

1 **The lemur baseline: How lemurs compare to monkeys and apes in the Primate Cognition**

2 **Test Battery**

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28 **ABSTRACT**

29 Primates have relatively larger brains than other mammals even though brain tissue is
30 energetically costly. Comparative studies of variation in cognitive skills allow testing of
31 evolutionary hypotheses addressing socioecological factors driving the evolution of primate
32 brain size. However, data on cognitive abilities for meaningful interspecific comparisons are
33 only available for haplorhine primates (great apes, Old- and New World monkeys) although
34 strepsirrhine primates (lemurs and lorises) serve as the best living models of ancestral primate
35 cognitive skills, linking primates to other mammals. To begin filling this gap, we tested
36 members of three lemur species (*Microcebus murinus*, *Varecia variegata*, *Lemur catta*) with
37 the Primate Cognition Test Battery, a comprehensive set of experiments addressing physical
38 and social cognitive skills that has previously been used in studies of haplorhines. We found no
39 significant differences in cognitive performance among lemur species and, surprisingly, their
40 average performance was not different from that of haplorhines in many aspects. Specifically,
41 lemurs' overall performance was inferior in the physical domain but matched that of
42 haplorhines in the social domain. These results question a clear-cut link between brain size and
43 cognitive skills, suggesting a more domain-specific distribution of cognitive abilities in
44 primates, and indicate more continuity in cognitive abilities across primate lineages than
45 previously thought.

46

47 **Keywords:** cognition, Primate Cognition Test Battery, primates, lemurs

48

49 INTRODUCTION

50 One central question in comparative cognition is why primates have evolved larger brains and
51 enhanced cognitive skills compared to other equally-sized mammalian species (Shettleworth
52 2010). Among primates, this effect is paralleled by a disproportionate increase in brain size
53 from strepsirrhines to haplorhines and humans (Dunbar 1992; Isler et al. 2008; Jerison 1973;
54 Martin 1981). Because larger brains are energetically more expensive (Aiello and Wheeler
55 1995), they are assumed to confer benefits with regard to enhanced cognitive abilities that
56 compensate this additional investment (Navarrete et al. 2011; Reader and Laland 2002; Reader
57 et al. 2011).

58 Several non-mutually exclusive hypotheses on the evolution of brain size have been
59 proposed to account for the distinctive cognitive abilities of primates (Dunbar and Shultz 2017).
60 According to the *General intelligence hypothesis*, larger brains are thought to confer an
61 advantage because of faster learning and larger memory capacities (Spearman 1904). The
62 *Ecological intelligence hypothesis* suggests that environmental and ecological challenges in
63 food acquisition, including spatial and spatio-temporal processes to memorize seasonally
64 available food or manipulative skills for extractive foraging, selected for larger brains (Byrne
65 1996; Clutton-Brock and Harvey 1980; Heldstab et al. 2016; Milton 1981; Powell et al. 2017).
66 Several versions of the *Social brain hypothesis* posit that increased cognitive skills in primates
67 evolved in response to the constant challenges associated with the complexity of social life,
68 such as competition and cooperation within larger social groups (Byrne and Whiten 1988;
69 Dunbar 1992; Dunbar and Shultz 2007; Humphrey 1976; Jolly 1966a; Kudo and Dunbar 2001).
70 However, support for the *Social brain hypothesis* is not uniform in other taxa, with brain size
71 correlating positively with measures of sociality in some insectivores, bats and ungulates (e.g.
72 Barton et al. 1995; Byrne and Bates 2010; Dunbar and Bever 1998; Shultz and Dunbar 2006),
73 but not in corvids (Emery et al. 2007; Shultz and Dunbar 2007), and it is equivocal in carnivores
74 (Benson-Amram et al. 2016; Dunbar and Bever 1998; Finarelli and Flynn 2009; Holekamp et

75 al. 2007; Pérez-Barbería et al. 2007). Moreover, recent comparative analyses among primates
76 indicated that brain size is associated with ecological (home range size, diet, activity period),
77 but not with social factors (DeCasien et al. 2017; Powell et al. 2017), also challenging the social
78 brain hypothesis.

79 Since these studies usually link interspecific variation in brain size with certain socio-
80 ecological factors, it is essential to understand how brain size actually impacts cognitive skills.
81 Hence, comparative studies of cognitive abilities, ideally using identical tests, across the
82 primate order and beyond are required. However, comparisons of performance in cognitive
83 experiments across species may fail due to variation in the experimental set-up and specific
84 methods (van Horik and Emery 2011; Krasheninnikova et al. 2019; MacLean et al. 2012).

85 To overcome this problem, Herrmann and colleagues (2007) assembled a systematic
86 toolbox for comparative analysis, called the *Primate Cognition Test Battery* (PCTB), which
87 compared cognitive skills in various tasks in the physical and social domain among 2.5-year-
88 old children, chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*). The physical
89 domain deals with the spatial-temporal-causal relations of inanimate objects, while the social
90 domain deals with the intentional actions, perceptions, and knowledge of other animate beings
91 (Tomasello and Call 1997). These tests revealed that children and chimpanzees have similar
92 cognitive skills for dealing with the physical world, but children have increased cognitive skills
93 for dealing with the social world, particularly in the scale of social learning. These results
94 support the *Cultural intelligence hypothesis*, a variant of the Social brain hypothesis, suggesting
95 that exchanging knowledge within human cultural groups requires specific socio-cognitive
96 skills, such as social learning or Theory of Mind (e.g. Boyd and Richerson 1998; Herrmann et
97 al. 2007; Whiten and van Schaik 2007).

98 Application of the PCTB to two other haplorhine primate species, long-tailed macaques
99 (*Macaca fascicularis*) and olive baboons (*Papio anubis*), revealed that both species performed
100 similarly to great apes in both the physical and the social domain (Schmitt et al. 2012).

101 Specifically, chimpanzees outperformed macaques only in tasks on spatial understanding and
102 tool use. Since chimpanzees have relatively larger brains than macaques or baboons (Isler et al.
103 2008; Jerison 1973), these results question the clear-cut relationship between cognitive
104 performance and brain size (Schmitt et al. 2012). In addition, four closely related macaque
105 species that differ in their degree of social tolerance, performed similarly in cognitive tests of
106 the PCTB in the physical domain. However, socially more tolerant species performed better in
107 one task of the social domain and the inhibitory control task, suggesting that social tolerance is
108 associated with a set of cognitive skills that are specifically required for cooperation (Joly et al.
109 2017). Thus, further studies on additional non-human primates are required to explore the
110 interrelationships among cognitive abilities, socio-ecological traits and brain size
111 (ManyPrimates et al. 2019).

112 Strepsirrhine primates are the obvious candidates for such an extended comparative
113 approach because they represent the best living models of the earliest primates and the link
114 between primates and other mammalian orders (Fichtel and Kappeler 2010; MacLean et al.
115 2008). Strepsirrhines split off from the main primate lineage approximately 60 million years
116 ago and retained many ancestral primate traits (Martin 1990; Yoder et al. 1996; Yoder and Yang
117 2004). Importantly, strepsirrhine primates have relatively smaller brains than haplorhines, and
118 their brain size does not correlate with group size (MacLean et al. 2009). Although older studies
119 suggested that strepsirrhine primates possess physical cognitive abilities that are inferior to
120 those of haplorhines (e.g. Ehrlich et al. 1976; Jolly 1964; Maslow and Harlow 1932), recent
121 studies indicated that their cognitive skills are similar to those of haplorhines (e.g. Deppe et al.
122 2009; Fichtel and Kappeler 2010; Kittler et al. 2015, 2018; Santos et al. 2005a, b). However,
123 existing studies of strepsirrhine cognition used isolated tests, hampering systematic
124 interspecific comparisons. Hence, a comprehensive study investigating a broad variety of tasks
125 addressing different cognitive skills in lemurs, and replicating the exact same methods used in
126 the PCTB, seems indicated for a systematic comparison across both primate suborders.

127 To this end, we applied the PCTB to three species of lemur that differ in key socio-
128 ecological traits: ring-tailed lemurs (*Lemur catta*), black-and-white ruffed lemurs (*Varecia*
129 *variegata*; in the following: ruffed lemurs) and gray mouse lemurs (*Microcebus murinus*, Table
130 1). Mouse lemurs have one of the smallest brain sizes among primates, and absolute brain size
131 increases from mouse lemurs over ring-tailed lemurs to ruffed lemurs (Isler et al. 2008). Ring-
132 tailed lemurs are diurnal opportunistic omnivores that live in groups of on average 14
133 individuals (Gould et al. 2003; Jolly 1966b; Sussman 1991). Ruffed lemurs are diurnal,
134 frugivorous and live in small groups (average 6 individuals), exhibiting a fission-fusion social
135 organization (Baden et al. 2015; Holmes et al. 2016; Vasey 2003). Gray mouse lemurs are
136 nocturnal, omnivorous solitary foragers that form sleeping-groups among related females
137 (Eberle and Kappeler 2006; Isler et al. 2008).

138 According to the *General intelligence hypothesis*, we predicted that the tested apes and
139 monkeys outperform lemurs because they have absolutely larger brains (Table 1). In accordance
140 with the *Ecological intelligence hypothesis* we predicted that the more frugivorous species or
141 those with a broader dietary breadth perform better (Table 1). Because lemurs generally live in
142 smaller groups than monkeys and apes (Kappeler and Heymann 1996), we predicted that they
143 should have inferior cognitive abilities than the already tested group-living species according
144 to the *Social intelligence hypothesis* (Table 1).

145

146 **METHODS**

147 Experiments were conducted with adult individuals of gray mouse lemurs (n=9-15), ring-tailed
148 lemurs (n=26-27) and black-and-white ruffed lemurs (n=13). All individuals were born in
149 captivity and housed in enriched or semi-natural environments, either at the German Primate
150 Centre (DPZ, Göttingen) or the Affenwald Wildlife Park (Straußberg, Germany). The lemurs
151 at the Affenwald range freely within a 3.5 ha natural forest enclosure. At the DPZ, ring-tailed
152 and ruffed lemurs are offered indoor and outdoor enclosures equipped with enriching climbing

153 materials and natural vegetation. The nocturnal mouse lemurs are kept indoors with an
154 artificially reversed day-night-cycle, and cages are equipped with climbing material, fresh
155 natural branches and leaves. All individuals were tested individually in their familiar indoor
156 enclosures and were unfamiliar with the presented tasks. Since some individuals passed away
157 during the course of the study, not all individuals participated in every task of the test battery
158 (Table S1, Supplemental). To ensure comparability with the previous studies, the experimental
159 setup was replicated after the PCTB (Herrmann et al. 2007; Schmitt et al. 2012), and only
160 objects presented in the tests were adjusted in size for lemurs.

161

162 ***Ethical statement***

163 All animal work followed relevant national and international guidelines. The animals were kept
164 under conditions documented in the European Directive 2010/63/EU (directive on the
165 protection of animals used for experimental and other scientific purposes) and the EU
166 Recommendations 2007/526/EG (guidelines for the accommodations and care of animals used
167 for experimental and other scientific purposes). Consultation and approval of the experimental
168 protocols by the Animal Welfare Body of the German Primate Center is documented (E2-17).

169

170 ***General testing procedure***

171 During the experiments, individuals were briefly separated from the group. The testing
172 apparatus for all tasks consisted of a table with a sliding board on top that was attached to the
173 fence of the subjects' enclosures (Figure S2, Supplemental). In most of the tasks two or three
174 opaque cups (ruffed- & ring-tailed lemurs: Ø 6.8 cm x 7.5 cm; mouse lemurs: Ø 2.5 cm x 3
175 cm), which were placed upside down in a row on the sliding board, were used to cover the food
176 reward (see also Supplemental). If necessary, a cardboard occluder was put on top of the sliding
177 board between the experimental setup and the individual to hide the baiting process from the
178 individuals. The position of the reward was randomized and counter-balanced across all

179 possible locations, and the reward was never put in the same place for more than two
180 consecutive trials. Once the board was pushed into reach of an individual, the experiment began
181 and, depending on the task, the individual had to manipulate an item or indicate its choice by
182 pointing or reaching towards the chosen item, to obtain the reward if chosen correctly. If the
183 choice was incorrect, the correct location of the reward was shown to the individual after each
184 trial.

185 For most of the tasks at least 6 trials were conducted per individual and setup (Table S1,
186 Supplemental). Raisins and pieces of banana served as rewards. During testing, no possible
187 cues to where the reward was located were provided by the experimenter; she simply put her
188 hands on her lap and her gaze was directed downwards. All experiments were videotaped and
189 responses of the subjects to the tasks coded afterwards from the videos. A naïve second observer
190 additionally scored 20% of all trials a second time to assess inter-observer reliability. The
191 Interclass Correlation Coefficient was excellent ($ICC = 0.985$).

192

193 ***The Primate Cognition Test Battery***

194 All experimental setups and methods were replicated from the *PCTB* (Herrmann et al. 2007;
195 Schmitt et al. 2012). Following Schmitt et al. (2012), we also doubled the number of trials for
196 all object-choice tasks of the test battery (Table S1, Supplemental) to evenly distribute objects
197 between all possible spatial positions and combinations of manipulations. In total, the *PCTB*
198 consists of 16 different experimental tasks, 10 investigating physical and 6 social cognitive
199 skills. These tasks can be grouped into 6 different scales: space, quantity and causality for the
200 physical and social learning, communication and Theory of Mind for the social domain.

201 In the *physical domain*, the *scale space* examines the ability to track objects in space in
202 four tasks: spatial memory, object permanence, rotation and transposition. The *scale quantity*
203 tests the numerical understanding of individuals and consists of two tasks: relative numbers and
204 addition numbers. The *scale causality* consists of four tasks: noise, shape, tool use and tool

205 properties to examine the ability to understand spatial-causal relationships. In the *social*
206 *domain*, the *scale social learning* examines in one task whether individuals use social
207 information provided by a human demonstrator to solve a problem. The *scale communication*
208 examines whether individuals are able to understand communicative cues given by humans in
209 three tasks: comprehension, pointing cups and attentional state. Finally, in the *scale Theory of*
210 *Mind*, individuals were confronted with two tasks: gaze following and intentions. A detailed
211 description of the general setup and the methodology of the experiments can be found in the
212 supplementary material (Supplemental).

213

214 ***Temperament, inhibitory control, rank and learning effect***

215 To assess the influence of temperament, inhibitory control and dominance rank on lemurs'
216 performances in the test battery, individuals participated in a set of additional tests (Herrmann
217 et al. 2007; Schmitt et al. 2012). Due to logistic constraints, the temperament tests could only
218 be conducted with ring-tailed and ruffed lemurs. For temperament, we measured whether
219 individuals would approach novel objects, people and foods (for details see Supplemental).
220 Inhibitory control was measured during an additional session of the spatial memory task, in
221 which out of three cups only the two outer ones were baited with a reward and hence,
222 individuals had to skip the cup in the middle. Dominance rank (high, middle or low-ranking)
223 was inferred by focal observations of ring-tailed and ruffed lemurs but not for the solitary mouse
224 lemurs, according to Pereira and Kappeler (1997). We also controlled for potential learning
225 effects within the trials of a task by calculating Pearson's correlations between performance in
226 the first and second half of trials.

227

228 ***Data analyses***

229 We measured the performance of individuals by the proportion of correct responses for each
230 task. We applied Wilcoxon tests followed by Benjamini-Hochberg corrections (for multiple

231 testing) for each task and lemur species to examine whether they performed above chance level.
232 Since no individual solved the social learning task and only one the tool use task, we omitted
233 both tasks from the interspecies comparisons. To analyse whether the three lemur species
234 differed in their performance in the tasks of the PCTB, we used multivariate analysis of variance
235 (MANOVA) with species, sex, rank, age and age:species as between-subject factor and their
236 performance in all tasks as dependent variable. To compare all three species' performances
237 between the different tasks, we used univariate analysis of variance (ANOVA, for normally
238 distributed data) or Kruskal-Wallis tests followed by *post hoc* analyses (with Bonferroni
239 correction). For significant results, we used an analysis of covariance (ANCOVA) to control
240 for age in these tasks.

241 Comparisons of performance in tests of the PCTB were conducted between the three
242 lemur species and four haplorhine species (chimpanzees, orangutans, olive baboons, and long-
243 tailed macaques) for which data on individual performance were kindly provided by E.
244 Herrmann and V. Schmitt. On the scale level we applied a MANOVA, followed by ANOVAs
245 or Kruskal-Wallis tests and *post hoc* corrections (Bonferroni) in case of significant results. All
246 statistical analyses were conducted in R version 3.2.2 (R Core Team, Vienna, Austria).

247

248 **RESULTS**

249 ***Lemurs' performance in the physical and social domain***

250 In the *physical domain*, the chance level was at 33% in all four tasks of the *scale space*. The
251 three lemur species performed significantly above chance level in the spatial memory and the
252 rotation task (Table 2, Fig. 1). In the object permanence tasks, only ruffed lemurs performed
253 above chance level, while in the control task, all three species performed above chance level
254 (Table 2, Fig. 1). In the *scale quantity*, the three lemur species performed significantly above
255 chance level (50%) in both tasks (Table 2, Fig. 1). In the *scale causality*, the tool use task was

256 successfully solved by only one ring-tailed lemur. However, in the shape and tool properties
257 tasks, all three lemur species performed above chance level (50%; Table 2).

258 In the *social domain*, no lemur solved the social learning task using a similar technique
259 as demonstrated by a human experimenter (Table 2, Fig. 1). In the *scale communication*, all
260 three lemur species performed significantly above chance level (50%) in the comprehension
261 task, whereas only mouse lemurs performed above chance level (50%) in the pointing cups
262 task. No lemur species performed above chance level in the attentional state task. In the *scale*
263 *Theory of Mind*, none of the lemur species did follow the gaze of the human experimenter
264 upwards significantly more often than in the control condition in which no cue was given
265 (baseline: 20%; Table 2, Fig. 1). In contrast, all lemur species performed significantly above
266 chance level (50%) in the intentions task (Table 2, Fig. 1).

267

268 ***Influence of age, sex and rank on performance of the three lemur species***

269 Because the tool use task was solved by only one individual and the social learning task by
270 none, these two tasks were excluded from this comparison. A multivariate analysis of variance
271 of the 14 remaining tasks revealed no differences in the average performance among the three
272 lemur species (MANOVA; Wilk's $\Lambda=0.498$, $F(19,14)=1.37$, $p=0.257$). Furthermore, average
273 performance was not influenced by sex (Wilk's $\Lambda=0.461$, $F(19,14)=1.59$, $p=0.173$), rank
274 (Wilk's $\Lambda=0.273$, $F(38,28)=1.24$, $p=0.268$), age (Wilk's $\Lambda=0.568$, $F(19,14)=1.03$, $p=0.466$) or
275 age within species (age:species; Wilk's $\Lambda=0.599$, $F(19,14)=0.91$, $p=0.566$).

276

277 ***Personality, inhibitory control and learning***

278 The three temperament measures (latency, proximity and duration) of ring-tailed or ruffed
279 lemurs did neither correlate with the performance in the physical domain of the PCTB
280 (Pearson's correlations, all $p>0.05$, see Supplemental), nor with the performance of ring-tailed
281 lemurs in the *social domain*. In ruffed lemurs, however, the latency to approach and proximity

282 to a novel stimulus correlated with performance in the social domain (latency to approach:
283 Pearson's correlation, $r(11)=0.61$, $p=0.026$; proximity: Pearson's correlation, $r(11)=-0.59$,
284 $p=0.032$). No correlation was found between time individuals spent close to the setup (duration)
285 and performance (Pearson's correlation, $r(11)=-0.30$, $p=0.323$). Performance in the inhibitory
286 control task did not correlate with performance in the physical and social domain (see Table
287 S4, Supplemental). In addition, we did not find a learning effect in performance between the
288 first and second half of trials within the tasks (Wilcoxon Signed-Rank test: $V=806.5$, $p=0.585$).

289

290 ***Comparison of lemurs and haplorhines in the physical and social domain***

291 The comparison of chimpanzees, orangutans, baboons, macaques, ruffed-, ring-tailed- and
292 mouse lemurs in their overall average performance in the two domains revealed differences
293 among species (Wilk's $\Lambda=0.383$, $F(406,12)=20.87$, $p<0.001$). Species differed in performance
294 in the *physical domain* (Kruskal-Wallis, $\chi^2=127.26$, $df=6$, $p<0.001$; Fig. 2), but not in the *social*
295 *domain* (Kruskal-Wallis, $\chi^2=10.25$, $df=6$, $p=0.115$; Fig. 2). In the *physical domain*, only
296 chimpanzees performed significantly better than ruffed lemurs, and chimpanzees and
297 orangutans outperformed ring-tailed and mouse lemurs (see Table S4, Supplemental).

298

299 ***Comparison of lemurs and haplorhines in the different scales***

300 For a more detailed comparison of all seven species, we conducted a MANOVA including each
301 individuals' overall performance in all six scales, which revealed significant differences among
302 species (Wilk's $\Lambda=0.284$, $F(833,36)=7.68$, $p<0.001$). Species differed in all scales except the
303 *scale communication* (ANOVAs or Kruskal-Wallis tests, see Table 3; Fig. 3). In the *scale space*,
304 chimpanzees outperformed all other species, except baboons. Orangutans performed better than
305 ruffed and ring-tailed lemurs, baboons performed better than all three lemur species, and
306 macaques performed similar to all lemur species (Table 4; Fig. 3). In the *scale quantity*, only
307 chimpanzees performed better than ring-tailed lemurs (Table 4; Fig. 3), and in the *scale*

308 *causality*, chimpanzees outperformed all other species, and orangutans performed better than
309 mouse lemurs (Table 4; Fig. 3). However, this scale was strongly biased by the results of the
310 tool use task, which was only solved by chimpanzees, orangutans and one ring-tailed lemur.
311 Excluding the tool use task from this comparison revealed that only chimpanzees performed
312 better than mouse lemurs (Table 4; Fig. S2, Supplemental).

313 In the *social domain*, all species, except great apes, performed poorly in the social
314 learning task, whereas all species performed equally well in the *scale communication* (Table 4;
315 Fig. 3). In the *scale Theory of Mind*, however, chimpanzees performed less good than macaques
316 and ring-tailed lemurs. All other species performed better than orangutans, except mouse lemurs
317 and macaques, and ring-tailed lemurs outperformed mouse lemurs (Table 4; Fig. 3).

318

319 **DISCUSSION**

320 In this study, we applied the Primate Cognition Test Battery to three lemur species differing in
321 socioecological traits and brain size and compared their performance with that of four
322 haplorhine species tested in previous studies with the exact same methods. In the *physical*
323 *domain*, apes and baboons performed better than lemurs in the *space scale*, chimpanzees
324 performed better than ring-tailed lemurs in the *quantity scale* but no differences among species
325 were found in the *causality scale*, after excluding the tool use task. In the *social domain*, lemurs
326 performed at level to apes and monkeys. Most interestingly, in the *Theory of Mind scale*, great
327 apes were outperformed by all other species except mouse lemurs. Since these species differ in
328 relative and absolute brains size (Table 1), with a more than 200-fold difference in brain size
329 between mouse lemurs and orangutans or chimpanzees, our results do not support the notion of
330 a clear-cut link between brain size and cognitive skills, but suggest a more domain-specific
331 distribution of cognitive abilities in primates.

332 In the *physical domain*, lemurs were outperformed by apes and baboons in the *space*
333 *scale*. The species with the largest brains (apes and baboons) performed better than all other

334 species, supporting the General intelligence hypothesis. These findings are in line with an
335 earlier study showing that apes and monkeys differ in their ability to track object displacements
336 (Amici et al. 2010). Spatial understanding is also important to remember food resources or to
337 track conspecifics (Dunbar and Shultz 2017), and species (chimpanzees, orangutans, baboons)
338 having a larger dietary breadth performed better in these tasks, but the species with the highest
339 amount of fruits in the diet (ruffed lemurs) did not perform better than other species, providing
340 only partial support for the Ecological intelligence hypothesis. There was no clear pattern
341 between group size and performance in the *space scale*, providing no support for the Social
342 intelligence hypothesis.

343 In the *quantity scale*, only chimpanzees performed better than ring-tailed lemurs, and
344 all other species performed similarly, indicating that a certain level of numerical understanding
345 appears to be a basal cognitive trait of all primates. These results support earlier studies
346 indicating that lemurs do not differ from haplorhine primates in numerosities and simple
347 arithmetic operations (Jones and Brannon 2012; Merritt et al. 2011; Santos et al. 2005a). Since
348 a comparable numerical understanding as tested in the PCTB has also been reported for various
349 taxa outside the primate order, including fish and insects (e.g. Agrillo et al. 2012; Chittka and
350 Geiger 1995; Pahl et al. 2013; but see Krasheninnikova et al. 2019), a basal numerical
351 understanding may be present in many animals.

352 In the *causality scale*, lemurs performed as well as both monkey species, but all
353 monkeys and lemurs were outperformed by chimpanzees, who excelled in the tool use task.
354 Even natural tool users, such as orangutans and long-tailed macaques (Brotcorne et al. 2017;
355 van Schaik et al. 2003), hardly solved this task (Schmitt et al. 2012). It required the ability to
356 use a stick to rake a food reward into reach, which might have been too challenging for species
357 exhibiting either a medium (baboons, macaques) or low (lemurs) level of precision grip
358 (Torigoe 1985). Although long-tailed macaques use stone tools to crack open nuts or mussels,
359 they do so mainly by applying force rather than using fine-motor skills (Gumert and

360 Malaivijitnond 2012). Thus, the tool use task appears unsuitable for a fair interspecific
361 comparison. Excluding this task from the *quantity scale* resulted in a rather similar overall
362 average performance of all species. Interestingly, lemurs that have never been observed to use
363 tools in the wild (Fichtel and Kappeler 2010; Kittler et al. 2015, 2018), appeared to exhibit an
364 understanding for the necessary functional properties of pulling tools (Santos et al. 2005b;
365 Kittler et al. 2018). Hence, except for the *space scale* we did not find systematic species
366 differences in performance, challenging the notion that there is a domain-general distinction
367 between haplorhines and strepsirrhines (Deaner et al. 2006). Our results instead suggest the
368 existence of domain-specific cognitive differences.

369 In the social domain, species differences were less pronounced, and lemurs' overall
370 performance in the *Theory of Mind scale* was equal to that of monkeys and even superior to that
371 of apes. In the *social learning scale* neither lemurs, nor baboons or long-tailed macaques solved
372 the task. However, long-tailed macaques exhibit cultural variation in stone handling techniques
373 in the wild, indicating that they are able to learn socially (Brotcorne et al. 2017). The ability to
374 learn socially has also been reported in ring-tailed and ruffed lemurs (e.g. Kappeler 1987;
375 Kendal et al. 2010; O'Mara and Hickey 2012; Stoinski et al. 2011), but remains unstudied in
376 mouse lemurs. Since individuals had to learn in this task from a human demonstrator, the
377 phylogenetic distance between species and the demonstrator might have influenced learning
378 abilities, because great apes performed better than Old World monkeys and lemurs (Schmitt et
379 al. 2012). Hence, it remains an open question whether monkeys and lemurs would perform
380 better when tested with a conspecific demonstrator. Moreover, the task required the ability to
381 shake a transparent tube or to insert a stick into the tube, which might have been too difficult
382 for species with limited dexterity (Torigoe 1985). Therefore, a social learning task adapted to
383 manipulative skills of Old World monkeys and lemurs (Schnoell and Fichtel 2012) might be
384 more informative in future studies.

385 In the *communication scale*, all species performed equally well, suggesting that all
386 species can make use of socio-visual cues given by others. This result is in line with those of
387 several other studies showing the ability to use social-visual cues presented by a human
388 demonstrator in object-choice experiments in birds (Schmidt et al. 2011), aquatic mammals (sea
389 lions: Malassis and Delfour 2015; dolphins: Tschudin et al. 2001), domestic animals (dogs:
390 Kaminski et al. 2005; Miklósi et al. 1998; pigs: Nawroth et al. 2016; goats: Wallis et al. 2015),
391 as well as other primates (Anderson et al. 1995; Itakura 1996).

392 In contrast, unexpected species differences emerged in the *Theory of Mind scale*, with
393 great apes performing inferior to both monkeys and lemurs. This difference was mainly due to
394 better performance of monkeys and lemurs in the intentions task, but not in the gaze following
395 task. In the gaze following task all lemurs performed below chance level, although it has been
396 shown that ring-tailed lemurs follow the gaze of conspecifics (Shepherd and Platt 2008) and
397 that they use human head orientation as a cue for gaze orientation in a food choice paradigm
398 (Botting et al. 2011, Sandel et al. 2011), questioning the validity of these gaze following tasks.
399 In the intention task, a human observer tried to reach a cup with a hidden reward repeatedly
400 with the hand. Monkeys and lemurs might have performed better than apes because they may
401 have solved the task by using spatial associations between the repeated hand movements and
402 the cup or by understanding the hand movements as a local enhancement (Shettleworth 2010;
403 Schmitt et al. 2012). Still, it remains puzzling why chimpanzees and orangutans did not use the
404 hand movement as a cue for the location of the hidden reward. Even more so because a
405 comparative study of Theory of Mind compatible learning styles in a simple dyadic game
406 between seven primate species, including chimpanzees and ring-tailed lemurs, and a
407 competitive human experimenter revealed that test performance was positively correlated with
408 brain volume but not with social group size, suggesting that Theory of Mind is mostly
409 determined by general cognitive capacity (Devaine et al. 2017). Hence, additional social

410 cognitive tests are required to obtain a better understanding of the relationship between brain
411 size and cognitive performance in the social domain.

412 Altogether, average species performances were generally not as different as it might
413 have been expected in view of the various hypotheses on the evolution of cognitive abilities.
414 Except for the scale space, the overall comparison does not provide support for the *General*
415 *intelligence hypothesis*, since variation in brain size cannot explain the observed results.
416 Similarly, performances of the seven species did not reflect any clear patterns concerning their
417 feeding ecology, i.e. the percentage of fruit in the diet or dietary breadth, except for the *space*
418 *scale* (see Table 1); hence, these results do not provide support for the *Ecological intelligence*
419 *hypothesis*. Moreover, our results do not provide support for the *Social intelligence hypothesis*
420 because lemurs, and especially the solitary mouse lemurs, should have performed inferior
421 compared to the haplorhine species (Dunbar and Shultz 2017).

422 Earlier comparative studies among primates linking performance in a range of
423 comparable cognitive tests in the physical or social domain revealed a link between
424 performance in these tasks and brain size (Deaner et al. 2006, 2007; Reader and Laland 2002;
425 Reader et al. 2011). However, studies using the exact same experimental set up revealed
426 contradictory results. Two studies addressing only one cognitive ability revealed a positive
427 relationship between brain size and performance in inhibitory control or Theory of Mind tests
428 (Maclean et al. 2014; Devaine et al. 2017), but all other studies applying various tests on
429 inhibitory control and spatial memory (Amici et al. 2008, 2010, 2012) or tasks of the Primate
430 Cognition Test Battery (Herrmann et al. 2007; Schmitt et al. 2012; this study), found no clear-
431 cut relationship between brain size and cognitive performance.

432 Even though lemurs performed at level with monkeys and great apes in many of these
433 experiments, we do not suggest that their cognitive abilities are *per se* on par with those of
434 larger-brained primates. In the physical domain, species differences emerged only in the space
435 scale, supporting the General intelligence hypothesis. However, no systematic species

436 differences were found in the quantity or causality scales, which address rather basal cognitive
437 abilities, which might not be variable enough to reveal actual differences between species.
438 Indeed, some fish and insects possess similar basal cognitive skills in the physical domain (Fuss
439 et al. 2014; Loukola et al. 2017; Schluessel et al. 2015). In the social domain, the social learning
440 task was not suitable for all species, and individuals might have recruited other abilities to solve
441 the problems, as discussed for the intention task above.

442 Many tests of the PCTB were based on two-or three-choice paradigms in which the costs
443 for choosing correctly were rather low, because the probability to receive a reward was either
444 50% or 33%, a random choice strategy might have been still relatively profitable. For example,
445 performance in a memory task increased in common marmosets (*Callithrix jacchus*) and
446 common squirrel monkeys (*Saimiri sciureus*) from a two-choice task to a nine-choice task, in
447 which the probability of success was lowered from 50% to 11%, making a wrong choice more
448 costly appeared to favour an appropriate learning strategy over a random choice strategy
449 (Schubiger et al. 2016). The application of a random choice strategy may also explain why four
450 parrot species that have been tested with the PCTB, may have failed to solve the tasks, besides
451 morphological differences in performing the tasks (Krasheninnikova et al. 2019).

452 In addition, the PCTB was designed to examine the spontaneous ability to solve the
453 tasks, and not to examine how long individuals need to learn the task. Hence, a test battery that
454 continued testing until individuals reached a certain criterion (e.g. 80 % correct responses) or
455 detailed analyses of applied learning strategies as in Devaine et al. (2017) may allow to compare
456 not only species differences in their spontaneous ability to solve the task, but also species-
457 specific learning curves as well as learning strategies, which might reveal more informative
458 differences.

459 To conclude, our study generated the first systematic results on cognitive abilities in
460 lemurs, and the comparison with haplorhines suggests that in many aspects of the physical and
461 social domain, the average performance in these tests of members of these two lineages do not

462 differ substantially from each other. These results reject the notion of a direct correlation
463 between brain size and cognitive abilities and question assumptions of domain-general
464 cognitive skills in primates. Overall, our results strengthen the view that when comparing
465 cognitive abilities among species, it is of vital importance to include a diverse set of tests from
466 both cognitive domains which are applicable to a diverse range of species and taxa (Auersperg
467 et al. 2011, 2013; Burkart et al. 2016; MacLean et al. 2012; Schmitt et al. 2012) and to carefully
468 consider the external validity of the specific tests (Krasheninnikova et al. 2019).

469

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701

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710

711 **AUTHORS' CONTRIBUTIONS**

712 C.F. and K.D. have a shared first-authorship, they conceived the study and analysed the data.

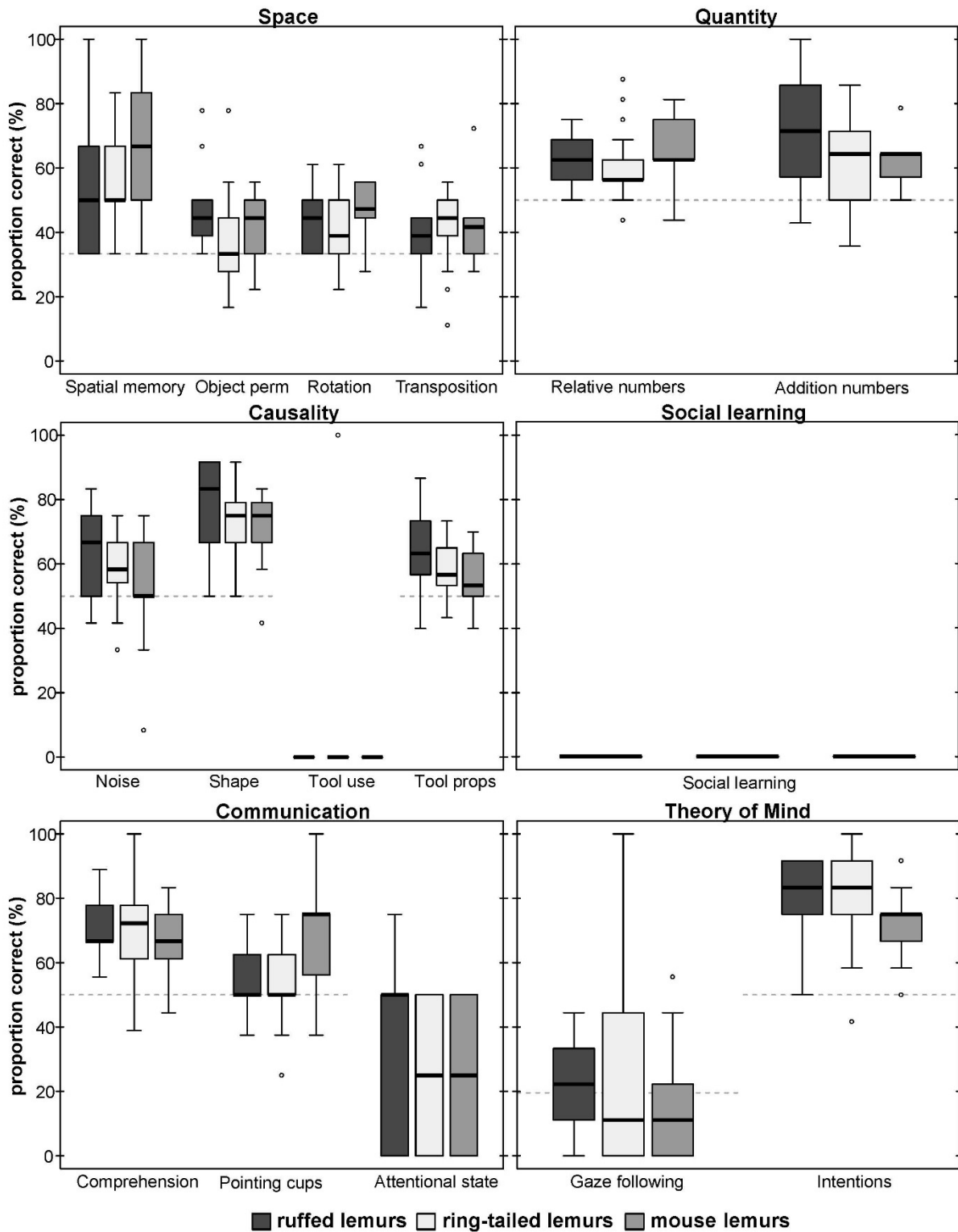
713 K.D. conducted the experiments. C.F., K.D. and P.M.K. wrote the manuscript. All authors gave
714 final approval for publication.

715

716 **COMPETING INTERESTS**

717 We have no competing interests.

718 **FIGURES**

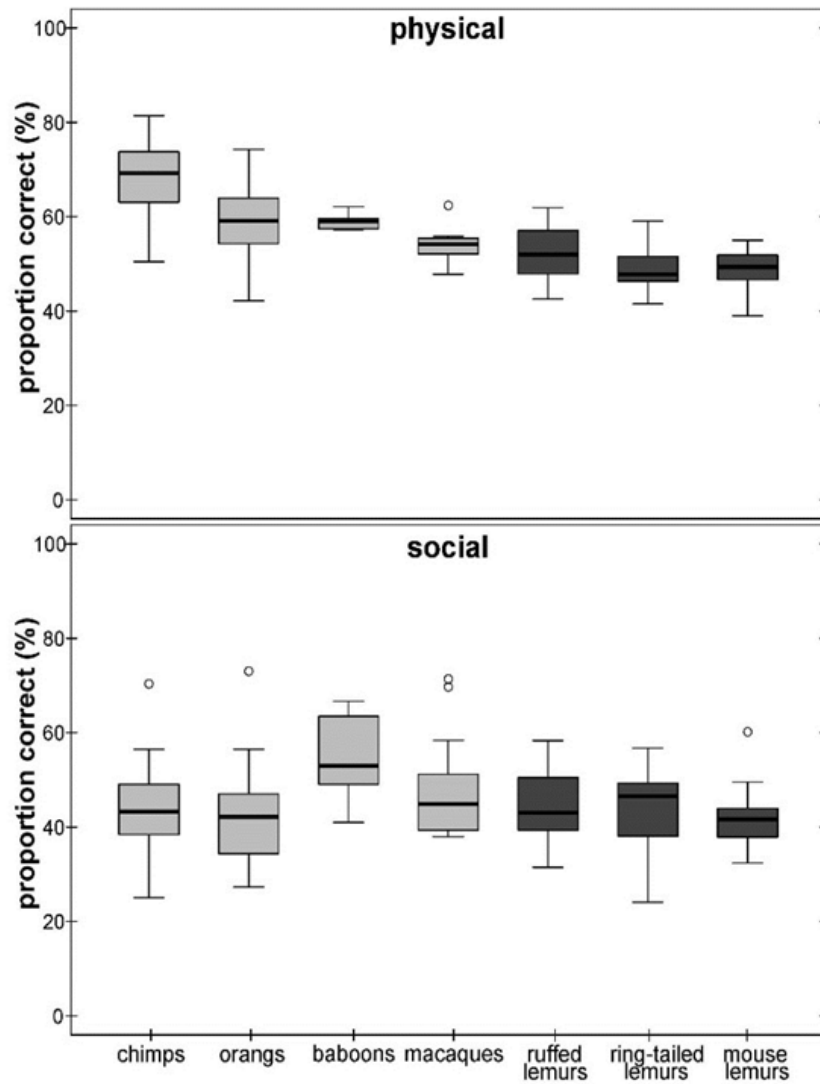


719

720 **Figure 1** Average performance of the three lemur species in all tasks of the PCTB. Represented are medians (black

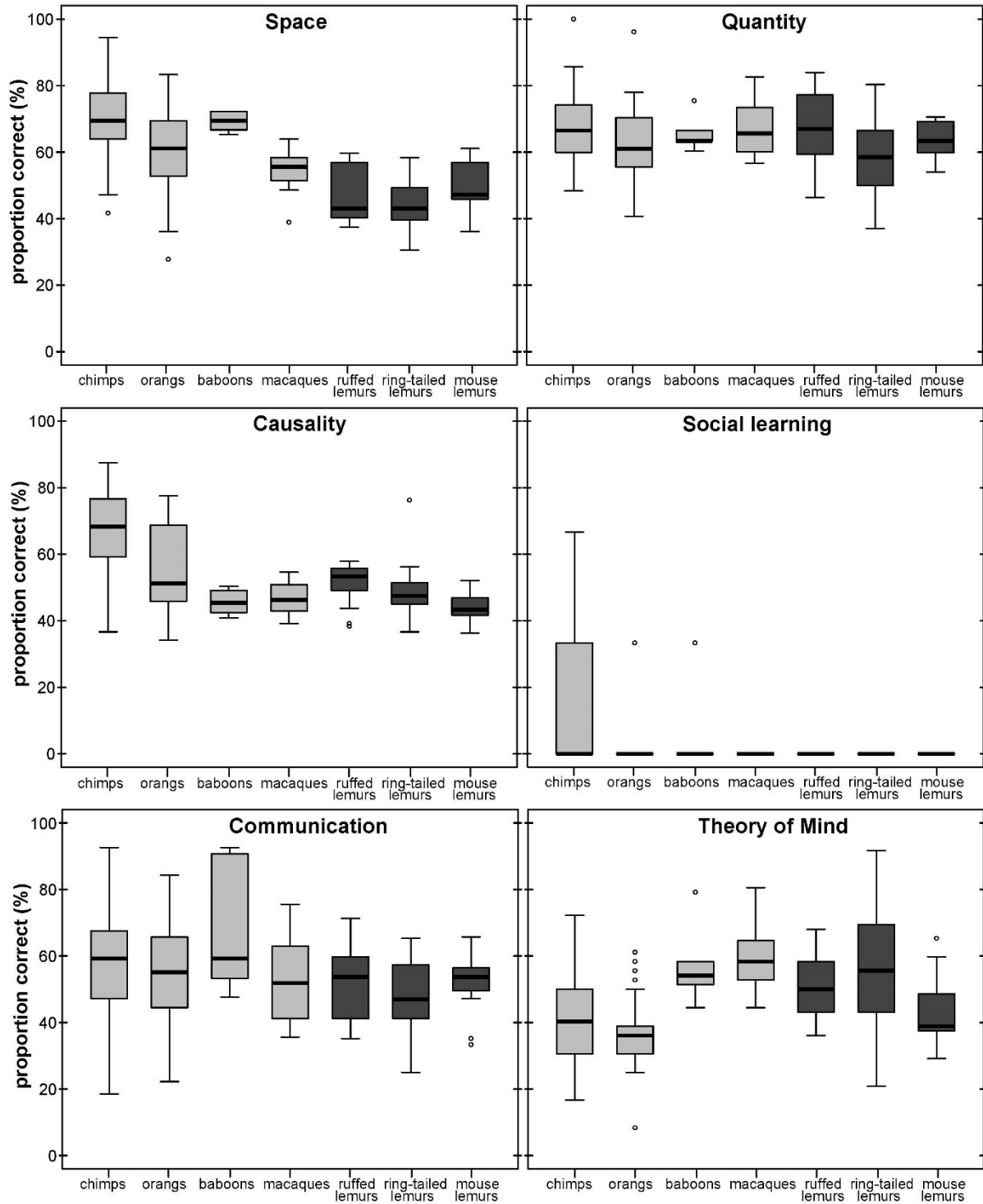
721 bars), interquartile ranges (boxes), upper and lower hinges (whiskers), and outliers (circles).

722



723

724 **Figure 2** Average performance of apes & monkeys (light grey) and lemurs (dark grey) in the two cognitive
725 domains. Represented are medians (black bars), interquartile ranges (boxes), upper and lower hinges (whiskers),
726 and outliers (circles).



727

728 **Figure 3** Average performance of apes & monkeys (light grey) and lemurs (dark grey) over the six scales.

729 Represented are medians (black bars), interquartile ranges (boxes), upper and lower hinges (whiskers), and outliers

730 (circles).

731 **TABLES**

732
733

Table 1 Summary of the most important traits for the seven non-human primate species.

species	n	ECV (cc)	% fruit	dietary breadth	social system	average group size
chimpanzees (<i>Pan troglodytes</i>)	106	368.4	66	6	group	47.6
orangutans (<i>Pongo pygmaeus</i>)	32	377.4	64	6	solitary	1.5
olive baboons (<i>Papio anubis</i>)	5	167.4	62	6	group	69
long-tailed macaques (<i>Macaca fascicularis</i>)	10-13	64	66.9	5	group	26
ruffed lemurs (<i>Varecia variegata</i>)	13	32.1	92	4	group	6
ring-tailed lemurs (<i>Lemur catta</i>)	26-27	22.9	54	5	group	11
grey mouse lemurs (<i>Microcebus murinus</i>)	9-16	1.6	31.3	4	solitary	1

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n=number of individuals, ECV=endocranial volume (absolute brain size), % fruit=percentage of fruit in the diet; Data from: Herrmann et al. 2007; Schmitt et al. 2012; Isler et al. 2008; MacLean et al. 2014; Dammhan and Kappeler 2006; Radespiel et al. 2006; Lahann 2007.

738 **Table 2** Summary of the mean proportions of correct responses of the three lemur species in all tasks and *scales* of the PCTB.

			Ruffed lemurs					Ring-tailed lemurs									
	trials	chance	n	M	adj p	SD	95% CI	n	M	adj p	SD	95% CI	n	M	adj p	SD	95% CI
Physical domain																	
Space				46.8		8	51.58		44.2		7	42.47		50.8		7	47.55
Spatial memory	6	33	13	53.9	0.017	23	42.66	27	55.6	0.001	17	49.62	15	66.7	0.004	18	58.68
Object permanence	18	33	13	47.9	0.006	12	41.55	27	38.3	0.112	15	32.44	12	42.1	0.074	10	36.48
Rotation	18	33	13	45.3	0.014	10	40.51	26	41.0	0.002	9	37.45	12	47.7	0.008	9	43.53
Transposition	18	33	13	40.2	0.052	13	33.47	27	42.2	0.001	11	38.46	12	41.2	0.019	12	35.48
Quantity				66.4		12	60.73		58.5		11	54.63		63.9		6	60.68
Relative numbers	16	50	13	62.0	0.006	7	58.66	27	60.4	0.007	10	57.64	9	66.0	0.019	11	59.73
Addition numbers	14	50	13	70.9	0.014	20	60.82	26	60.2	0.003	13	55.65	9	61.9	0.019	8	57.67
Causality				51.0		7	47.55		48.6		7	46.51		44.0		4	42.46
Noise	12	50	13	63.5	0.015	13	56.71	27	59.3	0.002	10	55.63	15	50.0	0.958	17	41.59
Shape	12	50	13	76.9	0.006	15	69.85	27	72.8	0.001	10	69.77	15	70.6	0.004	12	65.77
Tool use	1	-	13	0.0	-	-	-	27	3.7	-	19	-4.11	15	0.0	-	-	-
Tool properties	30	50	13	63.6	0.013	12	57.70	27	58.6	0.001	8	56.62	15	55.6	0.040	9	51.60
Social domain																	
Social learning	3	-	13	0.0	-	-	-	26	0.0	-	-	-	12	0.0	-	-	-
Communication				53.1		12	47.60		49.6		11	46.54		52.1		9	47.57
Comprehension	18	50	13	70.9	0.006	10	66.76	27	70.8	0.001	13	66.76	13	65.4	0.008	11	59.72
Pointing cups	8	50	13	53.9	0.220	9	49.59	27	55.1	0.050	12	51.59	15	68.3	0.008	16	60.76
Attentional state	4	-	13	34.6	-	28	19.50	26	21.2	-	22	13.30	14	25.0	-	22	14.36
Theory of mind				43.7		10	45.57		56.8		18	50.64		51.4		11	39.49
Gaze following	9	20 (bl)	13	23.9	0.326	17	15.33	27	30.0	0.340	33	18.42	15	11.1	0.713	17	2.20
Intentions	12	50	13	78.9	0.006	13	72.86	27	83.6	0.001	15	78.89	15	71.1	0.004	10	66.76

739 Numbers in boldface: Significant deviations from chance level (Wilcoxon tests); Trials=number of trials per task; chance=chance-level for each task; n=number of participating individuals;
 740 M=means of performance; adj= adjusted p-values (Benjamini-Hochberg-corrections); SD=standard deviation; CI=confidence interval; bl= baseline calculated from control condition.

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Table 3 Univariate analyses for the species differences for the six scales.

ANOVAs	Df	F-value	P-value
Quantity	6	3.49	0.0026 **
Communication	6	2.10	0.0549

Kruskal-Wallis tests	Df	χ^2	P-value
Space	6	111.68	<0.001 ***
Causality	6	68.59	<0.001 ***
Social learning	6	20.17	0.0026 **
Theory of Mind	6	55.08	<0.001 ***

<0.01; *<0.001 - significance levels

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747 **Table 4** Comparisons of performance among the seven non-human primate species for all six scales of the PCTB.
 748 Presented are the results of *post hoc* multiple comparisons (Bonferroni); significant results are in boldface.
 749 Causality II: The scale causality without the tools use task.

	Space	Quantity	Causality	Causality II	Social learning	Communication	Theory of Mind
Chimp - Orang	<0.001	0.275	<0.001	1	1	1	1
Chimp - Baboon	1	1	0.003	1	1	1	0.082
Chimp - Macaque	<0.001	1	<0.001	1	0.699	1	<0.001
Chimp - Ruffed lemur	<0.001	1	<0.001	1	0.352	1	0.077
Chimp - Ring-tailed lemur	<0.001	<0.001	<0.001	1	0.025	0.29	<0.001
Chimp - Mouse lemur	<0.001	1	<0.001	0.041	0.229	1	1
Orang - Baboon	1	1	1	1	1	0.677	0.014
Orang - Macaque	1	1	0.433	1	1	1	<0.001
Orang - Ruffed lemur	0.004	1	1	0.560	1	1	0.009
Orang - Ring-tailed lemur	<0.001	1	0.643	1	0.919	1	<0.001
Orang - Mouse lemur	0.237	1	0.046	0.918	1	1	1
Baboon - Macaque	0.176	1	1	1	1	0.591	1
Baboon - Ruffed lemur	0.001	1	1	1	1	0.653	1
Baboon - Ring-tailed lemur	<0.001	1	1	1	1	0.094	1
Baboon - Mouse lemur	0.023	1	1	1	1	0.424	0.816
Macaque - Ruffed lemur	1	1	1	1	1	1	1
Macaque - Ring-tailed lemur	0.074	0.307	1	1	1	1	1
Macaque - Mouse lemur	1	1	1	1	1	1	0.033
Ruffed lemur - Ring-tailed lemur	1	0.409	1	1	1	1	1
Ruffed lemur - Mouse lemur	1	1	1	0.008	1	1	1
Ring-tailed lemur - Mouse lemur	1	1	1	0.106	1	1	0.036

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