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Slow lorises (*Nycticebus* spp.*)* really are slow: A study into food passage rates

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Abstract

The characteristics of food ingested by a primate affect its assimilation of energy by modulating food passage rate. In general, digestive time increases in folivorous primates and decreases in frugivorous primates when they are fed higher fibre diets but this relationship is understudied in exudativorous primates. We compared the food passage rate of five slow loris species. We studied 34 wild-caught slow lorises (15 *Nycticebus coucang, 15 N. javanicus,* and four *N. menegensis*) in an Indonesian rescue centre and four captive-born slow lorises (two *N. bengalensis* and two *N. pygmaeus*) in a UK institution. We fed the Indonesian animals two different diets: a captive-type diet comprising fruits, vegetables and insects, and a wild-type diet formulated to be similar in nutrients to that consumed by slow lorises in the wild, consisting of gum, insects, vegetables and nectar. We fed the UK animals a diet of gum, vegetables, insects and hard-boiled eggs. We formulated this diet to mimic the wild diet, with notably higher fibre fractions and lower soluble sugars than the previous diet. We measured two variables: the transit time (TT) and the mean retention time (MRT). We mixed 1 tsp of glitter in bananas or gum as our markers and fed them to the slow lorises immediately prior to their main diet. We noted the date and time of feeding and of appearances of the marker in faeces. We weighed food given and left over for each animal to calculate ingested foods and nutrients. We found that TTs were not affected by diet treatment but MRTs were significantly longer for all species fed the wild type diet. Our results show that *Nycticebus* spp. have long MRTs for their body weight, and *N. pygmaeus* may have the slowest MRT of all primates in relation to body mass. The digestive flexibility of exudativorous primates should allow them to maximise fermentation opportunities when they ingest more (appropriate) fibre by increasing the amount of time the fibre substrate stays in the large intestine. Exudativorous primates appear to have plastic digestive strategies that may be an adaptation to cope with relatively nutrient-poor staple food sources such as gum. The provision of gum in a captive setting may therefore provide benefits for gut health in slow lorises.

Key words

Mean retention time, transit time, exudativory, diet, primate, gum

Introduction

Obtaining energy is a fundamental task of all animals, and underlies a finely tuned relationship between food composition and digestive ability. An animal's food passage rate varies with the nutrients ingested to maximize energetic gains. Obtaining energy from plant fibres (cellulose, hemicellulose, pectin, etc.) requires fermentation by microbes in the digestive systems of some animals. A fast passage rate may not allow enough time for the microbes to release a valuable amount of energy. The length of time food remains inside the gastrointestinal tract of an animal can influence many interrelated biological functions, such as the concentration and composition of intestinal microflora (Bailey and Coe 2002, Fogel 2015), extent of nutrient breakdown and absorption (Flores-Miyamoto *et al.* 2005), energetic yield (Blaine and Lambert 2012), metabolic rate (Muller *et al*. 2013) and detoxification of secondary plant metabolites (Cork and Foley 1991). Depending on the food ingested, some mammal species modulate this rate of passage (Edwards and Ullrey 1999a, Kuijper *et al.* 2004) to enhance the digestibility of poor quality food, speed up the intake of food items high in easily digestible nutrients (Caton *et al.* 1996, Sawada *et al.* 2011), or eliminate non-digestible food items (Dierenfeld *et al.* 1982, Power 2010). Measurements used to estimate the food passage rate include transit time (TT) and mean retention time (MRT) (Warner 1981). MRT values are difficult to measure in wild animals, so researchers use MRT in captive animals to infer information about the wild ecological niche, revealing information about energetic needs and digestive ecology (Blaine and Lambert 2012, Lambert 2002).

When primates undergo changes in their feeding regimes, changes in MRT values can be grossly predicted depending on feeding ecology and gastrointestinal tract anatomy. The MRTs of foregut fermenting folivorous proboscis monkeys (*Nasalis larvatus*) or hindgut fermenting folivorous gorillas (*Gorilla gorilla*) differ from those of poorly fermenting frugivores such as red ruffed lemurs (*Varecia rubra*) or granivorous white-faced saki monkeys (*Pithecia pithecia)* (Dierenfeld 2004, Dierenfeld *et al.* 1992, Edwards and Ullrey 1999b, Norconk *et al.* 1992). Changes in MRT may in part be caused by plant fiber in the diets of species with different feeding ecologies and the relative importance of fibrer to their overall energy balance. The folivorous colobine primates have the longest absolute MRTs (up to 49 h; Nijboer 2006), and folivorous hindgut fermenters vary greatly in their digestive capabilities and MRT ranging from 12-37 hr (Edwards and Ullrey 1999b). Such results are not surprising because colobine primates ingest foods high in fibre content compared to non-colobines, and must have a long MRT to allow their symbiotic microbes enough contact time to convert the cellulose and hemi-cellulose fibres into energy sources. Frugivorous species such as spider monkeys (*Ateles* spp.), in contrast, do not exploit the fibrous portions of their diets to the same extent as the soluble carbohydrates found in fruit and therefore do not require extended retention (Milton 1981). Numerous comparisons between the passage rates of frugivorous versus folivorous primates are available, but it is still difficult to draw general conclusions about primates of the same feeding ecology archetypes in relation to body mass (Lambert 1998).

Much of our understanding of exudativory (most notably tree gum eaters) in primates is based on the New World marmosets*,* which gouge trees throughout the year and trigger gum production that they harvest the next day or night (Isbell *et al.* 2013; Nash 1986, Smith 2010). Both the marmosets and the less-studied exudativorous slow lorises (*Nycticebus* spp.) possess gastro-intestinal tract anatomies (i.e., enlarged cecae) associated with digestion/fermentation of soluble polysaccharides found within tree gums (Coimbra-Filha and Mittermeier 1977, Ushida *et al.* 2006). This may be why marmosets decrease their food passage rates when they feed on gum (Power and Oftedal 1996). Gums are also high in minerals, particularly calcium, and once fermented, gums provide a concentrated source of energy; however, they are low in most other nutrients such as protein and lipids (Hladik 1979; Isbell *et al.* 2013). Amongst exudativores, *Callithrix jacchus* has a longer MRT to accommodate the opportunity for fermentation and energy gain (Power and Oftedal 1996). Studies of MRT in relation to exudativory have been limited to New World primates (Platyrrhini), despite the prevalence of this diet amongst the Strepsirrhini, notably the nocturnal slow lorises.

Recent research shows that exudates play a vital role across slow loris species in the wild (*Nycticebus pygmaeus, N. coucang, N. bengalensis* – all Vulnerable, and *N. javanicus* – Critically Endangered), with these taxa spending 43-87% of feeding time on exudates (Cabana *et al.* 2017, Das *et al.* 2014, Starr and Nekaris 2013, Wiens *et al.* 2006). In the past, *Nycticebus* spp. were classified as frugivores based on limited observations and comparisons to African pottos (*Perodicticus*) (Charles-Dominique 1977; Barrett 1984). This misconception has led zoos and rescue centres to feed slow lorises diets comprising largely fruits, a practice which has been implicated in reduced reproduction and high incidence of diseases, most notably dental and renal diseases (Cabana 2014, Cabana and Nekaris 2015, Debyser 1995, Fuller *et al.* 2013, Fuller *et al.* 2014).

We aimed to compare the TT and MRT of five slow loris species (*N. coucang, N. javanicus, N. menagensis, N. bengalensis, N. pygmaeus*) fed a traditional captive diet and a diet formulated to resemble wild diets to further understand the digestive strategy of exudativorous primates. We predicted that slow lorises should show a similar MRT response to common marmosets, namely increasing their MRT as fibre fractions in the form of gum in the diet is increased. We also compiled published primate TT and MRT values for comparison with our data.

Methods

Study Subjects and Locations

We conducted the study at two locations. The first location was Cikananga Wildlife Rescue Centre (CWRC), in Sukabumi, West Java, Indonesia. Animals housed at the centre and used in the study were: *Nycticebus coucang* (n=15)*, N. javanicus* (n=15) and *N. menagensis* (n=4). All animals at CWRC were wild born and had been at the centre for 14 - 20 months. We could not estimate the age of these animals; all were housed in single sex groups. We performed the second set of trials at Shaldon Wildlife Trust (SWT), Shaldon, United Kingdom, with *N. pygmaeus* (n=2) and *N. bengalensis* (n=2). Both *N. pygmaeus* were captive born, and both *N. bengalensis* were wild born. SWT housed all animals individually; veterinarians deemed animals healthy and kept them in non-breeding situations.

Estimation of Nutrient Intake

We estimated the nutrient intake of captive slow lorises fed two different diets. We quantified foods consumed by each slow loris as well as the uneaten foods the following morning using the methods of Britt *et al.* (2015). The captive diet at the CWRC was their current diet, comprising (on average per individual): katydids (*Scudderia* spp. - 3.4 g), peeled oranges (18.3 g), peeled banana (44.0 g), mealworms (*Tenebrio molitor* - 4.9 g), crickets (*Acheta domestica)* (1.3 g), peeled rambutans (*Nephelium lappaceum* - 12.2 g), hardboiled chicken egg without shell (2.2 g), sapodilla without seeds (*Manilkara zapota* - 17.1 g), honey (4.0 g), mangosteen (*Garcinia mangostana* - 12.9 g) and sago worms (*Rhynchophorus ferrugineus* - 2.1 g). We weighed the food before giving it to the animals, and weighed any uneaten food in the enclosure the following morning at 0700 h. We also set up desiccation dishes of food items and measured them at feeding time and the following morning at 0700 h. We filled them with the diet we gave the animals and kept them in a pest proof area with the same temperature and climate as the enclosures. We attributed the decrease in weight to evaporation, which allowed us to correct the diet intake values for this.

We based the wild type diet on a year-long ecological study of Javan slow lorises (Cabana *et al.* 2017). The wild type diet consisted of 20 g of various insects (including mealworms, crickets, wild caught katydids, sago worm larvae and pupae mix), carrots (10 g), green beans (10 g), young bamboo leaves (*Gigantochloa* cf. *ater*) (5 g) and gum directly from *Acacia decurrens* trees (20 g).

We changed the captive type diet to the wild type diet progressively over seven days. We then allowed seven days for acclimatisation then collected data forvthe following seven days. We used only food items that were affordable and available at the rescue centre and zoo.

We analysed the components of both CWRC diets for primary nutrients and fibre fractions (moisture, ash, crude protein, crude fat, acid detergent fibre (ADF), neutral detergent fibre (NDF), soluble fibre and soluble sugars) at the Indonesian Institute of Sciences (LIPI – Lembaga Ilmu Pengetahuan Indonesia) Nutrition Laboratory using methods in Cabana *et al.* (2017).

The SWT diet consisted of 50 g of vegetables (broccoli, peppers, cucumber), 50 g of various root vegetables (carrots, sweet potato, parsnip, swede), 2 g of nectar powder (Sunbird Nectar, Mazuri Europe, UK), 3 g of locusts (*Schistocerca gregaria*), 3 g of mealworms (*Tenebrio molitor)*, 1/2 hardboiled egg with shell, and 5 g of gum arabic powder from *A. senegalensis*.

Food Passage Rate

We used the methods described by Lambert (2002) to determine TT and MRT. Initially, we hid non-toxic plastic beads in bananas, guava and gum to use as the marker to calculate the TT and MRT by noting the time the beads were fed to animals and the time they appeared in faeces, but the slow lorises used their sublinguals (used to clean out their dental comb) to remove and spit out the beads. We then used glitter (unknown brand, Indonesia), previously described by Fuller *et al.* (2011) as a successful TT and MRT marker. To validate the glitter technique for slow lorises, we put it inside guavas and compared the TT and MRT of the guava seeds versus glitter in the same individuals of *N. javanicus*. Results were identical (TT of 24.00 ± 2.25 hr (SD) and MRT of 32.25 h ± 4.66). We then tried 5.0 g of glitter inside a banana in the captive diet, and in 10 g of gum for the wild type diet at CWRC and at SWT. We gave each animal the same amount of glitter. We always fed animals the markers first, before the rest of the diet. At CWRC we fed the animals markers at 1800 hr when the slow lorises awoke, and at SWT we fed slow lorises at 0800 hr due to the reversed light cycle of their nocturnal enclosures. After the slow lorises awoke, we checked each enclosure hourly and collected all faeces we could locate. If we found glitter in the faeces, we recorded the name of the individual and the time we found the marker. We alternated glitter colours (red and blue) between trials. We conducted four trials for each animal for each diet; trials lasted until we observed no more markers in the faeces and one extra day, making all trials four days long.

We defined the time between ingestion of the marker and its first appearance as TT, and we used MRT as the best estimate of food movement through the gastrointestinal tract (Warner 1981). We calculated this value by dividing the length of time from ingestion to each occurrence of the marker, divided by the total number of separate faeces with markers present for that trial (Lambert 2002). We took the mean of the four trials per animal to calculate individual MRT values.

We compiled the TT and MRT values of primates thus far for comparison between other species (Supplementary Table 1). We plotted MRT values against body mass and labelled species with their gross ecological feeding niche (folivore, frugivore, exudativore or granivore). We labelled generalist species and those with heavily seasonal diets frugivores.

Statistical Analysis

We conducted all statistical analyses using SPSS version 22.0 (IBM). We used a Generalized Linear Mixed Model (GLMM) to test for main effects of species and diet composition on the TT and MRT. We considered the assumptions associated with GLMMs and did not violate them. We used a gamma distribution for the response variables (TT and MRT), individual as a random factor and diet (captive and wild) and the three species (*N. coucang, N. javanicus* and *N. menagensis*) as fixed factors. We did not use data from SWT in this analysis since the animals only received the SWT diet. We also performed a Wilcoxon Signed Rank Test, comparing the nutrient concentrations ingested each CWRC slow loris when fed the captive diet and the wild diet.

Ethical Note

We received ethical clearance from the Oxford Brookes University (UK) Social Sciences Department Ethics Committee. Cabana obtained an Indonesian research visa for this research from the Indonesian government (Ministry of Research, Technology and Higher Education of the Republic of Indonesia). Animals were already captive and we did not handle them any more than usual. We expected the diet manipulations to lead to healthier and more naturalistic diets and thus we did not consider them to be a significant stress or danger to the animals.

Results

Transit and Mean Retention Times

The mean TT for CWRC *Nycticebus* spp. on the captive type diet ranged 24.2-25.6 hr, and on the wild type diet ranged 24.4 – 25.9 hr (Table 1). The MRT of *Nycticebus* at CWRC on the captive type diet ranged 29.7 - 33.4 hr and on the wild type diet ranged 34.1-88.5 hr. SWT slow lorises had TTs of 25.3-29 hr and MRTs of 42.6-58 hr. The TT was not affected by any variables we tested (overall model: χ^2=77.549, df=271, P=0.0001; diet χ^2=1.647, df=1, P=0.199; species χ^2=54.528, df=2, P=0.608) but for MRT, (overall model: (χ^2=211.394, df=271, P=0.0001) both diet (χ^2=710.276, df=1, P=0.0001) and species (χ^2=17.531, df=2, P=0.0001) had a significant effect. The captive type diet was associated with a significantly shorter MRT overall (B=-4.750 df= 1 P=0.0001). The MRTs of both *N. javanicus* (B=4.600 df=2 P=0.0001) and *N. coucang* (B=4.000 df=2 P=0.0001) were approximately four hours longer than *N. menagensis* fed the wild type diet. When we gave animals the captive diet, we recorded significantly shorter MRT values for *N. coucang* than for other species on this diet (B=-4.000, df=1 P=0.001).

Exudativores had the steepest line of best fit (y=40.45x) in our scatterplot of MRT and body mass values, followed by granivores (y=21.87x, although this was represented by only 2 samples), then folivores (y=6.80x) and finally frugivores (y=4.03x). These values should be used as loose comparisons only as species were fed different diets which may alter their TT or MRT.

Nutrients Ingested by Slow Lorises

The mean nutrient values ingested by slow lorises fed the captive type diet at CWRC were different to those in the wild type diet (Table 2). At SWT, *N. pygmaeus* and *N. bengalensis* had fibre intake concentrations (DMB) of 9.2-12.3% (ADF) and 12.0-13.6% (NDF). Our Wilcoxon signed rank test revealed that all nutrients ingested except iron were significantly different between the captive and wild diets (Table 3).

Discussion

The food passage rate of *Nycticebus* spp. was relatively long for their body mass compared to other primates. They showed a digestive response similar to that of leaf-eating monkeys (Colobinae), where MRT increased with fibre intake. This response is also comparable to that of exudativorous marmosets when dietary fibre intake increases (Power and Oftedal 1996). The wild type diet increased MRT by up to 42% but did not change TT values. The two different diets led to significantly different nutrient concentrations being ingested for every nutrient except iron, which also reflects how different captive diets can be to wild slow loris diets. The TT of the slow lorises did not vary with diet. Their long MRTs (ranging 29.70-33.40 hr) increased by 4-29 % when fed the wild type diet. This diet contained significantly more fibre fractions (soluble fibre, ADF and NDF), which may be the major reason underlying this altered gut passage rate. The SWT diet contained gum arabic, insects (crickets and mealworms), eggs, vegetables and fruit, effectively making it a hybrid of the captive and wild type diets, but the dietary fibre values were closer to the wild type diet. We did not have data to test whether MRT in *N. pygmaeus* or *N. bengalensis* increases if they are fed a higher fibre diet but we can compare their MRT values with those of other *Nycticebus* spp. The markers we used were not as sensitive as other validated methods. Our results are nonetheless useful for comparisons and to influence captive care due to the dearth of knowledge about *Nycticebus* physiology.

Strepsirrhines that depend on fermentable foods, such as leaves, have an enlarged large intestine and caecum (e.g., the sportive lemur *Lepilemur leucopus*, Perrin 2013). This anatomy most likely reflects an adaptation for efficient use of high fibre diets and active microbial populations. Slow lorises also appear to possess adaptations to high fibre diets, reflected in the large increase in MRT when we fed them wild type diets. Within the platyrrhines, howler monkeys (*Allouatta* spp.) also eat a very fibrous diet and display TTs of 20.4 - 35.0 hr and MRTs of 49.5 - 57.0 hr, in contrast with 5.3 hr in the frugivorous spider monkeys (*Ateles* spp, Crissey *et al.* 1990, Espinoza-Gomez *et al.* 2013, Milton 1984). This enables spider monkeys to pass indigestible materials rapidly through their less complex digestive tract, similar to tamarin species which pass whole undigested seeds within 2.2-2.5 hr (Heymann and Smith 1999, Knogge 1998). This response allows frugivores to ingest more food and exploit the easily absorbable nutrients in the diet faster than folivores. This also explains why frugivores had the lowest MRT to body size ratio. If preferred foods are not available in large quantity, a higher intake of lesser quality food may compensate. This strategy is useful for frugivorous tamarins (*Saguinus* spp.), spider monkeys, Japanese macaques (*Macaca fuscata*), white-handed gibbons (*Hylobates lar)* and de Brazza's monkeys (*Cercopithecus neglectus*)*,* which show decreased MRTs with increasing dietary fibre (Sawada *et al.* 2011). The dichotomy between the folivorous and frugivorous responses is further exemplified in the lemurs (Lemuridae). Frugivorou*s* lemurs *(Eulemur* spp.) have a rapid TT of 1.6 - 3.3 hr, but the fermenting eastern lesser bamboo lemur (*Hapalemur griseus)* has a much longer TT of 18.2 hr (Overdorff and Rasmussen 1995). Data for great apes also support this hypothesis. The more frugivorous orangutans (*Pongo pygmaeus)* and chimpanzee (*Pan troglodytes)* have an MRT of 37 and 37.0-48.0 hr while the highly folivorous lowland gorilla (*Gorilla gorilla)* has an MRT which may reach up to 97 hr (Milton 1984, Milton and Demment 1988, Remis 2000, Remis and Dierenfeld 2004). The slow loris in this study had a similar MRT to that of *P. pygmaeus*, which is 80 times larger.

There is a trend for frugivores to reduce their MRT when they ingest more fibre (Overdorff and Rasmussen 1995), while folivores (Remis and Dierenfeld 2004) and exudativores (Power and Oftedal 1996; this study) increase their MRT. The gouging marmosets (*Cebuella* and *Callithrix*) are often grouped with slow lorises due to their exudativorous feeding ecologies (Smith 2010). Although data are limited, they also grouped together when MRT was plotted against body mass (Figure 1). Slow lorises and marmosets are similar in their response to increased dietary fibre. Both groups of primates have unique traits and ecology, such as a low metabolic rate, the ability to ingest a diet high in plant secondary metabolites and the ability to subsist on a diet of mostly plant exudates (Nekaris 2014). Marmosets and slow lorises have basal metabolic rates 72 and 60% of expected primate values (Genoud *et al*. 1997, Muller 1979). Their low-quality diet coupled with a slow metabolism probably culminate to the high MRT values observed for exudativorous primates.

Slow lorises are well adapted to a high fibre diets. This may be important for their health (Campbell *et al.* 2001). Captive slow lorises suffer from many ailments including obesity, dental diseases and kidney diseases (Cabana 2014, Cabana and Nekaris 2015, Debyser 1995, Fuller *et al.* 2013). Overall, captive diets are lacking or low in gum (and coincidentally in fibre compared to the wild) and are high in soluble carbohydrates (Cabana and Nekaris 2015). A longer MRT means an increased opportunity for fermentation, resulting in higher concentration of short-chain fatty acids (Blaine and Lambert 2012, Lambert and Fellner 2012). A longer MRT also results in better digestive efficiencies for many nutrients. Moreover, the properties of volatile fatty acids created at the end of fermentation are associated with gut health benefits (Plaami 1997). These acids may contribute to positive gastrointestinal cell proliferation and increased substrate for cellular energy production, as well as a more stable luminal pH that allows bacterial metabolic functions to be most efficient (Walker and Buckley 2006). The acids can also have a protective effect against potential pathogens and diarrhoea, and reduce the negative effects of high soluble carbohydrates in the diet (Bailey and Coe 2002, Johnson *et al.* 1984). Increasing fibre in the diet may also increase satiation, possibly reducing stereotypies and other abnormal heath patterns (Britt *et al.* 2015, Remis and Dierenfeld 2004). There are no obvious downsides to increasing fibre in the diets of captive exudativorous primates and many possible benefits.

In conclusion, slow lorises, like marmosets, increase their MRT values when dietary fibre increases . Their response to a higher fibre diet is similar to folivorous primates. Exudativorous primates seem to digest low quality food slowly, presumably to allow fermentation, rather than quickly eating a larger amount of food with little to no opportunity for fermentation. Future studies should modify only fibre to derive more robust conclusions about the plasticity of exudativorous digestion, free from the possible effects of other nutrients.

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FIGURE LEGENDS

Figure I Published values for body mass and mean retention times for primates <20 kg with their ecological feeding niche: exudativores (orange diamond), granivores (grey triangle), folivores (blue circle) and frugivores (yellow X). Lines indicate lines of best fit where a steeper slope indicates a slower food passage rate per kg of body mass. Values and references are in supplementary Table S1.

Table I Transit and mean retention times for gut passage rates of *Nycticebus javanicus, coucang* and *menagensis* at Cikananga Wildife Rescue Centre (Sukabumi, Indonesia) in June 2015 under two different diet treatments, and *N. pygmaeus* and *N. bengalensis* at Shaldon Wildlife Trust (Shaldon, United Kingdom) in August 2015, on a diet of refined gum, vegetables and insects.

Species		*N. javanicus*	*N. coucang*	*N. menagensis*	*N. pygmaeus*	*N. bengalensis*
N		15	15	4	2	2
Mean (± SD) animal mass (g)		1050 (±236)	936 (±312)	902 (±53)	423(±25)	1020 (±93)
Mean (± SD) Transit Time (hours)	Captive Diet	25.6 (±2.6)	25.00 (±3.5)	24.2 (±3.2)	-	-
	Wild Diet	25.9 (±3.4)	24.4(±2.1)	24.5 (±2.9)	-	-
	SWT Diet	-	-	-	29.0 (±2.0)	25.3 (±2.2)
Mean (± SD) Retention Time (hours)	Captive Diet	33.40 (±1.0)	29.70 (±1.5)	32.88 (±3.1)	-	-
	Wild Diet	38.50 (±2.0)	38.0 (±2.5)	34.13 (±4.1)	-	-
	SWT Diet	-	-	-	39.75 (±1.5)	24.32 (±0.5)

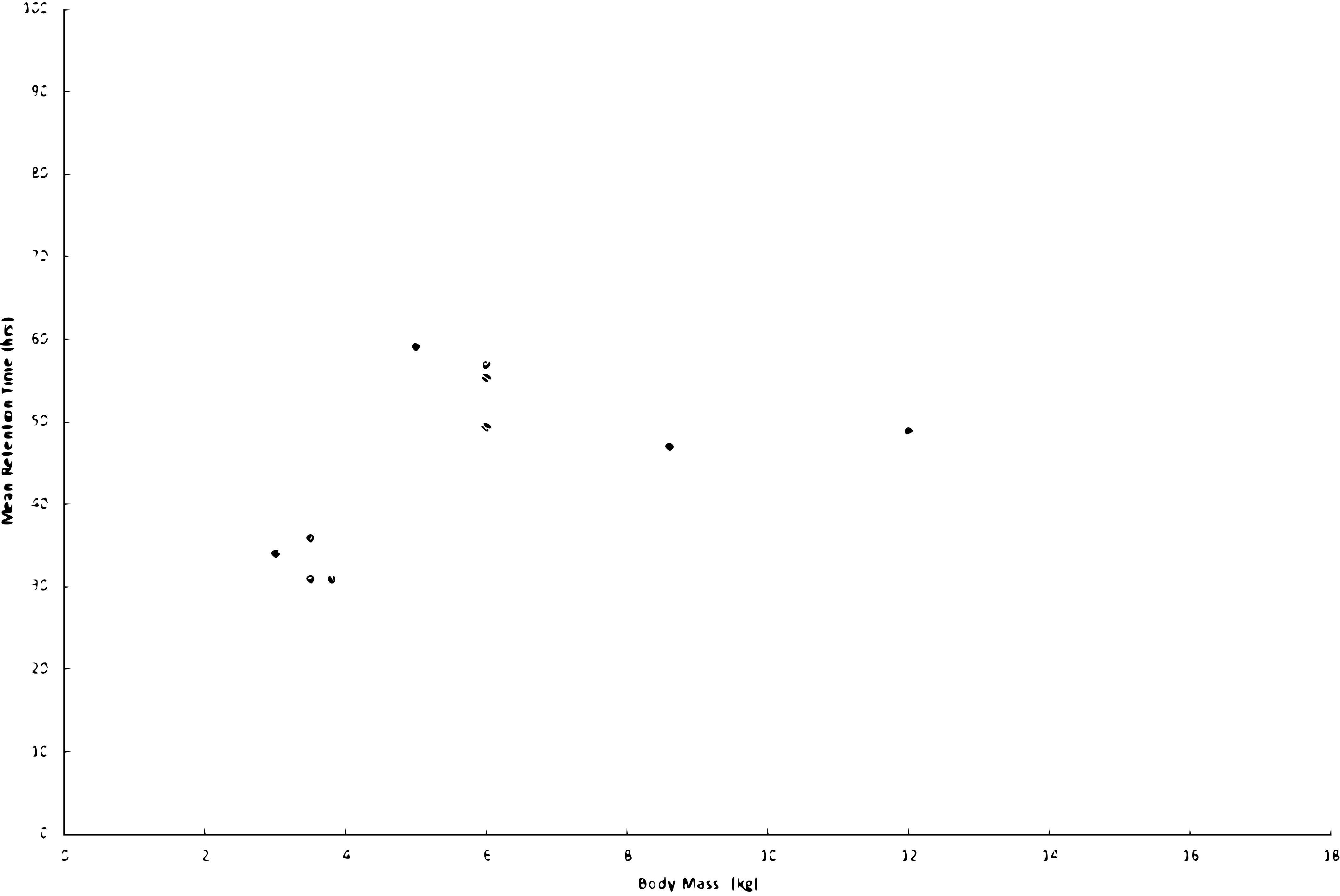
Table II Mean +/- SD daily nutrient intake for *Nycticebus javanicus, coucang* and *menagensis* at Cikananga Wildlife Rescue Centre (Sukabumi, Indonesia) in June 2015 under two dietary treatments and of *N. pygmaeus* and *N. bengalensis* at Shaldon Wildlife Trust (SWT - Shaldon, United Kingdom) in August 2015.

	N. javanicus		***N. coucang***		***N. menagensis***		***N. pygmaeus***	***N. bengalensis***
Nutrient	**Captive Diet**	**Wild Diet**	**Captive Diet**	**Wild Diet**	**Captive Diet**	**Wild Diet**	**SWT Diet**	**SWT Diet**
Ash (%)	2.90 (±2.51)	2.64 (±0.53)	3.11 (±2.65)	2.44 (±0.43)	2.88 (±2.44)	2.76 (±0.62)	5.67 (±2.34)	5.43 (±2.21)
Crude Protein (%)	12.79 (±4.59)	26.23 (±5.58)	12.11 (±4.91)	25.64 (±5.48)	13.69 (±4.34)	24.35 (±6.01)	24.08 (±3.56)	22.56 (±3.31)
Crude Fat (%)	7.58 (±2.03)	10.41 (±2.09)	7.81 (±1.98)	11.15 (±2.37)	8.30 (±2.00)	9.62 (±2.56)	14.75 (±6.75)	13.65 (±5.23)
Energy (Kcal/g)	3.92 (±0.68)	4.17 (±0.61)	3.91 (±0.74)	4.31 (±0.48)	4.25 (±0.51)	4.09 (±0.73)	4.02 (±0.34)	3.96 (±0.12)
Soluble fibre (%)	0.72 (±1.27)	3.11 (±2.71)	0.71 (±1.11)	3.09 (±2.31)	0.78 (±1.19)	3.24 (±3.01)	NA	NA
Acid Detergent Fibre (%)	5.28 (±4.05)	15.04 (±6.73)	4.35 (±3.93)	14.13 (±5.19)	8.41 (±3.99)	14.56 (±6.87)	9.24 (±2.59)	10.34 (±2.46)
Neutral Detergent Fibre (%	8.56 (±3.00)	18.72 (±6.81)	7.31 (±3.16)	17.72 (±6.27)	10.50 (±2.69)	19.01 (±7.23)	12.04 (±2.99)	13.56 (±2.64)
Sugars (%)	9.60 (±6.86)	3.88 (±10.76)	9.20 (±5.12)	4.10 (±10.32)	9.14 (±6.73)	3.56 (±11.38)	NA	NA
Calcium (%)	0.17 (±0.04)	0.33 (±0.09)	0.14 (±0.10)	0.35 (±0.12)	0.15 (±0.12)	0.31 (±0.11)	0.35 (±0.09)	0.37 (±0.11)
Phosphorous (%)	0.19 (±0.06)	0.30 (±0.08)	0.16 (±.09)	0.32 (±0.10)	0.20 (±0.11)	0.28 (±0.13)	0.40 (±0.13)	0.38 (±0.06)
Magnesium (%)	0.27 (±0.13)	0.54 (±0.24)	0.29 (±0.17)	0.49 (± 20)	0.24 (±0.11)	0.51 (±0.29)	0.10 (±0.02)	0.09 (±0.03)
Iron (mg/kg)	59.47(±13.71)	123.00 (±38.17)	57.26 (±11.57)	113.45 (±39.62)	69.12 (±13.56)	119.57 (±41.67)	43.69 (±9.16)	46.97 (±8.82)
Sodium (%)	0.43 (±0.63)	0.11 (±0.10)	0.36 (±0.72)	0.10 (±0.15)	0.12 (±0.59)	0.11 (±0.07)	0.24 (±0.14)	0.20 (±0.12)
Copper (mg/kg)	7.45 (±2.88)	6.67 (±1.46)	6.96 (±2.81)	6.79 (±)1.86	7.2 (±2.63)	6.41 (±1.75)	3.70 (±1.04)	3.98 (±0.94)
Calcium:Phosphorous	0.89	1.10	0.88	1.09	0.75	1.11	0.88	0.98

Table III Wilcoxon Signed Rank Test results comparing the nutrient intake of 34 slow lorises (*Nycticebus javanicus, coucang* and *menagensis)* at Cikananga Wildlife Rescue Centre (Sukabumi, Indonesia) under two different diet treatments: a captive diet high in fruits and a wild type diet high in gum.

	Nutrient	Z	P
Higher in Captive Diet	Ash	-3.17	0.0020
	Sugar	-7.73	0.0001
	Copper	-6.77	0.0001
Higher in Wild Diet	Crude Protein	-8.94	0.0001
	Crude Fat	-9.38	0.0001
	Energy Density	-4.59	0.0001
	Soluble Fibre	-7.73	0.0001
	Acid Detergent Fibre	-7.99	0.0001
	Neutral Detergent Fibre	-7.48	0.0001
	Calcium	-9.62	0.0001
	Phosphorous	-8.39	0.0001
	Magnesium	-5.30	0.0001
	Sodium	-8.14	0.0001
No Difference	Iron	-1.48	0.2780

Figure 1


Mean Retention Time (hrs)
100
90
80
70
60
50
40
30
20
10
0
0
2
4
6
8
10
12
14
16
18
Body Mass (kg)