

1 **Title**

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

3 **Authors**

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28 **Title:** Slow lorises (*Nycticebus* spp.) really are slow: a study of food passage rates

29 **Running Title:** Slow loris food passage rate

30 **Abstract**

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

51 strategies that may be an adaptation to cope with relatively nutrient-poor staple food sources such as gum.  
52 The provision of gum in a captive setting may therefore provide benefits for gut health in slow lorises.

### 53 **Key words**

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

### 55 **Introduction**

56 Obtaining energy is a fundamental task of all animals, and underlies a finely tuned relationship between  
57 food composition and digestive ability. An animal's food passage rate varies with the nutrients ingested to  
58 maximize energetic gains. Obtaining energy from plant fibres (cellulose, hemicellulose, pectin, etc.)  
59 requires fermentation by microbes in the digestive systems of some animals. A fast passage rate may not  
60 allow enough time for the microbes to release a valuable amount of energy. The length of time food  
61 remains inside the gastrointestinal tract of an animal can influence many interrelated biological functions,  
62 such as the concentration and composition of intestinal microflora (Bailey and Coe 2002, Fogel 2015),  
63 extent of nutrient breakdown and absorption (Flores-Miyamoto *et al.* 2005), energetic yield (Blaine and  
64 Lambert 2012), metabolic rate (Muller *et al.* 2013) and detoxification of secondary plant metabolites  
65 (Cork and Foley 1991). Depending on the food ingested, some mammal species modulate this rate of  
66 passage (Edwards and Ullrey 1999a, Kuijper *et al.* 2004) to enhance the digestibility of poor quality food,  
67 speed up the intake of food items high in easily digestible nutrients (Caton *et al.* 1996, Sawada *et al.*  
68 2011), or eliminate non-digestible food items (Dierenfeld *et al.* 1982, Power 2010). Measurements used  
69 to estimate the food passage rate include transit time (TT) and mean retention time (MRT) (Warner  
70 1981). MRT values are difficult to measure in wild animals, so researchers use MRT in captive animals to  
71 infer information about the wild ecological niche, revealing information about energetic needs and  
72 digestive ecology (Blaine and Lambert 2012, Lambert 2002).

73 When primates undergo changes in their feeding regimes, changes in MRT values can be grossly  
74 predicted depending on feeding ecology and gastrointestinal tract anatomy. The MRTs of foregut

75 fermenting folivorous proboscis monkeys (*Nasalis larvatus*) or hindgut fermenting folivorous gorillas  
76 (*Gorilla gorilla*) differ from those of poorly fermenting frugivores such as red ruffed lemurs (*Varecia*  
77 *rubra*) or granivorous white-faced saki monkeys (*Pithecia pithecia*) (Dierenfeld 2004, Dierenfeld *et al.*  
78 1992, Edwards and Ullrey 1999b, Norconk *et al.* 1992). Changes in MRT may in part be caused by plant  
79 fiber in the diets of species with different feeding ecologies and the relative importance of fiber to their  
80 overall energy balance. The folivorous colobine primates have the longest absolute MRTs (up to 49 h;  
81 Nijboer 2006), and folivorous hindgut fermenters vary greatly in their digestive capabilities and MRT  
82 ranging from 12-37 hr (Edwards and Ullrey 1999b). Such results are not surprising because colobine  
83 primates ingest foods high in fibre content compared to non-colobines, and must have a long MRT to  
84 allow their symbiotic microbes enough contact time to convert the cellulose and hemi-cellulose fibres into  
85 energy sources. Frugivorous species such as spider monkeys (*Ateles* spp.), in contrast, do not exploit the  
86 fibrous portions of their diets to the same extent as the soluble carbohydrates found in fruit and therefore  
87 do not require extended retention (Milton 1981). Numerous comparisons between the passage rates of  
88 frugivorous versus folivorous primates are available, but it is still difficult to draw general conclusions  
89 about primates of the same feeding ecology archetypes in relation to body mass (Lambert 1998).

90

91 Much of our understanding of exudativory (most notably tree gum eaters) in primates is based on the New  
92 World marmosets, which gouge trees throughout the year and trigger gum production that they harvest the  
93 next day or night (Isbell *et al.* 2013; Nash 1986, Smith 2010). Both the marmosets and the less-studied  
94 exudativorous slow lorises (*Nycticebus* spp.) possess gastro-intestinal tract anatomies (i.e., enlarged  
95 caecae) associated with digestion/fermentation of soluble polysaccharides found within tree gums  
96 (Coimbra-Filha and Mittermeier 1977, Ushida *et al.* 2006). This may be why marmosets decrease their  
97 food passage rates when they feed on gum (Power and Oftedal 1996). Gums are also high in minerals,  
98 particularly calcium, and once fermented, gums provide a concentrated source of energy; however, they  
99 are low in most other nutrients such as protein and lipids (Hladik 1979; Isbell *et al.* 2013). Amongst

100 exudativores, *Callithrix jacchus* has a longer MRT to accommodate the opportunity for fermentation and  
101 energy gain (Power and Oftedal 1996). Studies of MRT in relation to exudativory have been limited to  
102 New World primates (Platyrrhini), despite the prevalence of this diet amongst the Strepsirrhini, notably  
103 the nocturnal slow lorises.

104

105 Recent research shows that exudates play a vital role across slow loris species in the wild (*Nycticebus*  
106 *pygmaeus*, *N. coucang*, *N. bengalensis* – all Vulnerable, and *N. javanicus* – Critically Endangered), with  
107 these taxa spending 43-87% of feeding time on exudates (Cabana *et al.* 2017, Das *et al.* 2014, Starr and  
108 Nekaris 2013, Wiens *et al.* 2006). In the past, *Nycticebus* spp. were classified as frugivores based on  
109 limited observations and comparisons to African pottos (*Perodicticus*) (Charles-Dominique 1977; Barrett  
110 1984). This misconception has led zoos and rescue centres to feed slow lorises diets comprising largely  
111 fruits, a practice which has been implicated in reduced reproduction and high incidence of diseases, most  
112 notably dental and renal diseases (Cabana 2014, Cabana and Nekaris 2015, Debyser 1995, Fuller *et al.*  
113 2013, Fuller *et al.* 2014).

114

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

121

122

## 123 **Methods**

### 124 **Study Subjects and Locations**

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

### 133 **Estimation of Nutrient Intake**

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

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

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

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

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

162

### 163 **Food Passage Rate**

164 We used the methods described by Lambert (2002) to determine TT and MRT. Initially, we hid non-toxic  
165 plastic beads in bananas, guava and gum to use as the marker to calculate the TT and MRT by noting the  
166 time the beads were fed to animals and the time they appeared in faeces, but the slow lorises used their  
167 sublinguals (used to clean out their dental comb) to remove and spit out the beads. We then used glitter  
168 (unknown brand, Indonesia), previously described by Fuller *et al.* (2011) as a successful TT and MRT  
169 marker. To validate the glitter technique for slow lorises, we put it inside guavas and compared the TT

170 and MRT of the guava seeds versus glitter in the same individuals of *N. javanicus*. Results were identical  
171 (TT of  $24.00 \pm 2.25$  hr (SD) and MRT of  $32.25 \text{ h} \pm 4.66$ ). We then tried 5.0 g of glitter inside a banana in  
172 the captive diet, and in 10 g of gum for the wild type diet at CWRC and at SWT. We gave each animal  
173 the same amount of glitter. We always fed animals the markers first, before the rest of the diet. At CWRC  
174 we fed the animals markers at 1800 hr when the slow lorises awoke, and at SWT we fed slow lorises at  
175 0800 hr due to the reversed light cycle of their nocturnal enclosures. After the slow lorises awoke, we  
176 checked each enclosure hourly and collected all faeces we could locate. If we found glitter in the faeces,  
177 we recorded the name of the individual and the time we found the marker. We alternated glitter colours  
178 (red and blue) between trials. We conducted four trials for each animal for each diet; trials lasted until we  
179 observed no more markers in the faeces and one extra day, making all trials four days long.

180

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

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

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## 193 **Statistical Analysis**

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

202

## 203 **Ethical Note**

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

210

## 211 **Results**

### 212 **Transit and Mean Retention Times**

213 The mean TT for CWRC *Nycticebus* spp. on the captive type diet ranged 24.2-25.6 hr, and on the wild  
214 type diet ranged 24.4 – 25.9 hr (Table 1). The MRT of *Nycticebus* at CWRC on the captive type diet

215 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  
216 hr and MRTs of 42.6-58 hr. The TT was not affected by any variables we tested (overall model:  
217  $\chi^2=77.549$ ,  $df=271$ ,  $P=0.0001$ ; diet  $\chi^2=1.647$ ,  $df=1$ ,  $P=0.199$ ; species  $\chi^2=54.528$ ,  $df=2$ ,  $P=0.608$ ) but for  
218 MRT, (overall model: ( $\chi^2=211.394$ ,  $df=271$ ,  $P=0.0001$ ) both diet ( $\chi^2=710.276$ ,  $df=1$ ,  $P=0.0001$ ) and  
219 species ( $\chi^2=17.531$ ,  $df=2$ ,  $P=0.0001$ ) had a significant effect. The captive type diet was associated with a  
220 significantly shorter MRT overall ( $B=-4.750$   $df=1$   $P=0.0001$ ). The MRTs of both *N. javanicus* ( $B=4.600$   
221  $df=2$   $P=0.0001$ ) and *N. coucang* ( $B=4.000$   $df=2$   $P=0.0001$ ) were approximately four hours longer than *N.*  
222 *menagensis* fed the wild type diet. When we gave animals the captive diet, we recorded significantly  
223 shorter MRT values for *N. coucang* than for other species on this diet ( $B=-4.000$ ,  $df=1$   $P=0.001$ ).

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

228

### 229 **Nutrients Ingested by Slow Lorises**

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

235

### 236 **Discussion**

237 The food passage rate of *Nycticebus* spp. was relatively long for their body mass compared to other  
238 primates. They showed a digestive response similar to that of leaf-eating monkeys (Colobinae), where  
239 MRT increased with fibre intake. This response is also comparable to that of exudativorous marmosets  
240 when dietary fibre intake increases (Power and Oftedal 1996). The wild type diet increased MRT by up to  
241 42% but did not change TT values. The two different diets led to significantly different nutrient  
242 concentrations being ingested for every nutrient except iron, which also reflects how different captive  
243 diets can be to wild slow loris diets. The TT of the slow lorises did not vary with diet. Their long MRTs  
244 (ranging 29.70-33.40 hr) increased by 4-29 % when fed the wild type diet. This diet contained  
245 significantly more fibre fractions (soluble fibre, ADF and NDF), which may be the major reason  
246 underlying this altered gut passage rate. The SWT diet contained gum arabic, insects (crickets and  
247 mealworms), eggs, vegetables and fruit, effectively making it a hybrid of the captive and wild type diets,  
248 but the dietary fibre values were closer to the wild type diet. We did not have data to test whether MRT in  
249 *N. pygmaeus* or *N. bengalensis* increases if they are fed a higher fibre diet but we can compare their MRT  
250 values with those of other *Nycticebus* spp. The markers we used were not as sensitive as other validated  
251 methods. Our results are nonetheless useful for comparisons and to influence captive care due to the  
252 dearth of knowledge about *Nycticebus* physiology.

253

254 Strepsirrhines that depend on fermentable foods, such as leaves, have an enlarged large intestine and  
255 caecum (e.g., the sportive lemur *Lepilemur leucopus*, Perrin 2013). This anatomy most likely reflects an  
256 adaptation for efficient use of high fibre diets and active microbial populations. Slow lorises also appear  
257 to possess adaptations to high fibre diets, reflected in the large increase in MRT when we fed them wild  
258 type diets. Within the platyrrhines, howler monkeys (*Alouatta* spp.) also eat a very fibrous diet and  
259 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  
260 monkeys (*Ateles* spp, Crissey *et al.* 1990, Espinoza-Gomez *et al.* 2013, Milton 1984). This enables spider  
261 monkeys to pass indigestible materials rapidly through their less complex digestive tract, similar to

262 tamarin species which pass whole undigested seeds within 2.2-2.5 hr (Heymann and Smith 1999, Knogge  
263 1998). This response allows frugivores to ingest more food and exploit the easily absorbable nutrients in  
264 the diet faster than folivores. This also explains why frugivores had the lowest MRT to body size ratio. If  
265 preferred foods are not available in large quantity, a higher intake of lesser quality food may compensate.  
266 This strategy is useful for frugivorous tamarins (*Saguinus* spp.), spider monkeys, Japanese macaques  
267 (*Macaca fuscata*), white-handed gibbons (*Hylobates lar*) and de Brazza's monkeys (*Cercopithecus*  
268 *neglectus*), which show decreased MRTs with increasing dietary fibre (Sawada *et al.* 2011). The  
269 dichotomy between the folivorous and frugivorous responses is further exemplified in the lemurs  
270 (Lemuridae). Frugivorous lemurs (*Eulemur* spp.) have a rapid TT of 1.6 - 3.3 hr, but the fermenting  
271 eastern lesser bamboo lemur (*Hapalemur griseus*) has a much longer TT of 18.2 hr (Overdorff and  
272 Rasmussen 1995). Data for great apes also support this hypothesis. The more frugivorous orangutans  
273 (*Pongo pygmaeus*) and chimpanzee (*Pan troglodytes*) have an MRT of 37 and 37.0-48.0 hr while the  
274 highly folivorous lowland gorilla (*Gorilla gorilla*) has an MRT which may reach up to 97 hr (Milton  
275 1984, Milton and Demment 1988, Remis 2000, Remis and Dierenfeld 2004). The slow loris in this study  
276 had a similar MRT to that of *P. pygmaeus*, which is 80 times larger.

277 There is a trend for frugivores to reduce their MRT when they ingest more fibre (Overdorff and  
278 Rasmussen 1995), while folivores (Remis and Dierenfeld 2004) and exudativores (Power and Oftedal  
279 1996; this study) increase their MRT. The gougling marmosets (*Cebuella* and *Callithrix*) are often  
280 grouped with slow lorises due to their exudativorous feeding ecologies (Smith 2010). Although data are  
281 limited, they also grouped together when MRT was plotted against body mass (Figure 1). Slow lorises  
282 and marmosets are similar in their response to increased dietary fibre. Both groups of primates have  
283 unique traits and ecology, such as a low metabolic rate, the ability to ingest a diet high in plant secondary  
284 metabolites and the ability to subsist on a diet of mostly plant exudates (Nekaris 2014). Marmosets and  
285 slow lorises have basal metabolic rates 72 and 60% of expected primate values (Genoud *et al.* 1997,

286 Muller 1979). Their low-quality diet coupled with a slow metabolism probably culminate to the high  
287 MRT values observed for exudativorous primates.

288

289 Slow lorises are well adapted to a high fibre diets. This may be important for their health (Campbell *et al.*  
290 2001). Captive slow lorises suffer from many ailments including obesity, dental diseases and kidney  
291 diseases (Cabana 2014, Cabana and Nekaris 2015, Debyser 1995, Fuller *et al.* 2013). Overall, captive  
292 diets are lacking or low in gum (and coincidentally in fibre compared to the wild) and are high in soluble  
293 carbohydrates (Cabana and Nekaris 2015). A longer MRT means an increased opportunity for  
294 fermentation, resulting in higher concentration of short-chain fatty acids (Blaine and Lambert 2012,  
295 Lambert and Fellner 2012). A longer MRT also results in better digestive efficiencies for many nutrients.  
296 Moreover, the properties of volatile fatty acids created at the end of fermentation are associated with gut  
297 health benefits (Plaami 1997). These acids may contribute to positive gastrointestinal cell proliferation  
298 and increased substrate for cellular energy production, as well as a more stable luminal pH that allows  
299 bacterial metabolic functions to be most efficient (Walker and Buckley 2006). The acids can also have a  
300 protective effect against potential pathogens and diarrhoea, and reduce the negative effects of high soluble  
301 carbohydrates in the diet (Bailey and Coe 2002, Johnson *et al.* 1984). Increasing fibre in the diet may also  
302 increase satiation, possibly reducing stereotypies and other abnormal heath patterns (Britt *et al.* 2015,  
303 Remis and Dierenfeld 2004). There are no obvious downsides to increasing fibre in the diets of captive  
304 exudativorous primates and many possible benefits.

305

306 In conclusion, slow lorises, like marmosets, increase their MRT values when dietary fibre increases .  
307 Their response to a higher fibre diet is similar to folivorous primates. Exudativorous primates seem to  
308 digest low quality food slowly, presumably to allow fermentation, rather than quickly eating a larger  
309 amount of food with little to no opportunity for fermentation. Future studies should modify only fibre to

310 derive more robust conclusions about the plasticity of exudativorous digestion, free from the possible  
311 effects of other nutrients.

312

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531 **FIGURE LEGENDS**

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

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**Table I** Transit and mean retention times for gut passage rates of *Nycticebus javanicus*, *coucang* and *menagensis* at Cikananga Wildlife 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		<i>N. javanicus</i>	<i>N. coucang</i>	<i>N. menagensis</i>	<i>N. pygmaeus</i>	<i>N. bengalensis</i>
N		15	15	4	2	2
Mean ( $\pm$ SD) animal mass (g)		1050 ( $\pm$ 236)	936 ( $\pm$ 312)	902 ( $\pm$ 53)	423( $\pm$ 25)	1020 ( $\pm$ 93)
Mean ( $\pm$ SD) Transit Time (hours)	Captive Diet	25.6 ( $\pm$ 2.6)	25.00 ( $\pm$ 3.5)	24.2 ( $\pm$ 3.2)	-	-
	Wild Diet	25.9 ( $\pm$ 3.4)	24.4( $\pm$ 2.1)	24.5 ( $\pm$ 2.9)	-	-
	SWT Diet	-	-	-	29.0 ( $\pm$ 2.0)	25.3 ( $\pm$ 2.2)
Mean ( $\pm$ SD) Retention Time (hours)	Captive Diet	33.40 ( $\pm$ 1.0)	29.70 ( $\pm$ 1.5)	32.88 ( $\pm$ 3.1)	-	-
	Wild Diet	38.50 ( $\pm$ 2.0)	38.0 ( $\pm$ 2.5)	34.13 ( $\pm$ 4.1)	-	-
	SWT Diet	-	-	-	39.75 ( $\pm$ 1.5)	24.32 ( $\pm$ 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.

Nutrient	<i>N. javanicus</i>		<i>N. coucang</i>		<i>N. menagensis</i>		<i>N. pygmaeus</i>	<i>N. bengalensis</i>
	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 (±0.09)	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 (±0.20)	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

