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Hand pressures during arboreal locomotion in captive bonobos (*Pan paniscus*)

Diana S. Samuel¹, Sandra Nauwelaerts^{2,3}, Jeroen M.G. Stevens^{3,4}, and Tracy L. Kivell*^{1, 5}

¹Animal Postcranial Evolution (APE) Lab, Skeletal Biology Research Centre, School of Anthropology and Conservation, University of Kent, Canterbury CT2 7NR, United Kingdom

²Laboratory for Functional morphology, Department of Biology, University of Antwerp, Universiteitsplein 1, 2610 Wilrijk, Belgium

³Centre for Research and Conservation (CRC), Koningin Astridplein 20-26, 2018 Antwerp, Belgium

⁴Behavioral Ecology and Ecophysiology group, Department of Biology, University of Antwerp, Universiteitsplein 1, 2610 Wilrijk, Belgium

⁵Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, Leipzig 04103, Germany

***Corresponding author:**

Professor Tracy L. Kivell

t.l.kivell@kent.ac.uk

+44(0)1227 824959

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SUMMARY STATEMENT

Bonobo digit pressures are significantly greater during arboreal knuckle-walking than either vertical or suspensory locomotion, and the thumb experiences low or no pressure during all locomotor modes.

ABSTRACT

Evolution of the human hand has undergone a transition from use during locomotion to use primarily for manipulation. Previous comparative morphological and biomechanical studies have focused on potential changes in manipulative abilities during human hand evolution, but few have focused on functional signals for arboreal locomotion. Here, we provide this comparative context through the first analysis of hand loading in captive bonobos during arboreal locomotion. We quantify pressure experienced by the fingers, palm and thumb in bonobos during vertical locomotion, suspension and arboreal knuckle-walking. Results show that pressure experienced by the fingers is significantly higher during knuckle-walking compared with similar pressures experienced by the fingers and palm during suspensory and vertical locomotion. Peak pressure is most often experienced at or around the third digit in all locomotor modes. Pressure quantified for the thumb is either very low or absent, despite the thumb making contact with the substrate during all suspensory and vertical locomotor trials. Unlike chimpanzees, the bonobos do not show a rolling pattern of digit contact with the substrate during arboreal knuckle-walking but, instead, digits 3 and 4 typically touch down first and digit 5 almost always made contact with the substrate. These results have implications for interpreting extant and fossilised hand morphology; we expect bonobo (and chimpanzee) bony morphology to primarily reflect the biomechanical loading of knuckle-walking, while functional signals for arboreal locomotion in fossil hominins are most likely to appear in the fingers, particularly digit 3, and least likely to appear in the morphology of the thumb.

INTRODUCTION

The human hand is unique among primates in its enhanced ability to precisely and forcefully manipulate objects (e.g., Napier, 1955; Marzke, 1997, 2013). However, understanding how these abilities evolved requires a better understanding of what fossil human (hominin) ancestors may have been doing with their hands, both in terms of manipulation and

36 locomotion. Although there has been much research into the potential changes in
37 manipulative abilities throughout human evolution, from both morphological (e.g. Napier,
38 1955; Marzke, 1997; Marzke et al., 1999; Skinner et al., 2015) and biomechanical (e.g.
39 Marzke et al., 1998; Rolian et al., 2011; Williams et al., 2012; Key and Dunmore, 2014)
40 perspectives, comparatively little research has been done that may help us infer how our
41 ancestors may have used their hands for arboreal locomotion, particularly that of climbing
42 and suspension. Many fossil hominins show features of the hand (e.g. curved fingers) and
43 upper limb (e.g. superiorly-oriented shoulder joint) (e.g. Stern, 2000; Larson, 2007; Churchill
44 et al., 2013; Kivell et al., 2011, 2015; Kivell, 2015) that suggest arboreal locomotion may still
45 have been an important selective pressure on the hominin postcranium (for a review, see
46 Rose, 1991; Ward, 2002; Niemitz, 2010). More information about the biomechanics and, in
47 particular, the loads experienced by the hand during arboreal locomotion in our closest living
48 relatives, the African apes, will help to interpret the potential functional significance of
49 variation in hand morphology that we see among fossil hominins. To gain this insight, we
50 measure pressures experienced by the hand during vertical locomotion, suspension and
51 arboreal knuckle-walking in captive bonobos (*Pan paniscus*). Bonobos, in addition to their
52 close genetic relationship with humans (Prüfer et al. 2012), show greater stasis in their
53 anatomy compared with chimpanzees and thus are arguably a better extant ape model for
54 understanding human evolution (Diogo et al. 2017a, b).

55 Bonobo locomotion has been studied in a variety of ways, both in the wild and
56 captivity. Early work on locomotion in the wild highlighted greater arboreality in bonobos
57 compared with chimpanzees (Badrian and Badrian, 1977; MacKinnon, 1978), particularly
58 suspension, leaping and bipedal locomotion in the trees (Susman et al., 1980). Doran (1992,
59 1993) later confirmed these initial impressions with more detailed comparative studies,
60 noting that bonobos used more arboreal quadrupedalism, particularly palmigrade
61 quadrupedalism, suspension and leaping compared with chimpanzees (Susman, 1984;
62 Doran, 1993). With regards to hand use during arboreal locomotion, only chimpanzee hand
63 postures have been studied in the wild, highlighting the use of power grips, involving the
64 palm and thumb, and hook grips, using the fingers only, on differently-sized substrates
65 during suspension (Hunt, 1991; Marzke and Wullstein, 1996) and vertical climbing (Hunt,
66 1991; Neufuss et al., 2017b).

67 Unlike most natural environments, captive environments can provide a venue for
68 experimental studies that utilize specialist equipment to obtain biomechanical information,
69 such as three-dimensional kinematics, substrate reaction forces, or hand/foot pressures, that
70 are crucial to gaining a full understanding of locomotor biomechanics in primates and the
71 potential selective pressures on the skeletal morphology (Vereecke and Wunderlich, 2016
72 and references therein). Among the captive biomechanical studies that include bonobos or

73 chimpanzees, most analyse terrestrial locomotion, often with a focus on the hind limb (e.g.,
74 Kimura et al., 1979; Demes et al., 1994; Aerts et al., 2000; D'Août et al., 2001, 2002, 2004;
75 Vereecke et al., 2003, 2004; Li et al., 2004; Sockol et al., 2007; Raichlen et al., 2009). Some
76 of this research has revealed that chimpanzees (bonobos have not yet been studied), like
77 most primates, are distinct from many other mammals in having lower or equal vertical
78 forces on the forelimbs and hindlimbs (Kimura et al., 1979; Demes et al. 1994; Li et al.,
79 2004). Comparatively few studies have investigated the biomechanics of arboreal
80 locomotion, especially vertical climbing or suspension (Isler, 2002, 2005; Nakano et al.,
81 2006; Wunderlich and Jungers, 2009; Schoonaert et al., 2016; Wunderlich and Ischinger,
82 2017), likely in part because of the inherent logistical challenges associated with collecting
83 such data compared with terrestrial substrates. In Isler's (2002, 2005) investigation of gait
84 parameters (e.g., stride length, duty factor) and kinematics of the fore- and hind limbs during
85 vertical climbing, she found that vertical climbing in bonobos was highly variable in terms of
86 gait parameters, but that joint angles were similar to those of gorillas. Bonobo gait
87 parameters have been further studied during terrestrial locomotion (Aerts et al., 2000) and,
88 only recently, during arboreal knuckle-walking and climbing at a variety of different inclines
89 (Schoonaert et al., 2016). However, to our knowledge, substrate reaction forces during
90 arboreal locomotion in apes have only been measured in the hind limb during vertical
91 climbing in a single gibbon (Yamazaki and Ishida, 1984; for other non-hominoid primates,
92 see Hirasaki et al., 1993; Hanna et al. 2017).

93 Measures of substrate reaction force provide the net result of all forces experienced
94 by the limb and, although informative, such data lack detailed information on where the load
95 is applied. Pressure studies complement substrate reaction force analyses, as they provide
96 a dynamic map of vertical force distribution and changes in contact area across the region of
97 interest (e.g. hand or foot). Studies measuring changes in pressure during locomotion in
98 primates are limited, but have included bonobos (D'Août et al., 2001, 2004; Vereecke et al.,
99 2003, 2004). However, most have only investigated terrestrial locomotion and/or have
100 focussed on the feet (e.g. Wunderlich, 1999; Patel and Wunderlich, 2010; D'Août et al.,
101 2001, 2004; Vereecke et al., 2003, 2004; Kivell et al., 2010; Matarazzo, 2013; Wunderlich
102 and Ischinger, 2017). To our knowledge, the only pressure studies of non-horizontal arboreal
103 locomotion are on the hand of a gibbon during brachiation (Richmond, 1998) and, just
104 recently, the chimpanzee foot during vertical climbing (Wunderlich and Ischinger, 2017). Of
105 particular interest here, two studies have measured pressure experienced by the hand
106 during knuckle-walking in African apes. Wunderlich and Jungers (2009) measured digit
107 pressures of young (4-5 years) and old (7 years) chimpanzees during knuckle-walking on
108 both the ground and an arboreal horizontal pole. Although peak pressure was comparable
109 between the substrates, its distribution across the digits differed with digits 3 and 4

110 experiencing the greatest load on the arboreal substrate as opposed to digits 2-4 on the
111 ground (Wunderlich and Jungers, 2009). This variation in digit load was further influenced by
112 hand posture and whether a palm-in or pronated palm-back posture was used. This flexibility
113 in hand posture and digit load was corroborated by Matarazzo's (2013) study of chimpanzee
114 and gorilla digit pressures during terrestrial knuckle-walking.

115 To date, no studies have directly measured how the different anatomical regions of
116 the primate hand are loaded during different modes of arboreal locomotion. In particular,
117 vertical climbing and suspension are key components of the locomotor repertoire in African
118 apes (Susman, 1984; Susman et al., 1980; Hunt, 1991, 1992; Doran, 1993; Crompton et al.,
119 2010) and may also have been critical behaviours in the evolution of early hominin ancestors
120 (e.g., Rose, 1991; Schmitt, 2003). To fill this gap, we measure pressures experienced by the
121 bonobo hand (divided into regions of the palm, fingers and thumb) during three modes of
122 arboreal locomotion: vertical locomotor behaviours, suspension, and knuckle-walking. We
123 test four hypotheses, based on previous studies of hand use and posture during arboreal
124 locomotion in bonobos, or great apes in general, and pressure analyses of chimpanzee
125 arboreal knuckle-walking (Wunderlich and Jungers 2009):

126

127 **1.** Hand postures used during arboreal locomotion will be similar to those described
128 previously in chimpanzees during suspension and climbing (Hunt, 1991; Marzke and
129 Wullstein, 1996; Neufuss et al., 2017b) and arboreal knuckle-walking (Wunderlich and
130 Jungers, 2009).

131

132 **2a.** Pressure experienced by the palm and fingers will be similar within both vertical
133 locomotion and suspension as both regions of the hand are generally used to grasp the
134 substrate during these locomotor behaviours (Hunt, 1991).

135 **2b.** In contrast, pressure experienced by the thumb will be significantly lower than that of the
136 palm or fingers due to the thumb's short length relative to the fingers, small musculature
137 (Tuttle, 1969; Marzke et al., 1999), and the general assumption that the function role of the
138 thumb is limited during arboreal locomotion (e.g., Straus, 1942; Tuttle, 1967; Sarmiento,
139 1988).

140

141 **3.** Pressure experienced by the fingers will be highest during knuckle-walking, as only the
142 dorsum of the intermediate phalanges is in contact with the substrate (i.e. high force
143 distributed over a small area). In contrast, pressure experienced by the fingers and palm will
144 be lowest during vertical locomotion, as the hind limbs provide propulsion during vertical
145 locomotion and thus experience greater force than the forelimbs (Hirasaki et al., 1993;

146 Hanna et al., 2017) and most of the hand grips the substrate (i.e. relatively lower force
147 distributed over a larger area).

148

149 **4.** Loading of the fingers during arboreal knuckle-walking will be similar between bonobos
150 and chimpanzees (Wunderlich and Jungers, 2009), given their close evolutionary
151 relationship, similar anatomy (Diogo et al. 2017a, b), and similar biomechanical pattern of
152 knuckle-walking (Inouye, 1994).

153

154 Altogether, this study provides the first quantitative information on dynamic hand pressure
155 distribution during a variety of arboreal locomotor behaviours in a primate and, more
156 specifically, provides important biomechanical data needed to help make more informed
157 functional inferences about variation in hand morphology across extant and extinct
158 hominoids, including fossil hominins.

159

160 **MATERIALS AND METHODS**

161

162 **Sample**

163 Over a period of nine months, we measured the hand pressures during vertical locomotion,
164 suspension and arboreal knuckle-walking in captive bonobos (*Pan paniscus*) cared for at
165 Planckendael Zoo (Royal Zoological Society of Antwerp, Belgium). Eight adult individuals
166 from this captive group were included in this study (Table 1). Ethical approval for this study
167 was granted by the Centre for Research and Conservation in Antwerp, Belgium. The trials
168 were conducted within their indoor enclosure whilst all individuals were together. Contact
169 with or training of the bonobos was not possible, thus all data were collected *ad libitum* when
170 the individuals voluntarily decided to use the apparatus.

171

172 **[INSERT Table 1 about here]**

173

174 **Materials**

175 Hand pressures were measured using a flexible Novel® S2119 pressure mat (novel GmbH,
176 Munich, Germany) with an additional rubber coating for protection and durability. It is
177 composed of 512 sensors, each 1 cm × 1 cm, and arranged over 32 columns and 16 rows.
178 The mat was calibrated to have a pressure range of 15–1000 kPa. Data were read using a
179 Pliance®-xf-32 analyzer (novel GmbH, Munich, Germany) at a rate of 34-35 Hz, and
180 transferred to a laptop running Pliance®-xf-32 Recorder software (version 24.3.5; novel
181 GmbH, Munich, Germany).

182 The pressure mat was wrapped around a cylindrical wooden beam, 4 m in length and
183 12 cm in diameter. This diameter was chosen for three reasons. First, most substrates in the
184 enclosure were of a similar diameter, and thus the bonobos were used to using them for a
185 variety of locomotor behaviours. Second, bonobos commonly locomote on similar-sized
186 substrates in the wild, using tree trunks for 14-25% (males/females), “branches” (defined as
187 2-15cm in diameter) for 32-47% and “boughs” (defined as 15-20 cm in diameter) for 12-20%
188 of their time spent engaging in arboreal locomotion (Doran, 1993). Third, this diameter was
189 large enough to wrap the pressure mat around without overlapping the sensors. Polymer
190 shrink wrap was used to protect the mat and its associated cable from both the bonobos and
191 the high relative humidity within the enclosure. The shrink wrap was painted white to
192 highlight the position of the pressure mat. To ensure the bonobos were comfortable
193 locomoting on this material, the beam was covered with shrink wrap (without the pressure
194 mat) and placed inside the enclosure for a period of two weeks prior to data collection. This
195 period revealed that the bonobos were capable of locomoting easily on the shrink wrap
196 without slipping. To test for any effects of the shrink wrap on the data, weights were placed
197 on the pressure mat with and without the shrink wrap, both when the mat was laid flat and
198 when it was fixed to the beam (n = 30 per condition). The effect on peak pressure was found
199 to be in range of 0.4-0.9%. The Pliance® analyser was placed within a wooden box,
200 securely fixed to the bottom of the beam.

201 Hand pressure data were collected with the beam in two orientations. First, the beam
202 was secured in a vertical (i.e. 90 degrees) position and the pressure mat positioned 3 m from
203 the ground to collect data during vertical climbing (Fig. 1A). Second, the beam was
204 positioned horizontally 2.5 m above the ground to collect data during suspension and
205 arboreal knuckle-walking (Fig. 1B). An overview of the technical set-up is depicted in Figure
206 S1. To visualize how the hand grasped the pressure mat, three GigE ac640-120gm mono
207 high-speed video cameras (Basler AG, Ahrensburg, Germany), fitted with 50 mm lenses,
208 were strategically positioned to focus on the pressure mat. Each camera recorded at a
209 frequency of 120 Hz, with a resolution of 659 × 494 pixels. The cameras were powered and
210 synchronised with one another using a digital signal amplifier connected to the laptop
211 running StreamPix MultiCamera recording software (version 6; Norpix, Quebec, Canada).
212 The high-speed camera system was further synchronised with the pressure measurement
213 system using Pedar wireless sync boxes (novel GmbH, Munich, Germany) that triggered the
214 cameras using a TTL-signal input box (Fig. S1). The latency between contact with the mat
215 and triggering of the cameras was 0.2 s. When a minimum threshold (45-55 kPa, the
216 maximum noise range) was surpassed, the cameras were triggered. The cameras recorded
217 in a 20 s loop and, when triggered, data were saved 10 s before and after the trigger. In
218 addition, a HD Pro Webcam C920 (Logitech, Lausanne, Switzerland) was independently

219 synchronised with the pressure mat software to record an overall view of the animal and the
220 beam for each trial (Fig. S1).

221

222 **[INSERT Figure 1 about here]**

223

224 **Data analysis**

225 Only trials in which the individual engaged in continuous motion and the whole hand made
226 contact with the pressure mat were analysed. First, data pertaining to different anatomical
227 regions of the hand (i.e. palm, fingers and, where possible, the thumb) were defined using
228 the masking tool within the Pliance® software (novel GmbH, Munich, Germany). For each
229 region, peak pressure and the pressure-time integral (PTI) were computed. Peak pressure
230 (kPa) is the maximum pressure recorded in the area of interest. The pressure-time integral
231 (kPa*s) is the area under the pressure-time curve; in other words, it considers both peak
232 pressure and the duration of contact of a particular region. In addition, maximum contact
233 area (cm²), overall contact time for the hand (hereon referred to as 'stance time'), contact
234 time for each anatomical region, and the instant of peak pressure (as a percentage of stance
235 time) were calculated. Due to small sample sizes, both male and female individuals were
236 pooled together for data analyses. Thus, analyses of both raw pressure data (kPa) for the
237 entire sample and peak pressure standardized by body mass (peak kPa/body mass) for six
238 of the eight individuals (excluding n=2 vertical locomotion and n=1 suspension trials for
239 Louisoko and n=2 vertical locomotion trials for Lucuma; see Table 1) are presented.
240 Qualitative assessments of how the hand grasped the pressure mat were also made from
241 the high-speed video data.

242 Means and standard errors for raw peak pressure, relative peak pressure, PTI, the
243 instant of peak pressure and maximum contact area were calculated for each anatomical
244 region, for all locomotor modes. Statistical comparisons were made across anatomical
245 regions with each locomotor type and across all locomotor modes using paired t-tests or,
246 when data were not normally-distributed, Wilcoxon's test. Speed could not be calculated for
247 all trials given the variable use of the vertical substrate (see below) and the different
248 directions in which the animals travelled. For example, the bonobos used suspensory
249 locomotion along both the longitudinal and transverse axis of the horizontal beam.
250 Therefore, we calculated speed for all steady vertical climbing (both ascent and descent)
251 and knuckle-walking trials and found a significant negative correlation between speed and
252 stance time (vertical climbing, Pearson's coefficient = -0.851, $p = 0.032$; knuckle-walking,
253 Spearman's rho = -0.771, $p = 0.009$). Thus, stance time was used as a proxy for speed,
254 following Vereecke et al. (2003). To account for potential influence of variation in stance
255 time, we ran an analysis of covariance (ANCOVA) for all comparisons with stance time as

256 the covariate. All statistical tests were conducted in SPSS (version 22.0; IBM, Portsmouth,
257 UK).

258

259

RESULTS

260 An analysis of pressure and video data during all vertical locomotion, suspension and
261 knuckle-walking trials revealed that the bonobos generally held their fingers together. This
262 hand posture, in combination with the resolution of the pressure mat, meant that data for
263 individual digits, as done in previous studies (Wunderlich and Jungers, 2009; Matarazzo,
264 2013), could not be reliably quantified. Therefore, all of the fingers were analysed as a group
265 for all locomotor modes.

266

267 **Vertical locomotion**

268 Given that data were collected *ad libitum* and the animals could not be trained, the bonobos
269 used the vertical beam for a variety of locomotor behaviours. In addition to vertical climbing,
270 they used it for clambering and for swinging when moving from one substrate to another.
271 Since all of these locomotor modes are normal and natural for bonobos (Doran, 1993), we
272 have included all of them with the qualitative and quantitative analyses of “vertical
273 locomotion” (Table 1).

274

275 **Hand posture**

276 Although the bonobos used the vertical beam for variety of vertical locomotor behaviours,
277 the same hand posture was generally always used. The palm, thumb and fingers always
278 made contact with the substrate and the fingers were always held together. The thumb was
279 always separated from the palm, although its position varied from being fully opposed to
280 being more in line with the palm (Fig. 2). **In all trials, at least the palmar surface of the distal**
281 **half of the thumb, if not the full thumb, was clearly in contact with the beam based on the**
282 **video data, even though pressure data did not always register on the mat.** However, there
283 was variation in how the hand grasped the substrate; the first region to touchdown on the
284 substrate was most often the fingers (in 46% of n = 37 vertical locomotor trials) or the thumb
285 (36%), but in some trials the palm (18%) was the first to touch down. In 90% of all vertical
286 locomotor trials, digit 5 touched down before digit 2 and, concurrently, the medial side of the
287 palm touched down before the lateral side. The first region of the hand to lift off the substrate
288 varied, but was most often the thumb (65%), followed by either the fingers or the palm (both
289 17%). As with touchdown, digit 5 most often lifted off before digit 2 (74%), whilst palm lift off
290 initiated from the lateral or the medial side relatively equally (52% and 48%, respectively).

291 Mean stance time for all vertical locomotion trials was 0.9 (± 0.1) s. Contact time was
292 calculated for each anatomical hand region relative to stance time. The digits were generally
293 in contact with the substrate for 94% of the stance time, compared with 85% for the palm.
294 For the 12 trials in which loading of the thumb was registered by the pressure mat, the
295 thumb was in contact for 50% of the stance time. Additionally, the fingers and palm were first
296 loaded within 2% and 6%, respectively, into the stance time, and fully unloaded within 4%
297 and 8%, respectively, from the end of the stance time. Although video data showed that the
298 thumb often touched the pressure mat prior to the fingers and palm, loading of the thumb did
299 not register until much later (within 23% into the stance time) and was also unloaded much
300 earlier (within 20% from the end of the stance time).

301

302 **Hand pressure**

303 Pressure experienced by the hand during vertical locomotion was predominantly limited to
304 the palm and fingers. Loading of the thumb was only registered by the pressure mat in 32%
305 ($n = 12$) of the total vertical locomotion trials and was not limited to specific types of vertical
306 locomotor behaviours (e.g. climbing, clambering) (Fig. 3). There were no statistical
307 differences for any pressure variables in the palm and finger regions between trials with and
308 without thumb loading, thus data were pooled. Regional raw peak pressure, relative peak
309 pressure, pressure-time integral (PTI), the instant of peak pressure, and maximum contact
310 area results are presented in Table 2 and Figure 3. Results from the ANCOVA accounting
311 for variation in stance time found significant differences across all of the anatomical regions
312 (i.e., palm, thumb and fingers) for raw peak pressure (F -ratio = 16.398, $p < 0.001$), relative
313 peak pressure (F -ratio = 13.908, $p < 0.001$), PTI (F -ratio = 10.121, $p < 0.001$) and maximum
314 contact area (F -ratio = 22.966, $p < 0.001$). Raw and relative peak pressure was significantly
315 higher in the palm compared to the fingers ($p = 0.022$ and $p = 0.045$, respectively), and both
316 the palm and fingers were significantly higher than that of the thumb (palm, $p < 0.001$ and p
317 < 0.001 ; fingers, $p = 0.001$ and $p = 0.003$). PTI values for the palm and fingers were similar
318 ($p = 1.000$), but, again, both were significantly higher compared to that of the thumb (palm, p
319 < 0.001 ; digits, $p = 0.001$). For all hand regions, the instant of peak pressure occurred in the
320 first half of stance: at 38% of stance time for the fingers, 43% for the palm, and 45% for the
321 thumb. Peak pressure on the palm was predominantly located at the proximal part of the
322 palm (57% of the total vertical trials), and less often at the middle (38%) or distal (5%) palm.
323 Peak pressure for the fingers was almost always (89%) at the distal phalanges. In fact, often
324 it was only the distal area of the fingers that was loaded, such that there was a large gap
325 between the finger and palm regions indicating that the most of the proximal and
326 intermediate phalangeal regions were not loaded (Fig. 4). Whilst it was not possible to
327 determine exactly under which digit the peak occurred, it was frequently in the centre of the

328 distal portion of the finger region and thus was likely experienced by or near the third digit.
329 Maximum contact area was similar for the palm and fingers ($p = 0.431$), and both were
330 significantly larger than that of the thumb (both $p < 0.001$) (Table 2; Fig. 3).

331

332 **[INSERT Table 2 and Figures 2-4 about here]**

333

334 **Suspension**

335 The bonobos suspended under the horizontal beam along both its longitudinal axis and its
336 transverse axis (i.e. travelling both along the length of the beam, or suspending from it as
337 they moved transversely between substrates), but there were no obvious qualitative or
338 quantitative differences between the two directions (Fig. 5). Loading of the thumb was not
339 registered by the pressure mat for any of the suspensory trials and thus the thumb is only
340 discussed qualitatively.

341

342 **Hand posture**

343 During suspension, the palm, fingers and thumb always made contact with the substrate,
344 and the fingers were always held together. **Based on video data, the full palmar surface of**
345 **the thumb was in contact with the substrate, even though pressure data under the thumb did**
346 **not register on the mat (see below).** In contrast to vertical locomotion, the thumb was always
347 slightly abducted (Fig. 5a) or held in line (Fig. 5b) with the palm,

348 Touchdown of the hand during suspension was most often led by the fingers (in 50%
349 of $n = 16$ suspensory trials), in which digit 5 touched down before digit 2. The palm touched
350 down first in 30% of all suspensory trials, generally with the medial side of the palm touching
351 down before the lateral side (80% of these trials), while the thumb was the first to touch
352 down in 20% of all trials. The thumb was almost always the first region to lift off the substrate
353 (90% of all trials). Lift-off of the palm predominantly occurred from the lateral side (70%). The
354 fingers were always the last to lift off and all fingers tended to come off simultaneously (90%
355 of all trials).

356 Mean stance time for all suspensory trials was 1.1 (± 0.1) s. On average, the fingers
357 and palm were in contact with the substrate for similar amounts of time (both ca. 89% of the
358 stance time). The order of loading differs slightly from the qualitative analyses; the palm was
359 loaded first, within 4% into the stance time, whilst the fingers were loaded within 6% into the
360 stance. This suggests that although the fingers make contact with the substrate first, they
361 are not loaded enough to register on the pressure mat until slightly later in the stance. In
362 keeping with the qualitative analyses, the palm was unloaded within 6% before the end of
363 stance, whilst the fingers were unloaded last, within 2% before the end of stance.

364

365 **Hand pressure**

366 Regional raw and relative peak pressure, PTI, the instant of peak pressure, and maximum
367 contact area results for suspensory locomotion are presented in Table 2 and Figure 6.
368 Pressure was experienced by the palm and fingers, while the thumb, although in contact with
369 the substrate, did not register on the pressure mat (Fig. 4). The contact area of the fingers
370 was often divided into two distinct regions during stance, which correlated with the regions of
371 distal phalanges and the proximal phalanges, while pressures experienced by the
372 intermediate phalanges were more limited or not detected (Fig. 4).

373 Results from the ANCOVA show that only the PTI of the palm was significantly higher
374 than that of the fingers (F -ratio = 5.245, p = 0.029), while raw (F -ratio = 1.830, p =0.187) and
375 relative (F -ratio = 1.035, p =0.318) peak pressure and contact area (F -ratio = 1.770, p
376 =0.194) were similar between the two anatomical regions. The instant of peak pressure
377 occurred around mid-stance for both the fingers (47% of stance time) and palm (48%). Peak
378 pressure was most commonly experienced by the proximal portion of the palm (44% of n =16
379 trials), whilst for the fingers it was most often located at the distal phalanges (56%). Again,
380 while it was not possible to distinguish loading experienced by specific digits, peak pressure
381 was generally located around the centre of the distal digit area, suggesting that it was at or
382 near the third digit.

383

384 **[INSERT Figures 5 & 6 about here]**

385

386 **Arboreal knuckle-walking**

387

388 **Hand posture**

389 Only the dorsal surface of the intermediate phalanges of the fingers made contact with the
390 substrate during arboreal knuckle-walking and the fingers were generally held together (Fig.
391 7). All four fingers made contact with the substrate in every trial apart from one (88% of n =
392 11 trials), in which digit 5 did not make contact. The bonobos adopted a palm-back posture
393 most frequently (64% of all trials), as opposed to a palm-in posture (36%). In most trials
394 (63% of all trials), digit 3 or digit 3 and 4 together touched down first, followed by digit 2 and
395 then digit 5. The pattern of lift off was most often (75% of all trials) digit 5, followed by digit 4,
396 digit 2 and then digit 3. The average stance time for arboreal knuckle-walking was 1.1 (\pm 0.1)
397 s.

398

399 **Hand pressure**

400 Finger raw and relative peak pressure, PTI, the instant of peak pressure and maximum
401 contact area results are presented in Table 2 and Figure 8. Peak pressure was always

402 localized to the centre of the contact region; thus, it is likely that this pressure was
403 experienced by or surrounding digit 3 (Fig. 4). Unlike vertical locomotion and suspension, the
404 instant of peak pressure occurred after mid-stance, at 63% of stance time.

405

406 **Comparisons of hand pressures between locomotor modes**

407 Comparisons of pressure variables were made between vertical locomotion and suspension
408 for the palm, and across all locomotor modes for the fingers (Fig. 8). For the palm, only
409 maximum contact area was significantly different (F -ratio = 9.722, $p = 0.003$), with
410 suspension having a significantly ($p = 0.003$) greater contact area than vertical locomotion.
411 For the fingers, raw and relative peak pressure (F -ratio = 21.216, $p < 0.001$ and F -ratio =
412 19.898, $p < 0.001$, respectively), PTI (F -ratio = 19.475, $p < 0.001$) and maximum contact
413 area (F -ratio = 4.569, $p = 0.014$) differed significantly across all locomotor modes. Raw and
414 relative peak pressure and PTI were significantly larger for the fingers during arboreal
415 knuckle-walking compared with both suspension and vertical locomotion ($p < 0.001$ in all
416 cases), although there were no differences for these variables between the latter two
417 locomotor modes. Maximum contact area of the fingers was significantly smaller during
418 vertical locomotion compared to knuckle-walking ($p = 0.037$). The instant of peak pressure
419 also occurred later in stance during knuckle-walking compared to vertical locomotion and
420 suspension.

421

422 **[INSERT Figures 7 & 8 about here]**

423

424

425

DISCUSSION

426 This study quantified dynamic pressure distribution experienced by the bonobo hand during
427 a variety of arboreal locomotor behaviours. The results highlight several postural and loading
428 differences across the locomotor modes that are useful for future studies investigating the
429 relationship between hand posture, load distribution and morphology in extant and extinct
430 hominoids.

431

432 ***Hand posture***

433 In this study, we provide the first quantitative and detailed qualitative assessment of how the
434 bonobo hand made contact with an arboreal substrate during a variety of vertical locomotor
435 behaviours, suspension and arboreal knuckle-walking. During vertical locomotion and
436 suspension, the palm, fingers and thumb always made contact with the substrate, and the
437 fingers were typically held together during contact with the substrate for all modes of
438 locomotion. The position of the thumb varied during vertical locomotion, ranging from being

439 positioned parallel to the palm to being opposed to the fingers, while during suspension it
440 was generally positioned in line with the palm. Although the details of the exact position of
441 the fingers during climbing and suspension have not been previously described in bonobos,
442 the hand postures documented here are generally consistent with those described in
443 chimpanzees (Hunt, 1991; Marzke and Wullstein, 1996; Neufuss et al., 2017b) and other
444 great apes (Sarmiento 1988; Alexander, 1994), supporting our first hypothesis.

445 Furthermore, during vertical locomotion and suspension, the fingers were most often
446 the first part of the hand to touch down, while the thumb was most often the first to lift off.
447 During vertical locomotion and, less so, suspension, most often digit 5 touched down before
448 digit 2 and, similarly, the medial side of the palm before the lateral side. Richmond (1998)
449 found the same sequence of digit loading during brachiation in gibbons. This pattern is also
450 consistent with the adducted wrist posture that is used during climbing in chimpanzees,
451 which allows the digits to more effectively grasp a vertical substrate (Sarmiento, 1988; Hunt,
452 1991; Neufuss et al., 2017b) and the pronated hand and forearm posture used when
453 suspending from larger-diameter substrates (Sarmiento, 1988).

454 The bonobos used a typical knuckle-walking posture, in which only the dorsum of the
455 intermediate phalanges contacted the substrate, which has been described previously for
456 chimpanzees and bonobos on terrestrial and arboreal substrates (e.g., Tuttle 1967; Inouye,
457 1994; Wunderlich and Jungers, 2009). Bonobos most often used a pronated palm-back
458 posture (64% of all trials) and less so a palm-in posture. All fingers always made contact with
459 substrate, apart digit 5 in one trial, and the order in which the fingers made contact did not
460 vary based on the hand posture, in contrast to previous studies (Wunderlich and Jungers,
461 2009; Matarazzo, 2013). Digit 3 most often was the first digit to touch down and the last to lift
462 off. The bonobo hand posture differs slightly from that documented during arboreal knuckle-
463 walking in chimpanzees, contrary to our first hypothesis. Wunderlich and Jungers (2009)
464 found that chimpanzees used palm-in and palm-back postures with equal frequency. With a
465 palm-in posture, the chimpanzee digits touched down and lifted off in ulnar radial succession
466 (i.e., digit 5-4-3-2), as the hand rolled through the stance phase (Wunderlich and Jungers,
467 2009). This rolling pattern was not seen in the bonobos; instead digits 3 and 4 typically
468 touched down first, which is similar to the pattern found in chimpanzees when using a palm-
469 back posture (Wunderlich and Jungers, 2009). Furthermore, digit 5 rarely made contact with
470 the substrate in chimpanzees (Wunderlich and Jungers, 2009), but almost always did in
471 bonobos.

472 These differences between bonobo and chimpanzee arboreal knuckle-walking hand
473 posture may be a byproduct of samples used in each study; here, we had n=11 trials from
474 five individuals ranging from 8-30 years of age (Table 1), while Wunderlich and Jungers
475 (2009) had n=38 trials from two young juvenile chimpanzees aged 4-5 years. Although

476 Inouye (1994) found no significant differences in digit use throughout ontogeny between
477 bonobos and chimpanzees, her analysis was of terrestrial knuckle-walking only.
478 Furthermore, the bonobos knuckle-walked on a slightly wider substrate compared to the
479 chimpanzees (12 cm vs. 10.2 cm in diameter, respectively) that was much higher off the
480 ground (2.5 m vs. ~0.3 m, respectively) (Wunderlich and Jungers, 2009; Wunderlich, pers.
481 comm.). As such, the bonobo's greater use of the palm-back postures and simultaneous
482 digit contact (rather than the "rolling" touch down/lift off) may reflect both the increased
483 substrate surface area for digit contact and provide greater stability when being higher off
484 the ground. Further studies of the kinematics of African ape arboreal knuckle-walking are
485 needed to document potential variation in hand (and forelimb) posture and how this may
486 relate to differences in substrate size and height, and the overall requirements for stability.

487

488 ***Hand pressure***

489 This study tested three hypotheses in relation to hand pressures experienced by bonobos
490 during arboreal locomotion. First, we predicted that pressure experienced by the palm and
491 fingers would not differ within vertical locomotion and suspension, but that loading of the
492 thumb would always be significantly lower than that of the rest of the hand. We found partial
493 support for this hypothesis. Raw and relative peak pressure experienced by the palm and
494 fingers during suspension was similar, and the peak pressure and PTI experienced by the
495 thumb was always significantly lower than the rest of the hand during both locomotor modes
496 (also see below). Furthermore, the regions most often experiencing peak pressure – the
497 proximal portion of the palm and the distal region of the fingers – were similar in both vertical
498 and suspensory locomotion. However, raw and relative peak pressure during vertical
499 locomotion and PTI during suspension were significantly higher for the palm compared with
500 that of the fingers. When considering differences in contact area between the palm and
501 fingers (Figs. 3 and 6), this result suggests comparatively greater normal force being exerted
502 on the palm during suspension than during vertical locomotion.

503 Second, for comparisons across the different locomotor modes, we predicted that
504 pressure would be highest during knuckle-walking and lowest during vertical locomotion.
505 Again, we found only partial support for this hypothesis. Raw and relative peak pressure and
506 the PTI were significantly higher for the fingers during knuckle-walking compared with
507 vertical and suspensory locomotion. However, this was not due to a high compressive
508 loading over a relatively small contact area, as predicted. Instead, maximum contact area for
509 the digits during arboreal knuckle-walking was similar to that of the digits during suspension
510 and significantly larger than that of vertical climbing. This unexpected result may be
511 explained by two factors. First, African apes have broad, specialised "knuckle pads" covering
512 the dorsum of the intermediate phalanges (Tuttle 1967, 1969) that, during compressive loads

513 of knuckle-walking, create a large friction contact area with the substrate. Mean contact area
514 for chimpanzee arboreal knuckle-walking was even larger (26.1 cm², S.D. 4.9; data provided
515 by R. E. Wunderlich), suggesting that a relatively large contact area during bonobo knuckle-
516 walking (mean 18.4 cm², S.D. 3.8; Table 2) is not unexpected.

517 Second, although from the video data it appeared that the full hand was grasping the
518 substrate during vertical locomotion (and suspension), most often only the area under the
519 distal and, sometimes, proximal phalanges was loaded (Fig. 4). This may reflect the
520 diameter of the substrate; experimental studies of human hands grasping cylindrical handles
521 have shown that contact area of the palmar surface, as well as normal force, decrease with
522 an increase in diameter (Kong and Lowe, 2005; Seo et al., 2007; Seo and Armstrong, 2008).
523 This is because gripping flexes the fingertips and the curvature of larger diameter handles
524 (or, in this case, substrates) is too large to fit the curvature of the finger (Seo and Armstrong,
525 2008). A similar phenomenon may be occurring with bonobos when they grasp larger
526 substrates, such that pressure is mainly being incurred by only the distal fingers and palm.

527 We also found that raw and relative peak pressure and PTI for the digits and palm
528 did not differ significantly between vertical locomotion and suspension, which did not support
529 our prediction. This result was unexpected since the hind limbs have been shown in other
530 primates to provide most of the propulsive force during vertical climbing and bear more load
531 than the forelimbs (Hirasaki et al., 1993, 2000; Hanna et al., 2017), while the forelimbs bear
532 all of the load during suspension. This result suggests that even when the hind limbs are
533 helping to propel the body vertically, the hand still experiences high pressure to counter
534 gravitational forces. Although shear forces are not measured by the pressure mat, the hand
535 must exert higher loads to increase friction on the vertical substrate (Preuschoft 2002:180).
536 Furthermore, in primates with a high intermembral index (i.e., long forelimbs) like bonobos,
537 Nakano (2002) demonstrated that stance phase for the forelimbs increased with increasing
538 inclination of the substrate (while that of the hind limb remained constant) and that the
539 forelimbs played a more significant role in vertical climbing than in primates with lower
540 intermembral indices (e.g., macaques). Recent findings by Hanna et al. (2017) confirm this,
541 showing that the primate forelimb also serves a propulsive function during vertical climbing,
542 experiencing primarily tensile forces. Thus, pressures experienced by the bonobo hand
543 during vertical locomotion on a medium-sized substrate (i.e., between the diameter of
544 smaller “branches” and larger “boughs” used by bonobos and chimpanzees in the wild
545 [Doran 1992, 1993]), are similar to that of suspension, despite the dramatically different
546 biomechanical role of the hindlimb in these locomotor modes.

547 Finally, we predicted that loading experienced by the bonobo fingers during arboreal
548 knuckle-walking would be similar to those previously described in chimpanzees (Wunderlich
549 and Jungers, 2009). As discussed above, we found some differences in the hand postures

550 used by bonobos compared with chimpanzees. Raw pressure data are not directly
551 comparable between the two studies due to variation in the pressure mat sensor size (0.5cm
552 x 0.5cm vs. 1.0cm x 1.0cm in this study) and the way in which Pliance® software calculates
553 peak pressure. However, the general patterns appear similar; peak pressures for
554 chimpanzees were significantly higher on digit 3 than any other digit, while in bonobos peak
555 pressure was experienced in the middle of the “finger region”, consistent with peak pressure
556 occurring at or near digit 3 as well. Relative mean peak pressure on the third digit for juvenile
557 chimpanzees (236 kPa/ body mass of 25-29 kg) is 8.1-9.4 compared with a mean of 7.4
558 (S.D. 2.1) in bonobos. Furthermore, the instant of peak pressure occurred after mid-stance
559 in both bonobos (63% of total stance phase) and chimpanzees (55% of stance phase in the
560 palm-back posture; 70% of stance phase in the palm-in posture for digit 3) (Wunderlich and
561 Jungers, 2009). **Matarazzo (2013) also showed relatively high pressures on the third digit
562 during terrestrial knuckle-walking in chimpanzees and gorillas. However, comparisons with
563 the absolute pressure values are not made given the unusually low values reported in
564 Matarazzo (2013) (i.e. maximum pressure for an adult chimpanzee during knuckle-walking
565 was only 31.8 kPa, compared to 790 kPa in Wunderlich and Jungers (2009) and a mean of
566 234 kPa in this study).** Overall, these results are consistent with previous studies showing
567 general similarities between bonobo and chimpanzee knuckle-walking hand posture (e.g.
568 Inouye, 1994) and the kinematics and kinetics during terrestrial knuckle-walking (Pontzer et
569 al., 2014; Finestone et al. 2018), but further studies of both taxa on larger samples are
570 needed to determine if subtle differences in gait mechanics found in the hind limbs (D’Aout
571 et al., 2004; Ponzter et al., 2014) might also be revealed in the fore limbs.

572

573 ***The functional role of the thumb***

574 Of particular interest is the role of the thumb during arboreal locomotion. For decades, many
575 have downplayed the functional importance of the thumb in great apes, particularly during
576 suspensory locomotion (e.g. Ashley-Montagu, 1931; Straus, 1942; Tuttle, 1967; Rose, 1988;
577 Sarmiento, 1988). However, more recent studies have demonstrated that the great ape
578 thumb is used much more often for grasping arboreal substrates than previously thought
579 (McClure et al., 2012; Neufuss et al., 2017b), in addition to its important functional role
580 during manipulative activities (Bryne et al. 2001; Marzke et al., 2015; Neufuss et al., 2017a).
581 Here we show that the bonobo thumb always grasped the substrate during vertical and
582 suspensory locomotion. It was the first to touch the substrate in 36% of the vertical
583 locomotion trials and 20% of the suspensory trials. The bonobos’ use of the thumb may
584 reflect the relatively large diameter of the substrate in this experiment; chimpanzees typically
585 use a hook-grip, involving just the fingers (and sometimes the distal palm), on substrates
586 with an average diameter of 4.7 cm (Hunt, 1991). However, Hunt (1991) reports

587 chimpanzees using hook-grips on substrates up to 40.6 cm in diameter, suggesting that
588 bonobos would be capable of using hand postures that did not involve the thumb on a 12
589 cm-diameter substrate.

590 Despite the fact that video data demonstrated that thumb made contact with the
591 substrate in all vertical and suspensory locomotion trials, and was often the first part of the
592 hand to touchdown, the pressure experienced by the thumb was low. Loading of the thumb
593 was only registered by the pressure mat in 32% of the vertical locomotion trials, for which the
594 mean peak pressure, PTI and contact area was significantly lower than that of the digits or
595 palm. For the remaining vertical locomotion trials and suspensory trials, pressure
596 experienced by the thumb must have been lower than the minimum threshold of the mat
597 (i.e., <15 kPa) and/or was further mitigated by the polymer shrink wrap needed to protect the
598 mat. Furthermore, even when the thumb was the first part of the hand to touch down, it often
599 did not register on the mat until later in the stance, and was in contact with the substrate for
600 significantly less time than the digits and palm. This suggests that for bonobos locomoting on
601 a medium-sized substrate, the thumb does not appear to be playing an important
602 biomechanical role based on its variable position relative to the palm and its minimal loading.
603 However, this does not mean that the thumb is not functional during arboreal locomotion
604 (e.g., perhaps in guiding the hand during touchdown) and it may experience much higher
605 loading on differently-sized substrates, which remains to be tested.

606 In this first dynamic pressure study of bonobo arboreal locomotion, we revealed
607 biomechanical data that may be informative for making functional interpretations about
608 variation in extant ape and fossil hominoid and hominin hand bone morphology. We showed
609 the pressures experienced by the digits are significantly greater during arboreal knuckle-
610 walking than either vertical or suspensory locomotion. Thus, given the high frequency of
611 knuckle-walking by bonobos and chimpanzees (Doran, 1992, 1993), and assuming that
612 terrestrial knuckle-walking pressures are similarly high, as demonstrated by Wunderlich and
613 Jungers (2009) in chimpanzees, we would expect *Pan* external and/or internal hand
614 morphology to reflect more so the high biomechanical loading of knuckle-walking over the
615 lower loading and lower frequency of vertical climbing and suspension (Doran, 1993).
616 Indeed, recent studies of the internal trabecular structure of the third metacarpal is
617 consistent with the extended metacarpophalangeal posture of knuckle-walking in African
618 apes compared with flexed-finger grasping postures of Asian apes (Tsegai et al., 2013;
619 Chirchir et al., 2017).

620 This study also revealed some similarities across the different arboreal locomotor
621 behaviours. In all locomotor modes, peak pressure occurred in the centre of the finger
622 region, likely being experienced by or near the third digit. Furthermore, we found that bonobo
623 hand posture, grasping (i.e., touch down/lift off) and loading during vertical and suspensory

624 locomotion are more similar than might be initially predicted when engaging in such
625 fundamentally different types of locomotion (e.g. vertical climbing vs. suspension) on vertical
626 and horizontal arboreal substrates; the ulnar side of digits and palm most often grasped the
627 substrate first and pressures were similar across the two locomotor modes. Although the
628 pressures experienced by the hand during vertical and suspensory locomotion were
629 significantly lower than those during knuckle-walking, fossil hominins were not knuckle-
630 walkers (Richmond and Strait, 2000). Thus, if fossil hominins were still using their hands for
631 climbing or suspending in the trees, it is likely that this behaviour could be reflected in some
632 aspects of the hand morphology, particularly in digit 3, and may be least likely to appear in
633 the morphology of the thumb. Indeed, several fossil hominins have curved phalanges and
634 well-developed digit flexor tendon attachments (e.g. *Australopithecus afarensis*,
635 *Australopithecus sediba*, *Homo habilis*), even when the remainder of the hand is similar to
636 that of humans (i.e. *Homo naledi*), which have been interpreted as evidence of a functionally
637 significant component of arboreal locomotion in their behavioural repertoires (Bush et al.,
638 1982; Kivell et al. 2011, 2015; Kivell, 2015). In contrast to extant great apes, most fossil
639 hominins have (e.g. *A. sediba*, *H. naledi*) or are considered to have (e.g. *A. afarensis*) a long
640 thumb relative to the length of the fingers (Kivell et al., 2011, 2015; Rolian and Gordon,
641 2013; Almécija and Alba, 2014). If the comparatively low loading of the bonobo thumb
642 revealed in this study on a medium-sized (12 cm-diameter) substrate holds true across
643 differently-sized substrates, different locomotor strategies, and potentially other great apes
644 (but see Neufuss et al. 2017b), then it may imply that the thumb of the last common ancestor
645 was somewhat biomechanically “free” to adapt to the functional requirements of
646 manipulation in hominins. However, it must be recognised that the short fingers and long
647 thumb that characterise the hominin hand may better represent the hand proportions of the
648 last common ancestor (Almécija et al., 2015), and would likely elicit a different biomechanical
649 strategy when grasping arboreal substrates, one in which the thumb may incur greater loads.
650 Future studies of the pressures experienced by the hand during arboreal locomotion in
651 gorillas, which have more human-like hand proportions (Almécija et al., 2015), and humans,
652 particularly individuals that frequently engage in arboreal locomotion (e.g. Venkataraman et
653 al. 2013), in comparison to those of bonobos found here would help to inform our
654 understanding of the role of arboreal locomotion in hominin hand evolution.

655

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667

668 **Competing interests**

669 The authors declare no competing interests.

670

671 **Author contributions**

672 TLK and SN designed and supervised the project; JS provided access to animals; DSS, SN,
673 JS set up experiment; DSS collected data; DSS and TLK analysed the data; all authors
674 wrote the manuscript.

675

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681 **References**

682

683 **Aerts P., Van Damme R., Van Elsacker L. and Duchêne V.** (2000). Spatio-temporal gait
684 characteristics of the hind-limb cycles during voluntary bipedal and quadrupedal walking in
685 bonobo's (*Pan paniscus*). *Am. J. Phys. Anthropol.* **111**, 503-517.

686

687 **Alexander, C.J.** (1994). Utilisation of joint movement range in arboreal primates compared
688 with human subjects: an evolutionary frame for primary osteoarthritis. *Ann. Rheumatic*
689 *Diseases* **53**, 720-725.

690

691 **Almécija, S. and Alba, D.M.** (2014). On manual proportions and pad-to-pad precision
692 grasping in *Australopithecus afarensis*. *J. Hum. Evol.* **73**, 88-92.

693

694 **Almécija, S., Smaers, J.B. and Jungers, W.L.** (2015). The evolution of human and ape
695 hand proportions. *Nat. Commun.* **6**, 7717.

696

697 **Ashley-Montagu, F.M.** (1931). On the primate thumb. *Am. J. Phys. Anthropol.* **15**, 291-314.

698
699 **Badrian A. and Badrian N.** (1977). Pygmy chimpanzees. *Oryx* **13**, 463-468.
700
701 **Bush, M.E., Lovejoy, C.O., Johanson, D.C. and Coppens Y.** (1982). Hominid carpal,
702 metacarpal, and phalangeal bones recovered from the Hadar Formation: 1974-1977
703 collections. *Am. J. Phys. Anthropol.* **57**, 651-677.
704
705 **Byrne, R.W., Corp, N. and Byrne J.M.E.** (2001). Manual dexterity in the gorilla: biomanual
706 and digit role differentiation in a natural task. *Anim. Cogn.* **4**, 347-361.
707
708 **Chirchir, H., Zeininger, A., Nakatsukasa, M., Ketcham, R.A. and Richmond, B.G.** (2017).
709 Does trabecular bone structure within the metacarpal heads of primates vary with hand
710 posture? *Comptes Rendus Palevol* **16**, 533-544.
711
712 **Churchill, S.E., Holliday, T.W., Carlson, K.J., Jashashvili, T., Macias, M.E., Mathews, S.,**
713 **Sparling, T.L., Schmid, P., de Ruiter, D.J. and Berger, L.R.** (2013). The upper limb of
714 *Australopithecus sediba*. *Science* **340**, 1233477.
715
716 **Crompton, R.H., Sellar, W.I., and Thorpe, S.K.S.** (2010) Arboreality, terrestriality and
717 bipedalism. *Phil. Trans. R. Soc. B.* **365**, 3301-3314.
718
719 **D'Août, K., Aerts, P., De Clercq, D., Schoonaert, K., Vereecke, E. and Van Elsacker, L.**
720 (2001). Studying bonobo (*Pan paniscus*) locomotion using an integrated setup in a zoo
721 environment: preliminary results. *Primatologie* **4**, 191-206.
722
723 **D'Août, K., Aerts, P., De Clercq, D., De Meester, K., and van Elsacker, L.** (2002).
724 Segment and joint angles of the hind limb during bipedal and quadrupedal walking of the
725 bonobo (*Pan paniscus*). *Am. J. Phys. Anthropol.* **119**, 37-51.
726
727 **D'Août, K., Vereecke, E., Schoonaert, K., De Clercq, D., van Elsacker L. and Aerts, P.**
728 (2004). Locomotion in bonobos (*Pan paniscus*): differences and similarities between bipedal
729 and quadrupedal terrestrial walking, and a comparison with other locomotor modes. *J. Anat.*
730 **204**, 353-361.
731
732 **Demes, B., Larson, S.G., Stern J.T. Jr, Jungers, W.L., Biknevicius, A.R., and Schmitt,**
733 **D.** (1994). The kinetics of primate quadrupedalism. *J. Hum. Evol.* **26**, 353-374.
734

735 **Diogo, R., Molnar, J.L., and Wood, B.** (2017a). Bonobo anatomy reveals stasis and
736 mosaicism in chimpanzee evolution, and supports bonobos as the most appropriate extant
737 model for the common ancestor of chimpanzees and humans. *Sci. Rep.* **7**, 608.
738

739 **Diogo, R., Shearer, B., Potau, J.M., Pastor, J.F., de Paz, F.J., Arias-Martorell, J.,**
740 **Turcotte, C., Hammond, A., Vereecke, E., Vanhoof, M., et al.** (2017b) *Photographic and*
741 *Descriptive Musculoskeletal Atlas of Bonobos*. Springer, Cham.
742

743 **Doran, D.M.** (1992). The ontogeny of chimpanzee and pygmy chimpanzee locomotor
744 behavior: a case study of paedomorphism and its behavioural correlates. *J. Hum. Evol.* **23**,
745 139-157.
746

747 **Doran, D.M.** (1993). Comparative locomotor behavior of chimpanzees and bonobos: the
748 influence of morphology on locomotion. *Am. J. Phys. Anthropol.* **91**, 83-98.
749

750 **Finestone, E.M., Brown, M.H., Ross, S.R. and Pontzer, H.** (2018). Great ape walking
751 kinematics: implications for hominoid evolution. *Am. J. Phys. Anthropol.* DOI:
752 10.1002/ajpa.23397
753

754 **Hanna, J.B., Granatosky, M.C., Rana, P., and Schmitt, D.** (2017). The evolution of vertical
755 climbing in primates: evidence from reaction forces. *J. Exp. Biol.* doi: 10.1242/jeb.157628
756

757 **Hirasaki, E., Kumakura, H., and Matano, S.** (1993). Kinesiological characteristics of
758 vertical climbing in *Ateles geoffroyi* and *Macaca fuscata*. *Folia Primatol.*, **61**, 148-156
759

760 **Hirasaki, E., Kumakura, H. and Matano, S.** (2000). Biomechanical analysis of vertical
761 climbing in the spider monkey and the Japanese macaque. *Am. J. Phys. Anthropol.* **113**,
762 455-472.
763

764 **Hunt, K.D.** (1991). Positional behavior in the Hominoidea. *Int. J. Primatol.***12**, 95-118.
765

766 **Hunt , KD.** (1992). Positional behavior of *Pan troglodytes* in the Mahale Mountains and
767 Gombe Stream National Parks, Tanzania. *Am. J. Phys. Anthropol.* **87**, 83-105.
768

769 **Inouye , S.E.** (1994) Ontogeny of knuckle-walking hand postures in African apes. *J. Hum.*
770 *Evol.* **26**, 459-485.
771

772 **Isler, K.** (2002). Characteristics of vertical climbing in African apes. *Senckenbergiana*
773 *lethaea* **82**, 115-124.
774

775 **Isler, K.** (2005). 3D-Kinematics of vertical climbing in hominoids. *Am. J. Phys. Anthropol.*
776 **126**, 66-81.
777

778 **Key, A.J.M. and Dunmore, C.J.** (2014) The evolution of the hominin thumb and the
779 influence exerted by the non-dominant hand during stone tool production. *J. Hum. Evol.* **78**,
780 60-69.
781

782 **Kimura ,T., Okada, M. and Ishida, H.** (1979). Kinesiological characteristics of primate
783 walking: its significance in human walking. In: *Environment, behavior, and morphology:*
784 *dynamic interactions in primates* (ed. M.E. Morbeck , H. Preuschoft and N. Gomberg), pp
785 297-311. Gustav Fischer, New York.
786

787 **Kivell, T.L., Schmitt, D. and Wunderlich, R.E.** (2010). Hand and foot pressures in the aye-
788 aye (*Daubentonia madagascariensis*) reveal novel biomechanical trade-offs required for
789 walking on gracile digits. *J. Exp. Biol.* **213**, 1549-1557.
790

791 **Kivell, T.L., Kibii, J.M., Churchill, S. E., Schmid, P. and Berger, L.R.** (2011).
792 *Australopithecus sediba* hand demonstrates mosaic evolution of locomotor and manipulative
793 abilities. *Science* **333**, 1411-1417.
794

795 **Kivell, T.L., Deane, A.S., Tocheri, M.W., Orr, C.M., Schmid, P., Hawks, J., Berger, L.R.**
796 **and Churchill, S.E.** (2015). The hand of *Homo naledi*. *Nature Communications* **6**, 1-9.
797

798 **Kivell, T.L.** (2015). Evidence in hand: recent discoveries and the early evolution of human
799 manual manipulation. *Phil. Trans. R. Soc. B.* **370**, 20150105.
800

801 **Kong, Y-K. and Lowe, B.D.** (2005) Optimal cylindrical handle diameter for grip force tasks.
802 *Int. J. Ind. Ergonom.* **35**, 495-507.
803

804 **Larson, S.G.** (2007). Evolutionary transformation of the hominin shoulder. *Evol. Anthropol.*
805 **16**, 172-187.
806

807 **Li, Y., Crompton, R.H., Wang, W., Savage, R. and Günther, M.M.** (2004) Hind limb drive,
808 hind limb steering? Functional differences between fore and hind limbs in chimpanzee

809 quadrupedalism. In: *Shaping Primate Evolution* (eds. Anapol, F., German, R.Z. and
810 Jablonski, N.G.), pp 258-277. Cambridge University Press.

811

812 **Marzke, M. W.** (1997). Precision grips, hand morphology, and tools. *Am. J. Phys. Anthropol.*
813 **102**, 91–110.

814

815 **Marzke, M. W.** (2013) Tool making, hand morphology and fossil hominins. *Phil. Trans. R.*
816 *Soc. B* **368**, 20120414.

817

818 **Marzke, M. W. and Wullstein, K.L.** (1996). Chimpanzee and human grips: a new
819 classification with a focus on evolutionary morphology. *Int. J. Primatol.* **17**, 117-139.

820

821 **Marzke, M.W., Marchant, L.F., McGrew, W.C. and Reece, S.P.** (2015). Grips and hand
822 movements of chimpanzees during feeding in Mahale Mountains National Park, Tanzania.
823 *Am. J. Phys. Anthropol.* **156**, 317–326.

824

825 **Marzke, M. W., Toth, N., Schick, K., Reece, S., Steinberg, B., Hunt, K., Linscheid, R.**
826 **and An, K.N.** (1998). EMG study of hand muscle recruitment during hard hammer
827 percussion manufacture of Oldowan tools. *Am. J. Phys. Anthropol.* **105**, 315–332.

828

829 **Marzke, M. W., Marzke, R.F., Linscheid, R.L., Smutz, P., Steinberg, B., Reece, S. and**
830 **An, K.N.** (1999). Chimpanzee thumb muscle cross sections, moment arms and potential
831 torques, and comparisons with humans. *Am. J. Phys. Anthropol.* **110**, 163–178.

832

833 **Matarazzo, S.** (2013) Manual pressure distribution patterns of knuckle-walking apes. *Am. J.*
834 *Phys. Anthropol.* **152**, 44-50.

835

836 **McClure, N.K., Phillips, A.C., Vogel, E.R., and Tocheri, M.W.** (2012) Unexpected pollex
837 and hallux use in wild *Pongo pygmaeus wurmbii*. *Am. J. Phys. Anthropol.* **147**, 208.

838

839 **MacKinnon, J.** (1978). *The Ape Within Us*. New York, USA: Holt, Rinehart and Winston.

840

841 **Nakano, Y.** (2002). The effects of substratum inclination on locomotor patterns in primates.
842 *Z. Morph. Anthropol.* **83**, 189-199.

843

844 **Nakano, Y., Hirasaki, E., and Kumakura, H.** (2006) Patterns of vertical climbing in
845 primates. In *Human origins and environmental backgrounds*. (ed. H. Ishida, R. Tuttle, M.

846 Pickford, N. Ogiwara and M. Nakatsukasa) pp. 97-104. New York: Springer Publishing.
847

848 **Napier, J. R.** (1955). Form and function of the carpo-metacarpal joint of the thumb. *J. Anat.*
849 **89**, 362–369.
850

851 **Neufuss, J., Humle, T., Cremaschi, A. and Kivell, T.L.** (2017a). Nut-cracking behaviour in
852 wild-born, rehabilitated bonobos (*Pan paniscus*): a comprehensive study of hand-preference,
853 hand grips and efficiency. *Am. J. Primatol.* **79**, 1-16.
854

855 **Neufuss, J., Robbins, M.M., Baeumer, J., Humle, T., and Kivell, T.L.** (2017b).
856 Comparison of hand use and forelimb posture during vertical climbing in mountain gorillas
857 (*Gorilla beringei beringei*) and chimpanzees (*Pan troglodytes*). *Am. J. Phys. Anthropol.* **164**,
858 651-664.
859

860 **Niemitz, C.** (2010). The evolution of the upright posture and gait - a review and a new
861 synthesis. *Naturwissenschaften* **97**, 241-263.
862

863 **Patel, B.A. and Wunderlich, R.E.** (2010). Dynamic pressure patterns in the hands of olive
864 baboons (*Papio anubis*) during terrestrial locomotion: implications for cercopithecoid primate
865 hand morphology. *Anat. Rec.* **293**, 710-718.
866

867 **Plavcan, J.M. and van Schaik, C.P.** (1997). Intrasexual competition and body weight
868 dimorphism in anthropoid primates. *Am. J. Phys. Anthropol.* **103**, 37-68.
869

870 **Pontzer, H., Raichlen, D.A. and Rodman, P.S.** (2014). Bipedal and quadrupedal
871 locomotion in chimpanzees. *J. Hum. Evol.* **66**, 64-82.
872

873 **Preuschoft, H.** (2002). What does “arboreal locomotion” mean exactly and what are the
874 relationships between “climbing”, environment and morphology? *Z. Morph. Anthropol.* **83**, 171-
875 188.
876

877 **Prüfer, K., Munch, K., Hellmann, I., Akagi, K., Miller, J.R., Walenz, B., Koren, S., Sutton,
878 G., Kodira, C., Winer, R., et al.** (2012). The bonobo genome compared with the
879 chimpanzee and human genomes. *Nature* **486**, 527-531.
880

881 **Raichlen, D.A., Pontzer, H., Shapiro, L.J. and Sockol, M.D.** (2009). Understanding hind
882 limb weight support in chimpanzees with implications for the evolution of primate locomotion.
883 *Am. J. Phys. Anthropol.* **138**, 395-402.
884

885 **Richmond, B.G.** (1998). Ontogeny and biomechanics of phalanx form in primates. *PhD*
886 *thesis*, State University of New York at Stony Brook, Stony Brook, NY.
887

888 **Richmond, B.G. and Strait, D.S.** (2000). Evidence that humans evolved from a knuckle-
889 walking ancestor. *Nature* **404**, 382-385.
890

891 **Rolian, C., Lieberman, D. E. and Zermeno, J. P.** (2011). Hand biomechanics during
892 simulated stone tool use. *J. Hum. Evol.* **61**, 26–41.
893

894 **Rolian, C. and Gordon, A.D.** (2013). Reassessing manual proportions in *Australopithecus*
895 *afarensis*. *Am. J. Phys. Anthropol.* **152**, 393-406.
896

897 **Rose, M.D.** (1988). Functional anatomy of the cheiridia. In *Orang-utan Biology* (ed. J.H.
898 Schwartz), pp. 299-310. Oxford University Press, New York.
899

900 **Rose, M. D.** (1991). The process of bipedalization in hominids. In *Origine (s) de la bipédie*
901 *chez les hominidés*. (ed. Y. Coppens and B. Senut B), pp. 37-48. Paris: CNRS.
902

903 **Sarmiento, E.E.** (1988). Anatomy of the hominoid wrist joint: its evolutionary and functional
904 implications. *Int. J. Primatol.* **9**, 281-345.
905

906 **Schmitt, D.** (2003). Insights into the evolution of human bipedalism from experimental
907 studies of human and other primates. *J. Exp. Biol.* **206**, 1437-1448.
908

909 **Schoonaert, K., D’Aout, K., Samuel, D., Talloen, W., Nauwelaerts, S., Kivell, T.L. and**
910 **Aerts, P.** (2016). Gait characteristics and spatio-temporal variables of climbing in bonobos
911 (*Pan paniscus*). *Am. J. Primatol.* **78**, 1165-1177.
912

913 **Seo, N.J., Armstrong, T.J., Ashton-Miller, J.A. and Chaffin, D.B.** (2007). The effect of
914 torque direction and cylindrical handle diameter on the coupling between the hand and a
915 cylindrical handle. *J. Biomech.* **40**, 3236-3243.
916

917 **Seo, N.J. and Armstrong, T.J.** (2008). Investigation of grip force, normal force, contact
918 area, hand size, and handle size for cylindrical handles. *Human Factors* **50**, 734-744.
919

920 **Skinner, M.M., Stephens, N.B., Tsegai, Z.J., Foote, A.C., Nguyen, N.H., Gross, T., Pahr,**
921 **D.H., Hublin, J-J. and Kivell, T.L.** (2015). Human-like hand use in *Australopithecus*
922 *africanus*. *Science* **347**, 395-399.
923

924 **Sockol, M.D., Raichlen, D.A. and Pontzer, H.** (2007). Chimpanzee locomotor energetics
925 and the origin of human bipedalism. *Proc. Natl. Acad. Sci. USA* **104**, 12265-12269.
926

927 **Stern, J.T., Jr.** (2000). Climbing to the top: a personal memoir of *Australopithecus afarensis*.
928 *Evol. Anthropol.* **9**, 113-133.
929

930 **Straus, W.L.** (1942). Rudimentary digits in primates. *Quart. Rev. Biol.* **17**, 228-243.
931

932 **Susman, R.L.** (1984). The locomotor behavior of *Pan paniscus* in the Lomako Forest. In *The*
933 *Pygmy Chimpanzee: Evolutionary Biology and Behavior*. (ed. R.L. Susman), pp 369-393.
934 Plenum Press, New York.
935

936 **Susman, R.L., Badrian, N.L. and Badrian, A.J.** (1980). Locomotor behaviour of *Pan*
937 *paniscus* in Zaire. *Am. J. Phys. Anthropol.* **53**, 69-80.
938

939 **Tsegai, Z.J., Kivell, T.L., Gross, T., Nguyen, N.H., Pahr, D.H., Smaers, J.B., and**
940 **Skinner, M.M.** (2013). Trabecular bone structure correlates with hand posture and use in
941 hominoids. *PLoS ONE* **8**, e78781.
942

943 **Tuttle, R.H.** (1967). Knuckle-walking and the evolution of hominoid hands. *Am. J. Phys.*
944 *Anthropol.* **26**, 171-206.
945

946 **Tuttle, R.H.** (1969) Quantitative and functional studies on the hands of the Anthropoidea; I.
947 The Hominoidea. *J. Morph.* **128**, 309-364.
948

949 **Venkataraman, V.V., Kraft, T.S. and Dominy, N.J.** (2013). Tree climbing and human
950 evolution. *Proc. Natl. Acad. Sci. USA* **110**, 1237-1242.
951

952 **Vereecke, E., D'Août, K., De Clercq, D., Van Elsacker, L. and Aerts, P.** (2003). Dynamic
 953 plantar pressure distribution during terrestrial locomotion of bonobos (*Pan paniscus*). *Am. J.*
 954 *Phys. Anthropol.* **120**, 373-383.

955

956 **Vereecke, E., D'Aout, K., De Clercq, D., Van Elsacker, L. and Aerts, P.** (2004). The
 957 relationship between speed, contact time and peak plantar pressure in terrestrial walking of
 958 bonobos. *Folia Primatol.* **75**, 266-278.

959

960 **Vereecke, E.E. and Wunderlich, R.E.** (2016) Experimental research on hand use and
 961 function in primates. In *Evolution of the Primate Hand: Anatomical, Developmental,*
 962 *Functional and Paleontological Evidence* (ed. T.L. Kivell, P. Lemelin, B.G. Richmond and D.
 963 Schmitt), pp. 259-284. Springer-Verlag, New York.

964

965 **Ward, C.V.** (2002). Interpreting the posture and locomotion of *Australopithecus afarensis*:
 966 where do we stand? *Yrbk. Phys. Anthropol.* **45**, 185-215.

967

968 **Williams, E. M., Gordon, A. D., and Richmond, B. G.** (2012). Hand pressure distribution
 969 during Oldowan stone tool production. *J. Hum. Evol.* **62**, 520–32.

970

971 **Wunderlich, R.E.** (1999). Pedal form and plantar pressure distribution in anthropoid
 972 primates. *PhD thesis*, State University of New York at Stony Brook, Stony Brook, NY.

973

974 **Wunderlich, R.E. and Ischinger, S.B.** (2017). Foot use during vertical climbing in
 975 chimpanzees (*Pan troglodytes*). *J. Hum. Evol.* **109**, 1-10.

976

977 **Wunderlich, R.E. and Jungers, W.L.** (2009). Manual digital pressures during knuckle-
 978 walking in chimpanzees (*Pan troglodytes*). *Am. J. Phys. Anthropol.* **139**, 394-403.

979

980 **Yamazaki, N. and Ishida, H.** (1984). A biomechanical study of vertical climbing and bipedal
 981 walking in gibbons. *J. Hum. Evol.* **13**, 563-571.

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984 **Figure legends**

985

986 **Figure 1.** Images of the bonobo enclosure showing the orientation of the pressure beam for
 987 (A) vertical locomotion and (B) suspension and arboreal knuckle-walking. The beam is

988 covered in black shrink wrap; the position of the pressure mat has been painted white (black
989 dotted oval). ‘*’ in B indicate doors through which the bonobos enter their enclosure.

990

991 **Figure 2.** Hand posture during vertical locomotion. Three sets of still images taken from the
992 three high-speed cameras, showing contact of the palm and fingers with the substrate, how
993 the fingers were kept together, and variations in thumb position relative to the palm. In (A)
994 the thumb is more in line with the palm compared with an intermediate (B) or opposed (C)
995 posture.

996

997 **Figure 3.** Pressure results for vertical locomotion, showing differences in (A) raw peak
998 pressure, (B) relative peak pressure (kPa/body mass), (C) the pressure-time integral (PTI),
999 (D) the instant of peak pressure and (E) maximum contact area across the palm, fingers and
1000 thumb. A-C and E: Mean values are adjusted for covariation with stance time. There were
1001 significant statistical differences across anatomical regions for raw and relative peak
1002 pressure, PTI and contact area; ‘*’, $p < 0.05$; ‘***’, $p < 0.01$; ‘****’, $p < 0.001$.

1003

1004 **Figure 4.** Examples of representative pressure data and camera stills at point of peak
1005 pressure during vertical locomotion, suspension and arboreal knuckle-walking. Palm region
1006 highlighted in orange and digits in yellow. During vertical locomotion, typically only the distal
1007 portion of the fingers was loaded, and thus contact area for the fingers was small relative to
1008 the other types of locomotion. In the above examples, maximum contact area for the digits
1009 (which was not necessarily at the same time frame as peak pressure) was 10cm² during
1010 vertical locomotion, but 27 cm² for suspension and 28cm² for knuckle-walking.

1011

1012 **Figure 5.** Hand posture during suspensory locomotion. Still images taken from the three
1013 high-speed cameras, showing the typical grasping posture when (A) moving along the length
1014 of the beam and (B) transversing under it.

1015

1016 **Figure 6.** Pressure results for suspensory locomotion, showing differences in (A) raw peak
1017 pressure, (B) relative peak pressure (kPa/body mass), (C) the pressure-time integral (PTI),
1018 (D) the instant of peak pressure and (E) maximum contact area between the palm and
1019 fingers (the thumb was never loaded). A-C and E: Mean values are adjusted for covariation
1020 with stance time. There was a significant statistical difference across anatomical regions for
1021 PTI only. ‘*’, $p < 0.05$.

1022

1023 **Figure 7.** Hand posture during arboreal knuckle-walking. Still images taken from the three
1024 high-speed cameras, showing a palm-back (A) and palm-in (B) postures.

1025

1026 **Figure 8.** Comparisons of palm and finger pressures across different locomotor modes,
1027 showing differences in (A) raw peak pressure, (B) relative peak pressure (kPa/body mass),
1028 (C) the pressure-time integral (PTI), (D) the instant of peak pressure and (E) maximum
1029 contact area. There is only a statistical difference in maximum contact area for the palm
1030 between locomotor modes, but there are differences in raw and relative peak pressure, PTI
1031 and maximum contact area for the fingers across all modes. ‘*’, $p < 0.05$; ‘**’, $p < 0.01$; ‘***’,
1032 $p < 0.001$.

1033

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1036 **Tables**

1037

1038

1039 **Table 1:** The bonobo sample and number of trials for each individual and locomotor mode

1040

individual	age (yrs)	sex	weight (kg)	number of trials		
				vertical locomotion	suspension	knuckle- walking
Vifijo	21	male	35.0	17	3	1
Louisoko	17	male	-	2	1	-
Lucuma	12	male	-	2	-	-
Habari	9	male	32.7	7	2	-
Lina	30	female	33.4	3	-	5
Djanao	20	female	36.0	-	-	1
Busira	11	female	28.1	-	5	1
Lingoye	8	female	25.8	6	5	3
Total				37^a	16	11

1041 ^a Pressure data on the thumb was recorded in only 12 of these trials.

1042

1043

1044

1045

1046 **Table 2:** Peak pressure, both raw data and standardized for body mass, pressure-time integral (PTI), instant of peak pressure and maximum
 1047 (max.) contact area values for the different hand regions during vertical locomotion, suspension, and knuckle-walking. Mean values for peak
 1048 pressure, PTI and maximum contact area are adjusted for covariation with stance time.
 1049

		Mean values (\pmS.E)					
Mode	Hand region	N	Peak pressure (kPa)		PTI (kPa*s)	Max. contact area (cm²)	Instant of peak pressure (% of stance)
			raw	body mass^a			
Vertical							
locomotion	Palm	37	142.0 (\pm 12.9)	4.3 (\pm 0.4)	72.3 (\pm 10.6)	14.1 (\pm 1.0)	42.8 (\pm 3.4)
	Fingers	37	103.3 (\pm 7.6)	3.1 (\pm 0.2)	63.8 (\pm 9.0)	12.1 (\pm 1.0)	38.2 (\pm 3.8)
	Thumb	12	30.0 (\pm 3.4)	0.9 (\pm 0.1)	10.6 (\pm 1.8)	1.7 (\pm 0.2)	45.2 (\pm 8.4)
Suspension	Palm	16	129.7 (\pm 12.6)	4.3 (\pm 0.5)	84.6 (\pm 13.0)	21.6 (\pm 2.5)	48.2 (\pm 4.6)
	Fingers	16	99.7 (\pm 15.7)	3.4 (\pm 0.8)	59.3 (\pm 8.1)	17.1 (\pm 2.2)	46.8 (\pm 3.7)
Knuckle-							
walking	Fingers	11	233.6 (\pm 24.2)	7.4 (\pm 0.6)	154.3 (\pm 29.6)	18.4 (\pm 1.1)	63.1 (\pm 3.0)

1050 ^a Raw pressure data divided by body mass data (Table 1) for each individual, excluding trials from Louisoko (n=2 vertical locomotion and n=1
 1051 suspension trials) and Lucuma (n=2 vertical locomotion trials) individuals, for which body mass data is not known.

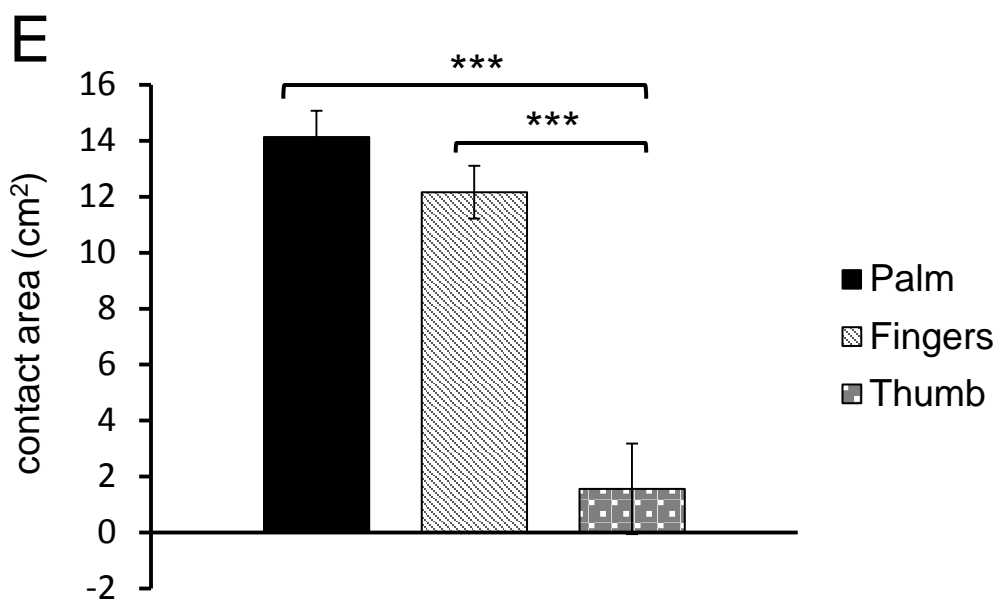
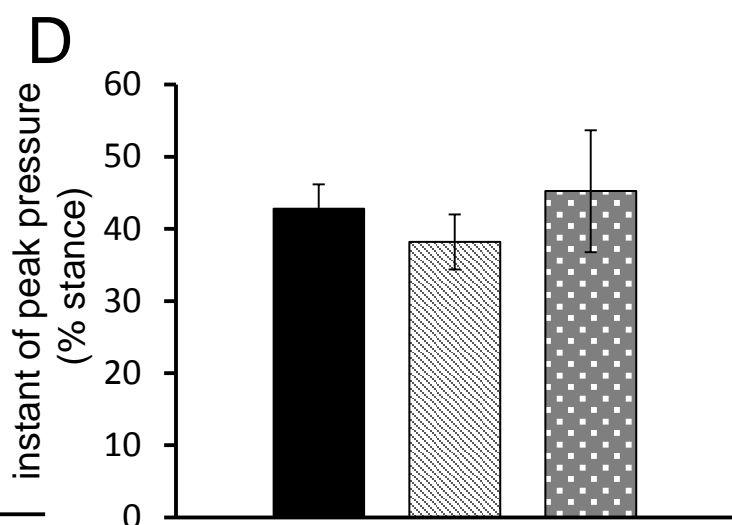
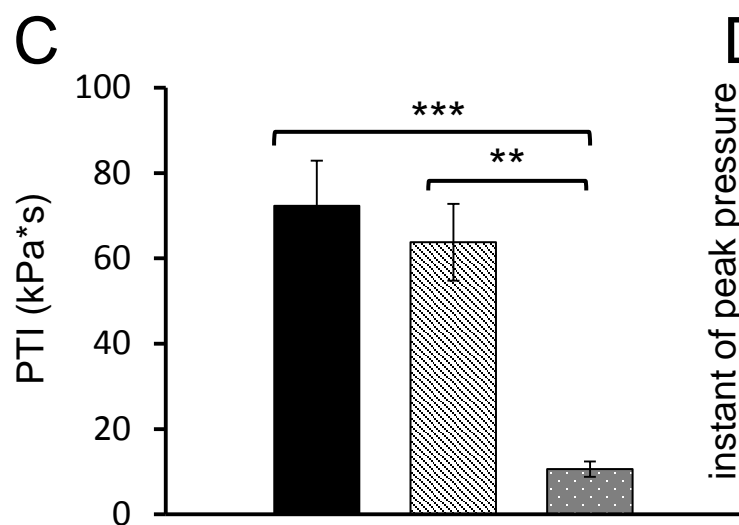
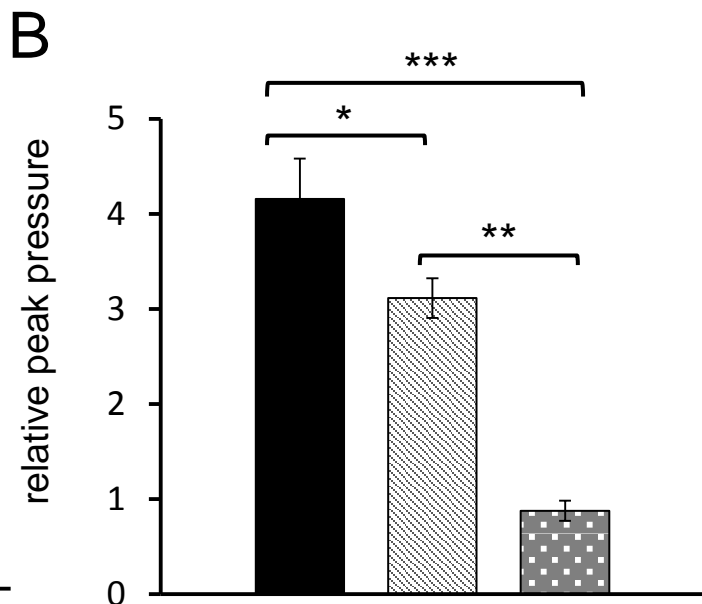
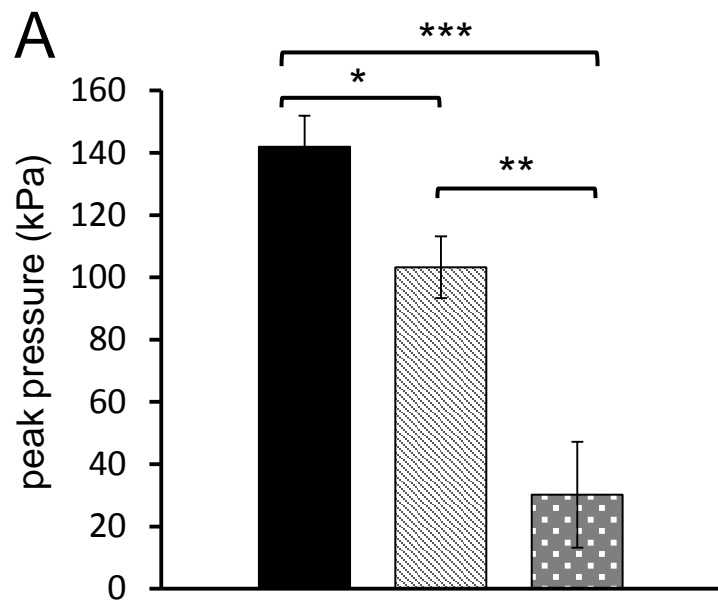
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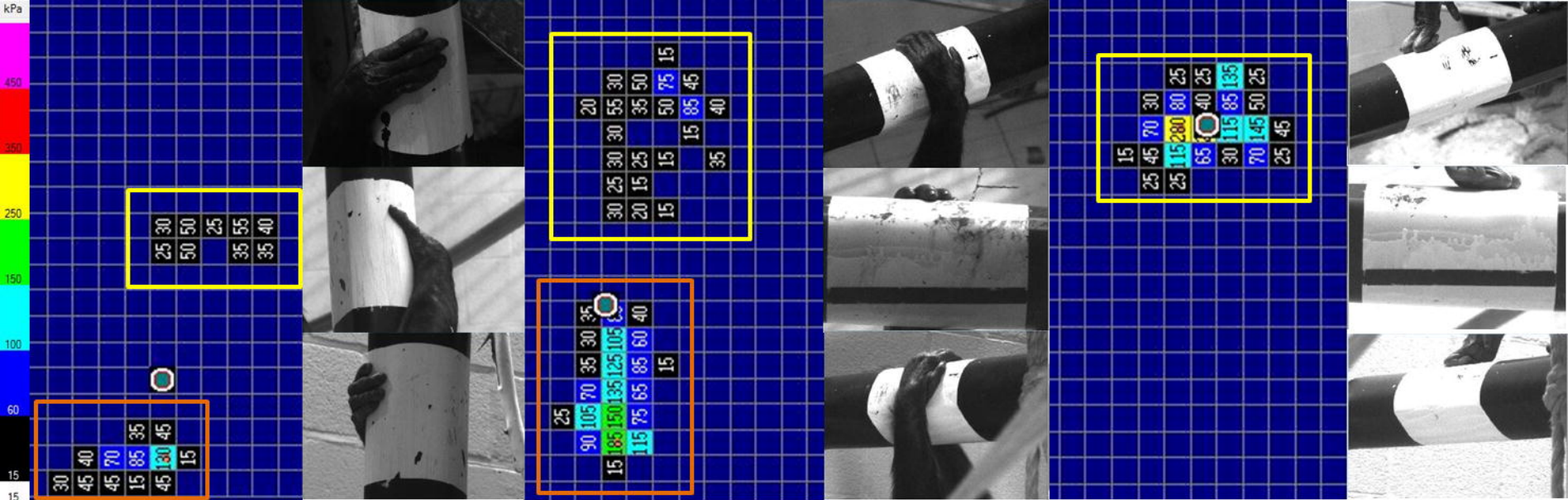
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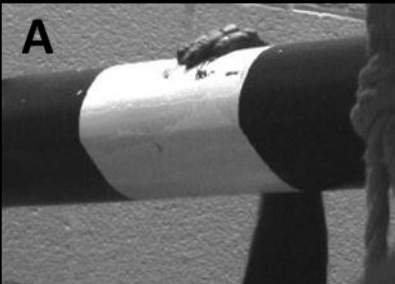
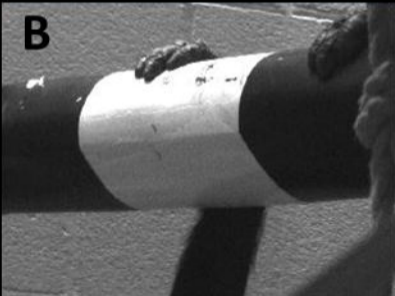


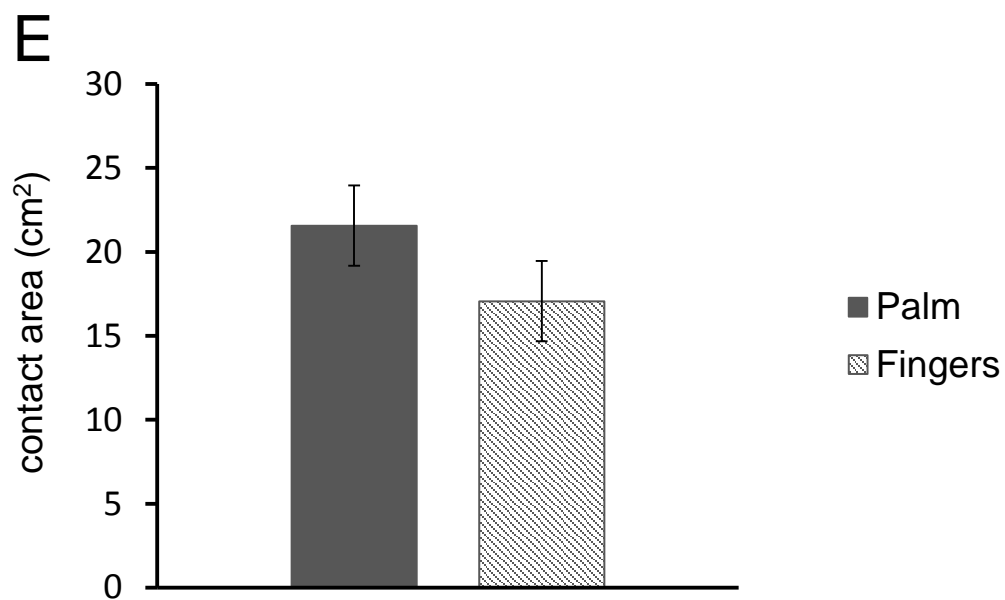
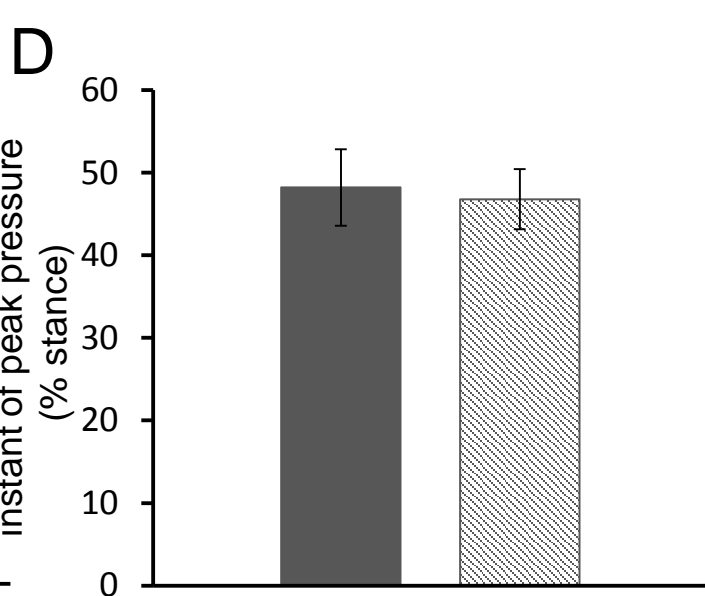
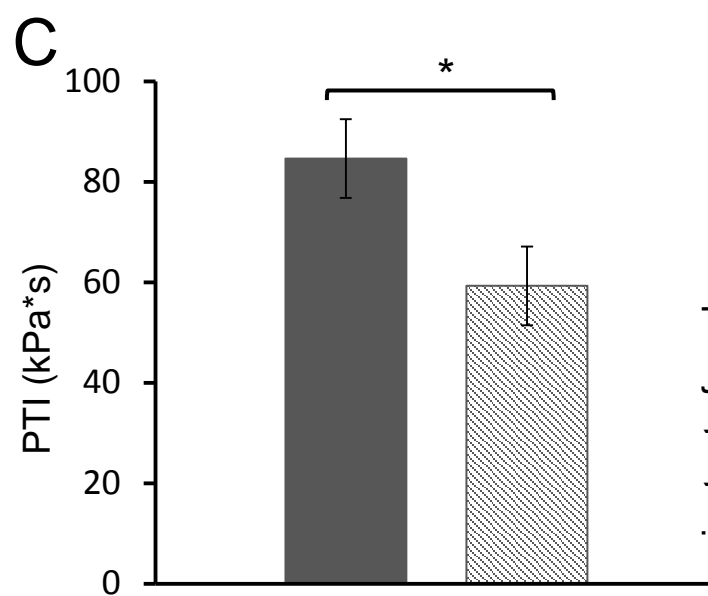
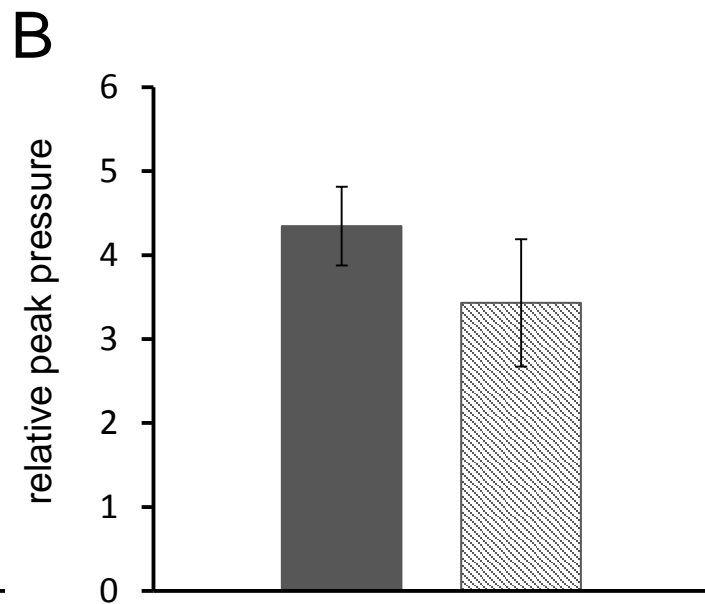
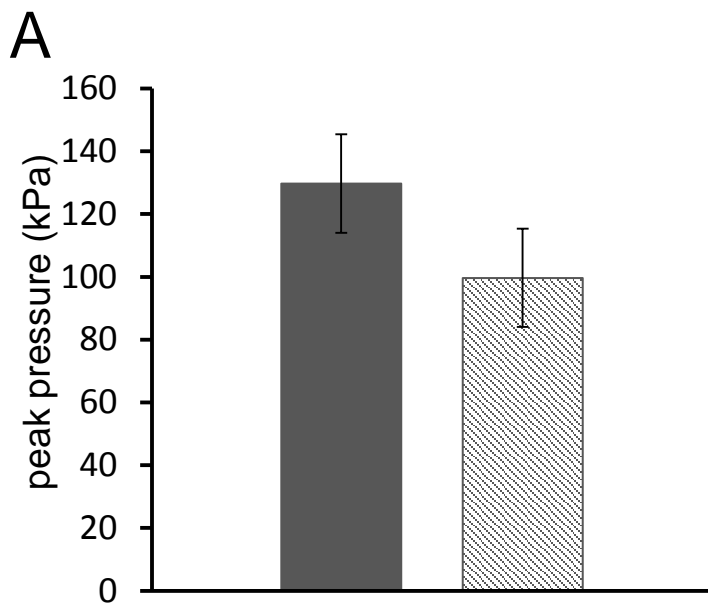


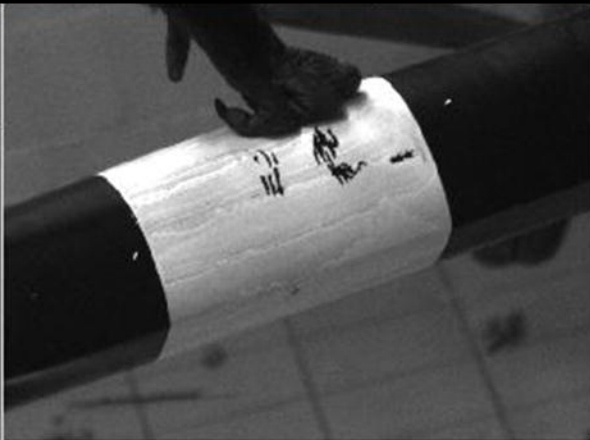
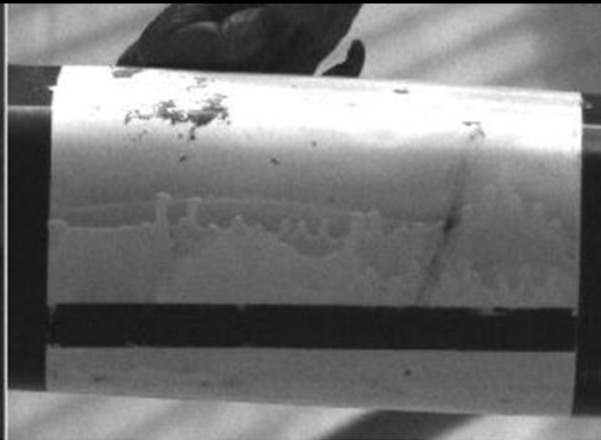
vertical locomotion

suspension

knuckle-walking

A**B**



A**B**