

RESEARCH ARTICLE

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

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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. The 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, bonobos do not show a rolling pattern of digit contact with the substrate during arboreal knuckle-walking – instead, we found that 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 fossilized 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.

KEY WORDS: Force, Biomechanics, African apes, Vertical climbing, Suspension, Knuckle-walking

INTRODUCTION

The human hand is unique among primate hands 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, in terms

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

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

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

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

Measures of substrate reaction force provide the net result of all forces experienced by the limb and, although informative, such data lack detailed information on where the load is applied. Pressure studies complement substrate reaction force analyses, as they provide a dynamic map of vertical force distribution and changes in contact area across the region of interest (e.g. hand or foot). Studies measuring changes in pressure during locomotion in primates are limited, but have included bonobos (D'Août et al., 2001, 2004; Vereecke et al., 2003, 2004). However, most have only investigated terrestrial locomotion and/or have focused on the feet (e.g. Wunderlich, 1999; Patel and Wunderlich, 2010; D'Août et al., 2001, 2004; Vereecke et al., 2003, 2004; Kivell et al., 2010; Matarazzo, 2013; Wunderlich and Ischinger, 2017). To our knowledge, the only pressure studies of non-horizontal arboreal locomotion are on the hand of a gibbon during brachiation (Richmond, 1998) and, just recently, the chimpanzee foot during vertical climbing (Wunderlich and Ischinger, 2017). Of particular interest here, two studies have measured pressure experienced by the hand during knuckle-walking in African apes. Wunderlich and Jungers (2009) measured digit pressures of young (4–5 years) and old (7 years) chimpanzees during knuckle-walking on both the ground and an arboreal horizontal pole. Although peak pressure was comparable between the substrates, its distribution across the digits differed, with digits 3 and 4 experiencing the greatest load on the arboreal substrate as opposed to digits 2–4 on the ground (Wunderlich and Jungers, 2009). This variation in digit load was further influenced by hand posture and whether a palm-in or pronated palm-back posture was used. This flexibility in hand posture and digit load was corroborated by Matarazzo's (2013) study of chimpanzee and gorilla digit pressures during terrestrial knuckle-walking.

To date, no studies have directly measured how the different anatomical regions of the primate hand are loaded during different modes of arboreal locomotion. In particular, vertical climbing and suspension are key components of the locomotor repertoire in African apes (Susman, 1984; Susman et al., 1980; Hunt, 1991,

1992; Doran, 1993; Crompton et al., 2010) and may also have been critical behaviours in the evolution of early hominin ancestors (e.g. Rose, 1991; Schmitt, 2003). To fill this gap, we measured pressures experienced by the bonobo hand (divided into regions of the palm, fingers and thumb) during three modes of arboreal locomotion: vertical locomotor behaviours, suspension and knuckle-walking. We tested four hypotheses, based on previous studies of hand use and posture during arboreal locomotion in bonobos, or great apes in general, and pressure analyses of chimpanzee arboreal knuckle-walking (Wunderlich and Jungers, 2009). (1) Hand postures used during arboreal locomotion will be similar to those described previously in chimpanzees during suspension and climbing (Hunt, 1991; Marzke and Wullstein, 1996; Neufuss et al., 2017b) and arboreal knuckle-walking (Wunderlich and Jungers, 2009). (2a) Pressure experienced by the palm and fingers will be similar within both vertical locomotion and suspension as both regions of the hand are generally used to grasp the substrate during these locomotor behaviours (Hunt, 1991). (2b) In contrast, pressure experienced by the thumb will be significantly lower than that experienced by the palm or fingers because of the thumb's short length relative to that of the fingers, small musculature (Tuttle, 1969; Marzke et al., 1999) and the general assumption that the function of the thumb is limited during arboreal locomotion (e.g. Straus, 1942; Tuttle, 1967; Sarmiento, 1988). (3) Pressure experienced by the fingers will be highest during knuckle-walking, as only the dorsum of the intermediate phalanges is in contact with the substrate (i.e. high force distributed over a small area). In contrast, pressure experienced by the fingers and palm will be lowest during vertical locomotion, as the hindlimbs provide propulsion during vertical locomotion and thus experience greater force than the forelimbs (Hirasaki et al., 1993; Hanna et al., 2017) and most of the hand grips the substrate (i.e. relatively lower force distributed over a larger area). (4) Loading of the fingers during arboreal knuckle-walking will be similar between bonobos and chimpanzees (Wunderlich and Jungers, 2009), given their close evolutionary relationship, similar anatomy (Diogo et al., 2017a,b) and similar biomechanical pattern of knuckle-walking (Inouye, 1994).

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

MATERIALS AND METHODS

Sample

Over a period of 9 months, we measured hand pressure during vertical locomotion, suspension and arboreal knuckle-walking in captive bonobos (*Pan paniscus* Schwarz 1929) cared for at Planckendael Zoo (Royal Zoological Society of Antwerp, Belgium). Eight adult individuals from this captive group were included in this study (Table 1). Ethical approval for this study was granted by the Centre for Research and Conservation in Antwerp, Belgium. The trials were conducted within the bonobos' indoor enclosure whilst all individuals were together. Contact with or training of the bonobos was not possible; thus, all data were collected *ad libitum* when the individuals voluntarily decided to use the apparatus.

Materials

Hand pressure was measured using a flexible Novel® S2119 pressure mat (Novel GmbH, Munich, Germany) with an additional

Table 1. Bonobos, number of trials for each individual and locomotor mode

| Individual | Age (years) | Sex | Mass (kg) | No. 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 |
| Djanaoa | 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 |

^aPressure data on the thumb were recorded in only 12 of these trials.

rubber coating for protection and durability. The pressure mat is composed of 512 sensors, each 1 cm×1 cm, arranged over 32 columns and 16 rows. The mat was calibrated to have a pressure range of 15–1000 kPa. Data were read using a Pliance[®]-xf-32 analyser (Novel GmbH) at a rate of 34–35 Hz, and transferred to a laptop running Pliance[®]-xf-32 Recorder software (version 24.3.5; Novel GmbH).

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

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

Data analysis

Only trials in which the individual engaged in continuous motion and the whole hand made contact with the pressure mat were analysed. First, data pertaining to different anatomical regions of the hand (i.e. palm, fingers and, where possible, thumb) were defined

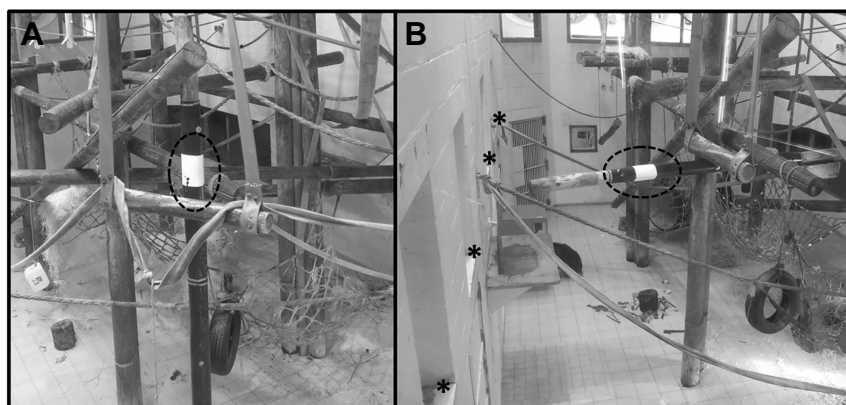


Fig. 1. Images of the bonobo enclosure showing the orientation of the pressure beam for the different types of locomotion. (A) Vertical locomotion; (B) suspension and arboreal knuckle-walking. The beam is covered in black shrink wrap; the position of the pressure mat has been painted white (black dotted oval). Asterisks in B indicate the doors through which the bonobos entered their enclosure.

using the masking tool within the Pliance[®] software (Novel GmbH). For each region, peak pressure and the pressure–time integral (PTI) were computed. Peak pressure (kPa) is the maximum pressure recorded in the area of interest. The pressure–time integral (kPa×s) is the area under the pressure–time curve; in other words, it considers both peak pressure and the duration of contact of a particular region. In addition, maximum contact area (cm²), overall contact time for the hand (hereafter referred to as ‘stance time’), contact time for each anatomical region, and the instant of peak pressure (as a percentage of stance time) were calculated. Because of the small sample sizes, male and female individuals were pooled together for data analyses. Thus, analyses of both raw pressure data (kPa) for the entire sample and peak pressure standardized by body mass (peak kPa/body mass) for six of the eight individuals (excluding $n=2$ vertical locomotion and $n=1$ suspension trials for Louisoko and $n=2$ vertical locomotion trials for Lucuma; see Table 1) are presented. Qualitative assessments of how the hand grasped the pressure mat were also made from the high-speed video data.

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

covariance (ANCOVA) for all comparisons with stance time as the covariate. All statistical tests were conducted in SPSS (version 22.0; IBM, Portsmouth, UK).

RESULTS

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

Vertical locomotion

Because the animals could not be trained, and data were therefore collected *ad libitum*, the bonobos used the vertical beam for a variety of locomotor behaviours. In addition to vertical climbing, they used it for clambering and for swinging when moving from one substrate to another. As all of these locomotor modes are normal and natural for bonobos (Doran, 1993), we included all of them in the qualitative and quantitative analyses of ‘vertical locomotion’ (Table 1).

Hand posture

Although the bonobos used the vertical beam for a variety of vertical locomotor behaviours, the same hand posture was generally always used. The palm, thumb and fingers always made contact with the substrate and the fingers were always held together. The thumb was always separated from the palm, although its position varied from being fully opposed to being more in line with the palm (Fig. 2). In all trials, at least the palmar surface of the distal half of the thumb, if not the full thumb, was clearly in contact with the beam, based on the video data, even though pressure data did not always register on the mat. However, there was variation in how the hand grasped the substrate; the first region to touch down on the substrate was most often the fingers (in 46% of $n=37$ vertical locomotor trials) or the

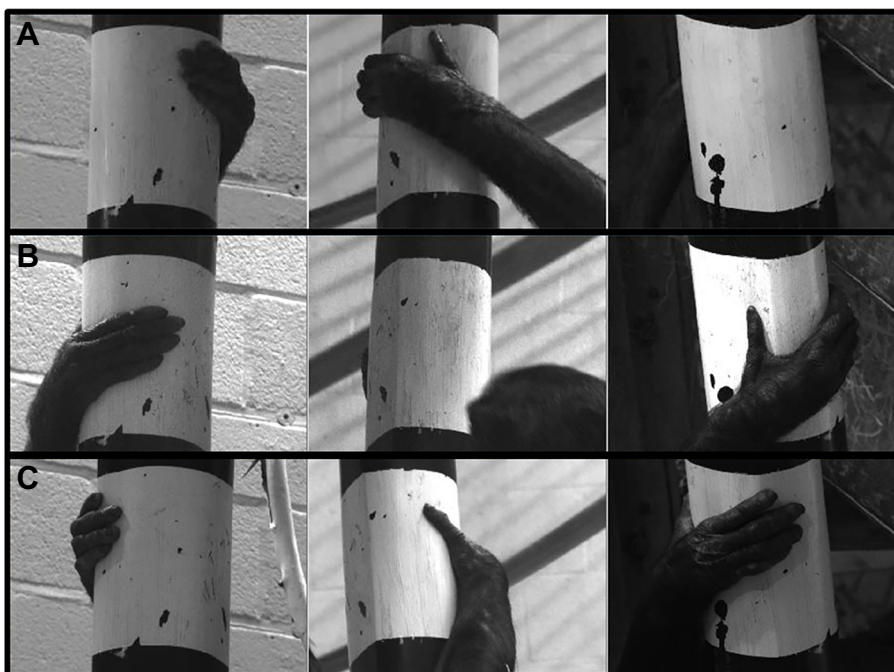


Fig. 2. Hand posture during vertical locomotion. (A–C) Three sets of still images taken from the three high-speed cameras, showing contact of the palm and fingers with the substrate, how the fingers were kept together, and variations in thumb position relative to the palm. In A, the thumb is more in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

thumb (36%), but in some trials the palm (18%) was the first to touch down. In 90% of all vertical locomotor trials, digit 5 touched down before digit 2 and, concurrently, the medial side of the palm touched down before the lateral side. The first region of the hand to lift off the substrate varied, but was most often the thumb (65%), followed by either the fingers or the palm (both 17%). As with touchdown, digit 5 most often lifted off before digit 2 (74%), whilst palm lift off initiated from the lateral or the medial side relatively equally (52% and 48%, respectively).

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

Hand pressure

Pressure experienced by the hand during vertical locomotion was predominantly limited to the palm and fingers. Loading of the

thumb was only registered by the pressure mat in 32% ($n=12$) of the total vertical locomotion trials and was not limited to specific types of vertical locomotor behaviours (e.g. climbing, clambering) (Fig. 3). There were no statistical differences for any pressure variables in the palm and finger regions between trials with and without thumb loading; thus, data were pooled. Regional raw peak pressure, relative peak pressure, PTI, the instant of peak pressure and maximum contact area results are presented in Table 2 and Fig. 3. Results from the ANCOVA accounting for variation in stance time found significant differences across all of the anatomical regions (i.e. palm, thumb and fingers) for raw peak pressure (F -ratio=16.398, $P<0.001$), relative peak pressure (F -ratio=13.908, $P<0.001$), PTI (F -ratio=10.121, $P<0.001$) and maximum contact area (F -ratio=22.966, $P<0.001$). Raw and relative peak pressure were significantly higher in the palm than in the fingers ($P=0.022$ and $P=0.045$, respectively), and raw and relative peak pressure for both the palm and fingers were significantly higher than those of the thumb (palm, $P<0.001$ and $P<0.001$; fingers, $P=0.001$ and $P=0.003$). PTI values for the palm and fingers were similar ($P=1.000$) but, again, both were significantly higher compared with that of the thumb (palm, $P<0.001$; digits, $P=0.001$). For all hand regions, the instant of peak pressure occurred in the first half of stance: at 38% of stance time for the fingers, 43% for the palm and 45% for the thumb. Peak pressure on the palm was predominantly located at the proximal part of the palm (57% of the total vertical trials), and less often at the middle (38%) or distal (5%) palm.

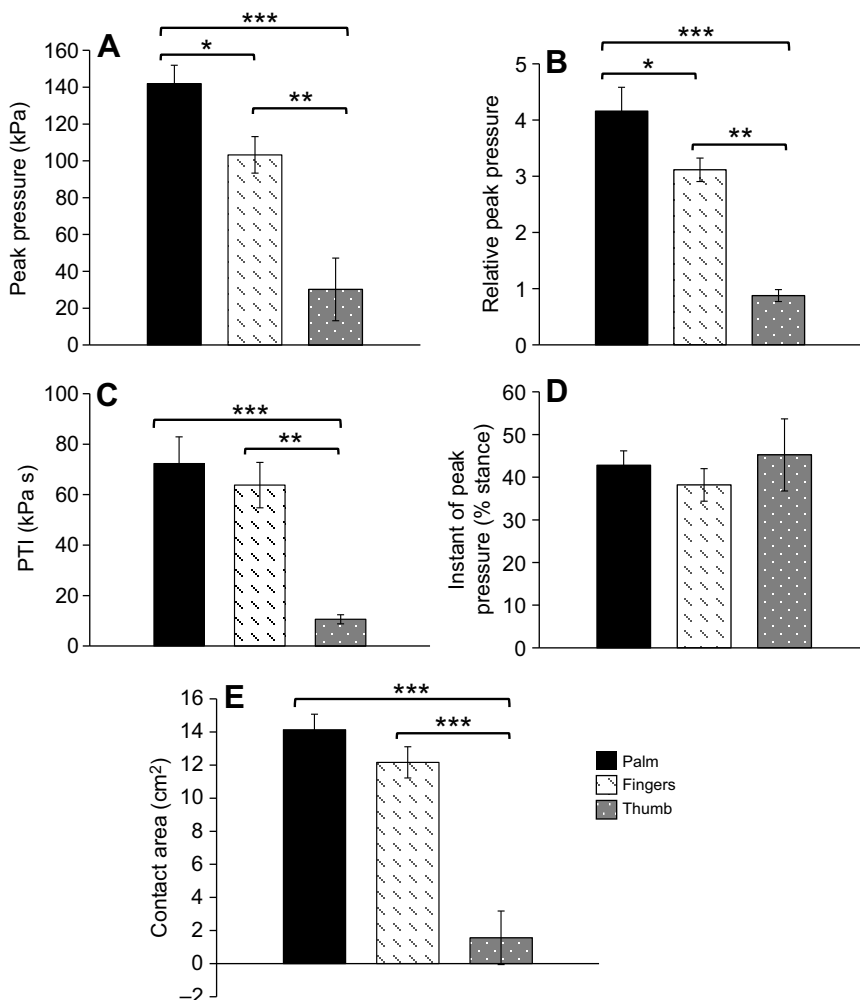


Fig. 3. Pressure results for vertical locomotion.

Differences in (A) raw peak pressure, (B) relative peak pressure (kPa/body mass), (C) the pressure–time integral (PTI), (D) the instant of peak pressure and (E) maximum contact area across the palm, fingers and thumb are shown. Data in A–C and E are mean values adjusted for covariation with stance time. There were significant statistical differences across anatomical regions for raw and relative peak pressure, PTI and contact area; * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

Table 2. Peak pressure, pressure-time integral, instant of peak pressure and maximum contact area values for the different hand regions during vertical locomotion, suspension and knuckle-walking

| Mode | Hand region | N | Peak pressure (kPa) | | PTI (kPa×s) | Max. contact area (cm ²) | Instant of peak pressure (% of stance) |
|---------------------|-------------|----|---------------------|------------------------|-------------|--------------------------------------|--|
| | | | Raw | Body mass ^a | | | |
| Vertical locomotion | Palm | 37 | 142.0±12.9 | 4.3±0.4 | 72.3±10.6 | 14.1±1.0 | 42.8±3.4 |
| | Fingers | 37 | 103.3±7.6 | 3.1±0.2 | 63.8±9.0 | 12.1±1.0 | 38.2±3.8 |
| | Thumb | 12 | 30.0±3.4 | 0.9±0.1 | 10.6±1.8 | 1.7±0.2 | 45.2±8.4 |
| Suspension | Palm | 16 | 129.7±12.6 | 4.3±0.5 | 84.6±13.0 | 21.6±2.5 | 48.2±4.6 |
| | Fingers | 16 | 99.7±15.7 | 3.4±0.8 | 59.3±8.1 | 17.1±2.2 | 46.8±3.7 |
| Knuckle-walking | Fingers | 11 | 233.6±24.2 | 7.4±0.6 | 154.3±29.6 | 18.4±1.1 | 63.1±3.0 |

Data are means±s.e.; mean values for peak pressure (shown as raw data and standardized for body mass), pressure–time integral (PTI) and maximum contact area were adjusted for covariation with stance time.

^aRaw pressure data divided by body mass data (Table 1) for each individual, excluding trials from Louisoko ($n=2$ vertical locomotion and $n=1$ suspension trials) and Lucuma ($n=2$ vertical locomotion trials), for which body mass data were not known.

Peak pressure for the fingers was almost always (89%) at the distal phalanges. In fact, often it was only the distal area of the fingers that was loaded, such that there was a large gap between the finger and palm regions, indicating that most of the proximal and intermediate phalangeal regions was not loaded (Fig. 4). Whilst it was not possible to determine exactly under which digit the peak occurred, it was frequently in the centre of the distal portion of the finger region and thus was probably experienced by or near the third digit. Maximum contact area was similar for the palm and fingers ($P=0.431$), and both were significantly larger than that of the thumb (both $P<0.001$) (Table 2, Fig. 3).

Suspension

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

Hand posture

During suspension, the palm, fingers and thumb always made contact with the substrate, and the fingers were always held together. Based on video data, the full palmar surface of the thumb was in

contact with the substrate, even though pressure data under the thumb did not register on the mat (see below). In contrast to vertical locomotion, the thumb was always slightly abducted (Fig. 5A) or held in line (Fig. 5B) with the palm,

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

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

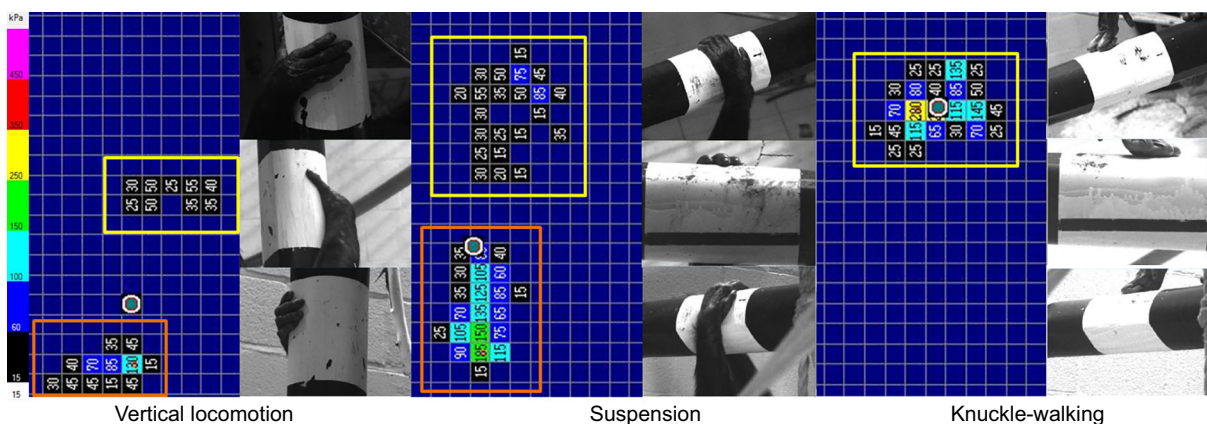


Fig. 4. Examples of representative pressure data and camera stills at the point of peak pressure during vertical locomotion, suspension and arboreal knuckle-walking. Data for the palm region are highlighted in orange and those for the digits are in yellow. During vertical locomotion, typically only the distal portion of the fingers was loaded, and thus contact area for the fingers was small relative to that for the other types of locomotion. Maximum contact area for the digits (which was not necessarily in the same time frame as peak pressure) was 10 cm² during vertical locomotion, but 27 cm² for suspension and 28 cm² for knuckle-walking.

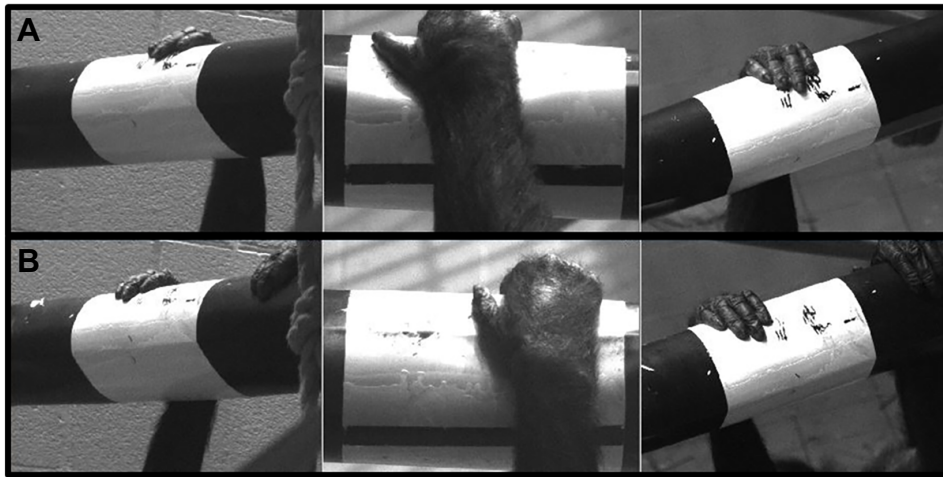


Fig. 5. Hand posture during suspensory locomotion. Still images taken from the three high-speed cameras, showing the typical grasping posture when (A) moving along the length of the beam and (B) traversing under it.

Hand pressure

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

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

Arboreal knuckle-walking

Hand posture

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

Hand pressure

Finger raw and relative peak pressure, PTI, the instant of peak pressure and maximum contact area results are presented in Table 2 and Fig. 8. Peak pressure was always localized to the centre of the contact region; thus, it is likely that this pressure was experienced by

or surrounding digit 3 (Fig. 4). Unlike vertical locomotion and suspension, the instant of peak pressure occurred after mid-stance, at 63% of stance time.

Comparison of hand pressures between locomotor modes

Comparisons of pressure variables were made between vertical locomotion and suspension for the palm, and across all locomotor

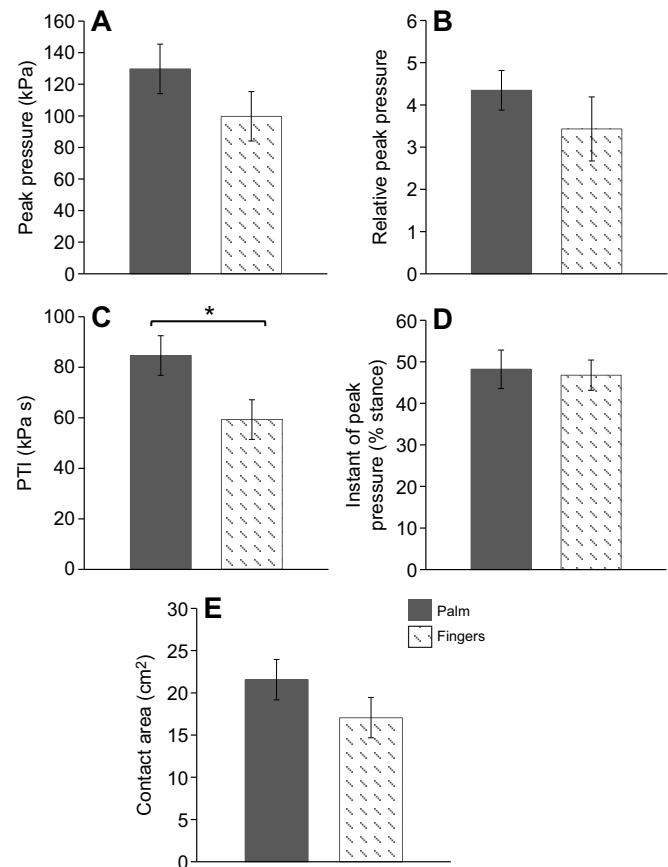


Fig. 6. Pressure results for suspensory locomotion. Differences in (A) raw peak pressure, (B) relative peak pressure (kPa/body mass), (C) PTI, (D) the instant of peak pressure and (E) maximum contact area between the palm and fingers (the thumb was never loaded) are shown. Data in A–C and E are mean values adjusted for covariation with stance time. There was a significant statistical difference across anatomical regions for PTI only. * $P < 0.05$.

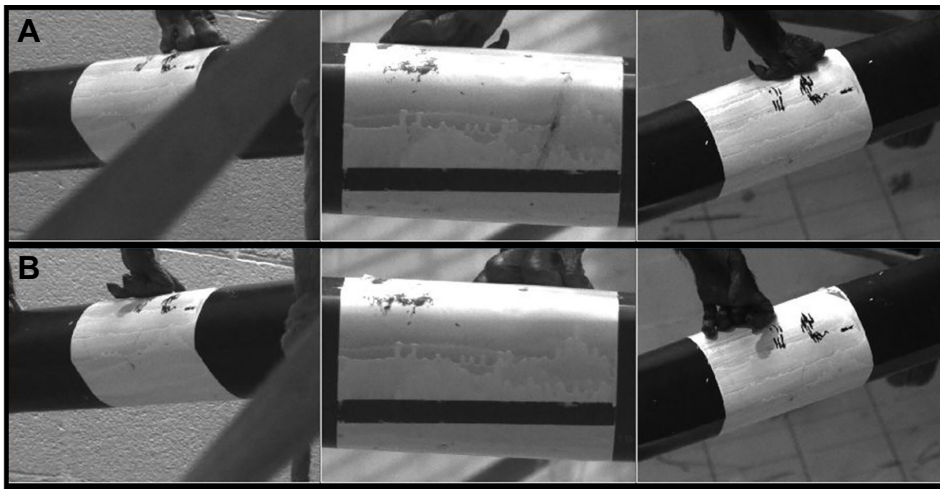


Fig. 7. Hand posture during arboreal knuckle-walking. Still images taken from the three high-speed cameras, showing a palm-back (A) and palm-in (B) posture.

modes for the fingers (Fig. 8). For the palm, only maximum contact area was significantly different (F -ratio=9.722, $P=0.003$), with suspension having a significantly ($P=0.003$) greater contact area than vertical locomotion. For the fingers, raw and relative peak pressure (F -ratio=21.216, $P<0.001$ and F -ratio=19.898, $P<0.001$, respectively), PTI (F -ratio=19.475, $P<0.001$) and maximum contact area (F -ratio=4.569, $P=0.014$) differed significantly across all locomotor modes. Raw and relative peak pressure and PTI were significantly larger for the fingers during arboreal knuckle-walking compared with both suspension and vertical locomotion ($P<0.001$ in all cases), although there were no differences for these variables between these last two locomotor modes. Maximum contact area of the fingers was significantly smaller during vertical locomotion than during knuckle-walking ($P=0.037$). The instant of peak pressure also occurred later in stance during knuckle-walking than during vertical locomotion and suspension.

DISCUSSION

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

Hand posture

In this study, we provide the first quantitative and detailed qualitative assessment of how the bonobo hand made contact with an arboreal substrate during a variety of vertical locomotor behaviours, suspension and arboreal knuckle-walking. During vertical locomotion and suspension, the palm, fingers and thumb always made contact with the substrate, and the fingers were typically held together during contact with the substrate for all modes of locomotion. The position of the thumb varied during vertical locomotion, ranging from being positioned parallel to the palm to being opposed to the fingers, while during suspension it was generally positioned in line with the palm. Although the details of the exact position of the fingers during climbing and suspension have not been previously described in bonobos, the hand postures documented here are generally consistent with those described in chimpanzees (Hunt, 1991; Marzke and Wullstein, 1996; Neufuss et al., 2017b) and other great apes (Sarmiento, 1988; Alexander, 1994), supporting our first hypothesis.

Furthermore, during vertical locomotion and suspension, the fingers were most often the first part of the hand to touch down, while

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

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

These differences between bonobo and chimpanzee arboreal knuckle-walking hand posture may be a byproduct of samples used in each study; here, we had $n=11$ trials from five individuals ranging from 8 to 30 years of age (Table 1), while Wunderlich and Jungers (2009) had $n=38$ trials from two young juvenile chimpanzees aged 4–5 years. Although Inouye (1994) found no significant differences in digit use throughout ontogeny between bonobos and chimpanzees, her analysis was of terrestrial knuckle-walking only. Furthermore, the bonobos knuckle-walked on a slightly wider substrate than did the chimpanzees (12 cm versus 10.2 cm in

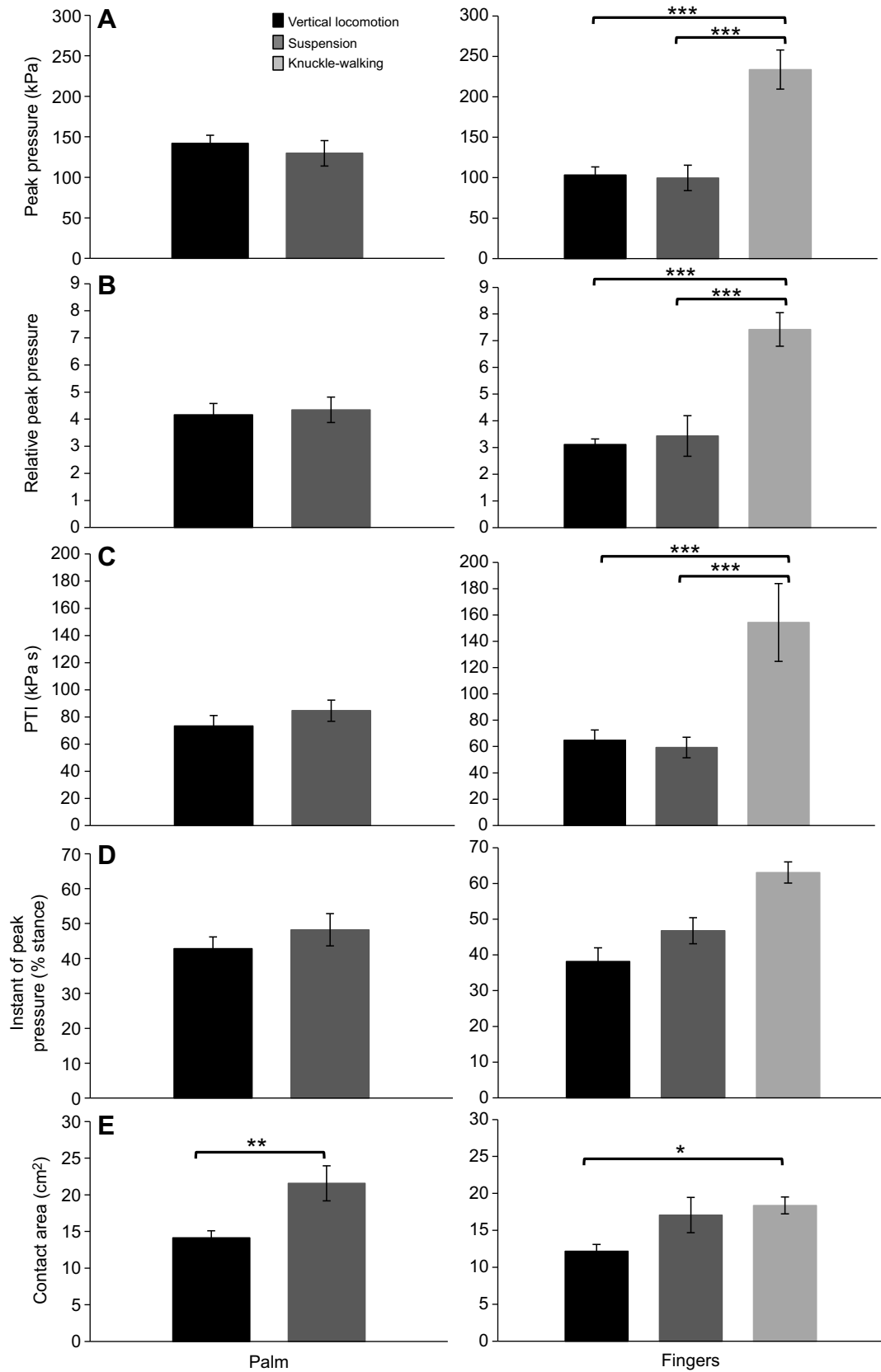


Fig. 8. Comparison of palm and finger pressures across different locomotor modes. Differences in (A) raw peak pressure, (B) relative peak pressure (kPa/body mass), (C) PTI, (D) the instant of peak pressure and (E) maximum contact area are shown. There was a statistically significant difference only in maximum contact area for the palm between locomotor modes, but there were differences in raw and relative peak pressure, PTI and maximum contact area for the fingers across all modes. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

diameter, respectively) that was much higher off the ground (2.5 m versus ~0.3 m, respectively) (Wunderlich and Jungers, 2009; R. E. Wunderlich, personal communication). As such, the bonobo's greater use of the palm-back postures and simultaneous digit contact (rather than the 'rolling' touch down/lift off) may both reflect the increased substrate surface area for digit contact and provide greater stability when higher off the ground. Further studies of the kinematics of African ape arboreal knuckle-walking are needed to document potential variation in hand (and forelimb) posture and how this may relate to differences in substrate size and height, and the overall requirements for stability.

Hand pressure

This study tested three hypotheses (hypotheses 2–4 in the Introduction) in relation to hand pressure experienced by bonobos during arboreal locomotion. First, we predicted that pressure experienced by the palm and fingers would not differ within vertical locomotion and suspension, but that loading of the thumb would always be significantly lower than that of the rest of the hand. We found partial support for this hypothesis. Raw and relative peak pressure experienced by the palm and fingers during suspension were similar, and the peak pressure and PTI experienced by the thumb was always significantly lower than that experienced by the rest of the hand during both locomotor modes (also see below). Furthermore, the regions most often experiencing peak pressure – the proximal portion of the palm and the distal region of the fingers – were similar in both vertical and suspensory locomotion. However, raw and relative peak pressure during vertical locomotion and PTI during suspension were significantly higher for the palm compared with those for the fingers. When considering differences in contact area between the palm and fingers (Figs 3 and 6), this result suggests comparatively greater normal force being exerted on the palm during suspension than during vertical locomotion.

Second, for comparisons across the different locomotor modes, we predicted that pressure would be highest during knuckle-walking and lowest during vertical locomotion. Again, we found only partial support for this hypothesis. Raw and relative peak pressure and the PTI were significantly higher for the fingers during knuckle-walking compared with vertical and suspensory locomotion. However, this was not due to a high compressive loading over a relatively small contact area, as predicted. Instead, maximum contact area for the digits during arboreal knuckle-walking was similar to that of the digits during suspension and significantly larger than that for vertical climbing. This unexpected result may be explained by two factors. (1) African apes have broad, specialized 'knuckle pads' covering the dorsum of the intermediate phalanges (Tuttle, 1967, 1969) that, during compressive loads of knuckle-walking, create a large friction contact area with the substrate. Mean contact area for chimpanzee arboreal knuckle-walking was even larger ($26.1 \pm 4.9 \text{ cm}^2$, mean \pm s.d.; data provided by R. E. Wunderlich), suggesting that a relatively large contact area during bonobo knuckle-walking (mean $18.4 \pm 3.8 \text{ cm}^2$, mean \pm s.d.; Table 2) is not unexpected. (2) Although from the video data it appeared that the full hand was grasping the substrate during vertical locomotion (and suspension), most often only the area under the distal and, sometimes, proximal phalanges was loaded (Fig. 4). This may reflect the diameter of the substrate; experimental studies of human hands grasping cylindrical handles have shown that contact area of the palmar surface, as well as normal force, decreases with an increase in diameter (Kong and Lowe, 2005; Seo et al., 2007; Seo and Armstrong, 2008). This is because gripping flexes the fingertips, and the curvature of larger diameter handles (or, in this

case, substrates) is too large to fit the curvature of the fingers (Seo and Armstrong, 2008). A similar phenomenon may be occurring with bonobos when they grasp larger substrates, such that pressure is mainly incurred by only the distal fingers and palm.

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

Finally, our fourth hypothesis predicted that loading experienced by the bonobo fingers during arboreal knuckle-walking would be similar to that previously described in chimpanzees (Wunderlich and Jungers, 2009). As discussed above, we found some differences in the hand postures used by bonobos compared with chimpanzees. Raw pressure data are not directly comparable between the two studies because of variation in the pressure mat sensor size ($0.5 \text{ cm} \times 0.5 \text{ cm}$ versus $1.0 \text{ cm} \times 1.0 \text{ cm}$ in this study) and the way in which Pliance[®] software calculates peak pressure. However, the general patterns appear similar; peak pressures for chimpanzees were significantly higher on digit 3 than on any other digit, and peak pressure in bonobos was experienced in the middle of the 'finger region', consistent with peak pressure occurring at or near digit 3 as well. Relative mean peak pressure on the third digit for juvenile chimpanzees ($236 \text{ kPa body mass}^{-1}$ of 25–29 kg) is 8.1–9.4 compared with a mean (\pm s.d.) of 7.4 ± 2.1 in bonobos. Furthermore, the instant of peak pressure occurred after mid-stance in both bonobos (63% of total stance phase) and chimpanzees (55% of stance phase in the palm-back posture; 70% of stance phase in the palm-in posture for digit 3) (Wunderlich and Jungers, 2009). Matarazzo (2013) also showed relatively high pressures on the third digit during terrestrial knuckle-walking in chimpanzees and gorillas. However, comparisons with the absolute pressure values were not made given the unusually low values reported in Matarazzo (2013) [i.e. maximum pressure for an adult chimpanzee during knuckle-walking was only 31.8 kPa, compared with 790 kPa in Wunderlich and Jungers (2009) and a mean of 234 kPa in this study]. Overall, these results are consistent with previous studies showing general similarities between bonobo and chimpanzee knuckle-walking hand posture (e.g. Inouye, 1994) and the kinematics and kinetics during terrestrial knuckle-walking

(Pontzer et al., 2014; Finestone et al., 2018), but further studies of both taxa on larger samples are needed to determine whether subtle differences in gait mechanics found in the hindlimbs (D'Aouit et al., 2004; Pontzer et al., 2014) might also be revealed in the forelimbs.

The functional role of the thumb

Of particular interest is the role of the thumb during arboreal locomotion. For decades, many studies have downplayed the functional importance of the thumb in great apes, particularly during suspensory locomotion (e.g. Ashley-Montagu, 1931; Straus, 1942; Tuttle, 1967; Rose, 1988; Sarmiento, 1988). However, more recent studies have demonstrated that the great ape thumb is used much more often for grasping arboreal substrates than previously thought (McClure et al., 2012; Neufuss et al., 2017b), in addition to its important functional role during manipulative activities (Byrne et al., 2001; Marzke et al., 2015; Neufuss et al., 2017a). Here, we show that the bonobo thumb always grasped the substrate during vertical and suspensory locomotion. It was the first to touch the substrate in 36% of the vertical locomotion trials and 20% of the suspensory trials. The bonobos' use of the thumb may reflect the relatively large diameter of the substrate in this experiment; chimpanzees typically use a hook-grip, involving just the fingers (and sometimes the distal palm), on substrates with an average diameter of 4.7 cm (Hunt, 1991). However, Hunt (1991) reports chimpanzees using hook-grips on substrates up to 40.6 cm in diameter, suggesting that bonobos would be capable of using hand postures that did not involve the thumb on a 12 cm-diameter substrate.

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

In this first dynamic pressure study of bonobo arboreal locomotion, we have revealed biomechanical data that may be informative for making functional interpretations about variation in extant ape and fossil hominoid and hominin hand bone morphology. We showed the pressures experienced by the digits are significantly greater during arboreal knuckle-walking than during either vertical or suspensory locomotion. Thus, given the high frequency of knuckle-walking by bonobos and chimpanzees (Doran, 1992, 1993), and assuming that terrestrial knuckle-walking pressures are similarly high, as demonstrated by Wunderlich and Jungers (2009) in chimpanzees, we would expect *Pan* external and/or internal hand morphology to better reflect the high biomechanical loading of knuckle-walking over the lower loading

and lower frequency of vertical climbing and suspension (Doran, 1993). Indeed, recent studies of the internal trabecular structure of the third metacarpal is consistent with the extended metacarpophalangeal posture of knuckle-walking in African apes compared with flexed-finger grasping postures of Asian apes (Tsegai et al., 2013; Chirchir et al., 2017).

This study also revealed some similarities across the different arboreal locomotor behaviours. In all locomotor modes, peak pressure occurred in the centre of the finger region, probably being experienced by or near the third digit. Furthermore, we found that bonobo hand posture, grasping (i.e. touch down/lift off) and loading during vertical and suspensory locomotion are more similar than might be initially predicted when engaging in such fundamentally different types of locomotion (e.g. vertical climbing versus suspension) on vertical and horizontal arboreal substrates; the ulnar-side digits and palm most often grasped the substrate first and pressures were similar across the two locomotor modes. Although the pressures experienced by the hand during vertical and suspensory locomotion were significantly lower than those experienced during knuckle-walking, fossil hominins were not knuckle-walkers (Richmond and Strait, 2000). Thus, if fossil hominins were still using their hands for climbing or suspending in the trees, it is likely that this behaviour could be reflected in some aspects of the hand morphology, particularly in digit 3, and may be least likely to appear in the morphology of the thumb. Indeed, several fossil hominins have curved phalanges and well-developed digit flexor tendon attachments (e.g. *Australopithecus afarensis*, *Australopithecus sediba*, *Homo habilis*), even when the remainder of the hand is similar to that of humans (i.e. *Homo naledi*), which have been interpreted as evidence of a functionally significant component of arboreal locomotion in their behavioural repertoires (Bush et al., 1982; Kivell et al., 2011, 2015; Kivell, 2015). In contrast to extant great apes, most fossil hominins have (e.g. *A. sediba*, *H. naledi*) or are considered to have (e.g. *A. afarensis*) a long thumb relative to the length of the fingers (Kivell et al., 2011, 2015; Rolian and Gordon, 2013; Almécija and Alba, 2014). If the comparatively low loading of the bonobo thumb revealed in this study on a medium-sized (12 cm-diameter) substrate holds true across differently sized substrates, different locomotor strategies and, potentially, other great apes (but see Neufuss et al., 2017b), then it may imply that the thumb of the last common ancestor was somewhat biomechanically 'free' to adapt to the functional requirements of manipulation in hominins. However, it must be recognized that the short fingers and long thumb that characterize the hominin hand may better represent the hand proportions of the last common ancestor (Almécija et al., 2015), and would probably elicit a different biomechanical strategy when grasping arboreal substrates, one in which the thumb may incur greater loads. Future studies of the pressures experienced by the hand during arboreal locomotion in gorillas, which have more human-like hand proportions (Almécija et al., 2015), and humans, particularly individuals that frequently engage in arboreal locomotion (e.g. Venkataraman et al., 2013), in comparison to those of bonobos found here would help to inform our understanding of the role of arboreal locomotion in hominin hand evolution.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: T.L.K.; Methodology: D.S.S., S.N., T.L.K.; Formal analysis: D.S.S., S.N., T.L.K.; Investigation: D.S.S., S.N.; Resources: J.M.S.; Writing - original draft: D.S.S., T.L.K.; Writing - review & editing: S.N., J.M.S., T.L.K.; Supervision: S.N., J.M.S., T.L.K.; Project administration: S.N., J.M.S., T.L.K.; Funding acquisition: T.L.K.

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Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.170910.supplemental>

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