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Comparison of hand use and forelimb posture during vertical climbing in mountain gorillas (*Gorilla beringei beringei*) and chimpanzees (*Pan troglodytes*)

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ABSTRACT

Objectives: Studies on grasping and limb posture during arboreal locomotion in great apes in their natural environment are scarce and thus, attempts to correlate behavioral and habitat differences with variation in morphology are limited. The aim of this study is to compare hand use and forelimb posture during vertical climbing in mountain gorillas (*Gorilla beringei beringei*) and chimpanzees (*Pan troglodytes*) to assess differences in the climbing styles that may relate to variation in hand or forelimb morphology and body size. **Materials and methods:** We investigated hand use and forelimb posture during both ascent and descent vertical climbing in 15 wild, habituated mountain gorillas and eight semi-free-ranging chimpanzees, using video records obtained ad libitum. **Results:** In both apes, forelimb posture was correlated with substrate size during both ascent and descent climbing. While climbing, both apes used power grips and diagonal power grips, including three different thumb postures. Mountain gorillas showed greater ulnar deviation of the wrist during vertical descent than chimpanzees, and the thumb played an important supportive role when gorillas vertically descended lianas. **Discussion:** We found that both apes generally had the same grip preferences and used similar forelimb postures on supports of a similar size, which is consistent with their overall similarity in hard and soft tissue morphology of the hand and forelimb. However, some species-specific differences in morphology appear to elicit slightly different grasping strategies during vertical climbing between mountain gorillas and chimpanzees.

INTRODUCTION

Arboreal locomotor behaviors, although generally practiced infrequently compared to terrestrial locomotion, are critical to the daily life and survival of African apes. In particular, vertical climbing is used to access important food sources (e.g., Remis, 1995; Pilbeam, 2002; Robbins, 2008), to change levels within the forest canopy, to exploit safer substrates for horizontal travel, for safety from predators and for access to sleeping sites (e.g., Hunt, 1992a; Preuschoft, 2002; Thorpe and Crompton, 2006; Garber, 2007). Records of the frequency of arboreal locomotion in wild African apes varies depending on the species and population (e.g., Tuttle and Watts, 1985; Doran, 1993, 1996; Remis, 1995; Crompton et al., 2010). Most studies agree that gorillas are less arboreal than chimpanzees and bonobos (Hunt, 1996; Crompton et al., 2010; Hunt, 2016). In particular, mountain gorillas (*Gorilla beringei beringei*) are typically considered the least arboreal of all the great apes are thought to spend less than 1% of total locomotor time engaging in vertical climbing (Tuttle and Watts, 1985).

Arboreal locomotor behaviors in mountain gorillas have to date only been broadly described (e.g., Schaller, 1963; Doran, 1996) and the frequency is likely underestimated (Crompton, 2016). One possible explanation for the much lower reported frequency of arboreal locomotion in mountain gorillas compared with western lowland gorillas (e.g., Tutin et al., 1991; Nishihara, 1992; Remis, 1994, 1995; Tutin, 1996) may be differences in habitat structure and resource availability, as these have a substantial influence on gorilla locomotion (Remis, 1995). Most mountain gorilla locomotor data come from the Volcanoes National Park, Rwanda (e.g., Doran 1996, 1997). Remis (1999) suggested that the high frequency of terrestrial knuckle-walking exhibited by mountain gorillas at sites like Karisoke in the

Virunga mountains represents an adaptation to a high-altitude dwarf forest environment, which likely limits their arboreality (average height climbed in trees <7 m; Fossey, 1983; Watts, 1984; Doran, 1996; Remis, 1998). However, little is known about gorilla arboreal locomotion in this type of environment and thus, the frequency of arboreal locomotor behaviors is generally based on estimates (e.g., Watts and Tuttle, 1985; Crompton et al., 2010).

The mountain gorillas of Bwindi Impenetrable Forest live at lower altitude (1,160-2,607 m; Robbins et al., 2006) with more trees and a denser forest canopy than that of Karisoke (canopy height ranges between 10-35 m; Shaw and Shewry, 2001). Tree use by gorillas is relatively common at Bwindi when, for example, foraging for fruits (Sarmiento et al., 1996, Robbins, 2008). Studies of feeding behaviors have revealed that Bwindi mountain gorillas climb trees for several months of the year, making use of arboreal fruit resources when they are seasonally available (Ganas et al., 2004; Robbins, 2008; see methods). For example, Bwindi gorillas spent 95 days of 324 observation days eating fruit in trees (29.3%), including 403 trees and 15 fruit species (Robbins, 2008), supporting recent assertion by Crompton (2016) that the <1% frequency for vertical climbing reported in mountain gorillas is likely an underestimation. However, to date, vertical climbing in wild mountain gorillas has not been examined in detail.

Arboreal locomotion in chimpanzees, by contrast, is more frequent (spending up to half of their time in trees; Tuttle and Watts, 1985). Chimpanzee habitats are typically located in mid-altitude (e.g., 1500 m; Pontzer and Wrangham, 2004) thicket woodland or tropical montane rainforest habitats with tree heights >30 m (e.g., Stanford and O'Malley, 2008). While several studies investigated different arboreal locomotor behaviors in wild chimpanzees, they were mainly associated with body

size effects, musculoskeletal adaptations of the upper body, or their daily energy cost (Hunt, 1991a,b, 1992b, 1994; Pontzer and Wrangham, 2004).

During arboreal locomotion, and particularly vertical climbing, primates face several biomechanical challenges that often require changes in forelimb and hand posture. For example, the difficulty of maintaining stability increases as substrates get smaller and/or are more inclined because the risk of toppling backwards becomes higher when propulsive forces in the hindlimbs increase (e.g., Cartmill, 1974; Preuschoft and Witte, 1991; Preuschoft, 2002). Our understanding of the ways in which primates cope with these challenges is largely based on small and medium-sized non-hominoid primates (e.g., mouse lemurs, cotton-top tamarins, lemurs or macaques; ranging from 0.06 to 11kg; Hirasaki et al., 1993; Nyakatura et al., 2008; Johnson, 2012; Shapiro et al., 2016) and theoretical models (e.g., Cartmill, 1974, 1979; Preuschoft and Witte, 1991; Preuschoft, 2002, 2004). However, the challenges of vertical climbing are amplified for larger-bodied primates, such that, both mechanical challenges and relative energetic costs of climbing increase in primates with a larger body size (Hanna et al., 2008). Larger-bodied primates appear to use their forelimbs mainly in tension and the hindlimbs mainly in compression, both when ascending and descending vertical substrates (Preuschoft, 2002; Hanna et al., 2017). When climbing on large substrates, wild chimpanzees have been observed to extend their elbows (“extended-elbow vertical climbing”) while the forelimbs assist in elevating the body through flexion of the elbow on small substrates (“flexed-elbow climbing”) (Hunt, 1991b, 1992; Hunt et al., 1996). General similarity in elbow joint morphology among apes is interpreted as an adaptation for elbow stability in varied forelimb postures used during vertical climbing and other forms of arboreal locomotion (e.g., Jenkins, 1973; Rose, 1988, 1993; Drapeau, 2008). The hands are

critically important to maintaining stability on differently-sized vertical substrates and providing a counterbalance to the feet (Hirasaki et al., 1993; Nakano, 2002; DeSilva, 2009; Johnson, 2012). Increased friction force between the prehensile hands (and feet) with the substrate (i.e., support phase) is needed when climbing upon vertical supports (Preuschoft, 2002).

Although previous studies demonstrate the importance of the primate forelimbs and hands during vertical climbing and the potential high loads that the hands may experience by gripping vertical substrates, they do not consider the actions that the hands are performing to facilitate this locomotion.

Detailed observations about how the hands grasp substrates during different arboreal locomotor behaviors have been reported in great apes, but these data were mainly obtained in captive settings and are limited, particularly in regards to the functional role of the thumb (Sarmiento, 1988, 1994; Hunt, 1991a; Marzke et al., 1992; Alexander, 1994; Marzke and Wullstein, 1996).

The short thumb of African apes is not used during knuckle-walking (e.g., Tuttle, 1967; Wunderlich and Jungers, 2009) and its functional importance during arboreal behaviors, particularly during suspensory locomotion, has traditionally been downplayed (Ashely-Montagu, 1931; Straus, 1942; Tuttle, 1967; Rose, 1988; Sarmiento, 1988). However, a preliminary study of orangutan arboreal locomotion revealed that they recruit the thumb much more often (i.e., more than 53% of hand postures included thumb use) when grasping arboreal substrates than traditionally believed (McClure et al., 2012). Among African apes, chimpanzee grips and hand postures have received the most attention. Chimpanzees use power grips, diagonal power grips and diagonal finger hook grips during vertical climbing as well as recruit

their thumbs in different postures relative to differently sized substrates (Napier, 1960; Marzke et al., 1992; Alexander, 1994; Marzke & Wullstein, 1996). In contrast, arboreal hand use in gorillas has only once been broadly described in captivity, showing that western lowland gorillas use a more flexed wrist posture on smaller than on larger vertical supports to enable that the hand can wrap around the grasped support (Sarmiento, 1994).

Gorillas have a significantly longer thumb relative to the length of their fingers compared to other great apes (Susman, 1979), such that their hand proportions (defined as thumb length relative to length of the fourth digit) are more similar to humans than those of chimpanzees (Almécija et al., 2015). A relatively longer thumb is thought to enhance opposability to the fingers during grasping (e.g., Napier, 1993; Marzke, 1997). Enhanced opposability is usually discussed within the context of manipulation (e.g., Marzke, 1997), but the variation in hand proportions, as well as differences in body size, between gorillas and chimpanzees may also result in different grip and thumb use strategies during vertical climbing. However, there are no studies of which we are aware that have investigated mountain gorilla arboreal hand use, or how grasping posture might vary with forelimb posture during vertical climbing on natural substrates in gorillas compared with chimpanzees.

The aim of this study was to provide the first insights into the hand use and forelimb posture of mountain gorillas and free-ranging chimpanzees used during vertical climbing (both ascent and descent) on natural substrates. First, we predict that shared features in forelimb morphology and body size within *Gorilla* (females 71.0-97.5 kg; males 162.5-175.2 kg across *G. beringei*, *G. gorilla*, *G. graueri*; Smith and Jungers, 1997) and within *Pan* (females 33.2-45.8 kg; males 42.7-59.7 kg across *P. paniscus* and *P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus*; Smith and

Jungers, 1997) will elicit similar forelimb postures during vertical climbing between (1) mountain gorillas and western lowland gorillas (Isler, 2002, 2003, 2005), and (2) between chimpanzees and bonobos (Isler, 2002, 2005). Second, we hypothesize that differences in hand and forelimb morphology, as well as body size, between mountain gorillas and chimpanzees will elicit different forelimb postures and grasping strategies on supports of a similar size. Third, we predict that given the relatively longer thumb length of mountain gorillas, they will more often oppose their thumbs during grasping than chimpanzees.

MATERIALS AND METHODS

Species and study sites

Mountain gorillas (*Gorilla beringei beringei*) were observed in the Bwindi Impenetrable National Park (331 km²) in the southwest corner of Uganda (0° 53'1°08'N; 29°35'–29°50'E), with an altitude of 2100–2600 m (Robbins and McNeilage, 2003; Ganas et al., 2004; Wright et al., 2015). Data were collected on two fully habituated groups of gorillas (Kyagurilo and Bitukura) between October-December 2014 and March-July 2015 during two fruiting seasons.

Chimpanzee (*Pan troglodytes* ssp.) vertical climbing data were collected between August-September 2014 on two colonies of semi-free-ranging chimpanzees at the Chimfunshi Wildlife Orphanage Trust (CWO), Zambia. Each colony was composed of a mixture of wild-born chimpanzees (e.g., from Tanzania, Uganda and Rwanda; Rawlings et al., 2014) and chimpanzees born at the CWO. All individuals in our study were living within a dry woodland natural environment in large outdoor enclosures (25-77 ha).

Data collection

Vertical climbing for any given individual was divided into 'sequences' and 'limb cycles'. A 'sequence' was defined as a continued period of climbing behavior. A sequence started when the right hindlimb was initially placed in contact with the substrate and stopped if climbing was interrupted by a change of the substrate using another locomotor mode, or by a switch in behavior, such as sitting or feeding. A sequence was generally composed of multiple limb cycles. A limb cycle was defined as the interval between touchdown of one limb and the subsequent touchdown of the same limb (i.e., right foot/ hand to right foot/hand).

The mountain gorillas were observed for an average of 4 hours/day. A minimum of 7 m had to be maintained between the gorillas and the observer to reduce the risk of disease transmission. High-definition video was filmed ad libitum at a frequency of 50Hz (HDR-CX240E, Sony, Japan).

All gorilla climbing sequences were recorded at relatively close range (7m to ~20m) during vertical ascent and descent on a sample of 15 individuals across the two study groups, including 10 adult females and five males, the latter including one subadult (6-8 years), one blackback (8-12 years) and three silverbacks (≥ 12 years) (Czekala and Robbins, 2001; Robbins, 2001). Video data also included a form of vertical descent in which the animal is sliding on vertical supports, where both forelimbs move alternately with a hand over hand movement to regulate velocity while both feet remain in contact with the substrate. This submode of vertical descent was classified as 'fire-pole slide' (Hunt et al., 1996). The gorillas had the opportunity to climb on various-sized substrates ranging from lianas to extremely large tree trunks. The dense understorey vegetation often limited access to climbing substrates, making direct measurements of their circumference difficult. Thus, we grouped substrate size into three categories consistent with previous reports (Napier,

1960; Marzke et al., 1992; Alexander, 1994): (1) medium, when the diameter was approximately 6-10 cm (e.g., lianas, thin trees); (2) large, when the diameter was approximately 11-50 cm (e.g., tree trunks); (3) extra-large, when the diameter was >50 cm (e.g., tree trunks). Neither gorillas nor chimpanzees in our study climbed on small substrates less than 6 cm diameter (e.g., thin lianas, vertical branches). We recorded a total of 75 climbing sequences, containing 231 limb cycles (Table 1) on 31 medium, 13 large and 31 extra-large substrates.

Similar to the mountain gorillas, the free-ranging chimpanzees were recorded with high-definition video (50Hz; HDR-CX240E, Sony, Japan) ad libitum at relatively close range (~10m) from both the ground and viewing platforms. We collected a total of 37 climbing sequences, containing 111 limb cycles, in eight adult chimpanzees (six females, two males) (Table 1). Data were collected on substrates of varying sizes, but given that it was a natural environment within a sanctuary, substrates were limited to tree trunks only. Data were collected on two medium-sized, 23 large and 12 extra-large substrates.

Table 1 Summary of vertical climbing in Bwindi mountain gorillas and Chimfunshi chimpanzees

Species	Individual	Sex/Age	Total no. of climbing sequences	No. of forelimb cycles for vertical ascent	No. of forelimb cycles for vertical descent	No. of limb cycles for fire-pole slide
G. b. beringei	JN	female/adult	11	17	6	3
	ST	female/adult	11	13	6	2
	KR	female/adult	9	18	-	8
	TN	female/ adult	5	10	-	13
	TW	female/adult	7	12	3	19
	MG	female/adult	8	2	9	10
	KG	female/adult	1	-	-	3
	BY	female/adult	5	3	4	6
	TD	female/adult	2	2	-	4
	BT	female/adult	1	-	-	10
	HP	male/subadult	2	-	-	9
	KA	male/blackback	4	7	2	5
	MK	male/silverback	6	13	-	3
	RC	male/silverback	2	3	-	3
	ND	male/silverback	1	-	-	6
Total			75	100	30	101
P. troglodytes ssp.	RI	female/adult	2	-	7	-
	KB	female/adult	8	7	19	-
	MI	female/adult	11	12	20	-
	KY	female/adult	7	6	13	-
	JU	female/adult	3	3	8	-
	UN	female/adult	4	-	10	-
	TA	male/adult	1	-	4	-
	CO	male/adult	1	-	2	-
Total			37	28	83	-

Forelimb posture in relation to substrate size during vertical climbing

We investigated the hand and forelimb posture during vertical climbing in relation to the size of the substrate (N= 75 sequences in 15 gorillas; N= 37 sequences in eight chimpanzees). Hunt and colleagues (1996) described two types of vertical climbing in African apes in relation to substrate size: (1) when climbing on smaller substrates, flexion of the elbow helps to elevate the body ('flexed-elbow' vertical climbing); (2) on larger substrates, the elbow is typically extended throughout the motion cycle ('extended-elbow' vertical climbing). We used these same categories when scoring and analysing our data (Figs. 1a, c, 2a, c). To reduce the dependence of data points, findings were reduced by pooling sequential observations for each individual in which forelimb posture did not change along a particular substrate size category, following Hunt (1992b). The reduced data set contained N=36 pooled observations in 15 gorillas (N= 10 medium-sized substrates; N=11 large substrates, N=15 extra-large substrates) and N=18 pooled observations in eight chimpanzees (N=2 medium-sized substrates, N=8 large substrates, N=8 extra-large substrates). Each individual only contributed one data point within a particular substrate size category. Individuals with missing data points were excluded from statistical analysis.

Hand grips and thumb use

We investigated hand use and grip types during vertical climbing in all 15 gorillas (N= 231 limb cycles) and eight chimpanzees (N= 111 limb cycles). We classified each hand grip within a limb cycle (as a limb cycle is defined as the use of one grip only between the two touchdowns by the same forelimb) for each individual and calculated the relative frequencies. Hand grips were categorized following previous descriptions of hand use and grips during climbing in chimpanzees (Sarmiento, 1988; Napier, 1960; Hunt, 1991a; Marzke et al., 1992; Alexander, 1994; Marzke and Wullstein, 1996). Our initial categorization centred on the **power grip**, in which larger

substrates are grasped by all five digits and the entire palm of the hand, the **diagonal power grip**, in which smaller substrates lie diagonally across the fingers and the palm, and the **diagonal finger hook grip** without the thumb and without active involvement of the palm (e.g., Napier, 1960; Hunt, 1991a; Marzke et al., 1992) (Figs. 1a, c, 2a, c).

We further investigated in detail the role of the thumb during ascent and descent climbing, including different thumb postures in relation to substrate size (N=231 limb cycles for 15 gorillas; N=111 limb cycles for eight chimpanzees). Three thumb positions were categorized following previously described climbing grips in chimpanzees (Marzke et al., 1992; Alexander, 1994; Marzke and Wullstein, 1996): (1) thumb held in adduction relative to index finger, (2) thumb held in abduction relative to index, (3) thumb held opposed to index finger, and was either wrapped around the substrate or held in line with the long-axis of the substrate (Figs. 1 and 2). Thumb posture was examined within a limb cycle for each individual and relative frequencies were calculated. As described above, dependence among data points was reduced by pooling limb cycles for each individual in which thumb posture did not change on a particular substrate size category. The reduced data set contained N=36 pooled observations for 15 gorillas (N=10 medium-sized substrates, N=11 large substrates, N=15 extra-large substrates) and N= 18 pooled observations for eight chimpanzees (N=2 medium-sized substrates, N=8 large substrates, N= 8 extra-large substrates). Each individual only contributed one data point within a particular substrate size category and individuals with missing data points were not included in the statistical analysis.

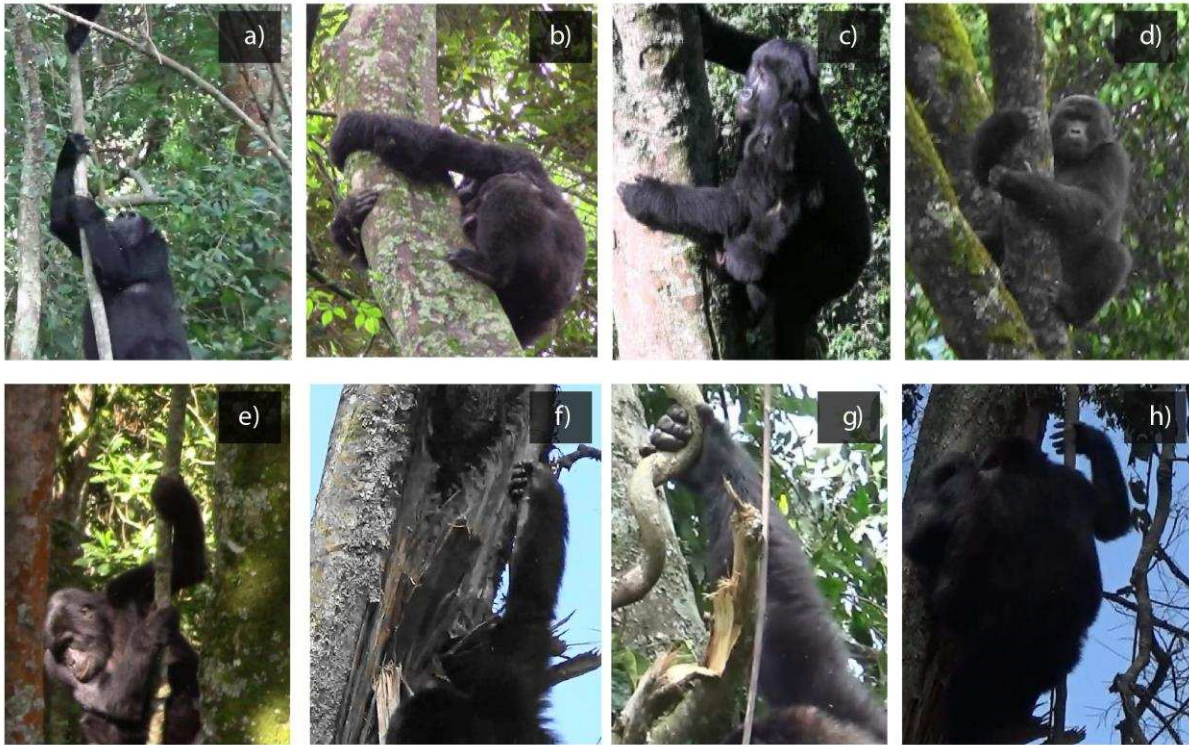


Figure 1 Forelimb (a-b) and hand (c-h) postures during vertical climbing in mountain gorillas. (a) Flexed-elbow climbing on medium-sized support and (b) a nearly extended-elbow posture during fire-pole slide on extra-large substrate in mountain gorillas. Hand grips and variable thumb postures in relation to supports of different size: (c) power grip with the thumb adducted to the index finger typically used on an extra-large substrate; (d) power grip with the thumb abducted from the index finger typically used on large substrates; (e) diagonal power grip with the thumb opposed to the index finger and held in line (right hand), exclusively used on medium-sized substrates; (f) the wrist is deviated in the ulna direction to an extreme degree, bringing the right hand's long axis relatively in the plane of the support's cross section with the thumb held opposed and wrapped around the medium-sized substrate; (g) form of diagonal power grip adjusted to the curved liana; (h) showing that opposed thumb of the right hand making first contact with the substrate and secure the substrate within the V-shaped region between thumb and extended Index while climbing down the irregular support.

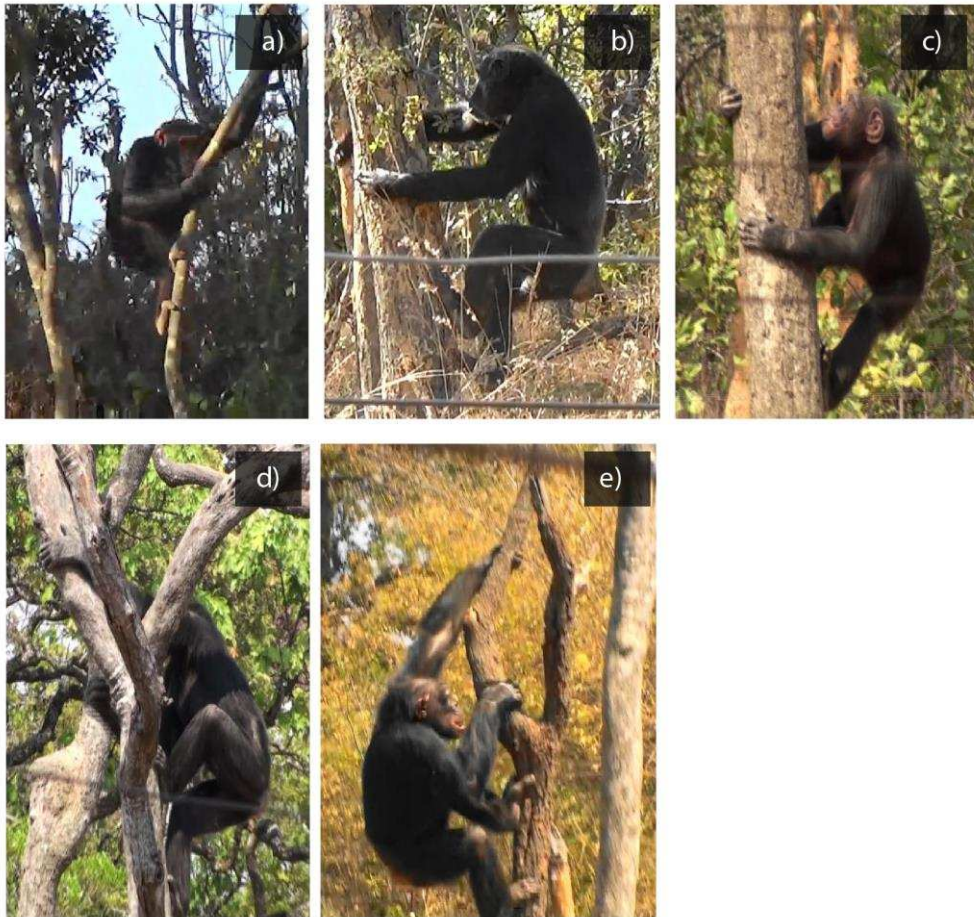


Figure 2 Forelimb (a-b) and hand (c-e) postures during vertical climbing in chimpanzees. (a) Flexed-elbow climbing on medium-sized support in chimpanzees and (b) extended-elbow climbing on large substrate during vertical descent. Hand grips and variable thumb postures in relation to supports of different diameter: (c) power grip with the thumb adducted to the index finger used on large substrate; (d) power grip with the thumb abducted from the index finger used on large substrate; (e) diagonal power grip with the thumb opposed to the index finger and held in line, exclusively used on medium-sized substrates (left hand).

Statistics

All statistical analyses were run in SPSS (IBM SPSS Statistics for Windows, Version 24.0). An exact binomial test was applied to test the probability of using a particular forelimb posture (50/50 distribution) within each substrate size category. Similarly, we used an exact binomial test to determine the probability of observing a particular thumb posture (50/50 distribution) within each substrate size category. In

chimpanzees, both flexed forelimb (N=2) and opposed thumb posture (N=2) used on medium-sized substrates were excluded from analysis due to small sample size. The significance threshold was set at $p=0.05$. However, since one data point for the same individual may be included in all three substrate categories, the data are not fully independent. The overall sample size was too small to allow more sophisticated statistical tests that could take into account dependency within the data. Therefore, results of these statistical analyses are interpreted with caution.

RESULTS

Forelimb posture during vertical climbing

We observed both flexed-elbow and extended-elbow vertical climbing during ascent and descent in mountain gorillas and chimpanzees. Gorillas always used a flexed-elbow posture on medium-sized substrates and an extended-elbow on large and extremely large substrates (Table 2). In gorillas, there was a significant use of a flexed elbow on medium-sized substrates (100% of 10 sequences, $p=0.002$) (Fig. 1a, h) and a highly significant use of an extended elbow on large (100% of 11 sequences, $p<0.001$) as well as on extra-large substrates (100% of 15 sequences, $p<0.001$) (Fig. 1b).

Table 2 Frequency (no. of climbing sequences) of forelimb-posture in relation to total climbing sequences and substrate size

Species	forelimb-posture	forelimb-posture relative to total climbing sequences	medium-sized substrate	large-sized substrate	extra-large substrate
mountain gorilla	extended-elbow	59% of total 75	-	29.5%	70.5%
	flexed-elbow	41% of total 75	100%	-	-
chimpanzee	extended-elbow	92% of total 37	-	65%	35%
	flexed-elbow	8% of total 37	67%	33%	-

“-“ denotes to absence of forelimb data.

During flexed-elbow climbing in mountain gorillas, which was only used on medium-sized substrates, the elbows were flexed and the torso was held nearly parallel to the support. Flexion of the elbow helped to elevate the body during the push of the hind limbs in ascent climbing, while the elbows were flexed throughout the support phase until the mid-swing phase. A strongly flexed position of the forelimb was occasionally used in late-swing phase until early-support phase during descent climbing (Fig. 1h). Strong horizontal abduction of the upper arm was obtained while reaching upward and at the very end of the support phase in flexed-elbow ascent (unpooled data set: 100% of 33 limb cycles), when the elbow was already being lifted but the hand was still in contact with the substrate. The elbow was always elevated far above the shoulder (Fig. 3a).

During extended-elbow ascent climbing on large substrates, the torso was held roughly parallel to the substrate, while on extra-large substrates, the torso was angled forward such that the shoulders were closer than the hips to the support. The elbows were never fully extended throughout the motion cycle in both ascent and descent climbing, but were clearly extended enough to allow both hands to control for friction while the feet appeared to experience more of the compressive load. When the hand lifted off the substrate, the humerus was slightly abducted and the

elbow was most often elevated to shoulder level (unpooled data set: 81% of 63 limb cycles) and less often slightly higher than the shoulder (Fig. 3b).

Gorillas most often descended trees by sliding downwards using only the forelimbs (14 individuals; 75% of total descent sequences), in which the forearms were either flexed or extended throughout support and swing phase. The forearms moved alternately in lift-off and touchdown while both hindlimbs remained in contact with the substrate.

Chimpanzees always used a flexed-elbow posture on medium substrates. An extended-elbow posture was used on large and extremely large substrates but flexed-elbow postures were occasionally used on large trees (Table 2). In chimpanzees, there was a significant use of an extended elbow on extra-large substrates (100% of 8 sequences, $p=0.008$), but the use of a flexed (25% of 8 sequences) and extended-elbow (75%) was not significantly different on large substrates ($p= 0.289$).

When chimpanzees engaged in flexed-elbow climbing during vertical ascent, we observed that flexion of the elbow occurred during the early to mid-support phase until early swing phase whereas during extended-elbow climbing, the elbow was extended throughout the motion cycle. In vertical descent, a flexed elbow posture was used during the mid-swing phase and throughout support phase while during extended-elbow climbing, extension of the elbow occurred throughout the motion cycle.

Like mountain gorillas, chimpanzees never fully extended the elbow during ascent and descent climbing but, the elbow was clearly extended enough to hold the body away from the support while the hindlimbs pushed-off from the substrate.

Chimpanzees were not observed to slide down tree trunks using only the forelimbs as documented in gorillas.

During both flexed- and extended-elbow climbing, chimpanzees slightly abducted their humerus when the hand lifted off the substrate (Fig. 3c, d). Chimpanzees varied in their degree of elbow elevation during both flexed- and extended-elbow climbing on larger substrates; sometimes both elbows would be elevated to shoulder level while at other times, individuals showed asymmetry with one elbow would be elevated to shoulder level and the other reaching slightly above or far above the shoulder (Fig. 3c).

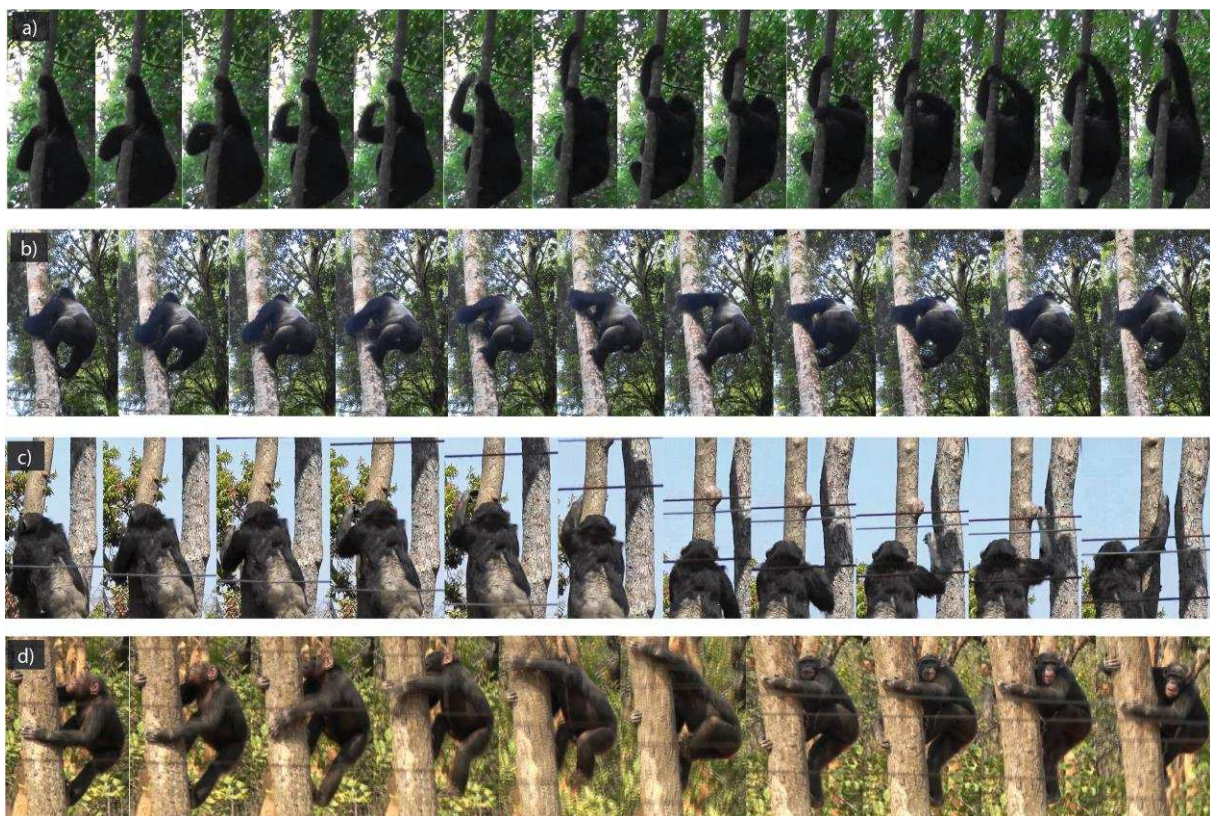


Figure 3 Typical vertical climbing sequences of mountain gorillas (a-b) and chimpanzees (c-d). (a) Female gorilla horizontally abducts the upper arm considerably and elevates the elbow far above the shoulder during flexed-elbow climbing on medium-sized support; (b) a silverback abducts the upper arm less of horizontal plane and elevates the elbow to shoulder level during extended-elbow climbing on a large substrate; (c) a female chimpanzee slightly abducts the upper arm and shows forelimb

asymmetry in the degree of elbow elevation during flexed-elbow climbing on a large substrate; (d) a female chimpanzee slightly abducts the upper arm and elevates the elbow to shoulder level during extended-elbow climbing on an extra-large substrate.

Hand grips and thumb use

Both mountain gorillas and chimpanzees used a power grip and a diagonal power grip during vertical ascent and descent (Figs. 1 and 2). Gorillas used a power grip only during extended-elbow climbing, a diagonal power grip only during flexed-elbow climbing and both grips during forelimb-only descent. Chimpanzees used a power grip during both extended- and flexed-elbow climbing while a diagonal power grip was only used during flexed-elbow climbing. Neither ape was observed to use the diagonal finger hook grip for climbing. Grip use depended upon the size of the substrate; both apes used the power grip only on large and extra-large substrates and the diagonal power grip only on medium-sized substrates. A power grip was used at high frequency in both gorillas (63% of total 231 limb cycles) and chimpanzees (95% of total 111 limb cycles). A diagonal power grip was used relatively frequently in gorillas (37% of total limb cycles) but rarely in our chimpanzee sample (5% of total limb cycles) and only on medium-sized substrates (Fig.1e). Both apes showed significant differences in using a particular thumb posture on differently-sized substrates. Opposition of the thumb was only used when both apes grasped medium-sized substrates in a diagonal power grip and the thumb was most frequently held in line with the long axis of the substrate (Figs. 1a and 2e; Table 3). Gorillas used an opposed thumb significantly more on medium-sized substrates (100% of 10 data points, $p=0.002$) and both gorillas (100% of 15 data points, $p<0.001$) and chimpanzees (100% of 8 data points, $p=0.008$) used an adducted thumb posture significantly more on extra-large substrates (Figs. 1c and 2b; Table

3). Neither ape showed a significant difference between thumb adduction and abduction on large substrates (gorillas: N=11, 23% vs. 73%, $p=0.227$; chimpanzees: N=8, 38% vs. 63%, $p=0.727$) (Figs. 1d and 2d; Table 3).

Table 3 Frequency (no. of limb cycles) of thumb positions in relation to substrate size

Species	Hand grip	Thumb posture	medium-sized substrate	large-sized substrate	extra-large substrate	total no. of limb cycles
mountain gorilla	Power grip	Thumb adducted to index	-	26 (19%)	112 (81%)	138
		Thumb abducted from index	-	10 (100%)	-	10
	Diagonal power grip	Thumb opposed to index and held in line with long axis of substrate	59 (100%)	-	-	59
		Thumb opposed to index and wrapped around substrate	24 (100%)	-	-	24
chimpanzee	Power grip	Thumb adducted to index	-	26 (41%)	37(59%)	63
		Thumb abducted from index	-	41 (95%)	2 (5%)	43
	Diagonal power grip	Thumb opposed to index and held in line with long axis of substrate	5 (100%)	-	-	5
		Thumb opposed to index and wrapped around substrate	-	-	-	-

The percentages of the total limb cycles are given in parentheses. “-” denotes absence of thumb data.

Both apes were observed to ulnarly deviate the wrist (tilting the wrist and hand towards the ulnar side of the forearm) such that the hand's long axis was orientated perpendicular to the substrate with the opposed thumb held either in line or wrapped around the substrate (Figs.1a, 2e). Only mountain gorillas ulnarly deviated the wrist to an extreme degree during both vertical descent and forelimb-only vertical descent on medium-sized substrates, bringing the hand perpendicular to the vertical substrate with the forelimb approaching a nearly parallel position with the substrate

(Fig. 1f). Gorillas used two different grasping strategies when climbing lianas, neither of which were documented in the chimpanzees (although they were not observed climbing lianas). The first grasping strategy was used when the individual moved downward along the liana (Fig. 1h). During the swing phase of the opposing forelimb, strong ulnar deviation of the wrist allowed the individual to grasp the vertical support within the V-shaped region between the opposed thumb and extended index finger. When descending lianas of irregular shape, the liana was grasped diagonally across all four fingers and mainly against the thenar area of the palm and proximal phalanx of the thumb (Fig. 1g). The different postures of the flexed fingers conformed to the irregular shape of the liana and firmly maintain the grip against the downward pull of the body during vertical descent. The pull appeared to be resisted mostly by the second, third and fourth fingers while the shorter fifth finger was not able to flex as much at the metacarpophalangeal joint to fully contribute to the grasp (Fig. 1g).

DISCUSSION

This study provides the first comparative study of wild mountain gorilla and free-ranging chimpanzee hand use and forelimb posture during both ascent and descent vertical climbing in natural environments. These new data, although sample sizes are small, provide greater insight into the potential range of grasping strategies that are capable with a given bony and muscular morphology in African apes, and generally provides a better understanding of the postural adaptations for vertical climbing in large-bodied primates.

Forelimb posture during vertical climbing

Mountain gorillas have the largest body mass among living primates (e.g., Sarmiento, 1994; Smith and Jungers, 1997) and thus locomotion and maintaining

stability in a complex, three-dimensional arboreal environment poses considerable challenges. We found partial support for our first prediction that similar forelimb morphology and body size within *Gorilla* and *Pan* would elicit similar forelimb postures (1) between mountain gorillas and western lowland gorillas and (2) between chimpanzees and bonobos (Isler 2002, 2003, 2005).

Our sample of mountain gorillas most often engaged in extended-elbow climbing (59% of total 75 sequences), both on extra-large and large substrates, and also frequently used flexed-elbow climbing (41% of total sequences), exclusively on medium-sized substrates (Fig. 1a, e).

The mountain gorillas commonly entered and left large trees by climbing on medium-sized vertical substrates (69% of total 26 instances). When ascending medium-sized substrates, flexion of the elbow joint appears to help pull the body upwards during the mid-support phase, and keeps the body positioned close to the substrate throughout the support phase, while the gorilla's strong muscular hindlimbs (Zihlman et al., 2011) provide most of the propulsive power and push against the substrate in the mid-support phase. Similar to previous reports on vertical climbing in chimpanzees (Hunt, 1991b, 1992), the flexed-elbow posture stabilizes the upper body against backward rotation caused by the propulsive force of the hindlimbs. As the demands are particularly high in flexed-elbow vertical climbing (Isler, 2005), mountain gorillas likely show, like all other apes, adaptations for large force production in the elbow flexors for pulling-up (Myatt et al., 2012) and have forearm flexor muscles that are nearly four times as large as in cursorial mammals (Alexander et al., 1981). Therefore, differences in the elbow joint morphology between mountain and lowland gorillas (Inouye, 2003) does not appear to inhibit the mountain gorilla's ability to climb safely upon medium-sized substrates. Western

lowland gorillas in captivity also used flexed-elbow climbing on smaller-sized substrates, which helped to elevate and stabilize the body when climbing up a vertical rope (see Figs. 3 and 4 in Isler, 2003). The mountain gorillas in our study occasionally used a stronger flexed forelimb posture when descending lianas (Fig. 1h) compared with ascent on smaller-diameter trees (Fig. 1a,e), bringing the torso even closer to the compliant support and providing greater stability against the potentially high gravitational pull of the heavy body.

We also observed that mountain gorillas abduct the humerus considerably during the process of reaching upward for the next grip during flexed-elbow climbing, elevating the elbow far above the shoulder. Isler (2002, 2003, 2005) noted a similar forelimb posture in captive western lowland gorillas. The abduction of the forelimb during climbing is consistent with interpretations of the gorilla's forelimb anatomy to accommodate shoulder joint mobility for vertical climbing and reaching while maintaining joint stability during terrestrial quadrupedal locomotion (Zihlman et al., 2011).

The semi-free-ranging chimpanzees in our sample used a flexed-elbow posture on smaller substrates, similar to that previously described in captive bonobos (Isler, 2005). However, unlike bonobos ascending a vertical rope, the chimpanzees did not abduct their humerus at the very end of the forelimb's support phase and varied in their degree of elbow elevation when ascending larger substrates (Fig. 3c). Similar to our observations, wild and captive chimpanzees have been observed to elevate the arm only slightly higher above shoulder level (Hunt, 1991a, 1992; Nakano et al., 2006) while humeral abduction has been documented in a study on scapulohumeral muscle function in captive chimpanzees during vertical climbing (Larson and Stern, 1986). Variations in the degree of elbow elevation across our chimpanzee individuals

may be related to speed modulation, if the speed increase were to be achieved more through an increase in forelimb stride length than through an increase in stride frequency (Isler, 2005). Comparisons to captive bonobo vertical climbing suggest that chimpanzees abduct their humerus less of horizontal plane, which may reflect a slower climbing speed as found in male bonobos (Isler, 2002). However, chimpanzees are adapted for highly abducted arm postures just like all other arboreal apes, based on shared features in joint morphology and muscular anatomy of the shoulder (for circumduction), elbow (rotation), and wrist (adduction) (e.g., Tuttle, 1969; Larson, 1998; Chan, 2008; Preuschoft et al., 2010; Zihlman et al., 2011; Myatt et al., 2012). Whether forelimb joint excursions increase with climbing speed in chimpanzees and other apes requires further testing as, at present, there are insufficient data on spatio-temporal gait parameters in primates to clarify this issue.

Our prediction that, due to differences in forelimb morphology and body mass, we would see differences in forelimb posture on similarly-sized substrates between mountain gorillas and chimpanzees was only partially supported. Mountain gorillas only used flexed-elbow climbing on smaller substrates, while chimpanzees flexed their elbows on both smaller and larger substrates (Fig. 2a and d). However, the chimpanzees in our sample climbed on trees of a lower diameter range (11-50 cm; see Methods), while Hunt and colleagues (1996) suggested that a substrate diameter larger than 20 cm is more likely to evoke extended-elbow climbing in chimpanzees. Similarly, both apes abducted the humerus less of horizontal plane and showed a lower degree of elbow elevation during ascent on larger-sized substrates (Fig. 3b, c). Finally, mountain gorillas commonly slid down vertical supports while this strategy of descending trees was not observed in the

chimpanzees of our sample and appears not to be used in other adult chimpanzees either (Table 3 in Sarringhaus, 2014).

The variation documented here in mountain gorilla and chimpanzee forelimb postures on different sized substrates, as well as differences in forelimb joint excursions, needs to be tested on a larger comparative data set including more individuals and substrate types to see if these patterns still hold. Furthermore, 3D kinematic analyses in a natural environment, although challenging, would provide more detailed insight into the biomechanical strategies used by large-bodied apes.

Hand use and the role of the thumb during vertical climbing

Both mountain gorillas and chimpanzees most frequently used a power grip only on larger substrates and less often a diagonal power grip, which was used only on medium-sized substrates during ascent and descent climbing. This result is consistent with previous reports on chimpanzees grasping locomotor supports of different sizes (Napier, 1960; Hunt, 1991; Marzke et al., 1992; Alexander, 1994; Marzke and Wullstein, 1996). In contrast to chimpanzees, gorillas used a power grip only during extended-elbow climbing while a diagonal power grip was used only during flexed-elbow climbing. Mountain gorillas also used both grips when sliding down tree trunks (which was not documented in chimpanzees). Neither ape was documented using a diagonal finger hook grip for climbing, although this grip has been reported in climbing chimpanzees to be typically used on smaller substrates, which were not used in this study (e.g., Marzke et al., 1992). Mountain and lowland gorillas use hook grips during food processing and stick tool-use (Byrne et al., 2001; Bardo, 2016) but whether they are capable of using this hand grip to support their large body mass during vertical climbing is not yet known. Their large body mass

typically limits the gorilla's substrate choice to larger and more robust substrates (Reynolds, 1969; Remis, 1998), which in turn limits their grip repertoire for climbing. Lowland gorilla phalanges are shorter and straighter than those of chimpanzees (Stern et al., 1995; Patel and Mailino, 2016) and assuming mountain gorillas are the same (Matarazzo, 2008), this morphology may place greater restrictions on the grasping postures that can be used on smaller substrates, especially for large-bodied mountain gorillas. Further investigation of grasping smaller natural substrates is needed, in all species of gorillas, to understand the full repertoire of available hand grips in an arboreal environment.

Although the frequency of vertical climbing is lower in mountain gorillas than in chimpanzees and other hominoids, all hominoids retain arboreal features in their hand and forelimb due to the selective advantage of being able to ascent and descent arboreal substrates of variable size and compliance effectively and safely (gorillas: Taylor, 1997; hominoids: Larson, 1998). Indeed, while species-specific differences in morphology between gorillas and chimpanzees appear to elicit slightly different grasping strategies during vertical climbing), general similarity in hard and soft tissue morphology of the hand and forelimb (i.e., long and powerful digital flexors; Schultz, 1969; Myatt et al., 2012) allow both apes to use the same grip preferences and similar forelimb postures on supports of a similar size. Grip strength is critical when climbing safely and both hand grips exert contact pressure for strong friction between the palmar surface of the hands and the support (Cartmill, 1979, 1985; Preuschoft, 2002). However, the mountain gorilla's ability to ulnarly deviate the wrist to an extreme degree appears to be particularly valuable when descending medium-sized supports, as the hand can fully wrap around the vertical support in a firm diagonal-power grip (Fig. 1f). Although we did not observe this high range of

ulnar deviation in our sample of climbing chimpanzees, ulnar deviation of the wrist is also used by chimpanzees on smaller-diameter vertical supports (e.g., Sarmiento, 1988; Marzke et al., 1992). Furthermore, chimpanzees are capable of a similar degree of wrist adduction as western lowland gorillas (Tuttle, 1969), and potentially mountain gorillas. The ulnar side of the hand appears to provide the strongest friction against the downward pull of gravitational force, which is consistent with Susman's (1979) observations of ape hand posture during vertical climbing.

We predicted that gorillas would oppose their relatively longer thumb when grasping arboreal substrates more frequently than chimpanzees. We found partial support for this hypothesis. The functional role of the thumb during vertical ascent and descent climbing, as well as during flexed-elbow and extended-elbow climbing, revealed the use of three different thumb postures relative to differently sized substrates in both mountain gorillas and chimpanzees. Both apes significantly used an adducted thumb in a power grip on extra-large substrates (Figs. 1c, 2c) and opposed their thumb to the index finger in a diagonal power grip on medium-sized substrates only (Figs. 1e, 2e). Both apes generally held the opposed thumb in line with the substrate, which is consistent with previous studies of chimpanzees (Napier, 1960; Marzke et al., 1992; Alexander, 1994). Only mountain gorillas wrapped their opposed thumb around the support during diagonal power grasping, supporting our prediction. However, the absence of this thumb posture in our chimpanzee sample is likely due to our limited sample size on the smaller-diameter substrates, as it has been reported previously in chimpanzees (e.g., Napier, 1960; Marzke et al., 1992; Alexander, 1994). Furthermore, in mountain gorillas the opposed thumb appeared particularly important when grasping lianas whereas the chimpanzees were not observed to climb on lianas (Fig. 1g). When gorillas grasped lianas, the downward pull of the body

appeared to be resisted mostly by the second, third and fourth fingers, while the thenar region of the palm and the proximal phalanx of the thumb counter stabilized the grip. Our observations of a relative frequent use of grasping with an opposed thumb (36% of total 231 limb cycles) together with the gorilla's need to resist the downward pull of its large body mass during descent climbing, suggest that the gorilla thumb may experience large loading during this arboreal behavior. This hypothesis is consistent with the robust first metacarpal in mountain gorillas (Hamrick and Inouye, 1995), suggesting that the mountain gorilla's thumb is adapted to meet the potentially high forces during vertical ascent and descent, that occur due to their great body mass. Finally, mountain gorillas and chimpanzees occasionally abducted the thumb at roughly a right angle to the index finger, typically in a power grip on large substrates (Figs. 1d, 2d). In this abducted posture, the thenar area of the palm is recruited for counter pressure and thus, the thumb may potentially experience forceful loading at the metacarpal region (Fig. 2).

Although the gorilla's hand proportions are closer to humans than those of other hominoids (Almécija et al., 2015), their thumb is still too short to lock with or stabilize against the index finger on medium-sized supports as seen in humans when power squeeze gripping (e.g., Napier, 1960; Marzke et al., 1992; but see illustrations in Sarmiento, 1988 and Hasley et al., 2017 for human arboreal behaviours). Nevertheless, the great range of ulnar deviation at the wrist that was used during vertical descent enabled mountain gorillas to use the opposed thumb as an additional point of contact on lianas if needed, so that the support can be grasped quickly and firmly in case of slipping off, especially when the substrate surface was uneven. The extremely ulnarly-deviated wrist posture allowed the liana to be held securely in the web at the V-shaped region (Marzke et al., 2015) between the

opposed thumb and extended index finger while the gorilla's forelimb moved downward along the substrate (Fig.1h). We did not observe this important supportive role of the thumb in the our chimpanzee sample and it has not been reported in other chimpanzees (e.g., Marzke et al., 1992; Hunt, 1991a, 1992; Alexander, 1994; Hunt et al., 1996). However, since the chimpanzees in our sample did not exhibit such an extreme degree of ulnar deviation (although they are anatomically capable of it; Tuttle, 1969) as compared with mountain gorillas during descent climbing, it needs to be further investigated whether chimpanzees use the same grasping strategy to overcome substrate irregularities.

This comparative study provides much needed data on how the hand and forelimb are used during vertical climbing in a natural environment that can, in turn, help interpret differences in both external and internal bony morphology. However, this study also makes clear that there is a complex relationship between species-specific morphology and the range of potential postures that may be used in a natural environment. Although recent work found clear differences in foot morphology between more arboreal western gorillas and less arboreal eastern gorillas that correlate well with differences in arboreality, slight differences between eastern gorilla subspecies (i.e., lowland gorillas vs. mountain gorillas) did not follow the functional predictions (Tocheri et al., 2011, 2016). Furthermore, previous work examining African ape hand and foot morphology in relation to frequencies of arboreality and terrestriality, did not find strong concordance between functional predictions and the observed morphology across species and subspecies (Jabbour, 2008). Together, these findings underline both the difficulty and critical importance of identifying skeletal features that have a clear functional and adaptive signal to "potential" and "actual" behaviors.

Conclusion

This is the first comparative study on hand use and forelimb posture in mountain gorillas and chimpanzees during vertical climbing. This study demonstrates the importance of powerful grasping and the use of variable thumb postures relative to substrate size in both ape species. Moreover, our study reveals for the first time the supportive role of the gorilla's thumb during vertical descent. However, this study shows that more work is needed to characterize the potential range of grasping and postural strategies that might be used by African apes in their natural environments.

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REFERENCES

Alexander RM, Jayes AS, Maloiy, GMO, Wathuta EM. 1981. Allometry of the leg muscles of mammals. *Journal of Zoology*, 194, 539-552.

Alexander CJ. 1994. Utilisation of joint movement range in arboreal primates compared with human subjects: an evolutionary frame for primary osteoarthritis. *Annals of the Rheumatic Diseases*, 53, 720-725.

Alexander, R.M., Jayes, AS., Maloiy, GMO., & Wathuta, EM. 1981. Allometry of the leg muscles of mammals. *Journal of Zoology*, 194, 539–552.

Almécija S, Smaers JB, Jungers WL. 2015. The evolution of human and ape hand proportions. *Nature Communications*, 6, 7717.

Ashely-Montagu FM. 1931. On the primate thumb. *American Journal of Physical Anthropology*, 15, 291-314.

Bardo A. 2016. Manipulation abilities among hominids: a multidisciplinary study with behaviour, morphology and modelling (unpublished doctoral dissertation). Université Paris Descartes, France.

Byrne RW, Corp N, Byrne JME. 2001. Manual dexterity in the gorilla: bimanual and digit role differentiation in a natural task. *Animal Cognition*, 4, 347-361.

Chan LK. 2008. The range of passive arm circumduction in primates: Do hominoids really have more mobile shoulders? *American Journal of Physical Anthropology*, 136, 265-277.

Cartmill M. 1974. Pads and claws in arboreal locomotion. In: Jenkins, Jr FA, editor. *Primate Locomotion*. New York: Academic Press. p 45-83.

Cartmill M. 1979. The volar skin of primates: its frictional characteristics and their functional significance. *American Journal of Physical Anthropology*, 50, 497-510.

Cartmill M. 1985. Climbing. In: Hildebrand M, Bramble D M, Liem KF, Wake DB, editors. *Functional Vertebrate Morphology*. Cambridge, MA: Harvard University Press. p 73-88.

Crompton RH, Sellers WI, Thorpe SKS. 2010. Arboreality, territoriality and bipedalism. *Philosophical Transactions of the Royal Society B*, 365, 3301-3314.

Crompton RH. 2016. The hominins: a very conservative tribe? Last common ancestors, plasticity and ecomorphology in hominidae. *Journal of Anatomy*, 228, 686-699.

Czekala NM, Robbins MM. 2001. Assessment of reproduction and stress through hormone analysis in gorillas. In: Robbins MM, Sicotte P, Stewart KJ, editors. *Mountain Gorillas: Three Decades of Research at Karisoke*. Cambridge: Cambridge University Press. p 317-339.

DeSilva JM. 2009. Functional morphology of the ankle and the likelihood of climbing in early hominins. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 6567-6572.

Doran, D.M. 1993. Comparative locomotor behavior of chimpanzees and bonobos: The influence of morphology on locomotion. *American Journal of Physical Anthropology*, 91, 83-98.

Doran DM. 1996. Comparative positional behavior of the African apes. In: McGrew WC, Marchant LF, Nishida T, editors. *Great Ape Societies*, Cambridge: Cambridge University Press. p 213-224.

Drapeu MSM. 2008. Articular morphology of the proximal ulna in extant and fossil hominoids and hominins. *Journal of Human Evolution*, 55, 86-102.

Fossey D. 1983. *Gorillas in the Mist*. Boston: Houghton Mifflin Co.

Ganas J, Robbins MM, Nkurunungi JB, Kaplin BA, McNeilage A. 2004. Dietary Variability of Mountain Gorillas in Bwindi Impenetrable National park, Uganda. *International Journal of Primatology*, 25, 1043-1072.

Garber PA. 2007. Primate locomotor behaviour and ecology. In: Campbell CJ, Fuentes A, Mackinnon KC, Panger M, Bearder SK. editors. *Primates in Perspective*. Oxford: Oxford University Press. p 543-560.

Hanna JB, Schmitt D, Griffin TM. 2008. The energetic cost of climbing in primates. *Science*, 320, 898.

Hanna JB, Granatosky MC, Rana, P., Schmitt D. 2017. The evolution of vertical climbing in primates: evidence from reaction forces. *Journal of Experimental Biology*. doi:10.1242/jeb.157628

Hamrick MW, Inouye SE. 1995. Thumbs, tools, and early humans. *Science*, 268, 586-587.

Hasley LG, Coward SRL, Crompton RH, Thorpe SKS. 2017. Practice makes perfect: Performance optimisation in 'arboreal' parkour athletes illuminates the evolutionary ecology of great ape anatomy. *Journal of Human Evolution*, 103, 45-52.

Hirasaki E, Kumakura H, Matano S. 1993. Kinesiological characteristics of vertical climbing in *Ateles geoffroyi* and *Macaca fuscata*. *Folia Primatologica*, 61, 148-156.

Hunt KD. 1991a. Mechanical implications of chimpanzee positional behavior. *American Journal of Physical Anthropology*, 86, 521-536.

Hunt KD. 1991b. Positional behavior in the Hominoidea. *International Journal of Primatology*, 12, 95-118.

Hunt KD. 1992a. Positional behavior of *Pan troglodytes* in the Mahale Mountains and Gombe Stream National Parks, Tanzania. *American Journal of Physical Anthropology*, 87, 83-105.

Hunt KD. 1992b. Social rank and body size as determinants of positional behavior in *Pan troglodytes*. *Primates*, 33, 347-357.

Hunt KD. 1994. Body size effects on vertical climbing among chimpanzees. *International Journal of Primatology*, 15, 855-865.

Hunt KD, Cant JGH, Gebo DL, Rose MD, Walker SE, & Youlatos, D. 1996. Standardized descriptions of primate locomotor and postural modes. *Primates*, 37, 363-387.

Hunt KD. 2016. Why are there apes? Evidence for the co-evolution of ape and monkey ecomorphology. *Journal of Anatomy*, 228, 630-685.

Inouye SE. 2003. Intraspecific and ontogenetic variation in the forelimb morphology of Gorilla. In: Taylor AB, Goldsmith ML. editors. *Gorilla Biology. A Multidisciplinary Perspective*. New York: Cambridge University Press. p 194-235.

Isler K. 2002. Characteristics of vertical climbing in African apes. *Senckenbergiana Lethaea*, 82, 115-124.

Isler K. 2003. Footfall patterns, stride length and speed of vertical climbing in spider monkeys (*Ateles fuscipes robustus*) and woolly monkeys (*Lagothrix lagotricha*). *Folia Primatologica*, 75, 133-149.

Isler K. 2005. 3D-Kinematics of vertical climbing in hominoids. *American Journal of Physical Anthropology*, 126, 66-81.

Jabbour RB. 2008. Geographic variation in the forelimb and hindlimb skeletons of African apes. [doctoral dissertation]. The City University of New York.

Jenkins FA. 1973. The functional anatomy and evolution of the mammalian humeroulnar articulation. *American Journal of Anatomy*, 137, 281-297.

Johnson L. 2012. Biomechanics of Vertical Clinging and Grasping in Primates (doctoral dissertation). UMI: 3505179, Duke University, Durham, NC.

Larson SG, Stern JT Jr. 1986. EMG of scapulohumeral muscles in the chimpanzee during reaching and "arboreal" locomotion. *American Journal of Anatomy*, 176, 171-190.

Larson SG. 1998. Parallel evolution in the hominoid trunk and forelimb. *Evolutionary Anthropology*, 6, 87-89.

Marzke MW, Wullstein KL, Viegas SF. 1992. Evolution of the power ("squeeze") grip its morphological correlates in hominids. *American Journal of Physical Anthropology*, 89, 283-298.

Marzke MW, Wullstein KL. 1996. Chimpanzee and human grips: a new classification with a focus on evolutionary morphology. *International Journal Primatology*, 17, 117-13.

Marzke, MW. (1997). Precision grips, hand morphology, and tools. *American Journal of Physical Anthropology*, 102, 91-110.

Marzke, MW, Marchant, LF, McGrew, WC, & Reece, SP. (2015). Grips and hand movements of chimpanzees during feeding in the Mahale Mountain National Park, Tanzania. *American Journal of Physical Anthropology*, 156, 317-326. 9.

Matarazzo S. 2008. Knuckle walking signal in the manual digits of Pan and Gorilla. *American Journal of Physical Anthropology*, 135, 27-33.

McClure NK, Phillips AC, Vogel ER, Tocheri MW. 2012. Unexpected pollex and hallux use in wild *Pongo pygmaeus wurmbii*. [abstract]. *American Journal of Physical Anthropology Supplement*, 147, 208.

Myatt JP, Crompton RH, Payne-Davis RC, Vereecke EE, Isler K, Savage R, D'Aout K, Guenther MM, Thorpe SKS. 2012. Functional adaptations in the forelimb muscles of non-human great apes. *Journal of Anatomy*, 220, 13-28.

Napier JR. 1960. Studies of the hands of living primates. *Proceedings of the Zoological Society of London*, 134, 647-657.

Napier, JR. 1993. *Hands*. Revised edition by Russell H. Tuttle. Princeton University Press, Princeton.

Nakano Y. 2002. The effects of substratum inclination on locomotor patterns in primates. *Zeitschrift fuer Morphologie und Anthropologie*, 83, 189-199.

Nakano Y, Hirasaki E, Kumakura H. 2006. Patterns of vertical climbing in primates. In: Ishida H, Tuttle R, Pickford M, Ogihara N, Nakatsukasa M, editors. *Human origins and environmental backgrounds*. New York: Springer Publishing. p 97-104.

Nayakatura JA, Fischer MS, Schmidt M. 2008. Gait parameters adjustments of cotton-top tamarins (*Saguinus oedipus*, Callitrichidae) to locomotion on inclined arboreal substrates. *American Journal of Physical Anthropology*, 135, 13-26.

Patel BA, Mallino SA. 2016. Morphological diversity in the digital rays of primate hand. In: Kivell TL, Lemelin P, Richmond BG, Schmitt D, editors. *The Evolution of the Primate Hand: Anatomical, Developmental, Functional and Paleontological Evidence*. New York: Springer Publishing. p 55-101.

Pilbeam D. 2002. Perspectives on the Miocene Hominoidea. In: Hartwig WC, editor. *The Primate Fossil Record*. Cambridge: Cambridge University Press. p 303-310.

Pontzer H, Wrangham RW. 2004. Climbing and the daily energy cost of locomotion in wild chimpanzees: implications for hominoid locomotor evolution. *Journal of Human Evolution*, 46, 315-333.

Preuschoft H, Witte H. 1991. Biomechanical reasons for the evolution of hominid body shape In: Coppens Y, Senut B, editors. *Origine(s) de la bipédie chez les hominides*. Paris: Editions du CNRS. p 59–77.

Preuschoft H. 2002. What does “arboreal locomotion” mean exactly and what are the relationship between “climbing”, environment and morphology? *Zeitschrift fuer Morphologie und Anthropologie*, 83, 171-188.

Preuschoft H. 2004. Mechanisms for the acquisition of habitual bipedality: are there biomechanical reasons for the acquisition of upright bipedal posture? *Journal of Anatomy*, 204, 363–384.

Preuschoft H, Hohn B, Scherf H, Schmidt M, Krause C, Witzel U. 2010. Functional analysis of the primate shoulder. *International Journal Primatology*, 31, 301-320.

Rawlings B, Davila-Ross M, Boyson ST. 2014. Semi-wild chimpanzees open hard-shelled fruits differently across communities. *Animal Cognition*, 17, 891-899.

Remis, MJ. 1994. Feeding ecology and positional behavior of western lowland gorillas (*Gorilla gorilla gorilla*) in the Central African Republic (unpublished doctoral dissertation). Yale University, New Haven.

Remis MJ. 1995. Effect of body size and social context on the arboreal activities of lowland gorillas in the Central African Republic. *American Journal of Physical Anthropology*, 97, 413-433.

Remis MJ. 1998. The gorilla paradox. In: Strasser E, Fleagle JG, Rosenberger AL, McHenry HM, editors. *Primate locomotion*. New York: Springer Publishing. p 95-106.

Remis MJ. 1999. Tree structure and sex differences in arboreality among western lowland gorillas (*Gorilla gorilla gorilla*) at Bai Hokou, Central African Republic. *Primates*, 40, 383-396.

Robbins MM. 2001. Variation in the social system of mountain gorillas: The male perspective. In: Robbins MM, Sicotte P, Stewart KJ, editors. *Mountain Gorillas: Three Decades of Research at Karisoke*. Cambridge: Cambridge University Press. p 29-58.

Robbins, MM., Nkurunungi, JB., & McNeilage, A. 2006. Variability of the feeding ecology of eastern gorillas. In: G. Hohmann, M. M. Robbins, & C. Boesch (Eds.), *Feeding Ecology in Apes and Other Primates: Ecological, Physical, and Behavioral Aspects* (pp. 24–46). Cambridge, U.K.: Cambridge University Press.

Robbins MM. 2008. Feeding competition and agonistic relationships among Bwindi Gorilla *beringei*. *International Journal Primatology*, 29, 999-1018.

Robbins MM, McNeillage A. 2003. Home range and frugivory patterns of mountain gorillas in Bwindi impenetrable national park, Uganda. *International Journal Primatology*, 24, 467-490.

Rose MD. 1988. Functional anatomy of the cheiridia. In: Schwartz J, editor. *Orangutan biology*. New York: Oxford University Press. p 299-310.

Rose MD. 1993. Functional anatomy of the elbow and forearm in primates. In: Gebo DL, editor. *Postcranial Adaptation in Nonhuman Primates*. DeKalb: Northern Illinois University Press. p 70-95.

Sarmiento EE. 1988. Anatomy of the hominoid wrist joint: Its evolutionary and functional implications. *International Journal of Primatology*, 9, 281-345.

Sarmiento EE. 1994. Terrestrial traits in the hands and feet of gorillas. *American Museum Novitates*, 3091, 56.

Sarmiento EE, Butynski TM, Kalina J. 1996. Gorillas of Bwindi-Impenetrable forest and the Virunga Volcanoes: taxonomic implications of morphological and ecological differences. *American Journal of Primatology*, 40, 1-21.

Schaller GB. 1963. *The Mountain Gorilla: Ecology and Behavior*. Chicago and London: The University of Chicago Press.

Schultz AH. 1969. Observations on the acetabulum of primates. *Folia Primatologica*, 11, 181-199.

Shapiro LJ, Kemp AD, Young JW. 2016. Effects of substrate size and orientation on quadrupedal gait kinematics in Mouse Lemurs (*Microcebus murinus*). *Journal of Experimental Zoology*, 325, 329-343.

Shaw P, Shewry M. 2001. Population density and habitat associations of restricted-range bird species at Ruhija, Bwindi Impenetrable Forest, Uganda. *Bird Conservation International*, 11, 161-174.

Smith RJ, Jungers WL. 1997. Body mass in comparative primatology. *Journal of Human Evolution*, 32, 523-559.

Stanford CB, O'Malley RC. 2008. Sleeping Tree choice by Bwindi chimpanzees. *American Journal of Primatology*, 70, 642-649.

Stern JT Jr, Jungers WL, Susman RL. 1995. Quantifying phalangeal curvature: an empirical comparison of alternative methods. *American Journal Physical Anthropology*, 97, 1-10.

Straus WL. 1942. Rudimentary digits in primates. *The Quarterly Review of Biology*, 17, 228-243.

Susman RL. 1979. Comparative and functional morphology of hominoid fingers. *American Journal Physical Anthropology*, 50, 215-236.

Thorpe SKS, Crompton RH. 2006. Orangutan positional behaviour and the nature of arboreal locomotion in hominidae. *American Journal Physical Anthropology*, 131, 384-401.

Tocheri MW, Solhan CR, Orr CM, Femiani J, Frohlich B, Groves CP, Harcourt-Smith, WE, Richmond BG, Shoelson B, Jungers WL. 2011. Ecological divergence and medial cuneiform morphology in gorillas. *Journal of Human Evolution*, 60, 171-184.

Tocheri, MW, Dommain R, McFalin SC, Burnett SE, Case DT, Orr CM, Roach NT, Villmoare B, Eriksen AB, Kalthoff DC, Senck S, Assefa Z, Groves CP, Junger WL.

2016. The Evolutionary Origin and Population History of the Grauer Gorilla. *Yearbook of Physical Anthropology*, 159, 4-8.

Tuttle RH. 1969. Quantitative and functional studies on the hands of the Anthroidea: The Hominoidea. *Journal of Morphology*, 128, 309-363.

Tuttle RH, Watts DP. 1985. The positional behaviour and adaptive complexes of Pan gorilla. In: Kondo S, editor. *Primate Morphophysiology, Locomotor Analyzes, and Human Bipedalism*. Tokyo: University of Tokyo Press. p 261-288.

Tutin CEG, Fernandez M, Rogers ME, Williamson EA, McGrew WC. 1991. Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lopé Reserve, Gabon. *Philosophical Transactions of the Royal Society of London. Series B Biological Science*, 334, 179-185.

Tutin CEG. 1996. Ranging and social structure of lowland gorillas in the Lopé Reserve, Gabon. In: MCGrew WC, Marchant LF, Nishida T, editors. *Great ape societies*. Cambridge: Cambridge University Press. p 58-70.

Watts DP. 1984. Composition and variability of mountain gorilla diets in the central Virungas. *American Journal of Primatology*, 7, 323-356.

Wright, E., Grueter, C. C., Seiler, N., Abavandimwe, D., Stoinski, T.S., Ortmann, S., & Robbins, M. M. (2015). Energetic responses to variation in food availability in the two mountain gorilla populations (*Gorilla beringei beringei*). *American Journal of Physical Anthropology*, 158, 487–500.

Wunderlich RE, Jungers WL. 2009. Manual digital pressures during knuckle-walking in chimpanzees (*Pan troglodytes*). *American Journal Physical Anthropology*, 139, 394-403.

Zihlman AL, McFarland RK, Underwood CE. 2011. Functional anatomy and adaptation of male gorillas (*Gorilla gorilla gorilla*) with comparison to male orangutans (*Pongo pygmaeus*). *The Anatomical Record*, 294,1842-1855.