

1 **Title:** Slow lorises (*Nycticebus* spp.) display evidence of handedness in the wild and in  
2 captivity

3 **Authors:** Stephanie A. Poindexter, Kathleen D. Reinhardt, Vincent Nijman, and K.A.I Nekarlis

4 **Running Title:** Laterality in *Nycticebus* Spp.

5 **Keywords:** Nocturnal Primate, Handedness, Hand Use, Indonesia, Feeding

6 **Abstract:**

7 It has been suggested that strepsirrhines (lemurs, lorises, and galagos) retain the more  
8 primitive left hand preference, whilst monkeys and apes more regularly display a right hand  
9 preference at the individual-level. We looked to address questions of laterality in the slow  
10 loris (*Nycticebus* spp.) using spontaneous observations of seven wild individuals, unimanual  
11 tests in six captive individuals, and photos of 44 individuals in a bilateral posture assessing  
12 handedness at the individual- and group-level. During the unimanual reach task, we found  
13 at the individual-level, only four slow lorises showed a hand use bias (R: 3, L:1), Handedness  
14 index (HI) ranged from -0.57-1.00. In the wild unimanual grasp task we found at the  
15 individual-level two individual showed a right-hand bias, the HI ranged from -0.19-0.70. The  
16 bilateral venom pose showed a trend toward a right hand dominant grip in those  
17 photographed in captivity, but an ambiguous difference in wild individuals. There are many  
18 environmental constraints in captivity that wild animals do not face, thus data collected in  
19 wild settings are more representative of their natural state. The presence of right-  
20 handedness in these species suggest that there is a need to re-evaluate the evolution of  
21 handedness in primates.

22

23 **Acknowledgements:**

24 We thank the two anonymous reviewers whose suggestions greatly improved the  
25 manuscript. We thank Amersfoort Zoo, Augsburg Zoo, Brevard Zoo, Cleveland Zoo and Zoo  
26 Society, Columbus Zoo, Conservation International Primate Action Fund and Margot Marsh  
27 Biodiversity Fund, Cotswolds Wildlife Park, Disney Worldwide Conservation Fund, Henry  
28 Doorly Zoo, International Primate Protection League, Longleat Safari and Adventure Park,  
29 Mohamed bin al Zayed Species Conservation Fund (152511813), Memphis Zoo, Nacey  
30 Maggioncalda Foundation, National Geographic (GEFNE101-13), People's Trust for  
31 Endangered Species, Phoenix Zoo, the Royal Geographical Society (with IBG), Shaldon  
32 Wildlife Trust, Shepreth Wildlife Park, Sophie Danforth Conservation Biology Fund, Whitley  
33 Wildlife Conservation Trust, Primate Society of Great Britain, and the European Human  
34 Behaviour and Evolution Society and ZGAP provided the funding for this project. We also  
35 thank our field team including Y. Nazmi, A. Nunur, D. Rustandi, R. Cibabuddhea, D. Spaan, J.  
36 Wise, R. O'Hagan, D. Bergin, F. Cabana, L. Beasley, C. Marsh, J. Wise, D. Geerah, E. J. Rode,

37 M. Rademaker, M. Siagud, and S. McCabe. We thank the team at the Cikananga  
38 Wildlife Center including N. Muqaddam and W. Eggen. The photos included in this project  
39 were taken by J. O'Neil, K. A. I. Nekaris and A. Walmsley. Ethical approval for this research  
40 was provided by the Animal Ethics Sub-Committee at Oxford Brookes University.

41

42

43 Tables: 2

44 Figures: 4

45 Word Count: 6175

46 Word Count Without References and abstract: 4108

47

## 48 **Introduction**

49 Humans show a bias for right-handedness across all populations, regardless of culture and  
50 geographic location (Faurie & Raymond, 2004; Faurie, Schiefenhvel, le Bomin, Billiard, &  
51 Raymond, 2005; McGrew & Marchant, 1994; Raymond & Pontier, 2004). No other species  
52 shows this level of consistency in hand preference (Cashmore, Uomini, & Chapelain, 2008;  
53 Cochet & Byrne, 2013). The roots of motor asymmetries can be traced back to early  
54 vertebrates (Vallortigara, Rogers, & Bisazza, 1999). To uncover the root of this asymmetry,  
55 researchers investigated handedness and laterality in invertebrates and vertebrates  
56 including non-human primates (MacNeilage, Rogers, & Vallortigara, 2009; Neufuss et al.,  
57 2015; Regaiolli, Spiezio, & Hopkins, 2016a; Regaiolli, Spiezio, & Vallortigara 2016b; Wiper,  
58 2017). Hopkins (2013) suggested that the lack of universal handedness in primates  
59 compared to humans was related to a qualitative difference in the way behavioural and  
60 brain asymmetries are expressed. Others noted that there is a more prominent  
61 disconnection between the species-wide handedness seen in humans versus non-human  
62 hand preference (Cashmore et al., 2008; Marchant & McGrew, 2013). Despite these  
63 debates, nearly 70% of non-human vertebrates that have been tested display hand  
64 preference (Ströckens, Güntürkün, & Ocklenburg, 2013).

65

66 Some researchers report the presence of an individual-level bias, but not a group-level bias  
67 in hand preference among various non-human primates (McGrew & Marchant, 1997;  
68 Papademetriou, Sheu, & Michel, 2005), as evidenced by studies of lemurs (Schnoell,  
69 Huebner, Kappeler, & Fichtel, 2014), Old World monkeys (Chapelain et al., 2012; Regaiolli,  
70 Spezio, & Hopkins, 2016b), and New World monkeys (Cameron & Rogers, 1999; Hook-

71 Costigan & Rogers, 1996; Hook & Rogers, 2008). Extensive research on chimpanzees,  
72 gorillas, baboons, and capuchins not only found an individual- and group-level bias, but they  
73 reported a preferential use of the right hand, similar to humans (Hopkins, 2006;  
74 Meguerditchian, Calcutt, Lonsdorf, Ross, & Hopkins, 2010; Vauclair, Meguerditchian, &  
75 Hopkins, 2005). At the individual-level, far more primate species display hand preferences in  
76 both unimanual and bimanual tasks, suggesting that individual-level handedness is not  
77 uniquely human (McGrew & Marchant 1997; Papademetriou et al., 2005; Hopkins, 2007).

78

79 MacNeilage, Studdert-Kennedy, & Lindblom (1987) suggested that strepsirrhines (e.g.,  
80 lemurs, lorises, pottos and galagos) are characterized by a left hand preference, whilst in all  
81 other primates the right hand is used preferentially. Despite this assertion, most formal  
82 studies examining handedness in strepsirrhines have reported various results. At the group-  
83 level, Papademetriou et al. (2005) found that strepsirrhines, New World monkeys, and Old  
84 World monkeys often showed a left-hand bias, whereas most apes show a right-hand bias  
85 (e.g. Lonsdorf & Hopkins, 2005). Studies on strepsirrhines have covered lemur species (e.g.  
86 Nelson, O’Karma, Ruperti, & Novak, 2009; Regaiolli et al., 2016a; Schnoell et al., 2014),  
87 galagos (e.g. Dodson, Stafford, Forsythe, Seltzer, & Ward, 1992; Sanford, Guin, & Ward,  
88 1984) and pottos (Karberger, 1980), using both spontaneous and experimental conditions in  
89 both unimanual and bimanual tasks though primarily were tested in captive settings (e.g.  
90 Fagot & Vauclair, 1991)

91

92 Reports of a right hand preference and a left hand preference at the individual- and group-  
93 level further contribute to the confusion and debate as to the primitive state of laterality in  
94 primates and ultimately humans. Rogers (2009) noted that hand preferences at the  
95 individual-level are linked to general aspects of behaviour. The task used to measure hand  
96 preference and laterality can have a strong effect on individual- and group-level  
97 preferences. Complex bimanual tasks are consistently associated with a stronger  
98 asymmetric response in primates at the individual- and group-level contrary to unimanual  
99 tasks (Cantalupo, Vauclair, & Meunier, 2013; Hopkins et al., 2011; Meguerditchian, Vauclair,  
100 & Hopkins, 2013). Thus it is vital to diversify the types of tasks examined in relation to  
101 laterality and to examine both the individual- and the group-level.

102

103 Slow lorises were once classified as solitary primates, but following more in-depth studies  
104 across species, we now know that they exhibit levels of social interaction comparable to  
105 many diurnal primates (Wiens & Zitzmann, 2003; Nekaris, 2014). Slow lorises display unique  
106 morphological and physiological features related to a hind-limb dominated non-leaping  
107 locomotion. They are characterised by a vice-like grip, as they hold on to branches for long  
108 durations throughout the day as they sleep, and when they cling to trunks for exudate  
109 feeding at night. In addition to this strong grip, they use precision while quickly grabbing  
110 insects, and reeling in flowers on fine branches to drink nectar, without damaging the flower  
111 (Nekaris, 2014). Physiologically, slow lorises are the only venomous primates. When  
112 preparing to bite, slow loris species regularly clasp their arms in a bilateral position called  
113 the venom pose (Nekaris, Moore, Rode, & Fry, 2013). This unique posture is similar to hand-  
114 clasping in humans and the hand clasp grooming of chimpanzees. In the venom pose, slow  
115 lorises use one hand to grasp the wrist of the other arm above their head in threatening  
116 situations; this position enables them to mix the oils secreted from a brachial gland with  
117 their saliva (Nekaris, Moore, Rode, & Fry, 2013). The venom pose is seen in most species of  
118 slow loris, during instances of handling both in captivity and in the wild, providing a unique  
119 opportunity to incorporate another behaviour to examine lateralization.

120

121 Most studies on strepsirrhine manual laterality focused on the influence of posture on hand  
122 preference and simple hand reach preferences, where 'primitive' primates used their right  
123 hand for holding on to branches, and their left hand for reaching and grasping items.  
124 (Sanford & Ward, 1986; Forsythe, Milliken, Stafford, & Ward, 1988; Forsythe & Ward, 1988;  
125 Sanford & Ward, 1986). Many studies on laterality in primates have been conducted in  
126 captivity, although it has been suggested that the surrounding environment can influence  
127 the development of a hand preference.

128

129 Researchers noted that strepsirrhines represent a valuable model for hemispheric  
130 lateralization because of their simple neural system and basal phylogenetic placement  
131 (Ward, 1991). Our goal in this study was to investigate hand preference in spontaneous  
132 unimanual tasks, including bilateral hand-clasp position in slow lorises, to determine if there

133 is an individual or group- level lateralization. For the unimanual task, handedness was  
134 assessed by observing simple reaching for presented food items in captivity and  
135 spontaneous grabbing in the wild. For the bilateral position, we observed which hand  
136 subjects used to clasp their wrist during physical examinations.

137

## 138 **Methods**

### 139 *Bilateral hand clasp position (Venom pose):*

140 We analyzed photos taken during physical examinations in both wild and captive  
141 populations of slow lorises. These photos were taken between 2006 and 2014, and included  
142 three species of slow lorises (Javan slow loris *Nycticebus javanicus*, greater slow loris *N.*  
143 *couang*, and Sumatran slow loris *N. hilleri*) as they employed the venom pose in which arms  
144 are crossed above the animal's head as a defensive position (Figure 1). Forty-two individuals  
145 made up the analysis of the slow loris bilateral clasp, which were photographed either at  
146 wild field sites or rescue centres (Table 1). The species was determined based on the  
147 geographic location and pelage coloration. We included only one photo of each of 42  
148 observed individuals in the analysis, because any subsequent photos were from the same  
149 session and lacked independence. We defined left hand preference as the left hand  
150 clasping the right wrist and the digits are forward facing, and right hand preference was the  
151 right hand grasping the left wrist and the digits are forward facing (Figure 1). The  
152 experienced handling team followed a protocol approved by the Animal Ethics  
153 Subcommittee at Oxford Brookes University and did not restrict arm movement in a way  
154 that would influence which hand clasp their wrist during the venom pose.

155

### 156 *Unimanual reach in captive slow lorises*

157 We observed six individually-housed adult Sumatran slow lorises (M: 3 | F: 3) at Cikananga  
158 Wildlife Center (CWC) in Sukabumi, West Java, Indonesia, as they reached for presented  
159 food items, which we classified as a unimanual reach tasks. We recorded which hand was  
160 used each time a study subject reached for a presented food item. Individuals were sitting  
161 symmetrically in front of three dishes presented to them outside of their cage. They had  
162 equal access to each dish and were presented with either a thin slice of fruit or a small  
163 mealworm in one of the dishes. All participants employed a single handed reach, which was  
164 the only way they could successfully access the dishes through the mesh of their enclosures.

165 Here each single handed reach was defined as a unimanual reach task event, where we  
166 coded right, as the animal's right hand reaching for the dish and left represented the  
167 animal's left hand reaching for the dish.

168

### 169 *Unimanual grasping in wild slow lorises*

170 From June 2015 - December 2017 we recorded the feeding techniques used in a population  
171 of wild Javan slow lorises as a part of ongoing research at the Little Fireface Project field  
172 station (LFP), Cipaganti, West Java, Indonesia (S7°6'6" 7°7' and E107°46' 107°46'5"). We  
173 collected direct observational data using five-minute instantaneous sample points and all  
174 occurrences of grasping behaviours (Altman, 1974). The main study area encompasses a 60  
175 ha area of patches of cultivated lands, bamboo, shrubs, and trees used as lines of  
176 demarcation (Nekaris et al., 2017). Nightly observations took place between 18:00 and  
177 05:00, which constitute the slow lorises' active hours. Here we defined instances where  
178 seven adult Javan slow lorises (M: 3 | F: 4) used their right or left hand to bring a food item  
179 towards their mouth, as a unimanual grasp task (Figure 2).

180

### 181 *Data analysis*

182 To analyse the bilateral hand clasp we used descriptive statistic due to the lack of repeated  
183 occurrence per individual. Results are reported as the mean count of either right- or left-  
184 handed clasping across all photos. To determine the preference at each site we used a one-  
185 sample binomial test. To determine individual preference in the two unimanual tasks, we  
186 calculated the Handedness index (HI), or manual preference index for each slow loris across  
187 all recorded hand grasping and reaching occurrences (Schmitt, Melchisedech,  
188 Hammerschmidt, & Fischer, 2008). An HI of -1 represents a totally left-handed individual  
189 and an HI of +1 represents a totally right-handed individual. A one-sample binomial test for  
190 each slow loris in the unimanual reach and grasp task determined the significant bias in the  
191 use of the right or left hand (Brand, Marchant, Boose, White, Rood, & Meinelt, 2017). To  
192 analyse the unimanual task and spontaneous unimanual grasping at the group-level, we  
193 performed a one-Sample T-test on the distribution of the Absolute Handedness index (ABS-  
194 HI) with significance set to  $p \leq 0.05$ .

195

## 196 **Results**

197 *Bilateral hand clasp position (venom pose):*

198 We found no significant difference between the two bilateral venom poses across all sites  
199 and species (binomial test, N=42, p=0.090). A total of 64% of lorises favoured the right  
200 position; 36% favoured the left position. The photos taken at the CWC centre (binomial test,  
201 N=16, p=0.804), IAR centre (binomial test, N=15, p=0.118), and SPC centre (binomial test,  
202 N=5, p=0.750) showed no significant difference. The mean right hand use was 56%, 73%,  
203 and 67%, respectively. The mean hand use for the photos taken of wild slow lorises was 50%  
204 right and 50% left, statistically there was no difference (binomial test, N=6, p=1.000).

205

206 *Unimanual reach in captive slow lorises*

207 At the group-level, we found a significant difference in the distribution of the HI (One-  
208 sample Test, N=6, t=4.92, p=0.004). When considered as one sample, the slow lorises used  
209 their right hand 57% of the observations and their left hand 43% of the observations. The  
210 mean absolute HI for this task was  $0.45 \pm 0.16$  (Figure 3). At the individual-level only four  
211 slow lorises showed a hand use bias (R: 3, L:1), HI ranged from -0.57-1, two individuals (FO &  
212 MD) displayed a negative HI value, the other four had positive HI values (Table 2).

213

214 *Unimanual grasping in wild slow lorises*

215 At the group-level, we found a significant difference in the distribution of HI (One-sample  
216 Test, N=7, t=3.29, p=0.016). When considered as one sample, slow lorises used their right  
217 hand 64% of the observations and their left hand 37% of the observations. The mean  
218 absolute Handedness Index (HI) for this task was  $0.56 \pm 0.34$  (Figure 4). At the individual-  
219 level two individual showed a right-hand bias (AL & FE), the HI ranged from -0.19-0.70, two  
220 individuals (MA & SH) displayed negative values, TE had a value of zero, and the others  
221 displayed positive values (Table 2).

222

223 **Discussion**

224 Despite the small sample size, the results of this study suggest that there is variation  
225 between hand preference in wild and captive individuals during unimanual reaching and  
226 grasping tasks, but not during bilateral positions. In the bilateral position, there was no  
227 difference in the preferred clasping hand during venom poses. In the unimanual task in  
228 captive slow lorises, there was a difference at the group-level. At the individual-level one

229 individual showed a left hand preference. The unimanual grasping in the wild slow lorises  
230 also displayed significant right-hand preferences as a group. In addition to a lack of  
231 continuity regarding strepsirrhine laterality, each tested task has a varying effect on the  
232 manifestation of hemispheric biases (Fagot & Vauclair, 1991). The results in this study offer  
233 a counterpoint to the idea that strepsirrhines have retained a left hand bias, as an assumed  
234 ancestral state for primates including humans (Papademetriou et al., 2005).

235

236 MacNeilage et al. (1987) observed that the hands of strepsirrhines showed some  
237 specialization such as grasping for supports with the right hand (left hemisphere) and  
238 striking prey with the left hand (right hemisphere), revealing that task demands elicited the  
239 obligate use of a particular hemisphere. It has been suggested that the left hemisphere  
240 develops before the right hemisphere (Fagard, 2013; MacNeilage, Rogers, & Vallortigara,  
241 2009) and based on studies of a wide range of vertebrates without forelimbs/hands it is  
242 known that the brain became lateralized well before handedness.  
243 Studies show that there may be subtle functional differences between the left and right  
244 hand (Sainburg, 2014; Schabowsky, Hidler, & Lum, 2007). These authors provide a structure  
245 for understanding the motor control process that lead to handedness. In this dynamic  
246 dominance model, the left hemisphere in right-handed animals is most proficient at  
247 processes that predict the effects of body and environmental dynamics, whereas left-  
248 handed animals relying on the right hemisphere are most proficient at object manipulation.  
249 Furthermore, zoo-housed gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes*)  
250 display varied hand use bias when engaging with animate and inanimate objects suggesting  
251 that object characteristics effect how the right and left hemisphere process manual actions  
252 (Foster, Quaresmini, Leavens, Spiezip & Vallortigara, 2012; Forrester, Quaresmini, Leavens &  
253 Vallortigara, 2011).

254

255 The right or left hand dominance in the slow loris venom pose at the included rescue  
256 centres and in the wild varied from one slow loris to the next, showing no group-level  
257 preference. Despite our insignificant findings, we did observe right-hand dominated clasping  
258 in 64% of the slow lorises compared to 36% of the slow loris using a left hand dominated  
259 clasp. We suggest that this variation may be linked to the strong I-V grasp known to slow  
260 loris species (Gebo, 1987). The I-V grasp relies heavily on the thumb, which Morino,



261 Uchikoshi, Bercovitch, Hopkins, & Matsuzawa (2017) suggested may motivate a shift in  
262 hemispheric involvement. Grips using the thumb in other primates including humans are  
263 typically associated with right hand use (Christel, 1994; Hopkins, Cantalupo, Wesley,  
264 Hostetter, & Pilcher, 2002; Hopkins & Russell 2004; Meguerditchian et al., 2015). In human  
265 studies of arm folding and hand clasping, there was no evidence of consistent lateral  
266 preferences that could be associated with handedness (Reiss & Reiss, 1998), noting that  
267 bilateral preference has a weak connection to hemispheric lateralization. There is another  
268 plausible factor, which may influence the left or right hand dominated grasp during the slow  
269 loris venom pose. This posture serves the function of delivering brachial oil to the mouth, to  
270 enable a venomous bite (Nekaris et al., 2013). Using either the right or left hand to grasp the  
271 other wrist could be linked to the amount of brachial oil present on the right or left brachial  
272 gland. To further discuss this theory, we would need to incorporate data on brachial oil  
273 production at each instance of observing the venom pose.

274

275 Hand clasping in non-human primates is very rarely reported in publications, outside of a  
276 posture used by chimpanzees. McGrew and Tutin (1978) described this pattern of behaviour  
277 as the grooming hand-clasp in the chimpanzees of K-group in the Mahale Mountains of  
278 western Tanzania. This behaviour was absent in other chimpanzee populations, nearby and  
279 in other countries (McGrew, Marchant, Nakamura, & Nishida, 2001). The presence or  
280 absence of hand-clasp grooming in chimpanzee groups is related to cultural differences  
281 between various populations (McGrew, Marchant, Nakamura, & Nishida, 2001). In humans  
282 hand-clasping shows a lateral preference but there appears to be an east to west variation.  
283 Indeed, left hand clasping (the thumb of the left hand resting on top of the thumb of the  
284 right hand) is more dominant in populations near the Greenwich Meridian, and decreases  
285 east of the Meridian, with the lowest level of left hand clasping in India and Australasia  
286 (McManus & Mascie-Taylor, 1979; Reiss, 1999). This cultural influence suggests that  
287 although hand-clasping shows lateral preference similar to manual tasks it has a weaker  
288 connection to brain hemispheric lateralization (Critchley, 1972; Reiss, 1999; Reiss M., Reiss  
289 G., & Freye, 1998). In this study we included three slow loris species in varying conditions.  
290 The lack of an identifiable preference supports what is seen in humans, that unlike other  
291 manual tasks this bilateral position displays less of a universal hand preference.

292

293 Our results in the unimanual task in captive lorises suggest a group-level bias. At the  
294 individual-level one of six individuals had a negative HI, representing a left hand bias, the  
295 other three that displayed a significant preference were right handed. These results refer  
296 back to Sanford and Ward's (1986) suggestion that posture has a significant influence in  
297 manual lateralization. As captive slow loris species generally maintain a sitting posture and  
298 did so throughout testing, our findings are congruent with findings in strepsirrhines (Sanford  
299 et al., 1984; Ward, Milliken, & Stafford, 1993), monkeys (Fagot & Vauclair, 1991; King &  
300 Landau, 1993; Roney & King, 1993), and apes (Hopkins, 1996). Similar to the bilateral  
301 posture, the simple unimanual hand reach recorded in the captive slow lorises is a poor  
302 indicator of hemispheric specialization, as seen in other quadrupeds (Vauclair et al., 2005).  
303 Merguerditchian and colleagues (2015) concluded that any hand preferences seen in this  
304 task are likely due to situational and postural conditions. Our observations support this  
305 assertion as individual slow lorises did not consistently rotate their bodies to use a specific  
306 hand, but instead often used the hand closest to the presented food dish, which varied  
307 based on where the individual was at the start of the testing session.

308

309 In the Javan slow loris we found a group-level right-hand bias in the unimanual grasping in  
310 wild individuals. This right-hand preference acts as a counter point to studies that report a  
311 higher right-hand bias for nongrasping actions (Cochet & Vauclair, 2010; Esseily, Nadel, &  
312 Fagard, 2010; Hopkins et al., 2005). If as suggested by Molesti et al. (2016) that precise and  
313 complex manipulative activities may be selective pressures for the evolution of handedness  
314 in the primate lineage, it is increasingly important for researchers exploring questions of  
315 laterality to consider strepsirrhines, who like most haplorhines, engage in precise and  
316 manipulative activities. In particular, Javan slow lorises observed in the wild used a precision  
317 grip to grasp and reel in thin braches to access the flowers located on the end, or to grab  
318 insects quickly (Moore, 2012). Given that precision and the visual demand of a motor action  
319 are hallmark traits of task complexity (Fagot & Vauclair, 1991; Meunier & Vauclair, 2007),  
320 the spontaneous unimanual grasping observed in free-ranging slow lorises could explain the  
321 lateralization seen at the individual- and group-level.

322

323 We found a right-hand bias, whereas prior studies of lemurs and galagos show a left-handed  
324 bias (Leliveld, Scheumann, & Zimmermann, 2008; Lhota, Jůnek, & Bartoš, 2009; Milliken,

325 Forsythe, & Ward, 1989; Rigamonti, Spiezio, Poli, & Fazio, 2005; Schnoell et al., 2014; Ward,  
326 Milliken, Dodson, Stafford, & Wallace, 1990). Hopkins et al. (2006) noted the impact of  
327 sample size especially in comparative studies, thus the reported findings may change when  
328 we analyse a larger dataset. Furthermore, it has been reported that right-handedness is  
329 more common among terrestrial compared to arboreal non-human primate species, given  
330 that they do not need their hands to support their posture (Hopkins et al., 2011; MacNeilage  
331 et al., 1987; Meguerditchian et al., 2013). Following this justification, the slow loris may  
332 deviate from other arboreal animals, due to their strong reliance on their hindlimbs to  
333 maintain their posture. They regularly use both hands to grasp insects as they stretch  
334 between discontinuous substrates using only their core and hindlimbs to support their  
335 position (Poindexter & Nekaris, 2017).

336

337 In this study we included both a bilateral posture and unimanual tasks, but to create a truly  
338 comprehensive picture of *Nycticebus* laterality, we should complete further research  
339 including a more complex bimanual task. Bimanual tasks require a higher level of fine motor  
340 skill and manipulation, thus they are believed to have a higher likelihood to induce hand  
341 preferences at the group-level (Colell, Segarra, & Sabater-Pi, 1995). In conclusion, results of  
342 this study revealed a group-level right hand preference in the Javan slow loris during  
343 observed unimanual grasping in the wild, but not in the bilateral venom pose or the  
344 unimanual reach observed in captivity. These findings suggest that lateralization can be  
345 elicited in unimanual tasks depending on the level of complexity needed to complete the  
346 task. Lastly, our findings support the need to further consider strepsirrhines in the wild and  
347 during more complex tasks as these results follow those in another strepsirrhine, the ring-  
348 tailed lemur (*Lemur catta*) (Ragaiolli, Spiezio, & Vallortigara, 2016a). The presence of right-  
349 handedness in this species and in these conditions highlights the importance of re-  
350 evaluating the evolution of hand preference in strepsirrhines.

351

## 352 **References**

353

354 Bisazza, A., Cantalupo, C., Capocchiano, M., & Vallortigara, G. (2000). Population  
355 lateralisation and social behaviour: a study with 16 species of fish. *Laterality: Asymmetries*  
356 *of Body, Brain and Cognition*, 5(3), 269-284.

357

358 Brand, C.M., Marchant, L.F., Boose, K.J., White, F.J., Rood, T.M. & Meinelt, A., 2017.  
359 Laterality of Grooming and Tool Use in a Group of Captive Bonobos (*Pan paniscus*). *Folia*  
360 *Primatologica*, 88(2), 210-222.

361  
362 Cameron, R., & Rogers, L. J. (1999). Hand preference of the common marmoset (*Callithrix*  
363 *jacchus*): Problem solving and responses in a novel setting. *Journal of Comparative*  
364 *Psychology*, 113(2), 149.

365  
366 Cashmore, L., Uomini, N., & Chapelain, A. (2008). The evolution of handedness in humans  
367 and great apes: a review and current issues. *Journal of Anthropological Sciences*, 86, 7-35.

368  
369 Chapelain, A., Laurence, A., Vimond, M., Maille, A., Meunier, H., Fagard, J., Vauclair, J. &  
370 Blois-Heulin, C. (2012). Hand preference and its flexibility according to the position of the  
371 object: a study in cercopithecines examining spontaneous behaviour and an experimental  
372 task (the Bishop QHP task). *Animal Cognition*, 15(5), pp.937-953.

373  
374 Cochet, H., & Vauclair, J. (2010). Pointing gestures produced by toddlers from 15 to 30  
375 months: Different functions, hand shapes and laterality patterns. *Infant Behavior and*  
376 *Development*, 33(4), 431-441.

377  
378 Cochet, H., & Byrne, R. W. (2013). Evolutionary origins of human handedness: evaluating  
379 contrasting hypotheses. *Animal Cognition*, 16(4), 531-542.

380  
381 Colell, M., Segarra, M. D., & Sabater-Pi, J. (1995). Manual laterality in chimpanzees (*Pan*  
382 *troglydites*) in complex tasks. *Journal of Comparative Psychology*, 109(3), 298.

383  
384 Dodson, D. L., Stafford, D., Forsythe, C., Seltzer, C. P., & Ward, J. P. (1992). Laterality in  
385 quadrupedal and bipedal prosimians: Reach and whole-body turn in the mouse lemur  
386 (*Microcebus murinus*) and the galago (*Galago moholi*). *American Journal of*  
387 *Primatology*, 26(3), 191-202.

388  
389 Esseily, R., Nadel, J. and Fagard, J. (2010). Object retrieval through observational learning in  
390 8-to 18-month-old infants. *Infant Behavior and Development*, 33(4), 695-699.

391  
392 Fagot, J., & Vauclair, J. (1991). Manual laterality in nonhuman primates: a distinction  
393 between handedness and manual specialization. *Psychological Bulletin*, 109(1), 76.

394  
395 Faurie, C., Schiefenhvel, W., leBomin, S., Billiard, S., & Raymond, M. (2005). Variation in the  
396 frequency of left-handedness in traditional societies. *Current Anthropology*, 46(1), 142-147.

397  
398 Forsythe, C., Milliken, G. W., Stafford, D. K., & Ward, J. P. (1988). Posturally related  
399 variations in the hand preferences of the ruffed lemur (*Varecia variegata variegata*). *Journal*  
400 *of Comparative Psychology*, 102(3), 248.

401  
402 Forsythe, C., & Ward, J. P. (1988). Black lemur (*Lemur macaco*) hand preference in food  
403 reaching. *Primates*, 29(3), 369-374.

404

405 Forrester, G. S., Leavens, D. A., Quaresmini, C., & Vallortigara, G. (2011). Target animacy  
406 influences gorilla handedness. *Animal Cognition*, 14(6), 903-907.  
407  
408 Forrester, G. S., Quaresmini, C., Leavens, D. A., Spiezio, C., & Vallortigara, G. (2012). Target  
409 animacy influences chimpanzee handedness. *Animal Cognition*, 15(6), 1121-1127.  
410  
411 Gebo, D. L. (1987). Locomotor diversity in prosimian primates. *American Journal of*  
412 *Primatology*, 13(3), 271-281.  
413  
414 Hook, M. A., & Rogers, L. J. (2008). Visuospatial reaching preferences of common  
415 marmosets (*Callithrix jacchus*): An assessment of individual biases across a variety of  
416 tasks. *Journal of Comparative Psychology*, 122(1), 41.  
417  
418 Hook-Costigan, M. A., & Rogers, L. J. (1996). Hand preferences in New World  
419 primates. *International Journal of Comparative Psychology*, 9(4).  
420  
421 Hopkins, W. D. (1996). Chimpanzee handedness revisited: 55 years since Finch  
422 (1941). *Psychonomic Bulletin & Review*, 3(4), 449-457.  
423  
424 Hopkins, W. D. (2006). Comparative and familial analysis of handedness in great  
425 apes. *Psychological Bulletin*, 132(4), 538.  
426  
427 Hopkins, W. D. (Ed.). (2007). *The evolution of hemispheric specialization in primates* (Vol. 5).  
428 Elsevier.  
429  
430 Hopkins, W.D. (2013). Neuroanatomical asymmetries and handedness in chimpanzees (*Pan*  
431 *troglydytes*): a case for continuity in the evolution of hemispheric specialization. *Annals of*  
432 *the New York Academy of Sciences*, 1288(1),17-35.  
433  
434 Hopkins, W. D., Cantalupo, C., Wesley, M. J., Hostetter, A. B., & Pilcher, D. L. (2002). Grip  
435 morphology and hand use in chimpanzees: Evidence of a left hemisphere specialization in  
436 motor skill. *Journal of Experimental Psychology*, 131 (3), 412–423  
437  
438 Hopkins, W.D., Phillips, K.A., Bania, A., Calcutt, S.E., Gardner, M., Russell, J., Schaeffer, J.,  
439 Lonsdorf, E.V., Ross, S.R. & Schapiro, S.J. (2011). Hand preferences for coordinated bimanual  
440 actions in 777 great apes: implications for the evolution of handedness in hominins. *Journal*  
441 *of Human Evolution*, 60(5), 605-611.  
442  
443 Hopkins, W. D., & Russell, J. L. (2004). Further evidence of a right hand advantage in motor  
444 skill by chimpanzees (*Pan troglodytes*). *Neuropsychologia*, 42(7), 990-996.  
445  
446 Hopkins, W. D., Russell, J., Freeman, H., Buehler, N., Reynolds, E., & Schapiro, S. J. (2005).  
447 The distribution and development of handedness for manual gestures in captive  
448 chimpanzees (*Pan troglodytes*). *Psychological Science*, 16(6), 487-493.  
449  
450 King, J. E., & Landau, V. I. (1993). Reaching in Squirrel Monkeys. *Primate Laterality: Current*  
451 *Behavioral Evidence of Primate Asymmetries*, 107.

452

453 Kraberger, A. (1980). Wahlstrategien des Verhaltens von *Percodicticus potto* am Beispiel des  
454 Handeinsatzes. Doctoral Thesis, FU Berlin.

455

456 Leliveld, L., Scheumann, M., & Zimmermann, E. (2008). Manual lateralization in early  
457 primates: A comparison of two mouse lemur species. *American Journal of Physical*  
458 *Anthropology*, 137(2), 156-163.

459

460 Lhota, S., Jůnek, T., & Bartoš, L. (2009). Patterns and laterality of hand use in free-ranging  
461 aye-ayes (*Daubentonia madagascariensis*) and a comparison with captive studies. *Journal of*  
462 *Ethology*, 27(3), 419-428.

463

464 MacNeilage, P. F., Rogers, L. J., & Vallortigara, G. (2009). Evolutionary origins of your right  
465 and left brain. *Scientific American*, 301, 60-67.

466

467 MacNeilage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987). Primate handedness  
468 reconsidered. *Behavioral and Brain Sciences*, 10(2), 247-263.

469

470 MacNeilage, P. F., Rogers, L. J., & Vallortigara, G. (2009). Evolutionary origins of your right  
471 and left brain. *Scientific American*, 301, 60-67.

472

473 Marchant, L. F., & McGrew, W. C. (2013). Handedness is more than laterality: lessons from  
474 chimpanzees. *Annals of the New York Academy of Sciences*, 1288(1), 1-8.

475

476 McGrew, W. C., & Marchant, L. F. (1994). Primate ethology: A perspective on human and  
477 nonhuman handedness. In P. K. Bock (Ed.), *Psychological Anthropology*, 171-184.

478

479 McGrew, W. C., & Marchant, L. F. (1997). On the other hand: current issues in and meta-  
480 analysis of the behavioral laterality of hand function in nonhuman primates. *American*  
481 *Journal of Physical Anthropology*, 104(S25), 201-232.

482

483 McGrew, W. C., Marchant, L. F., Nakamura, M., & Nishida, T. (2001). Local customs in wild  
484 chimpanzees: The grooming hand-clasp in the Mahale Mountains, Tanzania. In *American*  
485 *Journal of Physical Anthropology*, 107.

486

487 McGrew, W. C., & Tutin, C. E. (1978). Evidence for a social custom in wild  
488 chimpanzees?. *Man*, 234-251.

489

490 McManus, I. C., & Mascie-Taylor, C. G. N. (1979). Hand-clasping and arm-folding: A review  
491 and a genetic model. *Annals of Human Biology*, 6(6), 527-558.

492

493 Meguerditchian, A., Calcutt, S. E., Lonsdorf, E. V., Ross, S. R., & Hopkins, W. D. (2010). Brief  
494 communication: captive gorillas are right-handed for bimanual feeding. *American Journal of*  
495 *Physical Anthropology*, 141(4), 638-645.

496

497 Meguerditchian, A., Phillips, K.A., Chapelain, A., Mahovetz, L.M., Milne, S., Stoinski, T.,  
498 Bania, A., Lonsdorf, E., Schaeffer, J., Russell, J. & Hopkins, W.D. (2015). Handedness for

499 unimanual grasping in 564 great apes: the effect on grip morphology and a comparison with  
500 hand use for a bimanual coordinated task. *Frontiers in Psychology*, 6.  
501  
502 Meguerditchian, A., Vauclair, J., & Hopkins, W. D. (2010). Captive chimpanzees use their  
503 right hand to communicate with each other: implications for the origin of the cerebral  
504 substrate for language. *Cortex*, 46(1), 40-48.  
505  
506 Meguerditchian, A., Vauclair, J., & Hopkins, W. D. (2013). On the origins of human  
507 handedness and language: a comparative review of hand preferences for bimanual  
508 coordinated actions and gestural communication in nonhuman primates. *Developmental*  
509 *Psychobiology*, 55(6), 637-650.  
510  
511 Milliken, G. W., Forsythe, C., & Ward, J. P. (1989). Multiple measures of hand-use  
512 lateralization in the ring-tailed lemur (*Lemur catta*). *Journal of Comparative*  
513 *Psychology*, 103(3), 262.  
514  
515 Morino, L., Uchikoshi, M., Bercovitch, F., Hopkins, W. D., & Matsuzawa, T. (2017). Tube task  
516 hand preference in captive hylobatids. *Primates*, 1-10.  
517  
518 Nekaris, K. A. I., Moore, R. S., Rode, E. J., & Fry, B. G. (2013). Mad, bad and dangerous to  
519 know: the biochemistry, ecology and evolution of slow loris venom. *Journal of Venomous*  
520 *Animals and Toxins including Tropical Diseases*, 19(1), 21.  
521  
522 Nekaris, K. A. I., Poindexter, S., Reinhardt, K. D., Sigaud, M., Cabana, F., Wirdateti, W., &  
523 Nijman, V. (2017). Coexistence between Javan slow lorises (*Nycticebus javanicus*) and  
524 humans in a dynamic agroforestry landscape in West Java, Indonesia. *International Journal*  
525 *of Primatology*, 38(2), 303-320.  
526  
527 Nelson, E. L., O'Karma, J. M., Ruperti, F. S., & Novak, M. A. (2009). Laterality in semi-free-  
528 ranging black and white ruffed lemurs (*Varecia variegata variegata*): head-tilt correlates  
529 with hand use during feeding. *American Journal of Primatology*, 71(12), 1032-1040.  
530  
531  
532 Neufuss, J., Humle, T., Deschner, T., Robbins, M.M., Sirianni, G., Boesch, C. & Kivell, T.L.  
533 (2015). Diversity of hand grips and laterality in wild African apes. *Folia Primatologica*, 86(4),  
534 pp.329-329.  
535  
536 Papademetriou E., Sheu C.-F. & Michel G.F. (2005). A meta-analysis of primate hand  
537 preferences, particularly for reaching. *Journal of Comparative Psychology*, 119, 33-48.  
538  
539 Poindexter, S.A. and Nekaris, K.A.I. (2017). Vertical clingers and gougers: Rapid acquisition of  
540 adult limb proportions facilitates feeding behaviours in young Javan slow lorises (*Nycticebus*  
541 *javanicus*). *Mammalian Biology-Zeitschrift für Säugetierkunde*, 87, 40-49.  
542  
543 Raymond, M. and Pontier, D. (2004). Is there geographical variation in human  
544 handedness?. *Laterality: Asymmetries of Body, Brain and Cognition*, 9(1), 35-51.  
545

546 Regaiolli, B., Spiezio, C., & Hopkins, W. D. (2016a). Hand preference on unimanual and  
547 bimanual tasks in strepsirrhines: The case of the ring-tailed lemur (*Lemur catta*). *American*  
548 *Journal of Primatology*, 78(8), 851-860.

549

550 Regaiolli, B., Spiezio, C. and Vallortigara, G. (2016b). Manual lateralization in macaques:  
551 handedness, target laterality and task complexity. *Laterality: Asymmetries of Body, Brain*  
552 *and Cognition*, 21(2), 100-117.

553

554 Reiss, M. (1999). The genetics of hand-clasping a review and a familial study. *Annals of*  
555 *Human Biology*, 26(1), 39-48.

556

557 Reiss, M., & Reiss, G. (1998). Certain aspects of laterality research. *Archiv fur*  
558 *Kriminologie*, 201(3-4), 103-111.

559

560 Reiss, M., Reiss, G., & Freye, H. A. (1998). Some aspects of self-reported hand  
561 preference. *Perceptual and Motor Skills*, 86(3), 953-954.

562

563 Rigamonti, M. M., Spiezio, C., Poli, M. D., & Fazio, F. (2005). Laterality of manual function in  
564 foraging and positional behavior in wild indri (*Indri indri*). *American Journal of*  
565 *Primatology*, 65(1), 27-38.

566

567 Rogers, L. J. (2009). Hand and paw preferences in relation to the lateralized  
568 brain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1519), 943-  
569 954.

570

571 Roney, L. S., & King, J. E. (1993). Postural effects on manual reaching laterality in squirrel  
572 monkeys (*Saimiri sciureus*) and cotton-top tamarins (*Saguinus oedipus*). *Journal of*  
573 *Comparative Psychology*, 107(4), 380.

574

575 Sainburg, R. L. (2014). Convergent models of handedness and brain lateralization. *Frontiers*  
576 *in Psychology*, 5:1092.

577

578

579 Sanford, C., Guin, K., & Ward, J. P. (1984). Posture and laterality in the bushbaby (*Galago*  
580 *senegalensis*). *Brain, Behavior and Evolution*, 25(4), 217-224.

581

582 Sanford, C. G., & Ward, J. P. (1986). Mirror image discrimination and hand preference in the  
583 bushbaby (*Galago senegalensis*). *The Psychological Record*, 36(4), 439-449.

584

585 Schabowsky, C. N., Hidler, J. M., & Lum, P. S. (2007). Greater reliance on impedance control  
586 in the nondominant arm compared with the dominant arm when adapting to a novel  
587 dynamic environment. *Experimental Brain Research*, 182(4), 567-577.

588

589 Schmitt, V., Melchisedech, S., Hammerschmidt, K., & Fischer, J. (2008). Hand preferences in  
590 Barbary macaques (*Macaca sylvanus*). *Laterality*, 13(2), 143-157.

591



592 Schnoell, A. V., Huebner, F., Kappeler, P. M., & Fichtel, C. (2014). Manual lateralization in  
593 wild red fronted lemurs (*Eulemur rufifrons*) during spontaneous actions and in an  
594 experimental task. *American Journal of Physical Anthropology*, 153(1), 61-67.  
595

596 Ströckens, F., Güntürkün, O., & Ocklenburg, S. (2013). Limb preferences in non-human  
597 vertebrates. *Laterality: Asymmetries of Body, Brain and Cognition*, 18(5), 536-575.  
598

599 Vaucclair, J., Meguerditchian, A., & Hopkins, W. D. (2005). Hand preferences for unimanual  
600 and coordinated bimanual tasks in baboons (*Papio anubis*). *Cognitive Brain Research*, 25(1),  
601 210-216.  
602

603 Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: advantages and  
604 disadvantages of cerebral lateralization. *Behavioral and brain sciences*, 28(4), 575-588.  
605

606 Vallortigara, G., Rogers, L. J., & Bisazza, A. (1999). Possible evolutionary origins of cognitive  
607 brain lateralization. *Brain Research Reviews*, 30(2), 164-175.  
608

609 Ward, J. P., Milliken, G. W., Dodson, D. L., Stafford, D. K., & Wallace, M. (1990). Handedness  
610 as a function of sex and age in a large population of Lemur. *Journal of Comparative*  
611 *Psychology*, 104(2), 167.  
612

613 Ward, J. P., Milliken, G. W., & Stafford, D. K. (1993). Patterns of lateralized behavior in  
614 prosimians. *Primate Laterality: Current behavioral evidence of primate asymmetries*, 43-74.  
615

616 Watson, S. L., & Hanbury, D. B. (2007). Prosimian primates as models of laterality. *Special*  
617 *Topics in Primatology*, 5, 228-250.  
618

619 Wiens, F., & Zitzmann, A. (2003). Social structure of the solitary slow loris *Nycticebus*  
620 *coucang* (Lorisidae). *Journal of Zoology*, 261(1), 35-46.  
621

622 Wiper, M. L. (2017). Evolutionary and mechanistic drivers of laterality: A review and new  
623 synthesis. *Laterality: Asymmetries of Body, Brain and Cognition*, 1-31.  
624

625



626

627

Figure 1. *Nycticebus* venom pose.

628

629

630



631

632

633

Figure 2. Wild Javan slow loris (*Nycticebus javanicus*) in the process of grasping a flower in terminal branches of a tree in Cipaganti, West Java, Indonesia.

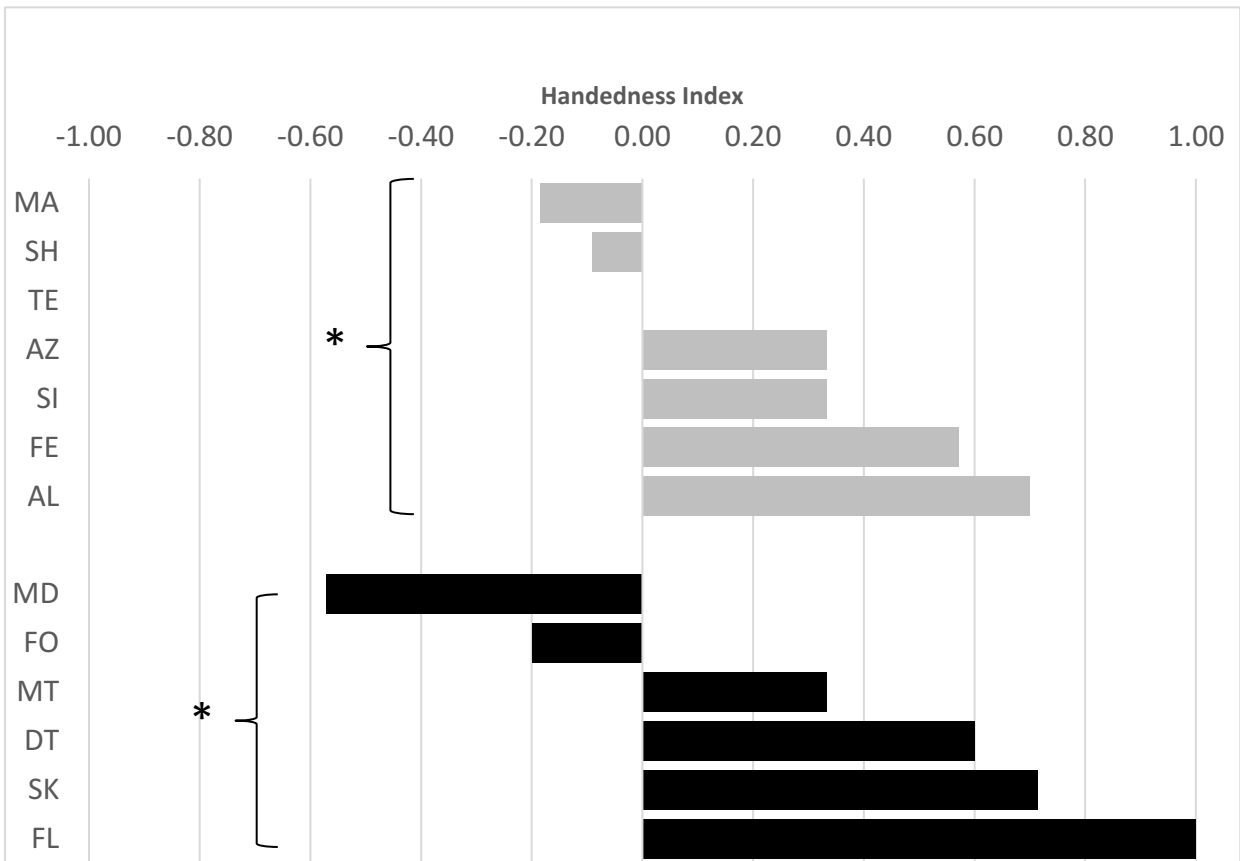
634

635



636  
637  
638  
639

Figure 3. The bilateral venom pose in two Javan slow lorises (*Nycticebus javanicus*), right-handed grasp (left) and the left-handed grasp (right).



640  
641  
642  
643  
644  
645  
646  
647  
648

Figure 4. HI value for wild grasping (grey) and captive reach (black) observations in slow lorises. Positive values represent a right hand preference and a negative value represents a left hand preference. The (\*) denotes a significant difference between the right and left hand use in the group.

649 Table 1. Details about the sample size and location of the photographed slow lorises.

650

<b>NYCTICEBUS SPECIES</b>	<b>N</b>	<b>LOCATION IN INDONESIA</b>
<b>SUMATRAN</b>	20	Cikananga Conservation Breeding Centre (CCBC), Sukabumi, Java
<b>JAVAN</b>	6	Little Fireface Project Field site (LFP), Garut, Java
<b>JAVAN</b>	9	International Animal Rescue (IAR), Bogor, Java
<b>GREAT</b>	7	Schmutzer Primate Center (SPC), Jakarta, Java

651

652

653

654 Table 2. Handedness of Unimanual reach and grasping in two species of slow loris

655 (*Nycticebus javanicus* and *N. coucang*).

656

657

	SEX	N	RH	LH	HI	ASB-HI	P-VALUE	HAND PREFERENCE
AL	M	20	17	3	0.70	0.70	0.003	R
AZ	M	6	4	2	0.33	0.33	0.688	A
FE	M	28	22	6	0.57	0.57	0.005	R
MA	F	27	11	16	-0.19	0.18	0.556	A
SH	F	11	5	6	-0.09	0.09	1	A
SI	F	6	4	2	0.33	0.33	0.688	A
TE	F	16	8	8	0.00	0.00	1	A
DT	F	15	12	3	0.60	0.60	0.035	R
FO	F	15	6	9	-0.20	0.20	0.607	A
FL	F	15	15	0	1.00	1.00	-	R
MD	F	28	6	22	-0.57	0.57	0.005	L
SK	M	21	18	3	0.71	0.71	-	R
MT	M	18	12	6	0.33	0.33	0.238	A

658 A, ambivalent hand preference index; HI, handedness index; ABS-HI, LH, left hand reach or

659 grasp; RH, right hand reach or grasp; L, left hand dominance during task; R, right hand

660 dominance during task

661