

RESEARCH ARTICLE

Feeding Ecology of Bornean Orangutans (*Pongo pygmaeus morio*) in Danum Valley, Sabah, Malaysia: A 3-Year Record Including Two Mast FruitingsTOMOKO KANAMORI^{1*}, NOKO KUZE², HENRY BERNARD³, TITOL P. MALIM⁴, AND SHIRO KOHSHIMA²¹Department of Biological Sciences, Graduate School of Bioscience and Biotechnology, Tokyo Institute of Technology, Ookayama Meguro-Ku, Tokyo, Japan²Wildlife Research Center of Kyoto University, Kyoto, Japan³Sabah University of Malaysia, Kota Kinabalu, Sabah, Malaysia⁴Sabah Wildlife Department, Kota Kinabalu, Sabah, Malaysia

We observed the diet and activity of Bornean orangutans (*Pongo pygmaeus morio*) in the primary lowland dipterocarp forests of Danum Valley, Sabah, Malaysia, during 2005–2007, including two mast fruitings. We collected 1,785 hr of focal data on 26 orangutans. We identified 1,466 samples of their food plants and conducted a fallen fruit census to monitor fruit availability in the study area. Their activity budget was 47.2% feeding, 34.4% resting, and 16.9% traveling. Fruits accounted for the largest part (60.9%) of feeding time, especially during mast fruiting periods (64.0–100%), although the percentages of leaves (22.2%) and bark (12.3%) were higher than those reported for *P. abelii* and *P. pygmaeus wurmbii*. Although 119 genera and 160 plant species were consumed by focal animals, only 9 genera accounted for more than 3% of feeding time (total: 67.8% for 9 genera). In particular, the focal orangutans fed intensively on *Ficus* and *Spatholobus* during most of the study period, especially in periods of fruit shortage. The percentage of fruit feeding changed markedly from 11.7 to 100% across different months of the year, and was positively correlated with the amount of fallen fruit. When fruit feeding and availability decreased, orangutans fed primarily on leaves of *Spatholobus* and *Ficus*, and the bark of *Spatholobus* and dipterocarp. The percentage of time devoted to feeding during mast fruitings, when the orangutans foraged almost exclusively on fruits, was lower than during seasons when the orangutan diet included leaves and bark as well as fruits. Resting increased as feeding decreased in the late stage of each fruiting season, suggesting that the orangutans adopted an energy-minimizing strategy to survive the periods of fruit shortage by using energy stored during the fruit season. Am. J. Primatol. 72:820–840, 2010. © 2010 Wiley-Liss, Inc.

Key words: Bornean orangutans; feeding ecology; mast fruiting; fallback foods; activity budget

INTRODUCTION

Southeast Asian dipterocarp forests are known for their supra-annual masting events approximately every 2–10 years, during which a majority of trees fruit in synchrony [Ashton et al., 1988]. Masts are periods of tremendous food abundance, permitting high energy intake for various frugivorous vertebrates [Curran & Leighton, 2000; Leighton & Leighton, 1983; Marshall & Leighton, 2006]. However, mast fruitings are often followed by periods of extremely low fruit availability [Knott, 1998]. Low fruit production during intermast intervals has been reported to cause famine-like emaciation or death in the sun bear (*Helarctos malayanus*) and bearded pigs (*Sus barbatus*) in mixed dipterocarp forests of Borneo [Curran & Leighton, 2000; Wong et al., 2005]. In addition to mast-fruiting events, smaller annual and seasonal changes in fruit production also occur [Knott & Kahlenberg, 2006]. Thus, orangutans, the frugivorous great apes living in Southeast

Asian tropical forests, experience much greater inter- and intra-annual variability in fruit production than do frugivorous primates in African and South American rain forests [Fleming et al., 1987].

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However, detailed information on their feeding ecology, especially during mast fruiting and their response to the drastic fluctuations in fruit availability, is limited [Knott, 1998; Morrogh-Bernard et al., 2009; Wich et al., 2006].

Pongo pygmaeus morio is the most eastern subspecies of Bornean orangutan, and inhabits forests in which mast-fruiting events occur in more tree species and individual trees than reported for habitats of other Bornean orangutan subspecies (*P. pygmaeus wurmbii* and *P. pygmaeus pygmaeus* in the central and western Borneo), and the Sumatran orangutan (*P. abelii*) [Curran et al., 1999; van Schaik et al., 2009a; Walsh, 1996]. Mast-fruiting events in Sumatra are less prominent than in Borneo because fewer mast-fruiting tree species exist in those forests [van Schaik, 1996]. Moreover, the influence of the El Niño/Southern Oscillation on mast fruiting is reportedly strongest in the eastern part of Borneo [Ashton et al., 1988; Wich & van Schaik, 2000]. Thus, *P. pygmaeus morio* living in the dipterocarp forests of East Kalimantan and Sabah, experience dramatic fluctuation in fruit availability [Leighton & Leighton, 1983; Rijksen & Meijaard, 1999]. *P. pygmaeus morio* exhibits the most robust jaw and smallest skull of any orangutan taxa, suggesting that this species has adapted to ecological conditions different from those of other Bornean subspecies and the Sumatran orangutan [Taylor, 2006, 2009; Taylor & van Schaik, 2007]. Thus, the study of *P. pygmaeus morio* is important for understanding orangutan feeding ecology and their ability to adapt to fluctuations in fruit availability. Earlier studies on *P. pygmaeus morio* have been conducted by Mackinnon in Ulu Segama and by Rodman and Leighton in Mentoko [Leighton, 1993; Mackinnon, 1974; Rodman, 1988]. Since these studies, however, detailed studies of the ecology of this subspecies in primary dipterocarp forests has not been undertaken, although studies have been conducted in logged forests in Kinabatangan, Sabah [Ancrenaz & Lackman-Ancrenaz, 1999; Ancrenaz et al., 2004, 2005].

In this study, we conducted field research on the feeding behavior and activity budget of *P. pygmaeus morio* living in the primary lowland dipterocarp forests of Danum Valley, Sabah, Malaysia, from 2005 to 2007, including two mast fruiting periods. We compared seasonal changes in the feeding time allocated to individual food items and plant species, and examined the dietary response of orangutans to major fluctuations in fruit availability.

METHODS

The Study Area

The study area was located in Danum Valley Conservation Area (DVCA, 438 km²), East Borneo, Sabah, Malaysia (Fig. 1A). DVCA is a Class I Protection Forest Reserve established by the Sabah

state government in 1996 and managed by the Sabah Foundation (Yayasan Sabah Group) for conservation, research, education, and tourism. The study area (5°01'17"N, 117°44'50"E, 231–384 m a.s.l.) is a primary forest of approximately 2 km² surrounding a tourist lodge, Borneo Rainforest Lodge (BRL). BRL was established in 2004 on the banks of the Danum River, a tributary of the Segama River. The forest is composed predominantly of lowland dipterocarp forest, interspersed with some lower-hill dipterocarp forest. Canopy height is approximately 50 m, with emergent trees more than 70 m. The mean tree density in this area was reported to be 470 trees per hectare (>30 cm dbh), and the trees in the forests (>30 cm dbh) included Euphorbiaceae (21%) and Dipterocarpaceae (16%), with basal areas of 7 and 49%, respectively [Newbery et al., 1992]. Approximately 88% of the total volume of the large trees in the conservation area was reported to be dipterocarps [Marsh & Greer, 1992].

Study Period

We conducted field research from March 2005 to December 2007, 27 months in total, although we only obtained limited data in April–May 2005 and November 2005–March 2006. We obtained no data in February 2006 owing to serious flooding in the area. The study period included two mast fruitings (July–August 2005 and May–September 2007). We defined a mast year as one with months in which fruit scores were higher than 1.96 standard deviations above the mean for the study period, following the definition for mast fruiting proposed by Wich and van Schaik [2000].

Climate

The mean, maximum, and minimum temperatures in the study period, recorded at Danum Valley Field Research Centre of DVCA next to the study area, were 27.1°C, 31.7°C, and 22.6°C, respectively (The Royal Society Southeast Asia Rain Forest Research Program, unpublished data). Mean monthly temperatures tended to be higher in April and May and lower in November and December. Annual rainfall in the area varied between 3,083.1 and 2,349.5 mm during 2005–2007. Mean monthly rainfall was 234.8 mm (SE = 22.1), ranging from 60.3 mm in April 2005 to 798.4 mm in February 2006. Although the seasonality of rainfall was not clear during the study period, 10-year mean values of monthly rainfall from 1988 to 2007 show that rainfall in this area tended to be higher in May–June and October–January and lower in March–April and July–September.

Observation of Animals

We observed 26 identified individuals, divided into the following six age–sex classes based on

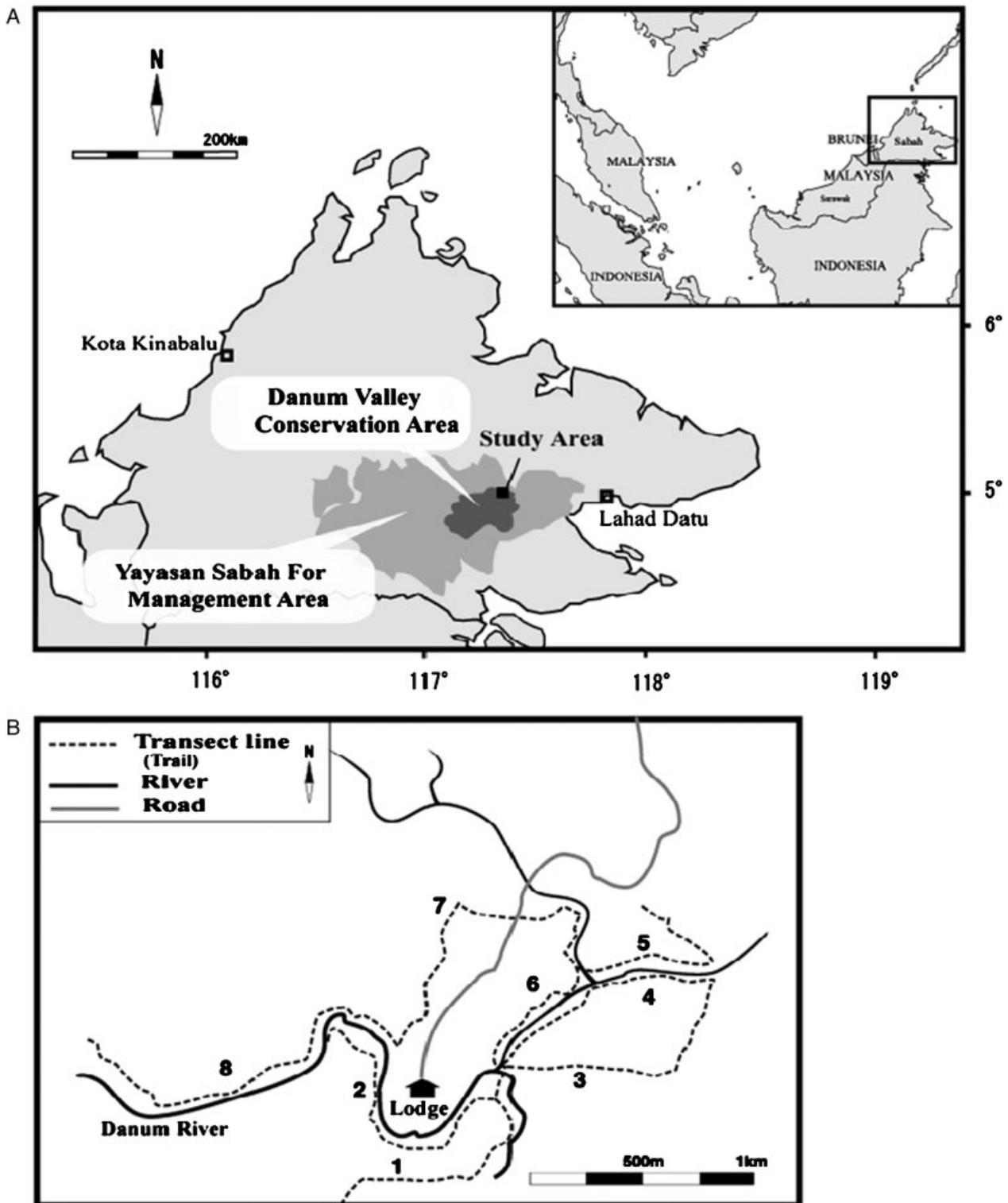


Fig. 1. Map of the study area. (A) The location of the study area, based at Borneo Rainforest Lodge in the state of Sabah, East Borneo. (B) Transect around Borneo Rainforest Lodge.

morphological characteristics [Kuze et al., 2005]: 3 flanged males, 9 unflanged males (UFM), 5 adult females (AF) with a dependent infant, 2 adolescent

females, 2 juveniles, and 5 infants (Table I). In this study, we analyzed the data on time budgets only from the fully habituated individuals that did not

TABLE I. Observation Times of Studied Animals

Age/sex class	Number of individuals	Names	Observation times (hours:minutes:seconds)	Days
Flanged male	3	CLIPPER	145:53:00	17
		KING	44:05:00	6
		PROFESSOR	27:38:00	3
Unflanged male	9	ONI	188:57:00	19
		JACK	72:46:00	7
		TONY	60:57:00	6
		GOTENZ	40:46:00	5
		SAM	20:56:00	2
		GOKU	8:50:00	1
		DENNY	10:23:00	1
		TOCH	114:49:00	11
		KAMCHONG	19:00:00	2
Adult female with an infant	5	YANTI	253:34:00	26
		BETH	208:19:00	22
		SUMI	28:59:00	3
		LINDA	16:58:00	2
		SITI	21:44:00	2
Adolescent female	2	SHEENA	124:34:00	15
		LINA	90:55:00	10
Juvenile female	2	JUN	203:03:00	19
Infant	5	WINA	8:00:00	1
		KAHI	47:35:00	5
		ACO	17:56:00	2
		TOY	8:59:00	1
		YAMATO	0:00:00	0
Total	26	BOB	0:00:00	0
			1,785:36:00	188

show any sign of disturbance. The total observation time of the orangutans was 1,785 hr and 36 min. We followed the focal orangutans from their morning nest to their night nest or until they were lost or abandoned. We recorded their activities (feeding, resting, traveling, and others) and food category every 1 min by direct observation, following a standardized method of orangutan data collection [Morrogh-Bernard et al., 2002]. In the analysis of the activity budget and dietary profile, we excluded the data of juveniles and infants and used only the data from days during which we followed the animals for more than 6 hr, following the method of Harrison et al. [2009].

The study includes data collected and analyzed using protocols approved by the Economic Planning Unit, Prime Minister's Department, and the Sabah Wildlife Department, Danum Valley Management Committee; such protocols adhered to the legal requirements of Malaysia. This research also adhered to the American Society of Primatologists principles for the ethical treatment of nonhuman primates.

Fallen Fruit Census

To estimate fruit availability, we conducted a census of fallen fruits by the line transect method [Furuichi et al., 2001] at the end of each month

during the study period (May 2005–December 2007; 33 months in total). In this census, we used tourist trails as transects because we were prohibited from making new line transects around the tourist lodge. It is possible that this use of tourist trails as transects caused some bias in the results, as the locations of the tourist trails were not random. The trails were about 2 m in width and 11.05 km total length, covering 2 km² (Fig. 1B). In each census session, the same local assistants walked all the trails, recording and sampling the fallen fruits found on the trail. We recorded the number of fallen fruit clusters (aggregation of fallen fruits), number of fruits in each cluster, size (length, width, and height), ripeness, and species of the fruit. In each census session, the number of fruiting trees observed in the area within 30 m of the trails were counted and recorded; trees were marked with tags to avoid double counting. In this study, fruit availability was represented by the following three indices: density of fruit cluster, volume of fallen fruit, and density of fruiting tree. These parameters were calculated only for the ripe fruits on which orangutans have been reported to feed.

Density of Fruit Cluster

We counted an aggregation of fallen fruits on the trail as a cluster even if it contained only one fruit.

Most clusters observed were less than 3 m in diameter, except those of Dipterocarpaceae fruit during mast fruiting periods. We counted the large clusters of Dipterocarpaceae more than 25 m in diameter as an aggregation of clusters with a diameter of 25 m, because the seeds of some Dipterocarpaceae (e.g. *D. crinitus*) were reported to be scattered within a radius of 20.1 m from the mother tree [Osada et al., 2001]. We could specify one mother tree for each fruit cluster in the area within 30 m of the trail in most cases (86.5%).

Volume of Fallen Fruit

This index (F) was calculated by the following formula: $F = \Sigma(V_i \times N_i)/T$, where V_i is the volume of each fruit, N_i is the number of fruits in each cluster, and T is the area within 2 m of the trails that was measured on a map with computer software NIH Image (<http://rsb.info.nih.gov/nih-image/>). The volume of each fruit was estimated from its dimension (a: major axis, b: minor axis, c: height) and the formula for ellipsoid volume ($V_i = 4\pi abc/3$), assuming that many fruits are close to this shape.

Density of Fruiting Tree

This index (Fd) was calculated by the following formula: $Fd = C/T$, where C is the number of fruiting trees observed in the area within 30 m of the trail, and T denotes the area within 30 m of the trail that was measured on a map with computer software, NIH Image.

Preference Index

This index (P) was calculated with the following formula:

$P = F_i/A_i$, where F_i is the ratio of each fruit type during feeding time and A_i is the ratio of each fruit type in the fallen fruit volume.

Statistics

Differences in food and activity budget between AF and UFM were analyzed using a Mann–Whitney

U test. Correlations between the feeding time on each food category and fruit availability indices and those among feeding, resting, and traveling time were analyzed using Spearman's rank correlation coefficient. Differences in the percentage of feeding time on each food plant genus and category by fruit-feeding periods were analyzed using the Tukey–Kramer HSD test for multiple comparisons that is recommended for unequal sample sizes [Sokal & Rohlf, 1995]. Statistical significance for all tests was set at $P < 0.05$ or $P < 0.01$. Data were presented as mean \pm standard deviation. The KyPlot Edition 5.0 statistical package was used for the analyses.

RESULTS

Overall Diet Composition: General Features

In Danum Valley, feeding time on fruits accounted for the largest part (60.9%) of the orangutan activity budget. Feeding time on leaves, bark, and the “other” food category accounted for 22.2, 12.3, and 4.6%, respectively (Table II). The “other” food category included flowers (2.48%), climbing bamboo (0.44%), monocotyledons (0.10%), ginger on the ground (0.30%), epiphyte (0.08%), fungi (0.007%), moss (0.007%), insects (0.55%), soil (0.004%), and unknown (0.63%). Almost all the orangutan feeding time was spent in trees (99.1%) and consuming plant parts (99.4%).

The percentage of feeding time for each food category did not differ significantly between UFM and AF (Table III; fruits: $N^{\text{UFM}} = 52$, $N^{\text{AF}} = 50$, $U = 1,378$, $P = 0.6$; leaves: $U = 1,266$, $P = 0.8$, bark: $U = 1,222$, $P = 0.6$; flower: $U = 1,386$, $P = 0.5$; insect: $U = 1,280$, $P = 0.8$; others: $U = 1,231$, $P = 0.6$).

We collected and identified 1,466 samples of the orangutans' food plants during 1,707 observations of plant feeding. We identified food plants from 119 genera (54 families), estimated to contain at least 160 species (Table II; Appendix A).

Although the list of food plants includes a large variety of species, orangutans in the study area

TABLE II. Food Plant at Danum Valley

Food category	Feeding time (%)		Family		Genus		Species
	Mean	Monthly range ^a	Number of identified	Number of major family ^b	Number of identified	Number of major genus ^b	Number of identified
Fruits	60.9%	11.7–100%	41	9 (79.8%)	77	6 (61.7%)	103
Leaves	22.2%	0.0–53.3%	30	4 (82.5%)	43	6 (85.7%)	57
Bark	12.3%	0.0–29.3%	19	4 (86.1%)	28	6 (82.0%)	36
Flowers	2.5%	0.0–17.4%	8	5 (96.5%)	9	6 (95.7%)	9

Total feeding time was 762 hr and 33 min.

^aMonthly ranges: the lowest and highest monthly values recorded from May 2005 to December 2007.

^bNumber of major family and genus that accounted for more than 3% of the feeding time on that food category. The value in parenthesis: total percentage of these major families or genera in feeding time on that food category.

TABLE III. Percentage of Feeding Time on Each Food Category in Each Age-Sex Class

Age-sex class (N)	Fruits	Leaves	Bark	Flowers	Insects	Others
Flanged male (3)	19.3 (0.0–50.7)	60.3 (27.1–82.8)	16.9 (15.3–18.4)	0.9 (0.0–2.3)	0.0 (0.0–0.0)	2.6 (0.0–6.4)
Unflanged male (7)	58.8 (0.0–83.1)	24.5 (0.0–45.4)	13.3 (0.0–21.1)	1.3 (0.0–3.7)	1.2 (0.0–9.5)	0.9 (0.0–1.9)
Adult female (5)	60.0 (34.8–69.9)	22.2 (18.2–32.7)	14.2 (3.3–32.1)	1.2 (0.0–4.9)	1.2 (0.0–5.4)	1.2 (0.0–3.7)
Adolescent female (2)	53.4 (38.3–68.4)	24.9 (20.4–29.3)	13.5 (7.8–19.2)	5.9 (2.5–9.3)	1.0 (0.0–1.9)	1.4 (0.0–1.9)

No significant difference was detected in all food categories between unflanged male and adult female (Mann-Whitney U tests, $P > 0.05$). The number of analyzed individuals of flanged males and adolescent females was not enough for statistical analysis.

intensively fed on a relatively limited number of taxa; nine genera, including ten species, each accounted for more than 3% of total feeding time (Tables II, IV). Feeding time on these major genera accounted for 67.8% of the total feeding time. In particular, *Ficus*, *Spatholobus*, and *Diospyros*, the top-ranked three genera, accounted for 42.9% of total feeding time. In most species of these three genera, various parts of the plants, including fruit, leaf, and bark, were foraged on during several months of the study. The density of these genera, especially *Ficus*, *Diospyros* and *Parashorea*, were higher than other genera (we could not estimate the density of lianas, such as *Spatholobus* and *Artabotrys*).

The most commonly foraged fruit genera were *Ficus* (27.2%), *Terminalia* (9.2%), and *Diospyros* (7.4%). In particular, the orangutans intensively fed on fruits of *F. virens* (11.0%), *T. citrina* (9.2%), *Alangium javanicum* (6.0%), *A. rosea* (4.4%), *F. microcarpa* (4.3%), and *D. macrophylla* (3.8%). Seventy-one percent of fruit-feeding time was spent consuming fruits with soft pulp, and 28.7% was spent feeding consuming hard fruits, such as acorns with hard skins and pulp. Given the proportion of soft (49.3%) and hard fruits (51.7%) that we collected on the ground, there is clear evidence that the orangutans preferred soft fruits to hard fruits. (preference index was 1.45 for soft fruits and 0.56 for the hard fruits).

Spatholobus leaves accounted for 38.3% of total leaf feeding time and *Ficus* leaves accounted for 15.0% of total leaf feeding time. In particular, the animals fed intensively on the leaves of *S. macropterus* (23%), *S. hirsutus* (5.6%), *F. benjamina* (3.3%), and *Xanthophyllum ecarinatum* (4.0%). In our observations, the orangutans typically fed on young leaves near the tip of the branch and rarely fed on mature leaves.

During our study, the orangutans fed intensively on the bark of *S. macropterus* (44.1%). When the orangutans fed on the bark of *Spatholobus*, they fed on the small stems near the tips of the branches. In contrast, when they fed on the bark of Dipterocarpaceae, they peeled off bark strips from the tree trunks, chewed the inner side of the bark strips (cambium), and regurgitated residue wadges. The most common flower species exploited by the orangutans were *Dillenia excelsa* (26.6% of the total

flower feeding time), *Poikilospermum* spp. (22.3%), and *Ludekia borneensis* (21.6%).

Seasonal and Supra-Annual Changes

Fruit Availability

Four parameters of fruit availability namely: the volume and cluster number of the edible fallen fruits (Fig. 2A) and the density and the number of genera producing fruits, along the observation trails (Fig. 2B), were characterized by marked changes both seasonally and supra-annually during the study period. In Figure 2A, there is evidence of two large peaks in the volume of fallen fruits during June–August 2005 and July–August 2007. In addition, in August 2005 and July 2007, there was a significant increase in fruit cluster number and fruiting tree density; we refer to these as the mast fruiting periods of 2005 and 2007. The number of fruiting genera also increased in August 2005 and June 2007. During these mast fruiting events, many dipterocarp trees fruited, as did various other tree species. In addition to these large fruiting peaks, we also identified smaller peaks in the volume of fallen fruits in July and December 2006, and February 2007. The cluster number, fruiting tree density, and the number of genera also increased between May and September 2006 and between January and March 2007 (Fig. 2A, B).

Additionally, increases in the volume and cluster number of fallen fruits and the density of fruiting trees, in January and March 2006, suggested peaks in these parameters between January and March, although we have no data for February 2006 owing to serious flooding at that time.

Based on the results, we defined fruit seasons as those periods characterized by peaks in one or more of the four fruiting measures and scored them as HA (high fruit availability) I–V; June–August 2005, January–March and May–September 2006, December 2006–March 2007, and June–August 2007, respectively. We also identified six periods with very low fruit availability. We defined these low fruit seasons as the periods covering all corresponding troughs of the four fruiting measures and scored them as LA (low availability) I–VI; April–May and October–December 2005, April–May and October–November 2006, and April–May and October–December 2007.

TABLE IV. Food Plants that Accounted for More than 3% of the Total Feeding Time

Rank	Genus (family)	Species ^a	% to the total feeding time	Eaten parts ^b	Rate of the months when the genus was eaten	Tree density in the area along the transect (tree/ha) ^c
1	<i>Ficus</i> (Moraceae)	<i>virens</i> 7.0%, <i>microcarpa</i> 2.7%, <i>benjamina</i> 1.3%, <i>punctata</i> 0.6%, <i>trichocarpa</i> 0.6%, <i>trichocarpa</i> 0.6%, <i>trichocarpa</i> 0.6%, <i>pumila</i> 0.5%, <i>callosa</i> 0.3%, <i>elastica</i> 0.2%, <i>stupenda</i> 0.06%, <i>xylophylla</i> 0.005%, U-spp. 7.8%	21.2	fr, le, bk	0.7 (23/27)	0.81
2	<i>Spatholobus</i> (Fabaceae)	<i>macropterus</i> 9.6%, <i>hirsutus</i> 1.2%, U-spp. 4.2%	14.9	fr, le, bk, fl	0.9 (24/27)	-
3	<i>Diospyros</i> (Ebenaceae)	<i>macrophylla</i> 3.1%, <i>frutescens</i> 0.8%, <i>tuberculata</i> 0.6%, <i>borneensis</i> 0.3%, <i>toposoides</i> 0.2%, <i>elliptifolia</i> 0.1%, <i>diepenhorstii</i> 0.03%, U-spp. 1.7%	6.8	fr, le, bk	0.6 (22/27)	0.39
4	<i>Terminalia</i> (Combretaceae)	<i>citrina</i> 5.9%	5.9	fr	0.2 (6/27)	0.03
5	<i>Artabotrys</i> (Annonaceae)	<i>rosea</i> 3.5%, U-spp. 0.9%	4.4	fr, le	0.7 (18/27)	-
6	<i>Durio</i> (Bombacaceae)	<i>zibethinus</i> 1.1%, <i>kutejensis</i> 0.05%, sp1 0.4%, U-spp. 2.5%	4.1	fr, le	0.5 (13/27)	0.06
7	<i>Alangium</i> (Alangiaceae)	<i>javanicum</i> 4.1%	4.1	fr, le	0.3 (9/27)	0.33
8	<i>Dacryodes</i> (Bursaceae)	sp1 1.7%, sp2 0.8%, sp3 0.5%, U-spp. 0.1%	3.3	fr, le	0.1 (3/27)	0.01
9	<i>Parashorea</i> (Dipterocarpaceae)	<i>tomentella</i> 1.8%, <i>malaanonan</i> 1.2%, U-spp. 0.06%	3.1	fr, le, bk, fl	0.5 (14/27)	0.39
10-119	Others (102 genus)		32.2			
Total	119 (54)	160	100			

Total feeding time was 692 hr and 32 min.

^aU-spp. means samples that we could not identify species.^bfr, fruit/seed; lv, leaves; bk, bark; fl, flower.^cThe density of liana could not be estimated.

These results suggested the existence of two high fruiting seasons (July–August and January–March) and two low fruiting seasons (April and October–November) per year. These fruiting seasons loosely correspond to the period from the end of the rainy to the dry season, and the period at the beginning of the rainy season, respectively.

During the mast fruiting season of 2005 (Fig. 2A), the marked increase in fruit production during July–August was principally owing to the fruiting of five Dipterocarpaceae genera (*Parashorea*, *Dryobalanops*, *Shorea*, *Hopea*, *Vatica*). Fruit production at the peak of these mast fruiting periods were 31 times and 4 times larger than that of the corresponding fruiting season of 2006 (HA III) and the mast fruiting period of 2007 (HAV). During the mast fruiting period of 2007, two Dipterocarpaceae genera (*Parashorea*, *Shorea*) fruited for 5 months, which was longer than that of the 2-month mast fruiting period in 2005.

The increase in fruit production between October and March was due largely to the fruiting of *Ficus* trees (Fig. 2A). The density of *Ficus* trees (>10 cm in dbh) in the study area was 0.81 individuals per hectare (Table IV). The mean density of fruiting *Ficus* trees ranged between 0 and 0.13 individuals per hectare (0.02 ± 0.04 individuals/ha, $n = 33$ months) during the study period.

Diet Composition

The ratio of feeding time devoted to each food category to the total feeding time changed markedly, both seasonally and supra-annually (Fig. 2C). In particular, the percentage of fruit-feeding time ranged from 11.7% and 100%, showing four notable peaks (high fruit-feeding periods, HF I–IV) and three troughs (low fruit-feeding periods, LF I–III) during the study period (Table II) (we have no data during the periods April–May 2005 and November 2005–March 2006). The peaks and troughs of the percentage of time devoted to fruit feeding roughly corresponded with the fruit availability index. Changes in the percentage of fruit feeding was positively correlated with the changes in the volume of fallen fruits ($R = 0.51$, $P < 0.01$, $n = 27$), the cluster number of fallen fruits ($R = 0.46$, $P < 0.05$), and the number of fruiting genera ($R = 0.18$, $P < 0.05$). Changes in the percentage of leaf feeding and bark feeding were negatively correlated with the changes in the volume of fallen fruits ($R = -0.65$, $P < 0.01$, $R = -0.47$, $P < 0.01$, respectively), the cluster number of fallen fruits ($R = -0.38$, $P < 0.05$, $R = -0.43$, $P < 0.01$), and the number of fruiting genera ($R = -0.41$, $P < 0.05$, $R = -0.49$, $P < 0.05$). The change in flower and insect feeding showed no significant correlation with these four parameters of fruit availability. The change in fruiting tree

density was not correlated with the percentage of feeding time devoted to any single food category.

Table V compares the average time feeding on each food category during the high and low fruit-feeding periods. In HF I and HF IV, corresponding to the two mast fruitings (HA I and HA V, respectively), the percentage of time devoted to fruit feeding was significantly greater than during the low fruit-eating periods (Tukey–Kramer HSD test, $P < 0.01$) and during the other high fruit-eating periods (HF IV > HF II, $P < 0.05$). In the low fruit-feeding periods, the percentage of feeding time devoted to leaves and bark was significantly greater than those in high fruit-eating periods ($P < 0.05$).

The food items that accounted for >3% of the total feeding time differed significantly between the high and low fruit-feeding periods (Table V). The most common food item exploited by orangutans throughout the entire study period was *Ficus* fruit. During mast fruiting periods, orangutans fed on more fruit genera (11 genera in both HF I and HF IV) than during other high fruit-feeding periods (4 and 5 genera in HF II and HF III, respectively) and during low fruit-feeding periods (1, 4, and 4 genera in LF I–III, respectively). Six of 11 fruit genera frequently fed on were different between the two mast fruitings. Orangutans fed more on Dipterocarpaceae fruits (12.8% in total; *Parashorea* 8.2%, *Dryobalanops* 4.4%, *Shorea* 0.2%) in HF I than in HF IV (only *Parashorea* 0.8%). In HF III, the percentage of time feeding on *Ficus* fruits was significantly higher than during all other periods (Tukey–Kramer HSD test: $P < 0.01$).

During low fruit-feeding periods, the orangutans fed primarily on leaves of *Spatholobus* (21.0% in mean for LF I–III), *Ficus* (9.5%), and *Durio* (4.4%), the bark of *Spatholobus* (8.4%) and Dipterocarpaceae (*Parashorea* and *Shorea*, 6.7%), and the fruits of *Ficus* (10.7%). Leaves of *Spatholobus*, *Ficus*, and *Durio* also were frequently eaten in the high fruit-feeding periods, including HF I. The bark of *Spatholobus* was frequently eaten during the non-mast fruiting seasons of HF II–III.

Ficus, *Spatholobus*, and *Diospyros* accounted for 52.4–62.6% of feeding time during the low fruit-feeding periods and 69.8% of feeding time during HF III. Even during mast fruiting periods, foods from these three genera accounted for 19.7–29.2% of total feeding time. These results indicate that orangutans in the study area depended on a relatively limited number of food plants during the study period, although food species diversity increased during mast fruiting periods.

Activity Budget

Orangutans in the study area spent 47.2% (24.0–70.7%) of the observation time feeding, 34.4% (13.1–63.5%) resting, 16.9% (4.8–26.6%) traveling,

TABLE V. Comparison of Major Food Plants ($\geq 3\%$ of the Feeding Time) During High and Low Fruit-Feeding Periods

Food category	Genus ^a	Fruiting cycle/seasonality ^b	High fruit-feeding periods ^c				Low fruit-feeding periods			
			HFI (a) ^d June–October 2005 5 months	HFI (b) June–October 2006 5 months	HFI (c) January–March 2007 3 months	HFI (d) June–December 2007 7 months	LFI (e) April–May 2006 2 months	LFII (f) November–December 2006 2 months	LFIII (g) April–May 2007 2 months	
Fruits $\geq 3\%$	<i>Ficus</i>	Sporadic	8.0	15.8	45.3 ($> a, b, d, e, f, g^{**}$)	6.7	17.5	6.9		
	<i>Diospyros</i>	Sporadic	3.3 ($> f^{**}$)	($> f^{**}$)	8.5 ($> f^{**}$)	8.9 ($> f^{**}$)	($> f^{**}$)	7.1 ($> f^{**}$)		3.5
	<i>Artabotrys</i>	Sporadic	11.2			8.9 ($> b^*$)				
	<i>Polyalthia</i>	Sporadic	3.6			3.1				
	<i>Chisocheton</i>	Annual/unclear	5.1			5.1				
	<i>Dryobalanops</i> (D)	Supra-annual	4.4							
	<i>Tetrastigma</i>	Supra-annual	4.4							
	<i>Artocarpus</i>	Supra-annual	3.1							
	<i>Shorea</i> (D)	Supra-annual	8.4							
	<i>Terminalia</i>	Annual/clear	6.2	17.6 ($> a, c, e, d^{**}$)						
	<i>Garcinia</i>	Annual/clear	6.6							
	<i>Dacryodes</i>	Supra-annual		11.0					3.6	
	<i>Bauhinia</i>	Annual/unclear			6.3 ($> a, e^*, b^{**}$)					
					4.2					
	<i>Parashorea</i> (D)	Supra-annual		7.9	7.5					
	<i>Alangium</i>	Annual/clear				8.6				
	<i>Durio</i>	Annual/clear				7.5				
	<i>Spatholobus</i>	Annual/unclear				4.9			4.3	
	<i>Canarium</i>	Annual/unclear				7.2				
	<i>Dimocarpus</i>	Supra-annual				4.6				
	<i>Zizyphus</i>	Supra-annual				3.7				
	<i>Barringtonia</i>	Annual/unclear							4.2	
	<i>Microcos</i>	Annual/unclear								5.4
Leaves $\geq 3\%$	<i>Spatholobus</i>		5.5	7.5			29.4 ($> a, b, c, d^{**}$)	23.1 ($> a, b, d^{**}, c^*$)	10.5	13.6 ($> b^{**}, g^*$)
	<i>Ficus</i>			3.5					5.3	5.4
	<i>Durio</i>			3.4			3.5		4.0	
	<i>Diospyros</i>						4.5		3.1	
	<i>Xanthophyllum</i>								6.5	
Bark $\geq 3\%$	<i>Spatholobus</i>			6.6	10.8 ($> a^{**}$)					14.1 ($> a^*, d^{**}$)

TABLE V. Continued

Food category	Genus ^a	Fruiting cycle/seasonality ^b	High fruit-feeding periods ^c			Low fruit-feeding periods			
			HFI (a) ^d	HFII (b)	HFIII (c)	HFIV (d)	LFI (e)	LFII (f)	LFIII (g)
	<i>Parashorea</i> (D)								
	<i>Shorea</i> (D)								
	<i>Diospyros</i>								
	<i>Lithocarpus</i>								
	<i>Ludokia</i>								
Flowers ≥ 3%									
Total of fruits (%)			82.7 (> e, f, g ^{**})	64.8 (> e, f ^{**})	66.6 (> e, f ^{**} , g [*])	93.7 (> b [*] , e, f, g ^{**})	20.2	20.2	29.2
Total of leaves (%)			12.6	20.7	17.9	2.3	44.6 (> a, b, c, d ^{**})	33.2 (> a, b, d [*])	42.6 (> a, d, c ^{**} , b [*])
Total of bark (%)			3.9	10.2	14.5	0.0	25.6 (> a, d ^{**})	25.6 (> a, d ^{**})	40.7 (> a, d ^{**})
Total of flowers (%)			0.3	2.4	0.6	0.0	2.0	2.0	23.8
Others (%)			0.5	1.9	0.4	4.0	0.0	0.0	6.4
The number of observed individuals (day)			12 (36)	10 (43)	5 (15)	11 (42)	6 (15)	6 (10)	6 (9)

^a(D): genus belonging to the family Dipterocarpaceae.

^bFruiting patterns: sporadic (fructed several times in a year), annual (fructed every year with clear or unclear seasonality), and supra-annual (fructed only once or only in the mast fruitings).

^cHF: high fruit-feeding period; LF: low fruit-feeding period (see Fig. 2).

^dWe abbreviated HFI, HFII, HFIII, HFIV to a, b, c, d, and LFI, LFII, LFIII to e, f, g, respectively.

Significant differences among seven fruit-feeding periods for each food plant genus or food category were shown in parenthesis (Tukey–Kramer post hoc test, * $P < 0.05$, ** $P < 0.01$). Genus with a significant difference was underlined.

and 1.5% (0.3–4.3%) in other activities, such as nest making, play, and social behaviors. The activity budget differed little between UFM and AF (Table VI). AF spent a significantly longer time feeding (Mann–Whitney *U*-test: $N^{AF} = 50$, $N^{UFM} = 52$, $U = 1691$, $P < 0.01$) and a shorter time resting ($U = 958$, $P < 0.05$) than did UFM. However, the differences were less than 10%, and no significant differences were detected in traveling time ($U = 1388$; $P = 0.56$).

The percentages of traveling and other activities did not show marked changes across seasons, although traveling increased slightly during HF I and II (Fig. 3A). In contrast, the percentage of time spent feeding changed markedly, showing a significant negative correlation with the percentage of resting time (Spearman, $R = -0.87$, $P < 0.01$, respectively, $n = 27$). The percentage of feeding time was higher than the mean value for that measure, during August–September 2006 (HF II)

TABLE VI. Active Budget of Each Age–Sex Class in Percentage

Age–sex class (N)	Feeding	Resting	Traveling
Flanged male (3)	56.6 (30.8–69.4)	33.7 (24.3–63.5)	8.0 (5.5–8.8)
Unflanged male (9)	41.2 (0.0–52.5)	40.6 (27.7–97.5)	16.7 (2.3–31.2)
Adult female (5)	50.6 (31.7–58.3)	31.3 (21.2–46.6)	16.6 (13.5–20.6)
Adolescent female (2)	53.5 (53.0–53.8)	24.2 (20.9–26.7)	21.2 (18.8–24.4)

Data were shown as percentage in the total observation time with range among individuals. N, number of observed individuals. Unflanged males fed less and rested more than adult female significantly (Mann–Whitney *U* tests, $*P < 0.05$, $**P < 0.01$). The number of analyzed individuals of flanged males and adolescent females was not enough for statistical analysis.

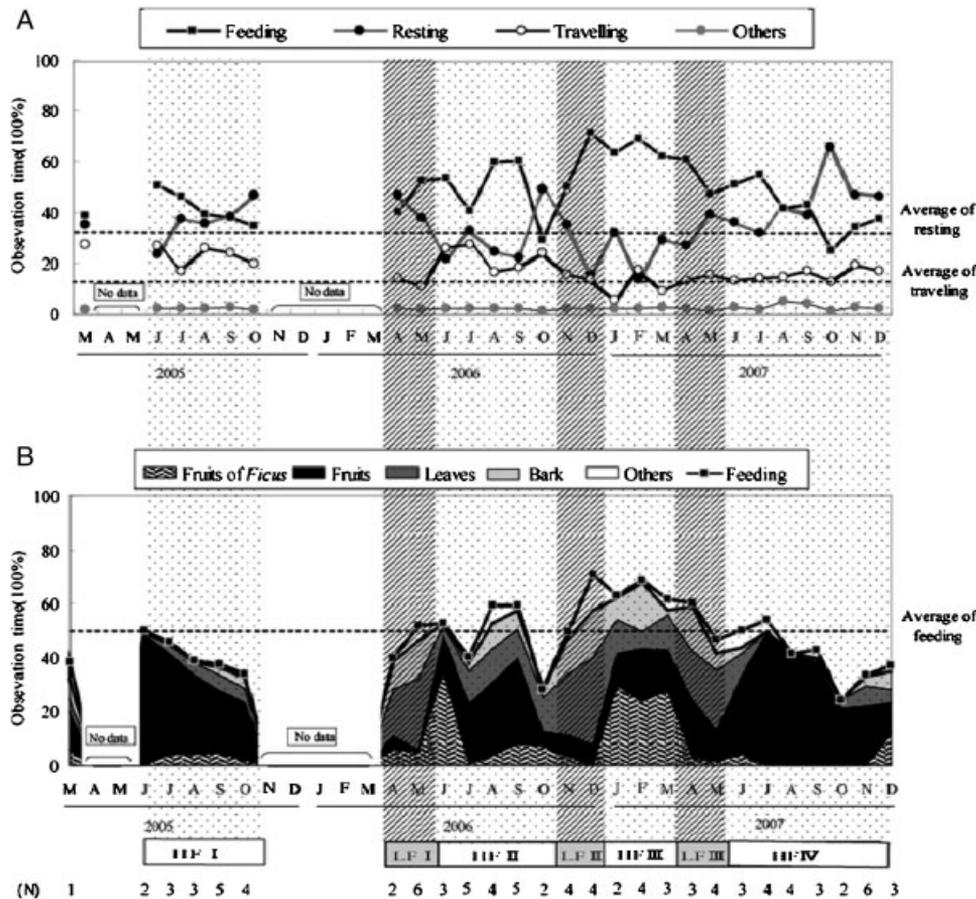


Fig. 3. Change in activity budget and time percentage of the feeding on each food category. (A) Active budget, (B) percentage of feeding time on each food category to the total observation time. Data for all age–sex classes are pooled. HF, high fruit-feeding period (shaded with dots); LF, low fruit-feeding period (shaded with slash lines) (see Fig. 2); N, the number of observed individuals in each month.

and December–April 2007 (around HF III), when orangutans frequently fed on leaves and bark as well as fruit (Fig. 3B). In contrast, the percentage of feeding time approximated the mean value at the beginning of the mast fruiting periods (HF I and IV), when the orangutans fed almost exclusively on fruits, but decreased continuously during the subsequent fruiting period (July–October in both 2005 and 2007). The percentage of feeding time on *Ficus* fruits during mast fruitings (HF I and IV) was smaller than during other fruiting seasons (HF II and III). As feeding time decreased in the later stages of mast fruitings, resting time increased. A similar decrease in feeding time and increase in resting time was observed in the last stage of HF II (August–October 2006).

DISCUSSION

Characteristics of the Diet of *P. pygmaeus morio* in Danum Valley

The percentage of time orangutans in Danum Valley fed on fruit, including during two mast fruiting periods, was higher than that observed at Mentoko and Ulu Segama, early study sites of

P. pygmaeus morio in mixed dipterocarp forest (Fig. 4) [Mackinnon, 1974; Rodman, 1988]. However, during other times of the year, time engaged in fruit feeding by Danum Valley orangutans (50.4%) was similar to that reported at Mentoko and Ulu Segama. At these latter two sites, data on orangutan feeding behavior did not include periods of mast fruiting.

The dietary composition of *P. pygmaeus morio* at Danum Valley, Mentoko, and Ulu Segama was similar, however, in an overall decrease in fruit and insect feeding and an increase in leaf and bark feeding compared with Sumatran orangutans (*P. abelii*) [Fox et al., 2004; Wich et al., 2006] and other subspecies of Bornean orangutans (*P. pygmaeus wurmbii*) [Galdikas, 1988; Knott, 1998]. The pattern seen at our site seems to characterize orangutans living in mixed dipterocarp forests with high fruiting seasonality and mast fruiting where peaks of high-quality fruit production are followed by extended periods of low fruit availability [Morrogh-Bernard et al., 2009; Wich et al., 2006].

Our results indicate that *P. pygmaeus morio* in the study area, markedly altered their diet in response to changes in seasonal and supra-annual

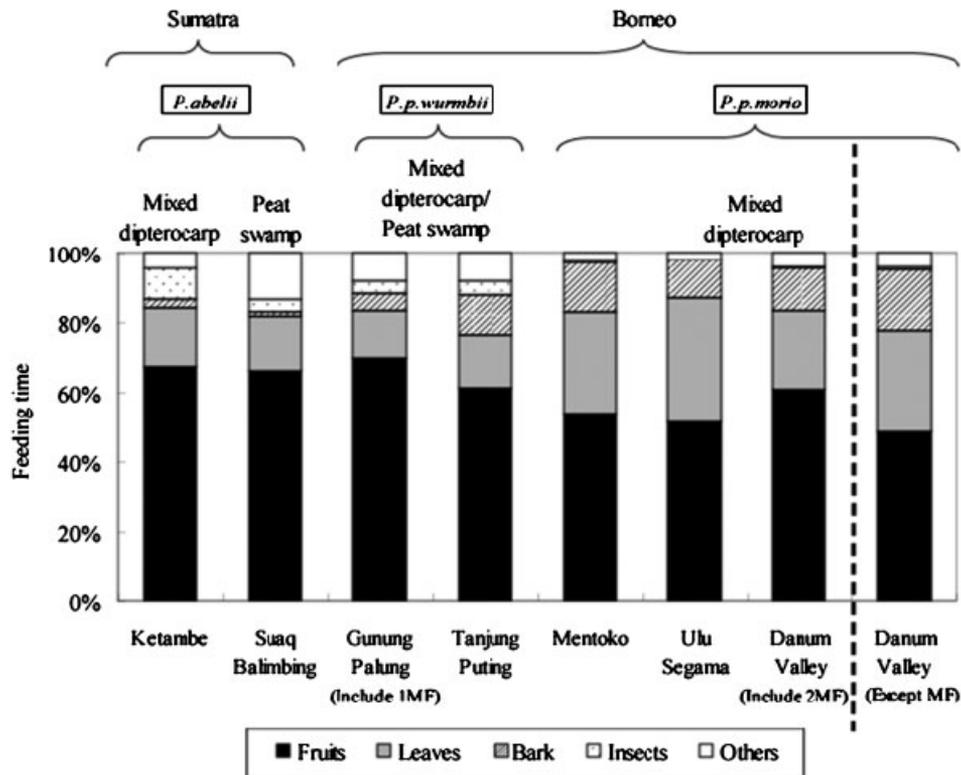


Fig. 4. The percentage of feeding time on each food category at Danum Valley, compared with other seven sites. (1) Data of Gunung Palung and Danum Valley include those during mast fruitings (MF). (2) Data of Danum Valley excluding those during two mast fruitings is shown separately (figure with “Except MF”). (3) Data of other sites are from Wich et al., 2006 (Ketambe), Fox et al., 2004 (Suaq Balimbing), Knott, 1998 (Gunung Palung), Galdikas, 1988 (Tanjung Puting), Rodman, 1988 (Mentoko), and Mackinnon, 1974 (Ulu Segama).

fruit availability. The positive correlation between the percentage of time for fruit feeding and availability, and the fact that the orangutans foraged almost exclusively on fruit during the peak of the mast fruiting (Fig. 2), suggest a dietary pattern of maximizing fruit/energy intake. In this regard, fruit represents a higher energy resource than leaves or bark. Knott [1998], who studied *P. pygmaeus wurmbii* in Gunung Palung, also reported a significant increase in fruit feeding during a fruit masting period. At our study site, however, the proportion of leaf and bark feeding was high, even during periods of high fruit availability (Fig. 3B). It has been suggested that Sumatran forests are more productive in some key orangutan food trees than Bornean forests [MacKinnon et al., 1996; Marshall et al., 2009a; Rijksen & Meijaard, 1999], and this may account for the fact that orangutans in Danum Valley devoted less time to fruit feeding than orangutans in Sumatra. Morphological data indicate that *P. pygmaeus morio* has a more robust jaw and smaller skull than other orangutan taxa [Taylor, 2006, 2009; Taylor & van Schaik, 2007]. Thus, it is possible that these anatomical changes represent an adaptation to habitats of limited productivity requiring the increased consumption of harder foods, such as bark, instead of softer ripe fruits [Taylor, 2006, 2009; Taylor & van Schaik, 2007]. The increased proportion of leaf and bark feeding in *P. pygmaeus morio* compared with *P. pygmaeus wurmbii* or *P. abelii* supports this view.

Orangutans in the study area consumed a diverse set of plants taxa. However, they intensively foraged on a relatively limited number of plant species, especially during nonmast fruiting periods. Although quantitative data comparable to our results are limited, a similar tendency was reported for *P. pygmaeus wurmbii* in Tanjung Puting [Galdikas, 1988]. Despite the fact that *P. pygmaeus wurmbii* at Tanjung Puting consumed resources from 229 plant species, only 24 plant species each accounted for more than 1% of feeding time (in total, they accounted for 61% of total feeding time). At that field site, *Gironniera nervosa* (leaves, bark, fruit, and possibly flowers; 10% feeding bouts) and *X. rufum* (bark, fruit, flowers, and leaves; 6% feeding bouts) were reported to be the most important food sources [Galdikas, 1988]. In Danum Valley, however, neither of these two plant species was eaten by the orangutans. At our study site, *S. macropterus* (liana) (leaves, bark, fruits, and flowers; 9.6% feeding time) and *F. virens* (tree) (fruits, leaves, and bark; 7.0%) were consumed most frequently. This difference in food choice is likely the result of differences in the vegetation at the two research sites. As indicated by Galdikas, large figs were virtually absent at her study site, which was comprised of mixed dipterocarp forest (63% of the area) and

peat swamp forest (27%) [Galdikas, 1988]. In Danum Valley, large figs (strangler figs) are common, and our site is a mixed dipterocarp forest along the river.

At our study site, orangutans frequently consumed the fruits of *Ficus* and *Diospyros* and the leaves and bark of *Spatholobus*, especially outside the mast fruiting period (Table V). *Ficus*, *Diospyros*, and *Spatholobus* represent the major food plants for *P. pygmaeus morio* at our study area. At the same time, *Ficus* fruits, *Spatholobus* leaves, and the bark of Dipterocarpaceae trees (especially *Parashorea*) represent important “fallback foods,” because they provide the major food items consumed by the orangutans during periods of fruit shortage (Table V). The term “fallback food” is generally used to refer to an abundant food of relatively low quality that is used during a period of low overall food availability [Hanya, 2004; Knott, 2005; Laden & Wrangham, 2005; Lambert et al., 2004; Wrangham et al., 1998]. Because many species of *Ficus* and *Diospyros* fruit several times a year and *Spatholobus* produces new leaves all year round, these foods were available during most of the study period. Additionally, the density of these tree species, especially *Ficus* and *Parashorea*, was high in the study area (Table IV). However, as is the case of the leaves and bark of *Spatholobus* and *Parashorea*, the nutritional quality of *Ficus* fruits is not high, as they generally contain significant amounts of fiber and are lower in energy than other fruits [Leighton, 1993].

The fruits of *Ficus* have been reported to be fallback foods for various primates and birds in the rain forests of Borneo and Central and South America [Leighton & Leighton, 1983; Terborgh, 1986]. Because strangler figs produce fruit year round, it has been reported that orangutans consume this fruit throughout the year [Sugardjito et al., 1987]. Sumatran orangutans (*P. abelii*) in Ketambe are reported to forage on *Ficus* fruits only when other fruits were scarce [Wich et al., 2006]. In Danum Valley, time devoted to *Ficus* fruit feeding was very low during mast fruiting periods compared with other fruit seasons (Fig. 3B), suggesting that the animals foraged for more nutritious fruits than *Ficus* during mast fruitings. That is, *P. pygmaeus morio* in our study area frequently foraged for low-quality, but always abundantly available, fallback foods, such as *Ficus* fruits and *Spatholobus* leaves, during both periods of fruit shortage and during the regular fruit season (but not during mast fruiting periods). It is possible, however, that the lower amount of fruit production documented during the regular fruiting seasons (especially in July 2006; Fig. 2A) did not reach normal levels. Data from other sites indicate that mast fruiting events are often followed by periods of extremely low fruit availability [Knott, 1998].

Sexual Difference in Activity Budget

Overall, we found evidence of sex-based differences in activity budget, similar to those reported for *P. pygmaeus morio* at other study sites and *P. abelii* (Table VI). In the Danum Valley, AF spent a significantly greater proportion of their activity budget feeding than UFM, and UFM spent a significantly greater time resting than AF. In *P. pygmaeus morio* at Mentoko and *P. abelii* at Ketambe and Suaq Balimbing, AF also were reported to feed for a significantly greater proportion of their activity budget than flanged and UFM [Fox et al., 2004; Mitani, 1989; Morrogh-Bernard et al., 2009; van Schaik et al., 2009b; Wich et al., 2006].

Changes in Activity

In our results (Fig. 3A), the percentage of the activity budget devoted to feeding during the mast fruiting period, when the animals foraged almost exclusively on fruit, was lower than during other fruiting seasons when leaf and bark consumption increased. This is probably because leaves and bark require greater processing time than fruits [Hladik, 1977]. Knott, who studied changes in caloric intake in *P. pygmaeus wurmbii* with changes in fruit availability reported that the caloric intake of orangutans during a mast fruiting was 2–5 times higher than that during a period of fruit shortage because orangutans increased their consumption of high-energy fruits [Knott, 1998; Knott & Kahlenberg, 2006]. *P. pygmaeus wurmbii* were reported to store large amounts of energy as fat during a mast fruiting [Knott, 1998]. In contrast, they lost weight during periods of fruit shortage, and ketones, products of fat metabolism, increased in their urine. This suggests that orangutans survive periods of fruit shortage using fats stored during periods of high fruit abundance [Knott, 1998; Robinson & Williamson, 1980]. In our results (Fig. 3A), resting increased as feeding decreased in the late stage of every fruit season, although a proportion of the activity budget devoted to traveling showed no major changes. This may indicate that orangutans exhibit a foraging strategy of storing energy during periods of fruit abundance to survive during periods of fruit shortage. Morrogh-Bernard et al. [2009], who compared the activity budget and diet of orangutans in various habitats, proposed that orangutans have two foraging strategies depending on the habitat in which they live. One, a “sit and wait” strategy, conserves energy by resting (and digesting low quality food) during periods of low fruit availability. The second is a “search and find” strategy, in which the orangutans feed continuously and move in search of high energy food. Our results suggest that *P. pygmaeus morio* adopted the “sit and wait” strategy. In contrast, Mackinnon [1974], who

studied *P. pygmaeus morio* in a mixed lowland dipterocarp forest of Ulu Segama, Sabah, reported that orangutans spent more time traveling, presumably in search of food, when fruit was scarce, suggesting a “search and find” strategy.

The results of this study indicate that in the primary low-land dipterocarp forests of northeastern Borneo, *P. pygmaeus morio* survive in a habitat with marked temporal fluctuations in fruit availability [Leighton & Leighton, 1983; Rijksen & Meijaard, 1999] and focus their feeding efforts on a relatively small number of food plants. Some of these plant species represent fallback foods, and are critical for understanding orangutan ecology and conservation. It has been argued that fallback foods are an important determinant of primate carrying capacity in a particular habitat [Marshall et al., 2009b]. In the reduced impact logging (RIL) guidelines that has been promoted in Danum Valley by the Sabah Forestry Department, lianas including *Spatholobus* were cut in areas where heavy lianas connect tree crowns (pre-harvest vine cutting) [Lohuji & Taumas, 1998]. However, to improve the quality of the forest for orangutans, *Spatholobus* lianas should not be cut because they represent an important food source for orangutans in this area. In these guidelines, approximately 11 genera of fruit trees were identified as valuable food resources for wild animals and are prohibited from cutting. Our results also suggest that more tree species should be protected in RIL for conservation of orangutan in this area.

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APPENDIX A: FOOD LIST OF ORANGUTANS IN DANUM VALLEY WITH TIME PERCENTAGE TO THE TOTAL FEEDING TIME

(a) Food Plants

Family	Genus	Species	% of feeding time					Total	Life Style
			Fruit	Leaves	Bark	Flower	Other plants		
ALANGIACEAE	<i>Alangium</i>	<i>javanicum</i>	3.547	0.028				3.576	Tree
ANACARDIACEAE	<i>Gluta</i>	sp1	0.105					0.105	Tree
	<i>Mangifera</i>	<i>pajang</i>	0.081					0.081	Tree
ANISOPHEACEAE	<i>Anisophyllea</i>	sp1	0.181					0.181	Tree
ANNONACEAE	<i>Artabotrys</i>	<i>rosea</i>	2.577	0.009				2.586	Liana
	<i>Artabotrys</i>	U-spp.	1.447					1.447	Liana
	<i>Enicosanthum</i>	<i>grandifolium</i>	0.013					0.013	Tree
	<i>Fissistigma</i>	sp1	0.007					0.007	Tree
	<i>Goniothalamus</i>	sp1	0.020					0.020	Tree
	<i>Meiogyne</i>	<i>virgata</i>		0.050				0.050	Tree
	<i>Meiogyne</i>	U-spp.	0.011					0.011	Tree
	<i>Orophea</i>	<i>odoardoii</i>	0.017					0.017	Tree
	<i>Polyalthia</i>	<i>rumphii</i>	0.293					0.293	Tree
	<i>Polyalthia</i>	<i>sumatrana</i>	0.063					0.063	Tree
	<i>Polyalthia</i>	<i>xanthopetala</i>	0.326	0.262	0.232			0.820	Tree
	<i>Polyalthia</i>	U-spp.	0.608	0.354	0.009			0.970	Tree
	<i>Popowia</i>	<i>pisocarpa</i>	0.020					0.020	Tree
	<i>Pseuduvaria</i>	U-spp.	0.431					0.431	Tree
	<i>Uvaria</i>	<i>sarsogonensis</i>	0.020					0.020	Liana
	<i>Uvaria</i>	U-spp.	0.015	0.009				0.024	Liana
ANNONACEAE 1			0.063					0.063	Tree
APOCYNACEAE	<i>Willughbeia</i>	<i>macropodem</i>	0.011					0.011	Liana
	<i>Willughbeia</i>	U-spp.	0.522					0.522	Liana
ARACEAE	<i>Calamus</i>	U-spp.					0.068	0.068	Mono-cotyledons
	<i>Chindapsus</i>	U-spp.					0.028	0.028	Epiphyte
	<i>Scindapsus</i>	U-spp.		0.120	0.044	0.013	0.033	0.210	Liana
ASCLEPIADACEAE 1				0.262				0.262	Liana
BIGNONIACEAE 1				0.002				0.002	Tree
BOMBACACEAE	<i>Durio</i>	<i>kutejensis</i>	0.037					0.037	Tree
	<i>Durio</i>	<i>zibethinus</i>	0.931	0.083				1.014	Tree
	<i>Durio</i>	sp1	0.378					0.378	Tree
	<i>Durio</i>	U-spp.	0.009	2.275				2.284	Tree
	<i>Neesia</i>	<i>synandra</i>	0.151					0.151	Tree
BURSERACEAE	<i>Canarium</i>	<i>denticulatum</i>	1.285		0.315			1.600	Tree
	<i>Canarium</i>	<i>odontophyllum</i>		0.011	0.035			0.046	Tree
	<i>Canarium</i>	U-spp.	0.170	0.004	0.007			0.177	Tree
	<i>Dacryodes</i>	sp1	1.502					1.502	Tree
	<i>Dacryodes</i>	sp2	0.752					0.752	Tree
	<i>Dacryodes</i>	sp3	0.411					0.411	Tree
	<i>Dacryodes</i>	U-spp.	0.153	0.138				0.291	Tree
	<i>Santiria</i>	<i>tomentosa</i>			0.028			0.028	Tree
	<i>Santiria</i>	U-spp.	0.254					0.254	Tree
CELASTRACEAE	<i>Bhesa</i>	<i>paniculata</i>	0.031					0.031	Liana
	<i>Lophopetalum</i>	U-spp.		0.009				0.009	Tree
CLUSIACEAE	<i>Garcinia</i>	<i>parvifolia</i>	0.070	0.022				0.092	Tree
	<i>Garcinia</i>	U-spp.	0.905	0.026				0.931	Tree
COMBRETACEAE	<i>Combretum</i>	sp1	0.057					0.057	Liana
	<i>Merrenia</i>	<i>gracilis</i>			0.195			0.195	Liana
	<i>Quisqualis</i>	sp1	0.068					0.068	Liana
	<i>Terminalia</i>	<i>citrina</i>	5.318					5.318	Tree
CONNARACEAE	<i>Agelaea</i>	<i>borneensis</i>	0.002	0.105	0.136			0.243	Liana
	<i>Agelaea</i>	U-spp.		0.188	0.050	0.007		0.245	Liana

CORNACEAE	<i>Mastixia</i>	<i>trichotoma</i>	0.199	0.011			0.210	Tree
	<i>Mastixia</i>	U-spp.		0.059			0.059	Tree
CUCURBITACEAE 1				0.035	0.017		0.052	Liana
DATISCAEAE	<i>Octomelis</i>	<i>sumatranus</i>		0.020			0.020	Tree
DILLENIAEAE	<i>Dillenia</i>	<i>excelsa</i>			0.007	0.645	0.651	Tree
DIPTEROCARPACEAE	<i>Dryobalanops</i>	U-spp.	0.588				0.588	Tree
	<i>Hopea</i>	<i>ferruginea</i>		0.026	0.059		0.085	Tree
	<i>Parashorea</i>	<i>malaanonan</i>	0.096	0.020	0.680	0.157	0.953	Tree
	<i>Parashorea</i>	<i>tomentella</i>	0.699		0.946		1.646	Tree
	<i>Parashorea</i>	U-spp.	0.131	0.011	0.039	0.037	0.219	Tree
	<i>Shorea</i>	<i>johorensis</i>		0.098	0.033		0.131	Tree
	<i>Shorea</i>	<i>leprosula</i>		0.011			0.011	Tree
	<i>Shorea</i>	<i>parvifolia</i>			0.044		0.044	Tree
	<i>Shorea</i>	<i>pauciflora</i>			0.313		0.313	Tree
	<i>Shorea</i>	U-spp.	1.123	0.105	0.044		1.272	Tree
	<i>Vatica</i>	<i>albiramis</i>			0.031		0.031	Tree
EBENACEAE	<i>Diospyros</i>	<i>borneensis</i>	0.079	0.063	0.138		0.280	Tree
	<i>Diospyros</i>	<i>diepenhorstii</i>		0.031			0.031	Tree
	<i>Diospyros</i>	<i>elliptifolia</i>	0.070	0.028			0.098	Tree
	<i>Diospyros</i>	<i>frutescens</i>	0.442	0.170	0.116		0.728	Tree
	<i>Diospyros</i>	<i>macrophylla</i>	2.225	0.498	0.120		2.844	Tree
	<i>Diospyros</i>	<i>toposioides</i>			0.195		0.195	Tree
	<i>Diospyros</i>	<i>tuberculata</i>	0.221	0.031			0.251	Tree
	<i>Diospyros</i>	U-spp.	1.283	0.420	0.087		1.790	Tree
ELAEOCARPACEAE	<i>Elaeocarpus</i>	sp1	0.035				0.035	Tree
	<i>Elaeocarpus</i>	sp2	0.151				0.151	Tree
EUPHORBIACEAE	<i>Aporosa</i>	<i>grandifolia</i>		0.024			0.024	Tree
	<i>Aporosa</i>	U-spp.	0.004	0.066			0.070	Tree
	<i>Baccaurea</i>	<i>lanceolata</i>		0.151			0.151	Tree
	<i>Baccaurea</i>	<i>macrocarpa</i>	0.149				0.149	Tree
	<i>Baccaurea</i>	<i>tetrandra</i>						Tree
	<i>Blumeodendron</i>	<i>tokbrai</i>		0.011			0.011	Tree
	<i>Croton</i>	<i>caudatus</i>	0.020				0.020	Tree
	<i>Drypetes</i>	<i>longifolia</i>			0.057		0.057	Tree
	<i>Endospermum</i>	<i>diadenum</i>	0.042				0.042	Tree
	<i>Endospermum</i>	<i>peltatum</i>			0.004		0.004	Tree
	<i>Endospermum</i>	sp1	0.280				0.280	Tree
	<i>Mallotus</i>	U-spp.			0.085		0.085	Tree
FABACEAE	<i>Bauhinia</i>	U-spp.	1.346	0.028	0.090	0.017	1.482	Liana
	<i>Callerya</i>	sp1	0.125				0.125	Liana
	<i>Crudia</i>	<i>veticulata</i>		0.026			0.026	Tree
	<i>Cynometra</i>	<i>elmeri</i>	0.013	0.155			0.168	Tree
	<i>Cynometra</i>	U-spp.		0.017			0.017	Tree
	<i>Derris</i>	U-spp.		0.227			0.227	Liana
	<i>Dialium</i>	<i>indum</i>			0.166		0.166	Tree
	<i>Intsia</i>	<i>palembanica</i>	0.022				0.022	Tree
	<i>Koompassia</i>	sp1	0.103				0.103	Tree
	<i>Peltophorum</i>	U-spp.		0.050			0.050	Liana
	<i>Saraca</i>	sp1	0.007				0.007	Tree
	<i>Sindora</i>	U-spp.		0.076			0.076	Tree
	<i>Spatholobus</i>	<i>hirsutus</i>		1.051			1.051	Liana
	<i>Spatholobus</i>	<i>macropterus</i>	0.063	4.345	4.304		8.712	Liana
	<i>Spatholobus</i>	U-spp.	1.071	1.853	0.619	0.243	3.786	Liana
	<i>Sympetalandra</i>	<i>borneensis</i>	0.066	0.068			0.133	Tree
	<i>Whitfordiodendron</i>	sp1	0.013				0.013	Liana
FABACEAE 1				0.175			0.175	Liana
FAGACEAE	<i>Castanopsis</i>	sp1	0.020				0.020	Tree
	<i>Lithocarpus</i>	<i>gracilis</i>	0.455				0.455	Tree
	<i>Lithocarpus</i>	U-spp.	0.564		0.284		0.848	Tree
FLACOURTIACEAE	<i>Hydnocarpus</i>	<i>woodii</i>		0.007			0.007	Tree
GNETACEAE	<i>Gnetum</i>	U-spp.	0.260				0.260	Liana
LAURACEAE	<i>Beilschmiedia</i>	<i>micrantha</i>	0.055				0.055	Tree
	<i>Beilschmiedia</i>	sp1			0.022		0.022	Tree
	<i>Litsea</i>	U-spp.	0.022	0.046			0.068	Tree
	<i>Nothaphoebe</i>	<i>umbellifera</i>	0.157				0.157	Tree

LECYTHIDACEAE	<i>Barringtonia</i>	<i>macrostachya</i>	0.002			0.002	Tree	
	<i>Barringtonia</i>	U-spp.	0.302		0.009	0.310	Tree	
	<i>Planchonia</i>	U-spp.		0.004		0.004	Tree	
LEEACEAE	<i>Leea</i>	<i>aculeata</i>			0.004	0.004	Tree	
	<i>Leea</i>	<i>indica</i>	0.076		0.068	0.144	Tree	
	<i>Leea</i>	U-spp.			0.026	0.026	Tree	
LYTHRACEAE	<i>Duabanga</i>	<i>moluccana</i>	0.020			0.020	Tree	
MAGNOLIACEAE	<i>Michelia</i>	<i>montana</i>	0.007			0.007	Tree	
MELIACEAE	<i>Aglaia</i>	<i>tomentosa</i>	0.098			0.098	Tree	
	<i>Chisocheton</i>	sp1	0.682			0.682	Tree	
	<i>Chisocheton</i>	sp2	0.002			0.002	Tree	
	<i>Chisocheton</i>	sp3	0.092			0.092	Tree	
	<i>Lansium</i>	<i>domesticum</i>	0.011			0.011	Tree	
	<i>Lansium</i>	U-spp.	0.002			0.002	Tree	
	<i>Sandoricum</i>	<i>koetjape</i>	0.142			0.142	Tree	
MELIACEAE1			0.271	0.175		0.446	Tree	
MORACEAE	<i>Artocarpus</i>	U-spp.	0.494	0.020	0.004	0.518	Tree	
	<i>Ficus</i>	<i>benjamina</i>	0.555	0.636		1.191	Tree	
	<i>Ficus</i>	<i>elastica</i>	0.188			0.188	Tree	
	<i>Ficus</i>	<i>microcarpa</i>	2.507			2.507	Liana/tree	
	<i>Ficus</i>	<i>pumila</i>	0.245	0.234		0.479	Tree	
	<i>Ficus</i>	<i>punctata</i>	0.063	0.470		0.533	Tree	
	<i>Ficus</i>	<i>stupenda</i>		0.052		0.052	Tree	
	<i>Ficus</i>	<i>trichocarpa</i>	0.415	0.096		0.511	Tree	
	<i>Ficus</i>	<i>virens</i>	6.360			6.360	Tree	
	<i>Ficus</i>	<i>xylophylla</i>	0.004			0.004	Tree	
	<i>Ficus</i>	U-spp.	5.482	1.353	0.601	7.436	Liana/tree	
MYRISTICACEAE	<i>Knema</i>	<i>laurina</i>	0.201			0.201	Tree	
	<i>Knema</i>	U-spp.	0.011		0.079	0.090	Tree	
MYRTACEAE	<i>Eugenia</i>	<i>kunstleri</i>	0.105			0.105	Tree	
	<i>Eugenia</i>	sp1	0.028			0.028	Tree	
	<i>Eugenia</i>	sp2	0.136			0.136	Tree	
	<i>Eugenia</i>	U-spp.	0.009			0.009	Tree	
	<i>Syzygium</i>	sp1	0.208			0.208	Tree	
OLACACEAE	<i>Ochanostachys</i>	<i>amentacea</i>	0.909			0.909	Tree	
ORCHIDACEAE	<i>Coelogyme</i>	U-spp.				0.004	0.004	Epiphyte
PANDANACEAE	<i>Pandanus</i>	U-spp.				0.033	0.033	Mono-cotyledons
POACEAE	<i>Dinochloa</i>	U-spp.				0.439	0.439	Climbing bamboo
POLYGALACEAE	<i>Drymoglossum</i>	U-spp.		0.007		0.007	Tree	
	<i>Xanthophyllum</i>	<i>affine</i>		0.415	0.098	0.514	Tree	
	<i>Xanthophyllum</i>	<i>ecarinatum</i>		0.754		0.754	Tree	
	<i>Xanthophyllum</i>	<i>ellipticum</i>		0.245		0.245	Tree	
	<i>Xanthophyllum</i>	<i>flavescens</i>		0.155		0.155	Tree	
	<i>Xanthophyllum</i>	U-spp.	0.068	0.334		0.402	Tree	
PROTEACEAE	<i>Helicia</i>	<i>artocarpoides</i>	0.026			0.026	Tree	
RHAMNACEAE	<i>Zizyphus</i>	<i>angustifolia</i>	0.452			0.452	Tree	
	<i>Zizyphus</i>	<i>borneensis</i>	0.190			0.190	Liana	
RUBIACEAE	<i>Ludkia</i>	<i>borneensis</i>			0.525	0.525	Tree	
	<i>Nauclea</i>	<i>subdita</i>			0.013	0.013	Tree	
	<i>Neolamarckia</i>	<i>cadamba</i>	0.066			0.066	Tree	
	<i>Uncaria</i>	U-spp.		0.024		0.024	Liana	
RUBIACEAE 1			0.083			0.083	Tree	
RUTACEAE	<i>Luvunga</i>	sp1	0.017			0.017	Liana	
SAPINDACEAE	<i>Dimocarpus</i>	<i>longan</i>	0.802			0.802	Tree	
	<i>Dimocarpus</i>	U-spp.		0.007		0.007	Tree	
	<i>Lepisanthes</i>	U-spp.	0.039			0.039	Tree	
	<i>Nephelium</i>	<i>ramboutan-ake</i>	0.107			0.107	Tree	
	<i>Nephelium</i>	U-spp.	0.044	0.083		0.127	Tree	
	<i>Paranephelium</i>	<i>xestopyllum</i>			0.068	0.068	Tree	
	<i>Pometia</i>	<i>pinnata</i>	0.048	0.039		0.087	Tree	
	<i>Pometia</i>	U-spp.	0.046			0.046	Tree	
SAPOTACEAE	<i>Madhuca</i>	U-spp.	0.070			0.070	Tree	
	<i>Palaquium</i>	sp1	0.068			0.068	Tree	

SAXIFRAGACEAE	<i>Payena</i>	<i>acuminata</i>	0.026				0.026	Tree	
	<i>Polyosma</i>	<i>integrifolia</i>		0.048	0.011		0.059	Tree	
	<i>Polyosma</i>	U-spp.		0.052			0.052	Tree	
STERCULIACEAE	<i>Pterospermum</i>	sp1	0.007				0.007	Tree	
SYMPLOCACEAE	<i>Symplocos</i>	<i>fasciculata</i>		0.138			0.138	Tree	
TILIACEAE	<i>Brownlowia</i>	<i>peltata</i>				0.092	0.092	Tree	
	<i>Grewia</i>	<i>fibrocarpa</i>	0.122				0.122	Tree	
	<i>Jarandersonia</i>	<i>rinoreoides</i>				0.011	0.011	Tree	
URTICACEAE	<i>Microcos</i>	<i>crassifolia</i>	0.822				0.822	Tree	
	<i>Dendrocnide</i>	<i>elliptica</i>		0.011			0.011	Liana	
	<i>Poikilos-</i> <i>permum</i>	U-spp.		0.177	0.072	0.540	0.789	Liana	
VERBENACEAE	<i>Callicarpa</i>	U-spp.				0.037	0.037	Tree	
	<i>Teijsman-</i> <i>niodendron</i>	U-spp.		0.046	0.024		0.070	Tree	
VERBENACEAE 1			0.050				0.050	Liana	
VITACEAE	<i>Tetrastigma</i>	U-spp.	0.684			0.042	0.726	Liana	
ZINGIBER- ACEAE	<i>Etlingera</i>	U-spp.				0.072	0.072	Ginger	
Unknown	<i>Plagiostachys</i>	U-spp.					0.046	0.046	Ginger
	<i>Zingiber</i>	U-spp.					0.177	0.177	Ginger
							0.083	0.083	Monocotyledons
							0.046	0.046	Epiphyte
							0.007	0.007	Fungus
			0.494	1.716	1.563	0.017	0.033	3.823	Liana
							0.007	0.007	Moss
			1.445	0.343	0.214	0.042	0.031	2.074	Tree
Total			60.92	22.22	12.47	2.49	1.41	99.51	

(b) Foods other than plant

		% of feeding time	Life style
Others			
Insects	Ant	0.081	Other
	Termite	0.466	Other
	Beehive (honey)	0.007	Other
Soil		0.004	Other
Total		0.56	

REFERENCES

- Ancrenaz M, Lackman-Ancrenaz I. 1999. Technical Progress Report January 1999–June 1999 (HUTAN).
- Ancrenaz M, Goossens B, Gimenez O, Sawang A, Lackman-Ancrenaz I. 2004. Determination of ape distribution and population size using ground and aerial surveys: a case study with orang-utans in lower Kinabatangan, Sabah, Malaysia. *Animal Conservation* 7:375–385.
- Ancrenaz M, Gimenez O, Ambu L, Ancrenaz K, Andau P, Goossens B, Payne J, Sawang A, Tuuga A, Lackman-Ancrenaz I. 2005. Aerial surveys give new estimates for orangutans in Sabah, Malaysia. *PLoS Biology* 3:30–37.
- Ashton PS, Givinish TJ, Appanah S. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting. *American Naturalist* 132:44–66.
- Curran LM, Leighton M. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecological Monographs* 70:101–128.
- Curran LM, Caniago II, Paoli GD, Astianti D, Kusneti M, Leighton M, Nirarita CE, Haeruman H. 1999. Impact of El Niño and logging on canopy tree recruitment in borneo. *Science* 286:2184–2188.
- Fleming TH, Breitwisch R, Whitesides GH. 1987. Patterns of tropical vertebrate frugivore diversity. *Annual Review of Ecology and Systematics* 18:91–109.
- Fox EA, van Schaik CP, Sitompul A, Wright DN. 2004. Intra- and inter-populational differences in orangutan (*Pongo pygmaeus*) activity and diet: implications for the invention of tool use. *American Journal of Physical Anthropology* 125:162–174.
- Furuichi T, Hashimoto C, Tashiro Y. 2001. Fruit availability and habitat use by chimpanzees in the Kalinzu Forest,

- Uganda: examination of fallback foods. *International Journal of Primatology* 22:929–945.
- Galdikas BMF. 1988. Orangutan diet, range, and activity at Tanjung Puting, Central Borneo. *International Journal of Primatology* 9:1–35.
- Hanya G. 2004. Diet of a Japanese macaque troop in the coniferous forest of Yakushima. *International Journal of Primatology* 25:55–71.
- Harrison ME, Vogel ER, Morrogh-Bernard HC, van Noordwijk MA. 2009. Methods for calculating activity budgets compared: a case study using orangutans. *American Journal of Primatology* 71:353–358.
- Hladik CM. 1977. A comparative study of the feeding strategies of two sympatric species of leaf monkeys: *Presbytis senex* and *Presbytis entellus*. In: Clutton-Brock TH, editor. *Primate ecology*. New York: Academic Press. p 324–354.
- Knott CD. 1998. Changes in orangutan caloric intake, energy balance, and ketones in response to fluctuating fruit availability. *International Journal of Primatology* 19:1061–1079.
- Knott CD. 2005. Energetic responses to food availability in the great apes: implications for Hominin evolution. In: Brockman DK, van Schaik CP, editors. *Primate seasonality*. Cambridge: Cambridge University Press. p 351–378.
- Knott CD, Kahlenberg SM. 2006. Orangutans in perspective: forced copulations and female mating resistance. In: Christina J, Campbell AF, MacKinnon KC, Panger M, Bearder SK, editors. *Primates in perspective*. Oxford: Oxford University Press. p 290–305.
- Kuze N, Malim TP, Kohshima S. 2005. Developmental changes in the facial morphology of the Borneo orangutan (*Pongo pygmaeus*): possible signals in visual communication. *American Journal of Primatology* 65:353–376.
- Laden G, Wrangham RW. 2005. The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopithecine origins. *Journal of Human Evolution* 49:482–498.
- Lambert JE, Chapman CA, Wrangham RW, Conklin-Brittain N. 2004. Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. *American Journal of Physical Anthropology* 125:363–368.
- Leighton M. 1993. Modeling dietary selectivity by Bornean orangutans—evidence for integration of multiple criteria in fruit selection. *International Journal of Primatology* 14:257–313.
- Leighton M, Leighton DR. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. In: Sutton SL, Whitmore TC, Chadwick AC, editors. *Tropical rain forest ecology and management*. Boston: Blackwell Scientific. p 181–196.
- Lohuji PL, Taumas R. 1998. RIL—operation guide book. Sabah: Sabah Forestry Department, Sandakan.
- Mackinnon JR. 1974. The behaviour and ecology of wild orangutans (*Pongo Pygmaeus*). *Animal Behaviour* 22:3–74.
- MacKinnon K, Hatta G, Halim H, Mangalik A. 1996. *The ecology of Kalimantan*. Hong Kong: Periplus Editions Ltd. 802p.
- Marsh CW, Greer AG. 1992. Forest land-use in Sabah, Malaysia: an introduction to Danum Valley. *Philosophical Transactions of the Royal Society* 335:331–339.
- Marshall AJ, Leighton M. 2006. How does food availability limit the population density of agile gibbons? In: Hohmann G, Robbins MM, Boesch C, editors. *Feeding ecology of the apes and other primates*. Cambridge: Cambridge University Press. p 311–333.
- Marshall AJ, Ancrenaz M, Brearley FQ, Fredriksson GM, Ghaffar N, Heydon M, Husson SJ, Leighton M, McConkey KR, Morrogh-Bernard HC, Proctor J, van Schaik CP, Yeager CP, Wich SA. 2009a. The effects of forest phenology and floristics on populations of Bornean and Sumatran orangutans: are Sumatran forests more productive than Bornean forests? In: Wich SA, Utami S, Setia TM, van Schaik CP, editors. *Orangutans*. Oxford: Oxford University Press. p 97–117.
- Marshall AJ, Boyko CM, Feilen KL, Boyko RH, Leighton M. 2009b. Defining fallback foods and assessing their importance in primate ecology and evolution. *American Journal of Physical Anthropology* 140:603–614.
- Mitani JC. 1989. Orangutan activity budgets—monthly variations and the effects of body size, parturition, and sociality. *American Journal of Primatology* 18:87–100.
- Morrogh-Bernard HC, Husson S, McLardy C. 2002. *Orangutan data collection standardization*. California: San Anselmo.
- Morrogh-Bernard HC, Husson SJ, Knott CD, Wich SA, van Schaik CP, van Noordwijk MA, Lackman-Ancrenaz I, Marshall AJ, Kanamori T, Kuze N, Sakong RB. 2009. Orangutan activity budgets and diet. In: Wich SA, Utami SSA, Setia TM, van Schaik CP, editors. *Orangutans*. Oxford: Oxford University Press. p 119–133.
- Newbery DM, Campbell EJF, Lee YF, Ridsdale CE, Still MJ. 1992. Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia—structure, relative abundance and family composition. *Philosophical Transaction of the Royal Society* 335:341–356.
- Osada N, Takeda H, Fukukawa A, Awang M. 2001. Fruit dispersal of two dipterocarp species in a Malaysian rain forest. *Journal of Tropical Ecology* 17:911–917.
- Rijksen H, Meijaard E. 1999. *Our vanishing relative: the status of wild orangutans at the close of the twentieth century*. Dordrecht: Kluwer Academic Publishers.
- Robinson AM, Williamson DH. 1980. Physiological role of ketone bodies as substrates and signals in mammalian tissues. *Physiological Reviews* 60:143.
- Rodman PS. 1988. Diversity and consistency in ecology and behavior. In: Schwartz JH, editor. *Orangutan biology*. Oxford: Oxford University Press. p 31–51.
- Sokal RR, Rohlf FJ. 1995. *Biometry—the principles and practice of statistics in biological research*. New York: W.H. Freeman and Company. 887p.
- Sugardjito J, te Boekhorst IJA, van Hooff JARAM. 1987. Ecological constraints on the grouping of wild Orangutans (*Pongo pygmaeus*) in the Gunung Leuser National Park, Sumatra, Indonesia. *International Journal of Primatology* 8:17–41.
- Taylor AB. 2006. Feeding behavior, diet, and the functional consequences of jaw form in orangutans, with implications for the evolution of *Pongo*. *Journal of Human Evolution* 50:377–393.
- Taylor AB. 2009. The functional significance of variation in jaw form in orangutans. In: Wich SA, Utami S, Setia TM, van Schaik CP, editors. *Orangutan*. Oxford: Oxford University Press. p 15–33.
- Taylor AB, van Schaik CP. 2007. Variation in brain size and ecology in *Pongo*. *Journal of Human Evolution* 52:59–71.
- Terborgh J. 1986. Community aspects of frugivory in tropical forests. In: Estrada A, Fleming TH, editors. *Frugivores and seed dispersal*. Dordrecht: Dr W. Junk. p 371–384.
- van Schaik CP. 1996. Strangling figs: their role in the forest. In: van Schaik CP, Supriatna J, editors. *Leuser: a Sumatran sanctuary*. Jakarta: Perdana Ciptamadri. p 111–119.
- van Schaik CP, Marshall AJ, Wich SA. 2009a. Geographic variation in orangutan behavior and biology: its functional interpretation and its mechanistic basis. In: Wich SA, Utami S, Setia TM, van Schaik CP, editors. *Orangutans*. Oxford: Oxford University Press. p 351–361.
- van Schaik CP, van Noordwijk MA, Vogel ER. 2009b. Ecological sex differences in wild orangutans. In: Wich SA, Utami S, Setia TM, van Schaik CP, editors. *Orangutans*. Oxford: Oxford University Press. p 255–269.
- Walsh RPD. 1996. Drought frequency changes in Sabah and adjacent parts of Northern Borneo since the late nineteenth

- century and possible implications for tropical rain forest dynamics. *Journal of Tropical Ecology* 12:387–407.
- Wich SA, van Schaik CP. 2000. The impact of El Niño on mast fruiting in Sumatra and elsewhere in Malesia. *Journal of Tropical Ecology* 16:563–577.
- Wich SA, Utami-Atmoko SS, Setia TM, Djoyosudharmo S, Geurts ML. 2006. Dietary and energetic responses of *Pongo abelii* to fruit availability fluctuations. *International Journal of Primatology* 27:1535–1550.
- Wong ST, Servheen C, Ambu L, Norhayati A. 2005. Impacts of fruit production cycles on Malayan sun bears and bearded pigs in lowland tropical forest of Sabah, Malaysian Borneo. *Journal of Tropical Ecology* 21: 627–639.
- Wrangham RW, Conklin-Brittain NL, Hunt KD. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance: I. antifeedants. *International Journal of Primatology* 19:949–970.