STRONGER THAN YESTERDAY: NEW NUTRIENT RECOMMENDATIONS FOR LORISINE PRIMATES

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Abstract
Asia's slow lorises (*Nycticebus* spp.) are heavily impacted by the illegal wildlife trade in Southeast Asia. Confiscated lorises by Customs officials find themselves in rescue centers with approximately 50% of them having had their lower teeth removed by the poachers and must remain in the rescue centre indefinitely, if they survive. Reintroductions do occur but success is very low. Despite evidence from four species in the wild that lorises largely consume exudates, insects and nectar, captive lorises are often fed a high fruit diet, with approximately 63% of facilities reporting diet-related health issues including dental, renal, facial problems, obesity and impaired breeding. The Javan slow loris (*Nycticebus javanicus)* is now critically endangered because of the pet trade and declining habitat. Understand their feeding ecology is essential to determining what they should be fed in captivity. We followed radio collared free-ranging Javan slow lorises (*N. javanicus*) (n = 17) for 10 months at a field site in Cipaganti (Java, Indonesia), itemising and quantifying their native diet and nutrient intake using various methods. Samples of food items were collected for chemical analysis. The food transit and mean retention time trials across five *Nycticebus* species show that the Javan slow loris is a suitable model for the genus and that their morphology and physiology is indeed adapted to digest structural carbohydrates. The current captive diet is far removed from the wild diet in terms of nutrients. The inclusion of gum into the diet increased micronutrient profiles considerably. The new diet trial removed all fruit and included vegetables, gum arabic and insects which created a nutrient profiles similar to wild intake. The new diet had a nutrient profile and food transit and mean retention time similar to wild type diets. This diet is believed to generate future health benefits as well as optimising physiological functions within *Nycticebus* primates.

Introduction
Eight species of slow lorises (*Nycticebus spp*.), small nocturnal primates, are distributed throughout Southeast Asia. A high demand for lorises as pets, photo props and traditional medicine makes illegal trade their greatest threat. To combat this problem, CITES, in 2007 placed *Nycticebus* spp. on Appendix 1, banning all international commercial trade. With a six month gestation leading to litters of one or two infants that require three to six months for weaning, their extremely slow life history does not lend well to this level of off-take (Fitch-Snyder and Ehrlich, 2003).

When enforcement does occur, the most likely destination for slow lorises in Indonesia is a rescue center. As rescue centers reach capacity, personnel investigate the possibilities of reintroduction. Unfortunately the success rate of reintroduction projects are low, with many reintroduced animals succumbing to predation or starvation, not adapting back to life in the wild, or simply unknown outcomes due to lack of follow-up (Soorae, 2008). For slow lorises, numerous newspaper articles report 'success' of individuals simply set free with no follow up. Indeed, only four systematic reintroduction studies are available (Streicher & Nadler 2003; Collins et al 2008). Of 51 confiscated pygmy slow loris (*Nycticebus pygmaeus*) in Vietnam, 15 (29%) died, eleven of which were juveniles (Streicher, 2005). In Java, of 180 confiscated lorises, 64% had their teeth removed. Of those 180, 61 (34%) died despite veterinary care; of 19 reintroduced animals, 90% died (Moore, 2012). Confiscated shipments of lorises show that what we see in markets is the tip of the iceberg. For example, of 102 pygmy lorises confiscated at a Taiwanese airport, > 80% died between confiscation and arrival at their final destination at Saigon Zoo.

Confiscated lorises number in the hundreds in Asia's rescue centers and are fed diets high in fruits, and include dairy, chicken and/or insects similar to diets fed to lorises found in western zoos (Fitch-Snyder et al., 2001; Cabana, 2014). Health issues such as dental problems, facial abscesses, obesity, renal impairment and impaired breeding are rampant in all captive populations (Debyser, 1995; Fitch-Snyder et al., 2001; Cabana, 2014; Fuller et al., 2013). Gum, nectar and insects form the majority of the wild loris diets, albeit minor differences occur in proportions for each species (Nekaris, 2014); no nutritional recommendations are available for any loris species, and current diets are based on anecdotes. There is a clear need to review feeding practices to cater for lorises' physiologic, morphological and behavioral needs if reintroductions are to become successful in their purpose of restoring dwindling wild populations (Kaumanns et al., 2000). This study aims to itemize and quantify both the food items and nutrients ingested by free-ranging critically endangered Javan slow lorises (*N. javanicus*) and to use the Javan slow loris as a model for the creation and validation of lorisine nutrient recommendations through a series of diet trials and validation methods.

Materials and Methods

Wild Data

We were based at the Little Fireface Project's (LFP) field station in the village of Cipaganti, West Java, on the volcano Mount Papandayan (7°16'44.30"S, 107°46'7.80"E, 1200 m ASL). The study area consisted of agriculture fields with interspersed tree and bamboo patches. We followed a group of collared free-ranging lorises (n = 17) using radio collars (BioTrak, UK) and a telemetry antenna and Sika receiver. They were observed six nights/week for a 12 month period with red next generation LED head lamps (CluLite Ltd., UK) and binoculars. Four lorises were also fitted with Activity logging collars (CamNtech, USA) which recorded activity bouts every minute for three months. Behaviors were recorded by instantaneous sampling and food intake was recorded continuously. Table 1 depicts how each food item quantity was measured during intake. Insects were recorded in small (smaller than hand), medium (larger than one hand but smaller than two) and large sizes (larger than two hands). After any fruit feeding occurred, we collected what was left and weighed it using a portable scale (AVI, UK) and compared this weight against a mean value for this fruit to determine weight of eaten portion. Any other food items not planned for was recorded as appropriate to the situation.

Table 1. Observations of food items consumed by slow lorises (n = 17) in Indonesia.

Food Item Category	Recording units
Gum	Seconds (s) of feeding
Nectar	Frequency (#) of flowers
Fruits	Weight of eaten portion
Insects	Frequency (#) of insects
Other	As appropriate

Five 10x10m phenology plots were established in random locations within the field site. Every 1st of the month phenological information was recorded as per Chapman et al. (2005). Presence of gum, mature leaves, young leaves, fruits in tree, fruits on ground and flowers were graded: 0 absent, 1 present but less than 60% of trees capacity, 2 present but more than 60% of tree's capacity. Insect Malaise traps were used in these phenology plots twice/week to calculate insect availability and to weigh a mean value for the different created categories of insects (small, medium, large).

Food Preference

Food preference was calculated by providing a rank to the food items eaten the most to least every month, and ranking the availability of each food resource from most to least. Gum availability did not change throughout the year, so gum tree density was used for its availability every month. These rankings were used in Ivlev’s selectivity index (Ivlev, 1961). This equation has been validated by Lehowicz (1982) and used to assign food preference scores in Watts (1984), Vedder (1989), Johnson (1980) and Ganas et al. (2008). Nutrient intake and nutrient proportions of natural food items were plotted on a graph using the Right-angled mixture triangle (RMT) method (Johnson et al., 2013; Raubenheimer, 2011) to determine how each food item contributes to wild diets.

Chemical Composition of Wild and Captive Foods

Samples of the wild diet components were collected and dried in indirect sunlight for 12 hours, then placed into a plastic zip lock bag with silica gel for a maximum of one week before being sent for analysis. Some samples were collected imminently before departure for nutrients which are better detected from fresh matter. A small portion of fresh samples were collected the day prior to going to the laboratory for specific nutrients which require immediate assay. The samples were processed in the same way as was observed eaten by the wild lorises; only ingested plant parts were analyzed. Assays were performed at the Lembaga Ilmu Pengetahuan Indonesia (Indonesian Institute of Science, also known as LIPI) in Bogor by Cabana and the LIPI staff. Gross energy, ash, crude protein, crude fat, simple sugars, soluble fiber, ADF, NDF, Ca, P, K, Na, Se, Fe, Vitamin A, Vitamin D and Vitamin E were all analyzed for wild food items as well as food items consumed in the rescue center. Chemical analysis methods are available in Appendix 1. Collecting and drying nectar in sufficient quantities was not possible, so the only sugar content was determined by using a portable hand held refractometer as per (Bolten et al. 1979); other nutrients were assumed to be present in negligible quantities. To estimate quantity of nectar per flower, 85 microlitre capillary tubes were used to estimate quantity based on volume of nectar collected within tube per flower (Morrant et al., 2009). We measured 100 inflorescences from 5 different plants, totaling 150 flowers over the course of 5 nights.

Captive Trials

After the field season, we collected data at Cikananga Wildlife and Rescue Centre, West Java for 12 weeks. The study population included 12 *N. javanicus*, 4 *N. menegensis* (Bornean slow loris) and 15 *N. coucang* (greater slow loris). All food items used at the rescue center were also sent for chemical analysis. Some individuals either had full, partial or no teeth however, this was not divulged to the researchers until after data collection, and was used as a variable for statistical analysis. At the center, the diet was separated into three meals. Menu 1 was presented at 1900 hr, menu 2 at 2300 hr and menu 3 at 0200 hr. Menus 1 and 2 consisted of one fruit portion and one insect portion each, sometimes with a hardboiled egg, and menu 3 was either more fruit or honey. Diets were evaluated as total daily intake.

Gum Intake Rate

One kg of wild gum from Cipaganti was collected and brought to the rescue centre. Gum intake rate was determined by feeding a known quantity of gum to *N. javanicus* individuals housed alone and using a stopwatch to time total consumption, subtracting any pauses during processing. Conversion (g gum/sec) was used to convert the wild gum intake into gram estimates.

Validation Methods: Intake and Food Mean Retention and Transit Time

The wild feeding data were converted into weights (g) using previously detailed methods. Food intake rates were calculated for each individual as a measure of g/hour on an as-fed (AF) basis. This was used in conjunction with the nutritional information for each food item previously analyzed to create a nutrient intake per hour metric for the Javan slow lorises. Nutrient intake per hour was adjusted by active periods (from logger data) to quantify daily nutrient intake.

Intake studies were conducted with the captive lorises fed their current diet as baseline data for seven days. Daily average amounts, per individual, of the original diets are: katydids (3.4g), Peeled oranges (18.3g), peeled banana (44.0g), mealworms (4.9g), crickets (1.3g), peeled rambutans (12.2g), hardboiled chicken egg without shell (2.2g), sapodilla without seeds (17.1g), honey (4.0g), mangusteen (12.9g) and pine beetle larvae (2.1g). Weights of food items offered and uneaten food removed from the enclosure were weighed. Dessication dishes of food items were also set up and measured at feeding time and at time of clean-up. Feces were collected every day at clean-up time (1000 hr) and individual species' feces were pooled to ensure adequate quantities for chemical analysis to determine apparent digestibility as per Graffam et al. (1998). The mean food retention time was calculated using a non-digestible marker that was fed immediately prior to intake/digestion trials (Lambert, 2002). Coloured plastic beads were used at first without success. The slow lorises were able to use their sublinguals to filter them out and push them out of their mouths. Instead, 1/8 tsp (0.1g) of glitter was mixed into a quarter of a guava fruit (60 g), per individual. The time of first appearance until last appearance was recorded for the glitter and the guava seeds. Four repeats per animal were conducted. Transit time and mean retention times (MRT) were recorded or calculated. A "wild type" diet was fed to the *N. javanicus* (n = 12) for 7 days (with a 25% diet change over 6 days prior to allow for acclimatization) using the proportions of wild food items observed ingested. Intake and transit and food MRT measurements were repeated on the "wild type" diet. MRT trials were also conducted on 2 pygmy slow loris (*N. pygmaeus)* at Paignton Zoo Environmental Park (UK) and on 2 Bengal slow lorises (*N. bengalensis*) at Shaldon Wildlife Trust (UK) for comparisons.

One new diet was created using the wild nutrients ingested as a framework. Only food items which were affordable and available for rescue centres, and were deemed morphologically and behaviorally appropriate for slow lorises, were used. Each individual loris was fed this diet for 14 days (with 25% diet change over 6 days prior to allow for acclimatization). Intake, transit and MRT were measured for this diet to assess if appeared more similar to the wild type diet, which we presume as our “gold standard”. The same validation methods were compared against the original captive diet and the three new diets to determine which appeared the most physiologically appropriate. The average daily new diet, as offered, consisted of mealworms (2.6g). crickets (6.9g), hardboiled chicken egg with shell (1.3g), palm beetle larvae, pupae and adult mix (6.5g), sweet potato (8g), peeled, semi boiled cassava (6.8g), green beans (9.7g), semi-boiled carrots (2g) and gum arabic (10g made with 2:1 parts powder to water).

Results

Wild Feeding Ecology

Wild *N. javanicus* were observed for 256 days for 1470 hours (5.8 hours/night on average) over 12 months totalling 7191 points of data. The unpredictable weather - namely rain and fog - made many nights impossible to find or observe any specimens. Using instantaneous focal sampling, the tally of each feeding observation for each individual was combined and averaged over the total number of data points to represent time spent feeding on different food items and is depicted in Figure 1. These data change substantially when the food items become weighted, and represent actual intake. Figure 2 shows that gum is not the item consumed in the largest amount.

Figure 1. Proportion of time spent consuming different food categories by free-ranging Javan slow loris *(Nycticebus javanicus; n* = 17*)* from instantaneous observations, indicating that almost half of the time is spent feeding on gum.

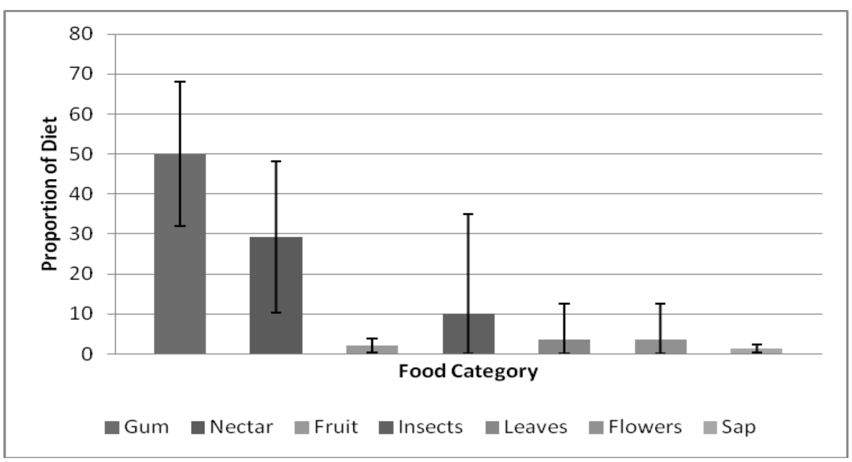
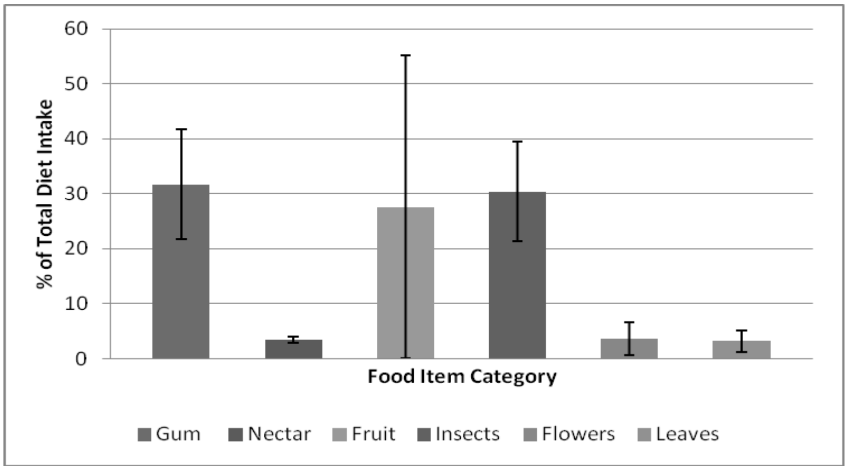


Figure 2. Proportion of actual intake (g as-fed) of different food categories consumed by free-ranging Javan slow loris, (*Nycticebus javanicus*; *n* = 17) according to average intakes measured over 12 months.



Each main staple food item was obtained from one or two plant species. Gum was from an Australian acacia tree, *Acacia decurens*, nectar from Caliandra (*Caliandra catothyrsus)*, fruits from jackfruit (*Arctocarpus heterophyllus*), and persimmon (*Diospyros kaki*), flowers from eucalyptus (*Eucalyptus spp.*) and leaves from bamboo (*Gigantochloa cf. ater*).

Nectar and Gum Intake Rates

One hundred total *Caliandra catothyrsus* inflorescences were sampled totaling 150 flowers. The average amount of nectar obtained from each flower was 22.55 (SD ±1.82) µL and the average sugar content was 22.82 (SD ±5.12) Brix which equates to 253 g of sugar per L of nectar, which we estimate to be 99% of DM and 22.55% as fed (AF).

Gum intake rate was calculated from sampling 12 captive Javan slow lorises which were given 10g of gum harvested from *Acacia decurrens.* On average they consumed gum at the rate of 0.021 g/s. SD ±0.006.

Food Preference

The only food item which had a relatively high preference score (>0.35) was young bamboo leaves as seen in Table 2. Food items which were always available in the same amounts, such as *A. decurrens* gum, resulted in low preference scores.

Table 2: Average values of importance of each food item in the overall diet of free-ranging Javan slow lorises (*N. javanicus; n* = 17), availability of these food items at the field site, and average food preference scores.

Plant Species	Part eaten	Yearly diet proportion (%)*	Avg. Diet rank (SD)	Avg. Avail rank (SD)	# Months observed consumed	Avg pref. score
Acacia decurrens	Gum	31.7	2.18(0.75)	5.33(0.89)	12	-0.42
Calliandra catothyrsus	Nectar	3.4	3.36(1.28)	4.25(1.55)	12	-0.15
Actocarpus heterophyllus	Fruit Pith	6.0	1(0.0)	3.5(0.67)	1	-0.5
Various Insects	Whole	30.4	2(0.89)	1.58(0.66)	12	0.09
Gigantochloa cf. ater	Young Leaf	3.2	4.5(0.58)	2.17(0.83)	4	0.57
Eucalyptus spp.	Flower	3.7	3.25(0.95)	6.17(0.83)	4	-0.33
Diospyros kaki	Fruit Pith	21.7	1(0.0)	5(2.55)	3	0

*Yearly diet proportion is based on intake rates of weighted values, # months refer to the number of calendar months that food was observed being consumed. Average preference scores between 0 and 1 show a preference, while values between 0 and -1 show no preference.

Activity Loggers

Activity logger results clearly delineated active from inactive periods. On average (*n* = 4) Javan slow lorises were active for 11 hours and 54 minutes per day. All 4 animals became active slightly before sunset, and were active only for a brief period of time after returning to their sleep sites before sunrise.

Chemical Composition of Food Items

The chemical composition of wild and captive food items can be found in Appendix 1.

Nutrient Intake

Average intake rate per night (using the 12 hour active period as determined above) of wild *N. javanicus* diet is listed in Table 3. Using the chemical compositions found within Table A1 and the proportional intake of Table 3, we calculated the average nutrients ingested by *N. javanicus* over a 12 month period (Table 4). The RMT is represented in Figure 3, and plots the proportions of NDF, crude fat and crude protein of wild food items as well as wild nutrient intake. Natural food values scaled tightly along the implicit axis ($y = -1.0978x + 98.796$) which represents crude fat, showing more variation between crude protein and NDF. Results of the captive intake studies for the usual captive diets, and the same diet but with the addition of wild gum, are reported in Table 5.

Table 3: Average food intake rates of free-ranging Javan slow lorises (*Nycticebus javanicus; n* = 17) over 12 months during daily 12-hour activity periods, showing the importance of gum and insects.

Food Category	Gum	Nectar	Fruit	Small Insect	Medium Insect	Large Insect	Flowers	Leaves
Intake rate g/night	10.90	1.17	9.52	0.34	3.08	7.03	1.27	1.11

Table 4: Average daily nutrient intake of Javan slow loris (*N. javanicus; n* = 17*)* with a diet consisting mainly of gum, insects and non cultivated fruits, calculated over 12 months with 12-hour daily activity periods, on a DM basis.

Nutrient	Concentration (DM basis)	Nutrient	Concentration (DM basis)
Energy (Kcal/g)	3.51	Ca:P (Ratio)	2.27
Crude Protein (%)	26.50	Cu (mg/kg)	15.93
Crude Fat (%)	3.38	Fe (mg/kg)	63.34
Soluble Fiber (%)	4.20	Mg (%)	0.10
ADF (%)	11.67	Na (%)	3.69
NDF (%)	18.44	Vit A (IU A/g)	0.72*
Ash (%)	3.74	Vit D (IU A/g)	0.30*
Ca (%)	0.59	Vit E (mg/kg)	1.01*
P (%)	0.26	Soluble Sugars (%)	3.33

*Values not representative of actual intake at time of writing.

Energy value presented above is gross energy; ADF = acid detergent fibre, NDF = neutral detergent fibre

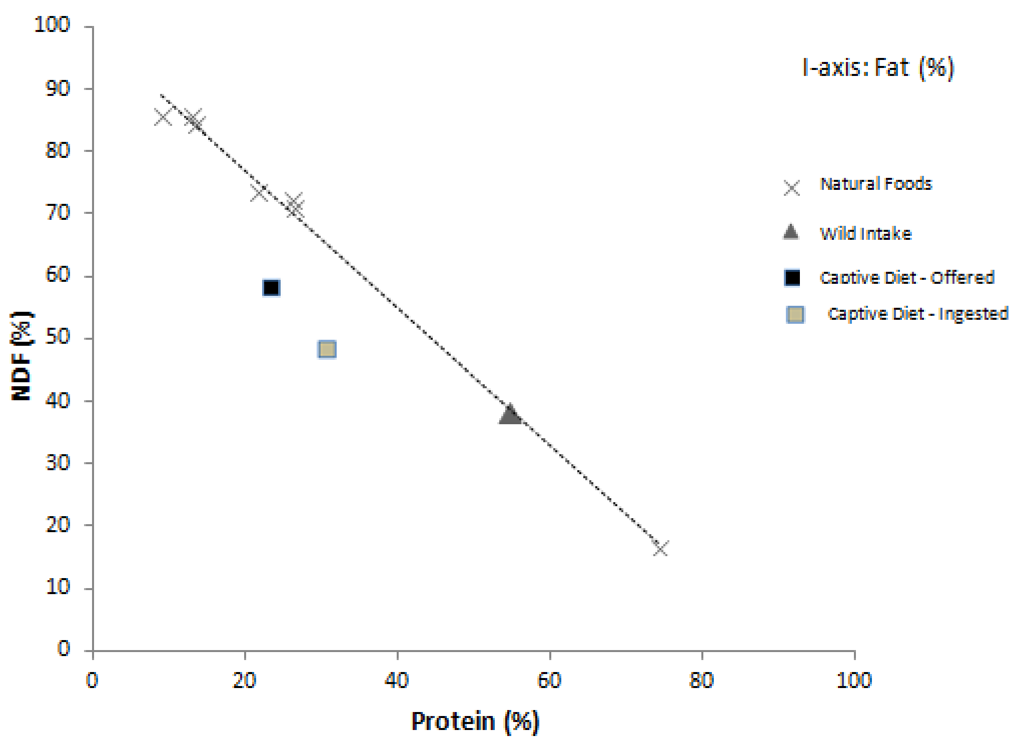


Figure 3 Right-angled mixture triangle (RMT) showing the relative proportions of NDF vs protein vs fat of *N. javanicus* food items (Xs) and the average nutrient intake of free-ranging specimens (triangle). Crude fat contribution is the implicit axis. The dashed line shows the linear regression of natural food compositions (y=-1.0978 + 98.769). The average contributions of crude protein vs NDF vs crude fat of the original captive diets as offered (black square) and as ingested (grey square) are also graphed.

Table 5 Nutrient intake of captive slow lorises (*n* = 31 from 3 *Ncyticebus* spp.) fed typical captive diets comprising fruits, insects and egg, with or without the addition of wild Acacia gum. All data presented on a DM basis.

Nutrient	N. Javanicus	N. Javanicus w/ gum	N. Coucang	N. Menegensis	New Diet N. Javanicus	New Diet N. Coucang
Ash (%)	2.9	2.68	3.11	2.88	3.78	4.03
Crude Protein (%)	12.79	17.46	12.11	13.69	24.38	26.59
Crude Fat (%)	7.58	9.71	7.81	8.3	5.96	6.71
Energy (Kcal/g)	3.92	3.93	3.91	4.25	3.34	3.56
Soluble fibre (%)	0.72*	2.11*	0.71*	0.78*	0.59*	0.61*
ADF (%)	12.28	10.51	24.35	8.41	1.21*	0.78*
NDF (%)	20.56	20.04	14.31	17.3	7.6*	6.15*
Sugars (%)	9.6	6.92	9.2	9.14	0.11*	0.13*
Ca (%)	0.17	0.27	0.14	0.15	0.52	0.53
P(%)	0.19	0.24	0.16	0.2	0.36	0.41
Mg (%)	0.27	0.23	0.29	0.24	0.25	0.16
Fe (mg/kg)	59.47	43.52	57.26	69.12	53.42	50.35
Na (%)	0.43	0.22	0.36	0.12	0.16	0.18
Cu (mg/kg)	7.45	8	6.96	0.2	7.17	7.64
Ca:P	0.89	1.12	0.88	0.75	1.44	1.29

Energy values are for gross energy

ADF = Acid detergent fibre, NDF = neutral detergent fibre

*Chemical analysis results not fully yet obtained so values are represented by less than 80% of diet (DM) at time of writing.

Food Mean Retention and Transit Times

Results of mean retention and transit times are presented in Table 6. All species of *Nycticebus* had comparable transit and retention times.

Table 6: Food transit and mean retention times of *Nycticebus* species held in captivity fed a typical captive diet and for some species, also when fed a naturalistic diet comprising only gum, insects and nectar.

	Diet Time	# of trials	*Javanicus* *n* = 15	*Coucang* *n* = 15	*Menegensis* *n* = 4	*Pygmaeus* *n* = 2	*Bengalensis* *n* = 2
Transit Time (hours)	Original Captive Diet (range)	4	25.6 (23.0-31.5)	25.00 (21.5-29.0)	24.2 (21.0-27.5)	29.0 (27.0-31.0)	
	Wild (range)	4	25.6 (24.0 - 29.0)	24.4 (24.0 - 26.5)	24.5 (22.5- 27.0)		
	New Captive Diet (range)	3	25.1 (23.0 - 28.8)	24.7 (22.0 - 28.3)			
Mean Retention Time (hours)	Original Captive Diet (range)	4	51.7 (51.0-52.5)	48.00 (47.0-49.5)	51.1 (48.0-53.4)	58.0 (56.5-59.5)	42.6 (42.8-42.5)
	Wild (range)	4	57.8 (54.5-59.0)	56.3 (54.0-57.5)	52.4 (50.0-54.8)		
	New Captive Diet (range)	3	56.7 (54.0-58.3)	55.9 (53.0-57.0)			
Average weight (g)			1050	936	902	423	1020

Transit time is the first appearance of the marker and MRT is the time until marker is no longer in feces.

Discussion

Wild Feeding Ecology

After observing wild *N. javanicus* for 12 months in an Indonesian agro forest, we were able to create a list of all of their food items. Unsurprisingly, their diets consisted of gum, insects and nectar, which is similar to the diet observed as consumed by *N. pygmaeus* (Starr and Nekaris, 2011). Due to our rigorous and detailed sampling methods of feeding behaviors, as well as excellent visibility, we may have been able to observe a more coherent and complete diet profile than other field sites, which focus on instantaneous data sampling. We were also able to see our specimens ingesting fruit, young bamboo leaves, flowers and sap. *Nycticebus coucang* has been described as spending the majority of its foraging time consuming fruit and nectar (Wiens, 2002). The only other slow loris which has been observed eating leaves as part of its diet is the largest of the genus, *Nycticebus bengalensis* (Das, 2014). It is hypothesised that due to their large size (up to 2 kg), *N. bengalensis* have a larger potential for hindgut fermentation and can exploit the energy of plant parts more effectively (Das, 2014). Without leaves, the large body size would also mean that they would have to catch many more insects to provide enough energy to support their body mass, which may not be sustainable. *N. javanicus* has an intermediate body size within their genus (up to 1.2 kg); omnivory and consumption of multiple plant parts such as bamboo leaves and eucalyptus flowers may not be unexpected, and also suggests this species may be capable of hindgut fermentation.

Food Preference

Our field site experiences one dry and one wet season evenly split throughout the year. Food abundance was expected to show a severe seasonality as seen in other tropical areas with only two seasons (Bearder and Martin, 1980; Chapman and Chapman, 1999). Actual phenological data showed that only fruits and flowers were seasonal, and to a lesser extent, bamboo leaves. Only bamboo leaves were shown to be preferred. The lorises were not observed taking advantage of the abundance of persimmon fruits during the dry season. Gum was a staple part of the diet and available all year round. The gum from *A. decurrens* was shown to have moderate amounts of many minerals, notably calcium, copper, iron and potassium which could help to balance out the high intake of phosphorus found in insects (as in Bearder and Martin 1980). Tree gum was also a source of presumed vitamin A precursors. Overall, the diet of the *N. javanicus* was high in macro nutrients such as crude fat, crude protein and structural carbohydrates. Total dietary calcium to phosphorous ratio was 1.24:1 which indicates that although loris consume a high proportion of insects, they are still able to select other foods that maintain a positive Ca:P ratio.
All of the food items ingested by free ranging *N. javanicus* were rather consistent in their low fat content (~3% of DM, ranging from <1 to a maximum of about 8%), and instead varied widely in fiber and protein (Figure 3). The majority of wild food items appear to be moderate to high in NDF (10 to 65 %) relative to lower protein content (4 to 12%) The opposite is true for the least-consumed food item(s) which are the average values for insects (NDF 14%, crude protein 64%). The insect values are clearly complimentary to the other food items as they are both found on the same axis, on either side of the nutrient intake proportions. The crude fat contents of the wild insects eaten by slow lorises are also relatively low compared with common domestically-reared substitutes (7.72% versus 28.1% for crickets and 27.9% for mealworms on a DM basis). The high prevalence of insects in loris diets may make duplication in captivity difficult. The preferred young bamboo leaves contain the highest NDF proportions (40 to 65% DM), yet do not stand out within the uppermost plant food item cluster; therefore their preference must be due to some micronutrient, possibly.

Captive Trials

Typical captive slow loris diets include domestic fruits and a small amount of a limited number of species of insects (Fitch-Snyder et al., 2001; Cabana, 2014). Zoo diets often include concentrate feeds; less than half of zoos surveyed provide gum, and almost none provide nectar, both of which were found to be staples in wild diets of lorises. These discrepancies lead to diets very rich in protein, soluble carbohydrates and microminerals in zoos (Cabana, 2014) and, as seen in this study, diets which can be nutritionally imbalanced in rescue centers. Lower protein amounts may be adequate for maintenance in captive settings, but the dependence on insects for protein in captivity creates an artificial increase in crude fat and phosphorus, which increases the need for a calcium supplement to balance the negative Ca:P ratio. The addition of gum to the captive diets increased the micronutrient amounts, as well as reversed the negative Ca:P ratio, and increased fibre fractions. The gum was found to be palatable, and even individual lorises which were described as "finicky" by the keepers ingested it readily. Addition of the gum in appreciable amounts (10 g/individual) was not sufficient to raise the nutrient concentrations to identical levels as seen in wild diets; however, it is believed that captive animals will have lower requirements in captivity than in the wild, due to less important physiological stressors and abiotic variations. A number of slow lorises in the rescue center, not used in this study, suffer from metabolic bone disease and dental disease, therefore the current high fruit diet is believed to be inadequate and unbalanced. Figure 3 shows exactly how misplaced and faraway current feeding practices are from wild intake. Zoo loris populations suffer from obesity, dental and kidney diseases as well as inferior quality pelages, thus diets appear inadequate in these instances as well. Diets in rescue centers seem to be too low in quality, and diets in zoos seem to be too rich in specific macronutrients which may all lead to diseases (Cabana, 2014). All captive diets seem to have at least one thing in common, - high soluble carbohydrate concentration owing to excessive fruit proportions. Nectar is the only significant source of soluble carbohydrates in the diets of free-ranging *N. javanicus*, but because nectar is found in such small amounts per flower, it does not translate into a high intake of sugars. Fruits do contain sugars and starches in appreciable amounts, however the wild fruits consumed also contain high amounts of fiber (see Appendix 1) and are not comparable to the cultivated fruits used in captive diets (Schwitzer and Oftedal, 1996; Dierenfeld et al., 2002; Plowman, 2014; Plowman et al., 2015).

Food Transit and Mean Retention Time

The food transit time for *Nycticebus* on a typical captive diet was more or less 25 hours, and did not show a significant difference between species despite large differences in body size. This transit time is much longer than other gummivorous primate groups, the marmosets (*Callithrix:* 3.2 hours and *Cebuella:* 6.3 hours) (Power, 1996). The mean retention time of slow lorises was surprisingly around 50 hours. This would indicate a very high potential for slow lorises to ferment soluble fibres found in gums, and perhaps even exert chitinolytic activity on the ingested insect chitin. The long passage rate of the slow lorises could inherently be caused by their slow metabolic rates, which could then also contribute to fermentation by their gut microflora. Food items should therefore be prioritised by their fibrous components, rather than sugar or starches as once considered. All species studied had very similar transit and mean retention times, which allows us to use the transit and MRT as validation values for the nutrient recommendation diet trials.

Suitability of Javan Slow Loris as a Model Species

The food transit and MRT of different loris species were not significantly different than the wild *N. javanicus* observed. Their digestive systems, feeding ecologies, and presumably physiology are also clearly similar. Captive diet intakes were not dissimilar across species, providing support to our claim that *N. javanicus* can be used as a model for all *Nycticebus spp.,* and that nutrient and feeding recommendations apply widely across this genus.

Slow lorises are known for their low metabolic rates. Muller (1979) successfully illustrated that *N. coucang* had a basal metabolic rate (BMR) of about half that of a primate of the same size , and assumed applicable to all other members of this genus. This observation, combined with Hayssen and Lacy’s estimate of BMR (1985), calculates to a mean basal energy requirement of $0.155(W)^{0.755}$ kcal per day, where W is the animal’s weight in grams. Using published average wild weights and the equation above, we would estimate the daily BMRs as 28.3, 24.9 and 24.1 kcal/day for *N. javanicus, N. coucang* and *N. menegensis* respectively. These minor differences in energy requirements may be met using identical diets differing only in total mass offered/consumed.

With the majority of captive *Nycticebus* diets containing high amounts of fruit and low amounts of exudates, current diets are not representative of slow loris feeding ecology adaptations (Cabana, 2014). Their digestive physiology and morphology are rather adapted to consume and exploit large amounts of exudates (Nekaris, 2014). It may be impossible for many centers to recreate these wild diets and their chemical and physical characteristics. Here we demonstrate that the removal of fruit and honey, and the regular inclusion of vegetables, gum Arabic and insects to the diet altered the nutrient profile to better reflect wild nutrient intake, and provide a more beneficial (nutritionally balanced) and positive physiologically functioning diet.

Conclusion

According to available results from this study, the Javan slow loris (*Nycticebus javanicus*) is a suitable model for the genus. Food transit and mean retention times, behavioural profiles and intake rates were similar for all species. This study is the first to describe nutritional profiles of foods eaten by free-ranging *Nycticebus* spp., and well as transit and food mean retention times of *Nycticebus* species held in captivity. We translated one year's worth of wild *N. javanicus* observations into nutrient recommendations that led to generalised captive feeding guidelines. Future research should focus on how changing the nutrient profile of the captive loris diets affects their health and the propensity of diseases long term.

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