

Responses to Spatial and Temporal Variation in Food Availability on the Feeding Ecology of Proboscis Monkeys (*Nasalis larvatus*) in West Kalimantan, Indonesia

Katie L. Feilen^a Andrew J. Marshall^b

^aProject Dragonfly, Department of Biology, Miami University, Oxford, OH, USA;

^bDepartment of Anthropology, Department of Ecology and Evolutionary Biology, Program in the Environment and School for Environment and Sustainability, University of Michigan, Ann Arbor, MI, USA

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Abstract

Folivorous primates have long been assumed to experience food competition less acutely than frugivores due to their ability to eat leaves, an abundant resource in most forest systems. Consequently, the behavioural responses of leaf-eating primates to variation in food availability are less well characterised than those of frugivores. Recent empirical studies have demonstrated that many colobine species are more affected by food availability and distribution than previously thought; they employ multiple strategies to survive during periods of food scarcity. We studied a population of proboscis monkeys (*Nasalis larvatus*) over 16 months in three forest types in West Kalimantan, Indonesia, to examine their responses to temporal fluctuation and spatial variation in food availability. We examined how feeding behaviour was influenced by the availability of plants in botanical plots to identify important and preferred foods of proboscis monkeys across months and in different forest types. Proboscis monkeys consumed foods from 68 genera, comprising 35% young leaves, 27% unripe fruit, 12% flowers and 6% mature leaves. Consumption of plant parts and genera by proboscis monkeys varied in response to monthly changes in food availability but did not vary among forest types despite substantial differences in phenology and floristics among them. The monkeys preferred unripe fruits and flowers and used young and mature leaves as fallback foods in mangrove forests. Documentation of proboscis monkey responses to variation in food availability contributes to our understanding of how monkeys respond to changes in their environments due to climate change and habitat degradation.

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Introduction

Understanding the effects of resource abundance and distribution on primate populations, groups and individuals is a central goal of primatology. Socioecological theory predicts that the quantity, quality and spatial distribution of resources influence primate social structure, movement patterns and social behaviours [Clutton-Brock and Harvey, 1977; Wrangham, 1980; van Schaik, 1983; Isbell, 1991; Sterck et al., 1997; Isbell, 2004]. Seasonal changes in resources can further influence feeding, ranging and grouping [van Schaik et al., 1993; Hemingway and Bynum, 2005]. Extensive empirical research has demonstrated the effects of spatiotemporal variation in food on the dietary choices, ranging, grouping and behaviour of primates [Milton, 1984; Chapman et al., 1995; Menon and Poirier, 1996; Doran, 1997; Ahumada et al., 1998; Isbell et al., 1998; Chapman and Chapman, 1999; Wallace, 2005; Roshier et al., 2008; Grueter et al., 2009b; Vogel et al., 2009; Struhsaker, 2010; Clink et al., 2017].

Folivorous primates were thought to be less acutely influenced by resource competition than frugivores as their diets usually contain a substantial proportion of leaves, a resource generally assumed to be relatively evenly distributed and consistently available [Isbell, 1991; Yeager and Kirkpatrick, 1998]. Several empirical observations have suggested that folivorous primates may be more severely affected by food scarcity than was previously assumed [Snaith and Chapman, 2007]. Folivores consume seeds and young leaves that are not evenly distributed in time or space [Yeager, 1989; Steenbeek and van Schaik, 2001; Grueter et al., 2009a], preferentially select leaves of certain species [McKey and Waterman, 1987; Harris and Chapman, 2007] and experience feeding competition [Steenbeek and van Schaik, 2001; Snaith and Chapman, 2007, 2008]. These results suggest that many folivorous primates should respond behaviourally to differences in spatial and temporal variation in food availability.

Proboscis monkeys (*Nasalis larvatus*) are colobine monkeys that, like many other colobines, consume a mixed diet of leaves, fruits, and flowers. The composition of their diet varies among study sites, forest types and seasons. At Samunsam Wildlife Sanctuary, Sarawak, Malaysia, the diet of the proboscis monkeys was 38% young leaves, 35% fruits and 3% flowers [Bennett and Sebastian, 1988], at a rubber plantation in South Kalimantan, the diet was 81% young leaves, 7% fruits and 11% flowers [Soendjoto et al., 2006] and at the Klias Peninsula in Sabah, Malaysia, the diet was 92% young leaves, 3% fruits and 4% flowers [Bernard et al., 2019]. The diets of proboscis monkeys also differ among forest types; at the Lower Kinabatangan River, Sabah, in a riverine forest the diet consisted of 73% young leaves and 7% fruits, while in a mangrove forest it was 50% young leaves and 21% fruits [Boonratana, 1994]. Seasonality also influences the diet; at Tanjung Puting National Park, fruits comprised more than 50% of the diet from January to May, but young leaves comprised more than 50% of the diet from June to December [Yeager, 1989].

Proboscis monkey populations usually inhabit spatially heterogeneous environments [Salter et al., 1985], living along rivers that flow through mangrove, lowland dipterocarp and *kerangas* (i.e. heath) forests. Additionally, many of their habitats have undergone human alteration. Given the spatial and temporal variation in their resources, monkeys should exhibit strategies to cope with fluctuations in food availability. With their ability to digest mature leaves due to foregut fermentation [Matsuda et al., 2017], it would be reasonable to hypothesise that proboscis monkeys would respond to reductions in the availability of high-quality foods (fruits and young leaves)

by incorporating greater amounts of lower-quality mature leaves in their diets. This does not, however, appear to be the case. Previous studies on proboscis monkeys had reported that when unripe fruits were plentiful, fruits comprised a large percentage of their diets, but when these unripe fruits were not available, the monkeys consumed more young leaves and flowers [Yeager, 1989; Boonratana, 1994; Matsuda et al., 2009]. Proboscis monkeys generally ate very few mature leaves [3%, Bennett, 1988; 2.5%, Yeager, 1989; 0.3%, Boonratana, 1994; 0.03%, Matsuda et al., 2009].

In this study, we investigated the responses of proboscis monkeys to both spatial and temporal variation in food availability by studying a population of monkeys in three forest types over 16 months in West Kalimantan, Indonesia. Our project had two primary goals: to compile a complete record of both the genera and types of food consumed by proboscis monkeys at Sungai Tolak and to determine how the consumption of distinct plant parts and dietary diversity changed in response to spatial and temporal variation of food availability. We predicted that proboscis monkeys (1) use similar strategies in each forest type to respond to spatial and temporal variation in food availability, (2) increase dietary breadth in places and during times of low food availability, and (3) consume young leaves and flowers when preferred foods are unavailable.

Methods

Study Site

K.L.F. collected data at Sungai Tolak (1°27'59" S, 110°4'54" E), located just outside Gunung Palung National Park, West Kalimantan, Indonesia [Feilen and Marshall, 2014, 2017]. The site consisted of 30 km of forest along the Tolak River, with mangrove forest found near the river's mouth, peat swamp forest located furthest upriver and riverine forest found between the two other forest sites (Fig. 1). The site was degraded by forest fires in 1997 and 2003. The site was also subject to light selective logging during the period of data collection, although we have no reason to believe this low-level activity had a substantial impact on the feeding ecology of the monkeys during the study period. Temperatures ranged from 21 to 39 °C, and monthly rainfall ranged from 28.6 to 633.8 mm with mean monthly rainfall = 213.8 mm ± standard deviation (SD) of 153.0 mm (Fig. 2).

To assess spatial and temporal variation in food availability, we placed 22 (25 × 20 m) plots using a stratified random design across the three forest types. We established 15 botanical plots along four 1,100 m transects across the three forest types in February 2011. In each transect, we placed a plot at 0, 125, 250 and 375 m from the river's edge in a north-to-south orientation. After performing an analysis on the sampling efforts of our site relative to the use of the site by the proboscis monkeys, we added four plots at the river's edge and three plots inland in August 2011. We used a nested design in each plot to maximise the sampling area for larger trees while limiting the time spent sampling smaller trees [Marshall and Leighton, 2006; Marshall and Wich, 2013]. We tagged and identified all trees within 5 m of the transect midline (both sides) with a diameter at breast height (DBH) greater than 5 cm, and all lianas greater than 1 cm. We tagged all trees with DBH greater than 10 cm and lianas greater than 6 cm located 5–10 m from the midline. We classified all stems as trees, lianas or figs. We placed all stems of the genus *Ficus* in the fig category, regardless of growth form (e.g. trees, lianas, hemiepiphytes) because of their distinct phenological patterns. An Indonesian field assistant with over 15 years of botanical experience in West Kalimantan identified all stems to genus using scientific names. We identified stems only to genus level as (1) conducting analyses of tropical stems at the species level may skew results due to phylogenetic non-independence [Chazdon et al., 2003; Davies et al., 2013], (2) many stems have yet to be described at the species level due to the high level of botanical diversity on Borneo, and (3) because many of the stems were impossible to identify to species level as they were reproductively inactive during sampling.

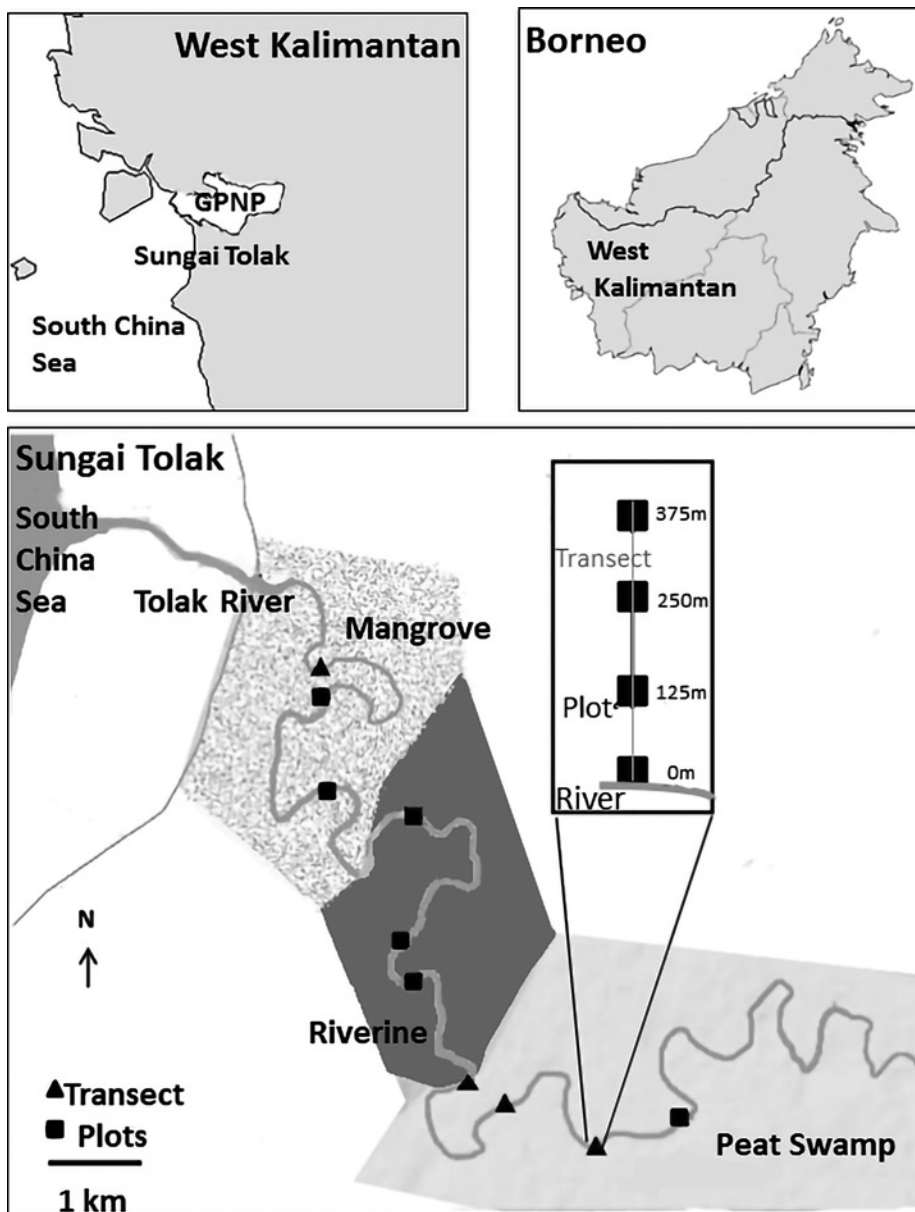
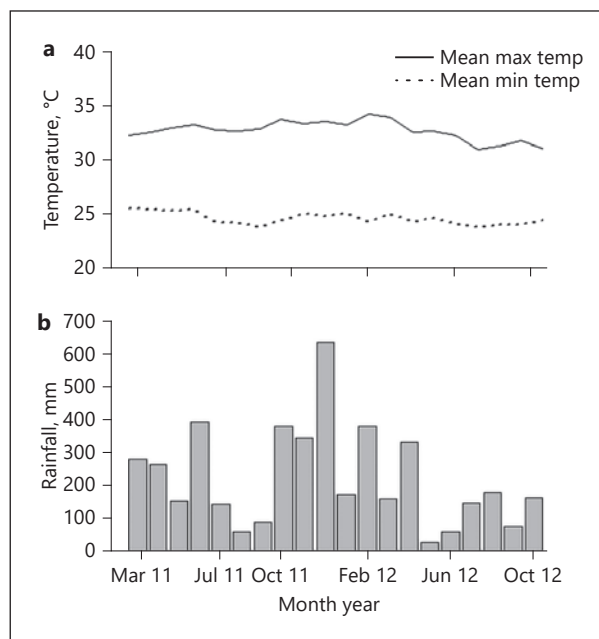


Fig. 1. Map of the research area at Sungai Tolak, West Kalimantan, Indonesia, indicating the locations of survey transects (squares) and botanical plots (triangles); GPNP, Gunung Palung National Park.

Fig. 2. Monthly average maximum and minimum temperatures (**a**) and total monthly rainfall (**b**) at Sungai Tolak, West Kalimantan, Indonesia, from March 2011 to October 2012.



Monthly Monitoring

Each month, we monitored the phenological state of each plant stem in our plots. From April 2011 to August 2011, we monitored 731 stems in 15 plots, and from September 2011 to October 2012 we monitored 1,274 trees in 22 plots. We recorded the presence or absence of young leaves, flower buds, flowers and fruits (immature, mature and ripe) on each stem. For fruits, we also estimated the crop size of each stem using the following categories: 0–10, 11–100, 101–1,000 and greater than 1,000 fruits.

Study Subjects and Feeding Data

We studied a population of proboscis monkeys at Sungai Tolak that consisted of approximately 20 groups varying in size between 2 and 35 individuals. Proboscis monkeys exhibit a multi-level grouping structure, with 1-male, multiple-female groups aggregating to form bands [Yeager, 1991]. At our site, bands consisted of 2–7 groups with banding occurring primarily at sleeping sites. As our goal was to understand the feeding ecology of the population of proboscis monkeys at Sungai Tolak rather than any specific group, we did not analyse feeding behaviours at the group level. To examine whether differences in life stage or sex influenced dietary intake, we characterised the diets of adult males, adult females, subadults and juveniles/infants separately [using age definitions of Bennet and Sebastian, 1988].

We collected feeding data for 16 days per month, from April 2011 to December 2011, and from April 2012 to October 2012 (total 16 months). We searched for groups of monkeys along four predefined sections of the river in the morning (05:00–12:30) and the evening (16:00–18:30) from a boat with a small motor. When we found a group of proboscis monkeys, we began collecting behavioural data. Every 15 min, we scanned the group and recorded the activities of each monkey [Altmann, 1974] as one of the following categories: resting, travelling, feeding and socialising. If the individual was feeding, we recorded the type (e.g. fruit, leaf, flower) and genus of the food item. In addition to group scans, we collected ad libitum data on feeding behaviours that occurred outside the group scans, because proboscis monkeys ate many items outside the group scans and the ad libitum data allowed us to collect a more comprehensive record of feeding. To

make the two types of behavioural data comparable, we collected the same data during ad libitum sampling as during group scan sampling; however, if multiple feeding events occurred on the same type and genus of food by the same individual during an ad libitum behavioural observation session, we recorded the feeding observation only once. We calculated the correlation between the proportion of food parts per month from the group scans ($n = 614$) and from the ad libitum ones ($n = 658$), and found them to be highly correlated (Pearson's correlation = 0.87, $p = 2.2 \times 10^{-16}$), suggesting that the inclusion of ad libitum data does not alter our results.

Data Analysis

We performed all statistical analyses in R version 2.15.3 [R Core Development Team, 2013]. We calculated the overall proportion of food parts in the diet by using the number of feeding observations of each food part divided by all feeding observations for all individuals, and for adult males, adult females, subadults and juveniles/infants. We also calculated the proportion of food parts in the diet within each forest type and during each month. We calculated means and SDs between months and plots within each forest type and tested for significance using ANOVA two-tailed tests at an α -level of 0.05. For comparison of count data, we tested significance with the χ^2 goodness-of-fit test.

We calculated the generic richness and diversity of feeding trees and available trees in each forest type. We summed the number of discrete genera for richness values, and we calculated Shannon's index using the "vegan" package in R for diversity values [Oksanen et al., 2013]. We compared richness and diversity of plot in each forest type using ANOVA, and of consumed genera using the χ^2 goodness-of-fit test. We made genus accumulation curves using the "specaccum" function in the "vegan" package, which demonstrated the effect of sampling size on the number of genera recorded as available and used. We used linear regression to examine the relationship between dietary richness and total food availability. Due to the curvilinear relationship between sampling effort and the number of genera recorded, we calculated the residuals from a curve fit to the number of genera consumed each month to the number of feeding observations in the corresponding month. We calculated the linear regression of the residuals of the number of genera to the percentage of stems with food available for each month.

We calculated selectivity coefficients to assess the preference of all consumed genera and plant parts. We calculated genus-level selectivity (S_i) by comparing the relative use of each genus to the relative availability of trees in our botanical plots ($n = 1,274$) [Savage, 1931] using the formula:

$$S_i = U_i/A_i,$$

where U_i = number of feeding observations of genus i / total number of feeding observations and A_i = number of trees of genus i in plots / total number of trees in plots.

Similarly, we calculated the preference of each food part by calculating the proportion of the diet for each plant part per month and dividing it by the proportion of stems in the plots that contained each corresponding plant part. We did not calculate the selectivity of mature leaves as they were consistently available in all stems in our plots. Scores >1 indicate positive selection (i.e. preference) of the genus or plant part while scores <1 indicate avoidance. We calculated genus-level feeding selectivity overall and by forest type. Proboscis monkeys ate 20 rare plant genera that were absent from our botanical plots. For these genera, we calculated selectivity coefficients based on the assumption of a density of 1 stem per 1,274 stems = 0.0008%. We defined important genera as those that comprise a large proportion of the diet, regardless of availability.

To determine the monkeys' responses to changes in food availability (in order to identify fallback foods), we calculated linear regressions between the monthly proportion of the diet comprising young leaves, mature leaves, unripe fruits, flower buds and flowers as well as the availability of unripe fruits (the most preferred food type – as determined by the results of this study). Although unripe fruits and flowers were both preferred foods, we propose that the most preferred food type would give us the most reliable indication of responses to food availability. Also, as the total number of food types was small, including flowers in our analysis would have meant that almost half the food types in our analysis would have been classified as preferred foods. We calculated linear regressions for the full data set and by forest type.

Table 1. Characteristics of used and available trees by forest types

	Forest type			
	all trees	mangrove	riverine	peat swamp
Number of families consumed	42	15	21	24
Number of families available	52	21	40	36
Number of genera consumed	68	37	39	46
Number of genera available	119**	25 ^{A, C}	74 ^{b, C}	86 ^{A, b}
Number of stems in plots	1,274	172	512	590
Mean diversity (SD) of trees in plots	3.7**	2.1 (0.5) ^{A, B}	3.1 (0.3) ^B	3.2 (0.2) ^A
Diversity of trees consumed	2.9	2.3	2.4	2.6
Mean density (SD) of trees, trees/m ²	0.11**	0.06 (0.03) ^{A, B}	0.15 (0.05) ^B	0.13 (0.02) ^A
Mean DBH (SD), cm	11.9 (8.6)**	14.7 (11.7) ^{A, B}	11.6 (11.8) ^B	11.3 (6.8) ^A

SD, standard deviation. * $p < 0.05$, ** $p < 0.01$; superscript letters demonstrate pairwise comparisons – lowercase letters $p < 0.05$, capital letters $p < 0.01$.

Results

Spatial Variation of Available Food Sources

Of the 1,274 stems in our plots, 94% were trees, 6% were lianas and 0.4% were figs. Tagged stems included 119 genera from 52 families (Table 1). Generic diversity differed significantly among forest types (ANOVA: $F = 27.62$, $df = 2$, $p = 0.000002$). Mangrove forest was significantly less diverse than peat swamp forest (Tukey HSD = 1.1, $p = 0.000003$) and riverine forest (Tukey HSD = 1.0, $p = 0.00004$). Riverine forest was not significantly different from peat swamp forest (Tukey HSD = -0.2, $p = 0.54$). Plant genus diversity was positively correlated with distance from the mouth of the river ($r^2 = 0.80$, $p = 0.00000002$, $n = 22$ plots).

Density and tree size also differed among forest types. Trees were less dense in the mangrove forest, most dense in the riverine forest and moderately dense in the peat swamp forest (ANOVA: $F = 11.75$, $df = 2$, $p = 0.01$; Tukey HSD peat-mangrove = 0.07, $p = 0.002$; mangrove-riverine = 0.09, $p = 0.0006$; riverine-peat = 0.0005, $p = 0.67$; Table 1). Mangrove forest had larger trees than riverine forest and peat swamp forest (ANOVA: $F = 10.99$, $df = 2$, $p = 0.00002$; Tukey HSD peat-mangrove = -3.4, $p = 0.00002$; mangrove-riverine = -3.1, $p = 0.0001$; riverine-peat = 0.3, $p = 0.9$; Table 1).

Temporal Variation of Available Food Sources

Besides mature leaves, young leaves were the most available food resource, as the mean percentage \pm SD of trees having young leaves was $40 \pm 9\%$ (range: 16–56%) per month (Fig. 3a). Immature fruits (mean \pm SD = $4 \pm 2\%$), flowers (mean \pm SD = $4 \pm 1\%$) (Fig. 3a) and flower buds (mean \pm SD = $6 \pm 2\%$) were relatively rare. Food availability also varied as a function of forest type (Fig. 3c, e, g). Flushing of young leaves was synchronised amongst mangrove and riverine forests ($r = 0.75$, $p = 0.0009$), riv-

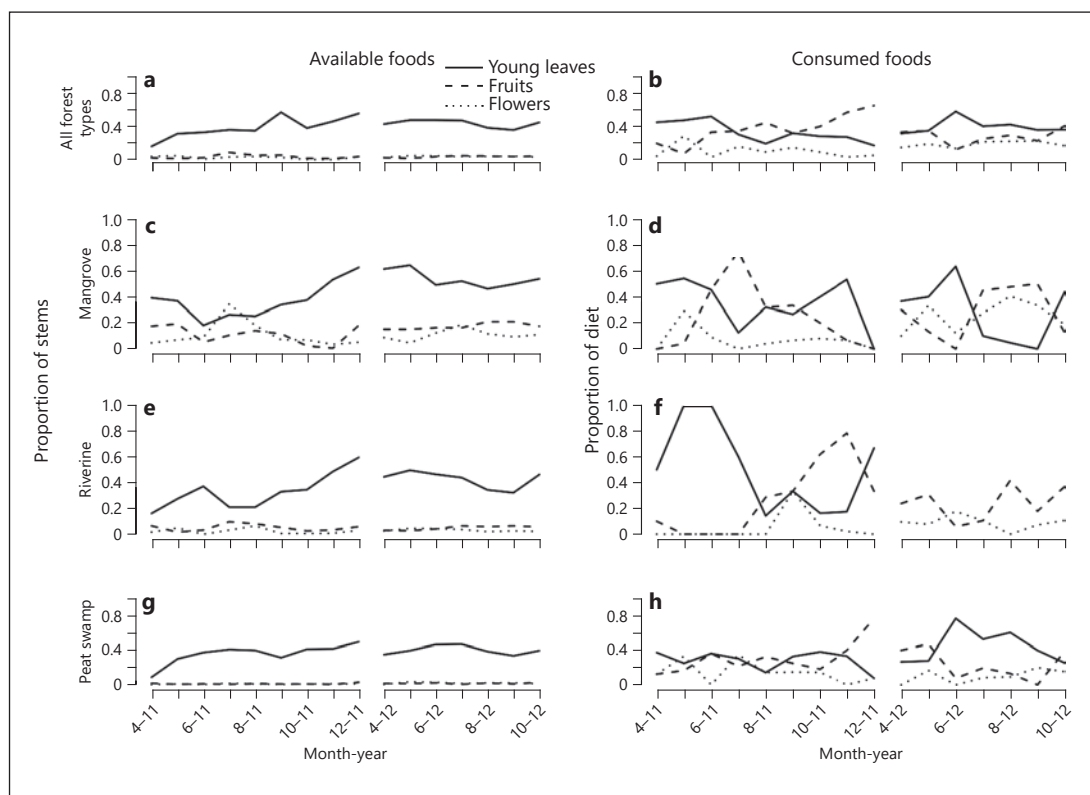


Fig. 3. Monthly variation in food availability (in 22 botanical plots) and dietary composition at Sungai Tolak, West Kalimantan, Indonesia, from April to December 2011 and April to October 2012 in all forests (**a, b**), mangrove (**c, d**), riverine (**e, f**), and peat swamp forests (**g, h**).

erine and peat swamp forest ($r = 0.66, p = 0.006$), but was not synchronised between mangrove and peat swamp forest ($r = 0.26, p = 0.33$). There was a correlation between the timing of flowering ($r = 0.51, p = 0.04$) and immature fruiting ($r = 0.72, p = 0.002$) between mangrove and riverine forests. There was no significant relationship between the timing of flowering between riverine and peat swamp forest ($r = 0.41, p = 0.09$) or peat swamp and mangrove forests ($r = 0.31, p = 0.24$). Similarly, there was no relationship in the timing of immature fruits in the riverine and peat swamp forest ($r = 0.09, p = 0.72$) or peat swamp and mangrove forest ($r = -0.25, p = 0.35$).

General Feeding Observations

During 1,271 recorded feeding bouts, the proboscis monkeys' diet consisted of 35% young leaves, 27% unripe fruit, 12% flowers, 6% mature leaves, 4% fruit of undetermined ripeness, 3% buds, 3% ripe fruit and 9% unidentified items (Table 2). The dietary composition varied slightly by age-sex of the individual (Table 3). The proboscis monkeys ate plant parts from at least 68 genera of trees and lianas in 42 families.

Table 2. Dietary composition of proboscis monkeys in all forest types, number of feeding observations for each genus and plant part, percentage of diet for each genus and selectivity coefficient values

Genus	Family	Plant part									Percent of diet	Selection coefficient
		buds	flowers	fruits ^c	ripe fruits	unripe fruits	mature leaves	young leaves	un-known	total		
	Proportion, % (n)	3 (36)	12 (157)	4 (56)	3 (33)	27 (346)	6 (80)	35 (450)	9 (113)	100 (1,271)	100.0	
<i>Syzygium</i>	Myrtaceae	24	46	12	6	62	13	115	21	299	23.5	1.7
<i>Palaquium</i>	Sapotaceae	3	8	5		122	7	26	3	174	13.7	1.2
<i>Bruguiera</i>	Rhizophoraceae	2	37	3		65	9	17	7	140	11.0	10.8
Unknown	n.a.		2	2	1	6	9	30	47	97	7.6	n.a.
<i>Ficus</i>	Moraceae	1		3	7	28	5	36	4	84	6.6	21.0
<i>Rhizophora</i>	Rhizophoraceae	1	7	21		18	3	18	7	75	5.9	3.8
<i>Heritiera</i>	Malvaceae	1	8				5	18	2	34	2.7	1.0
<i>Knema</i>	Myristicaceae		1	5	3	5	1	9	2	26	2.0	1.7
<i>Calophyllum</i>	Clusiaceae				4	9		9	2	24	1.9	2.2
<i>Derris</i>	Fabaceae	1				3	5	15		24	1.9	1.5
<i>Vatica</i>	Dipterocarpaceae		6	1		2		13	1	23	1.8	0.4
<i>Parkia</i>	Fabaceae							22		22	1.7	1.8
<i>Gluta</i>	Anacardiaceae		9				1	7		17	1.3	1.0
<i>Grewia</i>	Malvaceae		6	1	3		2	4		16	1.3	16.0
<i>Diospyros</i>	Ebenaceae						4	12		16	1.3	0.4
<i>Litsea</i>	Lauraceae	1	1		3	4		6		15	1.2	0.1
Unknown liana	n.a.		1			4		10	3	18	1.4	n.a.
<i>Vitex</i>	Lamiaceae		4	2				3	2	13	1.0	6.5
<i>Aglaia</i>	Meliaceae				3		2	8		13	1.0	0.7
<i>Hibiscus</i>	Malvaceae		1			1	1	5	2	10	0.8	0.7
<i>Lophopetalum</i>	Celastraceae		5		1	3				9	0.7	2.3
<i>Xylocarpus</i>	Meliaceae					1		8		9	0.7	0.5
<i>Uncaria</i>	Rubiaceae		4					5		9	0.7	0.3
<i>Excoecaria</i>	Euphorbiaceae				2			5		7	0.6	7.0
<i>Dillenia</i>	Dilleniaceae		3					3		6	0.5	3.0
<i>Rourea</i>	Connaraceae		1			4		1		6	0.5	3.0
<i>Archidendron</i>	Fabaceae					1		4		5	0.4	1.7
<i>Fragraea</i>	Gentianaceae					2	2			4	0.3	4.0
<i>Macaranga</i>	Euphorbiaceae	1	2				1			4	0.3	4.0
Pakis ^a	n.a.							3	1	4	0.3	4.0
<i>Pithecellobium</i>	Fabaceae						1	3		4	0.3	4.0
<i>Dialium</i>	Fabaceae							2	2	4	0.3	1.0
<i>Cerbera</i>	Apocynaceae		1					3		4	0.3	0.5
<i>Pternandra</i>	Melastomataceae		1	1			1	1		4	0.3	0.1
<i>Pandanus</i>	Pandanaceae							2	1	3	0.2	3.0
<i>Pometia</i>	Sapindaceae		2					1		3	0.2	3.0
<i>Austrobuxus</i>	Picrodendraceae							2	1	3	0.2	1.5
<i>Ziziphus</i>	Rhamnaceae							3		3	0.2	1.5
<i>Mangifera</i>	Anacardiaceae							3		3	0.2	0.4
Changalang ^a	n.a.							2		2	0.2	2.0
<i>Hydnocarpus</i>	Achariaceae					1	1			2	0.2	2.0
<i>Barringtonia</i>	Lecythidaceae						1	1		2	0.2	1.0
<i>Cnestis</i>	Connaraceae						1	1		2	0.2	1.0
<i>Nephelium</i>	Sapindaceae						1	1		2	0.2	0.5
<i>Ilex</i>	Aquifoliaceae		1					1		2	0.2	0.2
<i>Elaeocarpus</i>	Elaeocarpaceae							2		2	0.2	0.1
<i>Memecylon</i>	Melastomataceae					2				2	0.2	0.1
<i>Acacia</i>	Fabaceae							1		1	0.1	1.0
<i>Asplenium</i>	Aspleniaceae							1		1	0.1	1.0
Genus spp.	Fagaceae								1	1	0.1	1.0
Genus spp.	Icacinaceae								1	1	0.1	1.0
Genus spp.	Linaceae								1	1	0.1	1.0
Genus spp.	Orchidaceae							1		1	0.1	1.0
<i>Intsia</i>	Fabaceae	1								1	0.1	1.0
Labung ^a	n.a.								1	1	0.1	1.0
<i>Nypa</i>	Arecaceae						1			1	0.1	1.0

Table 2 (continued)

Genus	Family	Plant part								Percent of diet	Selection coefficient	
		buds	flowers	fruits ^c	ripe fruits	unripe fruits	mature leaves	young leaves	un-known			total
<i>Polyalthia</i>	Annonaceae							1		1	0.1	1.0
Genus spp.	<i>Pteridophyta</i> ^b							1		1	0.1	1.0
Rambang ^a	n.a.							1		1	0.1	1.0
<i>Stemonurus</i>	Stemonuraceae							1		1	0.1	1.0
<i>Melanochyla</i>	Anacardiaceae							1		1	0.1	0.5
<i>Melanorrhoea</i>	Anacardiaceae								1	1	0.1	0.5
<i>Uvaria</i>	Annonaceae					1				1	0.1	0.3
<i>Mezzettia</i>	Annonaceae					1				1	0.1	0.1
<i>Combretum</i>	Combretaceae						1			1	0.1	0.1
<i>Dacryodes</i>	Burseraceae							1		1	0.1	0.1
<i>Lithocarpus</i>	Fagaceae					1				1	0.1	0.1
Genus spp.	Araceae							1		1	0.1	0.1
Number of genera		10	23	11	10	23	25	52		68		
Genera are listed in descending order of importance (% of diet). Genus spp. means plants only identified to family. ^a Species that were only identified by the local Indonesian name. ^b Not a family, but a group of vascular plants. ^c Scored as fruits if unable to be categorised as ripe or unripe.												

Table 3. Dietary composition (%) of proboscis monkeys in all forest types by age-sex classes

	Plant part			
	leaves	fruits	flowers	other
Adult males	43	30	17	10
Adult females	43	35	14	8
Subadults	37	39	16	8
Juveniles/infants	46	24	20	10

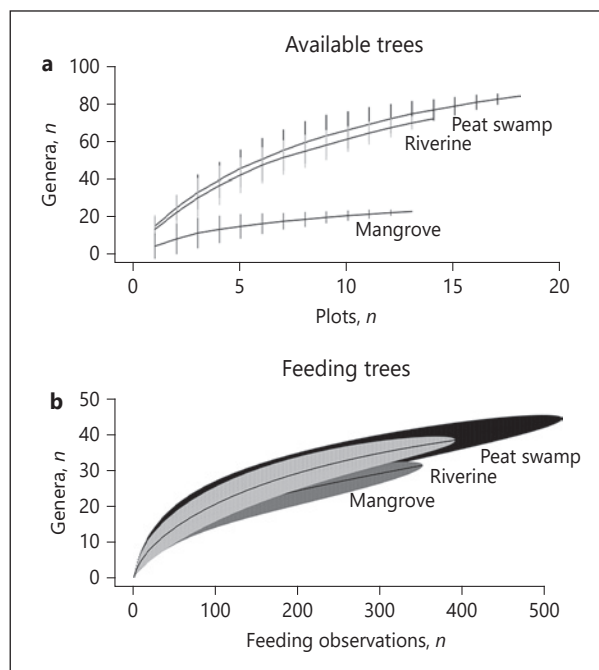
The genus most frequently fed upon was *Syzygium* (Myrtaceae), which accounted for 23.5% of the 1,271 feeding observations, although it was not a strongly preferred food (selectivity coefficient = 1.7). Other frequently eaten food sources varied in their preference (Table 2).

Spatial Variation in Feeding Behaviour

Of the 350 feeding observations in mangrove forest, 402 feeding observations in riverine forest and 519 feeding observations in peat swamp forest, proboscis monkeys fed on a similar number of genera in each forest type (Fig. 4; Table 1; $\chi^2 = 1.1$, $df = 2$, $p = 0.58$).

Plant parts eaten by proboscis monkeys did not differ substantially among forest types (Fig. 3d, f, h). Flowers comprised 17% of the feeding observations in mangrove forest, 7% of the feeding observations in riverine forest and 17% of the feeding observations in peat swamp forest (ANOVA: $F = 2.38$, $df = 2$, $p = 0.12$; Tukey HSD peat-mangrove = -0.03 , $p = 0.71$; mangrove-riverine = -0.08 , $p = 0.10$; riverine-peat = -0.05 , $p = 0.38$). Proboscis monkeys consumed slightly different proportions of unripe fruits in each forest: mangrove forests (22%), riverine (36%) and peat (23%); ANOVA: $F = 0.05$, $df = 2$, $p = 0.96$; Tukey HSD peat-mangrove = 0.2 , $p = 0.96$; river-

Fig. 4. Genus accumulation curves of available (a) and consumed food resources (b) by forest types (mangrove, riverine and peat swamp forests).



ine-mangrove = -0.0001 , $p = 0.99$; riverine-peat = 0.02 , $p = 0.96$). Young leaves comprised 32% of the diet in mangrove, 37% in riverine and 36% in peat swamp forests (ANOVA: $F = 2.4$, $df = 2$, $p = 0.10$; Tukey HSD peat-mangrove = 0.011 , $p = 0.89$; mangrove-riverine = 0.15 , $p = 0.13$; riverine-peat = 0.14 , $p = 0.17$).

Although the plant parts that the monkeys consumed did not differ significantly among forest types, the genera of foods fed upon did. In the mangrove forest, proboscis monkeys most frequently fed on *Bruguiera* (Rhizophoraceae; 35%), *Rhizophora* (Rhizophoraceae; 21%) and *Heritiera* (Malvaceae; 8%); the most preferred genus was *Bruguiera* (selectivity coefficient = 4.5). In the mangrove forest, the monkeys ate 12 rare genera that were not present in the plots. The most frequently eaten genera in the riverine forest were *Palaquium* (Sapotaceae; 29%), *Syzygium* (Myrtaceae; 25%) and *Ficus* (Moraceae; 10%). *Ficus* was the most preferred genus (selection coefficient = 25.4), while *Grewia* (Malvaceae) was the second most preferred genus (selection coefficient = 7.7) in the riverine forest. In the peat swamp forest, proboscis monkeys also consumed foods from *Syzygium* (37%), *Palaquium* (11%) and *Ficus* (7%); *Ficus* was highly preferred (selection coefficient = 40.9), and proboscis monkeys rarely fed on *Knema* (Myristicaceae), but it had the second-highest selectivity coefficient (10.7).

Temporal Variation of Feeding

The availability of food sources varied from month to month (Fig. 3a), as did the diet of the proboscis monkeys (Fig. 3b). Young leaves varied from 18 to 58% of their diet (mean \pm SD = $35 \pm 14\%$), flowers from 3 to 29% (mean \pm SD = $13 \pm 7\%$) and unripe fruits from 3 to 65% (mean \pm SD = $26 \pm 17\%$). The monkeys ate foods from 5 to

Fig. 5. Selectivity of food parts. The monthly use (proportion of the diet) as a function of the availability (proportion of stems in plots in each phenological stage) of plant parts. Points above the grey dashed line indicate preference of a plant part in a month, while points below the line indicate avoidance.

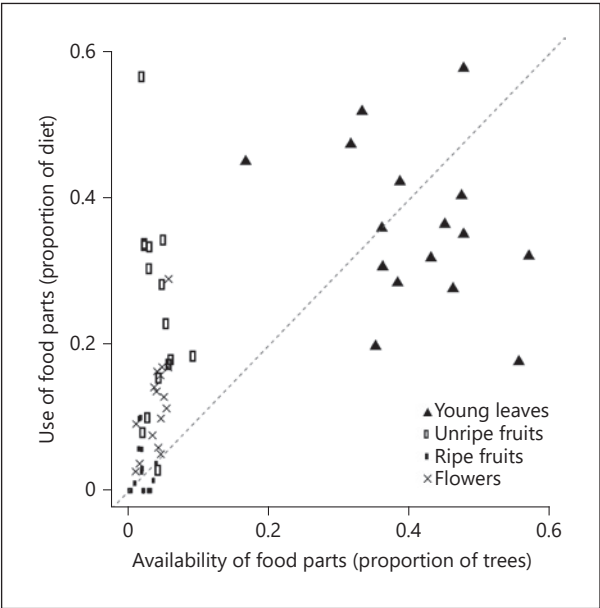


Table 4. Means (and standard deviations) of monthly selectivity coefficients of plant parts by forest type

	Food type		
	new leaves	unripe fruits	flowers
Mangrove	0.8 (0.7)	2.4 (1.8)	1.8 (2.7)
Riverine	1.5 (1.0)	6.5 (7.6)	6.1 (14.4)
Peat swamp	1.1 (0.9)	24.9 (18.2)	11.4 (11.4)

Each value was calculated across 16 months

23 genera per month, and diversity ranged from 1.0 in December 2011 to 2.6 in September 2011. We interpret these results with caution, as the number of genera used is closely related to the number of feeding observations in each month ($r^2 = 0.76$, $p = 9.7 \times 10^{-6}$). The number of genera fed from per month was unrelated to the total available food ($r^2 = 0.01$, $p = 0.69$).

The preference for plant parts differed among months, but not among forest types. Overall, the monkeys preferred unripe fruits (mean selectivity coefficient \pm SD = 7.9 ± 7.0), with selectivity varying from 0.6 to 27 (Fig. 5). Flowers were also a preferred food part (mean selectivity \pm SD = 3.2 ± 1.8). Proboscis monkeys generally avoided ripe fruits; in most months there was not a single feeding observation of ripe fruit. Monkeys ate young leaves in relation to their availability, showing neither a preference nor an avoidance (mean selectivity \pm SD = 1.0 ± 0.6). Given the high availability of mature leaves and their poor representations in the diet, proboscis monkeys appear to have avoided mature leaves as a part of their diet. The patterns of preference

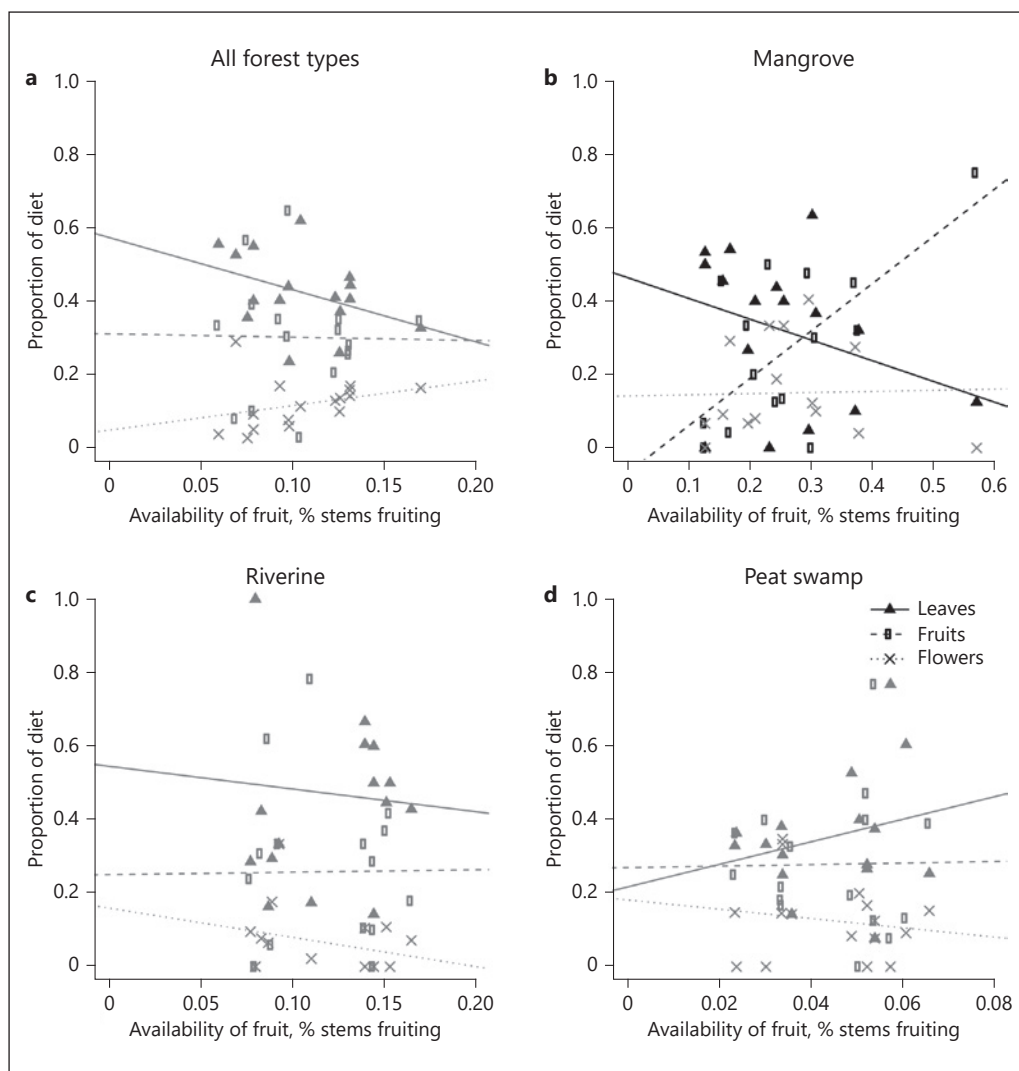


Fig. 6. Consumption of food parts as a function of the availability of preferred foods (unripe fruits) in all forest types (a), mangrove (b), riverine (c) and peat swamp forests (d). Black symbols and lines represent significant relationships ($p < 0.05$), grey symbols and lines represent non-significant relationships.

were similar across forest types, although the preference of unripe fruits and flowers was stronger in riverine and peat swamp forests than in mangrove forest (Table 4).

As unripe fruits were the most preferred food type of proboscis monkeys, we calculated the changes in dietary composition in response to changes in the availability of unripe fruits to identify their fallback foods. When we analysed the data from all forest types, there was no significant relationship between changes in unripe fruit

availability and proportion of young leaves ($r^2 = 0.07$, $p = 0.33$), all leaves ($r^2 = 0.16$, $p = 0.12$), unripe fruits ($r^2 = 0.0003$, $p = 0.95$) or flowers ($r^2 = 0.09$, $p = 0.25$; Fig. 6a) in the diet. In the mangrove (Fig. 6b) forest, consumption of all leaves was inversely related to the availability of stems fruiting (mangrove: $r^2 = 0.4$, $p = 0.008$), suggesting that both mature and young leaves are fallback foods [sensu Marshall and Wrangham, 2007]. Although proboscis monkeys ate young leaves and mature leaves (when analysed independently) more when unripe fruits were unavailable, the relationship was not significant (mangrove mature leaves: $r^2 = 0.14$, $p = 0.16$; mangrove young leaves: $r^2 = 0.10$, $p = 0.22$). Unripe fruit consumption increased proportionally with unripe fruit availability in mangrove ($r^2 = 0.46$, $p = 0.004$). The consumption of flowers in mangrove forest did not change significantly ($r^2 = 0.007$, $p = 0.92$) with unripe fruit availability. In the riverine (Fig. 6c) and peat swamp forest (Fig. 6d), there was no relationship between the availability of unripe fruits and the proportion of leaves (riverine $r^2 = 0.08$, $p = 0.28$; peat $r^2 = 0.06$, $p = 0.36$), unripe fruits (riverine $r^2 = 0.00009$, $p = 0.97$; peat swamp $r^2 = 0.0003$, $p = 0.97$), or flowers (riverine $r^2 = 0.08$, $p = 0.28$; peat swamp $r^2 = 0.03$, $p = 0.55$). The proportion of flower buds in the diet was not influenced by the availability of unripe fruits in any forest type (mangrove: $r^2 = 0.005$, $p = 0.79$; riverine: $r^2 = 0.08$, $p = 0.28$; peat swamp: $r^2 = 0.04$, $p = 0.44$).

Discussion

Proboscis monkeys at Sungai Tolak ate a varied diet, consisting of primarily young leaves, unripe fruit and flowers. In accordance with our prediction, we found that the overall composition of plant parts in the diet was consistent across three forest types; however, the dietary composition of plant parts varied substantially over time. The monkeys ate a similar number of genera in each forest type despite differences in the number of available genera. Although we predicted that flowers would be fallback foods, flowers were preferred foods in all forest types, as were unripe fruits. Supporting our prediction, young and mature leaves were fallback foods in the mangrove forests, but a fallback food could not be identified in the riverine and peat swamp forests.

Although the diet of the proboscis monkeys at Sungai Tolak had some similarities with studies at other sites, the diet was also distinct. At 35%, the percentage of young leaves in the diet of proboscis monkeys at our site was comparable to some other sites including the 38% found in mixed forest type at Samunsan Wildlife Sanctuary, Sarawak, Malaysia [Bennett and Sebastian, 1988] and the 40% found in peat swamp forest at Tanjung Puting National Park, Indonesia [Yeager, 1989]. However, all-day follows of single groups of proboscis monkeys in the riverine forests located in the Lower Kinabatangan River found much higher percentages of young leaves in the diet of proboscis monkeys than our study [66%, Matsuda et al., 2009; 73%, Boonratana, 2003]. A study in the rubber forest in South Kalimantan, Indonesia [80.9%, Soendjoto et al., 2006] and a study from the river's edge in mangrove forest and riverine forest performed in Klias Peninsula in Sarawak, Malaysia, also found higher percentages of leaves in the diet [91.6%, Bernard et al., 2019]. The consumption of flowers also differed, with proboscis monkeys at our site having a much higher percentage of flowers (12%) in their diets than at other sites [3%, Bennett and Sebastian, 1988; Yeager, 1989; 4%, Bernard et al., 2019]. The proportion of plant parts consumed at our study most closely matched that from a mangrove forest on the Lower Kin-

abatangan River [Boonratana, 1994, 2003]. These findings suggest that there may be considerable dietary variation among sites and forest types, although it is likely that differences in sampling methods (duration of the study, number of groups, time of days) explain at least some of the variation.

Across forest types, proboscis monkeys fed on similar numbers of genera even though the number of available genera differed. This pattern may be driven by the inclusion of rare genera in the mangrove forest compared to other forest types. Many colobine species, including other proboscis monkeys, have increased dietary breadth during times and areas with low availability or quality of resources [Yeager, 1989; Hu, 2011; Clink et al., 2017]. The broader dietary breadth in the mangrove forests compared to availability matches the predictions of the optimal foraging theory; animals should increase their dietary breadth in areas with low food quality [MacArthur and Pianka, 1966]. Proboscis monkeys may also increase the breadth of their diet to fulfill their nutritional requirements [Matsuda et al., 2017] and minimise the consumption of antifeedants [Freeland and Janzen, 1974; Janzen, 1974].

Although proboscis monkeys had a preference for unripe fruits and flowers in all forest types, the monkeys did not have a clear fallback food in all forest types. There are various potential explanations for our inability to identify a fallback food in the riverine and peat swamp forests. First, the feeding behaviours in riverine and peat swamp forests may not be a response to the food available in that forest type, but the availability of food in other forests types. As the availability of food sources between forest types was not synchronised, proboscis monkeys may switch habitats in response to changes in food available. Habitat switching in response to food available is a behavioural strategy used by many primates [Hemingway and Bynum, 2005]. Second, the variability of unripe fruit in the riverine forest and peat swamp forests was less than the variability of unripe fruits in mangrove forest. Therefore, the changes in fruit availability in the riverine and peat swamp forests were not different enough to cause an apparent response to the feeding of the proboscis monkeys. Further studies are needed to test these hypotheses.

Our study highlights the importance of forest type and composition in interpreting the feeding ecology of primates. By analysing our data by forest type, we were able to identify relationships between the availability of preferred foods and dietary composition that were obscured when forest types were lumped together. As forest types often vary in species composition and phenological patterns, it is critical to account for such variation in studies of primate feeding ecology. By monitoring food availability, we were able to distinguish between important (i.e. frequently eaten) and preferred foods [Marshall and Wrangham, 2007; Marshall et al., 2009; Marshall and Wich, 2013]. In both plant parts and genera, proboscis monkeys had different preferred and important foods. Many items that were frequently eaten were fed on in proportion to their availability, while highly preferred food sources were often a small percentage of the total diet.

Understanding the plasticity of feeding behaviours can assist the conservation management of this and other endangered animals. Understanding species' responses to seasonal variation of food sources may inform our predictions regarding how animals respond to climate changes, while elucidating species responses to spatial variation in their habitats may shed light on how species respond to human-altered habitat changes, including logging and fires. Finally, information from feeding ecology studies may help to prioritise land protection and inform restoration activities.

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Statement of Ethics

Animal experiments conformed to internationally accepted standards and complied with the rules and regulations of the Institutional Animal Care Committee at the University of California – Davis and were approved by the Indonesian Foreign Research Permit Division under the Indonesian Ministry of Research, Technology and Higher Education.

Disclosure Statement

The authors have no conflicts of interest to declare.

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Author Contributions

K.L.F. and A.J.M. designed the study, interpreted the data and revised the manuscript. K.L.F. collected and analysed the data, produced the figures and wrote the manuscript.

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