

1 **Title:** Vertical clingers and gougers: rapid acquisition of adult limb proportions facilitates  
2 feeding behaviours in young Javan slow lorises (*Nycticebus javanicus*)

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12 **Abstract:**

13 Animals of all ages need to access essential food resources, either on their own or with the  
14 assistance of conspecifics. Rapid physical and behavioural development is one strategy to  
15 help young animals reach adulthood. Specialized gum-feeding mammals exploit a food type  
16 that is relatively difficult to access and digest and must possess the appropriate adaptations to  
17 access large vertical substrates, i.e. tree trunks. Unlike other gum feeding mammals, the  
18 Javan slow loris (*Nycticebus javanicus*) lacks physical structures, such as keeled nails or  
19 claws, which animals commonly use to secure themselves to large vertical substrates. To  
20 understand how slow lorises of all ages exploit gum, we examined their vertical gouging  
21 posture, locomotor behaviour, habitat use during feeding, and their morphometric measures  
22 across three age classes (adult, sub-adult, juvenile). Using data collected in Cipaganti, Java,  
23 Indonesia between April 2012 and April 2016, we found that individuals of *N. javanicus* rely  
24 on their hand, foot, and limb morphology to maintain vertical gouging postures, in place of  
25 claws or keeled nails. Locomotor behaviour, position in tree, and tree DBH showed no  
26 significant difference across age classes while feeding. Juveniles were indistinguishable  
27 from adults and sub-adults in regards to limb proportion indices, lower leg length, hand span  
28 and foot span. Some morphometric measures scaled isometrically e.g. arm length, but  
29 those highlighted during prolonged vertical postures scaled allometrically e.g. leg, hand, and  
30 foot measures. These findings suggest that the rapid behavioural and physical development  
31 of key features may act as an ontogenetic adaptation to facilitate access to a stable food  
32 resource at a young age. The Javan slow loris exemplifies the complex relationship that  
33 exists between an animal's diet and the specializations that facilitate access to these food  
34 resources.

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36

37 **Keyword:** Exudativory, Gum, Ontogeny, Morphometrics, Strepsirrhine, Substrate Use,  
38 Habitat Use

## 40 Introduction

41 Mammals that rely on specific food resources must also possess a suite of adaptations to  
42 facilitate the access and digestion of these food items. Behavioural and morphological  
43 specialisations associated with feeding ecology are notable among mammal species (De  
44 Muizon and Lange-Badre, 1997; Dierenfeld, 1982; Ercoli and Youlatos, 2016; Koyabu et al.,  
45 2009; Ley et al., 2008; Naples, 1999; Ravosa et al., 2010; Tan, 1999). Mammals typically  
46 acquire needed feeding skills long before sexual maturity, allowing them to access vital  
47 resources before adulthood (Schuppli et al., 2012). One developmental strategy, rapid  
48 growth in infants, is a known adaptation to aid in reducing infant vulnerability and to help  
49 them surpass the “juvenile bottleneck”, a period in which the mortality rate for juveniles is  
50 higher than that of adults (Case, 1978; Williams, 1966; Yonger and Heard-Booth 2016).

51 Specialised gummivory is only seen in a small number of Australian marsupials and primates  
52 (Irlbeck and Hume, 2003; Viguier, 2004). These animals have evolved morphological traits  
53 and behavioural specializations to access and digest gums (Cabana et al., 2017a; Nash,  
54 1986; Smith, 2010). P-linked polysaccharides, such as gums, require specific microbes for  
55 fermentation (Booth and Henderson, 1963; Monke, 1941; Power and Myers, 2009).

56 Mammals that eat gums enable fermentation through having a longer cecum and large  
57 intestine (Chivers and Hladik, 1980; Power and Myers, 2009; Smith, 1982). In addition to  
58 digestive specializations, gummivory is often consistent with postcranial adaptations,  
59 including keeled nails or claws, which allow animals to climb and cling to large tree trunks  
60 and branches for extended periods, reducing the amounts of energy necessary during  
61 gouging (Kubota and Iwamoto, 1966). Across gouging mammals, mandibular variation is  
62 associated with the percentage of gum in a species’ diet (Viguier, 2004). Gougers use  
63 specialized dentition to damage a tree’s bark to elicit gum production and flow (Petter, 1978).  
64 In strepsirrhine primates, this adaptation takes the form of a specialised toothcomb used to  
65 elicit flow of or to scrape gum.

66 Charles-Dominique (1977) proposed that gums were inaccessible to mammals that lacked  
67 claws or modified nails. A number of primates consume gum and lack these features,  
68 including lesser galagos (*Galago senegalensis*) mouse lemurs (*Microcebus* spp.), and the  
69 slow lorises of Asia (*Nycticebus* spp.). Despite lacking claws or modified nails, Nekaris  
70 (2014) noted that *Nycticebus* spp. are “true gougers” characterised by stout mandibles, U-  
71 shaped hind limbs, and camouflaged fur that allow them to specialize on exudates up to  
72 97.5% their feeding time (c.f. Swapna et al., 2010). *Nycticebus* spp. possess a specialised  
73 toothcomb and a reduced last lower molar compared to *Loris* spp. further supporting their

74 distinction as obligatory gougers (Burrows et al. 2015). In order to cling to trees in the  
75 absence of specialized nails or claws, they possess a host of characteristics, including a firm  
76 grip, reduced second digit, and a vascular artery bundle that lowers the temperature of their  
77 limbs called the *retia mirabilia*, enabling them to maintain long-duration static postures  
78 necessary for gouging gum (Ishida et al., 1992; Kingston et al., 2010; Nekaris, 2014).

79 Despite a general lack of research regarding *Nycticebus* ontogeny in the wild, the consensus  
80 is that for an animal of its size, *Nycticebus* has a long gestation period (6 months) and  
81 delayed dispersal (~ 16 months) (Izard et al., 1988; Nekaris, 2014; Zimmermann, 1989). The  
82 period between these developmental milestones is poorly understood and previous reports  
83 on this topic offer varying results on the emergence of key behaviours (Ehrlich and  
84 Macbride, 1989; Fitch-Snyder and Ehrlich, 2003; Rasmussen, 1986; Zimmerman, 1989).  
85 This variation is attributed to variable captive conditions and small samples sizes. In  
86 captivity, infants were first observed consuming solid foods at ~40 days (Zimmerman, 1989)  
87 and in the wild Wiens and Zitzmann (2003) observed the solid feeding behaviour of an eight-  
88 week old infant. In regards to exudates, individuals as young as three months elicit gums  
89 from tree trunks (Nekaris, 2014).

90 Until now, there has been no exploration of either the behavioural repertoire used to access  
91 tree gums or the ontogenetic development of these behaviours. Here, we aim to explore the  
92 mechanisms used by the Javan slow loris to access gum from the juvenile period to  
93 adulthood. We address three research questions: 1) What physical adaptations facilitate the  
94 prolonged vertical postures needed to access tree trunks? 2) Do Javan slow lorises display  
95 any ontogenetic variation in their locomotor behaviour and habitat use during feeding? 3)  
96 What, if any, are the morphometric differences across age classes and do they influence  
97 locomotor behaviour or habitat use? Following these question we hypothesise that young  
98 Javan slow lorises will quickly attain the necessary physical and behavioural competence to  
99 gouge trees, as gum is a key component of their wild diet (Cabana et al., 2017b). In  
100 accordance with this hypothesis, we also predict that there will be little to no difference in  
101 habitat utilization, as defined by their position in tree, and the diameter at breast height  
102 (DBH) of feeding trees.

## 103 **Methods**

### 104 *Study site:*

105 We collected data from April 2012-April 2016 as part of an on-going project in Cipaganti,  
106 West Java, Indonesia (S7°6'6" 7°7' & E107°46' 107°46'5"). The field site lies at the  
107 unprotected base of the mountain Gunung Puntang, which is a part of the Java-Bali Montane

108 Rain Forests ecoregion. The area between the adjacent village and the protected forest is  
109 primarily patches of cultivated land, bamboo, and shrubs. The primary gum-producing tree  
110 species consumed in the area is green wattle (*Acacia decurrens*), with this species  
111 comprising 38-60% of the population's diet and 62-84% of all exudates consumed  
112 depending on the time of year (Cabana et al., 2017b). The area where we conducted nightly  
113 observations encompasses 50 ha with elevations varying between 900-2000 m asl.

114 *Radio collaring, aging, measuring and weighing:*

115 Following a protocol approved by the Animal Ethics Subcommittee at Oxford Brookes  
116 University, experienced team members handled non-anesthetized individuals. The radio  
117 collars (BioTrack, UK) weighed 17 g, which is on average less than 2% of the body weight of  
118 an adult Javan slow loris and less than 4% of an immature Javan slow loris. Using a 2.5 kg  
119 spring (Pesola, Canada) and a clean cloth bag, we weighed individuals either annually or  
120 every three months. Using digital callipers and soft measuring tape, KAI Nekaris measured  
121 the total body length, hand and foot span, upper arm, lower arm, upper leg, lower leg length,  
122 head width, and head length, for each individual (Nekaris and Jaffe, 2007). We assessed  
123 age classes for 58 individuals including 54 of the Javan slow lorises included in our nightly  
124 observations. We determined ages either from observing the animal from birth or using body  
125 size, pelage characteristics, and proximity to mother (Rode-Margono et al., 2014), but are  
126 reaffirmed here using morphometric data, including calculated limb proportion indices  
127 (Intermembral, Humerofemoral, Brachial, and Crural: Fleagle, 2013) and the whole arm and  
128 leg length in relation to total body length. Approximately, infants are less than 12 weeks old,  
129 juveniles are between 12 weeks and 9 months old, sub-adults are between 9 months and 16  
130 months old, and adults are older than 16 months.

131 *Nightly observations:*

132 We engaged in nightly observations over two shifts between 18:00 to 00:00 and 00:00 to  
133 05:00 (Wiens and Zitzmann, 2003), totaling 29,204 observation points for 54 individuals. We  
134 recorded data using instantaneous sampling with 15-minute intervals and *ad libitum* notes  
135 following Altman (1974) and Nekaris (2001). At each sample point we recorded the  
136 behaviour (alert, feed, forage, freeze, groom, rest, sleep, social, travel, other)  
137 locomotor/postural mode (Table 1 and Figure 1), position in tree (central, crown, periphery,  
138 terrestrial, trunk, undergrowth), and DBH (in cm). During each shift we followed one slow  
139 loris, unless other animals were within the vicinity of the collared focal, in which case we  
140 used instantaneous scan sampling. We tracked individuals using an antenna (Yagi, Biotrack,  
141 UK) and receiver (Sika, Biotrack, UK).

142 *Data analyses:*

143 Using SPSS version 22 and R 3.3.3, we calculated the mean and standard deviation of  
144 observed points in each of the above variables. To test for significant differences across the  
145 age classes in locomotor behaviour, habitat utilization, and the morphometric measures we  
146 used the nonparametric Kruskal-Wallis and Mann-Whitney U test with significance set at  $p <$   
147 0.05. We applied the Bonferroni correction to the post-hoc comparisons following significant  
148 results from the Kruskal-Wallis test, changing significance to  $p < 0.016$ . We used a  
149 Canonical variate analysis (CVA) to identify the morphometric variables that are most  
150 different between the age classes (Dytham, 2011). We ran four General Linear Models  
151 (GLM), in which we individually tested the proportion of time spent engaging in locomotor  
152 modes Vertical Suspension 3 Up/Down and Vertical Suspension 4 Up/Down as response  
153 variables. In each model, we tested eight morphometric measures as covariates. A test of  
154 multicollinearity using Spearman's rho test of the eight morphometric measures produced no  
155 collinearity coefficients greater than 0.90 (Field, 2013). Each response variable underwent a  
156  $\log_{10}$  transformation for normality. To look at the differential growth patterns of the reported  
157 morphometric measures, we calculated the allometry coefficient (slope) using least-square  
158 (LS) regression for each log transformed measure against the log-transformed body weight  
159 (Lawler, 2006).

## 160 **Results**

161 *Vertical gouging posture:*

162 While feeding and foraging specifically on tree trunks, Javan slow lorises of all age classes  
163 used either an upward or downward facing vertical posture. Animals had either three or four  
164 limbs in contact with the substrate, while feeding but we never observed them on tree trunks  
165 with only two limbs in contact with the substrate. When gripping the substrate, slow lorises  
166 pressed their distal phalanges into the surface of the substrate; the joint between the midline  
167 and proximal phalanges was bent. The pollex was perpendicular to the other digits and is  
168 similarly pressed into the surface. Both feet were used in a reversed position, where the  
169 hallux was adducted along the substrate, while the other four digits were parallel to one  
170 another. On larger substrates, arms were fully extended, but on smaller trunks, arms may be  
171 flexed at the elbow. The hind limbs were flexed and depending on the size of the substrate  
172 we observed varying degrees of abduction, as they wrapped around the substrate. Together  
173 with the reversed foot position, the flexed and abducted hind limb created a U-shaped  
174 appearance (Figure 2).

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176

177 *Locomotor behaviour during feeding:*

178 During all feeding bouts including those involving non-gum items the Javan slow loris  
179 displayed a wide range of locomotor and postural modes in equal measure across all three-  
180 age classes (Table 1). Vertical suspension 2 ( $H= 14.1$ ,  $df= 2$ ,  $p= 0.001$ ) and horizontal  
181 suspension 3 ( $H= 11.31$ ,  $df= 2$ ,  $p= 0.003$ ) were the only postures that statistically differed,  
182 where juveniles and sub-adults display these postures less than adults or not at all. In  
183 juveniles three postures in particular made up 57.6% of their repertoire, stand (20.7%),  
184 vertical suspension 4 up (15.6%), and vertical suspension 4 down (15.8%) The most used  
185 postural modes used in sub-adults were both vertical suspension 4 up ( $24.8 \pm 4.2$  %) and  
186 down ( $16.8 \pm 13.7$  %). Vertical suspension 3 up and down was rarely observed in adults and  
187 sub-adults (adults:  $1.3 \pm 1.0$  % sub-adults:  $3.9 \pm 0.8$  %) and was absent in juveniles. The  
188 locomotor modes employed across all behaviours show statistically significant differences in  
189 more modes compared to the locomotor behaviours during feeding alone (Table 1). These  
190 differences appear in walk ( $H = 9.09$ ,  $df = 2$ ,  $p = 0.011$ ), bridge ( $H = 19.83$ ,  $df = 2$ ,  $p = 0.001$ ),  
191 vertical suspension 2 ( $H = 17.34$ ,  $df = 2$ ,  $p < 0.0001$ ), and horizontal suspension 3 ( $H = 26.05$ ,  
192  $df = 2$ ,  $p < 0.0001$ )

193

194 *Habitat utilization during feeding:*

195 Table 2 presents the mean and standard deviation for each tree position variable in adults,  
196 sub-adults, and juvenile Javan slow lorises. None of the measured variables while feeding  
197 provided any significant differences. We observed the following trends in the age specific  
198 distribution of tree and environment locations during feeding; in adults feeding took place at  
199 the centre of the tree canopy ( $30.7 \pm 17.5$  %), the crown ( $17.9 \pm 20.9$ ), trunk ( $17.4 \pm 11.4$  %),  
200 and periphery ( $17.1 \pm 9.7$  %), with the remaining locations used less than 1% of the time.  
201 Juveniles spent most of their time in the periphery ( $32.5 \pm 22.1$  %), then the centre ( $32.0 \pm$   
202  $16.7$  %) and finally the trunk ( $21.7 \pm 14.1$  %). We found no significant difference in the mean  
203 DBH of the trees used by adults ( $38.0 \pm 16.9$  cm), sub-adults ( $34.9 \pm 14.0$  cm), and  
204 juveniles ( $37.6 \pm 16.7$  cm).

205 *Morphometric measures:*

206 We observed significant differences in five measures, body mass ( $H = 38.3$ ,  $df = 2$ ,  $p <$   
207  $0.0001$ ), total body length ( $H = 9.2$ ,  $df = 2$ ,  $p = 0.010$ ), head length ( $H = 8.8$ ,  $df = 2$ ,  $p = 0.012$ ),  
208 upper arm length ( $H = 8.6$ ,  $df = 2$ ,  $p = 0.013$ ), and lower arm length ( $H = 11.0$ ,  $df = 2$ ,  $p <$

0.0001) Table 3 displays the mean, N number of measurements, and standard deviation for each morphometric measure for each age class. The juveniles had the smallest mean body mass ( $609.7.6 \pm 121.4$  g), followed by the sub-adults ( $819.39 \pm 38.5$  g), then adults ( $907.2 \pm 72$  g). In contrast to the upper and lower arm lengths, which were lower in juveniles, the upper and lower leg lengths showed very little difference across and within age classes. Head length, head width, hand span, foot span, the proportional indices, both arm/body length and hindlimb/body length (Figure 3) showed no substantial variations. The two canonical axes identified by the Canonical discriminant analysis (CVA) accounted for 89.2% and 10.8% of age class variation (Wilk's  $\lambda = 0.235$ ,  $p < 0.0001$ ) (Figure 4). Body weight contributed the main discrimination along the first axis and total body length was the second. Overall, age classes were correctly classified 90% of the time, 95.6% for Adults, 50% for Sub-adults, 100% for Juveniles. The results of the GLMs showed that none of the morphometric measures had predictive power for the response variables, proportion of time spent in vertical suspension 4 up/down or vertical suspension 3 up/down. The growth allometries provided by LS regression for head length, head width, hand span, foot span, upper arm, lower arm, upper leg and lower leg are presented in Figure 5. Footspan (0.03), handspan (0.07), and upper leg (0.06) had the lowest coefficients; upper arm (0.23), lower leg (0.18), and head length (0.17) were the highest.

227

228

## 229 **Discussion**

230 We observed that Javan slow lorises rely on their hand, foot, and limb morphology in place  
231 of specialized nails or claws to maintain vertical postures on large tree trunks. In relation to  
232 this important feeding adaptation, young animals obtain adult body proportions and gain  
233 locomotor and postural competence by three months of age. Some variables such as arm  
234 measures scaled isometrically, while leg, hand, and feet measures scaled allometrically and  
235 thus were relatively larger in juveniles. The age classes showed little difference in habitat  
236 utilization, and the general morphometric measures were not determinants of the proportion  
237 of vertical postural modes. Feeding on gums and exudates in slow lorises is reflected to  
238 some extent in their pelage, life history, mandible morphology, and social behaviour (Nekaris  
239 et al., 2010). In conjunction with all of the physiological, morphological, and behavioural  
240 adaptations that facilitate gouging and exudate consumption in Javan slow lorises, data  
241 presented here suggest an ontogenetic adaptation as well.

242 *Vertical gouging posture:*

243 **Javan slow lorises** across all age classes used their hands, feet, and limbs to maintain  
244 vertical postures on large tree trunks. Mammals that lack specializations like claws or suction  
245 cups such as Javan slow lorises can only grasp large vertical substrates if they can exert  
246 enough force on the surface through adducting limbs inwards (Cartmill, 1979). To thwart  
247 gravity these animals must rely on a static friction grip, which is maintained through the  
248 interaction of their volar pads, the substrate surface, and the normal component of frictional  
249 force created from pressing against the substrate (Johnson, 2015). Considered unique  
250 among primates for their locomotor and physical characteristics (Ishida et al., 1992; Sellers,  
251 1996), Javan slow lorises may also use aspects of these features to create the needed force  
252 to uphold vertical postures on tree trunks; to confirm this notion further studies on the force  
253 of the *Nycticebus* grip in a controlled setting is required.

254 Although we did not record specific grasping behaviours in this study, it is clear during our  
255 live observations and through photos that as stated by Gebo (1985) *Nycticebus* spp. use a I-  
256 V grasp, while engaging with substrates, which uses the flexing force of the hallux to oppose  
257 the flexing force of the four laterally placed digits. Gebo (2011) later revisited vertical clinging  
258 and leaping, detailing the morphological features present in strepsirrhines that inherently  
259 facilitate access to vertical substrates, noting that strepsirrhines evolved modified upper  
260 ankle joints to improve foot abduction and lateral rotation, which ultimately improves their  
261 ability to utilize vertical substrates. Though Gebo (2011) stated that only indriids, lepilemurs,  
262 galagos, and to some extent gentle lemurs, could be considered vertical clingers; Javan slow  
263 lorises, generally regarded only as a slow climber, possess many of the same morphological  
264 modifications as vertical clingers. **Our data** showed that vertically clinging is one of their most  
265 common postures in the wild.

#### 266 *Locomotor behaviour and habitat utilization during feeding:*

267 While feeding, Javan slow lorises display adult-like locomotor and postural competence  
268 during development, only displaying two significantly different locomotor modes among  
269 adults, sub-adults, and juveniles. The increased number of significant differences seen  
270 across all behaviours contrasts the low level of difference seen during feeding, highlighting  
271 the importance of locomotor and postural competence to access certain food resources.  
272 Knowing that gums elicited from trees can make up as much as 97.5% of the *Nycticebus*  
273 feeding time (Swapna et al., 2010), it is not surprising that juveniles and adults use tree  
274 trunks in equal measure during feeding bouts. Typically used on smaller sized trunks and  
275 branches while individuals begin to bridge from one substrate to the next, Vertical  
276 Suspension 2 is virtually unobserved in juveniles. Bridging, which is associated with Vertical  
277 Suspension 2 requires individuals to maintain their balance and quickly re-establish stability



278 once they cross a gap (Ishida et al. 1992). Horizontal Suspension 3 again is a rarely seen  
279 mode, but is associated with grabbing insects during Suspensory Walk and is typically  
280 classified as Suspensory Walk instead of Horizontal Suspension 3, because it can be difficult  
281 to see the fast moving hand of slow lorises while they grasp insects in the wild (Streicher et  
282 al. 2012).

283 In contrast, the ontogenetic differences seen in locomotor modes across all behaviours  
284 suggest that indeed there are some physical or behavioural differences that prevent juvenile  
285 Javan slow lorises from fully mirroring adults within the same environment. Researchers  
286 working on ontogeny and positional behaviour, cite exploratory behaviour, changing  
287 musculoskeletal systems and varying environmental pressures as explanations for  
288 significant differences in locomotor behaviour between juveniles and adults (Workman and  
289 Covert 2005; Bezanson 2009; Dunham 2015). The morphometric scaling reported in this  
290 study highlights how vertical clinging and gum feeding are essential aspects of Javan slow  
291 loris survival and allows juveniles to access tree trunks the way adults do.

292

#### 293 *Morphometric measures:*

294 The basic morphometric differences among adult, sub-adult, and juvenile Javan slow lorises  
295 were limited to their body mass, total body length, arm length, and head length. The mean  
296 body mass in juveniles was almost two-thirds of the mean in adults, with sub-adults nearly  
297 100 g less than the adults. Within juveniles we found a wide range of variation, **evident in the**  
298 high standard deviation. The ontogenetic difference in body mass, which is a proposed  
299 influential factor for locomotion and substrate selection (Fleagle and Mittermeier 1980;  
300 Hurov, 1991), did not have an effect on the observed individuals' ability to secure necessary  
301 resources successfully. These data further support the assertion by Preushoft et al. (1998)  
302 that strepsirrhines and tarsiers show no apparent correlation between body size and  
303 preferred locomotor mode, due to their limited absolute body size variation.

304 Similar to previous studies on young mammal individuals compared to adult conspecifics,  
305 young Javan slow lorises had a hand and foot span comparable to both adults and sub-  
306 adults, while maintaining a relatively smaller body size. This relationship is a mechanism to  
307 improve stability in arboreal environments (Jungers and Fleagle, 1980; Lammers and  
308 German, 2002; Young, 2009); we also note that both hands and feet are key proponents in  
309 vertical clinging. As we predicted, young Javan slow lorises quickly attain the necessary  
310 physical and behavioural competence to vertically cling and gouge trees. These findings are  
311 supported by the fact that Javan slow lorises possess what Martin (1975) believed to be a

312 vital gouging tool, their toothcomb, at a young age. Reports on slow loris dental eruption  
313 vary, where some report that they are either born with a full set of teeth (Pournelle, 1955),  
314 complete their adult dentition as early as a six months (Smith et al., 1994), or no later than  
315 nine months (Hill, 1937). Martin (1975) thought that access to gums was the main  
316 evolutionary purpose of the toothcomb and that grooming developed secondarily. To  
317 reinforce these findings we would need to look at the ontogenetic trajectory in a broader  
318 phylogenetic context, comparing various primate species.

319 Focused on the results presented here we suggest that more primates could be adapted to  
320 utilize rapid growth to reduce infant vulnerability. This notion is supported by the rapid  
321 physical competence during feeding observed in this study, and suggestions from other  
322 researchers of dissociation among life history traits, including body mass, brain size, age of  
323 maturation, and ontogenetic positional patterns (Bezanson, 2009; Godfrey et al., 2001;  
324 Leigh, 2004; Pereira and Leigh, 2003). Acquiring adult-like physical features and behaviours  
325 is present in other animals that share the same behavioural and physiological traits as Javan  
326 slow lorises, including nocturnality (*Aotus*), low basal metabolic rate (*Tarsius*), slow  
327 quadrupedal climbing (*Choloepus*) and neonate parking (*Varecia*) (Dixson and Fleming,  
328 1981; Pereira, 1987; Roberts, 1994; Veselovsky, 1966). Leigh (1994) found that compared  
329 to frugivorous anthropoids, folivorous anthropoids attained adult body size at an earlier age.  
330 She suggested a number of factors that would lead to this difference, focusing on diet type  
331 and the varying risks each group faces to retrieve food resources. Like foliage, exudates are  
332 considered to be a more stable food resource compared to fruits, which may account for the  
333 ontogenetic similarity between folivorous anthropoids, pilosans and Javan slow lorises. In  
334 primates, the influence of ontogeny on locomotor behaviour and habitat utilization varies  
335 from species to species. Despite differences in body size and age, a number of primate  
336 species employ various locomotor and postural modes in equal measure (Lawler 2006;  
337 Bezanson 2009; Doran 1992, 1997; Thrope and Crompton 2005; Zhu et al., 2014; Wells and  
338 Turnquist 2001).

339

340 We have yet to understand the origin and potential impact that tree gouging and gum  
341 feeding may have had on the development and evolution of *Nycticebus* species. Burrows et  
342 al. (2015) noted that it is unlikely that tree-gouging existed in the last common ancestor of  
343 Lorisiformes, but that it evolved multiple times following the split of Lorisidae and Galagidae.  
344 If exudativory evolved independently multiple times, the varying adaptations seen in how  
345 species elicit gums or access tree trunks is representative of their individual lineages and the  
346 specific environmental pressures at the time exudativory emerged. As a non-leaping and

347 cryptic primate, Javan slow lorises have seemingly modified their limb, hand, and foot  
348 morphologies to facilitate access to vertical substrates. Having highlighted the importance of  
349 physical competence to access gums, Javan slow lorises may limit the period of time where  
350 these specializations are out of reach, to increase the likelihood that offspring reach sexual  
351 maturity, surpassing the “juvenile bottleneck”.

352 In the present study we focused on the gum feeding diet of Javan slow lorises and the  
353 potential ontogenetic adaptations used to facilitate it, but this case only exemplifies the  
354 complex relationship between feeding ecology and the specialized adaptations that evolved  
355 to enable it. Across all mammal species, unique adaptations emerge to increase the  
356 likelihood of survival, including reducing predation risks or maternal energetic expenditure.  
357 Gaining adult-like body proportions is yet another of many strategies used to achieve this  
358 goal.

359

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## 375 **References**

- 376 Altmann, J., 1974. Observational study of behavior: sampling methods. *Behav.* 49, 227-266.  
377 doi: 10.1163/156853974X00534
- 378 Bearder, S.K., Martin, R.D., 1980. Acacia gum and its use by bushbabies, *Galago*  
379 *senegalensis* (Primates: Lorisidae). *Int. J. Primatol.* 1, 103-128. doi:10.1007/BF02735592

380 Bezanson, M., 2009. Life history and locomotion in *Cebus capucinus* and *Alouatta palliata*.  
381 Am. J. Phys. Anthropol. 140, 508-517. doi: 10.1002/ajpa.21099

382 Booth, A.N., Henderson, A.P., 1963. Physiologic effects of three microbial polysaccharides  
383 on rats. Toxicol. Appl. Pharmacol. 5, 478-484. doi: 10.1016/0041-008X(63)90019-X

384 Burrows, A.M., Hartstone-Rose, A., Nash, L.T., 2015. Exudativory in the Asian loris,  
385 *Nycticebus*: Evolutionary divergence in the toothcomb and M3. Am. J. Phys. Anthropol. 158,  
386 663-672. doi: 10.1002/ajpa.22829

387 Cabana, F., Dierenfeld, E., Donati, G., Nekaris, K. A. I., 2017a. Exploiting a readily available  
388 but hard to digest resource: A review of exudativorous mammals identified thus far and how  
389 they cope in captivity. J. Integr. Zool.

390 Cabana, F., Dierenfeld, E., Wirdateti, W., Donati, G. and Nekaris, K.A.I., 2017b. The  
391 seasonal feeding ecology of the javan slow loris (*nycticebus javanicus*). Am. J. Phys.  
392 Anthropol., 162, 768-781. doi:10.1002/ajpa.23168

393 Cartmill, M., 1979. The volar skin of primates: its frictional characteristics and their functional  
394 significance. Am. J. Phys. Anthropol. 50, 497-509. doi: 10.1002/ajpa.1330500402

395 Cartmill, M., 1985. Climbing, in: Hildebrand, M., Bramble, D.M., Liem, K.F., Wake, D.B.  
396 (Eds.), Functional vertebrate morphology. Harvard University Press, Cambridge, pp. 73-88.

397 Case, T. J., 1978. On the evolution and adaptive significance of postnatal growth rates in  
398 terrestrial vertebrates. Q. Rev. of Biol. 53, 243–282. doi: 10.1086/410622

399 Charles-Dominique, P., 1977. Ecology and behaviour of nocturnal prosimians. London:  
400 Duckworth.

401 Chivers, D.J., Hladik C.M., 1980. Morphology of the gastrointestinal tract in primates:  
402 comparisons with other mammals in relation to diet. J. Morphol. 166, 337–386. doi:  
403 10.1002/jmor.1051660306

404 Das, N., Nekaris, K. A.I., Bhattacharjee, P., 2014. Medicinal plant exudativory by the Bengal  
405 slow loris *Nycticebus bengalensis*. Endanger Species Res. 23, 149-157. doi:  
406 10.3354/esr00560

407 De Muizon, C., Lange-Badré, B., 1997. Carnivorous dental adaptations in tribosphenic  
408 mammals and phylogenetic reconstruction. Lethaia, 30, 353-366. doi: 10.1111/j.1502-  
409 3931.1997.tb00481.x

410 Dierenfeld, E.S., Hintz, H.F., Robertson, J.B., Van Soest, P.J., Oftedal, O.T., 1982.  
411 Utilization of Bamboo by the Giant Panda. J. Nutr. 112, 636-641.

412 Dixson, A., Fleming, D., 1981. Parental behaviour and infant development in owl monkeys  
413 (*Aotus trivirgatus griseimembra*). J. Zool. 194, 25-39. doi: 10.1111/j.1469-  
414 7998.1981.tb04576.x

415 Doran, D.M., 1992. The ontogeny of chimpanzee and pygmy chimpanzee locomotor  
416 behavior: a case study of pedomorphism and its behavioral correlates. J. Hum. Evo., 23,  
417 139-157. doi: 10.1016/0047-2484(92)90104-H

- 418 Doran, D.M., 1997. Ontogeny of locomotion in mountain gorillas and chimpanzees. *J.Hum.*  
419 *Evo.*, 32, 323-344. doi: 10.1006/jhev.1996.0095
- 420 Dunham, N.T., 2015. Ontogeny of positional behavior and support use among *Colobus*  
421 *angolensis palliatus* of the Diani Forest, Kenya. *Primates*, 56, 183-192. doi:10.1007/s10329-  
422 015-0457-3
- 423 Dytham, C., 2011. Choosing and using statistics: a biologist's guide. John Wiley & Sons,  
424 West Sussex, pp.251-254.
- 425 Ehrlich, A. and Macbride, L., 1989. Mother-infant interactions in captive slow lorises  
426 (*Nycticebus coucang*). *Am. J. Primatol.*, 19, 217-228. doi; 10.1002/ajp.1350190404
- 427 Ercoli, M.D, Youlatos, D., 2016. Integrating locomotion, postures and morphology: The case  
428 of the tayra, *Eira barbara* (Carnivora, Mustelidae). *Mamm. Biol.* 81, 464-476. doi:  
429 10.1016/j.mambio.2016.06.002
- 430 Field, A., 2013. Discovering statistics using SPSS, fourth ed. Sage, London  
431
- 432 Fitch-Snyder, H. and Ehrlich, A., 2003. Mother-infant interactions in slow lorises (*Nycticebus*  
433 *bengalensis*) and pygmy lorises (*Nycticebus pygmaeus*). *Folia Primatol*, 74, 259-271. doi:  
434 10.1159/000073313
- 435 Fleagle, J.G., 2013. Primate adaptation and evolution, third ed. Academic Press, San Diego.
- 436 Fleagle, J.G., Mittermeier, R.A., 1980. Locomotor behavior, body size, and comparative  
437 ecology of seven Surinam monkeys. *Am. J. Phys. Anthropol.* 52, 301-314. doi:  
438 10.1002/ajpa.1330520302
- 439 Gebo, D. L., 1985. The nature of the primate grasping foot. *Am. J. Phys. Anthropol.* 67, 269 -  
440 278.
- 441 Gebo, D.L., 2011. Vertical clinging and leaping revisited: vertical support use as the  
442 ancestral condition of strepsirrhine primates. *Am. J. Phys. Anthropol.* 146, 323-335. doi:  
443 10.1002/ajpa.21595
- 444 Godfrey L.R., Samonds, K.E., Jungers, W.L., Sutherland, M.R., 2001. Teeth, brains, and  
445 primate life histories. *Am. J. Phys. Anthropol.* 114, 192–214. doi: 10.1002/1096-  
446 8644(200103)114:3<192::AID-AJPA1020>3.0.CO;2-Q
- 447 Godfrey, L.R., Samonds, K.E., Jungers, W.L., Sutherland, M.R., Irwin, M.T., 2004.  
448 Ontogenetic correlates of diet in Malagasy lemurs. *Am. J. Phys. Anthropol.* 123, 250-276.  
449 doi: 10.1002/ajpa.10315
- 450 Hill, W.C.O., 1937. On the breeding and rearing of certain species of primates in captivity.  
451 *Ceylon J. Sci. B. Zool.* 20, 369-389.
- 452 Hurov, J.R., 1991. Rethinking Primate Locomotion: What can we Learn from Development.  
453 *J. Motor. Behav.* 23, 211-218. doi: 10.1080/00222895.1991.10118364

- 454 Irlbeck, N.A., Hume, I.D., 2003. The role of acacia in the diets of Australian marsupials - a  
455 review. *Aust. Mammal.* 25, 121-134.
- 456 Izard, M.K., Weisenseel, K.A. and Ange, R.L., 1988. Reproduction in the slow loris  
457 (*Nycticebus coucang*). *Am. J. Primatol.*, 16, 331-339. doi: 10.1002/ajp.1350160405
- 458 Ishida H. Hirasaki E. Matano S., 1992. Locomotion of the slow loris between discontinuous  
459 substrates. in: Matano, S., Tuttle, R. H., Ishida, H., Goodman, M., (Eds.), *Topics in*  
460 *primatology*. Vol. 3. *Evolutionary Biology, Reproductive Endocrinology, and Virology*,  
461 University of Tokyo Press, Tokyo, Japan, pp. 139–152.
- 462 Johnson, L.E., Hanna, J., Schmitt, D., 2015. Single-limb force data for two lemur species  
463 while vertically clinging. *Am. J. Phys. Anthropol.* 158, 463-474. doi: 10.1002/ajpa.22803
- 464 Jungers W.L., Fleagle, J.G., 1980. Postnatal growth allometry of the extremities in *Cebus*  
465 *albifrons* and *Cebus apella*: a longitudinal and comparative study. *Am. J. Phys. Anthropol.*  
466 53, 471-478. doi: 10.1002/ajpa.1330530403
- 467 Kingston, A.K., Boyer, D.M., Patel, B.A., Larson, S.G., Stern, J.T., 2010. Hallucal grasping in  
468 *Nycticebus coucang*: further implications for the functional significance of a large peroneal  
469 process. *J. Hum. Evol.* 58, 33-42. doi: 10.1016/j.jhevol.2009.08.002
- 470 Koyabu, D.B., Oshida, T., Dang, N.X., Can, D.N., Kimura, J., Sasaki, M., Motokawa, M.,  
471 Son, N.T., Hayashida, A., Shintaku, Y., Endo, H., 2009. Craniodental mechanics and the  
472 feeding ecology of two sympatric callosciurine squirrels in Vietnam. *J. Zool.* 279, 372-380.  
473 doi: 10.1111/j.1469-7998.2009.00629.x
- 474 Kubota, K., Iwamoto, M., 1966. Comparative anatomical and neurohistological observations  
475 on the tongue of slow loris (*Nycticebus coucang*). *Anat. Rec.* 158, 163-176. doi:  
476 10.1002/ar.1091580206
- 477 Lammers, A.R., German, R.Z., 2002. Ontogenetic allometry in the locomotor skeleton of  
478 specialized half-bounding mammals. *J. Zool.* 258, 485-495. doi:  
479 10.1017/S0952836902001644
- 480 Lawler, R.R., 2006. Sifaka positional behavior: ontogenetic and quantitative genetic  
481 approaches. *Am. J. Phys. Anthropol.*, 131, 261-271. doi: 10.1002/ajpa.20430
- 482 Leigh, S.R., 1994. Ontogenetic correlates of diet in anthropoid primates. *Am. J. Phys.*  
483 *Anthropol.* 94, 499-522. doi: 10.1002/ajpa.1330940406
- 484 Leigh, S.R., 2004. Brain growth, life history, and cognition in primate and human evolution.  
485 *Am. J. Primatol.* 62, 139–164. doi: 10.1002/ajp.20012
- 486 Ley, R.E., Hamady, M., Lozupone, C., Turnbaugh, P.J., Ramey, R.R., Bircher, J.S.,  
487 Schlegel, M.L., Tucker, T.A., Schrenzel, M.D., Knight, R., Gordon, J.I., 2008. Evolution of  
488 mammals and their gut microbes. *Science*, 320, 1647-1651. doi: 10.1126/science.1155725
- 489 Martin, R.D., 1975. The bearing of reproductive behaviour and ontogeny on strepsirhine  
490 phylogeny, in: Lockett, W.P., Szalay, F.S. (Ed.), *Phylogeny of the Primates*. Springer, US,  
491 pp. 265-297. doi: 10.1007/978-1-4684-2166-8\_12

492 McGraw, W.S., Sciulli, P.W., 2011. Posture, ischial tuberosities, and tree zone use in West  
493 African cercopithecids. In: D'Aout, K., Vereecke, E.E. (Eds.), Primate Locomotion. Springer,  
494 New York, pp. 215-245. doi: 10.1007/978-1-4419-1420-0\_12

495 Monke J.V., 1941. Non-availability of gum arable as a glycogenic foodstuff in the rat. Proc.  
496 Soc. Exp. Biol. Med. 46, 178-179.

497 Napier, J.R., Napier, P.H., 1967. A handbook of living primates. Academic Press,  
498 Cambridge.

499 Naples, V.L., 1999. Morphology, evolution and function of feeding in the giant anteater  
500 (*Myrmecophaga tridactyla*). J. Zool. 249, 19-41. doi: 10.1111/j.1469-7998.1999.tb01057.x

501 Nash, L.T., 1986. Dietary, behavioural, and morphological aspects of gummivory in primates.  
502 Yearb. Phys. Anthropol. 29, 113-137. doi: 10.1002/ajpa.1330290505

503 Nekaris, K., 2001. Activity budget and positional behaviour of the Mysore slender loris (*Loris*  
504 *tardigradus lydekkerianus*): implications for slow climbing locomotion. Folia Primatol. 72,  
505 228-241. doi:10.1159/000049942

506 Nekaris, K.A.I., 2014. Extreme primates: Ecology and evolution of Asian lorises. Evol.  
507 Anthropol. 23, 177-187. doi:10.1002/evan.21425

508 Nekaris K.A.I, Jaffe, S., 2007. Unexpected diversity of slow lorises (*Nycticebus* spp.) within  
509 the Javan pet trade: implications for slow loris taxonomy. Contrib. Zool. 76, 187-196.

510 Nekaris, K.A.I., Starr, C.R., Collins, R.L. and Wilson, A., 2010. Comparative ecology of  
511 exudate feeding by lorises (*Nycticebus*, *Loris*) and pottos (*Perodicticus*, *Arctocebus*), in:  
512 Burrows, A.M., Nash, L.T. (Eds.), The Evolution of Exudativory in Primates. Springer, New  
513 York, pp. 155-168. doi: 10.1007/978-1-4419-6661-2\_8

514 Pereira, M.E., Klepper, A., Simons, E.L., 1987. Tactics of care for young infants by forest-  
515 living ruffed lemurs (*Varecia variegata variegata*): Ground nests, parking, and biparental  
516 guarding. Am. J. Primatol. 13, 129-144. doi: 10.1002/ajp.1350130204

517 Petter, J.J., 1978. Ecological and physiological adaptations of five sympatric nocturnal  
518 lemurs to seasonal variations in food production. Recent Adv. Primatol. 1, 211-223.

519 Pournelle, G.H., 1955. The bashful clown. Zoonooz 28, 23-25.

520 Power, M.L., Myers, E.W., 2009. Digestion in the common marmoset (*Callithrix jacchus*), a  
521 gummivore–frugivore. Am. J. Primatol. 71, 957-963. doi: 10.1002/ajp.20737

522 Preuschoft, H., Günther, M., Christian, A., 1998. Size dependence in prosimian locomotion  
523 and its implications for the distribution of body mass. Folia Primatol. 69, 60-81.  
524 doi:10.1159/000052699

525 Prost, J.H., 1965. A definitional system for the classification of primate locomotion. Am.  
526 Anthropol. 67, 1198-1214. doi: 10.1525/aa.1965.67.5.02a00060

527 Rasmussen, D. T., 1986. Life history and behavior of slow loris and slender loris:  
528 implications/or the LorisineGalagine divergence. Unpublished Ph. D. thesis, Duke University,  
529 Durham.

530 Ravosa, M.J., Daniel, A.N., Costley, D.B., 2010. Allometry and evolution in the galago  
531 skull. *Folia Primatol.* 81,177-196. doi: 10.1159/000317737

532 Roberts, M., 1994. Growth, development, and parental care in the western tarsier (*Tarsius*  
533 *bancanus*) in captivity: Evidence for a “slow” life-history and nonmonogamous mating  
534 system. *Inter. J. Primatol.* 15, 1-28. doi: 10.1007/BF02735232

535 Rode-Margono, E.J., Nijman, V., Wirdateti, N.K., 2014. Ethology of the critically endangered  
536 Javan slow loris *Nycticebus javanicus* E Geoffroy Saint-Hilaire in West Java. *Asian Primates*  
537 4, 27-41.

538 Rubin, C., Xu, G., Judex, S., 2001. The anabolic activity of bone tissue, suppressed by  
539 disuse, is normalized by brief exposure to extremely low-magnitude mechanical stimuli.  
540 *FASEB J.* 15, 2225-2229. doi: 10.1096/fj.01-0166com

541 Rubin, C., Turner, A.S., Müller, R., Mittra, E., McLeod, K., Lin, W., Qin, Y.X., 2002. Quantity  
542 and quality of trabecular bone in the femur are enhanced by a strongly anabolic, noninvasive  
543 mechanical intervention. *J. Bone Miner Res.* 17, 349-357. doi: 10.1359/jbmr.2002.17.2.349

544 Russell, J.B., Wilson, D.B., 1996. Why are ruminal cellulolytic bacteria unable to digest  
545 cellulose at low pH? *J. Dairy Sci.* 79, 1503-1509. doi: 10.3168/jds.S0022-0302(96)76510-4

546 Schuppli, C., Forss, S.I., Meulman, E.J., Zweifel, N., Lee, K.C., Rukmana, E., Vogel, E.R.,  
547 van Noordwijk, M.A. and van Schaik, C.P., 2016. Development of foraging skills in two  
548 orangutan populations: needing to learn or needing to grow?. *Front. Zool.*,13, 43.  
549 doi:10.1186/s12983-016-0178-5

550 Sellers, W.I., 1996. A biomechanical investigation into the absence of leaping in the  
551 locomotor repertoire of the slender loris (*Loris tardigradus*) *Folia Primatol.* 67, 1-14.  
552 doi:10.1159/000157202

553 Smith, A.C., 2010. Exudatory in primates: interspecific patterns,in: *The evolution of*  
554 *exudatory in primates*, Springer: New York. pp. 45-87

555 Smith, A.P., 1982. Diet and feeding strategies of the marsupial sugar glider in temperate  
556 Australia. *J. Anim. Ecol.* 51, 149-166. doi: 10.2307/4316

557 Smith, B. H., Crummett, T.L., Brandt, K.L., 1994. Ages of eruption of primate teeth: a  
558 compendium for aging individuals and comparing life histories. *Am. J. Phys. Anthropol.* 37,  
559 177-231. doi: 10.1002/ajpa.1330370608

560 Stevenson, M.F., Rylands, A.B., 1988. The marmosets, genus *Callithrix*, in: Mittermeier,  
561 R.A., Rylands, A.B., Coimbra-Filho, A.F., da Fonseca, G.A.B. (Eds.), *Ecology and behaviour*  
562 *of neotropical primates*, Vol. 2. World Wildlife Fund, Washington, DC, pp. 131–222.

563



- 564 Streicher, U., Wilson, A., Collins, R.L. and Nekaris, K.A.I., 2012. Exudates and Animal Prey  
565 Characterize Slow Loris (*Nycticebus pygmaeus*, *N. coucang* and *N. javanicus*) Diet in  
566 Captivity and After Release into the Wild, in: Masters, J., Marco Gamba, M., Génin, F.(Eds),  
567 Leaping Ahead. Springer, New York, pp. 165-172
- 568 Swapna, N., Radhakrishna, S., Gupta, A.K., Kumar, A., 2010. Exudatory in the Bengal  
569 slow loris (*Nycticebus bengalensis*) in Trishna Wildlife Sanctuary, Tripura, northeast  
570 India. Am. J. Primatol. 72, 113-121.  
571
- 572 Tan, C.L., 1999. Group composition, home range size, and diet of three sympatric bamboo  
573 lemur species (genus *Haplemur*) in Ranomafana National Park, Madagascar. Int. J.  
574 Primatol. 20, 547-566. doi: 10.1023/A:1020390723639
- 575 Thorpe, S.K. and Crompton, R.H., 2006. Orangutan positional behavior and the nature of  
576 arboreal locomotion in Hominoidea. Am. J. Phys. Anthropol., 131,384-401.  
577 doi:10.1002/ajpa.20422
- 578 Veselousky, Z., 1966. A contribution to the knowledge of the reproduction and growth of the  
579 two-toed sloth *Choloepus didactylus* at prague zoo. Int. Zoo Yearb., 6, 147-153. doi:  
580 10.1111/j.1748-1090.1966.tb01732.x
- 581 Viguier, B., 2004. Functional adaptations in the craniofacial morphology of Malagasy  
582 primates: shape variations associated with gummivory in the family Cheirogaleidae. Annals  
583 of Anatomy-Anatomischer Anzeiger, 186, 495-501. doi:10.1016/S0940-9602(04)80093-1
- 584 Wells, J.P. and Turnquist, J.E., 2001. Ontogeny of locomotion in rhesus macaques (*Macaca*  
585 *mulatta*): II. Postural and locomotor behavior and habitat use in a free-ranging colony. Am. J.  
586 Phys. Anthropol., 115, 80-94. doi:10.1002/ajpa.1059
- 587 Wiens, F., Zitzmann, A., 2003. Social dependence of infant slow lorises to learn diet. Inter. J.  
588 Primatol. 24, 1007-1021. doi: 10.1023/A:1026272127727
- 589 Williams, G.C., 1966. Adaptation and natural selection: A critique of some current  
590 evolutionary thought. Princeton University Press, NJ.
- 591 Workman, C. and Covert, H.H., 2005. Learning the ropes: The ontogeny of locomotion in  
592 red-shanked douc (*Pygathrix nemaeus*), Delacour's (*Trachypithecus delacouri*), and Hatinh  
593 langurs (*Trachypithecus hatinhensis*) I. positional behavior. Am. J. Phys. Anthropol.,  
594 128,371-380. doi: 10.1002/ajpa.20205
- 595 Young, J.W., 2009. Ontogeny of joint mechanics in squirrel monkeys (*Saimiri boliviensis*):  
596 functional implications for mammalian limb growth and locomotor development. J. Exp. Biol.  
597 212, 576-1591. doi: 10.1242/jeb.025460
- 598 Zimmermann, E., 1989. Reproduction, physical growth and behavioral development in slow  
599 loris (*Nycticebus coucang*, Lorisidae). Hum. Evol., 4, 171-179. doi:10.1007/BF02435445
- 600 Zhu, W.W., Garber, P.A., Bezanson, M., Qi, X.G. and Li, B.G., 2015. Age- and sex-based  
601 patterns of positional behavior and substrate utilization in the golden snub-nosed monkey  
602 (*Rhinopithecus roxellana*). Am. J. Primatol., 77, 98-108. doi: 10.1002/ajp.22314

<b>Locomotor Mode</b>	<b>Definition</b>
<b>Sit (a)</b>	Remain stationary with body hunched and head erect
<b>Stand (b)</b>	Remain stationary in upright position using all four limbs
<b>Horizontal Suspension-2 (c)</b>	Hanging from two feet
<b>Horizontal Suspension-1 (d)</b>	Hanging from one foot (rare but can occur when playing)
<b>Horizontal Suspension-3 (f)</b>	Hanging from three feet
<b>Sleeping Ball (e)</b>	Remain stationary with body hunched and head erect, head between the knees
<b>Horizontal Suspension-4 (g)</b>	Hanging from four feet
<b>Vertical Suspension-2 (h)</b>	Hanging towards the side of a support, with 2 feet
<b>Vertical Suspension-3 Up</b>	Hanging towards the side of a support, with 3 feet, either facing upwards or
<b>Vertical Suspension-3 Down</b>	downwards(not pictured in Figure 1)
<b>Vertical Suspension-4 Up</b>	Hanging towards the side of a support, with 4 feet, either facing upwards or
<b>Vertical Suspension-4 Down (i)</b>	downwards
<b>Climb Horizontally (j)</b>	Moving horizontally through 90 or +/- 45 degree support
<b>Walk (k)</b>	Quadrupedal walking on support
<b>Suspensory Walk (l)</b>	Locomoting while hanging from 0 degree or +/- 45 degree support
<b>Climb Up (m)</b>	Moving upwards on support
<b>Climb Down (n)</b>	Moving downwards on support
<b>Bridge (o)</b>	Climbing from one support to the next, stretching over a gap of more than 15 cm

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605 Table 1. Locomotor/postural mode definitions for wild Javan slow lorises in Cipiganti West Java.

606 Figure 1 presents images of modes a-o.

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**Locomotor/Postural Modes**

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641 Table 2. Proportion of locomotor and postural modes used while feeding and across all behaviours in wild  
642 Javan slow lorises. Proportions are presented as the mean and standard deviation (SD), with the number  
643 of included individuals listed at the top (N).

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Feeding	Adult (22)		Sub-adult (5)		Juvenile (9)	
	Mean	SD	Mean	SD	Mean	SD
Stand	20.3	11.9	10.2	7.3	20.7	17.7
Vertical Suspension 4 Up	14.4	9.6	24.8	4.2	15.7	22.5
Vertical Suspension 4 Down	11.0	6.5	16.8	13.7	21.3	19.4
Vertical Suspension 2**	9.2	10.4	6.8	4.0	0.2	0.7
Sit	8.6	9.8	6.4	2.9	6.2	11.5
Horizontal suspension 4	8.2	5.5	8.8	6.0	6.0	10.4
Horizontal Suspension 2	6.5	6.2	7.8	11.8	1.2	3.3
Climb Down	3.9	3.5	2.8	3.7	9.0	22.0
Bridge	3.5	3.8	2.4	3.6	4.4	13.3
Climb Up	2.9	2.6	5.0	4.0	1.6	3.1
Horizontal Suspension 1	2.8	4.8	0.2	0.4	0.8	2.0
Horizontal Suspension 3*	2.4	2.6	0.4	0.9	-	-
Suspensory Walk	1.5	2.2	1.6	3.6	0.1	0.3
Vertical Suspension 3 Up	1.4	2.1	3.2	4.4	5.6	16.7
Walk	1.3	2.0	1.4	1.9	0.2	0.7
Vertical Suspension 3 Down	1.1	3.0	0.6	1.3	-	-
Climb Horizontal	1.0	1.9	-	-	0.8	2.0
Horizontal Position	1.0	3.1	0.8	1.8	6.7	20.0
<b>All Behaviours</b>						
	<b>Adult (24)</b>		<b>Sub-adult (7)</b>		<b>Juvenile (23)</b>	
Sit	20.7	6.9	14.0	16.6	16.2	15.7
Climb Down	15.5	5.7	12.0	8.4	20.7	23.5
Climb Up	11.5	5.7	11.2	8.7	15.8	13.6
Stand	9.2	9.6	3.2	2.3	12.6	22.2
Walk*	8.3	4.7	18.9	36.0	8.1	20.7
Sleeping Ball***	6.8	5.7	0.8	1.0	1.2	3.1
Climb Horizontal	4.6	2.3	4.5	3.6	5.0	5.9
Vertical Suspension 4 up	4.3	2.4	4.7	4.4	3.8	5.4
Horizontal suspension 4	3.8	2.2	2.9	2.3	2.5	4.4
Bridge**	3.1	1.4	2.0	2.1	1.3	2.4
Suspensory Walk	2.8	1.8	2.2	2.8	1.2	4.2
Vertical suspension 4 down	2.6	1.5	17.7	36.4	3.1	4.8
Horizontal suspension 2	1.5	1.3	2.5	3.7	1.5	3.3
Vertical suspension 2***	1.3	1.9	0.8	1.2	0.5	2.1
Horizontal suspension 1*	1.0	1.3	0.9	2.3	0.5	1.0
Horizontal suspension 3***	0.7	0.6	0.4	0.6	0.1	0.4
Race walk	0.5	0.7	0.5	0.6	4.5	20.8
Play hang	0.2	0.5	0.0	0.0	0.0	0.0
Vertical suspension 3 up	0.2	0.2	0.6	0.9	0.7	2.5
Vertical suspension 3 down	0.1	0.2	0.2	0.3	0.4	1.5

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Significant p-values are denoted with a (\*),  $\leq 0.01$ ,  $** \leq 0.001$ ,  $*** \leq 0.0001$ .

Table 3. Mean, N and standard deviation (SD) of wild Javan slow lorises habitat use variable described as Position in Tree.

Position in Tree	Adult (16)		Juvenile (6)	
	Mean	SD	Mean	SD
<b>Central</b>	30.6	17.6	32.0	16.7
<b>Crown</b>	18.0	21.0	13.0	6.9
<b>Trunk</b>	17.4	11.4	21.7	14.1
<b>Periphery</b>	17.1	9.8	32.5	22.1
<b>Undergrowth</b>	0.8	1.0	1.0	2.4
<b>Terrestrial</b>	0.1	0.3	-	-

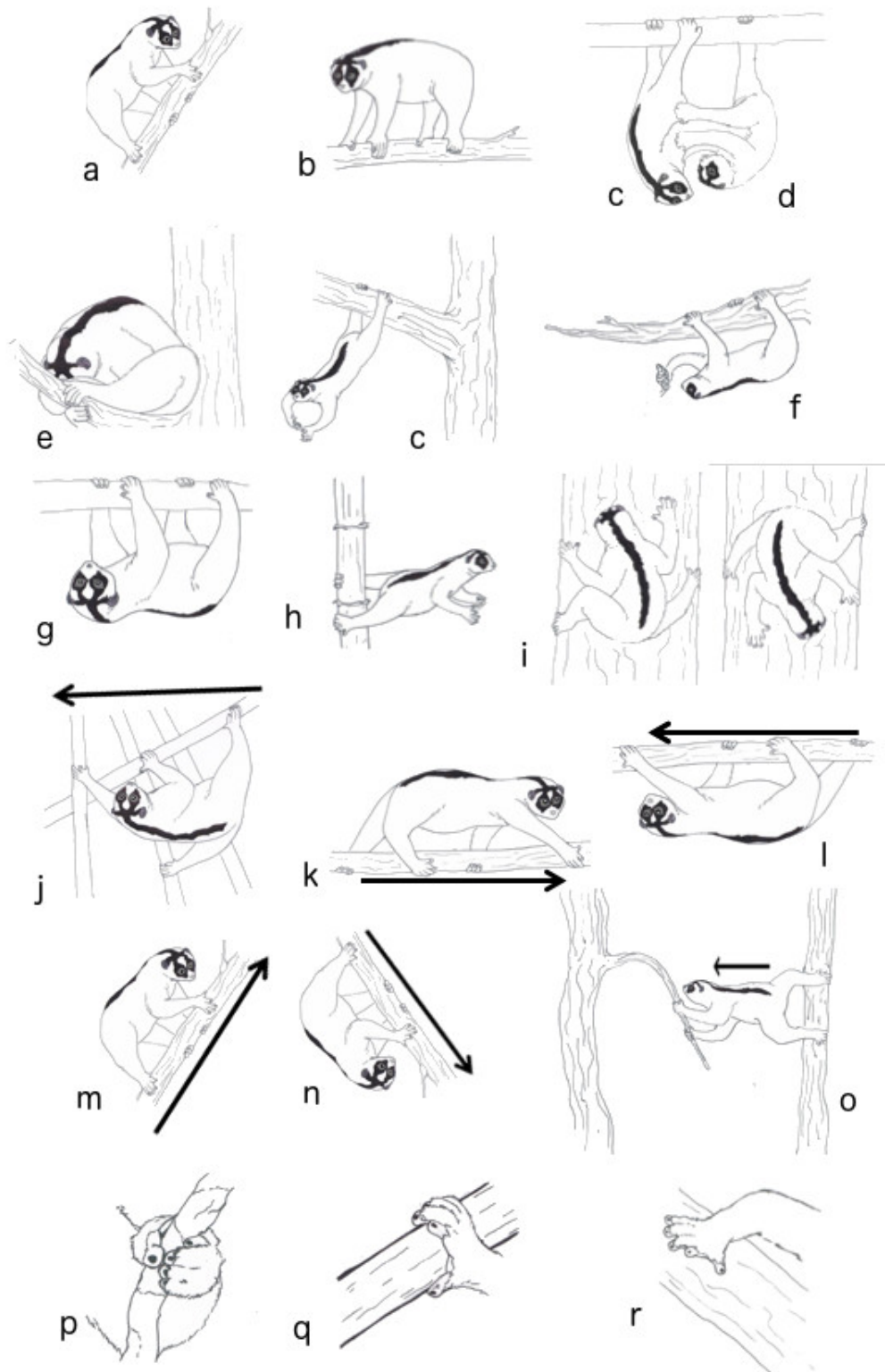
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Table 4. Morphometric measures of wild Javan slow lorises, results include the mean weight in grams (g) and length in millimeters (mm), the number of individuals measured (N) and the standard deviation (SD).

	Adult			Sub-adult			Juvenile		
	Mean	SD	N	Mean	SD	N	Mean	SD	N
<b>Body Weight ***</b>	907.2	72.0	32	819.3	38.5	12	609.7	121.4	14
<b>Total Body Length*</b>	244.4	32.1	29	250.8	11.2	10	252.4	40.5	11
<b>Head Width</b>	51.5	9.2	30	47.8	5.2	12	45.6	15.8	12
<b>Head length*</b>	54.7	11.2	29	50.7	5.5	12	38.5	20.4	12
<b>Foot Span</b>	73.3	6.0	28	72.9	7.3	11	71.4	9.8	10
<b>Hand Span</b>	59.0	6.7	29	57.8	5.3	10	57.4	5.1	10
<b>Lower Leg Length</b>	87.9	10.9	29	84.5	5.8	12	81.3	8.0	11
<b>Upper Leg Length</b>	83.7	9.6	28	81.7	5.4	12	79.4	9.4	11
<b>Lower Arm Length*</b>	75.0	4.2	30	73.1	5.0	12	64.4	16.0	12
<b>Upper Arm Length*</b>	79.4	5.9	30	74.6	6.8	12	72.3	9.1	11

713 Significant p-values are denoted with a (\*), \* $\leq 0.01$ , \*\*  $\leq 0.001$ , \*\*\*  $\leq 0.0001$ .

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717 Figure 1. Locomotor behaviour and substrate size ethogram, a-o are defined in table 1. p:  
 718 Small Substrate, loris can fully grip the branch, less than 20 mm diameter q: Medium  
 719 Substrate, hand of the loris can curve around the branch, greater than 20 mm and less than  
 720 100 mm in diameter r: Large Substrate, hand is flat on the branch/trunk, greater than 100  
 721 mm in diameter. Drawings by Mark Rademaker.

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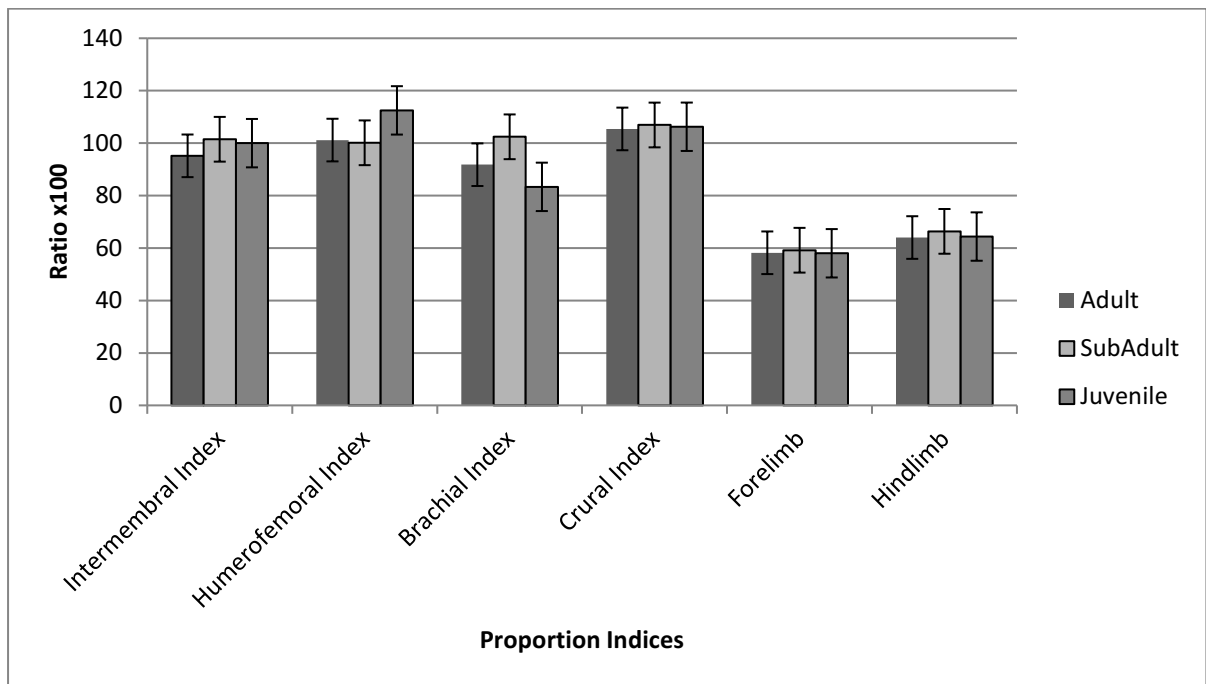


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730 Figure 2. Images of three Javan slow lorises in vertical postures on large substrates. Photos  
731 taken at the LFP field station.

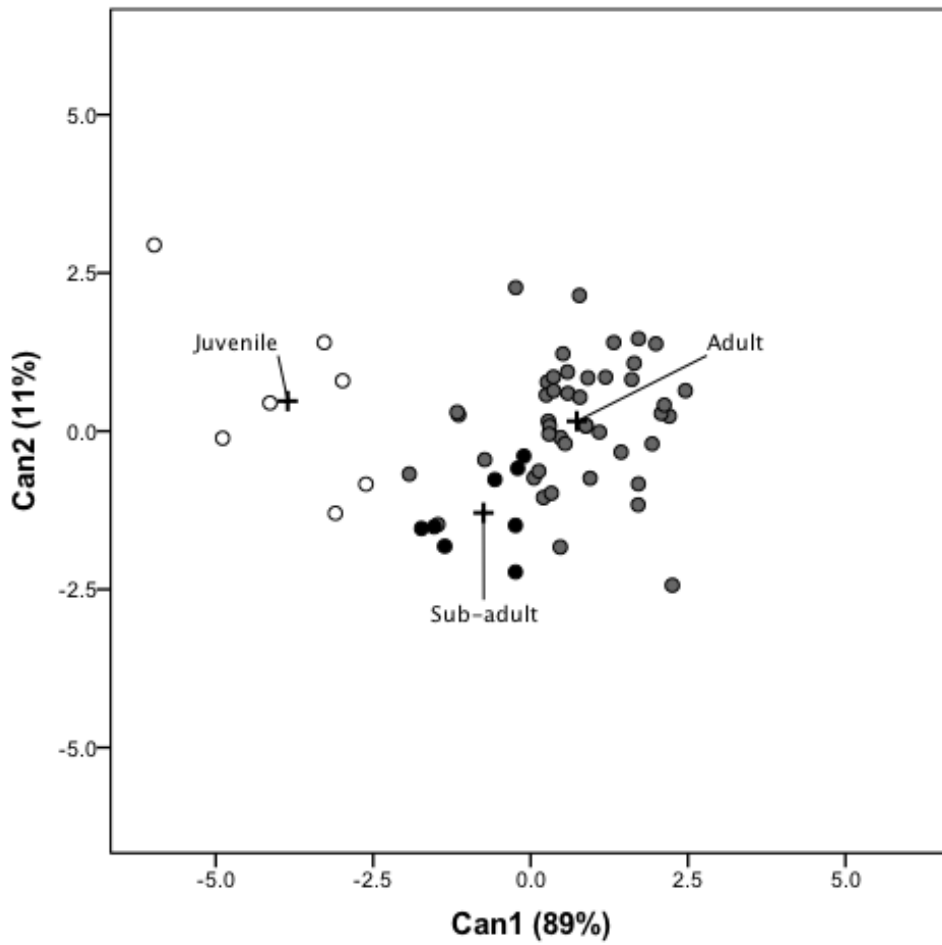
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736 Figure 3. Proportion indices, forelimb/total body length and hindlimb/ total body length  
737 calculated from the limb measurements taken from  $N_A = 30$ ,  $N_{SA} = 11$ ,  $N_J = 8$ . Error bars  
738 represent standard error.

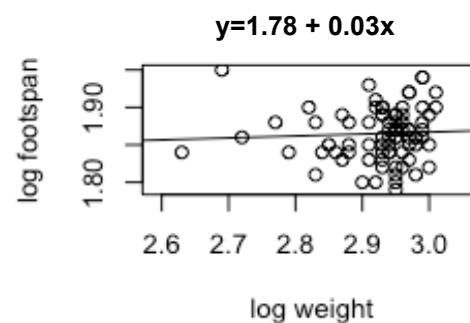
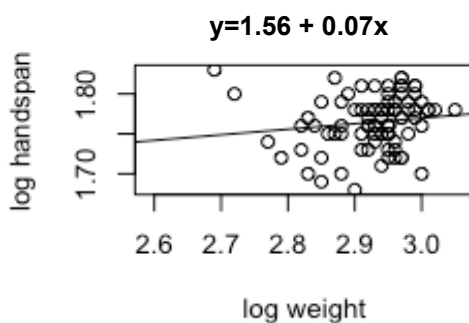
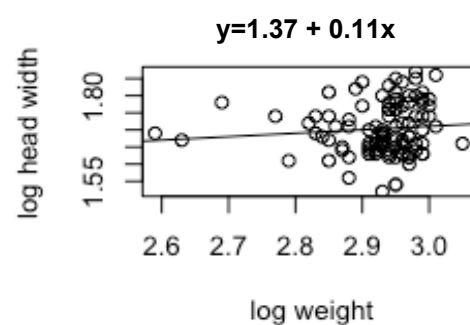
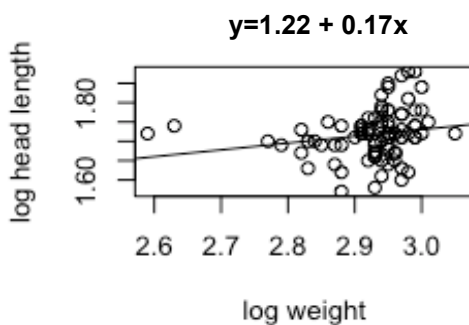
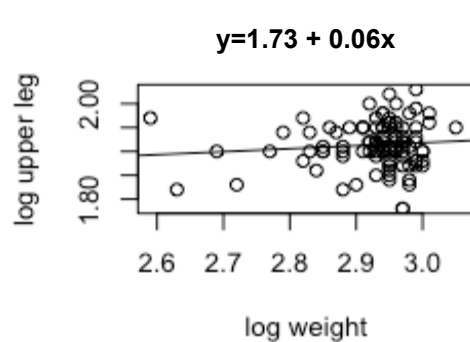
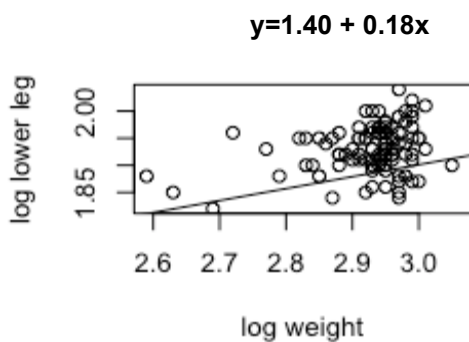
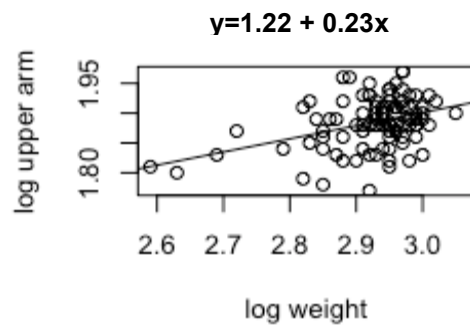
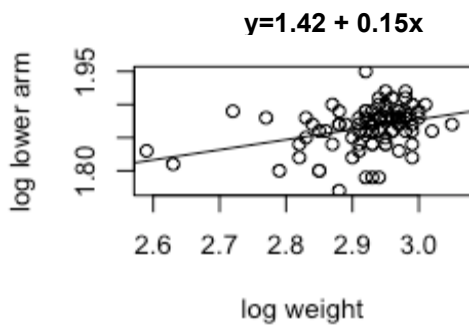
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Figure 4. Canonical variate analysis (CVA) calculated with eight morphometric measures and three age class identifiers (Adult, Sub-adult, and Juvenile) (Wilk's  $\lambda = 0.235$ ,  $p < 0.0001$ ). Crosses indicate the centroid of each group that defined the canonical component axes for Can1 and Can2, percentage represents the influence of the two functions in identifying group differences.

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804 Figure 5. Bivariate plots of morphometric measures and body weight in Javan slow lorises.

805 The generated least square regression formula is presented above each plot.

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