DIET OF PHAYRE'S LEAF-MONKEY IN THE PHU KHIEO WILDLIFE SANCTUARY, THAILAND

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ABSTRACT

Trachypithecus is reported to rely more on leaves, and predicted to eat more mature leaves, than other Asian colobines. I therefore predicted that leaves should dominate the diet of Phayre's Leaf-monkeys *Trachypithecus phayrei* (Blyth). To test this, I conducted five 20-minute focal samples each month (June 2004 to May 2005) for all adult monkeys in three social groups (N=23), with instantaneous sampling of behavior at one-minute intervals (N=24,439). Based on feeding time, the percentage of instantaneous samples within each dietary category, leaves were the dominant food item (46.2%) as predicted, with young leaves (31.3%) eaten more than mature leaves (12.4%). Fruit represented 39.5% of the diet, with monkeys consuming seeds and pulp from immature fruits (23.9%) more than mature fruits (12.6%). Flowers comprised 8.9% of the diet, while bamboo shoots, insects, and other items represented less than 5%. Insects and bamboo shoots were important for a period of less than two months. Diet varied across the year, with immature fruits becoming important as immature leaves disappeared from the diet. Most food items came from 28 plant genera, many of which are consumed throughout the year. *Trachypithecus phayrei* consumed more mature leaves than reported for *Presbytis* and *Nasalis*, providing support for stronger adaptation to a leaf diet.

Keywords: Asian colobines, folivorous diet, Phayre's Langur, *Trachypithecus phayrei*, *Trachypithecus*

INTRODUCTION

Colobines receive the name "leaf-eating monkeys" from their dietary preference for the consumption of leaves. This preference derives from a set of anatomical adaptations shared across taxa that allows them to maximize their nutritional intake from difficult-to-digest leaves. These adaptations include molar teeth with high cusps and ridges for breaking down leaf cellulose, and multi-chambered stomachs with associated symbiotic bacteria that aid in the degradation of plant fibers while maximizing opportunities to absorb carbohydrates and proteins (Kay & Davies, 1994). This adaptive morphological complex allows Asian colobines to subsist on the ubiquitously-available leaves found in a wide variety of forest habitats. Consequently, leaves feature prominently in the diets of many Asian colobines.

While specialized teeth and stomachs allow Asian colobines to digest nutritionally-challenging mature leaves, many Asian colobines demonstrate a behavioral bias towards selecting young leaves, which are lower in plant fiber, and therefore easier to break down in the mouth and stomach, and have fewer plant secondary compounds, making them easier to digest (Yeager & Kool, 2000). For example, 46% of the total feeding time of *Trachypithecus auratus* (É. Geoffroy) is directed towards the acquisition and consumption of young leaves (Kool, 1992; 1993).

Asian colobines complement their leafy diets with additional food items. Like many other primate species, fruits and seeds make up an important part of colobine diets. Many Asian colobines appear to target fruits when they are immature, avoiding the negative effects that the fruits' simple sugars have on the ability of the stomach's microflora to break down the cellulose in leaves (Waterman & Kool, 1994). Asian colobines show a similar preference for the seeds of immature fruits, as the seeds of mature fruits typically contain greater concentrations of plant secondary compounds, which are known to interfere with digestion and absorption of nutrients (Waterman & Kool, 1994). When *Trachypithecus vetulus* (Erxleben) consumed fruits, for example, they targeted fruits that were unripe, dry and fibrous, rather than ripened fruits (Hladik, 1977), and *Rhinopithecus avunculus* (Dollman) consumed more immature fruits than mature ones (Le *et al*., 2007). In addition to fruits and seeds, Asian colobines may also consume soil and gum (Oates *et al*., 1980), but typically not animal matter (Oates *et al*., 1980; Stanford, 1991), with the exception of Hanuman langurs *Semnopithecus entellus* (Dufresne), for whom insects made up 2.8% of the annual diet.

The dietary preferences of Asian colobine species varies seasonally, in response to environmental changes

in food abundance, patch density and distribution, and food quality. When preferred foods such as mature fruits and young leaves are scarce, Asian colobines shift their diets to include more low-quality, subsistence items such as mature leaves (Hladik, 1977; Newton, 1992; Bennett & Davies, 1994).

In addition to preferences for particular categories of food, Asian colobines also demonstrate preferences for particular food species. For example, *T. vetulus* was found to consume 23 different plant species over the course of a study, yet 70% of the annual food intake came from only three species (Hladik, 1977). Even Asian colobines with a broader diet demonstrate strong preferences for only a few plant species; *Trachypithecus johnii* (J. Fischer) consumed 102 different plant species, yet 45% of their diet came from only three species (Oates *et al*., 1980). Preference for particular food items is typically measured with a selectivity index, and is calculated as the ratio of the prevalence of a food species in the monkey's diet to the prevalence of the food species in the environment (Krebs, 1989). Preferred or selected foods occupy much of the feeding time, but are relatively less common in the environment. For example, *Trachypithecus francoisi* (Pousargues) in China chose a large proportion of their diet from ten plant species, and only three of these were among the ten predominant species at the site (Zhou *et al*., 2009). Also, when Asian colobines rely heavily on a few particular species of plants, different parts of each plant are harvested at different times of the year. Some trees, for example, are sources of young leaves, flowers, and fruits, depending on phenological condition (Hladik, 1977).

While it is possible to generalize about the diet of Asian colobines, there is also a lot of variation in feeding behavior across taxa. A big part of the variation arises from the broad geographic distribution of Asian colobines, which range from Pakistan and India to China, and down to Borneo (Groves, 2001). And while many species occupy tropical or sub-tropical forests in these areas, others live in extreme habitats, such as high-altitude, high-latitude, or karst rock formations (Li *et al*., 2009; Zhou *et al*., 2009; Workman, 2010).

Potentially important taxonomic variation in diet can be found in members of the genus *Trachypithecus*, which consume a greater amount of leaves than do most other Asian colobines (Kirkpatrick, 2011). Anatomical specialization may explain this preference, as members of the genus *Trachypithecus* have more effective shearing crests on molar teeth, and larger forestomachs than other Asian colobines, both of which are adaptations for breaking down the hard-to-digest cellulose found in leaves, and in mature leaves particularly (Kay & Hylander, 1978; Chivers & Hladik, 1980; Davies, 1991; Chivers, 1994; Kirkpatrick, 2011). Kirkpatrick hypothesizes that these adaptations make *Trachypithecus* better adapted to digest leaves than other Asian colobine genera, leading to the expectation that leaves should feature in the diets of *Trachypithecus*. Additionally, an unstated implication here is that these adaptations could permit a heavier reliance on mature leaves for *Trachypithecus*, as the anatomical adaptations appear to aid in the digestion of cellulose, found in higher proportions in mature leaves than in immature leaves (Milton, 1979). Kirkpatrick (2011) suggests that the mechanical ability of *Trachypithecus* to consume leaves may drive niche separation where *Presbytis* species overlap with *Trachypithecus*. It also may explain the broad distribution of species of *Trachypithecus*, allowing them to shift to leaves in marginal environments (Kirkpatrick, 2011). Kirkpatrick does note an important exception to this hypothesis, however; based on an eight-month study *T. auratus* does not consume more leaves than do other sympatric Asian colobine species (Rodman, 1978; Ruhiyat, 1983; Kool, 1993; Kirkpatrick, 2011). Other more recent research seems to support a preference in *Trachypithecus* for leaves, but also indicates a preference for young leaves over mature leaves, despite their anatomical specializations. These data come primarily from studies of monkeys living in marginal environments characterized by limestone karst rock formations, perhaps leading to phenotypic differences compared to monkeys found in non-karst evergreen tropical forests (Li *et al*., 2009; Zhou *et al*., 2009; Workman, 2010).

In this paper, I present the dietary and ecological data collected on three groups of *Trachypithicus phayrei* (Blyth) studied across a full year in a seasonal, subtropical habitat in northeastern Thailand, and examine the diet in light of Kirkpatrick's hypothesis that *Trachypithecus* species derive a higher proportion of their annual diet from leaves, and his hypothesis of a heavier reliance on the more difficult-to-digest mature leaves, compared with other Asian colobines, particularly the closely related *Presbytis* species.

METHODS

Data were collected at the Phu Khieo Wildlife Sanctuary (N16°05-35', E101°20-55'), located in northeastern Thailand (Fig. 1). The Phu Khieo Wildlife Sanctuary is part of the Western Isaan Forest Complex, and covers an area of approximately 5,948 km^2. The study

site, Huai Mai Sot, is located within the center of the sanctuary (N16°27', E101°38') at an altitude of 600-800 meters above sea level, and is characterized by a mosaic of forest types, including dipterocarp forest, bamboo stands, primary and secondary wet forest, and dry evergreen forest (Borries *et al*., 2002). The field site is also home to White-handed Gibbons *Hylobates lar* (Linneaus), Assamese Macaques *Macaca assamensis* M'Clelland, Southern Pig-tailed Macaques *Macaca nemestrina* (Linnaeus), Rhesus Macaques *Macaca mulatta* (Zimmermann), and the Bengal Loris *Nycticebus bengalensis* (Lacépède); Stump-tailed Macaques *Macaca arctoides* (I. Geoffroy) have been only rarely encountered.

I studied the diets of three groups of *T. phayrei*, designated as PA, PB, and PS, whose ranges were entirely within the study area. With the help of project field assistants, I followed each group for one week each month from June 2004 to May 2005. For each follow, I conducted five 20-minute focal observations on each adult male and female monkey in the group, using a stratified random design with observations spread evenly throughout the daylight hours. During the focal observations, I conducted instantaneous sampling of the focal subject's behavior at one-minute intervals. When focal subjects were engaged in a foraging or feeding behavior (feeding, handling a food object, or reaching for the next food object), I recorded the category of food (leaves, fruit, animal matter, etc.), the phenophase of plant parts (immature or mature), and the parts of the plants consumed (leaves, petiole, flowers, flower buds, etc.). With the help of assistants, I then marked the feeding patch for later data collection.

At the end of each week with a group, a field assistant and I returned to all of the marked feeding patches. As an estimate of crown volume and potential productivity, we measured the diameter of each tree at breast height (DBH, an effective approximation of patch size: Chapman, 1992). We collected plant samples for identification. Botanical samples were identified by two Thai botanists, Dr Wichan Ed-thong and Tosaporn Naknakled. Where identifications differed, I present the identifications from Dr Ed-thong who compared them to botanical samples available at Botany Department of Kasetsart University.

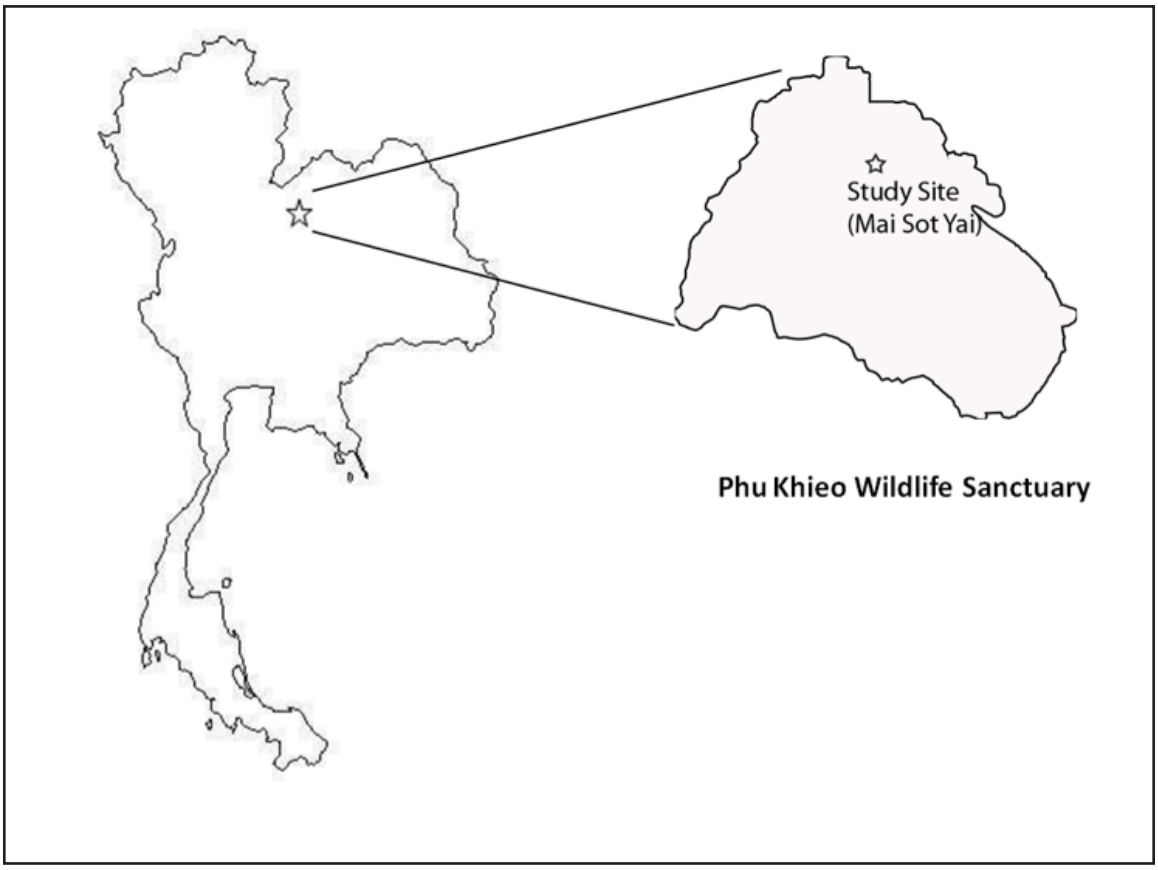


Fig. 1. Location of the Phu Khieo Wildlife Sanctuary, Thailand.

I calculated time spent feeding as the percentage of instantaneous sample points in which focal monkeys actively consumed food items, divided by the total number of sample points. The relative importance of particular food items is calculated as the total number of instantaneous sample points feeding on that food item, divided by the total number of instantaneous sample points during which feeding was observed.

At the time of the study, three 50 m x 50 m botanical plots had been established within the home ranges of the three groups. Within each plot, local botanists identified all trees with DBH greater than 10 cm and all climbers with DBH greater than 5 cm. I calculated the relative density of each species as the number of stems of that species within the plots, divided by the total number of stems of the respective size category within the plot. Systematic phenological data for these plant species had not begun at the time of this research, and thus, phenological data are not available; the results of this project were used to inform future phenological data collection.

I calculated a selectivity index to measure the preference of the focal subjects for particular plants. Because of difficulties of correlating species identifications between botanical plots and those plants sampled in the diet of focal subjects, I calculated selectivity at the generic level rather than the species level. While some selectivity indexes use basal area to estimate abundance of each plant type, the mix of trees and climbers in the plots and diet made comparisons between each difficult. Therefore, I relied on the proportion of individual stems to represent the abundance of plant species in the environment. The selectivity index was consequently calculated as the proportion of each genus as represented in the diet, divided by the proportion of each genus as represented in the botanical plots (Krebs, 1989). For each genus, a selectivity index of greater than one is taken to represent a preferred food item, while a selectivity index of less than one represents food items that are avoided. I ranked each genus for preference in the diet as well as representation in the botanical plots, and tested correlations between these ranks using Spearman's Rank correlation. All statistical tests were conducted using the JMP 8.0.1 statistical package (Copyright 2009 SAS Institute Incorporated).

RESULTS

During the year of data collection on focal animals of the three groups, I collected a total of 24,439 instantaneous sample points, of which 29% (7197 samples) included observations of focal subjects engaged in feeding or food-processing behavior. For all data collected across the year, leaves were the most important food item (46%), followed by fruits (39.5%), and flowers (8.9%), with all other feeding categories consisting of less than 5% of the annual diet (Table 1). Phayre's Leaf-monkeys consumed more young leaves than mature leaves, and immature fruits were consumed more than mature fruits (Table 1). While many of the young fruits were consumed whole, for most young fruits, only the immature seeds were consumed.

Table 1. Annual diet of Phayre's Leaf-monkeys.

Food Category	Percentage of Annual Diet
Leaves (all)	46.2%
Young leaves	31.3%
Mature leaves	12.4%
Fruit (all)	39.5%
Immature fruit	23.9%
Mature fruit	12.6%
Flowers	8.9%
Animal matter	3.6%
Shoots	0.2%
Drink	0.4%
Bark	0.3%
Wood	0.2%
Salt lick	0.5%
Pith	0.1%
Gum	<0.1%
Unidentified	0.3%

The categories Leaves (all) and Fruit (all) include food items of unknown maturity or ripeness.

The monthly proportion of feeding categories varied seasonally across the year, with different feeding categories becoming important in the diet during different months throughout the year (Table 2). The percentage of young leaves in any particular month is inversely correlated with the percentage contribution of immature fruits in that month (Spearman's Rho=-0.7552, p=0.0045), while all other pair-wise comparisons of food categories showed no statistically significant correlations.

Table 2. Monthly variation in diet composition of Phayre's Leaf-monkeys.

	Mature fruit	Young fruit	Mature leaves	Young leaves	Flowers	Bamboo shoots	Proportion of monthly diet
Jun. 2004	8.8%	3.5%	50.8%	18.8%	4.6%	0.4%	86.9%
Jul. 2004	8.7%	23.0%	18. 7%	25.7%	1.2%	2.3%	79. 7%
Aug. 2004	14.7%	49.0%	2.3%	9.3%	1.5%	0.4%	77.3%
Sep. 2004	34.2%	17.8%	9.1%	10.3%	5.3%	1.6%	78.3%
Oct. 2004	24.8%	28.1%	18.7%	20.5%	1.1%	0.0%	93.2%
Nov. 2004	3.0%	41.5%	21.5%	22.4%	0.5%	0.0%	88.9%
Dec. 2004	13.0%	25.9%	21.7%	23.7%	5.1%	0.1%	89.6%
Jan. 2005	10.2%	51.8%	19.0%	5.8%	3.3%	0.0%	90.2%
Feb. 2005	5.8%	0.8%	3.6%	62.5%	12.6%	0.0%	85.4%
Mar. 2005	15.0%	2.4%	0.5%	29.7%	50.0%	0.0%	97.8%
Apr. 2005	3.8%	0.0%	2.7%	91.0%	0.3%	0.0%	97.8%
May 2005	0.0%	5.3%	13.5%	64.9%	9.8%	0.0%	93.5%

The percentage contribution of young leaves in a month is inversely correlated with the percentage contribution of young fruits in the diet. (Spearman's Rho=-0.7552, p=0.0045). All other pair-wise comparisons are non-significant. The dry season begins in mid-October, and continues through March, while the wet season runs from April through September.

While Phayre's Leaf-monkeys fed primarily in trees (67% of the total feeding patches), they also spent a large amount of time feeding in climbers (28% of the total feeding patches), with the rest of their foraging efforts dedicated to feeding in epiphytes and stranglers. Feeding trees vary greatly in size, with mean DBH of 38.8 cm (N=86, SD=23.1). Though infrequent, Phayre's Leaf-monkeys also feed on or close to the ground when consuming bamboo shoots or soil, or when drinking water from creeks or from standing water.

The Phayre's Leaf-monkeys consumed parts from an average of 18.8 different plant species per month. Over the one-year study period, the monkeys consumed plant parts from more than 117 different plant species, comprising more than 43 different families. A majority of the feeding effort, however, was concentrated on only a few of these, with only 18 families and 22 species contributing more than 1% of the annual diet (Table 3), and only two species contributing more than 5% of the annual diet. Overall, 58.6% of the annual feeding time was spent consuming parts of these 22 species.

The results of selectivity analysis are presented in Table 4. Not all trees represented in the diet were also represented in the botanical plots. The results for the remaining 41 genera are presented here. These 41 genera represent 78% of the annual diet for Phayre's Leaf-monkeys. Twenty-eight genera, accounting for 66% of the annual feeding time, were represented at a higher proportion in the diet than in the botanical plots, and 13 at a lower proportion.

DISCUSSION

Phayre's Leaf-monkeys living in the Phu Khieo Wildlife Sanctuary in northeastern Thailand relied most heavily on leaves in their diet. Phayre's Leaf-monkeys spent most of their feeding time consuming young leaves and immature fruits and seeds, which together comprised 55.2% of the annual diet (Table 1). While leaves in general occupied almost 50% of the total annual feeding time, mature leaves accounted for only 12.4%, or 25% of all time eating leaves. This pattern contrasts with several published studies of this genus that show an equal or greater reliance on mature leaves, compared with immature leaves. For example, for *T. vetulu*s, mature leaves were the most important food item, comprising 40% of the annual diet and 66% of the leaf diet (Hladik, 1977), with a similar proportion representing the annual diet of *T. pileatus* (Stanford, 1991). However, it does fit with observations from other studies of *Trachypithecus*. *Trachypithecus auratus* consumed more young leaves than mature leaves (46% compared with <10%) (Kool, 1993), as did *T. francoisi* (39% cf. 14%) (Zhou *et al*., 2006), *T. pileatus*

Table 3. Plant species comprising more than 1% of the annual diet based on number of feeding observations, with their individual and cumulative contribution to diet.

Family	Species	Plant part consumed	% of total diet	Cumulative contribution to total diet
Leguminosae	*Afzelia xylocarpa* Kurz	yl, fl, le, se, ex	10.7%	10.7%
Leguminosae	*Millettia leucantha* (Kurz) Craib	yl, fl	8.9%	19.5%
Moraceae	*Maclura cochinchinensis* (Lour.) Corner	yl, ml	4.5%	24.0%
Leguminosae	*Peltophorum dasyrrhachis* (Miq.) Kurz	se	4.3%	28.3%
Ulmaceae	*Ulmus lanceifolia* Roxb. ex Wall.	fl, yl, imm wh	2.6%	30.9%
Rubiaceae	*Psydrax umbellata* (Wight) Bridson	wh, imm wh	2.6%	33.5%
Leguminosae	*Dalbergia oliveri* Prain	se, imm se, yl	2.5%	35.9%
Leguminosae	*Bauhinia* sp.	yl, se	2.0%	37.9%
Leguminosae	*Albizia lebbeck* (L.) Benth.	imm wh, imm se	1.9%	39.8%
Asclepiadaceae	*Streptocaulon* sp.	ml, yl, wh	1.9%	41.7%
Leguminosae	*Albizia myriophylla* Benth.	imm se	1.7%	43.4%
Moraceae	*Artocarpus lakoocha* Roxb.	wh	1.7%	45.1%
Apocynaceae	*Amalocalyx microlobus* Pierre ex Spire	yl, ml, imm se	1.7%	46.8%
Ebenaceae	*Diospyros bejaudii* Lecomte	yl	1.6%	48.4%
Moraceae	*Ficus drupacea* Thunb.	wh	1.6%	50.0%
Labiatae	*Vitex* sp.	yl, ml, imm wh	1.6%	51.6%
Leguminosae	*Pterocarpus macrocarpus* Kurz	fl, yl, imm wh	1.5%	53.1%
Annonaceae	*Alphonsea elliptica* Hook.f. & Thomson	imm wh	1.3%	54.4%
Malpighiaceae	*Hiptage gracilis* Sirirugsa	yl, ml	1.1%	55.5%
Fagaceae	*Quercus augustinii* Skan	imm wh, wh	1.1%	56.6%
Sterculiaceae	*Pterocymbium macranthum* Kosterm.	unk	1.0%	57.6%
Euphorbiaceae	*Suregada multiflora* (A.Juss.) Baill.	imm wh, ml	1.0%	58.6%

Key: imm=immature, wh=whole fruits, se=seeds, ex=exocarp, yl=young leaves and leaf buds, ml=mature leaves, fl=flowers and flower buds, unk=unknown.

"Cumulative contribution to diet" refers to the total percentage of observations contributed by the important species up to and including the species mentioned.

Table 4. Selectivity Index for genera in the diet of Phayre's Leaf-monkeys.

Genus	Minimum number of species	Proportion of plot stems	Proportion of annual diet	Selectivity Index
Afzelia	1	0.13%	14.45%	108.62
Peltophorum	1	0.07%	4.68%	70.34
Canthium	2	0.07%	3.08%	46.34
Albizia	3	0.13%	4.53%	34.02
Artocarpus	1	0.13%	2.23%	16.76
Millettia	1	0.80%	11.39%	14.27
Gmelina	1	0.07%	0.79%	11.83
Atalantia	1	0.07%	0.77%	11.50
Vitex	2	0.27%	2.14%	8.05
Dehaasia	1	0.07%	0.44%	6.57
Ficus	6	0.86%	5.27%	6.09
Ulmus	1	0.66%	3.46%	5.19
Dalbergia	2	0.73%	3.76%	5.14
Adenanthera	1	0.13%	0.42%	3.12
Ziziphus	1	0.07%	0.20%	2.96
Xanthophyllum	1	0.07%	0.17%	2.63
Psydrax	1	0.13%	0.33%	2.46
Siphonodon	1	0.13%	0.31%	2.30
Pterocarpus	1	0.40%	0.92%	2.30
Celtis	1	0.20%	0.44%	2.19
Walsura	1	0.13%	0.28%	2.14
Bauhinia	3	1.20%	2.43%	2.03
Quercus	1	0.93%	1.40%	1.50
Schefflera	1	0.33%	0.48%	1.50
Sapium	1	0.53%	0.74%	1.40
Suregada	1	0.07%	0.09%	1.40
Bombax	3	0.27%	0.33%	1.23
Apodytes	1	0.33%	0.35%	1.23
Sterculia	1	0.27%	0.24%	0.90
Ventilago	2	1.40%	1.18%	0.84
Rourea	1	0.66%	0.42%	0.62
Garcinia	3	2.12%	1.29%	0.60
Aporosa	1	0.66%	0.22%	0.33
Cananga	1	0.40%	0.13%	0.33
Tarennoidia	1	0.33%	0.09%	0.26
Mitrephora	1	2.73%	0.61%	0.22
Diospyros	4	13.44%	2.54%	0.19
Tetrastigma	1	2.26%	0.33%	1.14
Drypetes	1	4.86%	0.52%	0.11
Cratoxylum	1	1.60%	0.07%	0.04

The proportion of the plot stems is calculated as the number of stems for each genera found within the botanical plots for trees greater than 10 cm DBH and climbers greater than 5 cm DBH. Proportion of the annual diet is calculated as the number of instantaneous samples for all focal subjects feeding on a particular genus, divided by the total observed feeding time for all focal subjects. The selectivity index is calculated as the proportion in the annual diet divided by the proportion in the plot stems, where a value greater than one indicates a preference and a value below one indicates avoidance.

(Blyth) (57% cf. 6%) (Solanki *et al*., 2008) and *T. obscurus* (Reid) (36% cf. 22%) (Curtin, 1976). The lower reliance on mature leaves for Phayre's Leaf-monkeys in this study was evident across all months and seasons, with the exception of June 2006 (Table 2). While these data do support the hypothesis that dietary and digestive adaptations in *Trachypithecus* may permit a reliance on leaves in the diet, they do not fit the implication that anatomical adaptations should necessarily lead to a preference for mature leaves.

These data, however, are consistent with the implication of Kirkpatrick's hypothesis that *Trachypithecus* relies more heavily on the more difficult to digest mature leaves than do other Asian leaf-monkeys. Many studies of the diets of *Presbytis* and *Nasalis* suggest that mature leaves contribute less than 10% of the annual diet (Kirkpatrick, 2011). Observations of Phayre's Leaf-monkeys at the Phu Khieo Wildlife Sanctuary fit with other observations of *Trachypithecus* indicating an (albeit slightly) higher reliance on mature leaves, even when they are not the most important food item (Curtin, 1980).

One factor potentially contributing to the high proportion of young leaves in the annual diet of Phayre's Leaf-monkeys is that there are few competing folivorous species present in the Phu Khieo Wildlife Sanctuary (Hassel-Finnegan *et al*., 2008). For example, *T. obscurus* at Kuala Lompat, Malaysia, consumed more mature leaves than *Presbytis melalophos* (Raffles) at the same site (Curtin, 1980), presumably due to resource competition, as both species were seen to compete directly in shared resources (Curtin, 1980). The main dietary competitors at Phu Khieo Wildlife Sanctuary are *H. lar*, and several species of *Macaca*, all known to be primarily frugivorous when food sources are available and abundant (Thierry, 2007). Competing folivores are, therefore, not present at the site.

Across the year, Phayre's Leaf-monkeys spent most of their feeding time consuming young leaves and immature fruits and seeds, together comprising 55.2% of the annual diet (Table 1). As is consistent with the reported dietary preferences of many other Asian colobine monkeys (Curtin, 1980; Davies *et al*., 1988; Bennett & Davies, 1994; Yeager & Kool, 2000), Phayre's Leaf-monkeys consumed young leaves (31.3% of the annual diet) more than twice as often as mature leaves (12.4% of the annual diet) (Table 1). When whole fruits were consumed, they tended to be mature, typically fleshy, but not particularly sugary species such as *Ficus drupacea* Thunb., *Artocarpus lakoocha* Roxb. and *Quercus augustinii* Skan (pers. obs.). The second most important food item in the diet was immature seeds. Phayre's Leaf-monkeys frequently discarded the tough outer exocarps of immature fruits to consume immature seeds contained inside, to such a degree that it may be appropriate to describe them as seed predators (Davies, 1991).

The diet of Phayre's Leaf-monkeys varied across months in the year (Table 2). During this study, there was an inverse relationship between the quantities of immature fruits and young leaves in the diet. Most of the immature fruits were consumed during the dry season, which ran from October 2004 to March 2005. During these months, young-leaf consumption was low. Towards the end of the dry season, however, young leaves became increasingly important in the diet, as did flowers. It was during this time of the year that the common, small trees of *Millettia leucantha* Kurz were simultaneously presenting young leaves and flowers, and the Phayre's Leaf-monkeys spent a lot of time moving from tree to tree consuming both.

Other foods were seasonal for Phayre's Leaf-monkeys. Bamboo shoots were consumed during the wet season from June through August 2004. The monkeys descended close to the ground in large bamboo stands in order to break off bamboo shoots, which they broke open to consume the moist pith inside. While the annual and even monthly bamboo-shoot consumption time remained low, the monkeys invested a great deal of energy breaking into the bamboo shoots, suggesting they were a prized item. Feeding on bamboo is not described for most Asian colobines, with the exception of *T. johnii* (Oates *et al*., 1980), *Presbytis rubicunda* (Müller) (Davies, 1991) and *Rhinopithecus bieti* Milne-Edwards (Yang & Zhao, 1991).

Like a few other Asian colobines, Phayre's Leaf-monkeys also consumed animal matter during parts of the year (Oates *et al*., 1980; Davies, 1991; Stanford, 1991; Newton, 1992). During the month of September 2004, the leaf-monkeys spent part of the day traveling from one *Hopea ferrea* Laness. tree to another in *Hopea*-dominant forest to consume the unidentified caterpillars that had hatched on those trees. During this month, caterpillar consumption made up 25% of the diet, similar to the amount of caterpillar consumption seen in a single month's diet for *S. entellus* at the Kanha Tiger Reserve, India (Newton, 1992). Insects contributed less than one percent of the annual diet, however, which is consistent with relative unimportance of insects to most Asian colobines.

Phayre's Leaf-monkeys have a diet that is at the higher end of diet diversity for Asian colobine monkeys, though by no means the most diverse. The study subjects consumed 117 different plant species, from more than 43 different families (Table 3), and had a diet that was similar in species breadth to that of *T. johnii* at Kakichi (Oates *et al*., 1980) and *T. francoisi* at Nonggang Nature Reserve (Zhou *et al*., 2006). By comparison, other year-long studies found that *T. vetulus* consumed only 28 plant species at Polonnaruwa (Hladik, 1977) and *T. pileatus* consumed 35 at Madphur (Stanford, 1991). The number of plant species consumed is almost certainly a reflection of the productivity and diversity of the habitats. For example, tree-species diversity has been shown to be high in dipterocarp forests of Southeast Asia (Whitmore, 1984), and dietary diversity appears to be lower in leaf-monkeys living in habitats dominated by karst limestone formations (Zhou *et al*., 2006; Li *et al*., 2009; Workman, 2010). The Huai Mai Sot study area used by the Phayre's Leaf-monkeys in this study is characterized by a patchy array of habitat types, varying from open dipterocarp forest, *Hopea*-dominant forest, primary and secondary wet forest, and forest dominated by large bamboo stands. This patchy habitat may contribute to floral diversity, leading to the broad diet diversity of the monkeys in this study.

Phayre's Leaf-monkeys concentrate their feeding efforts on only a few of the 117 different plant species that they consume, a pattern seen in other Asian primate species (Oates *et al*., 1980; Davies, 1991; Zhou *et al*., 2006; Li *et al*., 2009; Zhou *et al*., 2009), with 22 species making up almost 60% of their annual diet, and the top three species making up almost 25% of the annual diet (Table 3). Twenty-eight genera, accounting for 42 species in the diet, could be considered to be preferred by Phayre's Leaf-monkeys, with selectivity indexes greater than 1.0 (Krebs, 1989). The rest are consumed less often than they are encountered. The most preferred genus, with the single species *Afzelia xylocarpa* (Kurz) Craib, is consumed year-round, and serves as a source of young leaves, flowers, and immature seeds. This pattern of heavy reliance on a few available tree species year-round is typical for Asian colobine monkeys (Hladik, 1977; Curtin, 1980; Oates *et al*., 1980; Zhou *et al*., 2006; Li *et al*., 2009; Zhou *et al*., 2009).

Despite Kirkpatrick's suggestion that *Trachypithecus* may differ dietarily from other Asian colobines, these data support the assertion that *T. phayrei* fit the overall dietary pattern for Asian Leaf-monkeys.

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Post-acceptance Editor's Note:

Semnopithecus vetulus (Erxleben) and *Semnopithecus johnii* (Fischer) were until recently classified as members of the genus *Trachypithecus*, but due to genetic studies reclassified as members of *Semnopithecus* (Zinner *et al.,* 2013). However, both genera are closely related (Roos *et al*., 2011).

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