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Gait characteristics of vertical climbing in mountain gorillas and chimpanzees

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Abstract

Biomechanical analyses of arboreal locomotion in great apes in their natural environment are scarce and thus attempts to correlate behavioral and habitat differences with variations in morphology are limited. The aim of this study was to investigate the gait characteristics of vertical climbing in mountain gorillas (*Gorilla beringei beringei*) and chimpanzees (*Pan troglodytes*) in a natural environment to assess differences in the climbing styles that may relate to variation in body size. We investigated temporal variables (i.e., cycle duration, duty factors, and stride frequency) and footfall sequences (i.e., diagonal vs. lateral sequence gaits) during vertical climbing (both ascent and descent) in 11 wild mountain gorillas and compared these data to those of eight semi-free-ranging chimpanzees, using video records *ad libitum*. Comparisons of temporal gait parameters revealed that large-bodied mountain gorillas exhibited a longer cycle duration, lower stride frequency and generally a higher duty factor than small-bodied chimpanzees. While both apes were similarly versatile in their vertical climbing performance in the natural environment, mountain gorillas most often engaged in diagonal sequence/diagonal couplet gaits and chimpanzees most often used lateral sequence/diagonal couplet gaits. This study revealed that mountain gorillas adapt their climbing strategy to accommodate their large body mass in a similar manner previously found in captive western lowland gorillas, and that chimpanzees are less variable in their climbing strategy than has been documented in captive bonobos.

Introduction

Vertical climbing is essential to the locomotor and foraging strategies of great apes (e.g., Hunt, 1992; Remis, 1995; Pilbeam, 2002; Robbins & McNeilage, 2003). Records of the frequency of vertical climbing in wild African apes vary depending on the species and population studied as well as on differences in habitat structure and resource availability (e.g., Tuttle & Watts, 1985; Doran, 1993, Doran, 1996; Remis, 1995; Crompton, Sellers & Thorpe, 2010). Most studies agree that mountain gorillas (*Gorilla beringei beringei*) are less arboreal than chimpanzees (*Pan troglodytes*) (Tuttle & Watts, 1985; Remis, 1998; Hunt, 2004, 2016; Crompton *et al.*, 2010) and are thought to spend less than 1% of total locomotor time engaging in vertical climbing (Tuttle & Watts, 1985). However, 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).

During arboreal locomotion, and particularly vertical climbing, primates face several biomechanical challenges. As substrate inclination increases, the difficulty in maintaining stability also increases, and these challenges are greatest on vertical supports (Cartmill, 1974, 1985; Preuschoft, 2002). When climbing up inclined substrates primates must use their limbs to overcome gravitational force (e.g., Hirasaki, Kumakura & Matano, 1993, 2000; Nakano, 2002; Preuschoft, 2002; Hanna *et al.*, 2017), while a shear force acts against the direction of movement (Preuschoft, 2002). The higher forces that are required for propel the body upwards, together with the shift in body weight towards the hind limbs, increases the risk of toppling backwards if an animal is not able to make secure substrate contact (e.g., Cartmill, 1974; Preuschoft & Witte, 1991; Preuschoft, 2002). Primates typically must use their hands/forelimb (to pull) and feet/hind limb (to push) to generate greater propulsive forces as substrate incline increases (Hirasaki *et al.*, 1993; Hanna *et al.*, 2017), although smaller primates (<1 kg) show greater versatility in limb use (Hanna *et al.*, 2017). In contrast, when descending an inclined or vertical substrate, greater braking may be applied to resist acceleration (e.g., Cartmill, 1985; Preuschoft, 2002). Heavier animals will, typcially, exhibit a prolonged support phase or higher duty factor (i.e., increased limb contact with the substrate) during vertical climbing to increase stability, enabling a more cautious movement (e.g., Cartmill, 1974; Cartmill & Milton, 1977). On vertical supports, primates overcome some of these biomechanical challenges using powerful grasping and adapting their forelimb and hand posture (Hunt, 1991; Hunt *et al.*, 1996; Hirasaki *et al.*, 2000; Isler, 2005; Nakano, Hirasaki & Kumakura, 2006). For example, recent work has found that mountain gorillas and chimpanzees generally use the same hand grips, power grips and diagonal power grips, as well as similar forelimb postures on vertical supports of a similar size, which is consistent with their general similarity in hard and soft tissue morphology of the hand and forelimb (Neufuss *et al.*, 2017).

Attempts to correlate variations in African ape morphology (e.g., hand or limb proportions, body mass) with behavioral and habitat differences are limited because kinematics (e.g., movement of body segments, gait parameters) of arboreal locomotion, such as vertical climbing, are scarce especially in the wild. A few studies have investigated the spatio-temporal parameters and gait characteristics of vertical climbing in apes and other primates, all of which have been conducted in captivity (Hirasaki *et al.*, 1993, 2000; Isler, 2002, 2003, 2005; Isler & Grueter, 2006; Schoonaert *et al.*, 2016). Within great apes, there is only one naturalistic study that compared the gait parameters of vertical climbing in rehabilitated and wild Sumatran orangutans to captive individuals (Isler & Thorpe, 2003). Captive chimpanzee climbing patterns and limb joint kinematics have been briefly described (Nakano *et al.*, 2006) but gait parameters of fore-and hind limbs have not been examined. Current knowledge about the spatio-temporal gait characteristics of gorilla vertical climbing stems solely from a captive study of western lowland gorillas (*Gorilla gorilla gorilla*) using a rope as locomotor support (Isler, 2002). Isler (2002) identified key differences in gorilla climbing performance associated with age and sex; vertical climbing in an adult male gorilla was characterized by higher duty factors, relatively shorter strides and more variable footfall patterns compared with adult female gorillas and bonobos. Isler (2002) interpreted these kinematic differences as evidence that vertical climbing on a rope was more challenging for adult male gorillas due to their larger body mass. However, the vertical climbing 'characteristics' in mountain gorillas and chimpanzees within a natural environment have never been investigated, and the potential differences in the climbing performance between these two apes that differ significantly in body size (e.g., Sarmiento, 1994; Smith & Jungers, 1997) are not yet known.

The aim of this study was to provide further insights into the arboreal locomotor strategies of mountain gorillas and chimpanzees by describing the temporal gait parameters and footfall sequences during vertical climbing (both ascent and descent) on differently sized natural substrates. We predict that vertical climbing of large-bodied mountain gorillas will be characterized by longer cycle durations, higher duty factors, lower stride frequencies, a higher number of limbs used as support and less variable footfall patterns compared to small-bodied chimpanzees. More specifically, we hypothesize that mountain gorillas will adapt their climbing strategy to accommodate their large body mass in a similar manner to that documented in captive western lowland gorillas (females 71.0–97.5 kg; males 162.5–175.2 kg across *G. beringei, G. gorilla, G. graueri*; Smith & Jungers, 1997) and, likewise, vertical climbing of small-bodied chimpanzees will be similar to that of bonobos given their generally similar body size (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 & Jungers, 1997).

Materials and methods

Species and study sites

Mountain gorillas (*Gorilla beringei beringei*) were observed in the Bwindi Impenetrable National Park (331 km^2). Data were collected on one fully habituated group of gorillas (Kyagurilo) between October–December 2014 and March–July 2015 during two fruiting seasons.

Chimpanzee (*P. troglodytes* ssp.) vertical climbing data were collected between August and September 2014 on two colonies of semi-free-ranging chimpanzees at the Chimfunshi Wildlife Orphanage Trust (CWO), Zambia.

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 hind limb was initially placed in contact with the substrate and a sequence ended when the individual stopped vertical climbing. 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).

Both apes were filmed *ad libitum* during vertical ascent and descent climbing using a high-definition HDR-CX240E video camera (Sony, Japan) at a frequency of 50 Hz. The mountain gorillas were observed for an average of 4 h day^{-1}. All gorilla climbing sequences were recorded at relatively close range (7 m to ~20 m) on a sample of 11 individuals (Table 1). The gorillas had the opportunity to climb on differently sized substrates ranging from lianas (6–10 cm diameter) to extremely large tree trunks (>50 cm diameter) (for more details on substrate sizes see Neufuss *et al.*, 2017). A total of eight adult semi-free-ranging chimpanzees were filmed at relatively close range (~10 m) (Table 1). Although the chimpanzees climbed in a natural environment, the sanctuary is located in a miombo woodland, and thus, substrates were limited to tree trunks of different sizes (i.e., no data were collected on lianas).

Types of vertical climbing

Two types of vertical climbing have been previously described in relation to substrate size (Hunt *et al.*, 1996): (1) when climbing

Table 1 Studied individuals and number of sequences and limb cycles analyzed

Species	Individual	Sex/age	Total no. of climbing sequences	No. of hind limb cycles for vertical ascent	No. of hind limb cycles for vertical descent
G. b. beringei	JN	Female/adult	11	17	6
	ST	Female/adult	11	13	6
	KR	Female/adult	9	18	–
	TN	Female/adult	5	10	–
	TW	Female/adult	7	10	3
	MG	Female/adult	8	2	8
	BY	Female/adult	5	3	–
	TD	Female/adult	2	2	–
	KA	Male/blackback	4	7	–
	MK	Male/silverback	6	12	–
	RC	Male/silverback	2	3	–
Total			70	97	23
P. troglodytes ssp.	RI	Female/adult	2	–	6
	KB	Female/adult	8	12	7
	MI	Female/adult	11	9	15
	KY	Female/adult	7	6	6
	JU	Female/adult	3	–	8
	UN	Female/adult	4	–	5
	TA	Male/adult	1	–	4
	CO	Male/adult	1	–	2
Total			37	27	53

on smaller substrates, such a liana or thin tree, flexion of the elbow helps to elevate the body (‘flexed-elbow’ vertical climbing); (2) on larger substrates, such as tree trunks, the elbow is typically extended throughout the motion cycle (‘extended-elbow’ vertical climbing). In both mountain gorillas and chimpanzees, smaller substrates evoke flexed-elbow climbing while a substrate diameter larger than 20 cm is likely to evoke extended-elbow climbing (Hunt *et al.*, 1996; Neufuss *et al.*, 2017).

Analysis of gait characteristics

The footfall sequence and gait parameters such as cycle duration, duty factor and stride frequency were determined by reviewing video sequences frame-by-frame using video analysis freeware Kinovea 0.8.15 (www.kinovea.org, France). *Cycle duration* (CD) is defined as the time between two initial contacts with the substrate (or ‘touchdowns’) by the same limb (e.g., Isler, 2002; Isler & Thorpe, 2003). The relative duration of the stance phase, or *duty factor* (S), is the fraction of the cycle duration that a particular limb contacts the substrate (Hildebrand, 1966). *Stride frequency* is the number of strides per unit of time, or 1/CD (Schoonaert *et al.*, 2016). The limb cycles were classified as either symmetrical or asymmetrical gaits according to the timing of footfalls, following Hildebrand (1967). *Stride symmetry* was calculated as the percentage of cycle duration separating the time between touchdowns of the right and left hind limbs (Hildebrand, 1966). A cycle was considered symmetrical if the opposing limb’s touchdown occurred between 40% and 60% of the cycle duration, allowing comparisons with results of Isler (2002, 2003, 2005) and Schoonaert *et al.* (2016). A cycle that was outside of this range (i.e., <40% or >60%) was considered as asymmetrical.

Symmetrical cycles were then further classified as being either diagonal sequence (DS) or lateral sequence (LS) gaits. In a *DS gait*, hind limb touchdown is followed by the touchdown of the opposite forelimb (right hind limb > left forelimb), whereas in a *LS gait* the ipsilateral forelimb follows (right hind limb > right forelimb) (Hildebrand, 1966). *Limb phase* (D, also called diagonality) is a quantitation of the timing of the footfalls and defined as the duration of time between hind limb touchdown and touchdown of the ipsilateral forelimb, expressed as a percentage of the stride cycle (Hildebrand, 1966; Cartmill, Lemelin & Schmitt, 2002). DS and LS strides can be further subdivided into five categories: diagonal couplets (DC), lateral couplets (LC), single foot (SF), pace and trot (Hildebrand, 1967) based on the relative timing of touchdown of the limbs (see Fig. 1; Table 2). Finally, we further investigated the average number of limbs supporting the animal’s body during ascent and descent climbing (i.e., two- vs. three-limb support). Limb support was categorized as diagonal, lateral, tripedal, or quadrupedal following Vielnsky & Gankiewicz (1989) (Table 2).

Statistics

All statistical analyses were performed using SPSS (IBM SPSS Statistics for Windows, Version 24.0). Gait parameters were analyzed using mean values for all cycles/individual, so that each individual was contributing only a single observation within each condition to ensure independence of data points. Given the small sample size for each species, statistical analyses are used here primarily to summarize the observed patterns rather than to explicitly test hypotheses. Differences in gait parameters between fore- and hind limbs during vertical ascent versus descent, including flexed- versus extended-elbow

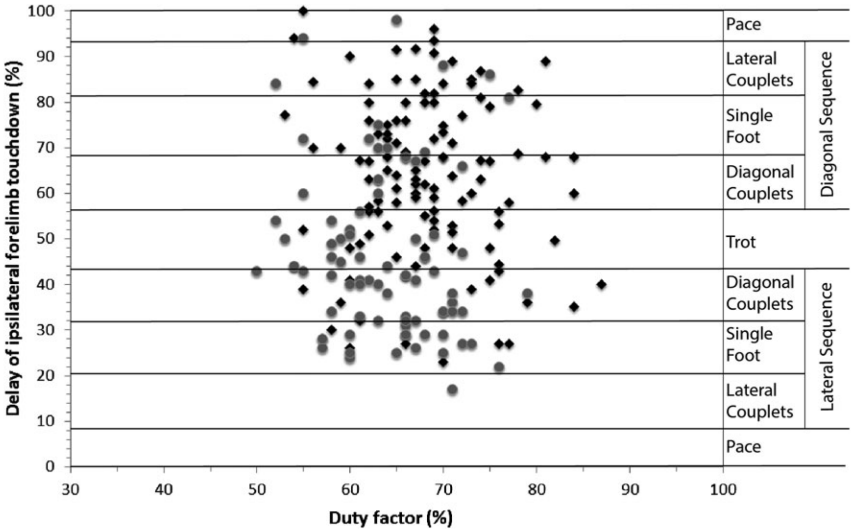

Figure 1 Classification of footfall patterns during symmetrical strides of vertical climbing in mountain gorillas (black diamonds) and chimpanzees (grey circles) following Hildebrand (1967). The *x*-axis shows the duty factor, or relative duration of the stance phase in percent of total cycle duration. The *y*-axis shows the delay of the ipsilateral forelimb following hind limb touchdown, as a percentage of total cycle duration. Both mountain gorillas and chimpanzees used lateral and diagonal sequence gaits.

Table 2 Definitions of gait sequence patterns[a] and types of limb support[b]

Gait sequence pattern	Definition
Diagonal couplets (DC)	Diagonally opposite fore-and hind limb touchdown at the same time
Lateral couplets (LC)	The footfalls on the same body side are evenly spaced in time
Single foot (SF)	The footfalls of all the limbs are evenly spaced
Pace	The footfalls of the fore- and hind limb on the same SIDE are evenly spaced
Trot	Diagonally opposite limbs are evenly spaced in time
Types of limb support	**Definition**
Diagonal pair	Support by either combination of diagonal limbs
Lateral pair	Support by either pair of limbs on the same side
Tripedal	Support by any combination of three limbs
Quadrupedal	Support by all four limbs

[a] Gait sequence patterns defined according to Hildebrand (1967).

[b] Type of limb support follow definitions by Vielnsky & Gankiewicz (1989) and Isler (2002).

climbing, were assessed with independent-samples *t*-tests. Following Isler (2002), significance of inter- and intraspecific (sex classes) differences in the gait parameters between gorillas and chimpanzees was tested using a one-way ANOVA and a Scheffé's *post-hoc* test ($a = 0.05$). The overall sample size was too small to allow more sophisticated statistical tests that would account for species, sex, or type of vertical climbing etc. as fixed effects and the individual as a random effect. Therefore, results of these statistical analyses should be interpreted with caution.

Results

We recorded a total of 70 climbing sequences, containing $N = 120$ limb cycles (ascent: 97; descent: 23), for 11 mountain gorillas and 37 climbing sequences, containing $N = 80$ limb cycles (ascent: 27; descent: 53), for eight chimpanzees (Table 1).

Gait sequence patterns

Mountain gorillas used DS gaits more often (68%) than trot (18%) and LS gaits (14%) during both ascent and descent climbing (Table 3, Fig. 1). Most of these DS gaits were further classified as diagonal couplets, followed by lateral couplets and single foot. Lateral couplets and LS pace were not observed. Chimpanzees showed the opposite pattern, using LS gaits (58%) more often than DS gaits (23%) and trot (20%; Table 3; Fig. 1) during both ascent and descent climbing. Most of these strides were diagonal couplets and single foot gaits. LS pace was not observed in chimpanzees (Fig. 1).

In mountain gorillas, limb phase was significantly higher [mean: 0.62, SD: 0.08; $t(17) = 3.59$, $P = 0.002$] for most limb cycles (20 cycles: 50–59%, 30 cycles: 60–69%, 18 cycles: 80–89%) than in chimpanzees (mean: 0.46, SD: 0.12; 15 cycles:

Table 3 Frequency of gait sequence patterns in mountain gorillas and chimpanzees

	Diagonal sequence gaits						Lateral sequence gaits				
	DS (%)	DC (%)	SF (%)	LC (%)	Pace (%)	Trot (%)	LS (%)	DC (%)	SF (%)	LC (%)	Pace (%)
Mountain gorillas	68	42	23	24	11	18	14	59	41	–	–
Chimpanzees	23	33	39	17	11	20	58	59	39	2	–

DC, diagonal couplet; DS, diagonal sequence; LC, lateral couplet; LS, lateral sequence; SF, single foot.

Note that the total number of strides was $N = 120$ in gorillas and $N = 80$ in chimpanzees. In gorillas, the number of DS gaits types was $N = 81$, trot: $N = 22$ and LS gaits: $N = 17$. In chimpanzees, the number of DS gait types was $N = 18$; trot: $N = 16$ and LS gaits: $N = 46$.

20–29%, 21 cycles: 40–49%, 14 cycles: 30–39%). This difference in limb phase is consistent with the more frequent use of DS gaits in mountain gorillas and LS gaits in chimpanzees.

Temporal gait parameters

Table 4 summarizes the mean cycle duration and the relative duration of the support phases (i.e., duty factor) of fore- and hind limbs of mountain gorillas and chimpanzees. When comparisons could be made, there were no significant species differences in either variable in the gait parameters between fore- and hind limbs during (1) ascent and descent climbing and (2) flexed-elbow and extended-elbow climbing (Table 5). Thus, all results were pooled for each species.

There were no intraspecific significant differences in forelimb or hind limb cycle duration, stride frequency, or duty factor between males and females within both gorillas and chimpanzees (Table 6). Interspecifically, however, significant variation was found across all gait parameters (Fig. 2, Table 6). Overall, gorillas (i.e., sexes pooled) showed a significantly longer cycle duration [mean: 2.7, SD: 0.8; ANOVA, $F(3) = 9.52$, MSE=1.45, $P = 0.001$] than chimpanzees (mean: 1.6, SD: 0.3) (Fig. 2). Cycle duration was significantly longer in female gorillas (mean: 2.7, SD: 0.9) than in female (mean: 1.6, SD: 0.2) and male (mean: 1.3, SD: 0.4) chimpanzees (Table 6). In contrast, male gorillas had a significantly longer cycle duration (mean: 2.4, SD: 0.4) than male chimpanzees but not compared to female chimpanzees (Table 6).

The duty factor was significantly higher in gorillas overall [mean: 69%, SD: 3; ANOVA, $F(3) = 5.71$, MSE=53.16, $P = 0.009$] than in chimpanzees (mean: 63%, SD: 3.6) (Fig. 2). The duty factor was significantly different between female gorillas (mean: 70%, SD: 3) and female (mean: 63%, SD: 3) and male (mean: 58%, SD: 0) chimpanzees (Table 6). Similarly, male gorillas showed a significantly higher duty factor (mean: 69%, SD: 2.9) than female and male chimpanzees (Table 6). In both apes, the duty factor was most frequently between 60 and 69% (gorillas: 65 limb cycles; chimpanzees: 42 limb cycles), but in gorillas the duty factor was higher for more limb cycles (36 limb cycles: 70–79%, 8 cycles: 80–89%) than in chimpanzees (18 limb cycles: 70–79%) (Fig. 2).

The stride frequency was significantly lower in gorillas overall [mean: 0.40, SD: 0.11; ANOVA, $F(3) = 22.16$, MSE=0.12, $P < 0.001$] compared to chimpanzees (mean: 0.65, SD: 0.13) (Fig. 2). Interspecific differences showed that female gorillas exhibited a significantly lower stride frequency (mean: 0.38, SD: 0.12) than female (mean: 0.62, SD: 0.14) and male chimpanzees (mean: 0.78, SD: 0.04). Male gorillas similarly had a significantly lower stride frequency (mean: 0.43, SD: 0.03) than female and male chimpanzees (Table 6).

The average number of supporting limbs was not significantly different between gorillas (ascent: 2.7, SD: 0.4; descent: 2.4, SD: 0.05) and chimpanzees (ascent: 2.6, 273 SD: 0.3; descent: 2.4, SD: 0.1), with both apes using on average three limbs as support more frequently during vertical ascent than during descent (Table 7).

Discussion

This study provides the first description of gait characteristics in mountain gorillas and chimpanzees during vertical climbing in a natural environment. These new data provide a broader comparative context to understand variation in primate locomotion in general, and particularly the biomechanical adaptations for vertical climbing in large-bodied primates. Our study found support for the hypothesis that, due to variation in body size, gait characteristics (i.e., temporal gait parameters, footfall sequences and limb support pattern) of vertical climbing differs between large-bodied mountain gorillas and small-bodied chimpanzees. However, due to limited sample sizes in the analysis, we caution that any species differences (or intraspecific similarities) found in this study need to be validated on larger samples and perhaps on more varies natural substrates. First, we found no intraspecific sex differences within the temporal gait parameters in mountain gorillas or chimpanzees (Table 6). Male and female gorillas showed similarly high duty factors when their hands contacted the substrate (female mean: 70%; male mean: 69%), suggesting that ascent and descent climbing as well as flexed-elbow and extended-elbow climbing are similarly mechanically challenging for both sexes, despite their large variation in body mass (e.g., Schultz, 1934; Sarmiento, 1994; Smith & Jungers, 1997). However, a larger sample size on male individuals is needed to clarify whether mountain gorillas differ more between the sexes during vertical climbing than is found in this study.

As predicted, mountain gorillas and chimpanzees showed striking differences in their temporal gait parameters, with gorillas having significantly longer cycle duration, higher duty factor and lower stride frequency than chimpanzees (Table 6). The higher duty factor of the mountain gorilla's forelimb indicates that the gorilla's hand is held in contact with the substrate for longer compared to chimpanzees. Forceful hand grips and the use of variable thumb postures relative to substrate size are, therefore, likely particularly important in large-bodied

Table 4 Cycle duration and duty factor of vertical ascent and descent in mountain gorillas and chimpanzees

Species	Individual	Sex/age	No. of limb cycles (hind/fore)	Cycle durationHind limb (s)	Cycle duration Forelimb (s)	Duty factor Hind limb (%)	Duty factor forelimb (%)
Vertical ascent							
Extended-elbow climb							
G. b. beringei	JN	Female adult	12/12	1.93 (0.20)	1.87 (0.32)	66 (0.04)	69 (0.04)
	ST	Female adult	13/11	2.76 (0.61)	2.49 (0.68)	70 (0.09)	69 (0.07)
	KR	Female adult	18/18	2.32 (0.54)	2.32 (0.52)	63 (0.04)	68 (0.05)
	TN	Female adult	10/10	2.04 (0.54)	2.45 (0.87)	71 (0.06)	72 (0.07)
	TW	Female adult	10/10	2.37 (0.38)	2.48 (0.58)	68 (0.09)	69 (0.06)
	BY	Female adult	3/3	2.22 (0.08)	2.10 (0.15)	68 (0.02)	71 (0.05)
	TD	Female adult	2/2	3.41 (0.53)	2.96 (0.74)	69 (0.09)	73 (0.08)
	KA	Male blackback	7/7	3.03 (0.53)	2.63 (0.16)	76 (0.06)	71 (0.05)
	MK	Male silverback	10/8	2.26 (0.71)	2.50 (1.65)	72 (0.04)	66 (0.05)
	RC	Male silverback	3/3	2.19 (0.35)	1.93 (0.13)	65 (0.05)	71 (0.03)
P. troglodytes ssp.	KB	Female adult	7/7	1.82 (0.38)	1.82 (0.21)	68 (0.05)	63 (0.07)
	MI	Female adult	9/8	1.73 (0.78)	1.73 (0.72)	65 (0.08)	59 (0.04)
	KY	Female adult	6/5	1.90 (0.47)	1.94 (0.67)	69 (0.07)	66 (0.09)
Flexed-elbow climb							
G. b. beringei	JN	Female adult	5/5	2.35 (0.13)	2.35 (0.22)	64 (0.03)	64 (0.04)
	MG	Female adult	2/2	1.86 (0.14)	1.76 (0.21)	72 (0.03)	68 (0.00)
	MK	Male silverback	2/2	2.22 (0.30)	3.39 (0.72)	71 (0.03)	69 (0.01)
Vertical descent							
Extended-elbow climb							
G. b. beringei	JN	Female adult	4/3	1.65 (0.24)	2.49 (1.40)	66 (0.03)	65 (0.05)
	ST	Female adult	6/6	2.62 (0.76)	4.53 (0.93)	71 (0.04)	76 (0.04)
	TW	Female adult	3/3	4.34 (3.02)	3.35 (1.91)	69 (0.07)	71 (0.08)
	MG	Female adult	8/8	2.40 (0.70)	3.50 (1.59)	66 (0.06)	65 (0.11)
P. troglodytes ssp.	RI	Female adult	6/6	1.43 (0.38)	1.56 (0.55)	61 (0.09)	61 (0.08)
	KB	Female adult	12/12	1.83 (0.71)	1.78 (0.43)	66 (0.11)	62 (0.08)
	MI	Female adult	15/15	1.40 (0.31)	1.48 (0.34)	64 (0.06)	67 (0.07)
	KY	Female adult	6/6	1.60 (0.32)	1.71 (0.33)	65 (0.04)	65 (0.08)
	JU	Female adult	8/6	1.38 (0.20)	1.40 (0.15)	62 (0.03)	63 (0.07)
	UN	Female adult	5/5	1.81 (0.33)	1.55 (1.60)	68 (0.02)	68 (0.03)
	TA	Male adult	4/4	1.34 (0.14)	1.45 (0.18)	61 (0.02)	58 (0.03)
	CO	Male adult	2/2	1.23 (0.00)	0.94 (0.04)	62 (0.17)	58 (0.05)
Flexed-elbow climb							
G. b. beringei	JN	Female adult	2/2	2.42 (0.52)	4.75 (0.47)	73 (0.00)	71 (0.01)
P. troglodytes ssp.	JU	Female adult	2/2	1.28 (0.18)	1.22 (0.47)	68 (0.06)	66 (0.16)
	UN	Female adult	2/2	1.62 (0.30)	1.87 (0.08)	55 (0.04)	68 (0.02)

mountain gorillas (Neufuss *et al.*, 2017), as they face greater biomechanical challenges during vertical climbing than small-bodied chimpanzees. The lower cycle duration and stride frequency combined with longer contact times, represents a more cautious and stable climbing strategy of mountain gorillas, which would increase safety when traversing unfamiliar or irregular substrates in an arboreal environment (Pontzer & Wrangham, 2004), as well as likely reduce energetic costs as found in other climbing primates (Isler, 2003; Isler & Thorpe, 2003; Hanna & Schmitt, 2011). Indeed, several studies have indicated that arboreal great apes display energy-saving adaptations in their locomotion to cope with their large body mass in an energetically challenging environment (Thorpe, Crompton & Alexander, 2007; Pontzer *et al.*, 2010). An interspecific comparison between western lowland gorillas and bonobos, as well as between juvenile and adult gorillas and orangutans, supports both suggestions on climbing safety and energy-saving adaptations (Isler, 2002, 2005). Further investigation of the spatio-temporal gait parameters will show whether mountain gorillas also use relatively long strides and climb at a slow speed similar to western lowland gorillas (Isler, 2005).

We also predicted that mountain gorillas would adapt their climbing strategy to accommodate their large body mass in a similar manner to that previously described in western lowland gorillas (Isler, 2002, 2003) and, likewise, that small-bodied chimpanzees would show a similar climbing style to that of bonobos (Isler, 2002). This prediction was only partially supported.

Similar to mountain gorillas, Isler (2002) also found high mean duty factors in captive western lowland gorillas, although she attributed this in part to their difficulty in climbing up a vertical rope (Isler, 2002, 2003). Although all of the chimpanzees in our study exhibited comparatively lower mean duty factors like that of bonobos, Isler (2002) found that female and

Table 5 Independent-samples *t*-test of gait parameters between fore- (RF) and hind limbs (RH) during vertical ascent and descent

Species	Cycle duration	Stride frequency	Duty factor
RF versus RH during vertical ascent			
Mountain gorillas (*N* = 10)	*t*(22) = 0.21, *P* = 0.834	*t*(22) = 0.16, *P* = 0.871	*t*(24) = −0.25, *P* = 0.8
Chimpanzees (*N* = 3)	*t*(4) = −1.71, *P* = 0.873	*t*(4) = 0.00, *P* = 1.00	*t*(4) = 1.98, *P* = 0.119
RF versus RH during vertical descent			
Mountain gorillas (*N* = 4)	*t*(8) = −1.4, *P* = 0.194	*t*(8) = −5.78, *P* = 0.571	*t*(8) = 0.51, *P* = 0.63
Chimpanzees (*N* = 8)	*t*(19) = 0.35, *P* = 0.728	*t*(18) = −0.2, *P* = 0.82	*t*(14) = −1.53, *P* = 0.8

Table 6 Scheffé's *post-hoc* test of gait parameters in mountain gorillas and chimpanzees

	Cycle duration	Stride frequency	Duty factor
Intraspecific			
Female versus male gorillas (*N* = 10)	*P* = 1.000	*P* = 0.999	*P* = 0.566
Female versus male chimpanzees (*N* = 8)	*P* = 0.888	*P* = 0.287	*P* = 0.811
Interspecific			
Female gorillas versus female chimpanzees	*P* < 0.001	*P* = 0.001	*P* = 0.002
Female gorillas versus male chimpanzees	*P* = 0.003	*P* < 0.001	*P* < 0.001
Male gorillas versus female chimpanzees	*P* = 0.075	*P* = 0.004	*P* = 0.040
Male gorillas versus male chimpanzees	*P* = 0.005	*P* = 0.001	*P* = 0.003

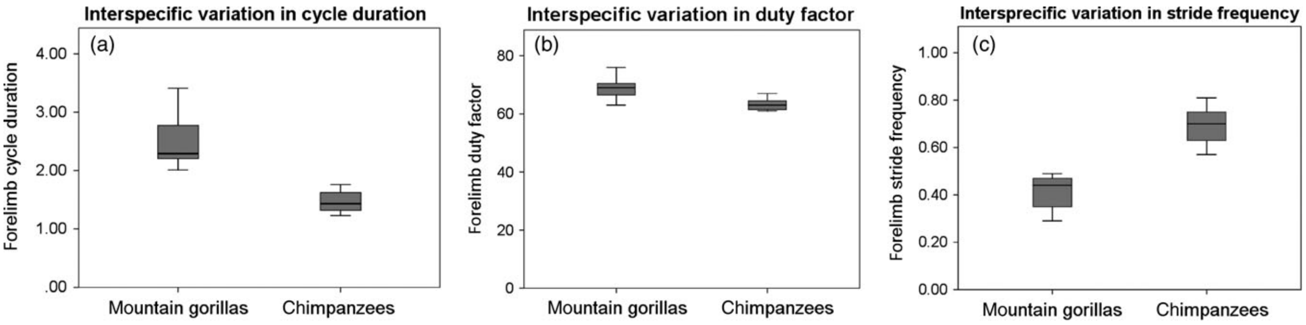

Figure 2 Box-and-whisker plots of interspecific variation in forelimb cycle duration, duty factor and stride frequency between mountain gorillas and chimpanzees. These differences were significant.

male bonobos differed considerably in their gait parameters during rope climbing, with females showing a shorter cycle duration and lower duty factor than males. Female bonobos could climb at a faster speed while the male bonobos would typically climb more slowly, combining long strides with a long cycle duration (Isler, 2002). However, a recent study of bonobos climbing a pole found similar gait parameters between the sexes (Schoonaert *et al.*, 2016), suggesting that a flexible rope may pose a greater locomotor challenge than climbing on a rigid support. This is in contrast to climbing in gorillas, where a compliant rope or liana might become stiffer in the line of action while a gorilla climbs up, using their large body mass against the substrate. However, since the sample sizes for male chimpanzees in this study and for female bonobos in Schoonaert *et al.* (2016) were small, a more comprehensive analysis of the spatio-temporal gait parameters in a larger sample on different substrate types will clarify whether chimpanzees also show the same level of intraspecific variation reported in bonobos (Isler, 2002).

This study also found that the climbing performance of mountain gorillas is not less versatile than that of chimpanzees in a natural environment, but that gorilla individuals most often used a different footfall sequence pattern (diagonal sequence gaits) compared to chimpanzees (Fig. 2; Table 3). However, at a given duty factor, mountain gorillas used a significantly higher limb phase on vertical supports than that of chimpanzees, likely leading to an increase in the frequency of simultaneous footfalls of diagonally opposite limbs (diagonal sequence-diagonal couplet, DSDC) to improve balance in an arboreal environment (e.g., Cartmill *et al.*, 2002; Stevens, 2006; Cartmill, Lemelin & Schmitt, 2007). Using DSDC gaits, the mountain gorilla hind limb can touch down before the contralateral forelimb to secure a firm foothold on the substrate and both limbs can provide body support for part of the gait cycle. Changes in duty factor and gait sequence patterns result in a higher proportion of strides with support by more limbs at one time on substrates that challenge stability (Stevens, 2006). This holds true for our sample of mountain gorillas, which

Table 7 Limb support during vertical ascent and descent in mountain gorillas and chimpanzees

Species	Individual	Sex/age	Total no. of hind limb cycles (100%)	*D*	*L*	*T*	*Q*	Mean no. of supp. limbs
Vertical ascent								
Gorilla beringei b.	JN	Female adult	17	3 (17.6%)	1 (5.9%)	12 (70.6%)	1 (5.9%)	2.8
	ST	Female adult	13	3 (23.1%)	4 (30.8%)	6 (46.2%)	0 (0.0%)	2.5
	KR	Female adult	18	3 (16.7%)	0 (0.0%)	15 (83.3%)	0 (0.0%)	2.8
	TN	Female adult	10	2 (20.0%)	1 (10.0%)	7 (70.0%)	0 (0.0%)	2.7
	TW	Female adult	10	0 (0.0%)	0 (0.0%)	60 (60%)	40 (40%)	3.4
	MG	Female adult	2	0 (0.0%)	0 (0.0%)	2 (100%)	0 (0.0%)	2.0
	TD	Female adult	2	2 (100%)	0 (0.0%)	0 (0%)	0 (0.0%)	2.0
	BY	Female adult	3	2 (66.7%)	0 (0.0%)	1 (33.3%)	0 (0.0%)	2.3
	KA	Male blackback	7	0 (0.0%)	0 (0.0%)	7 (0.0%)	0 (0.0%)	3.0
	MK	Male silverback	12	0 (0.0%)	2 (16.7%)	10 (83.3%)	0 (0.0%)	2.8
	RC	Male silverback	3	0 (0.0%)	0 (0.0%)	3 (100%)	0 (0.0%)	3.0
Pan troglodytes ssp.	KB	Female adult	7	2 (28.6%)	1 (14.3%)	4 (57.2%)	0 (0.0%)	2.6
	MI	Female adult	12	1 (8.3%)	5 (41.6%)	6 (50.0%)	0 (0.0%)	2.5
	KY	Female adult	6	0 (0.0%)	2 (33.3%)	4 (66%)	0 (0.0%)	2.7
Vertical descent								
Gorilla beringei b.	JN	Female adult	6	1 (16.7%)	2 (33.3%)	3 (50.0%)	0 (0.0%)	2.4
	ST	Female adult	6	4 (66.7%)	1 (16.7%)	1 (16.7%)	0 (0.0%)	2.4
	TW	Female adult	3	0 (0.0%)	2 (66.7%)	1 (33.3%)	0 (0%)	2.3
	MG	Female adult	8	5 (62.5%)	0 (0.0%)	3 (37.5%)	0 (0%)	2.4
Pan troglodytes ssp.	RI	Female adult	8	3 (37.5%)	2 (25%)	3 (37.5%)	0 (0%)	2.4
	KB	Female adult	7	0 (0%)	3 (42.8%)	4 (57.2%)	0 (0%)	2.6
	MI	Female adult	16	1 (6.3%)	5 (31.3%)	10 (62.5%)	0 (0%)	2.6
	KY	Female adult	5	0 (0%)	0 (0%)	5 (100%)	0 (0%)	3.0
	JU	Female adult	8	5 (62.5%)	0 (0%)	3 (37.5%)	0 (0%)	2.4
	UN	Female adult	5	2 (40%)	1 (20%)	2 (40%)	0 (0%)	2.4
	TA	Male adult	4	2 (50%)	2 (50%)	0 (0%)	0 (0%)	2
	CO	Male adult	2	0 (0%)	2 (100%)	0 (0%)	0 (0%)	2

D = support by a diagonal pair of limbs; *L* = support by an ipsilateral pair of limbs; *T* = support by any combination of three limbs; *Q* = support by all four limb.

used mainly three limbs as body support during vertical ascent (Table 7). This is consistent with the climbing strategy documented in western lowland gorillas in captivity, in which they also used mainly three-limb support and mostly engaged in trot or DSDC gaits (Isler, 2002). However, our sample size of individuals descending substrates was comparatively small and thus, results on limb support pattern during vertical descent should be interpreted with caution (Table 7). More data on vertical descent climbing will clarify whether mountain gorillas also support their body mainly by three limbs as during vertical ascent.

In contrast, small-bodied chimpanzees used lateral sequence, and particularly diagonal couplet (LSDC) gaits most often, in which the hind foot touches down slightly later than the contralateral forelimb and the body is balanced on two diagonally opposite limbs. This is perhaps not surprising as it has long been acknowledged that either DS or LS gaits can be used in combination with diagonal limb couplet support patterns (e.g., Muybridge, 1887; Hildebrand, 1966, 1976). The diagonal couplet support enables primates to arrange the limbs as a widely splayed diagonal bipod and allows the center of mass to be contained within the base of support, reducing the risk of slipping and falling off the support during climbing (Cartmill *et al.*, 2002). Similar to our sample of chimpanzees, bonobos also used LS gaits more often than lowland gorillas during rope climbing but used two-limb, rather than three-limb, supports (Isler, 2002). Bonobo pole climbing showed a similar pattern to our study with a more frequent use of LS gaits than DS gaits (Schoonaert *et al.*, 2016). However, the variation in footfall sequences between gorillas and chimpanzees suggests that hypotheses (i.e., limb interference avoiding: Hildebrand, 1980; stability: Cartmill *et al.*, 2002; energetic benefit: Griffin, Main & Farley, 2004) of primate-specific DS gait adaptations for arboreal locomotion require further investigation. A computer simulation of chimpanzee quadrupedal locomotion found a preference for LS/lateral couplet gaits (Sellers *et al.*, 2013). Furthermore, Stevens (2006) showed that primates could readily switch between DS and LS gaits on different arboreal supports likely because of differences in relative stance and swing phase durations. These results suggest that neither DS nor LS gaits offer a particular advantage for stability on horizontal (e.g., Shapiro & Raichlen, 2005; Stevens, 2006, 2008) and potentially vertical supports. This may reflect the need for most primates to use both arboreal and terrestrial substrates and thus, gait flexibility is the key feature of primate locomotion rather than the choice of a specific footfall sequence (Stevens, 2006; Higurashi, Hirasaki & Kumakura, 2009).

Conclusion

This quantitative analysis of temporal gait chacteristics of mountain gorillas and chimpanzees in a natural environment showed that the climbing style can vary within each species. However, further field research and additional laboratory studies on more challenging (i.e., differently sized, less stable, irregular surface) supports are needed to clarify if captive studies are adequately representative for the patterns found in natural environments. Likewise, more work is needed to further characterize arboreal kinematic variability and gait choice among a wider range of primates (body proportions, body size) during vertical ascent and descent.

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Conflict of interest

We declare we have no competing interests.

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