

Research article

Comparative diet and nutrition of primates at the Singapore Zoo

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Abstract

Considerable variability in dietary and digestive strategies exists across primate taxa. The Singapore Zoo houses a diverse collection of primate species and their diets are formulated with consideration for their natural diets. We evaluated five species of primates with different diets managed by providing different proportions of fruits/vegetables and leaves to replicate their natural diet compositions. We examined the typical proportion of foods provided and consumed by the different species, and compared the nutrients consumed from the respective food types provided. We found that the primates consumed proportions of the two food types provided consistent with the quantities provided. However, all species consumed a higher proportion of fruits/vegetables to leaves than was provided. Species with more folivorous diets often consumed all fruits/vegetables provided to them, but species with more frugivorous diets did not, and supplemented their diets with leaves. More folivorous species obtained the majority of their nutrition from the leaf component of their diet whereas more frugivorous primates obtained relatively equal proportions from both food types. Nutrient selection in preferred food items was not strongly exhibited but the primates generally preferred food items with higher protein and non-structural carbohydrate (NSC) content; species with more folivorous diets preferred leaf items with higher protein–fibre ratio while the converse applied to species with more frugivorous diets. Dietary fibre consumption levels for all species were relatively high; and NSC consumption levels for species with more folivorous diets were close to the recommended upper limits for foregut fermenters. Although current diets provided for these primate species are appropriate, adjustments should be made to refine the proportions and compositions of major food types provided to ensure nutritional goals are met while minimising food wastage. Diets for primates with different dietary specialisations should be customized whenever possible, within the constraints of practical captive management.

Introduction

The primate order is highly diverse and this is reflected in the range of dietary and digestive specialisations found amongst different species (Chivers and Hladik 1980; National Research Council 2003). Most primate species have diets consisting of proportions of different food types that can be differentiated along broad continuums, for example, frugivory to folivory (Chivers and Hladik 1980, 1984; Lambert 1998). Wild primates meet their nutritional goals by prioritising certain nutritional parameters when choosing the types and quantities of different foods within the constraints of the spatial and temporal distribution of food resources within their habitats (Schoener 1971; Oates 1987; Felton et al. 2009). Primate species with more folivorous diets primarily select foods of high protein and protein–fibre ratio (McKey et al. 1981; Waterman 1984; Waterman and Kool 1994; Yeager et al. 1997) and species with more frugivorous diets select foods rich in digestible carbohydrate content (Oftedal 1991; Nakagawa 2003).

Digestive strategies are required to process and absorb nutrients according to the chemical, physical and nutritional component of the different diets that primates consume, for example, gastrointestinal morphology, adaptations for mechanical processing and symbiotic microbial fermentation (Milton 1981; Lambert 1998). Digestive strategies are also reflected in different digesta passage rates required for optimal processing and absorption of nutrients from different food types (Chivers and Hladik 1980; Lambert 2002; Clauss et al. 2008). Forestomach fermentation is most efficient for primates that rely on foods high in structural carbohydrates, while caeco-colic fermentation is most efficient for primates that typically rely on foods high in readily digestible fibres (Lambert 1998). Primate species with more folivorous diets often consume leaves that contain high proportions of fibre and plant secondary compounds, which act as digestion inhibitors (Milton 1979; Waterman and Kool 1994). They have large multi-chambered stomachs containing anaerobic cellulolytic bacteria to assist in the breakdown of cellulose-based food and secondary toxins

in leaves (Bauchop and Martuchi 1968; Davies and Oates 1994). However, there are exceptions to such generalisations, whereby simple-stomached primate species can also have highly variable folivorous diets and long digestion retention times; for example, mountain gorillas (*Gorilla beringei*) (Ganas et al. 2003; Clauss et al. 2008). Primates with more frugivorous diets are generally caeco-colic fermenters that use enlarged caecums or colons as fermentation chambers (Chivers 1994). Such digestive adaptations allow for more efficient absorption of nutrients from foods high in readily digestible components (Alexander 1993). They are generally inefficient fermenters of complex carbohydrates, although there are exceptions, i.e. species that exhibit a high degree of microbial fermentation (Clemens and Phillips 1980; Brounron and Perrin 1991; Norconk et al. 2002).

Wild primates have the opportunity to adapt their foraging strategies to a higher diversity and variability of food within their natural habitats, in order to satisfy their primary nutritional goals; whereas captive animals are presented with more limited food choices, albeit often less variable and inadvertently of higher nutritional quality. Successful maintenance of captive primates requires appropriate dietary husbandry to meet the nutritional needs of different species. Optimal nutritional management of primates in captivity is dependent on meeting their nutrient needs, taking into consideration the foraging strategies, dietary and digestive characteristics of different species, and replicating these requirements within the constraints of captive dietary management (Ullrey 1986; NRC 2003). In captivity, there are limitations posed by the availability of suitable food plants that mimic the nutritional content of wild foods. Natural fodder for primates is particularly difficult to obtain in sufficient quantities in non-tropical countries, requiring storage measures such as freezing and drying or growing under artificial (greenhouse) conditions (Koontz et al. 1988; Nijboer and Dierenfeld 1996). Wild foods differ nutritionally from commercial produce that is often more readily available for primates in captivity. One important difference between wild and cultivated fruits is that sugar in the pulp of wild fruits tends to be hexose-dominated (some fructose and considerable glucose) while that of cultivated fruits tends to be highest in sucrose (Milton 1999). They also tend to contain lower protein, minerals and vitamins compared to wild foods (Schwitzer et al. 2009). Due to the substitution of cultivated fruits for wild fruits, the nutritional composition of zoo diets do not appear to duplicate, for example, high fibre levels, but include substantially more soluble carbohydrate and available protein instead (Kay & Davies 1994; Waterman & Kool 1994; Nijboer & Dierenfeld 1996). Historical diets for primates with more folivorous diets in European and North American zoos, for example, contain low fibre concentrations of 12.5% neutral detergent fibre (NDF) in dry matter (DM) and 6.3% acid detergent fibre (ADF) in DM. One of the reasons for these low fibre levels may be the low proportion of leaves in such diets. For example, at the New York Zoological Park, leaves constituted only about 20% of total diet for proboscis monkeys (Dierenfeld et al. 1992). The consequences of not providing appropriate specialised diets have been particularly demonstrated for highly folivorous species, in which provision of a high level of rapidly fermentable foods with highly digestible sugars can lead to health problems and death (Hollihn 1973; Collins and Roberts 1978; Albert 1983; Janssen 1994).

The Singapore Zoo manages a collection of 37 species of primates (as of March 2014). The diversity of species in the collection requires formulation of different diets to cater to the specialisations of different species. In this study, we examined five species of primates with diets formulated with broad considerations of their natural diets; and variations in type and quantities of food types such as fruits/vegetables and leaves were provided to replicate natural diet compositions. We examined the proportion

of fruit/vegetables to leaves provided and consumed by these primates, and how they obtained major nutrients from these two food types. We compared our results to nutrient compositions of the diets of wild conspecifics and/or recommended nutritional requirements for these species in captivity, where available. We hypothesise that current dietary management through the provision of different proportions and compositions of food types appropriately caters to the dietary specialisations of different primate species. However, broad generalisations about their diets may need to be further refined to provide more optimal nutritional management and to minimise food wastage.

Methods

Subjects

One male and one female subject from each of five species of primates were used – ring-tailed lemur (*Lemur catta*), white-faced saki (*Pithecia pithecia*), red-shanked douc langur (*Pygathrix nemaeus*), proboscis monkey (*Nasalis larvatus*) and Javan langur (*Trachypithecus auratus*) (Table 1). All subjects were housed in pairs at the Primate Holding, an off-exhibit facility area of the Singapore Zoo.

Diet and feeding

The primates were fed with a mixed diet of leaves, vegetables and fruits, between twice and three times daily at 0900, 1330 and 1530. The staple leaf diet consisted of five to seven plant species – acalypha (*Acalypha siamensis*), hibiscus (*Hibiscus* sp.), miracle (*Leucaena leucocephala*), ketapang (*Terminalia catappa*) and mulberry (*Morus alba*). Small quantities of an additional three to four species of leaves (from a total of 54 different plant species from 26 families) were also included according to seasonal availability of young leaves. This was because the leaf diets were pre-selected for high quantities of young leaves whenever possible. Fruits/vegetables were also fed on a daily basis. These consisted of a mix of fruits such as oranges, apples, pears, papayas and bananas, and vegetables including sweet potatoes, long beans, carrots, sweet corn, tomatoes and cucumbers. Species considered to have more frugivorous diets, such as the ring-tailed lemur and white-faced saki, were provided with a wider variety

Table 1. Details of study subjects.

Species	Age class	Sex	Age (yrs)	*Body mass (kg)
Ring-tailed lemur	Adult	M	8.8	3.0
Ring-tailed lemur	Adult	F	4.1	2.0
White-faced saki	Adult	M	6.0	2.0
White-faced saki	Adult	F	12.8	1.5
Red-shanked douc langur	Sub-adult	M	3.8	6.5
Red-shanked douc langur	Sub-adult	F	3.1	5.0
Proboscis monkey	Adult	M	19.8	19.0
Proboscis monkey	Adult	F	5.3	8.0
Javan langur	Adult	M	5.0	6.5
Javan langur	Adult	F	16.0	5.0

*Body mass was measured prior to commencement of the study using a custom-made flatbed weighing scale placed inside the enclosures of the subjects. Individual subjects were baited by food to climb onto the scale for measurements.

Table 2. Study species, food type and average quantities provided per day over the study period.

Food type	Species				
	Ring-tailed lemur	White-faced saki*	Red-shanked douc langur	Proboscis monkey	Javan langur
Mixed leaves	538 g	682 g	2320 g	7899 g	2461 g
Mixed fruits and vegetables	568 g	535 g	911 g	1447 g	433 g
Primate pellet	3 pellets	2 pellets	2 pellets	4 pellets	2 pellets
Nutroplex multivitamin	2 tsp	½ tsp	1 tsp	2 tsp	1 tsp
Bread	25 g	15 g	35 g	45 g	25g
Rice ball with boiled egg and chicken meat	–	50 g	100 g	100 g	100 g

*The white-faced sakis' mixed fruit and vegetable diet included approximately 35 g of sunflower seeds.

of high-sugared cultivated fruits in their diet mix, for example, mangoes and grapes. Seed-eating species such as the white-faced saki were also given additional items including sunflower seeds and almonds. All primates also received daily supplements of Mazuri® Primate Browse pellets (Mazuri®, Indiana, USA) and Nutroplex multivitamins syrup (Myra Pharmaceutical Inc, Binan Laguna, Philippines). Water was available in water troughs at all times. The types of food and average quantities provided per day are given in Table 2.

Food consumption

Food consumption was recorded quantitatively over a period of five consecutive days for each species. Food items were weighed before they were offered to the subjects and left in their enclosures until the next feeding session. Prior to subsequent feeding sessions, all leftover food was removed and the enclosure cleaned, before fresh food items were offered. Each feeding session lasted from two to four hours. All food items that were 5g and below were weighed using an Ohaus CL series portable scale (500g x 0.1g), while items above this weight were weighed using a Hokotow digital weighing scale (15kg x 5g). Weights were adjusted by deriving a desiccation factor from the estimated moisture lost from similar sets of food placed in a desiccation pan in an area adjacent to the primate enclosures; and accounting for the actual duration of each feeding session at different times of the day. As individuals of each species were housed together, food consumption, calculated by subtracting leftover food from total food offered, represented consumption for both individuals. We also calculated the percentage of food wastage from each species using the total amount of food left over divided by the total amount of food given x 100.

Food preference

Preferences for leaf items were recorded by focal sampling (Altmann 1974) of individuals over 90 minutes from the start of each feeding session, by observing the number of times an individual picked up a leaf item. We ranked items in order of preference by computing the average number of pickups over different feeding sessions.

Preferences for fruit/vegetable items were similarly recorded by focal sampling; but by observing the sequence an individual consumed a fruit/vegetable item. Fruit/vegetable items were assigned reverse order ranks, with a maximum score assigned to the first item consumed and a minimum score assigned to the last item consumed. Cumulative scores for each feeding session were then computed and preferred items ranked in order of highest to lowest score. We then examined food preference by comparing the top and bottom five leaf and fruit/vegetable items consumed by each species and examining the mean nutrients present in these food items.

Nutritional analysis

Sets of typical leaf and fruit/vegetable diets for each species as well as individual food items were sent to ZARGO Pacific Lab Services laboratory (Singapore) for nutritional analysis. To minimise moisture loss from samples, we sealed the samples in a ziplock bag and sent the samples to the laboratory within an hour of collection. The following nutritional components were analysed using standard procedures – moisture (vacuum oven drying at 135° C for 2 h), ash (gravimetry), crude protein (CP) (Kjeldahl method using the calculation: 6.25 x nitrogen value), crude fat (CF) (acid hydrolysis method), neutral detergent fibre (NDF) (gravimetry) and acid detergent fibre (ADF) (nitrogen determination by Kjeldahl). Dry matter (DM) was calculated by subtracting moisture content from wet weight; carbohydrate was calculated by subtracting moisture and ash content from wet weight; non-structural carbohydrate (NSC) was calculated by subtracting NDF from carbohydrate. All nutrition values were calculated as weight per 100 g. The actual nutrient consumption of each subject during the study was obtained by dividing the nutritional content of each nutrition component by 100 and multiplied by the actual amount of food (in grams) consumed.

Statistical analysis

We tested for differences between the proportions of fruit/vegetable to leaf offered and consumed by the five primate species using One-Way Anova. We used paired-sample t-tests to test for differences between the proportion of fruits/vegetables offered and consumed, and for differences in nutrient values (DM, CP, CF, NSC, NDF and ADF) between consumed fruit/vegetable and leaf diets. We used Independent-sample t-tests to look for differences in nutrient values (CP, protein–fibre ratio and NSC) between preferred and non-preferred fruit/vegetable and leaf items. All data were checked for normality using Kolmogorov–Smirnov tests, and as all data were normal, parametric statistical tests were chosen. All analysis was done using the Statistical Package for the Social Sciences, version 20.0 (SPSS Inc., Chicago, USA). Statistical significance was set at $p < 0.05$.

Results

Diet

The daily average proportions of fruits/vegetables and leaves offered and consumed by the different species are shown in Figure 1.

The proportion of fruits/vegetables to leaves offered to the individual species did not differ significantly from what was consumed (one-way ANOVA: $F=1.165$; $d.f.=9$; $p=0.312$). However, the consumption of fruits/vegetables for all species was significantly higher than the proportion offered (paired t-test: $t=4.521$; $d.f.=4$; $p=0.011$).

All three species of primates with more folivorous diets i.e. douc langur, proboscis monkey and Javan langur, consumed almost all fruits/vegetables offered, with a daily average wastage of less than 0.5%. For species with more frugivorous diets, i.e. ring-tailed lemur

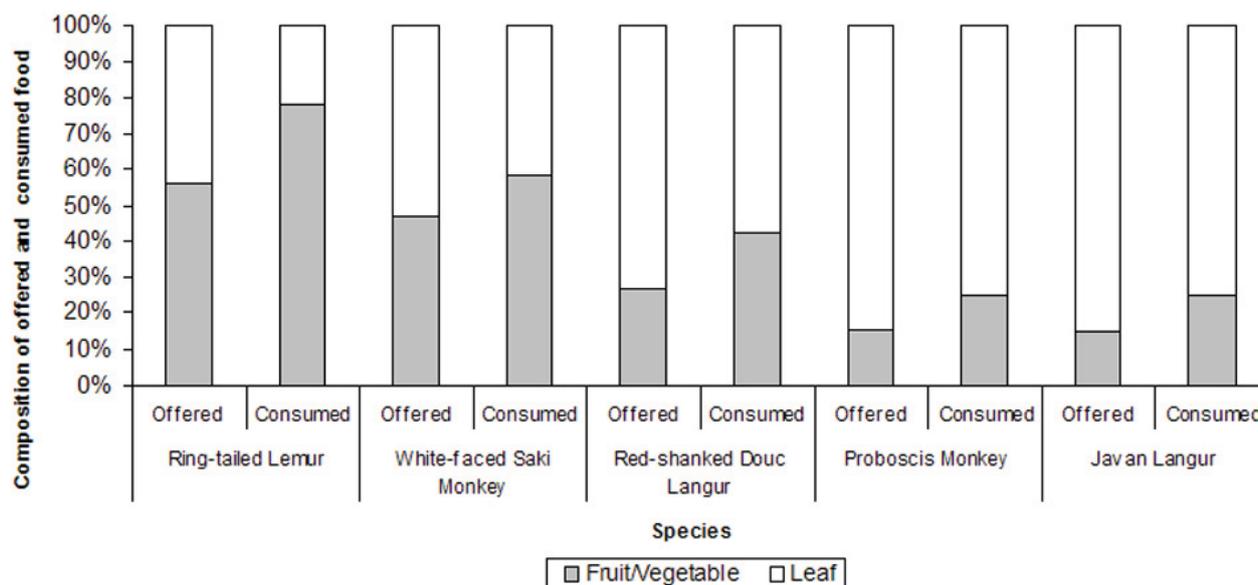


Figure 1. Daily average percentage of fruits/vegetables and leaves offered and consumed by the primate species.

and white-faced saki monkey, although the proportion of fruits/vegetables to leaves consumed was higher than the proportion offered, there was still daily average fruit/vegetable wastage of 3% and 18% respectively. Leaf wastage was high across species, averaging between 17% and 55% daily, although this also included larger stem parts that the primates generally do not consume.

Nutrient composition of diet

The nutrient values of major food items in the fruit/vegetable and leaf diets of the primates are given in Appendix I (available online at www.jzar.org).

The nutrient values of fruit/vegetable and leaf diets consumed by the primates are given in Table 3 and differences compared in Table 4. Consumption of all major nutrients from the leaf diets of the three species with more folivorous diets was significantly higher than from their fruit/vegetable diets (with the exception of the douc langur, which derived similar amounts of NSC from both diets).

Consumption of DM and CP for the two species with more frugivorous diets did not differ significantly between their fruit/

vegetable and leaf diets. Consumption of NSC for both species was significantly higher from fruit/vegetables compared to leaves. The white-faced saki monkey derived significantly higher CF from its fruit/vegetable diet but fibre consumption (ADF and NDF) was not significantly different. The ring-tailed lemurs derived significantly higher fibre content (ADF and NDF) from their leaf diets but CF consumption was not significantly different.

Overall fibre consumption level (ADF and NDF) was highest for the white-faced saki and lowest for the ring-tailed lemur, with corresponding lowest and highest NSC consumption levels.

Food preference

The mean nutrient contents of preferred and non-preferred items in the leaf diet of the primates are given in Table 5a and in the fruit/vegetable diet in Table 5b.

The more frugivorous species generally preferred leaf items with lower protein content and protein–fibre ratios, while the more folivorous species preferred leaf items with higher protein content and protein–fibre ratio. However, these differences were only significant for the ring-tailed lemur for protein–fibre ratio

Table 3. Nutrient values in food consumed in fruit/vegetable and leaf components of diets.

Nutrients	Ring-tailed lemur			White-faced saki			Red-shanked douc langur			Proboscis monkey			Javan langur		
	F/V	L	O	F/V	L	O	F/V	L	O	F/V	L	O	F/V	L	O
Dry matter	62.6	53.7	116.3	93.7	105.3	199.0	125.9	394.3	520.2	124.0	1259.8	1383.8	51.3	501.1	552.4
Crude protein	7.3	8.0	7.6	13.1	18.9	16.1	8.2	12.8	11.7	16.6	18.9	18.6	9.3	16.1	15.4
Crude fat	1.5	3.9	2.6	11.2	3.6	7.2	0.5	2.2	3.1	2.7	2.9	2.9	2.1	2.7	2.7
Non-structural carbohydrate	63.2	29.9	47.9	23.0	15.3	14.6	58.6	26.9	34.6	44.7	21.9	23.9	45.0	36.2	37.0
NDF	19.5	50.1	33.6	53.4	56.6	55.1	26.1	48.1	42.8	27.4	48.7	46.8	35.9	37.1	37.0
ADF	11.9	35.0	22.5	37.7	42.5	40.2	18.6	37.6	40.0	20.2	33.2	32.1	15.8	35.6	33.8

F/V=Fruit/Vegetable; L=Leaf; O=Overall diet. DM is presented in grams (g); other nutritional values as % of DM.

Table 4. Differences in nutrient consumption between fruit/vegetable and leaf diet.

	Ring-tailed lemur	White-faced saki	Red-shanked douc langur	Proboscis monkey	Javan langur
Dry matter	t=1.370; p=0.242	t=-0.258; p=0.809	t=-8.756; p=0.001	t=-12.852; p=0.001	t=-7.638; p=0.005
Crude protein	t=0.643; p=0.555	t=-0.909; p=0.415	t=-11.216; p<0.001	t=-13.147; p=0.001	t=-5.637; p=0.011
Crude fat	t=-3.576; p=0.023	t=4.216; p=0.014	t=-13.594; p<0.001	t=-13.116; p=0.001	t=-7.798; p=0.004
Non-structural carbohydrate	t=8.053; p=0.001	t=7.532; p=0.005	t=-2.505; p=0.066	t=-10.161; p=0.002	t=-7.132; p=0.006
NDF	t=-3.580; p=0.023	t=2.632; p=0.078	t=-11.822; p<0.001	t=-13.565; p=0.001	t=-7.638; p=0.005
ADF	t=-3.840; p=0.018	t=2.129; p=0.123	t=-12.117; p<0.001	t=-13.616; p=0.001	t=-8.926; p=0.003

Paired-sample t-tests (df = 4) were used to test for differences with a significance level of p<0.05. All nutrition values used for this calculation were expressed per unit DM. Significant values are highlighted in italics.

and for the douc langur and Javan langur for protein content. All species preferred leaf items with higher NSC content, although these were not significantly different from non-preferred items.

All species except the Javan langur generally preferred fruit/vegetable items with higher protein content and protein-fibre ratio. They also preferred fruit/vegetable items with higher NSC content. None of the differences in nutrient values between preferred and non-preferred fruit/vegetable items were significant, however.

Discussion

The overall consumption of fruits/vegetables and leaves by the primate species in this study followed the proportions offered i.e. diet specialisations were appropriately accounted for by provision of relevant proportions of the two major food types to mimic dietary compositions. The overall consumption of fruits/vegetables was higher than what would be expected from the

Table 5a. Nutrient contents in preferred and non-preferred leaves.

Species	Protein		Protein-fibre ratio		NSC	
	Preferred	Non-preferred	Preferred	Non-preferred	Preferred	Non-preferred
Ring-tailed lemur	3.66±0.12 t=-0.656; p=0.548	4.45±1.08	0.24±0.06 t=-8.218; p=0.001	0.65±0.07	6.28±2.73 t=0.374; p=0.727	5.40±3.02
White-faced saki	3.38±0.59 t=-1.256; p=0.227	4.59±3.14	0.23±0.05 t=-1.716; p=0.161	1.07±0.84	8.74±6.77 t=0.286; p=0.789	7.33±5.21
Douc langur	4.53±0.82 t=2.674; p=0.028	3.40±0.46	0.54±0.19 t=1.884; p=0.096	0.32±0.17	7.82±2.83 t=0.063; p=0.951	7.55±5.67
Proboscis monkey	5.11±1.67 t=1.614; p=0.145	3.82±0.61	0.56±0.22 t=1.122; p=0.295	0.41±0.22	6.83±4.14 t=1.884; p=0.096	5.36±2.78
Javan langur	5.75±1.52 t=2.739; p=0.029	4.60±3.78	0.71±0.35 t=2.046; p=0.080	0.35±0.16	7.18±2.78 t=0.146; p=0.888	6.81±4.26

Table 5b. Nutrient contents in preferred and non-preferred fruits/vegetables.

Species	Protein		Protein-fibre ratio		NSC	
	Preferred	Non-preferred	Preferred	Non-preferred	Preferred	Non-preferred
Ring-tailed lemur	0.77±0.52 t=-1.012; p=0.369	1.35±0.84	1.31±0.81 t=0.309; p=0.773	1.11±0.84	9.83±1.16 t=1.941; p=0.124	3.76±5.30
White-faced saki	0.97±0.49 t=-0.112; p=0.915	1.20±0.97	1.20±0.69 t=0.369; p=0.727	0.97±0.94	9.02±1.25 t=1.929; p=0.112	3.81±5.38
Douc langur	1.33±0.85 t=1.619; p=0.149	0.51±0.08	0.91±0.55 t=0.186; p=0.857	0.83±0.69	6.31±3.93 t=-0.115; p=0.912	6.65±4.64
Proboscis monkey	1.52±0.96 t=1.774; p=0.136	0.51±0.08	1.05±0.63 t=0.451; p=0.671	0.83±0.69	7.36±3.79 t=0.225; p=0.831	6.65±4.64
Javan langur	1.65±1.63 t=1.159; p=0.311	0.74±0.46	0.74±0.44 t=-0.179; p=0.867	0.83±0.56	4.71±3.87 t=-0.779; p=0.480	7.44±4.11

Differences in mean nutrient content between preferred and non-preferred food items were tested using independent-samples t-tests (df = 8). Significant values are italicised.

proportions offered. This was because all species consumed a higher proportion of their provided fruit/vegetable diet and a lower proportion of the leaf diet, indicating a preference for fruits/vegetables, even for the species with more folivorous diets: the douc langur, proboscis monkey and Javan langur consumed almost all the fruits/vegetables provided to them. A study on proboscis monkeys at the New York Zoological Park similarly found that a higher proportion of sweet fruits such as plantain and banana were consumed compared to leaf browse (Dierenfeld et al. 1992). Species with more frugivorous diets, on the other hand, did not consume all the fruits/vegetables provided to them, but supplemented their diets with leaves instead. This was particularly evident for the white-faced saki, where high fruit/vegetable wastage of about 18% was observed on average per day. Species with more folivorous diets also generally had a higher percentage of leaf wastage compared to frugivores, while frugivores had a higher wastage of fruits/vegetables. This was probably due to the higher absolute quantities of fruits/vegetables and leaves provided to the primates according to their expected diet types, but these high wastage levels could imply that more food was provided than required.

Species with more folivorous diets derived a higher proportion of all major nutrients from their leaf diets compared to their fruit/vegetable diets, due to the higher consumption of leaves with inherently higher DM content. The exception was for NSC consumption for the douc langur, which was not significantly different between the two food types, due to a higher proportion of fruits/vegetables consumed compared to the other two species. We did not measure fibre digestion efficiency or metabolisable energy gain from different food types in this study, but more folivorous species such as the colobines are known to be able to process difficult-to-digest carbohydrates in dietary fibre, so the consumption of major nutritional components from their leaf diets should be sufficient to provide the required nutrients. Species with more frugivorous diets generally derived higher NSC from their fruit/vegetable diets and higher fibre consumption from their leaf diets. This was because they preferred leaf items with a lower protein-fibre ratio.

The fibre consumption levels of species with more folivorous diets exceeded recommended levels by the National Research Council (2003) of ADF 15% and NDF 30% for colobine species. For the proboscis monkey, fibre levels were also close to that found in leaves consumed in the wild (Yeager et al. 1997; Matsuda et al. 2013). High fibre diets for species with more folivorous diets are desirable for faecal consistency and overall gastrointestinal health (Edwards 1995; Nijboer et al. 2006a,b). The fibre consumption levels of species with more frugivorous diets in this study generally exceeded the fibre concentrations of 5–10% ADF and 10–20% NDF recommended by the National Research Council (2003) for non-colobine species. This was due to the consumption of leaves that contained higher fibre concentrations compared to the leaf diets provided to species with more folivorous diets. Unexpectedly, the white-faced saki and ring-tailed lemur actually preferred leaves higher in fibre content. For the ring-tailed lemur, consumption of such leaves could be used as a supplement to the high NSC/low fibre content in their fruit/vegetable diets. The white-faced saki has also been shown to be capable of a high degree of fibre fermentation to cope with relatively high consumptions of NDF and ADF in the wild (Norconk et al. 2002). Consequently, the diet of the white-faced saki in this study showed the highest fibre level (NDF and ADF) amongst the study subjects. There are, however, potential negative effects of high fibre diets in non-human primates; for example, reduction in mineral absorption and decreased fat and protein digestibility (Schneeman 1990), and the loss of energy to the metabolism of symbiotic microbes before nutrients can be digested and absorbed (Alexander 1993).

Frugivorous caeco-colic fermenters may, however, have a higher than expected flexibility to process high fibre foods; for example, Japanese macaques can expand gut size (Sawada et al. 2010), and gorillas have longer than expected average gut retention times for a simple-stomached species (Remis 2000; Remis and Dierenfeld 2004) to deal with high consumption of high-fibre foods.

All species generally preferred food items with high NSC content in both their leaf and fruit/vegetable diets. Consequently, the primates showed high NSC consumption levels, particularly for species with more folivorous diets, which were close to or fell within the limits of not more than 30–40% recommended for foregut fermenters (NRC 2001). This was contributed by the availability of fruits/vegetables high in NSC content but could also be attributed to the consumption of leaf diets that were preselected for high compositions of young leaves. The leaves provided in this study also contained higher protein-fibre ratios compared to, for example, wild proboscis monkeys (Yeager et al. 1997; Matsuda et al. 2013) and douc langurs (Otto 2005). Species with more folivorous diets, for example proboscis monkeys, preferred these leaves due to the high protein-fibre ratios (Abdul Wahid and Richardson, unpublished). However, young leaves also generally contain higher NSC content compared to mature leaves (Milton 2008). The consequences of consuming a high level of rapidly fermentable foods have been widely reported and captive feeding programmes for folivorous primates recommends limiting the amount of fermentable carbohydrates (Edwards et al. 1997). For example, Paignton Zoo implemented the removal of all fruit, bread and eggs from primate diets, in order to reduce the levels of readily available energy and particularly sugar (Plowman 2013).

Historically, dietary management of primates in captivity was often based on experience rather than applied research; for example, diets for colobine monkeys in European and North American zoos consists of 149 different ingredients with no agreement as to what foods should be fed to these primates (Nijboer and Dierenfeld 1996). This may largely be due to the limited availability of standardised and suitable fodder in non-tropical regions. In tropical zoos, wild fodder that better mimics the nutritional qualities of those consumed by primates in their natural habitats is fortunately more readily available. A well-balanced diet that is phytochemically similar to the wild diet is largely responsible for the success in maintaining colobine species with highly specialised digestive systems, such as proboscis monkeys (Agoramoorthy et al. 2004).

However, diets provided to primates in captivity still vary considerably from their wild conspecifics. The most marked difference can be found in the provision of cultivated fruits in captivity, instead of wild fruits that are usually not readily available as staple provisions for captive primates. For example, proboscis monkey diets in the wild consist of up to 26% fruits (but less than 3% ripe fruits) (Boonratana 2003; Matsuda et al. 2009).

Although the broad differences between species with more frugivorous and folivorous diets were appropriately managed with the provision of suitable types and proportions of food types, improvements to the dietary management of these primates should be considered. For example, reduction of the general consumption of fermentable carbohydrates by species with more folivorous diets should be implemented by reducing the provision of fruit items high in NSC that do not contribute significantly to their overall nutritional consumption. The type and composition of fruits/vegetables and leaves provided to species with different natural diets could also be adjusted, for example, by providing higher proportions of young leaves (which are generally higher in readily digestible fibre and lower in non-digestible fibre content) to species with more frugivorous diets, and provision of vegetables and fruits that are lower in readily digestible fibre and higher in non-digestible fibre content to species with more folivorous diets.

Efforts should also be made to source appropriate substitutes for unripe fruits to better mimic the nutritional composition of wild diets.

Some of these diet changes have since been implemented at the Singapore Zoo. Food items such as rice balls and bread have since been removed from the diets of colobine species. Reduction of fruit items high in NSC content, for example apples and pears, has also been implemented. The gradual total removal of fruits that are high in digestible sugar, similar to the regime that has been implemented at Paignton Zoo (Plowman 2013), is currently being considered. In addition, further customisation of diets for individual or groups of primate species that vary in natural diet compositions are in progress, to refine the proportions and compositions of major food types provided to ensure nutritional goals are met while minimising food wastage.

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