Feeding Ecology of the Proboscis Monkey (*Nasalis larvatus*)

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Proboscis monkey (Nasalis larvatus) *feeding behavior and ecology were studied at the Natai Lengkuas Station, Tanjung Puting National Park, Kalimantan Tengah, Indonesia. Data on feeding behavior were collected using scan sampling during group follows. Three vegetational plots containing 1,732 trees were established and monitored monthly for changes in fruit, flower, and young leaf production. Basal area and canopy cover were calculated and used in estimating food abundance. Proboscis monkeys were found to be folivore/frugivores, specializing in seed consumption. At least 55 different plant species were used as food sources, with a marked preference for* Eugenia sp. 3/4, Ganua motleyana *and* Lophopetalum javanicum. *These tree species were among the most frequent and most dominant. However, proboscis monkeys were selective feeders; use of tree species as food sources was not based simply on relative density. During times of low food abundance and/or availability proboscis monkeys switched dietary strategies and increased dietary diversity. The average total home range was estimated to be 130.3 ha, with an average group density of 5.2 groups per km². The average biomass per km² was estimated to be 499.5 kg. Given their high biomass and predilection for consuming seeds of dominant species, proboscis monkeys may help to maintain and increase vegetational diversity.*

INTRODUCTION

The general trend in colobine diets is towards folivory (Struhsaker and Leland, 1987). Their specialized digestive physiology and anatomy (sacculated stomachs with anaerobic, cellulytic bacteria in the forechambers)

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(Bauchop, 1978; Bauchop and Martucci, 1968) is assumed to allow them to break down anti-feedants (digestion inhibitors and/or secondary toxins) commonly found in the parts of some plant species (Bennett, 1983; Hladik, 1977; Waterman, 1984). This antipredator strategy is presumably costly to the plants in terms of energy consumption and anti-feedants are usually restricted to specific plant parts or specific developmental stages of the parts. In tropical rain forests, young leaves often have the highest concentrations of anti-feedants (Choo *et al.,* 1981; Milton, 1979; Oates *et al.,* 1980—but see Hladik, 1978 for an opposing view). Colobines are thus able to use potential food sources unavailable to sympatric species. However, this unique ability may also place a constraint upon their food choices. The high sugar content of ripe, pulpy fruits (Waterman, 1984) may induce increased fermentation and bloat (Collins and Roberts, 1978), which may account for the preference for unripe fruits reported by Struhsaker and Leland (1987). Similarly, the higher concentrations of fiber (digestion inhibitor) (Choo *et al.,* 1981; Milton, 1979) and lower protein content usually found in mature leaves may account for their preference for young leaves (Waterman, 1984).

The proboscis monkey (*Nasalis larvatus*), a member of the subfamily Colobinae, is a riverine dwelling, sexually dimorphic species endemic to the island of Borneo in Southeast Asia. The principal social units are one-male groups, which are further organized into bands with fission-fusion of stable groups within bands. The one-male groups appear to be female-bonded and are non-territorial (Yeager, 1986, 1989, 1990, in press). Minimal information has been available concerning the feeding behavior and ecology of this threatened species. Prior reports indicated a high degree of folivory and low dietary diversity (Kawabe and Mano, 1972; Kern, 1964; Macdonald, 1982). Kern (1964) suggested that mangrove trees (i.e. *Rhizophora* spp., *Brugiera* spp.) were a "key feature" of their diet. In contrast to these reports, Bennett and Sebastian (1988) and Yeager (1984) found that fruit played an important role in the proboscis monkey's diet.

The data presented here are based on a field study undertaken at the Natai Lengkuas station at the Tanjung Puting National Park in Kalimantan Tengah, Indonesia, from January through December 1985. An additional three months were spent before then to establish the study site and to habituate animals.

METHODS

Study Site

The primary study area is located along a 2 km stretch of the Sekonyer Kiri river in a fresh water peat swamp that had been lightly hand logged previ-
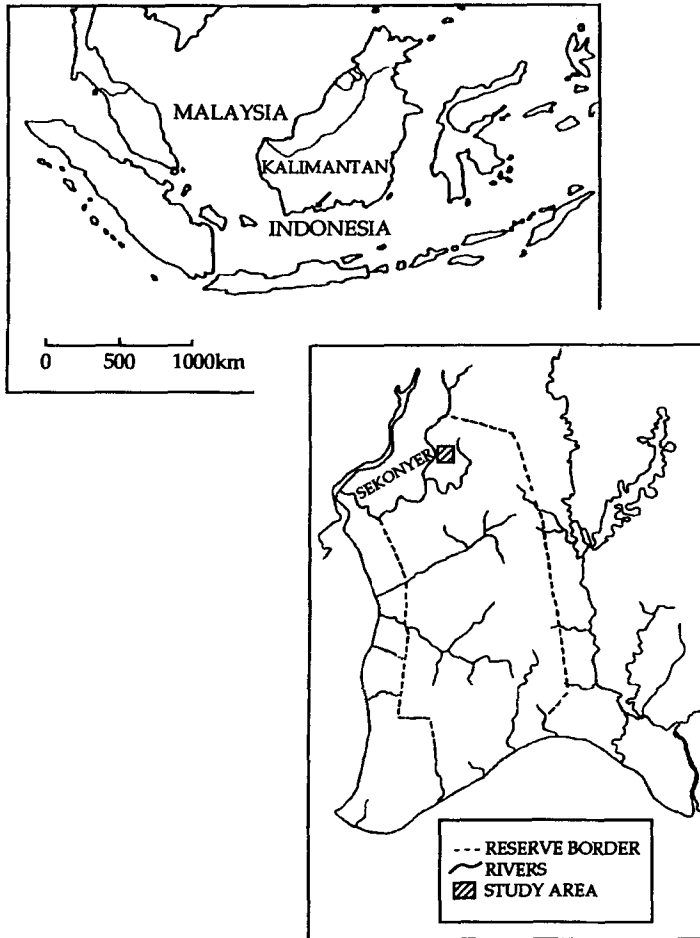
Fig. 1. The Natai Lengkuas Station located in Tanjung Puting National Park, Kalimantan Tengah, Indonesia.

ously (Fig. 1). Additional observations were made outside this area when possible. A trail system was established on the South bank of the river and trail markers (metal tags and survey tape) were placed every 25 m (the North river bank was outside of the park boundaries). Twenty trails, 100 m apart, and perpendicular to the river's edge, were made, with an additional two access trails horizontal to the river. The average canopy height was 11.39 m, with some emergents reaching 25 m or more.

Tanjung Puting National Park contains a diverse fauna, including six other primate species. These are the long-tailed macaque (*Macaca fascicularis*), the pigtailed macaque (*Macaca nemestrina*), the red langur (*Pres-*

bytis rubicunda), the agile gibbon (*Hylobates agilis*), the orangutan (*Pongo pygmaeus*), and the slow loris (*Nycticebus coucang*). Of these species, only *M. fascicularis* was regularly observed within the study area. A variety of hornbill species and fruit-eating bats are also present. More complete faunal lists can be found in MacKinnon *et al.,* (1983).

Weather

Temperature was recorded once daily using a Taylor minimum-maximum gauge located inside a screened box placed 1.5 m above ground within the forest perimeter. The average minimum temperature was approximately 22°C; the average maximum temperature was approximately 29°C, with minimal variation recorded throughout the course of the study (Fig. 2). The river level fluctuated greatly, varying more than 2 m due to seasonal flooding. Although there is no true dry season, with over 150 mm of rain each month, somewhat less rain fell from July through October (Fig. 3).

Subjects

At least 12 groups of proboscis monkeys (10 one-male groups and 2 all-male groups) had part of their home ranges located within the study site.
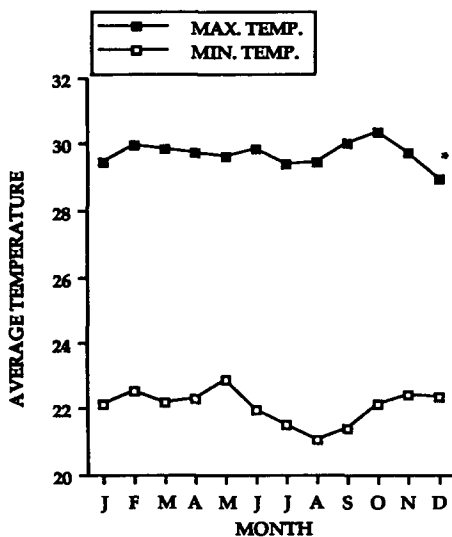

Fig. 2. The average minimum and maximum temperature per month from January-December, 1985. *Only one-half month's data available for December.
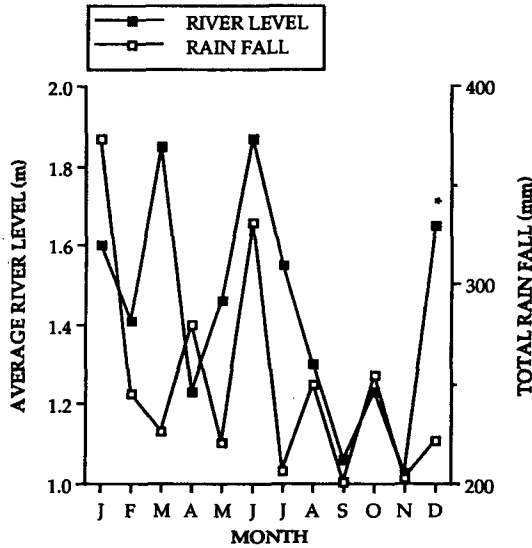
Fig. 3. The average river level (in meters) and the total rainfall (in millimeters) per month from January-December, 1985. *Only one-half month's data available for December.

Habituation to the observer varied between groups and among individuals within groups. All groups were habituated to approaches within 25 m by canoe and 100 m on foot; some groups allowed observers within 5 m on foot. Groups were identified through the presence of "marker" individuals (animals with distinctive scars or natural features) and the age/sex composition. Group size ranged from 3 to 23 at the close of the study, with a mean of 12.1 for all groups ($N = 145$ animals) (mean of 12.6 for one-male groups; $n = 126$ animals). Groups were found through evening census surveys and were chosen for following based on degree of habituation, location, and the possibility of observing an unusual event. There was a preference for most closely approachable groups, groups located within the trail grid, and groups in which an unusual event had occurred. The majority of follows were made between 0600 and 1200h.

Home Range, Density, and Biomass Estimates

Proboscis monkeys return regularly to the river's edge to sleep each night; they use both sides of the river (Bennett, 1986; Yeager, 1983, 1989, in press) and rarely travel more than 500 m from the river's edge (Yeager, 1986). Home range estimates were calculated for each group based on observations at the

sleeping site and the assumption that 500 m was the mean average distance moved away from the river bank. This assumption may overestimate habitat use near the river and underestimate habitat use further from the river; unfortunately, a more accurate estimate was not possible given observational constraints (Bennett and Sebastian, 1988, and Yeager, 1990). For each river bank, the distance (in meters) between each group's farthest sighting downriver and upriver was calculated. This distance was summed for the two river banks and multiplied by 500 (the presumed distance traveled from the river's edge), then divided by 10,000 to obtain an estimate of the total area in hectares used by a group. This is termed its *total* home range. Known unused area (i.e., the base camp) was deleted from these estimates. To estimate group density, the areas in which the home ranges of groups overlapped had to be partitioned between those groups (Janson and Terborgh, in press). Overlap areas were divided equally between the total number of groups using that area. An *adjusted* home range was calculated by summing the proportions of overlap allotted each group and those areas it used exclusively. Good estimates of adjusted home ranges and total home ranges were obtained for four groups (R, FB, K, GR). The average adjusted home range and average total home range were calculated based on those four groups. The average group density was obtained by dividing the average adjusted home range (in ha) for a group into 100 (km² = 100 ha). The average number of individuals per km² was obtained by multiplying the average group density per km² by the average group size. The average biomass per km² was obtained by multiplying the average estimated weight by the average number of individuals per km². Estimates were not rounded until the final calculation.

Behavioral Data Collection

Feeding data were obtained from instantaneous group scans made every 5 min (scan event) for 30 min per follow hour. Feeding included both the manipulation and ingestion of food items. Food items were identified by species and plant part (young leaves, mature leaves, fruit flesh or seed, flower) when possible. In approximately 1700 h of observation during follows, 3,739 individual activity records of feeding during a scan (hereafter referred to as IARFs) were recorded. Because several individuals might be seen feeding during a single scan, but on different items, adjusted scores, based on the proportion of individuals feeding on various items for each scan event, were calculated. Each IARF was weighted based on its proportion per scan event, with each scan event given a total score of one. The adjusted scores did not vary significantly from the raw data ($r = 0.98, p < 0.01$), thus the IARFs were used for this paper. As individuals could not always be identified, the IARFs were pooled.

Vegetational Data Collection

Three vegetational plots perpendicular to the river's edge were established (on trails 4, 10, and 20 within the study area). The plots were 10 m wide and totalled 2020 m in length. All trees (stems) 30 cm or larger in girth at breast height (1.5 m) were tagged, identified, and measured (height, girth, and crown spread). Girth was used to determine basal area (i.e., the area covered by the tree stem; basal area = [½ diameter]^2 *π) (Mueller-Dombois and Ellenberg, 1974). Crown spread was used to determine canopy cover (i.e., the area covered by the tree crown; canopy cover = [diameter$_1$ + diameter$_2$/4]^2 *π) (Mueller-Dombois and Ellenberg, 1974). There were 1,732 · trees of 90 species in the plots. They were examined monthly to assess their phenological state (i.e., presence/absence of young leaves, ripe or unripe fruit and flowers). Each tree was visually examined with binoculars and given a numeric rating based on the estimated percentage of the canopy containing a particular phytophase. Plots on trails 4 and 20 were examined on the first Saturday of each month and the plot on trail 10 was examined on the third Saturday of each month (except for December 1985, when the plots on trails 4 and 20 were examined on the first Sunday).

Feeding Ecology

A particular food item's frequency of use may be affected by such factors as its relative density (i.e., the percent of stems of a particular species relative to the total number of stems present in a vegetational plot), and percent total canopy cover (i.e., the percent of canopy cover of a particular species relative to the total canopy cover of all stems combined in a vegetational plot). Relative dominance (i.e., the percent of basal area of a particular species relative to the total basal area of all stems combined in a vegetational plot) has also been used as an indicator of canopy cover. The relationship between these variables was examined using correlations and selection ratios. Selection ratios were calculated using Clutton-Brock's (1975) method. Each food item's percentage of the total diet was divided by its relative density then multiplied by 10. A food item with a selection ratio greater than 10 is one for which a preference was shown.

Interspecific Competition for Food Resources

Of the nonhuman primate species found within the National Park, the long-tailed macaque (*M. fascicularis*) is the only other regular riverine dwelling monkey. At least 5 orangutans (*P. pygmaeus*) had part of their home ranges

located within the study area; they were observed occasionally. Other species were rarely or never observed. As long-tailed macaques were potential competitors for the same resources, data on their feeding behavior (over 800 observation hours) were collected during this study. A brief summary is provided here; details will be reported later.

RESULTS

Home Range, Density, and Biomass Estimates

The average total home range, based on groups R, FB, K and GR, is approximately 130.3 ha (range 125–137.5 ha) (Table I). The average adjusted home range for these groups is approximately 19.3 ha (range 18.1–20.5 ha). Based on this estimate of adjusted home range the average density per km² is approximately 5.2 groups. The average number of individuals per km² is approximately 62.6, based on a mean group size of 12.1 for all groups combined. Based on the data in Table I, the average estimated biomass per group is approximately 96.4 kg (range 32.2 kg–148.4 kg), based on the mean group size and an average weight of 7.97 kg for all individuals combined. The average biomass per km² is approximately 499.5 kg, based on the average number of individuals per km² and the average weight. As seen in Table II, there was extensive home range overlap for groups R, FB, K, and GR; home ranges overlapped an average of 95.9% (range 92.0%–97.7%).

Table I. Estimates of Home Range Size and Biomass for Proboscis Monkey Groups

Group	Home Range Estimate (ha)	Adjusted Home Range Estimate (ha)	Biomass Estimate (kg)[a]
R	127.50	18.11	54.1
FB	125.00	18.60	32.2
K	137.50	20.51	133.5
GR	131.25	19.90	49.1
S	117.50	20.57	130.5
MG	77.50	12.40	82.0
TK	68.75	12.85	59.1
TW	64.00	10.13	119.5
EP	79.25	15.45	148.4
BO	6.25	5.31	123.6
AMD[b]	105.00	52.12	108.6
AMU[b]	118.00	23.92	115.6

[a]Biomass estimates based on Schultz (1942) (adult male: 20.3 kg, adult female: 9.9 kg) and personal estimates (infant: 2 kg, juvenile: 5 kg, adolescent female: 9 kg, adolescent male: 12 kg).
[b]All-male group.

Table II. Total Length of Riverbank Observed Used by Proboscis Monkey Groups R, FB, K and GR, and the Average Percent Overlap Between These Four Groups for Each Group (Based on Sightings at the Sleeping Site).

Group	Number sightings	Length of riverbank used (m)	Average percent spatial overlap
R	116	1575	97.7
FB	103	1625	97.7
K	122	1725	96.3
GR	108	1750	92.0

Feeding Behavior

Diet

Proboscis monkeys used at least 47 plant species as food sources during scan samples (Table III); use of an additional 8 species was observed outside of the sampling period. These 47 species belonged to 19 families. Based on IARFs for these 47 plant species, 17 species were used primarily for their reproductive parts (fruit, seed, flower) and 30 species were used primarily for their leaves. There was a marked preference for four species, with over 60% of all IARFs accounted for by *Eugenia* sp. 3/4, *Ganua motleyana*, and *Lophopetalum javanicum*. (*Eugenia* sp. 3 and *Eugenia* sp. 4 were not distinguishable except when fruiting; all fruit eaten was from *Eugenia* sp. 3.)

Proboscis monkeys are folivores/frugivores; leaves and fruit account for 51.9% and 40.3% of all IARFs, respectively (Fig. 4). Of leaves eaten, the majority (79.3%) were young leaves (Fig. 5A). Observations of mature leaf-eating were primarily made in September and October, 1985. Of fruits eaten, the seed or the seed and the flesh were consumed in 91.7% of the IARFs on fruits (Fig. 5B). Fruit ripeness was not assessed quantitatively, but they generally appeared to be unripe and/or nonfleshy.

Animal material comprised less than 1% of the IARFs. The ingestion of mosquitos, caterpillars, and insect larvae were all observed during the course of this study. Animal material in the proboscis monkeys' diet may be underestimated, as some rotting fruits contain insect larvae.

Monthly Variation in Diet

The number of identified species used as food sources in a given month ranged from 10 to 23 with a mean of 14.9 (Table IV). The total number of months an identified species was used as a food source ranged from 1 to 12 (Table V). The overall preferences for *Eugenia* sp. 3/4, *Ganua*

Table III. Proboscis Monkey Plant Food Sources

Family	Genus species	Local Name	Number IARFs per Plant Part				
			Fruit[a]	Seed	Flower	Leaf	Other/?
Anacardiaceae	Mangifera sp.	Rangas[d]	2	0	3	38	0
Annonaceae	Polyalthia glauca	Mahabi	0	0	1	0	0
Annonaceae	Polyalthia lateriflora	Banitan	0	0	1	6	0
Annonaceae	Xylopia fusca	Jampang	0	0	0	9	0
Burseraceae	Santiria rubiginosa	Pempadu	0	0	0	8	0
Clusiaceae	Calophyllum sp. 1	Pempasir	1	0	0	2	0
Clusiaceae	Calophyllum sp. 2	Poga	2	0	0	0	0
Clusiaceae	Garcinia dulcis	Penaga[d]	19	0	0	4	3
Clusiaceae	Garcinia forbesii	Kemanjing[d]	7	0	0	2	0
Celastraceae	Kokoona ochracea	Penempalaan	0	31	0	1	0
Celastraceae	Lophopetalum jcvanicum	Bentukak[d]	0	486	6	22	0
Connaraceae	Rourea mimosoides	Gamat sawa[d]	0	4	0	0	0
Dipterocarpaceae	Shorea smithiana	Lanan	2	0	0	6	0
Ebenaceae	Diospyros maingayi	Belamanaduk[d]	37[b]	0	0	2	0
Euphorbiaceae	Baccaurea racemosa	Puak[d]	0	1	1	6	0
Euphorbiaceae	Laccaurea bracteata	Puak hijau[d]	0	18	0	0	0
Euphorbiaceae	Macaranga hypoleuca	Mahang	0	0	4	1	0
Euphorbiaceae	Neoscortechinia sp.	Bekapas[d]	0	48	0	17	0
Fabaceae	Crudea teyamannii	Mampai[d]	0	2	0	67	0
Fabaceae	Dialium indum	Keranji	0	0	0	4	0
Fagaceae	Lithocarpus sundaicus	Kumpat rawa	1	0	0	0	0
Flacourtiaceae	Ryparosa javanica	Bekapas natai	12	0	0	0	0
Gonystylaceae	Gonystylus macrophyllus	Ramin	0	0	0	2	0
Lauraceae	Litsea sp.	Piayis	0	0	0	28	0
Melastomataceae	Pternandra rostrata	Pisulan[d]	4[c]	0	0	7	0
Meliaceae	Aglaia sp.	Papung[d]	1	0	0	4	0
Myristicaceae	Knema latifolia	Kumpang rawa	0	0	0	4	0
Myrtaceae	Eugenia reinwardtiana	Telihai	0	0	0	1	0

Family	Species	Local name					
Myrtaceae	*Eugenia* sp. 1	Jinjit[d]	14	0	0	18	0
Myrtaceae	*Eugenia* sp. 2	Ubar hijau	0	9	0	0	0
Myrtaceae	*Eugenia* sp. 3/4	Ubar merah/putih[d]	0	159	62	899	3
Myrtaceae	*Eugenia zeylanica*	Bati bati	5[c]	0	0	1	0
Moraceae	*Ficus acamtophylla*	Akar kariwayak	1[c]	0	0	26	0
Moraceae	*Ficus globosa*	Kariwayak	2[c]	0	7	17	0
Pandanaceae	*Pandanus* sp.	Rassau	0	0	0	33	0
Pteris group	*Stenophlaea palustris*	Lembiding	78[c]	0	0	6	0
Rosaceae	*Licania splendens*	Bentan[d]	0	0	14	17	1
Rubiaceae	*Ixora blumei*	Sariwakak	1	0	0	2	0
Rubiaceae	*Lucinaea montana*	Akar kayas[d]	3[c]	0	0	14	0
Rubiaceae	*Uncaria glabrata*	Akar kekait[d]	2[b]	0	0	73	0
Rebiaceae	?	Randa[d]	532[c]	0	0	117	0
Rubiaceae	*Ganua motleyana*	Ketiau[d]	0	0	5	217	2
Symplocaceae	*Symplocos fasciculata*	Habu habu rawa	0	0	2	4	1
		Besirak[d]	0	0	0	7	0
		Epiphyte	0	0	0	1	0
		Tentalang[d]	2	0	0	0	0
		Unidentified sp.	22	0	5	249	165
Araceae	*Thaipadoohora silvatica*	Akar keliding air	•			•	
Apocynaceae	*Dyera lowii*	Jelutung	•			•	
Lauraceae	*Actinodaphne procera*	Medang rawa	•				
Lauraceae	*Dehasia cuneata*	Gembor					
Theaceae	*Tetrameriste glabra*	Merang					
		Akar kepiting					
		Anggrek					
		Fungus					
		Ubai[d]	•				

[a] Unless specified, not certain whether seed, flesh or both eaten.
[b] Feed on flesh only.
[c] Feed on seed and flesh.
[d] Also used as a food source by *Macaca fascicularis*.
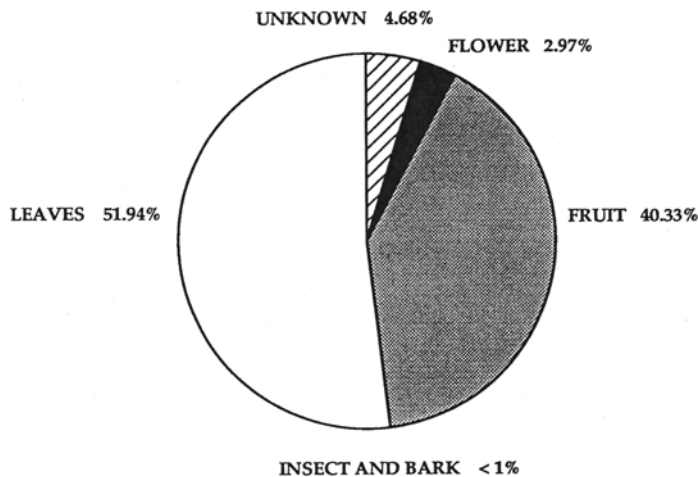[e] Observed outside scan samples.

Fig. 4. The percent of proboscis monkey IARFs presented as a function
of food type (N = 3739).

motleyana, and *Lophopetalum javanicum* were clearly seen here as well. Based
on monthly rankings, each of these species was among the top three species
used per month for at least 7 months (Table VI). Monthly use of each known
food source based on IARFs is presented in Table V.

Food type use varied monthly. Proboscis monkeys were frugivorous
from January through May, turning to leaves in June through December (Fig.
6). There was a significant difference in the total number of different spe-
cies used between the months of January through May versus June through

Table IV. Proboscis Monkey Dietary Diversity Calculated
Monthly Using the Shannon-Wiener Index of Diversity (H')
and Number of Identified Food Species Used per Month

Month	Shannon-Wiener Index of Diversity	Number Identified Food Species
January	2.13	10
February	1.70	10
March	1.81	11
April	1.36	11
May	2.67	23
June	2.05	18
July	2.09	16
August	2.21	18
September	2.16	18
October	1.75	18
November	1.64	14
December[a]	0.86	12

[a]Only one-half month's data.

UNKNOWN 15.5%   A

MATURE LEAVES 5.2%

YOUNG LEAVES 79.3%

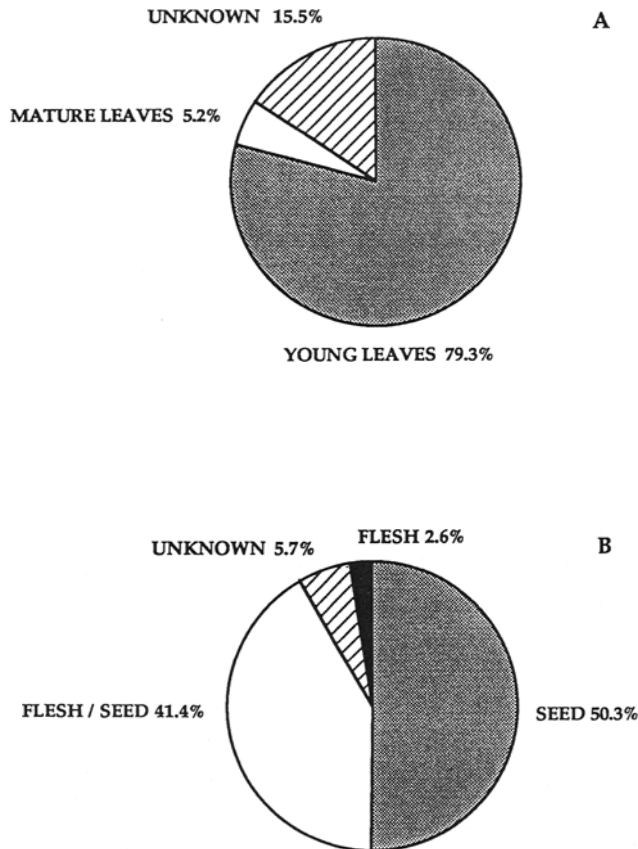UNKNOWN 5.7%   FLESH 2.6%   B

FLESH / SEED 41.4%   SEED 50.3%

Fig. 5A. The percent of proboscis monkey leaf IARFs presented as a function of category (n = 1944). B The percent of proboscis monkey fruit IARFs presented as a function of category (n = 1508).

December (X^2 = 11.26, $df(1)$, p < 0.01), with fewer species used during January through May.

Dietary Diversity

The Shannon-Weaver index of Diversity (H') (Pielou, 1966) was used to calculate dietary diversity for each month (Table IV). Both plant part (fruit, leaves, and flowers) and plant species were used in the analysis; unidentified plants and/or plant parts were not included. H' ranged from 0.86 to 2.67. Highest diversity was found in May and August. Most of the diversity is attributable to leaves.

Table V. Proboscis Monkey Monthly IARFs for Each Food Source

Genus species (Local)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec[a]	Total	Percent
Aglaia sp.	0	0	0	0	2	2	0	1	0	0	0	0	5	0.13
Baccaurea racemosa	0	1	0	0	1	1	2	2	0	1	0	0	8	0.21
(Besirak)	0	0	0	0	0	1	3	3	0	0	0	1	8	0.21
Calophyllum sp. 1	0	0	0	0	3	0	0	0	0	0	0	0	3	0.08
Calophyllum sp. 2	0	0	0	0	0	0	0	2	0	0	0	0	2	0.05
Crudea teyamannii	0	1	3	8	6	20	9	9	8	5	0	0	69	1.85
Dialium indum	0	0	0	0	4	0	0	0	0	0	0	0	4	0.11
Diospyros maingayi	26	4	6	0	1	0	0	1	1	0	0	0	39	1.04
(Epiphyte)	0	0	0	0	0	0	0	0	0	0	0	1	1	0.03
Eugenia reinwardtiana	0	0	0	0	0	0	0	1	0	0	0	0	1	0.03
Eugenia sp. 1	0	0	0	5	9	0	1	0	17	0	0	0	32	0.86
Eugenia sp. 2	0	0	9	0	0	0	0	0	0	0	0	0	9	0.24
Eugenia sp. 3/4[b]	102	61	67	5	23	168	119	23	136	131	100	188	1123	30.03
Eugenia zeylanica	0	0	0	0	0	0	0	0	0	1	0	0	1	0.02
Ficus acamtophylla	2	0	0	0	1	4	1	4	14	0	1	4	31	0.83
Ficus globosa	7	0	0	0	10	0	0	0	0	1	0	0	18	0.48
Ganua motleyana	164	19	91	253	75	42	59	7	23	16	7	0	756	20.22
Garcinia dulcis	0	0	0	0	20	0	0	0	5	0	1	0	26	0.70
Garcinia forbesii	0	0	0	2	7	0	0	0	0	0	0	0	9	0.24
Gonystylus macrophyllus	0	0	0	0	0	0	0	1	0	1	0	0	2	0.05
(Insect)	0	0	0	0	0	0	0	2	0	0	0	0	2	0.05
Ixora blumei	0	0	0	0	0	0	0	0	1	0	0	1	2	0.05
Knema latifolia	0	0	0	0	0	0	0	0	0	4	0	0	4	0.11
Kokoona ohracea	0	0	0	0	0	0	26	0	5	0	1	0	32	0.86
Laccaurea bracteata	0	0	0	2	0	16	0	0	0	0	0	0	18	0.48

Species													Total	%
Licania splendens	20	26	24	16	3	7	1	11	0	0	1	1	110	2.94
Lithocarpus sundaicus	0	0	0	0	0	0	1	0	0	0	0	0	1	0.03
Litsea sp.	0	0	0	0	0	0	0	0	0	16	12	0	28	0.75
Lophopetalum javanicum	23	12	18	30	1	29	58	50	147	87	51	8	514	13.75
Lucinaea montana	0	0	0	0	0	0	7	0	3	2	2	1	15	0.40
Macaranga hypoleuca	0	0	0	0	0	0	0	1	4	0	0	0	5	0.13
Mangifera sp.	0	0	8	10	5	7	7	0	3	2	1	0	43	1.15
Neoscortechinia sp.	34	8	3	0	3	7	0	10	0	0	0	0	65	1.74
Pandanus sp.	0	1	0	0	0	2	0	0	30	2	0	7	42	1.12
Polyalthia glauca	0	0	0	0	0	0	0	0	0	1	0	0	1	0.03
Polyalthia lateriflora	0	0	0	0	1	6	0	0	0	0	0	0	7	0.19
Pternandra rostrata	0	0	0	0	2	6	0	1	1	1	0	0	11	0.29
(Randa)	0	0	2	7	5	16	18	0	16	26	2	27	119	3.18
Rourea mimosoides	0	0	0	0	0	0	0	0	0	0	4	0	4	0.11
Ryparosa javanica	0	0	0	0	12	0	0	0	0	0	0	0	12	0.32
Santiria rubiginosa	0	0	0	0	0	0	0	0	0	0	8	0	8	0.21
Shorea smithiana	2	0	0	0	0	0	0	0	0	6	0	0	8	0.21
Stenophlaea palustris	0	0	0	0	0	1	1	0	4	0	0	0	6	0.16
Symplocos fasciculata	3	0	0	1	0	3	0	0	0	0	0	0	7	0.19
(Tentalang)	0	1	1	0	0	0	0	0	0	0	0	0	2	0.05
Uncaria glabrata	0	0	0	0	1	15	32	0	22	2	2	2	76	2.03
Xylopia fusca	0	0	0	0	5	0	0	4	0	0	0	0	9	0.24
Unidentified	25	12	40	26	7	48	56	13	45	72	48	49	441	11.79
Total	383	134	232	339	198	345	350	132	440	305	193	242	3739	100.00

a Only one-half month's data.

b *Eugenia* sp. 3 (Ubar merah) and *Eugenia* sp. 4 (Ubar putih) are combined in *Eugenia* sp. 3/4 as it was not usually possible to distinguish between their leaves in the field. All fruit eaten were *Eugenia* sp. 3.

Table VI. Top Three Food Sources Used by Proboscis Monkeys Each Month[a]

| Month | Food Source Rank | | |
	No. 1	No. 2	No. 3
January	*Ganua motleyana*	*Eugenia* sp. 3	*Ryparosa javanica*
February	*Eugenia* sp. 3	*Licania splendens*	*Ganua motleyana*
March	*Ganua motleyana*	*Eugenia* sp. 3	*Licania splendens*
April	*Ganua motleyana*	*Lophopetalum javanicum*	*Licania splendens*
May	*Ganua motleyana*	*Eugenia* sp. 3/4	*Garcinia dulcis*
June	*Eugenia* sp. 3/4	*Ganua motleyana*	*Lophopetalum javanicum*
July	*Eugenia* sp. 3/4	*Ganua motleyana*	*Lophopetalum javanicum*
August	*Lophopetalum javanicum*	*Eugenia* sp. 3/4	*Ryparosa javanica*
September	*Lophopetalum javanicum*	*Eugenia* sp. 3/4	*Pandanus* sp.
October	*Eugenia* sp. 3/4	*Lophopetalum javanicum*	(Randa)
November	*Eugenia* sp. 3/4	*Lophopetalum javanicum*	*Litsea* sp.
December	*Eugenia* sp. 3/4	*Garcinia tubifera*	*Lophopetalum javanicum*

[a]*Eugenia* sp. 3 and *Eugenia* sp. 4 were only distinguishable when fruiting.

<center>*Dietary Overlap*</center>

Monthly dietary overlap for all possible pairs of months was calculated using the Holmes-Pitelka method (Holmes and Pitelka, 1968). This method takes into account the plant part (leaves, fruit, and flowers were used in this analysis) as well as the plant species used (Struhsaker, 1975; Waser, 1987). The amount of overlap ranged from 4% to 79.4% with a mean of 33%. Adjacent months generally had the greatest amount of overlap (Table VII).

<center>## Vegetational Analyses</center>

<center>*Descriptive*</center>

The 1,732 trees found in the plots represented 90 different species of 63 genera from 33 different families. The average height, canopy cover, and basal area per species (as defined in Mueller-Dombois and Ellenberg, 1974) are presented in Table VIII. The average tree height for all trees combined was 11.4 m (6.0 m-27.0 m). The average tree diameter at breast height (1.5 m) for all trees combined was 18.4 cm (9.6 cm-45.2 cm). The average basal area per tree for trees combined was 350.3 cm² (71.6 cm²-1604.6 cm²). The average canopy cover per tree for all trees combined was 22.9 m² (9.1 m²-54.0 m²). The total basal area for all plots was 60.7 m². The total canopy cover for all plots was 39,273.8 m². The total basal area and canopy cover provided by each family is summarized in Table IX. The family providing the greatest total basal area and canopy over was Sapotaceae. *Ganua motleyana,* a highly used food source by the proboscis monkeys, is a member of this family. The average basal area and average canopy cover per species were significantly positively correlated (r_s = 0.60, $p < 0.01$).

Over 71% of the trees in the plots were potential food sources (as determined from scan samples of feeding behavior) at some time. An examination of the basal area and canopy cover yields the same pattern, with the majority of the total basal area (80.4%) and total canopy cover (76.6%) provided by potential food sources. Potential food sources appeared to be fairly evenly dispersed in space, with a mean of 6.1 stems per 10 m² area (S.D. = 4.3). The most highly used food sources (*Eugenia* sp. 3/4, *Ganua motleyana,* and *Lophopetalum javanicum*) were among the most frequent and most dominant, making up over 22% of the stems in the vegetational plots.

<center>*Phenology*</center>

Data on the production of fruit, flowers, and young leaves over the 12 months are presented in Fig. 7. The percent of trees containing fruit (ripe
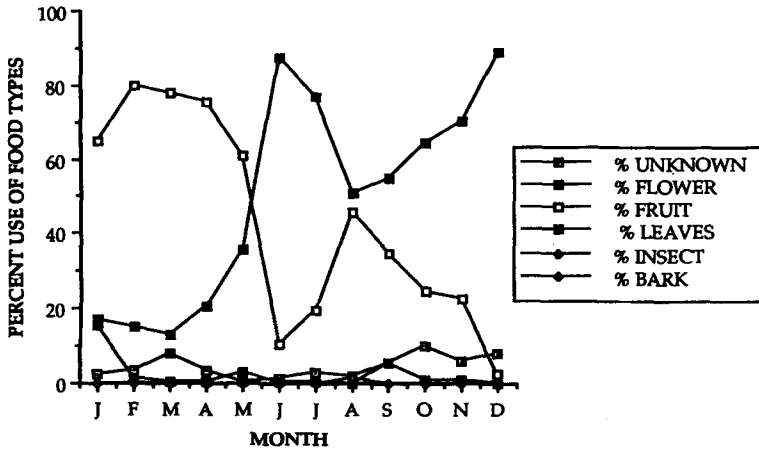
Fig. 6. Monthly variation in the percent of proboscis monkey IARFs as a function of food type.

or unripe) varied from 4.3 to 19.1. Fruit was most available from January through May, declining in June and beginning to increase again in November and December. There was a minor fruit peak in August (see Fig. 8). The percent of trees containing young leaves ranged from 61% to 90%, with May, August, and September being the periods of lowest availability. The percent of trees containing flowers ranged from 4% to 11%, with February, May, and August being the periods of greatest availability. Phenological data concerning fruiting for *Eugenia* sp. 3, *Ganua motleyana,* and *Lophopetalum javanicum* combined are presented in Fig. 8. Note that fruit availability does not increase in November, in comparison with the data from all trees combined; and, there is no minor fruit peak in August.

Feeding Ecology

Correlations and Selection Ratios

Significant positive correlations were found between percent diet and relative density for 33 food species for which information concerning percent diet (from scans) and percent stems present (from vegetational plots) are available (r_s = 0.50, p < 0.01). Significant positive correlations were found also between percent diet and relative dominance for each food item (r_s = 0.46, p < 0.01), and percent diet and percent total canopy cover for each food item (r_s = 0.52, p < 0.01). Selection ratios (Clutton-Brock, 1975) were calculated for these 33 food species. Of these species, 11 were more

Table VII. Monthly Dietary Overlap for Proboscis Monkeys

Month:	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec[a]
January	-	0.37	0.58	0.52	0.49	0.22	0.21	0.20	0.20	0.17	0.17	0.10
February		-	0.56	0.27	0.13	0.18	0.20	0.18	0.15	0.14	0.13	0.04
March			-	0.57	0.40	0.14	0.16	0.20	0.16	0.16	0.13	0.06
April				-	0.45	0.24	0.26	0.23	0.20	0.20	0.16	0.07
May					-	0.29	0.23	0.23	0.21	0.19	0.17	0.13
June						-	0.67	0.38	0.51	0.61	0.63	0.60
July							-	0.39	0.60	0.61	0.57	0.44
August								-	0.56	0.51	0.46	0.21
September									-	0.70	0.60	0.42
October										-	0.79	0.57
November											-	0.55
December												-

[a]Only one-half month's data.

Table VIII. Relative Density (DN), Average Height (HT), Average Basal Area (BA), and Average Canopy Cover (CC) of Tree Species Located within Established Vegetational Plots

Family	Genus species	Local Name	N	DN	HT (m)	BA (cm²)	CC (m²)[a]
Anacardiaceae	Mangifera sp. 1	Rangas (104)	105	6.06	12.44	557.30	28.89[a]
Annonaceae	Fissistigma fulgens	Penyeluangan rawa	4	0.23	13.50	341.68	18.93
Annonaceae	Polyalthia glauca	Mahabi	2	0.12	10.50	144.24	15.33
Annonaceae	Polyalthia lateriflora	Banitan	11	0.64	11.55	309.96	18.72
Annonaceae	Xylopia sp. 1	Jampang	20	1.15	9.55	193.12	18.34
Annonaceae	Xylopia sp. 2	Jangkang	10	0.58	12.50	179.69	14.48
Apocynaceae	Alstonia angustifolia	Ular ular	2	0.12	16.50	131.12	9.11
Apocynaceae	Dyera lowii	Jelutung	16	0.92	11.50	336.84	16.42
Burseraceae	Santiria rubiginosa	Pempadu	11	0.64	15.09	728.19	36.03
Celastraceae	Evonymus javanicus	Kopi hutan	1	0.06	8.00	179.55	30.19
Celastraceae	Kokoona ochracea	Penempalaan (12)	13	0.75	11.77	217.63	25.67[a]
Celastraceae	Lophopetalum javanicum	Bentukak (106)	108	6.24	12.14	749.69	16.15[a]
Clusiaceae	Calophyllum sp. 1	Pempasir	4	0.23	14.75	336.93	32.49
Clusiaceae	Calophyllum sp. 2	Poga	2	0.12	13.00	413.69	32.77
Clusiaceae	Garcinia aff. memecyloide	Idat (82)	83	4.79	13.02	175.58	11.76[a]
Clusiaceae	Garcinia forbesii	Kemanjing	9	0.52	8.89	133.29	16.59
Clusiaceae	Garcinia rostrata	Kayu aci	1	0.06	7.00	202.94	25.74
Clusiaceae	Garcinia sp. 1	Pandau	1	0.06	11.00	106.02	10.04
Clusiaceae	Garcinia sp. 2	Galam tikus	6	0.35	12.67	198.46	17.80
Clusiaceae	Garcinia sp. 3	Penaga	2	0.12	10.00	281.90	24.69
Clusiaceae	Garcinia sp. 4	Berok	5	0.29	11.80	260.33	28.18
Cunnoniaceae	Weinmania blumei	Jaring hantu	2	0.12	11.50	490.46	43.47
Dipterocarpaceae	Anisoptera thurifera	Ketimpun	1	0.06	9.00	76.47	16.44
Dipterocarpaceae	Shorea smithiana	Lanan	45	2.60	13.37	508.73	31.43
Dipterocarpaceae	Vatica umlonata	Rasak	6	0.35	10.33	302.92	38.03
Ebenaceae	Diospyros frutescens	Bekunyit	42	2.42	10.14	268.20	21.26
Ebenaceae	Diospyros maingayi	Belamanduk	51	2.94	13.71	506.32	27.10
Ebenaceae	Diospyros sp. 1	Jungkung	4	0.23	9.50	418.00	19.86
Elaeocarpaceae	Elaeocarpus valetonii	Semono	2	0.12	14.25	530.96	54.04
Euphorbiaceae	Antidesma sp. 1	Lurangan natai	3	0.17	9.00	175.19	14.79

Family	Species	Local name					
Euphorbiaceae	*Aporosa falcifera*	Lurangan rawa	2	0.12	9.50	150.76	16.15
Euphorbiaceae	*Baccaurea racemosa*	Puak (120)	121	6.99	10.96	248.62	25.48[a]
Euphorbiaceae	*Glochidian sericeum*	Katu hutan	2	0.12	9.00	81.51	23.99
Euphorbiaceae	*Marcaranga trichocarpa*	Kelantit kering (0)	1	0.06	7.00	106.02	0.00[a]
Euphorbiaceae	*Neoscortechinia sp. 1*	Bekapas	48	2.77	10.73	224.83	21.09
Fabaceae	*Crudea teyamannii*	Mampai	27	1.56	10.26	349.49	28.18
Fabaceae	*Dialium indum*	Keranji	9	0.52	8.44	247.33	20.93
Fabaceae	*Koompasia malaccensis*	Bangaris	1	0.06	27.00	1604.6	47.36
Fabaceae	*Sindora beccariana*	Sindur	2	0.12	10.50	256.65	24.24
Fagaceae	*Lithocarpus andersonii*	Pempaning	58	3.35	11.85	165.97	20.23
Gonystylaceae	*Gonystylus macrophyllus*	Ramin	17	0.98	16.18	723.13	32.57
Icacinaceae	*Stemonurus macacensis*	Bedaru rawa	14	0.81	8.57	127.59	15.91
Lauraceae	*Actinodaphene glomerata*	Medang sandok	14	0.81	9.79	200.61	27.96
Lauraceae	*Actinodaphene procera*	Medang rawa (69)	70	4.04	10.29	143.12	14.98[a]
Lauraceae	*Dehasia cuneata*	Gembor	10	0.58	10.80	428.12	20.21
Lecythidaceae	*Barringtonia reticulata*	Putat	1	0.06	13.00	395.52	11.19
Magnoliaceae	*Michelia montana*	Asam asam	22	1.27	12.91	414.09	24.15
Melastomataceae	*Memecylon laevigatum*	Tembaras	3	0.17	7.33	78.25	25.29
Melastomataceae	*Pternandra caerulescens*	Pisulan laki	1	0.06	10.00	250.72	9.62
Metastomataceae	*Pternandra rostrata*	Pisulan	139	8.03	8.16	174.80	26.36
Meliaceae	*Aglaia cf. longfolia*	Parak	5	0.29	11.60	270.06	28.18
Meliaceae	*Aglaia sp. 1*	Papung	11	0.64	12.36	317.55	21.23
Moraceae	*Artocarpus kemando*	Pudu	3	0.17	14.67	224.20	16.01
Moraceae	*Ficus globosa*	Kariwayak	2	0.12	12.00	191.98	37.93
Myristicaceae	*Knema latifolia*	Kumpang rawa	49	2.83	11.79	308.26	19.84
Myrtaceae	*Eugenia acuminatissima*	Haring para	2	0.12	9.00	124.18	14.67
Myrtaceae	*Eugenia zeylanica*	Bati bati	1	0.06	13.00	245.12	16.08
Myrtaceae	*Eugenia sp. 1*	Jinjit	2	0.12	13.00	489.72	52.29
Myrtaceae	*Eugenia sp. 2*	Ubar hijau	1	0.06	9.00	103.13	9.08
Myrtaceae	*Eugenia sp. 3*	Ubar merah (34)	35	2.02	10.54	216.25	30.62[a]
Myrtaceae	*Eugenia sp. 4*	Ubar putih	23	1.33	9.65	243.93	25.98
Myrtaceae	*Syzygium panzeri*	Jambu burung	1	0.06	6.00	108.94	2.84
Myrtaceae	*Tristania whitiana*	Pelewan	3	0.17	9.50	130.46	19.69
Mysinaceae	*Ardisia sp. 1*	Serapungan	1	0.06	19.00	108.94	50.27
Oleaceae	*Chionanthus rupicalus*	Kaya bunga	1	0.06	20.00	673.54	49.95

Table VIII. Continued

Family	Species	Local name	N				
Polygalaceae	*Xanthophyllum excelsum*	Rambai hutan	3	0.17	11.00	234.18	18.52
Proteaceae	*Helicia pescotomentosa*	Bengkaning tikus	30	1.73	10.00	120.43	17.41
Rhizophoraceae	*Anisophyllea disticha*	Ribu ribu	1	0.06	11.00	127.32	16.26
Rhizophoraceae	*Combretocarpus rotundus*	Perepat bangkit	4	0.23	14.75	1262.65	51.77
Rhizophoraceae	*Gynostroches axillaris*	Mata keli	3	0.17	11.33	332.17	28.68
Rosaceae	*Licania splendens*	Bentan (38)	39	2.25	12.87	424.12	39.61[a]
Rubiaceae	*Ixora blumei*	Sariwakak	28	1.62	9.93	156.87	14.49
Rubiaceae	*Jackia ornata*	Selumbar	4	0.23	17.25	1392.19	32.58
Rubiaceae	*Petunga microcarpa*	Sesapit	1	0.06	7.00	71.62	13.20
Rubiaceae	*Timonius lasianthoides*	Bengkel	1	0.06	10.00	509.30	21.44
Rubiaceae	*?*	Randa	30	1.73	8.17	145.79	22.66
Sapotaceae	*Ganua motleyana*	Ketiau (212)	218	12.59	13.01	537.75	22.26[a]
Sapotaceae	*Palaquium rostratum*	Nyatoh jangkar	1	0.06	13.00	111.91	9.76
Sapotaceae	*Payena leerii*	Sundi	1	0.06	15.00	522.11	34.47
Sapotaceae	*?*	Nyatoh	1	0.06	12.00	179.55	10.75
Symplocaceae	*Symplocos fasciculata*	Habu habu rawa	22	1.27	9.86	236.80	21.10
Theaceae	*Adinandra collina*	Betapai	1	0.06	13.00	236.36	17.72
Theaceae	*Tetramerista glabra*	Merang	15	0.87	10.67	607.02	23.83
		Besirak	24	1.39	9.25	200.11	15.97
		Gambor belitung	4	0.23	11.00	128.01	23.57
		Lebang	3	0.17	12.33	696.49	35.56
		Pintau rawa	4	0.23	8.50	108.77	16.94
		Ramania	4	0.23	9.75	141.93	16.13
		Tentalang	15	0.87	10.20	135.09	24.15
		Ubai	1	0.06	13.00	137.05	16.26

[a] N for some tree species was smaller due to mortality or broken stems. N for these tree species is given in parentheses next to local name.
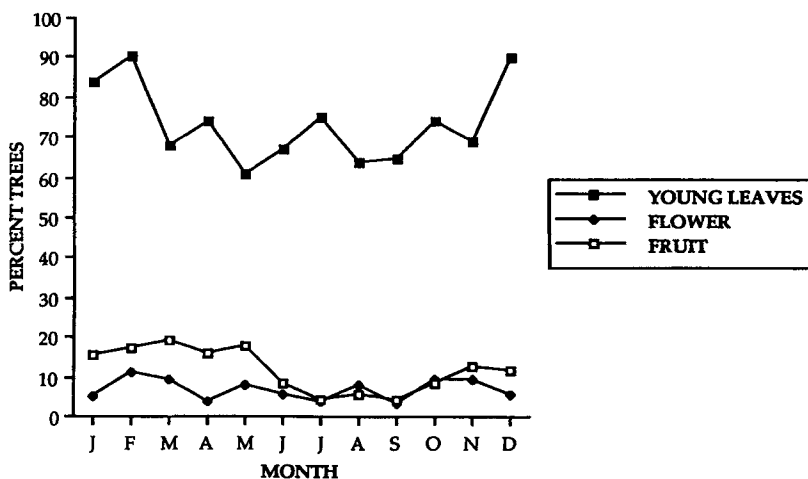
Fig. 7. Monthly variation in the percent trees within the vegetational plots (N = 1732) exhibiting a particular phytophase (young leaves, flower, fruit).

preferred based on their selection ratio score; their frequency of use was greater than expected given their density (see Fig. 9). They contributed 75.1% of the proboscis monkey diet.

Phenology and Diet

The use of fruits as a food source by proboscis monkeys correlates positively (r_s = 0.66, p < 0.02) with the phenological data on abundance presented in Fig. 7. Although proboscis monkeys fed on fruit when it was available, they continued to feed primarily on leaves in November/December when overall fruit abundance increased. As seen in Fig. 8, the species comprising the majority of fruit IARFs did not offer many fruits during this period.

No significant correlation was found between the phenological patterns of young leaves and flowers and their monthly variations as a percentage of the proboscis monkey's diet. However, there was a significant negative correlation between dietary diversity and young leaf phenology (r_s = −0.64, p < 0.02); dietary diversity increased as the number of trees containing young leaves decreased.

Interspecific Competition for Food Resources

Long-tailed macaques used many of the same food species as the proboscis monkeys (22 species in common) (Table III) and often the same

Table IX. Total Basal Area and Canopy Cover Provided by Each
Family

Family	Total Basal Area (cm²)	Total Canopy Cover (m²)
Anacardiaceae	58516.4	3004.8
Annonaceae	10724.1	822.9
Apocynaceae	5651.7	280.9
Burseraceae	8010.1	396.4
Celastraceae	83975.7	2050.0
Cunnoniaceae	980.9	86.9
Dipterocarpaceae	24787.0	1658.9
Ebenaceae	38758.9	2354.6
Elaeocaarpaceae	1061.9	108.1
Euphorbiaceae	41970.6	4194.6
Fabaceae	13780.1	1024.0
Fagaceae	9626.4	1173.5
Gonystylaceae	12293.2	553.7
Icacinaceae	1786.2	222.8
Lauraceae	17108.0	1627.4
Lecythidaceae	395.5	11.2
Magnoliaceae	9110.0	531.2
Melastomataceae	24782.2	3749.6
Meliaceae	4843.4	374.4
Moraceae	1056.6	123.9
Mysinaceae	108.9	972.4
Myrtaceae	15255.4	1859.6
Myristicaceae	15104.7	50.3
Oleaceae	673.5	50.0
Polygalaceae	702.6	55.6
Proteaceae	3613.0	522.2
Rhizophoraceae	6174.4	309.4
Rosaceae	16540.8	1505.1
Rubiaceae	14915.8	1250.4
Sapotaceae	118043.6	4773.2
Symplocaceae	5209.5	464.2
Theaceae	9341.6	375.1
Unidentified	8543.9	1094.9

food part. They were primarily frugivorous (66.7% of all IARFs, N = 813)
but also ate foliage (17.2%), flowers (8.9%), and insects (4.1%) (unidentified accounts for the remaining 3.2%). Monthly dietary overlap between long-tailed macaques and proboscis monkeys was calculated using the Holmes-Pitelka method. It ranged from 2.5% to 58.7% with a mean of 28.9% (Fig. 10). Overlap was highest from January through June and in November through December. Proboscis monkey and long-tailed macaque diets diverged most between July and October; this divergence was primarily due to the long-tailed macaques use of flowers and insects during this period (Yeager, 1987). Further, long-tailed macaques and orangutans were observed to displace proboscis monkeys at feeding sites on at least two occasions.
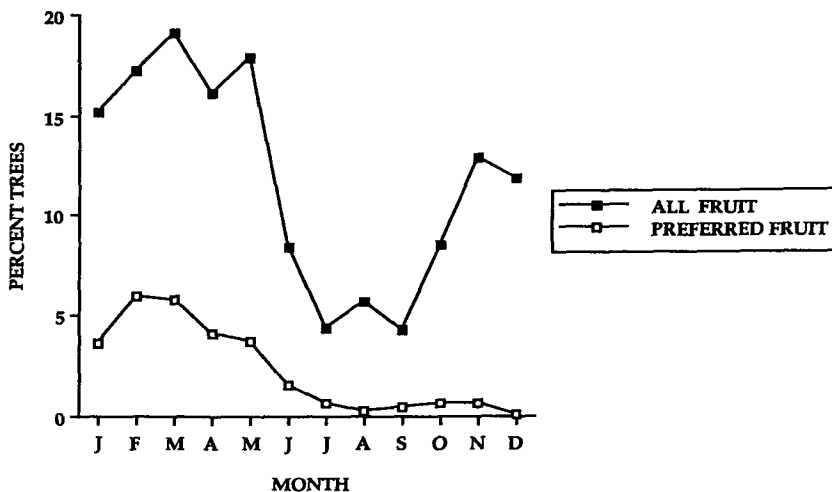
Fig. 8. Monthly variation in the percent of all trees versus preferred fruit trees carrying fruit within the vegetational plots ($N = 1732$).

DISCUSSION

Home Range, Density, and Biomass Estimates

Bennett and Sebastian (1988) report a home range estimate of approximately 900 ha (non-adjusted for group overlap) for one group of proboscis monkeys in the Samunsan Reserve of Sarawak, Malaysia. This is considerably larger than the estimate of 137 ha (non-adjusted for group overlap) reported here. Bennett and Sebastian (1988) estimate group density at 0.52 groups per km², individual density at 5.93 individuals per km², and a biomass of 45.8 kg per km² based on 14 groups ($N = 160$ individuals) along a 13.5 km stretch of river. Proboscis monkeys at the Natai Lengkuas site have smaller home ranges and occur at a higher density and biomass than reported by Bennett and Sebastian (1988). Part of the difference concerning population density and biomass appears due to differing assumptions concerning riverbank used in calculating these estimates (1 km versus 0.5 km per river bank). However, even if these methodological differences are controlled, by using the same assumptions in calculating population density and biomass, differences still exist between the Samunsam and Natai Lengkuas sites. Hunting pressure and low food availability have been suggested as possible explanations for the low density at Samunsam (Bennett, 1986; Bennett and Sebastian, 1988). Low food availability also may account for the large home ranges
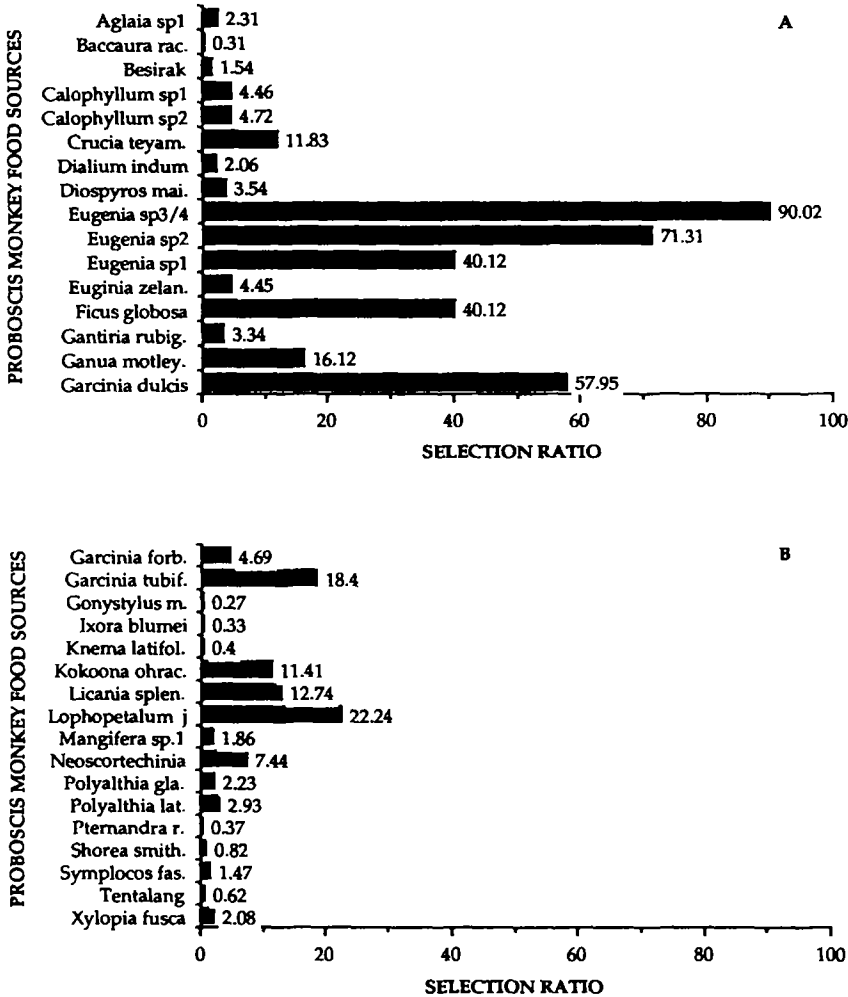
Fig. 9. Selection ratios for selected proboscis monkey foods.

at Samunsam (Bennett, 1986; Bennett and Sebastian, 1988). There is no known hunting pressure on proboscis monkeys within the Tanjung Puting National Park (personal observation, MacKinnon *et al.,* 1983); this proba-bly accounts for part of the difference between sites. Additionally, food avail-ability may be greater at Natai Lengkuas than at Samunsam; over 70% of the stems located within the vegetational plots at Natai Lengkuas were poten-tial food sources at some point during this study. Thus, food availability may also contribute to the differences between sites. Vegetational data from the Samunsam site are needed to assess this possibility.
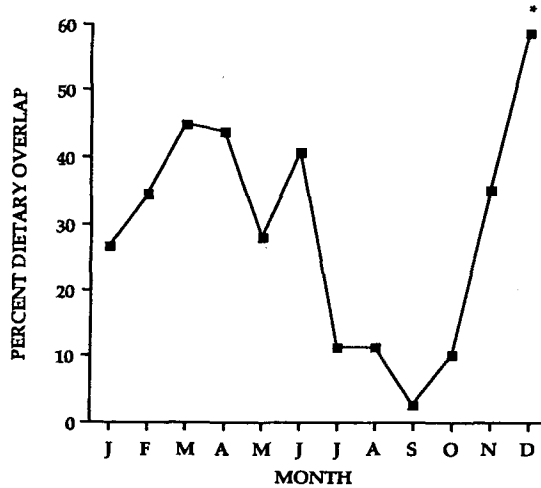
Fig. 10. Dietary overlap between proboscis monkeys and long-tailed macaques. *Only one-half month's data available for December.

Among primates, colobines generally occur at higher biomasses than monogastric primates, apparently due to their ability to use a wider range of food sources (i.e., increased number of food species and food types) than sympatric monogastric primate species (e.g., Bennett, 1983). In Tanjung Puting National Park, proboscis monkeys are sympatric with long-tailed macaques (*M. fascicularis*) and orangutans (*P. pygmaeus*). Biomass estimates for these two species are not available from this study as home ranges were not determined. Reported biomass estimates for orangutans and long-tailed macaques from Kutai Nature Reserve in Kalimantan Timor are 160 kg/km² and 16 kg/km², respectively (Waser, 1987, Table 18-1). Other biomass estimates for long-tailed macaques come from Malaysia (189 kg/km², Bennett, 1983; 89 kg/km², MacKinnon and MacKinon, 1980). These estimates are considerably lower than the biomass estimates for the proboscis monkey reported here. The pigtailed macaque (*M. nemestrina*), the red leaf-eating monkey (*P. rubicunda*), and the agile gibbon (*H. agilis*) were rarely observed within the study site. The slow loris (*N. coucang*), although reported to be present within the park, was never observed.

Diet and Feeding Ecology

Proboscis monkeys are folivore/frugivores, with an emphasis on the seeds of fruits consumed. Bennett and Sebastian (1988) also report an emphasis on fruits (35% of feeding observations), and seeds contribute an ad-

ditional 15%. Although based on a much smaller sample (34 feeding observations), they indicate the same general trend as found in this study. The proboscis monkey's feeding behavior appears to follow the general colobine pattern (an emphasis on young leaves, fruits that are unripe and nonfleshy or sweet). The emphasis on seeds has also been observed in several other colobine species. Although only one colobine species is reported to be gramnivorous, *Colobus satanas,* with at least 53% of its diet composed of seeds (McKey *et al.,* 1981; Harrison, 1986), seeds constitute 30% of *Presbytis rubicunda's* diet and over 25% of *Presbytis melalophos'* diet (Davies and Bennett, 1988). Struhsaker (1987) suggested two other colobine species that potentially may include a large portion of seed in their diets: *Presbytis entellus* and *Presbytis obscura.* Fruit comprises from 32% to 47% of their diets (*P. entellus,* Hladik and Hladik, 1972; *P. obscura,* Curtin, 1980; MacKinnon and MacKinnon, 1980) and an unknown portion of this may be seeds. Additionally, Gurmaya (1986) reported *Presbytis thomasi* to have a diet containing more than 50% fruit. Again, it is not clear what proportion of fruit use includes seeds.

Seeds can be high in protein, and are often high in carbohydrates and lipids (Waterman, 1984). Lipids are a second source of high energy nutrients, following sugars (Waterman, 1984). Seeds eaten by *C. satanas* are typically oil-rich and may contain high levels of protein (McKey *et al.,* 1981). However, seeds eaten by *P. rubicunda* and *P. melalophos* (Davies and Bennett, 1988) provided relatively less protein than foliage but were higher in fermentable carbohydrates and more digestible than foliage. Phytochemical analyses are needed to determine whether this is true of the seeds used by proboscis monkeys and other Asian colobine species.

Proboscis monkeys at Natai Lengkuas probably underwent their highest period of food stress between August and October. There was a decrease in the availability of both preferred fruits and young leaves during this period. New items, that had been previously available but not used were added to their diet; and, they ate more mature leaves. Proboscis monkeys may be "energy economists"; during periods of food scarcity they start using resources which may be poorer in nutrient quality but are widely available (i.e., leaves, particularly mature leaves). Nutrient quality may not be a major constraint on their feeding behavior, as specialized microflora found in the foregut may be able to provide vitamins and break down fiber (Bauchop, 1978).

Monthly dietary diversity increased as the number of trees with young leaves declined. It appears that much of the diversity found in the diet of proboscis monkeys is attributable to the young leaf portion of their diet. As overall abundance and availability of particular species of young leaves declined, the proboscis monkeys were forced to expand the number of different species used. Dietary diversity also increased when preferred foods (fruits)

were scarce. More diversity was seen during the proboscis monkeys' folivorous period than when they were frugivorous. Bennett (1983), in her study of the banded leaf monkey (*Presbytis melalophos*), also found increased dietary diversity when favorite foods were scarce.

Previous studies (Kern, 1964; Macdonald, 1982) have suggested that mangrove species (i.e., *Brugiera* sp., *Soneratia* sp., *Rhizophora* sp.) were the "key feature" of proboscis monkey diet and habitat. This study and a study by Bennett (1986) document much greater dietary diversity.

Proboscis monkeys appear to be selective feeders. The greater part (75.1%) of the proboscis monkey diet consists of species with selection ratios greater than expected based on the species' relative density.

Clutton-Brock and Harvey (1977, p. 562) state that "Within phylogenetic groups, larger species tend to feed more on foliage." Based on this statement, the proboscis monkey diet should be high in leaves, given their large body size. Yet, the proboscis monkey diet does not contain a larger percentage of foliage, relative to that reported for many colobine species. The diet of *P. entellus,* another large-bodied colobine, also does not contain a relatively large percentage of foliage (Hladik and Hladik, 1972). In fact, amongst colobines, the diet of *P. aygula* is reported to contain one the highest percentages of foliage (Ruhiyat, 1983). *P. aygula* is one of the smallest colobines. Within the colobines, recent data do not appear to support a positive linear relationship between body size and folivory.

Parra (1978) suggests that, for the use and maintenance of ruminant-like digestion (foregut fermentation), the colobines are actually below the lower weight limit necessary for efficient energy regulation. Foliage digestion is time-consuming, particularly for foregut as opposed to hindgut fermenters. As foregut fermenters appear to be better at detoxification, colobines may be making a trade-off between energy efficiency (i.e., hindgut fermentation strategy) and the ability to break down anti-feedants (Freeland and Janzen, 1974; Parra, 1978). Waterman (1984) states "it seems likely that they must either (a) be able to exploit foliage highly favorable to their digestive system or (b) be able to 'top up' their diet with concentrates such as seeds or fruits" (p. 183). No data concerning the phytochemistry of proboscis monkey food sources are available; however, proboscis monkeys do appear to "top up" their diet with seeds.

Interspecific Competition for Food Resources

Cords (1987) and Gautier-Hion (1980) stated that dietary overlap between cercopithecine species is higher for fruits than for less popular items such as leaves. In keeping with this conclusion, dietary overlap between

proboscis monkeys and long-tailed macaques was greatest when fruit was highly available and a major part of the diet. In Schoener's (1982) review of interspecific competition, he states that dietary overlap is generally least during periods of food scarcity. Waser (1987) stated that, if interspecific competition is present, the difference in overlap between periods of food abundance and periods of food scarcity should be more than 10%. This was observed in this study, supporting the idea that long-tailed macaques (*Macaca fascicularis*) and proboscis monkeys are interspecific competitors for food resources. Recall that long-tailed macaques displaced proboscis monkeys at a feeding site. Schoener (1982) suggested that:

> "During lean times, strong directional selection resulting from interspecific competition produces in each species adaptations most suited for resources used relatively exclusively by the species...During times of plenty, different types of resources increase differentially in abundance, and it then becomes more profitable to use types other than those for which the trophic phenotype has specifically been selected. Moreover, the newly profitable resource types are the same for a number of species, and the species converge upon them" (p. 591).

Physiological differences between proboscis monkeys and long-tailed macaques probably account for different dietary strategies during periods of resource scarcity. A sacculated stomach and specialized bacteria (Bauchop, 1978; Bauchop and Martucci, 1968) may allow proboscis monkeys to break down secondary toxins and digestion inhibitors in some food sources (Bennett, 1983; Hladik, 1977; Waterman, 1984). However, this specialization probably prevents them from using quantities of ripe fruits and animal protein because (due to fermentation processes) they are subject to bloat (Collins and Roberts, 1978). Waterman (1984) states that "even if not capable of permanently supplying the dietary needs of the animal the colobine digestive system will be advantageous in allowing the monkey greater dietary flexibility during periods of food stress" (p. 183).

Consequences of Seed Predation

One effect of the proboscis monkey's seed and foliage consumption may be to increase or to help maintain vegetational diversity. Janzen (1970) examined the role herbivores play in tropical forest diversity. He states that "as conditions become more favorable for the seed and seedling predators in a habitat (for example, in moving from moist temperate to moist tropical forests), that habitat will support more species of trees because no one species can become common enough to competitively oust most of the others" (p. 521). Although stating that the most important seed-predators before dispersal are insects, he does include some facultatively host-specific seed-eating vertebrates within his model, particularly monkeys. Proboscis monkeys are

definitely seed eaters; in over 100 fecal samples collected for parasitological analyses (Ranglack and Yeager, 1986) no whole seeds were found (whole seeds were observed in fecal samples from long-tailed macaques). Proboscis monkeys feed extensively upon the seeds of three species that are among the most dominant and most abundant plant species (*Eugenia* sp. 3, *Ganua motleyana,* and *Lophopetalum javanicum*); by acting as partial controls on these species, proboscis monkeys may "increase equitability and permit a larger number of minor plant species to survive in the community" (Whitaker, 1975, p. 103). This increases vegetational diversity, with a concomitant increase in the variety of resources available. Proboscis monkeys, given their relatively large biomass and predilection for the consumption of seeds of dominant tree species, probably play an important role, not only in increasing and maintaining vegetational diversity, but in maintaining and providing suitable habitat for other riverine fauna.

CONCLUSION

Proboscis monkeys are folivore/frugivores, that specialize in seeds. Their ability to switch dietary strategies during times of low food abundance and/or availability is probably the result of specialized physiological adaptations which allow them to use food sources unavailable to other primate species. This ability also allows them to exist at a relatively higher proportion of the primate biomass. Given their higher biomass and predilection for seed consumption, they probably have a significant impact on the vegetation and may help to maintain and to increase vegetational diversity.

ACKNOWELDGMENTS

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