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1 **Increased performance in juvenile baboons is consistent with ontogenetic changes in**
2 **morphology.**

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21 **Abstract**

22 **Objectives:** In many primates, the greater proportion of climbing and suspensory behaviors in
23 the juvenile repertoire likely necessitates good grasping capacities. Here we tested whether
24 very young individuals show near-maximal levels of grasping strength, and whether such an
25 early onset of grasping performance could be explained by ontogenetic variability in the
26 morphology of the limbs in baboons.

27 **Material and methods:** We quantified a performance trait, hand pull strength, at the juvenile
28 and adult stages in a cross-sectional sample of 15 olive baboons (*Papio anubis*). We also
29 quantified bone dimensions (i.e., lengths, widths and heights) of the fore- (n=25) and hind
30 limb (n=21) elements based on osteological collections covering the whole development of
31 olive baboons.

32 **Results:** One-year old individuals demonstrated very high pull strengths (i.e., 200% of the
33 adult performance, relative to body mass), that are consistent with relatively wider phalanges
34 and digit joints in juveniles. The mature proportions and shape of the forelimb elements
35 appeared only at full adulthood (i.e., ≥ 4.5 years), whereas the mature hind limb proportions
36 and shape were observed much earlier during development.

37 **Discussion:** These changes in limb performance and morphology across ontogeny may be
38 explained with regard to behavioral transitions that olive baboons experience during their
39 development. Our findings highlight the effect of infant clinging to mother, an often-neglected
40 feature when discussing the origins of grasping in primates. The differences in growth patterns
41 we found between the forelimb and the hind limb further illustrate their different functional
42 roles, having likely evolved under different ecological pressures (manipulation and
43 locomotion, respectively).

44 **KEYWORDS**

45 allometry, development, grasping performance, limb morphology, primate evolution

46 INTRODUCTION

47 The precise functional and ecological contexts that have driven the evolution of the
48 primate grasping abilities remain unclear. Different hypotheses about the ancestral primate
49 prehensile and locomotor system have been proposed and remain debated (Cartmill, 1974;
50 Godinot, 1991; Sussman, 1991). In order to more precisely infer behavioral transitions during
51 primate evolution it is crucial to better understand the relations between form and function
52 (Kay & Cartmill, 1977). However, the functional significance of morphological variation in both
53 fossil and extant primates remains poorly understood. Morphological variation further
54 provides only partial clues about behavioral capacity. Indeed, different species can share
55 similar morphologies and display different behaviors, and conversely, they can display a same
56 behavior but have different morphologies (Lauder, 1996; Pouydebat, Laurin, Gorce, & Bels,
57 2008; Pouydebat, Gorce, & Bels, 2009; Pouydebat, Fragaszy, & Kivell, 2014). This renders the
58 understanding of the relationships between behavior and morphology difficult. Although
59 grasping performance remains rather poorly investigated, information thereof would be
60 particularly insightful to understand the link between morphology and behavior (Morbeck,
61 Preuschoft, & Gomberg, 1979; Young & Shapiro, 2018).

62 As juveniles are not ‘miniature adults’, but rather experience concomitant changes in
63 morphology and behavior during growth (Carrier, 1996; Herrel & Gibb, 2006; Young & Shapiro,
64 2018), studying ontogeny offers the opportunity to simultaneously and in “real-time” explore
65 the relations between behavior, performance, and morphology (Boulinguez-Ambroise,
66 Zablocki-Thomas, Aujard, Herrel, & Pouydebat, 2019; Druelle, Young, & Berillon, 2017a;
67 Hurov, 1991; Russo & Young, 2011; Thomas, Pouydebat, Le Brazidec, Aujard, & Herrel, 2016).
68 Such an approach might thus provide unique insights into the behavioral transitions that likely
69 occurred during the evolution of the primate prehensile and locomotor systems. Moreover,
70 the physiological and behavioral changes that occur during development may be more
71 pronounced than the differences observed between species (Young & Shapiro, 2018),
72 increasing our resolution to identify relations between form and function.

73 A growing number of studies have demonstrated developmental variability of
74 locomotor behaviors in primates. In chimpanzees (*Pan troglodytes*), gorillas (*Gorilla beringei*
75 *beringei*), and olive baboons (*Papio anubis*), juveniles display a much more arboreal locomotor

76 repertoire (i.e., climbing, clinging, suspension) than when they become adult (Doran, 1992,
77 1997; Druelle et al., 2017a; Sarringhaus, MacLatchy, & Mitani, 2014). In many primates, the
78 greater proportion of climbing and suspensory behaviors in the juvenile repertoire likely
79 necessitates good grasping capacities (Lawler, 2006; Druelle et al., 2017a). Yet, ontogenetic
80 data on the acquisition of grasping performance in primates are rare. A previous study on
81 mouse lemurs (*Microcebus murinus*) showed that juveniles display more powerful grip
82 postures and a relative maximal hand pull strength on par with adults (Boulinguez-Ambroise,
83 Herrel, & Pouydebat, 2020). Considering the performance as the “ability of an individual to
84 perform a task when maximally motivated” (Careau & Garland, 2012), grasping performance
85 has been previously assessed through a pull strength task (mice, Smith, Hicks, Ortiz, Martinez,
86 & Mandler, 1995; Iwanami et al., 2005; chameleons, Herrel et al., 2013; *Macaca mulatta*,
87 Bozek et al., 2014; *Microcebus murinus*, Thomas et al., 2016). The measurement of maximal
88 pulling force allows an assessment of how well a subject can grasp and hold onto a substrate
89 with the forelimbs or the hind limbs. Physical performance is often determined by different
90 intrinsic factors, such as age, size, but also musculo-skeletal anatomy (Aerts, 1998; Channon,
91 Usherwood, Crompton, Günther, & Vereecke, 2012; Chazeau, Marchal, Hackert, Perret, &
92 Herrel, 2013; Le Brazidec et al., 2017; Thomas et al., 2016). Ontogenetic variability in the
93 morphology of the prehensile system in primates may explain such an early onset of grasping
94 performance in young primates.

95 Several studies have documented variability in the morphology of the prehensile and
96 locomotor systems across ontogeny. Juveniles of a wide range of primate species display
97 relatively larger extremities (i.e., segment lengths, bone cross-sectional robustness) than
98 adults (Druelle et al., 2017a; Druelle, Aerts, D’Août, Moulin, & Berillon, 2017b; Patel, Organ,
99 Jashashvili, Bui, & Dunsworth, 2018; Poindexter & Nekaris, 2017; Young & Heard-Booth,
100 2016). It has been previously documented that relatively larger hands and feet may increase
101 grasping ability by increasing effective grip span in primates (Jungers & Fleagle, 1980; Lawler,
102 2006; Raichlen, 2005; Young & Heard-Booth, 2016). Moreover, wider segments of the hands
103 and feet may allow for increased muscle insertion areas, an increase in the cross-sectional
104 second moments of area (Carrier, 1983), and thus increased grip strength. Also, longer
105 forearms likely enhance the attachment surface for finger and hand flexors (Thomas et al.,
106 2016), thus promoting stronger grip. Relative longer limbs have consequently been observed

107 to be related to high grasping performance in juvenile mouse lemurs (Boulinguez-Ambroise et
108 al., 2019). Furthermore, a greater anatomical mechanical advantage of the forearm extensors
109 and flexors (i.e., triceps and biceps brachii) has been demonstrated in juvenile capuchin
110 monkeys (Young, 2005) such that young individuals may produce greater output forces for a
111 given amount of muscle force compared to adults.

112 Interestingly, previous studies have suggested different functional roles for the hind
113 limb and the forelimb during primate locomotion, with grasping feet having a more substantial
114 role in locomotion, freeing the forelimbs for other functions such as foraging (Boulinguez-
115 Ambroise et al., 2019; Chadwell & Young, 2015; Charles-Dominique, 1977; Cartmill, 1974b;
116 Patel et al., 2015). Recent studies on locomotor development have also revealed
117 morphological or behavioral differences between the grasping functions of the hand and the
118 foot. For example, in olive baboons (*Papio anubis*) changes in foot proportions are correlated
119 with the time spent climbing and clinging, whereas hand proportions are not (Druelle et al.,
120 2017a). Moreover, young mouse lemurs (*Microcebus murinus*) display a pedal grasping that
121 provides a powerful secure grasp throughout development, whereas manual secure grasps
122 decrease during development, being most used only shortly after birth (Boulinguez-Ambroise
123 et al., 2020).

124 In the present developmental study, we explore the relations between grasping
125 performance and morphology across ontogeny in a cross-sectional sample of olive baboon
126 (*Papio anubis*) housed in social groups at the Primatology Station of the CNRS (Rousset sur
127 Arc, France). The behavioral transitions occurring during their locomotor development make
128 the olive baboon a relevant model for our study, as we can expect concomitant changes in
129 performance and morphology. Indeed, during their first month, newborn olive baboons are
130 transported by their mother, clinging onto their fur, and do not display quadrupedal walking
131 (Altmann & Samuels, 1992; Rose, 1977). Juveniles develop a wide arboreal locomotor
132 repertoire during the following months, with a significant proportion of climbing, clinging and
133 suspensory behaviors. When reaching the age of two years, the time spent grasping has
134 significantly decreased, and as the adults, they mostly walk quadrupedally on the ground.

135 To perform cross-sectional analyses of performance and morphology, we first
136 quantified pull strength at the juvenile and adult stages. Second, we quantified bone

137 dimensions (i.e., axial length, mediolateral width and dorsoventral thickness) of the fore- and
138 hind limb elements (from scapula to middle manual phalanges and from femur to middle
139 pedal phalanges, respectively) based on osteological collections covering the entire
140 development of olive baboons (i.e., from birth to adulthood). In comparison with a previous
141 ontogenetic study on olive baboon morphology (Druelle et al, 2017a), we added
142 measurements of the bones of the glenohumeral and acromioclavicular joints, which are
143 involved in both walking and suspensory locomotor behaviors, and measurements of the
144 digits during the first months of life, during which the infant is mostly cradled and relies
145 strongly on clinging to the mother's fur. As young olive baboons actively cling onto their
146 mother's fur during the first months of life, and then display a greater proportion of climbing
147 and suspensory behaviors than adults, we first predict very high relative maximal pulling force
148 (i.e., scaled to body mass) in young individuals (i.e., younger than two years of age). We further
149 expect juveniles to show a different forelimb morphology than adults, with the limb segments
150 being relatively longer and more robust (i.e., wider and thicker) in younger individuals. Finally,
151 we predict differences in the growth patterns of the fore- and the hind limb as they may
152 display different functional roles throughout ontogeny.

153 **MATERIAL AND METHODS**

154 **Experimental Model and Osteological Material**

155 We measured *in vivo* pull strength in 15 olive baboons (*Papio anubis*) born and raised
156 at the Primatology Station of the CNRS (UPS846 CNRS, Rousset-Sur-Arc, France, Agreement
157 C130877). They were housed in a large enriched enclosure containing multiple climbing
158 facilities. All selected individuals had no medical history and were healthy at the time of the
159 experiments. We tested four adult males and six adult females, as well as five juveniles aged
160 between one and one-and-a-half years of age (two males and three females). We tested
161 juveniles at this age as it matches the developmental stage described by Druelle et al. (2017a)
162 during which young baboons develop a wide locomotor repertoire with a greater proportion
163 of climbing, clinging and suspensory behaviors compared to adults. At the age of two years,
164 the time spent grasping has significantly decreased, and similar to adults, animals mostly walk
165 quadrupedally on the ground. Also, at one year of age, baboons are weaned allowing us to
166 isolate them (i.e., for no longer than 20 minutes) in an aviary adjoined to the group enclosure

167 to perform the test. We obtained body mass data for adult individuals from veterinary check-
168 ups and estimated the body mass of juveniles using the models previously constructed by
169 Druelle et al. (2017b) for a longitudinal sample of 30 individuals of the same species (*Papio*
170 *anubis*) and raised at the same Primate Center (Rousset-Sur-Arc, France). The study was
171 approved by the “C2EA-71 Ethics Committee of Neurosciences” (INT Marseille), and all
172 methods were performed in accordance with the relevant CNRS guidelines and the European
173 Union regulations (Directive 2010/63/EU). For ethical reasons, we did not collect direct
174 morphological data on the individuals studied for the pull strength, but collected instead data
175 on an osteological sample coming from the same colony of the Primatology Station of the
176 CNRS.

177 Our osteological material (*Papio anubis*) is composed of 34 individuals of the joint
178 osteological collection of the Primatology Station of the CNRS (UPS846 CNRS, Rousset-Sur-Arc,
179 France) and the UMR7194 CNRS (Paris, France). This collection derived from deceased
180 individuals born and raised in captivity in the same colony at the Primatology Station of the
181 CNRS (Agreement C130877). We supplemented this osteological sample by analyzing 3D
182 surface models at the technical plateau “Workstation” of the UMR7194 CNRS (Paris) for an
183 additional six hind limbs; these 3D models were segmented from CT-Scans taken at the
184 radiology service of the Clinique Bachaumont (Paris, France). Our sample contains a majority
185 of females: 19 forelimbs and 18 hind limbs versus 6 forelimbs and 3 hind limbs for males;
186 based on the availability in the collections. Our total sample covers the whole development of
187 olive baboons with bones of individuals ranging from 1 day old to 20 years at the time of death.
188 A summary describing the ontogenetic sample by age group and sex, as well as the availability
189 or absence of the hind limb and the forelimb for each individual, is provided in the
190 supplementary material (see supplementary Table 1). Newborns were individuals younger
191 than 1 month. Juveniles’ were 1 month to 4 years old. We identified adult individuals
192 according to previous studies showing that adulthood is achieved at around 4.5 years in
193 females and around 5 to 6 years in males (Druelle et al., 2017b; Leigh, 2009).

194 **Data Collection**

195 **a) Performance measurements**

196 **Device:** We designed a device inspired by the experimental setup used by Bozek et al. (2014)
197 for testing pull strength in adult macaques. A representation of the device and its location in
198 the enclosure is given in figure 1. Our device consists of an electronic dynamometer (Tractel
199 dynafor™ LLX2 500kg; Saint-Hilaire-sous-Romilly, France) fixed on a sliding tray. The
200 dynamometer has two attachment eyes arranged on its sides. A handle is attached on one
201 side, whereas adjustable weights are attached on the other side. The handle is a metal chain
202 made of 1.5 cm wide links, enabling both juveniles and adults to wrap their fingers around it.
203 Food is placed on the sliding tray. By pulling the handle, the subject pulls the respective weight
204 attached, and moves the tray closer to obtain access to the food reward. The pull strength is
205 registered by the dynamometer (in kg to nearest 0.5 g). A detachable display housing with a
206 maximum display mode allowed to record the maximal pull force. We placed the handle close
207 to the baboons' home enclosure, allowing the animals to reach and grab the handle and the
208 reward. Subjects pulled sitting, grasping the chains with the two hands, engaging both
209 forelimbs during the pulling movement (see supplementary Fig. 1). We did not consider
210 pulling occurrences engaging only one hand, the feet (i.e., pulling with the hands and pushing
211 with the feet against the wire of the enclosure), or trials during which the baboon wrapped
212 the chain around its wrists, or stood up.

213 **Training:** We trained the animals, before carrying out the performance test, to get them
214 habituated to applying a force to pull the chain and obtain the reward placed on the sliding
215 tray. First, food items (i.e., pieces of fruits) were placed inside the links of a chain. The chain
216 was kept loose and placed close to the baboon's enclosure. The subject could grab and pull
217 the chain towards it in order to pick up the food, training them to pull a chain to get a food
218 reward. Second, the dynamometer, the sliding tray and a light weight (i.e., 5kg) were added
219 to the experimental setup. The links of the chain were still associated with food items, but
220 additional items were placed on the sliding tray, training them to apply a force to pull the
221 chain and get the rewards placed on the sliding tray. Finally, individuals were tested with
222 weights of increasing mass (i.e., 20, 30 and 40 kg) and food items placed only on the tray only,
223 training them to apply a high pull strength to obtain the food reward. It took 20 minutes, on
224 average, for a subject to successfully perform all the successive training phases.

225 **Test:** After pulling weights of increasing mass (i.e., 20, 30 and 40 kg), the subject has to pull a
226 weight of 120 kg to move the tray. As this last mass is too heavy for the baboons to pull, the
227 animal will apply a near-maximal level of pull strength, when trying to get the reward. The
228 same procedure was followed for juveniles but with 5kg, 20kg, and 90kg. For each individual,
229 three measurements of maximal pulling force were recorded.

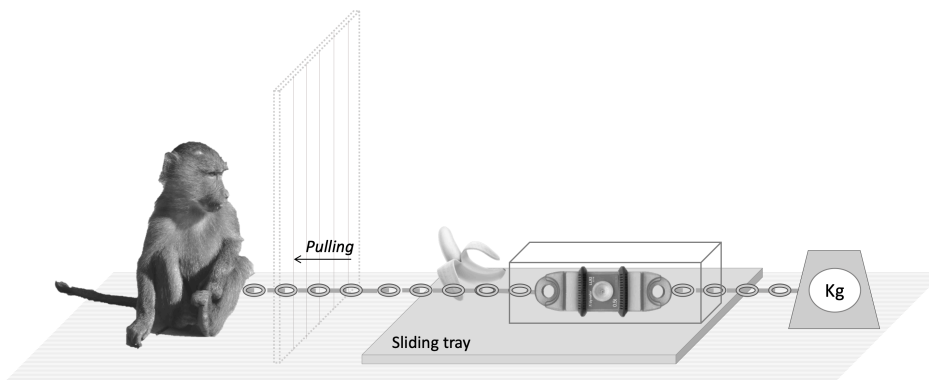
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237 **Figure 1. Schematic representation of the experimental setup used to measure pull strength**
238 **in *Papio anubis*.** By pulling the handle, the subject pulls the tray providing the food reward
239 and attached weight closer. The pull strength is registered by the dynamometer (i.e., fixed on
240 the sliding tray).

241 **b) Bone measurements**

242 We performed linear measurements of bone segments of the fore- and hind limbs. An
243 exhaustive list of bone measurements is provided in Table 1. Forelimb elements included
244 scapula, clavicle, the long bones (i.e., humerus, radius, ulna), and the metacarpals, proximal,
245 and middle phalanges of all rays. Hind limb elements included the long bones (i.e., femur,
246 tibia, fibula), and the metatarsals, proximal, and middle phalanges of all rays. We took the
247 following measurements: 1) the axial length, 2) the mediolateral width and 3) the dorsoventral
248 thickness at the level of both proximal and distal metaphyses (i.e., except for the clavicle),
249 and at the central level of the diaphysis (Begun, 1993; Green & Gordon, 2008; Madar, Rose,

250 Kelley, MacLatchy, & Pilbeam, 2002). As the epiphyses were not fully ossified at early
 251 developmental stages, we did not consider the total length but we selected length
 252 measurements that are comparable across ontogeny (see figure 2). We also reported the
 253 maximal length, width and height (i.e., spine height) of the scapula. We performed the
 254 measurements using a digital caliper (0.01 mm; Mitutoyo, Japan) for the osteological
 255 collections, and analyzed the 6 CT-scanned limbs using the software Geomagic Studio 2012
 256 (3D Systems Corporation, Rock Hill, NC, USA) and its distance measurement analysis tool.

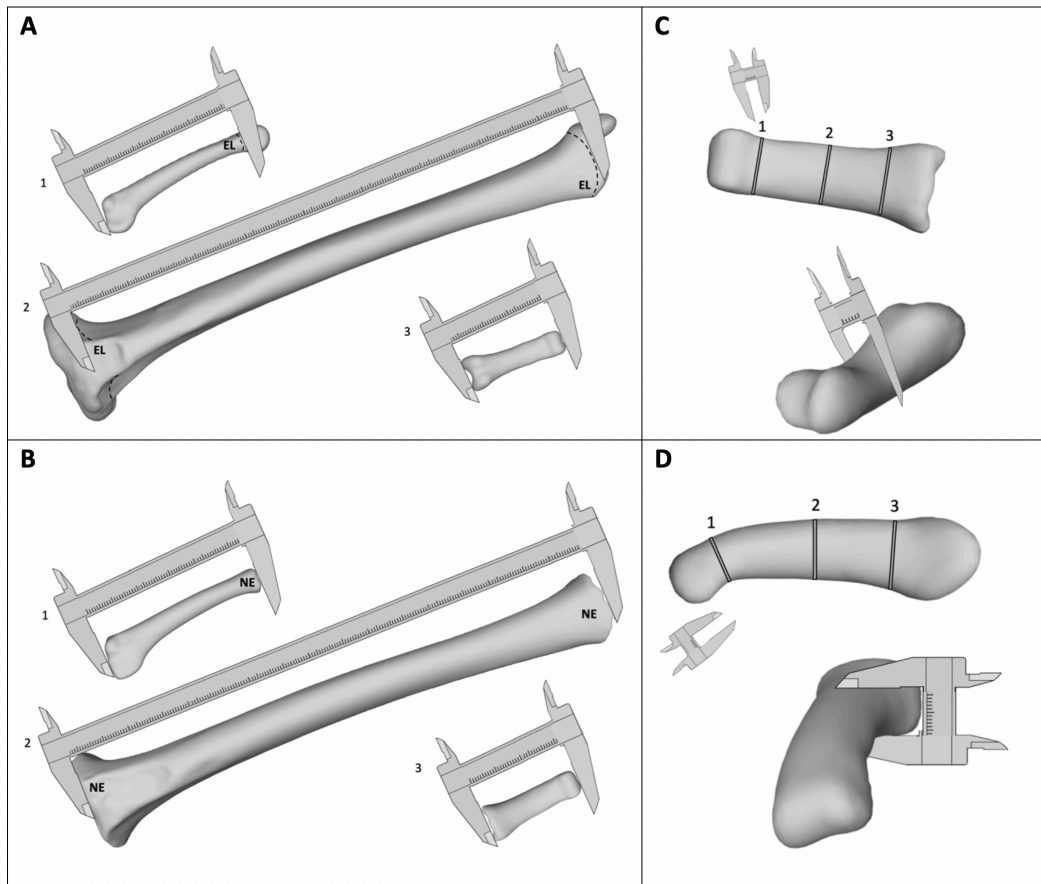
257 **Table 1** List of bone measurements of the olive baboon (*Papio anubis*) forelimb and hind limb,
 258 with abbreviations.

BONES	MEASUREMENTS	ABBREVIATIONS
Long bones: humerus radius ulna femur tibia fibula	Maximal length between proximal and distal epiphyseal lines	SEL
	Width at the central level of the diaphysis	DW
	Thickness at the central level of the diaphysis	DT
	Width at the proximal metaphysis	PMW
	Thickness at the proximal metaphysis	PMT
	Width at the distal metaphysis	DMW
	Thickness at the distal metaphysis	DMT
Scapula	Maximal length	L
	Maximal width	W
	Maximal height (i.e., spine height)	H
Clavicula	Maximal length between proximal and distal epiphyseal lines	SEL
	Width at the central level of the diaphysis	DW
	Thickness at the central level of the diaphysis	DT
Metapodia: rays 1 to 5, fore- and hind limbs	Maximal length between the proximal epiphysis and the distal epiphyseal line	MET_L
	Width at the central level of the diaphysis	DW
	Thickness at the central level of the diaphysis	DT
	Width at the proximal metaphysis	PMW
	Thickness at the proximal metaphysis	PMT
	Width at the distal metaphysis	DMW
	Thickness at the distal metaphysis	DMT
Proximal and middle phalanges,	Maximal length	L
	Width at the central level of the diaphysis	DW
	Thickness at the central level of the diaphysis	DT
	Width at the proximal metaphysis	PMW

rays 1 to 5, fore- and hind limbs	Thickness at the proximal metaphysis	PMT
	Width at the distal metaphysis	DMW
	Thickness at the distal metaphysis	DMT

259

260



261

262 **Figure 2. Illustration of the bone measurements.** **A** Measurements on fully ossified bones: 1)
 263 Maximal axial length of metapodia between the proximal epiphysis and the distal epiphyseal
 264 line (EL). 2) Maximal axial length of long bones between the proximal and distal epiphyseal
 265 lines. 3) Maximal axial length of phalanges. **B** illustrates measurements on immature bones,
 266 with missing epiphyses (NE) because of non-ossified epiphyseal plate. **C** illustrates
 267 measurements of the bone's mediolateral width at the level of both proximal (3) and distal (1)
 268 metaphyses and at the central level of the diaphysis (2). **D** illustrates measurements of the
 269 bone's dorsoventral thickness at the same levels.

270

271 **Statistical Analysis**

272 **Performance data:** For each individual, we kept the highest value of the three acquisitions of
273 maximal pulling force for analysis. We scaled the performance data to body mass by dividing
274 the force (N) by the product of the body mass (kg) and the standard gravitational acceleration
275 (9.81 m/s^2), as described by Hof (1996). We ran linear models with age as fixed variable to
276 investigate possible differences in maximal pulling force across ontogeny. Data were \log_{10} -
277 transformed before analyses to meet assumptions of normality and homoscedasticity of
278 residuals.

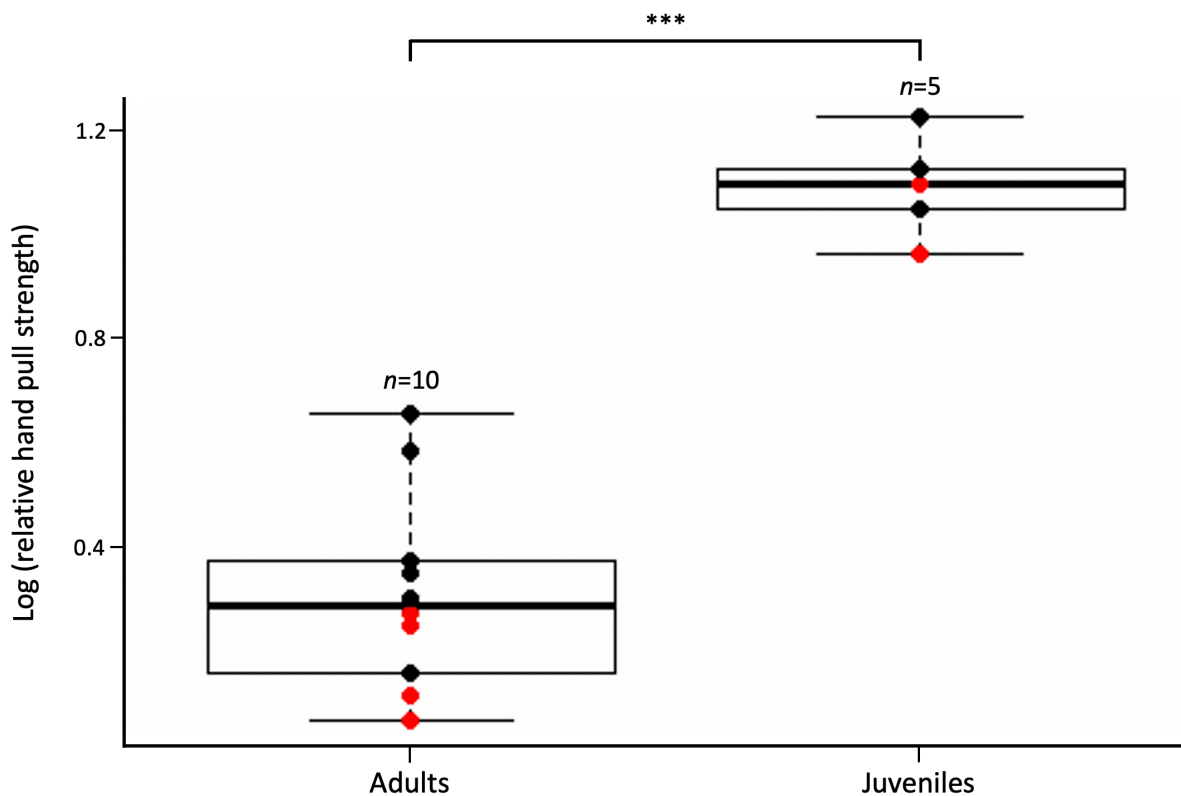
279 **Osteological data:** First, we conducted analyses on forelimbs and hind limbs separately: 1)
280 we calculated Log-shape ratios (see: Mosimann, 1970; Mosimann & James, 1979) based of the
281 raw \log_{10} -transformed linear dimensions. A measure of overall size was calculated as the
282 geometric mean of all measurements for each individual after \log_{10} -transformation. 2) We
283 conducted a principal component analysis (PCA) on the Log-shape ratios. 3) We explored
284 allometry by regressing the first principal components on overall size. We also regressed the
285 first PC-axes on age. By inspecting the individuals factor map, we visually identified groups of
286 individuals sharing a similar morphology. 4) We tested these groups of individuals by running
287 a k-nearest neighbor classification with cross-validations (using $k=1$, number of neighbours
288 considered). 5) To investigate potential differences between the sexes, we ran a multivariate
289 analysis of variance (MANOVA) on the principal component scores representing 90% of the
290 total variation. In addition, we ran analyses of variance (ANOVA) to test the effect of the sex
291 and size on the first principal component. Next, we carried out these five analysis steps with
292 a reduced sample of individuals ($n=11$) for which we had measurements for both fore- and
293 hind limbs. To investigate covariation between both limbs, we performed a Monte-Carlo Test
294 (i.e., on the sum of eigenvalues of a co-inertia analysis, RV coefficient; Heo & Gabriel, 1998)
295 on the first principal components of the PCAs run on the forelimb and hind limb datasets. As
296 the forelimb and the hind limb of one adult female were not complete (i.e., bones missing),
297 and PCA cannot deal with missing data, we had to exclude this individual from the PCA
298 analyses.

299

300 RESULTS

301 1) Pulling force

302 A linear model indicated that performance (scaled to body mass) was strongly negatively
303 related to age ($F_{1,13} = 40.24, P < 0.001$). Juveniles (between 1 and 1,5 years old) displayed
304 maximal pulling forces that were greater than that those of adults, relative to body mass (Fig.
305 3). Means of raw and scaled data are provided in Table 2.



306

307 **Figure 3. Boxplot comparing relative hand pull strength (i.e., scaled to body mass) between**
308 **one-year-old and adult *Papio anubis*.** Individual data points are overlaid on top of the
309 boxplots, males are colored in red and females are in black. (***: p-value < 0.001).

310

311

312

313 **Table 2 Summary detailing differences in maximal pulling force between juvenile and adult olive baboons**
 314 **(*Papio anubis*).** Raw and scaled data for pull strength (HPS), as well as body mass are provided (table entries are
 315 means \pm SD). Scaled data are the forces (N) divided by the product of the body mass (kg) and the standard
 316 gravitational acceleration (9.81 m/s^2). Juveniles (2 males, 3 females) were between one year and one year and a
 317 half of age. Adulthood is reached between 4.5 and 5 years of age.

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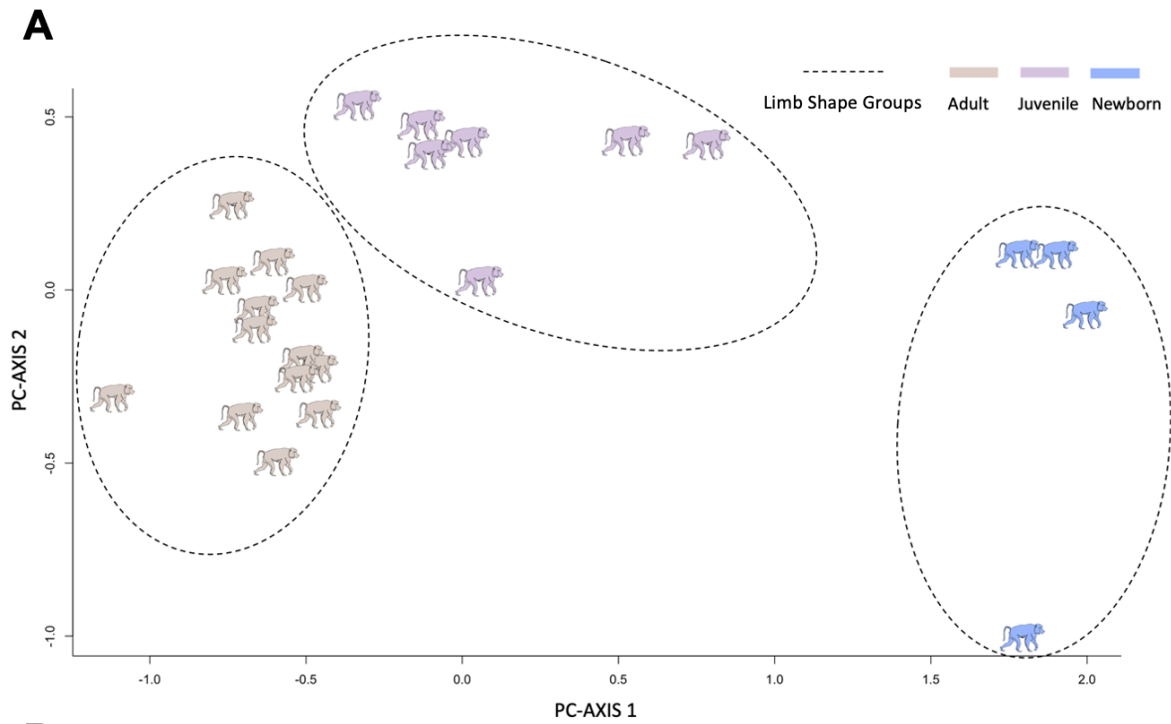
Stage	Body mass (Kg)	Absolute HPS (N)	Scaled HPS
Adult males, n=4	26 \pm 1.6	300 \pm 20	1.2 \pm 0.12
Adult females, n=6	19.5 \pm 3.3	286 \pm 53	1.51 \pm 0.3
Juveniles, n=5	4.2 \pm 0.8	122 \pm 20	2.98 \pm 0.3

319

320 **2) Ontogenetic trajectory of limb conformation**

321 **a) Forelimb**

322 The PCA resulted in 11 axes together explaining more than 90% of the overall variation in the
 323 data set. The first two principal components of the PCA accounted respectively for 50.3% and
 324 7.6% of the variance. Regressions showed strong allometry in our dataset, with the first PC-
 325 axis being significantly and strongly explained by the overall size ($R^2 = 0.90$; $P < 0.001$; the
 326 regression plot is provided in the supplementary Fig. 2) and age ($R^2 = 0.39$; $P < 0.001$).
 327 Allometry was not significant for the other PC-axes. The first principal component opposed
 328 the lengths and width of the diaphyses of the long bones and metacarpals with the width of
 329 the diaphysis of the phalanges as well as their sub-epiphyseal width, and the width of distal
 330 metacarpals. Further details are provided in Figure 4. We found no effect of sex on the limb
 331 conformation ($F_{1,22} = 0.11$, $P = 0.74$). The Individual factor map (see Fig. 4) identified three
 332 groups, confirmed by a k-nearest neighbor cross-validation ($k=1$, 22 well classified individuals
 333 of the 24). The three groups corresponded to newborns (i.e., first month), juveniles and adults
 334 (older than 4.5 years). We thus found young individuals to have relative wider phalanges and
 335 digital joints than adults. Adults are characterized by relative longer and wider long bones than
 336 juveniles.



B

PC 1 20 POSITIVE TOP-SCORER VARIABLES			PC 1 20 NEGATIVE TOP-SCORER VARIABLES		
BONE	DIMENSION	SCORE	BONE	DIMENSION	SCORE
MP 4	DW	0.20	Scapula	H	-0.25
PP 5	DW	0.15	Scapula	L	-0.25
Ulna	DMT	0.15	Ulna	SEL	-0.22
Ulna	DMW	0.14	Scapula	W	-0.19
MP 5	DMW	0.14	Radius	SEL	-0.18
PP 5	PMW	0.13	Clavicula	DT	-0.18
PP 4	DW	0.13	Humerus	SEL	-0.17
MP 4	DMW	0.13	Humerus	DT	-0.16
MP 5	DW	0.12	MC 5	MET_L	-0.14
MP 3	DMW	0.12	Clavicula	DW	-0.14
MP 3	PMW	0.12	Radius	DW	-0.13
MC 4	DMT	0.12	MC 2	MET_L	-0.12
PP 5	PMW	0.12	Ulna	DT	-0.12
MC 5	DMT	0.12	MC 4	MET_L	-0.12
PP 3	DMW	0.11	MC 3	MET_L	-0.11
MP 4	PMW	0.11	Radius	DT	-0.11
PP 3	PMW	0.11	Clavicula	SEL	-0.10
PP 4	DMW	0.11	Ulna	DW	-0.10
PP 2	PMW	0.11	MC 5	PMT	-0.10
PP 4	PMW	0.10	Humerus	DW	-0.09

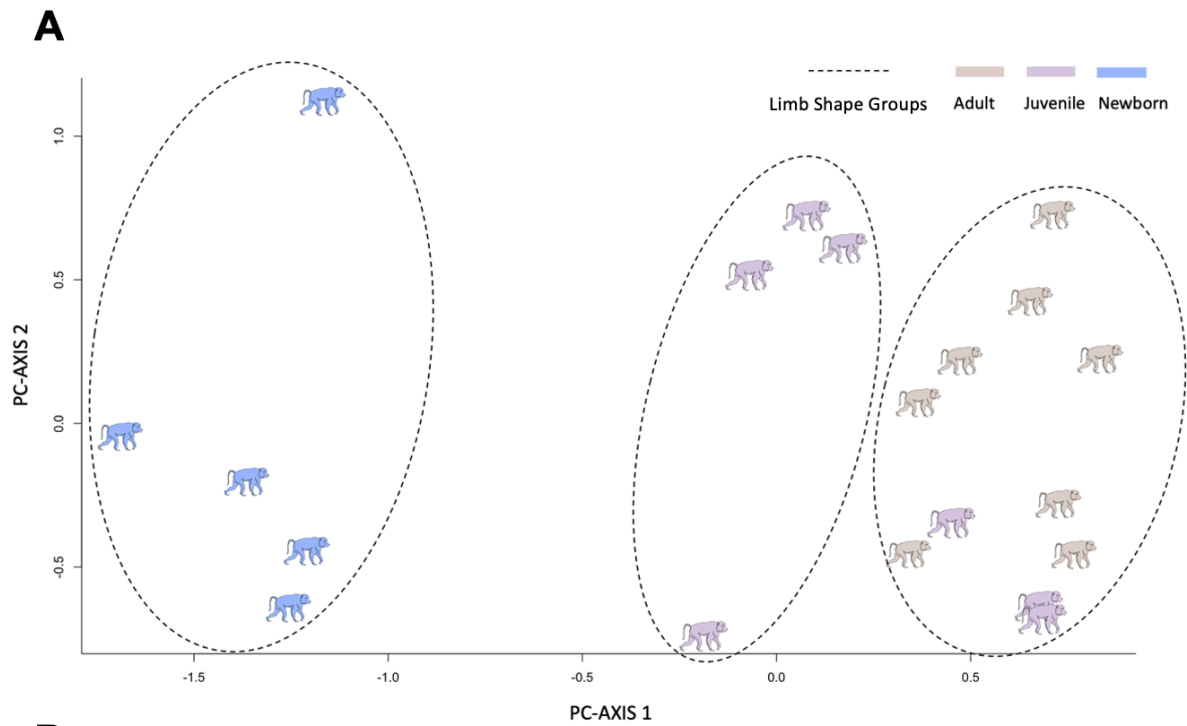
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339 **Figure 4. Outputs of principal component analyses (PCA) run on forelimb segments' Log-**
340 **shape ratios of an ontogenetic sample of olive baboons (*Papio anubis*).** **A** Individuals factor
341 map. Subjects are colored according to their age (i.e., three developmental stages), while they
342 are grouped together, surrounded by dashed lines, according to the limb shape groups they
343 belong (i.e., three groups statistically validated by a k-nearest neighbor cross-validation). **B**
344 Summary detailing the bone segments' dimensions that contribute the most to the
345 morphological conformation of the forelimb across ontogeny. We listed the 40 variables
346 contributing most to the principal component (i.e., showing strong allometry). MC, PP, MP
347 stand for metacarpus, middle and proximal phalanges respectively; the ray is provided (i.e., 1
348 to 5, 1 being the thumb). All abbreviations are explained in the Table 1. PCAs clearly
349 discriminated a juvenile and an adult conformation at the extremes of the major axis (PC 1).

350 **b) Hind limb**

351 The PCA resulted in 9 axes together explaining more than 90% of the overall variation in the
352 data set. The first two principal components accounted respectively for 44.7% and 19.5% of
353 the variance. Regressions showed strong allometry in our dataset, with the first PC-axis being
354 significantly and strongly explained by overall size ($R^2 = 0.86$; $P < 0.001$; the regression plot is
355 provided in the supplementary Fig. 2), and age ($R^2 = 0.25$; $P < 0.05$). Allometry was not
356 significant for the other PC-axes. As for the forelimb, the first axis opposed the lengths and
357 widths of the long bones and metacarpals with the widths of the phalangeal diaphyses and
358 sub-epiphyses, and of the distal metacarpals. Further details are provided in Figure 5. We
359 found no effect of sex on the limb conformation ($F_{1,18} = 0.43$, $P = 0.52$). The Individual factor
360 map (see Fig. 5) allowed to identify three groups, confirmed by a k-nearest neighbor cross-
361 validation ($k=1$, 19 well classified individuals of the 20). We found that the development of
362 the hind limb is achieved from 2 years of age, far before the adulthood. As for the forelimb,
363 we found younger individuals to have relative wider phalanges and digit joints than adults,
364 which are characterized by relative longer and wider long bones.



B

PC 1 20 POSITIVE TOP-SCORER VARIABLES			PC 1 20 NEGATIVE TOP-SCORER VARIABLES		
BONE	DIMENSION	SCORE	BONE	DIMENSION	SCORE
Fibula	PMW	0.21	MP 4	DMW	-0.18
Femur	SEL	0.21	MP 3	DMW	-0.17
Tibia	DT	0.20	MP 5	DMW	-0.16
Fibula	SEL	0.20	PP 2	DMW	-0.16
Fibula	DT	0.19	MP 2	DMW	-0.15
Tibia	SEL	0.18	PP 2	DW	-0.15
MT 5	MET_L	0.18	MT 1	DMT	-0.14
Fibula	DW	0.17	PP 4	DW	-0.14
Femur	DW	0.16	PP 3	DMW	-0.13
MT 2	MET_L	0.15	PP 1	DMW	-0.13
MT 4	MET_L	0.14	PP 4	DMW	-0.13
Femur	DT	0.12	PP 3	DW	-0.13
MT 3	MET_L	0.12	MP 3	DW	-0.13
Tibia	PMT	0.12	MP 4	DW	-0.13
MT 3	PMW	0.10	MP 5	DW	-0.12
MT 1	MET_L	0.10	MP 4	PMW	-0.12
MT 4	PMW	0.09	MP 3	PMW	-0.12
MT 5	DT	0.08	MT 3	DMT	-0.11
PP 1	DT	0.07	MP 2	DW	-0.10
MT 5	PMT	0.07	PP 4	PMW	-0.10

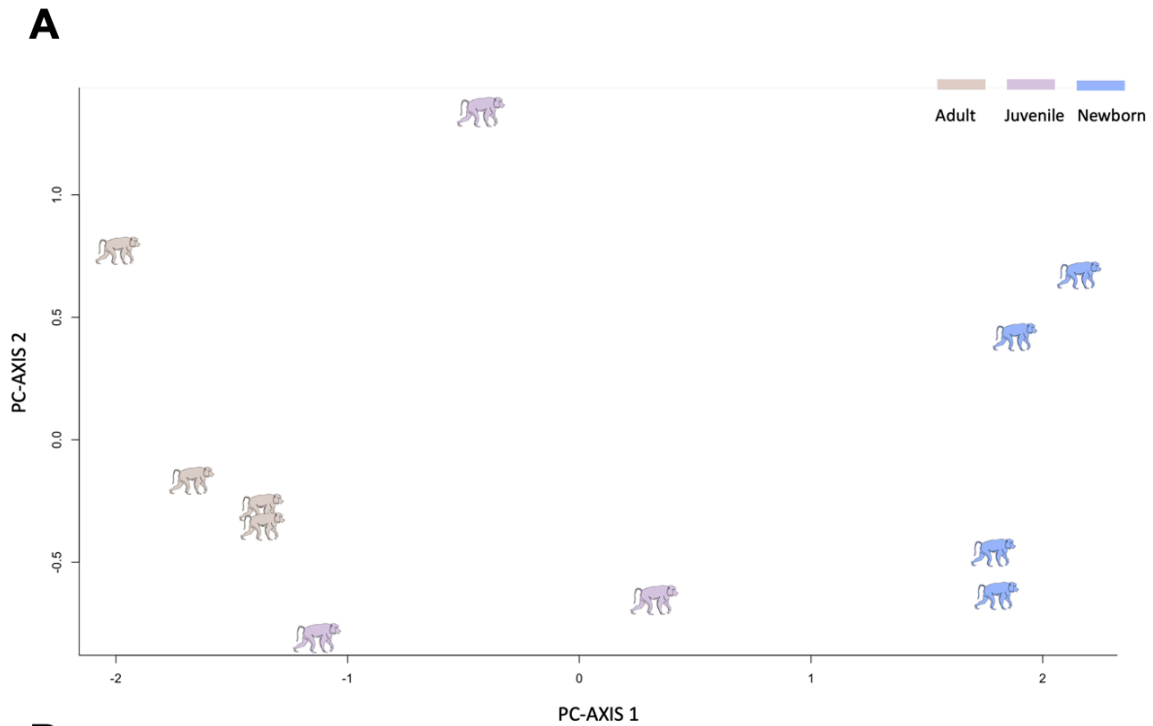
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367 **Figure 5. Outputs of principal component analyses (PCA) run on hind limb segment Log-**
368 **shape ratios of an ontogenetic sample of olive baboons (*Papio anubis*).** **A** Individuals factor
369 map. Subjects are colored according to their age (i.e., three developmental stages), while they
370 are grouped together, surrounded by dashed lines, according to the limb shape groups they
371 belong (i.e., three groups statistically validated by a k-nearest neighbor cross-validation). **B**
372 Summary detailing the bone segment dimensions contributing most to the morphological
373 conformation of the hind limb across ontogeny. We listed the 40 variables contributing most
374 to the principal component (i.e., showing strong allometry). MT, PP, MP stand for metatarsus,
375 middle and proximal phalanges respectively; the ray is provided (i.e., 1 to 5, 1 being the
376 hallux). All abbreviations are explained in the Table 1. PCAs clearly discriminated a juvenile
377 and an adult limb conformation at the extremes of the major axis (PC 1).

378 **c) Covariation**

379 A Monte-Carlo Test on the first principal components of the PCAs run on the forelimb and
380 hind limb datasets demonstrated a high covariation between the growth trajectories of the
381 two limbs ($RV = 0.92$, $P < 0.001$). Also, when running a PCA with the reduced sample of
382 individuals ($n=12$), for which we had measurements of both fore- and hind limbs, the PCA
383 resulted in six axes together explaining more than 90% of the overall variation in the data set.
384 The first two principal components of the PCA accounted respectively for 55.7% and 10.3% of
385 the variance. The first PC-axis was significantly and strongly explained by overall size ($R^2 = 0.95$;
386 $P < 0.001$; the regression plot is provided in the supplementary Fig. 2), and age ($R^2 = 0.79$; $P <$
387 0.001). We found that the dimensions of the manual phalanges more strongly characterized
388 newborns than dimensions of pedal phalanges: 18 of the 20 variables that loaded strongly
389 were manual dimensions (see Fig. 6).



B

PC 1 20 POSITIVE TOP-SCORER VARIABLES			PC 1 20 NEGATIVE TOP-SCORER VARIABLES		
BONE	DIMENSION	SCORE	BONE	DIMENSION	SCORE
H_MP 4	DW	0.16	Scapula	H	-0.21
H_MP 3	PMW	0.13	Scapula	L	-0.17
H_MP 5	DMW	0.12	Ulna	SEL	-0.16
H_PP 5	DW	0.11	Femur	SEL	-0.14
H_PP 4	DW	0.11	Tibia	DT	-0.14
H_PP 5	PMW	0.11	Radius	SEL	-0.13
H_MP 4	DMW	0.11	Fibula	DT	-0.13
H_PP 5	DMW	0.11	Fibula	SEL	-0.13
H_MP 3	DMW	0.11	Tibia	SEL	-0.12
Ulna	DMT	0.11	Humerus	SEL	-0.12
H_MP 5	DW	0.10	Fibula	PMW	-0.12
F_MP 4	DMW	0.10	MT 5	length	-0.11
H_PP 3	DMW	0.10	Clavicula	DT	-0.11
H_PP 2	DW	0.10	Fibula	DW	-0.11
H_MP 4	PMW	0.09	Femur	DW	-0.10
H_PP 2	DMW	0.09	MT 2	MET_L	-0.10
H_PP 4	DMW	0.09	Humerus	DT	-0.10
Ulna	DMW	0.09	MC 5	MET_L	-0.09
F_MP 3	DMW	0.09	Scapula	W	-0.09
MC 1	DMT	0.09	Tibia	PMT	-0.09

390

391

392 **Figure 6. Outputs of principal component analyses (PCA) run on forelimb and hind limb**
393 **segments' Log-shape ratios of an ontogenetic sample of olive baboons (*Papio anubis*). A**
394 Individuals factor map. Subjects are colored according to their age (i.e., three developmental
395 stages); **B** Summary detailing the bone segment dimensions that contribute the most to the
396 morphological conformation of the forelimb and the hindlimb across ontogeny. We listed the
397 40 variables contributing most to the principal component (i.e., showing strong allometry).
398 MC, MT, PP, MP stand for metacarpus, metatarsus, middle and proximal phalanges,
399 respectively. In front of PP and MP, H indicates phalanges of the hand, and F phalanges of the
400 foot. The ray is provided (i.e., 1 to 5, 1 being the thumb/hallux). All abbreviations are explained
401 in the Table 1.

402 **DISCUSSION**

403 We first predicted that very young olive baboons would display high levels of grasping
404 performance (scaled to body mass). In fact, we found that, between 1 to 1.5 years of age, the
405 relative maximal pulling force reached more than 200% of the adult strength (although
406 absolute pull strength does increase with age). Previous studies on the arboreal mouse lemur
407 (*Microcebus murinus*) found relative maximal hand pulling force to not vary across ontogeny,
408 reaching 92% of the adult strength as soon as the first week of life (Boulinguez-Ambroise et
409 al., 2020). The relative strength of juvenile olive baboons is much higher, which may be
410 explained by different motor experiences early in life between the two species. Whereas
411 young olive baboons cling to the mother's fur during their first months of life, young mouse
412 lemurs are not transported by the mother (though the mother will orally transport infants
413 when escaping predators) (Colas et al., 1999; Peckre et al., 2016). Grasping narrow substrates,
414 as young mouse lemurs do, requires strong grasping abilities (Boulinguez-Ambroise et al.,
415 2020), yet, young olive baboons have to bear their whole weight when holding onto their
416 mother's fur. Very few studies have investigated possible evolutionary links between infant
417 carrying and grasping skills in primates. However, Peckre et al. (2016) compared oral-carrying
418 with fur-clinging strepsirrhines species. They found a link between fur-grasping and hand
419 dexterity with species that cling to parental fur using their hands more to grasp items. When
420 clinging on the parental fur, young primates commonly press each finger toward the next (i.e.,
421 involving a close contact between phalanges), while the fingertips are pressed toward the

422 palm (Bishop, 1962; Peckre et al., 2016). This fur-grasping grip thus engages different hand
423 surface areas and contacts than the ones recruited when grasping branches during arboreal
424 locomotion (i.e., the whole palm and all palmar parts of the fingers; Reghem, Byron, Bels, &
425 Pouydebat, 2012; Peckre et al., 2016). Bishop (1962, p. 329) and Peckre et al. (2016) thus
426 suggested about fur-grasping that “such focus of control on the touch-pads is a likely
427 forerunner of fine control of the hand”. Infant carrying may thus have a fundamental role in
428 grasping development (Raichlen, 2005). Further studies are needed to investigate possible
429 links between infant carrying and grasping skills in primates. Moreover, the pull strength we
430 measured is obviously delivered by other muscles (e.g., back or hind limb muscles) than the
431 ones used in a strict grasping task only. The rationale for using the maximal pulling force as a
432 measure for grasping performance is that the animals must be able to keep grip on the handle
433 (i.e., to resist the handle reaction forces resulting from their own pulling). Some sensors exist,
434 measuring the grasping force during a strict grasping action (Young, Chadwell, O’Neill, & Patel,
435 2016). However, the existing tests are too dependent on the motivation of the subject to grasp
436 the item, and do not necessarily provide a maximal performance; to compare data between
437 individuals is therefore difficult. We stress the necessity to create a device and design a test
438 that will allow to obtain maximal performance when measuring grasping force. Quantifying
439 juvenile grasping strength, and not pull strength, will allow to better assess and quantify the
440 role of distal muscles more specifically.

441 Our second prediction was that juveniles and adults should show differences in the
442 limb morphology, associated with the early onset of relatively high maximal pulling forces in
443 immature individuals. We expected the limb segments to be relatively longer and more robust
444 (i.e., wider and thicker) in younger individuals. Previous studies on olive baboons focused on
445 the length of limb segments, showing relatively longer digits at young ages (Druelle et al.,
446 2017a). In our analyses, we included both length and width measurements of the different
447 segments of the limbs. Our data showed that juveniles were characterized by larger widths of
448 the diaphyses and sub-epiphyses of all phalanges, and of the distal part of the metapodia. The
449 width of phalanges and of the joints of the digits (i.e., between metapodia and proximal
450 phalanges, and between phalanges) were better indicators of the juvenile limb morphology
451 than their lengths. By contrast, the length and thickness of the long bones and metapodia (i.e.,
452 relative bigger proximal part of metapodia on the contrary of the relative bigger distal part in
453 juveniles) best described the adult limb morphology. Additionally, the section of the ulna’s

454 distal sub-epiphysis, which corresponds to the joint between the forearm and the hand, was
455 one of the top variables characterizing juveniles.

456 It has been previously documented that relatively larger hands and feet may increase
457 grasping capacity by increasing effective grip span in primates (Boulinguez-Ambroise et al.,
458 2019; Jungers & Fleagle, 1980; Lawler, 2006; Raichlen, 2005; Young & Heard-Booth, 2016).
459 Thus, the patterns of juvenile morphology match the very high relative grasping performance
460 we observed in this age class, and suggests selection on grasping ability early in development.
461 More than increasing grip span, the wider phalanges and joints may enhance muscle insertion
462 areas, cross-sectional second moments of area (Carrier, 1983), and thus grip strength. These
463 changes in limb performance and morphology across ontogeny may be explained in the light
464 of the behavioral transitions that the olive baboons experience during their development.
465 During the first months following birth, infant olive baboons are dependent on the mother for
466 transport, feeding, and predator evasion (Altmann & Samuels, 1992). They actively cling onto
467 their mother's fur, supporting their body weight when carried on the belly, while their mother
468 is free to walk, run, climb, or leap (i.e., exhibits the full locomotor repertoire). High grasping
469 abilities thus appear to be fundamental to their survival. Moreover, when gaining motor
470 independence, young olive baboons exhibit a greater proportion of climbing and suspensory
471 behaviors than adults (Druelle et al., 2017a); adults being mainly terrestrial quadrupedal
472 walkers. The relatively larger and more robust phalanges and digits, we report here, may be
473 involved in compensatory mechanisms allowing newborns to have a secure grasp despite
474 being immature, and providing effective clinging to the fur of the mother. However, in our
475 study, we collected our morphological data from osteological material, while we measured
476 the pull strength *in vivo*; this limited our ability to highlight direct relationships between
477 morphology and performance. Further long-term longitudinal studies are thus required to
478 investigate the morphological changes and the associated performance simultaneously.
479 Collecting morphological data (i.e., external or radiographic measurements) on the same
480 individuals tested for pull strength would allow to more clearly assess the morphological
481 determinants of pull strength in olive baboons. The acquisition of data on the development of
482 the limb muscles would be very insightful as well.

483 Our last prediction involved differences between the fore- and the hind limb growth
484 patterns associated with their different functional roles (i.e., manipulation for the hands, and
485 a more substantial role of the feet in primate locomotion). The mature morphological
486 proportions and shape of the limbs appear at different developmental stages. The mature
487 conformation of the forelimb appeared only at full adulthood (i.e., ≥ 4.5 years), whereas the
488 mature hind limb conformation was present much earlier during development, from 2 years
489 of age onwards. Moreover, we found that the dimensions of the manual phalanges to better
490 characterize newborns than the dimensions of pedal phalanges. Across ontogeny it appears
491 that forelimbs, and more specifically the hands, are associated with high grasping skills. This
492 is in accordance with the high level of hand pull strength observed in juveniles. The hind limbs,
493 on the other hand, seem to play a more substantial role in locomotion, being more sensitive
494 to the locomotor behavioral transitions that occur during growth. Prior to two years of age,
495 foot proportions promote increased hind limb grasping ability (Druelle et al., 2017a). After
496 two years of age, when the proportion of grasping behaviors (i.e., climbing, clinging) has
497 significantly declined (Druelle et al., 2017a), our results highlight a hind limb morphology
498 which is similar to that of adults which display mainly terrestrial quadrupedal walking. The
499 more substantial role of the feet during locomotion has been suggested in other studies in
500 primates. For instance, in mouse lemurs (*Microcebus murinus*), pedal grasping provides a
501 secure grasp from birth to adulthood, ensuring anchor and balance on narrow substrates,
502 while manual secure grasps decrease quickly during development, the forelimbs thus being
503 freed for manipulative behaviors (Boulinguez-Ambroise et al., 2019; Boulinguez-Ambroise et
504 al., 2020; Toussaint et al., 2013). Moreover, in red ruffed lemurs (*Varecia rubra*), toe flexors
505 show greater electromyographic activation than finger flexors during arboreal quadrupedal
506 locomotion, suggesting that these animals rely more on their hind limbs than on their
507 forelimbs (Patel et al., 2015). These differences observed between the fore- and hind limb
508 grasping extremities suggest that they evolved in different selective contexts, with the hind
509 limb having a more substantial role in locomotion, freeing the hands for manipulation.

510 This study assessed a grasping performance trait, the maximal pulling force, in an Old-
511 World monkey across ontogeny. One-year old olive baboons demonstrated very high grasping
512 performance (i.e., 200% of the adult performance, relative to body mass), that are consistent
513 with relative wider phalanges and digit joints in juveniles. As baby baboons actively cling onto

514 the mother's fur during their first months of life, the effect of an infant's holding should be
515 considered when discussing the origins of grasping in primates. Finally, the differences in
516 growth patterns we found between the forelimb and the hind limb further illustrate their
517 different functional roles, having likely evolved under different ecological pressures
518 (manipulation and locomotion, respectively).

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526 **CONFLICT OF INTEREST STATEMENT**

527 The authors declare no competing interests.

528 **DATA AVAILABILITY STATEMENT**

529 The datasets supporting this article are available from the corresponding author on
530 reasonable request and will be moved to an external repository upon publication.

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SUPPLEMENTARY MATERIALS

Table 1 Summary detailing the ontogenetic osteological sample of *Papio anubis* by age group and sex. Among the 34 individuals we had access to the forelimbs of 25 individuals and to the hind limbs of 21 individuals; we had access to both the forelimbs and the hind limbs of 12 individuals. *3D surface models segmented from CT-Scans.

Stage	Age (days)	Sex	Forelimb	Hind Limb
Newborn	1	Female	X	X
	3	Female	X	X
	1	Male	X	X
	36	Female	X	X
	2	Female		X*
Juvenile	217	Female	X	X
	458	Male	X	X*
	607	Female	X	
	1157	Male	X	
	1437	Female	X	
	737	Female	X	X
	792	Male	X	
	575	Female		X*
	201	Female		X*
	912,5	Female		X
	910	Female		X
Adult	5110	Female	X	
	1641	Female	X	X
	6570	Female	X	
	4743	Female	X	
	2896	Female	X	
	6298	Male	X	
	5573	Female	X	
	3137	Female	X	
	5341	Female	X	
	1808	Female	X	X
	2190	Female	X	X
	7498	Female	X	
	2203	Male	X	X*
	4383	Female		X*
	6840	Female		X
	5385	Female		X
	1810	Female		X
5537	Female	X	X	

Fig. 1 Picture of an olive baboon tested with the experimental setup used to measure pull strength. By pulling a 20kg weight, this adult male moves the tray providing the food reward closer. The pull strength is registered by a dynamometer fixed on the sliding tray (inside the wooden box).



Fig. 2 Additional PCA outputs: Plots of the regression of the first principal component on overall size. **A** Analysis conducted on linear measurements of bone segments of *Papio anubis* forelimbs, **B** of hind limbs, **C** of both forelimbs and hind limbs (reduced sample). All statistics are provided in the main text.

