB, Rubiaceae; SAPI, Sapindaceae; VERB, Verbenaceae.

^bFruit (frt) or seed (sd).

^cAnnual diet (%).

^dPlant form: E, emergent tree; MT, middle-story tree; UT, understory tree; T, tree; L, Liane.

^eWhite (W), yellow (Y), orange (O), red (R), brown (B), or green (G).

^fA, thin (as a cherry); B, thick (as an orange and/or tougher).

^gO, minimal; A, tough testa (e.g., apple pip); S, stone.

^h0, no flesh; 1, juicy/soft; 2, juicy/fibrous; 3, dry/soft; 4, dry/fibrous.

ⁱS, small (<1-cm diameter); L, large (>1-cm diameter at widest point).

^jP destroyed; ?D, possible, by unlikely dispersal.

^kJA January; F, February; MR, March; AP, April; MY, May; JN, June; JL, July; AG, August; S, September; O, October; N, November; D, December.

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