

Gait parameters in vertical climbing of captive, rehabilitant and wild Sumatran orang-utans (*Pongo pygmaeus abelii*)

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Summary

Vertical climbing is central to the locomotor and foraging strategies of the great apes and, indeed, to theories about the evolution of locomotor specialisations of hominoid primates. Nevertheless, its kinematics have yet to be fully evaluated. Here, we present spatio-temporal parameters of 80 climbing sequences containing 560 limb cycles obtained from video recordings of captive, rehabilitant and wild Sumatran orang-utans (*Pongo pygmaeus abelii*). Gait parameters such as cycle duration, duty factor, laterality of footfalls, relative stride length and normalised speed were analysed to identify the influence of body size (through an intraspecific comparison of age/sex classes), the influence of the environment (through an intraspecific comparison of animals living in different habitats) and the influence of morphology (through an interspecific comparison with the climbing characteristics of other primates) on climbing ability in orang-utans. Results show that there are only few differences between the climbing of wild, rehabilitant and captive individuals. Cycle duration is longer and speed is lower for the wild individuals than for other groups due to the complexity of their environment and

lack of familiarity with each substrate, which results in a more cautious gait. Sex/age-related differences in climbing were found to be small, although juveniles generally exhibited a shorter cycle duration and lower duty factor than other groups. The spatio-temporal gait parameters of adult females carrying infants were not found to differ significantly from those for females without an infant, which suggests that climbing kinematics are not affected by the presence of a clinging infant. Extended-elbow vertical climbing is primarily characterised by a higher duty factor than flexed-elbow climbing, indicating that the former is an energetically more demanding form of locomotion. In comparison with other primates, orang-utans exhibit a longer cycle duration, longer strides but lower climbing speed, reflecting a compromise between the demands of a large body mass and extreme joint mobility.

Key words: kinematics, animal locomotion, vertical climbing, spatio-temporal gait parameters, primates, orang-utans, *Pongo pygmaeus abelii*.

Introduction

Vertical climbing, defined as ascent on substrates angled at more than 45° to the horizontal (Hunt et al., 1996), is a key locomotor behaviour in large arboreal primates. Not only does it allow access to food resources situated high in the canopy but it also enables large primates to easily change levels vertically in order to exploit larger, safer substrates for horizontal travel, thus reducing the risk of substrate breakage or falls (Thorpe et al., submitted). However, these benefits are achieved at some cost for animals of large body mass, due to the energy expenditure required to oppose gravity during climbing. Vertical climbing has also played an important role in theories about the evolution of locomotor specialisations of hominoid primates and it has been proposed as being preadaptive for the acquisition of habitual bipedalism in early hominids (e.g. Fleagle et al., 1981; Prost, 1980). Nevertheless, until recently (Isler, 2002a,b, 2003), the kinematic details of

climbing in hominoids have never been adequately evaluated. In the present study, spatio-temporal gait parameters of vertical climbing in Sumatran orang-utans (*Pongo pygmaeus abelii*) are reported, with the aim of elucidating the characteristics of climbing in animals of different body size, but of geometrically similar body build, living in different habitats.

Orang-utans are the only extant great apes in Asia. They live in Sumatran and Bornean rainforests and are seriously threatened by extinction through habitat destruction. The two subspecies *Pongo pygmaeus pygmaeus* (from Borneo) and *Pongo pygmaeus abelii* (from Sumatra) differ in general appearance, behaviour and biochemistry (for an overview, see Delgado and van Schaik, 2000). No differences in postcranial morphology between the two subspecies have been documented, but they may exist. Orang-utans exhibit pronounced sexual dimorphism in body mass (adult females

weighing 35 kg and males 78 kg on average; Smith and Jungers, 1997), which might be expected to influence vertical climbing behaviour. They possess exceptionally long arms, whereas their hindlimbs are relatively short (Jungers and Susman, 1984). Both fore- and hindlimb joints are very flexible (Morbeck and Zihlman, 1988; Tuttle and Cortright, 1988). Whilst their locomotor behaviour is best characterized as orthograde suspension (after Hunt et al., 1996), which incorporates clamber, brachiation and orthograde bridging behaviour (Cant, 1987; MacKinnon, 1974; Sugardjito, 1982; Sugardjito and van Hooff, 1986), vertical climbing accounts for approximately a quarter of all observed locomotion (Cant, 1987; Thorpe et al., submitted), although note that Sugardjito and van Hooff (1986) recorded smaller frequencies. Quadrupedal walking is less frequent, and leaping is rarely performed. Vertical climbing has been observed to occur with approximately the same frequency in adult females, adult males and adolescents (Thorpe et al., submitted), ranging from 22% to 26% of total locomotor bouts. These results reveal that classic predictions based on geometric scaling, which imply that large animals should climb less than smaller ones, are not borne out by orang-utan behaviour. However, it is possible that the lack of size-related differences in climbing behaviour may be partly explained by the presence of size-related, kinematically distinct, climbing strategies. Consequently, to obtain valuable results for the kinematics of vertical climbing in orang-utans that can be used for comparisons with the locomotion of other species, it is necessary to start by investigating the extent of intraspecific variation.

During human walking on level substrates, gait parameters such as cycle duration, the duration of the support phase relative to cycle duration, stride length or speed are correlated with the costs of locomotion relative to the subject's physical ability or fitness (reviewed, for example, by Whittle, 1996). For example, walking gaits of very young or elderly humans are characterised by high duty factors, short strides and slow speed (Murray et al., 1969; Sutherland et al., 1988). For nonhuman primates, Isler (2002a) has identified key differences in the climbing performance of gorillas and bonobos associated with the age and sex of the individuals by comparing similar gait parameters. She showed that the vertical climbing behaviour of an adult male gorilla was characterised by higher duty factors, relatively shorter strides and more variable footfall patterns compared with adult female or juvenile gorillas. These results showed that the adult male climbed with apparent difficulty due to his large body mass and indicate that heavier animals will, in general, exhibit a prolonged support phase or higher duty factor, as well as a decrease in stride length relative to leg length, reflecting the higher energy expenditure relative to muscular strength that is predicted by theoretical considerations (Cartmill, 1972, 1974; Cartmill and Milton, 1977; Taylor et al., 1972). In the present study, we investigate whether differences in gait parameters can also be observed between adult and juvenile orang-utans or between adult males and females, which differ significantly in body mass, although

their limb lengths differ to a lesser extent than does body mass. In humans, carrying a child also has a significant influence on locomotion costs (Kramer, 1998). Similarly, in female orang-utans, the additional load of a clinging infant might be expected to reduce climbing speed and increase the duty factor to compensate for the increased mass. Thus, we compare the climbing performance of females with a clinging infant with that of females without an infant.

The second focus of this study is to identify the influence of different environments on vertical climbing performance of orang-utans. Due to their large body size, arboreal lifestyle and extensive home range, the confined living quarters of captive orang-utans present a strongly contrasting environment to that of primary rainforest. Motivation to climb is also reduced, as zoo animals are generally not dependent on locomotion for foraging. Cage furniture, which is often rigid and of uniform type and diameter, differs substantially from the compliant and complex nature of the rainforest. This results in the captive habitat providing a less challenging climbing environment than that experienced by wild individuals. Captive animals become so familiar with their enclosure that one might expect climbing performance to be characterised by increased speed and reduced duty factors in comparison with their wild counterparts, who may be expected to move more slowly due to the unknown or unstable nature of their substrates. On the other hand, captive orang-utans generally exhibit a far larger proportion of terrestrial locomotion than do their arboreal counterparts, which places very different biomechanical demands on the musculo-skeletal system. During terrestrial locomotion, compressive weight is distributed consistently between the four limbs, and limited mobility is required at the joints. By contrast, locomotion in an arboreal environment requires muscles capable of generating greater stresses, both in compression and tension, in order to oppose gravity during climbing and to cope with uneven and varied distribution of body mass on the weight-bearing limbs. Forces also need to be exerted in a wide range of joint positions, requiring full mobility at the joints. Sarmiento (1985) has argued that this results in the development of skeletal proportions of captive adult orang-utans that are detrimental to climbing due to adaptations to terrestrial quadrupedalism and consequently may result in less-confident climbing than that exhibited by wild individuals and thus higher duty factors and/or reduced speed. Rehabilitant orang-utans have also generally been kept in confined living conditions (although often more restrictive than those of zoos) and may not have received adequate nutrition, potentially hampering musculo-skeletal development. After a period of rehabilitation they are reintroduced back into a wild environment. Comparing the climbing performance of these animals with those of wild and captive orang-utans will shed light on the ability of the musculo-skeletal system to readapt to a locomotor repertoire that includes a significant climbing component from one dominated by terrestriality.

Thus, in this study, we present data on vertical climbing obtained both from captive individuals and from wild and

rehabilitant orang-utans in Sumatra, permitting a comparison of the gait parameters of wild, rehabilitant and captive animals of all age and sex categories. To our knowledge, this is the first quantitative comparison of locomotor kinematics in wild and captive primates. Additionally, in an interspecific comparison with the vertical climbing gait parameters of other hominoids (Isler, 2002a,b, 2003), we investigate the influence of the specialised locomotor anatomy of orang-utans on their climbing style.

Materials and methods

Subjects

Subject details and the numbers of analysed climbing sequences for all captive, rehabilitant and wild individuals are listed in Table 1. All climbing sequences were recorded with a digital video camera (Sony DCR-TRV 900E) at a speed of 50 frames s⁻¹. Observations on captive animals were made at the Durrell Wildlife Conservation Trust (Jersey Zoo), where five Sumatran orang-utans (*Pongo pygmaeus abelii* Lesson 1827) climbed on vertical rubber ropes (4–7 m in length and 5 cm in diameter) that were fixed to the ground. The elasticity of these ropes can be compared with that of lianas in natural surroundings. Male A was 16 years old, weighed 50 kg and had been castrated for medical reasons in early adolescence, consequently showing no secondary sex features. For comparison with the rehabilitant and wild orang-utans in Sumatra, he is classified as a subadult. Juvenile D is the son of

female B, and juvenile E is the son of female C. The animals are housed in a large enclosure that includes a 7.6 m-high indoor facility and two spacious islands of approximately 2350 m² (Mallinson and Carroll, 1995; Mallinson et al., 1994). A total of 31 climbing sequences, containing 184 limb cycles, were analysed.

Rehabilitant and wild orang-utans were observed at Bukit Lawang rehabilitation centre and Ketambe Research Station, respectively, in the Leuser Ecosystem, Sumatra, Indonesia. The Ketambe area is described in detail by Rijksen (1978) and van Schaik and Mirmanto (1985). In Bukit Lawang, all records were taken at a feeding platform at which rehabilitants, who roamed freely through the forest, would congregate twice a day for food supplements (bananas and milk). Consequently, calibration of the locomotor sequences was possible. Records of wild orang-utans were obtained throughout the Ketambe research area and, as a result, it was not possible to calibrate these sequences.

Types of vertical climbing

In the literature, two types of vertical climbing are described (Hunt et al., 1996): (1) when climbing large-diameter substrates, such as tree trunks, the elbows are always more or less extended ('extended-elbow vertical climbing'); (2) 'flexed-elbow vertical climbing' is used when the animal is climbing on a substrate of small diameter, such as a rope, liana or thin tree, with flexion of the elbow helping to elevate the body. The occurrence of these two types is

Table 1. Studied individuals

Individual	Sex	Age group	Age	Lower leg length ^a (cm)	Origin	Name	No. of climbing sequences
Captive ^b							
A	Male	Subadult	16 years	25	Jersey	Mokko	8
B	Female	Adult	~35 years	25	Wild born	Gina	6
C	Female	Adult	24 years	25	Bristol	Julitta	3
D	Male	Juvenile	4 years 2 months	16	Jersey	Kluet	13
E	Male	Juvenile	3 years 7 months	16	Jersey	Wirawan	1
Wild/rehabilitant ^c							
F	Male	Subadult		25	Rehabilitant		4
G	Female	Adult		25	Rehabilitant	Mina	2
H	Female	Adult		25	Rehabilitant		7
I	Female	Adult		25	Rehabilitant		2
J ^d	Females	Adult		25	Rehabilitant		7
K	Female	Adult		25	Rehabilitant		6
L ^d	Females	Adult		25	Rehabilitant		3
M	Male	Adolescent		23	Rehabilitant	Darwin	6
N	Indet	Juvenile		16	Rehabilitant		2
O	Male	Adult		27	Wild (Bukit Lawang)		3
P	Male	Subadult		25	Wild (Bukit Lawang)		2
Q	Female	Adult	24 years	25	Wild (Ketambe)	Ans	5

^aLower leg lengths (distance from knee to heel) were estimated as described in the text.

^bIndividuals A–E were observed at Jersey Zoo in September 1999.

^cIndividuals F–Q were observed at either Bukit Lawang rehabilitation centre or Ketambe Research Station in June–October 1999.

^dThe results were pooled from several animals that could not be recognised individually.

influenced by the animal's size, as flexed-elbow climbing requires the individual to grip the substrate with one hand. In adult orang-utans, a substrate diameter larger than 20 cm is likely to evoke extended-elbow climbing. In total, 47 sequences of flexed-elbow vertical climbing in Sumatra were recorded: 42 in Bukit Lawang (337 limb cycles) and five in Ketambe (47 limb cycles). Additionally, two extended-elbow vertical climbing sequences on a large-diameter tree trunk were recorded in Bukit Lawang (39 limb cycles). Five of the adult females in the rehabilitant and wild groups had dependent infants, and these were generally carried on the mother's hip whilst climbing. Subadult males do not exhibit the characteristics of fully adult males (e.g. cheek flanges) and weigh about the same as adult females (Delgado and van Schaik, 2000).

Analysis of gait parameters

Spatio-temporal gait parameters were analysed from the video sequences. The footfall sequence and spatio-temporal gait parameters such as cycle duration, duty factor and stride length were determined by reviewing the video sequences frame-by-frame using NIH Image 1.62. Statistical analyses were carried out with Statview 5 (SAS Institute Inc.). Cycle duration is defined as the time between two initial contacts with the substrate (or 'touchdowns') by the same extremity. The relative support phase, or duty factor, is the fraction of the cycle duration that a particular limb contacts the substrate. The cycles were classified as symmetrical or asymmetrical according to the timing of the footfalls, following Hildebrand (1967). If the opposing limb's touchdown occurred at between 40% and 60% of the cycle duration, the cycle was considered symmetrical. Symmetrical cycles of the hindlimbs were further classified as being either diagonal sequence or lateral sequence. In a diagonal sequence gait, hindlimb touchdown is followed by the touchdown of the opposite forelimb, whereas in a lateral sequence gait the ipsilateral forelimb follows. The precise timing of the footfalls is expressed as the percentage of the stride interval between the touchdown of the hindlimb and the following touchdown of the ipsilateral forelimb. This yields a further subdivision of the strides into the categories pace, diagonal couplets, single foot, lateral couplets and trot (Hildebrand, 1967). For statistical analysis, the laterality of a hindlimb cycle was calculated as the interval between the touchdown of the hindlimb and the following touchdown of the ipsilateral forelimb in percent of total cycle duration minus 50%. Thus, a diagonal couplets gait results in a low value of laterality, whereas a lateral couplets gait yields high values of laterality.

All climbing sequences were further divided into strides of either the left or the right hindlimb to analyse the type of limb support, according to the scheme proposed by Vilensky and Gankiewicz (1989). Stride length is defined as the distance between two successive points of contact by the same extremity; the reference point is the second joint of the middle finger or toe. To compare the dynamics of climbing of the different-sized animals, stride length and speed were normalised (following Aerts et al., 2000). As a size

determinant of the individual subject, and for calculating relative stride length (s_1), the lower leg length (l = distance from knee to heel) was used. Stride length was measured relative to lower leg length at the moment when this segment was held in parallel with, and close to, the climbing substrate. This was usually the case at the end of the support phase. Segment lengths were estimated from the video recordings for the captive subjects and most of the rehabilitated subjects. They correspond well with data on mean long bone lengths reported in the literature for the corresponding sex and age groups (e.g. Shea, 1981), which were thus used for all individuals (Table 1). Climbing speed (v) was then calculated by dividing the stride length by the cycle duration (cd). The square root of the Froude number (F) is used for normalising climbing speed to a dimensionless parameter (see Alexander, 1992):

$$F = \frac{v^2}{gl} = \frac{s_1^2 l}{gcd^2}$$

where $g=9.81 \text{ m s}^{-2}$. Theoretically, a longer cycle duration (or shorter cadence) could be compensated for by an increase in

Table 2. Scheffé's post-hoc tests for factorial ANOVA of vertical climbing within sex/age groups

	Cycle duration	Duty factor	Laterality	Rel. stride length	Normalised speed
Females					
B, C	ns	*	ns	*	***
B, K	ns	ns	ns	ns	ns
B, L	ns	ns	*	*	***
C, K	ns	ns	ns	ns	ns
C, L	ns	ns	ns	ns	ns
K, L	ns	ns	ns	ns	ns
Mothers					
G, H	ns	ns	ns	ns	ns
G, I	ns	ns	ns	ns	ns
G, J	ns	ns	ns	ns	ns
H, I	ns	ns	ns	ns	**
H, J	ns	ns	ns	ns	*
I, J	ns	ns	ns	ns	ns
Subadult males					
A, F	ns	ns	ns	ns	ns
A, P	ns	ns	ns	ns	ns
F, P	ns	ns	ns	ns	ns
Juveniles					
D, E	ns	ns	ns	ns	*
D, N	ns	ns	ns	ns	ns
E, N	ns	ns	ns	ns	ns
Wild individuals (O, P and Q)					
O, P	ns	ns	ns	ns	**
O, Q	ns	ns	ns	*	***
P, Q	**	ns	ns	***	***

Asterisks mark statistically significant differences between individuals: * $P<0.05$; ** $P<0.01$; *** $P<0.001$; ns, not significant.

stride length to obtain an equivalent climbing speed. Therefore, all three parameters are reported here.

Statistics

For statistical comparison of the gait parameters in different sex/age categories, the individuals were classified into the following groups: carrying adult females ('mothers'), non-carrying adult females, adult males, subadult males, adolescent males and juveniles. Being the only individual from Ketambe (and therefore the only wild individual in a truly wild environment), the results for adult mother Q are presented separately to those of the other individuals. For comparisons between localities, results for juveniles and adolescents were omitted from the captive and rehabilitant populations, as they were not represented in the wild group. Significance of intraspecific differences in the gait parameters was tested with factorial analysis of variance (ANOVA) and Scheffé's *post-hoc* tests. Differences in gait parameters between fore- and hindlimbs were tested with unpaired Student's *t*-tests. Relationships between the relative stride length and normalised speed were analysed with least-squares regressions on log₁₀-transformed data. Intraspecific differences of speed modulation were tested using analysis of covariance (ANCOVA), with normalised speed as a covariate.

Results

Flexed-elbow vertical climbing

To determine whether the grouping of individuals was reasonable, individuals of each sex/age group were compared with a factorial ANOVA and Scheffé's *post-hoc* tests (Table 2). Reasonable consistency was found within each sex/age group, although some significant differences between individuals for the speed of travel were found and there was some individual variation within the adult female group. Differences in the adult female group appear to be largely associated with captive adult female B. As our wild sample consisted of only three individuals, and two of these were sampled within the vicinity of the feeding platform at Bukit Lawang, Table 2 also tests for compatibility within the wild group. Some individual variation is apparent, primarily in speed and stride length.

Significant differences in gait parameters were also found between sex/age and locality (wild, rehabilitant, captive) categories. These are summarised in Table 3 and discussed below.

Mean cycle duration and duty factor of fore- and hindlimbs during vertical climbing of Sumatran orang-utans are shown in Table 4 and Fig. 1A,B. In most individuals, neither the cycle duration nor the duty factor differed significantly between fore-

Table 3. Scheffé's *post-hoc* tests for factorial ANOVA of vertical climbing between sex/age and locality groups

	Cycle duration	Duty factor	Laterality	Rel. stride length	Normalised speed
Between sex/age groups					
Wild mother (Q) vs adult male (O)	ns	ns	ns	ns	ns
vs juveniles	***	ns	ns	**	***
vs adolescent male (M)	***	ns	ns	ns	***
vs subadult males	***	ns	ns	**	***
vs adult females	***	ns	**	ns	***
vs mothers	***	ns	*	ns	***
Adult male (O) vs juveniles	***	ns	ns	ns	***
vs adolescent male (M)	ns	ns	ns	ns	ns
vs subadult males	*	ns	ns	ns	ns
vs adult females	*	ns	ns	ns	ns
vs mothers	**	ns	ns	ns	ns
Juveniles vs adolescent male (M)	***	ns	ns	ns	*
vs subadult males	***	ns	ns	ns	ns
vs adult females	***	ns	**	***	***
vs mothers	**	ns	*	ns	*
Adolescent male (M) vs subadult males	ns	ns	ns	ns	ns
vs adult females	ns	ns	ns	*	ns
vs mothers	ns	ns	ns	ns	ns
Subadult males vs adult females	ns	ns	ns	***	*
vs mothers	ns	ns	ns	ns	ns
Mothers vs adult females	ns	ns	ns	*	*
Between localities (subadult and adult males, adult females and mothers only)					
Captive vs rehabilitant	ns	ns	ns	**	***
Captive vs wild	***	ns	***	ns	***
Rehabilitant vs wild	***	ns	**	ns	***

Asterisks mark statistically significant differences between groups: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant.

and hindlimbs. The duty factor was not significantly different between sex/age or locality groups (ANOVA, Scheffé's *post-hoc* tests; Table 3). The cycle duration, however, is significantly shorter in juveniles than in all other groups. The wild adult female (Q) and wild adult male (O) exhibit similar cycle durations, and these are significantly longer than all other groups [except the adolescent male (M), who differs significantly from Q but not from O]. Accordingly, wild orang-utans exhibit a significantly longer cycle duration than both captives or rehabilitants.

In 78.4% of all hindlimb cycles, the footfalls of the hindlimbs were symmetrical according to the definition of

Hildebrand (1967). Most individuals preferred a diagonal sequence/diagonal couplets or single foot gait (Table 5). Lateral sequence gaits occurred very rarely, but, on occasion, lateral couplets were exhibited, especially by juvenile D in Jersey Zoo and the wild mother (Q). Wild individuals appear to exhibit a more diverse range of gaits than do rehabilitants or captives, although this is largely influenced by the results for wild mother Q.

Table 6 shows the types of limb support that the orang-utans used during vertical climbing. The body was mostly supported by three limbs, although two-limb support phases were also observed relatively frequently, with diagonal pairs being the

Table 4. Cycle duration and duty factor of vertical climbing in *Pongo pygmaeus abelii*

Individual	Sex/age	N (hind/fore)	Cycle duration		Duty factor	
			Hind	Fore	Hind	Fore
Individuals						
Jersey Zoo						
A	Male subadult	16/17	2.57 (0.80)	2.88 (1.12)	0.75 (0.05)	0.75 (0.07)
B	Female adult	15/23	1.86 (0.43)	1.97 (0.53)	0.67 (0.07)	0.72 (0.07)*
C	Female adult	11/10	2.70 (0.64)	2.58 (0.37)	0.77 (0.08)	0.75 (0.05)
D	Male juvenile	37/45	1.52 (0.38)	1.61 (0.32)	0.69 (0.08)	0.68 (0.09)
E	Male juvenile	5/5	1.97 (0.33)	1.89 (0.18)	0.70 (0.06)	0.70 (0.04)
Sumatra						
F	Male subadult	23/20	2.35 (0.49)	2.43 (0.49)	0.71 (0.07)	0.66 (0.12)
G+	Female adult	11/12	2.82 (0.85)	2.84 (0.98)	0.74 (0.07)	0.69 (0.10)
H+	Female adult	28/22	2.38 (0.65)	2.68 (0.42)	0.73 (0.11)	0.73 (0.08)
I+	Female adult	6/7	1.88 (0.67)	2.45 (0.29)	0.64 (0.05)	0.69 (0.09)
J+	Female adult	22/22	2.36 (0.54)	2.31 (0.53)	0.68 (0.10)	0.68 (0.08)
K	Female adult	10/9	2.20 (0.41)	2.32 (0.37)	0.74 (0.05)	0.77 (0.05)
L	Female adult	17/16	2.39 (1.14)	2.77 (1.00)	0.74 (0.06)	0.72 (0.09)
M	Male adolescent	31/28	2.46 (0.87)	2.46 (0.83)	0.71 (0.11)	0.72 (0.11)
N	Indet. juvenile	8/7	1.72 (0.69)	1.97 (0.43)	0.64 (0.04)	0.66 (0.06)
O	Male adult	11/11	3.50 (0.86)	3.25 (0.69)	0.76 (0.07)	0.75 (0.05)
P	Male subadult	9/7	2.44 (0.37)	3.25 (0.64)**	0.74 (0.06)	0.76 (0.07)
Q	Female adult	5/5	4.56 (0.74)	4.88 (0.77)	0.76 (0.06)	0.71 (0.08)
Q+	Female adult	17/20	4.32 (1.33)	4.09 (1.00)	0.75 (0.11)	0.76 (0.10)
Extended-elbow vertical climbing						
H+	Female adult	9/8	2.37 (0.26)	2.32 (0.25)	0.79 (0.06)	0.79 (0.04)
K	Female adult	11/11	2.32 (0.18)	2.33 (0.24)	0.80 (0.04)	0.78 (0.09)
Groups						
Flexed-elbow vertical climbing						
Adult females (B, C, K, L)		53/58	2.27 (0.81)	2.35 (0.73)	0.73 (0.07)	0.73 (0.07)
Mothers (G+, H+, I+, J+)		67/63	2.40 (0.68)	2.56 (0.61)	0.71 (0.10)	0.70 (0.09)
Wild mother (Q)		22/25	4.37 (1.21)	4.25 (1.00)	0.75 (0.10)	0.74 (0.10)
Adult male (O)		11/11	3.50 (0.86)	3.25 (0.69)	0.76 (0.07)	0.75 (0.05)
Subadult males (A, F, P)		48/44	2.44 (0.59)	2.73 (0.85)	0.73 (0.06)	0.71 (0.10)
Adolescent male (M)		31/28	2.46 (0.87)	2.46 (0.83)	0.71 (0.11)	0.72 (0.11)
Juveniles (D, E, N)		50/57	1.60 (0.45)	1.68 (0.35)	0.68 (0.08)	0.68 (0.08)
Captive (A, B, C)		42/50	2.35 (0.73)	2.40 (0.86)	0.73 (0.08)	0.74 (0.06)
Rehabilitant (F, G, H, I, J, K, L)		117/108	2.37 (0.71)	2.55 (0.65)	0.72 (0.08)	0.70 (0.09)
Wild (O, P, Q)		42/43	3.73 (1.25)	3.83 (0.99)	0.75 (0.08)	0.75 (0.08)
Extended-elbow vertical climbing						
Adult females (H+, K)		20/19	2.34 (0.22)	2.32 (0.24)	0.79 (0.05)	0.79 (0.06)

+ signifies an adult female carrying an infant. Values represent means, with s.d. given in parentheses. Asterisks mark statistically significant differences between fore- and hindlimbs: * $P < 0.05$; ** $P < 0.01$.

preferred support base in all subjects, except for the juvenile N and the adult female Q, who exhibited a greater percentage of lateral pairs. Thus, the index of laterality of limb support was higher in juveniles and the wild female (Q) than in the other groups (Fig. 1C). Support by only one limb, by both forelimbs or by both hindlimbs was extremely rare. The mean number of limbs used for support was also calculated for each subject (see Table 6). It was generally lower for juveniles than for adults, but this did not result in significant differences

between the age and sex groups. In comparison to rehabilitants and captives, wild individuals had a slightly higher mean number of supporting limbs, but again this result was not significant.

Mean relative hindlimb stride length and normalised speed of vertical climbing in orang-utans are shown in Table 7 and Fig. 1D,E. To account for body size differences between the animals studied, the gait parameters were normalised using lower leg length as an individual size determinant. Normalised

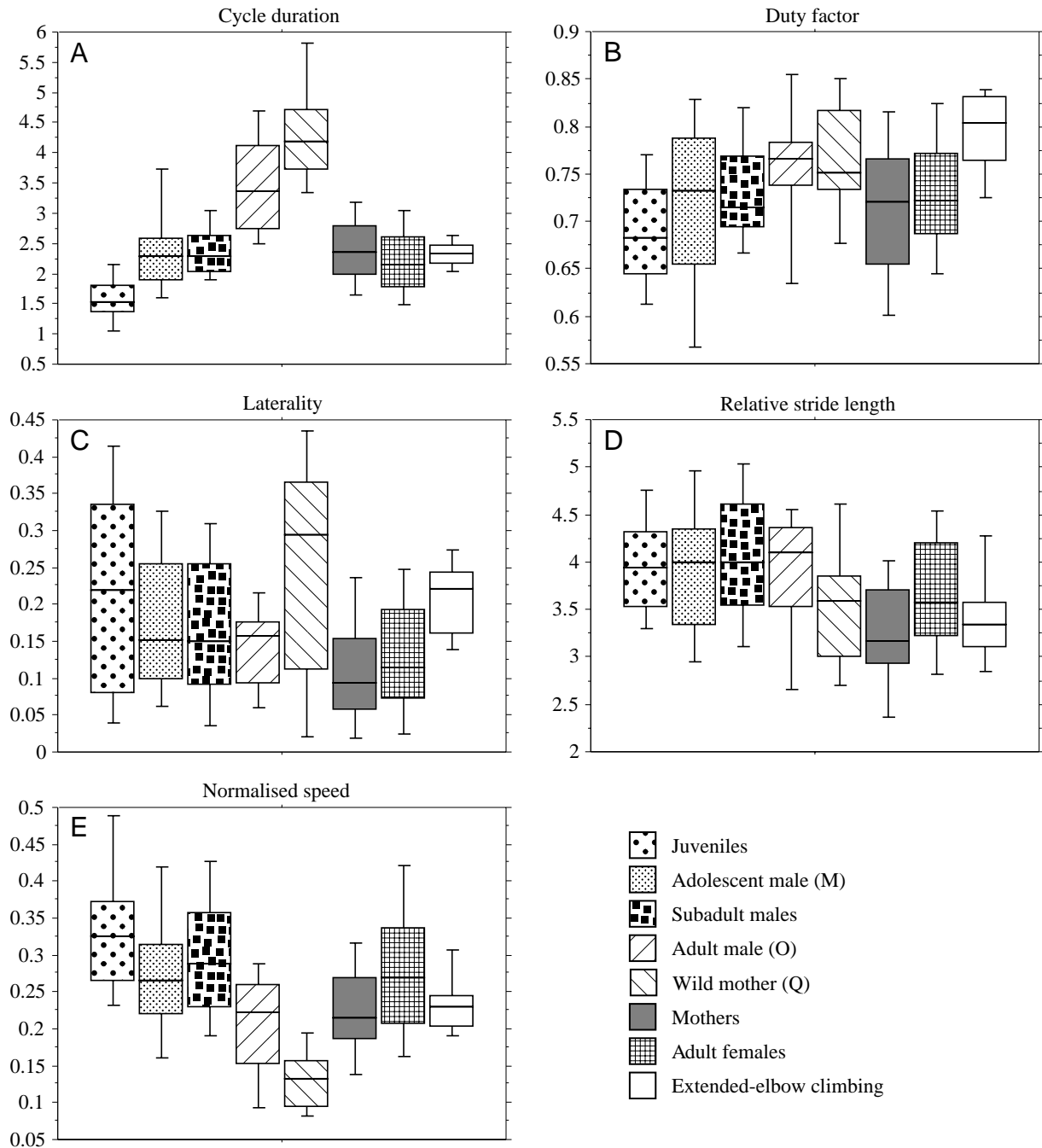


Fig. 1. Box plot of hindlimb cycle duration (A), duty factor (B), laterality of footfalls (C), relative stride length (D) and normalised speed (E) in vertically climbing orang-utans. For each sex/age group, the median value is presented as a straight line, surrounded by a box representing ± 1 quartile, and the bars represent ± 90 th percentiles.

speed of the wild mother (Q) is significantly lower than that of the other groups, while juveniles climb faster than adult females, mothers and the adult male (Factorial ANOVA, Scheffé's *post-hoc* test; see Table 3). Climbing speed is higher in captives than in rehabilitants, and higher in rehabilitants than in wild individuals, although the latter result is mainly caused by the very slow climbing speed of the wild adult mother (Q). The relative stride length is shorter in adult females than in juveniles, the adolescent male (M) and the subadult males (Table 3). Captive orang-utans exhibit significantly longer strides than rehabilitants.

The relationships between log₁₀-transformed hindlimb stride

length and speed during vertical climbing are shown in Table 8 and Fig. 2. All gait parameters are normalised as described above. The slopes of the linear regression equations are significantly different from zero in most groups, with the exception of the wild mother (Q) and the adolescent male (M) (see Table 8). Intraspecific differences in the regression parameters are tested with an ANCOVA (Table 9), with normalised speed as a covariate. Adult females, the adolescent male and the juveniles do not differ significantly with respect to speed modulation in flexed-elbow vertical climbing. Subadult males take longer strides at the same dimensionless speed than adult females or juveniles. The wild adult male (O)

Table 5. Footfall patterns of symmetrical hindlimb cycles in vertically climbing orang-utans

Individual	Sex/age	N	P	LD	SD	DD	T	DL	SL	LL
Individuals										
Jersey Zoo										
A	Male subadult	8	0	0	0	62.5	37.5	0	0	0
B	Female adult	13	0	0	23.1	30.8	46.2	0	0	0
C	Female adult	9	0	0	11.1	66.7	22.2	0	0	0
D	Male juvenile	26	7.7	38.5	19.2	23.1	7.7	3.8	0	0
E	Male juvenile	5	0	0	20.0	80.0	0	0	0	0
Sumatra										
F	Male subadult	16	0	0	43.8	50.0	0	6.3	0	0
G+	Female adult	5	0	0	0	60.0	40.0	0	0	0
H+	Female adult	22	0	0	22.7	59.1	18.2	0	0	0
I+	Female adult	4	0	25.0	0	50.0	25.0	0	0	0
J+	Female adult	13	7.7	7.7	0	53.8	30.8	0	0	0
K	Female adult	8	0	5.9	52.9	41.2	0	0	0	0
L	Female adult	11	0	0	36.4	27.3	18.2	9.1	0	9.1
M	Male adolescent	13	0	0	30.8	53.8	15.4	0	0	0
N	Indet. juvenile	5	0	0	80.0	0	0	0	0	20.0
O	Male adult	9	0	0	22.2	66.7	11.1	0	0	0
P	Male subadult	3	0	33.3	0	33.3	33.3	0	0	0
Q	Female adult	2	0	50.0	0	0	0	0	0	50.0
Q+	Female adult	7	14.3	28.6	28.6	14.3	14.3	0	0	0
Extended-elbow vertical climbing										
H+	Female adult	10	0	0	60	40	0	0	0	0
K	Female adult	9	0	11.1	77.8	11.1	0	0	0	0
Groups										
Flexed-elbow vertical climbing										
Adult females (B, C, K, L)		41	0	0	24.4	46.3	24.4	2.4	0	2.4
Mothers (G+, H+, I+, J+)		45	2.2	4.4	11.1	55.6	26.7	0	0	0
Wild mother (Q)		9	11.1	33.3	22.2	11.1	11.1	0	0	11.1
Adult male (O)		9	0	0	22.2	66.7	11.1	0	0	0
Subadult males (A, F, P)		27	0	3.7	25.9	51.9	14.8	3.7	0	0
Adolescent male (M)		13	0	0	30.8	53.8	15.4	0	0	0
Juveniles (D, E, N)		36	5.6	27.8	27.8	27.8	5.6	2.8	0	2.8
Captive (A, B, C)		30	0	0	13.3	50.0	36.7	0	0	0
Rehabilitant (F, G, H, I, J, K, L)		80	1.3	2.5	22.5	52.5	17.5	2.5	0	1.3
Wild (O, P, Q)		21	4.8	19.0	19.0	38.1	14.3	0	0	4.8
Extended-elbow vertical climbing										
Adult females (H+, K)		19	9	5.3	68.4	26.3	0	0	0	0

P, pace; LD, lateral couplets/diagonal sequence; SD, single foot/diagonal sequence; DD, diagonal couplets/diagonal sequence; T, trot; DL, diagonal couplets/lateral sequence; SL, single foot/lateral sequence; LL, lateral couplets/lateral sequence. + signifies an adult female carrying an infant. The most frequent footfall pattern for each individual/group is highlighted in bold, where appropriate.

takes even longer strides at the same dimensionless speed than subadult males. Between females that carry an infant and females that climb alone, there is no significant difference in speed modulation. The wild adult mother (Q), however, takes longer strides at the same dimensionless speed than other adult females.

Extended-elbow vertical climbing

At Bukit Lawang, two sequences of extended-elbow vertical climbing on large-diameter tree trunks were recorded, one of

a mother carrying an infant (H+) and one of an unaccompanied adult female (K). When compared with the flexed-elbow vertical climbing sequences of adult females (both carrying an infant and alone) at Bukit Lawang, the following results were apparent: the cycle duration was not significantly different between flexed-elbow and extended-elbow vertical climbing (unpaired *t*-test, $P=0.240$). The duty factor, however, was higher in extended-elbow vertical climbing ($78.9\pm 5.7\%$ vs $71.4\pm 8.7\%$; unpaired *t*-test, $P<0.001$). Accordingly, the mean number of limbs used for support was also higher for extended-

Table 6. Limb support in % of cycle duration in vertically climbing orang-utans

Individual	Age/sex	<i>N</i>	Unipod.	Biped.	Biman.	Diag. pair	Lateral pair	Triplet	Quadrupedal	Mean no. of supp. limbs
Individuals										
Jersey Zoo										
A	Male subadult	7	0	0	0	30.0	0.3	44.1	25.6	2.95
B	Female adult	8	0	0	0	42.0	3.1	38.0	16.8	2.71
C	Female adult	6	0	0	0	25.6	4.3	41.4	28.7	2.99
D	Male juvenile	16	0.2	0	0	22.8	19.6	42.9	14.6	2.72
E	Male juvenile	3	0	0	0	20	8.9	63.1	7.9	2.79
Sumatra										
F	Male subadult	12	0	0	0	32.8	4.5	49.5	13.1	2.76
G+	Female adult	6	0	0	2.1	31.8	3	41.3	23.9	2.93
H+	Female adult	13	0	0	0	21.7	1.7	53.0	23.6	3.00
I+	Female adult	3	0	0	0	29.3	5.9	54.6	10.2	2.75
J+	Female adult	10	2.5	0	0	30.8	7.1	44.4	15.2	2.72
K	Female adult	5	0	0	0	23.2	5.2	56.1	15.4	2.87
L	Female adult	7	0.7	0	0	26.0	6.7	46.5	20.1	2.86
M	Male adolescent	13	0.8	0.2	0	29.3	2.5	51.0	16.4	2.83
N	Indet. juvenile	4	4.9	0	0	21.0	24.1	41.3	8.6	2.53
O	Male adult	6	0	0	0	16.1	1.2	66.9	15.9	2.99
P	Male subadult	4	0	0	0	20.6	3.8	52.8	22.8	2.98
Q	Female adult	2	0	0	0	0	13.8	71.2	15.1	3.02
Q+	Female adult	7	0	0	0	11.2	9.0	62.1	17.6	2.97
Extended-elbow vertical climbing										
H+	Female adult	6	0	0	0	8	0.8	66.2	24.9	3.16
K	Female adult	5	0	0	0	3.3	1.9	72.1	22.7	3.18
Groups										
Flexed-elbow vertical climbing										
Adult females (B, C, K, L)		27	0.2	0	0	30.1	4.8	45.3	19.6	2.84
Mothers (G+, H+, I+, J+)		32	0.8	0	0.4	27.1	4.1	48.3	19.8	2.88
Wild mother (Q)		9	0	0	0	8.7	10.1	64.1	17.0	2.98
Adult male (O)		6	0	0	0	16.1	1.2	66.9	15.9	2.99
Subadult males (A, F, P)		23	0	0	0	29.9	3.1	48.5	18.6	2.86
Adolescent male (M)		13	0.8	0.2	0	29.3	2.5	51.0	16.4	2.83
Juveniles (D, E, N)		23	1.0	0	0	22.1	19.0	45.3	12.7	2.70
Captive (A, B, C)		21	0	0	0	33.3	2.5	41.0	23.1	2.87
Rehabilitant (F, G, H, I, J, K, L)		57	0.5	0	0.2	27.8	4.6	49.3	17.8	2.85
Wild (O, P, Q)		19	0	0	0	13.6	6.0	62.6	17.9	2.98
Extended-elbow vertical climbing										
Adult females (H+, K)		11	0	0	0	5.9	1.3	68.9	23.9	3.17

Support types are classified according to Vilensky and Gankiewicz (1989). Quadrupedal = support by all four limbs; triplet = support by any combination of three limbs; Diag. pair = support by either combination of diagonal limbs; Lateral pair = support by either pair of ipsilateral limbs; Unipod. = support by any single limb; Biped. = support by both feet; Biman. = support by both hands. + signifies an adult female carrying an infant. For each individual/group, the most frequent limb combination is highlighted in bold.

elbow vertical climbing (see Table 6). The preferred gait pattern was diagonal sequence, as in flexed-elbow climbing. Trot did not occur, but a single limb gait was used more often than diagonal couplets. The laterality of the footfall patterns was therefore higher (unpaired *t*-test, $P=0.001$), although lateral couplets gaits were equally rare in both flexed- and extended-elbow vertical climbing.

The relative stride length, normalised speed and speed modulation were not significantly different between extended-elbow and flexed-elbow vertical climbing (ANCOVA; Table 9; Fig. 2B).

Infant-carrying

The flexed-elbow climbing characteristics of female *Pongo p. abelii* carrying an infant at Bukit Lawang were compared with non-carrying adult females at the same site. Cycle duration was not significantly different between these two groups (unpaired *t*-test, $P=0.899$). Speed modulation was also not different (ANCOVA; Table 9). The duty factor was even higher in adult females climbing alone than in carrying mothers ($73.8\pm 6.6\%$ vs $70.4\pm 9.3\%$; unpaired *t*-test, $P=0.015$). The other significant difference between carrying and non-carrying females was the laterality of hindlimb cycles (unpaired *t*-test, $P=0.042$). Both

Table 7. Hindlimb stride length and speed of vertical climbing in *Pongo pygmaeus abelii*

Individual	Age/sex	N (hind/fore)	Relative stride length		Normalised speed	
			Hind	Fore	Hind	Fore
Individuals						
Jersey Zoo						
A	Male subadult	10/11	4.07 (0.69)	4.20 (0.76)	0.28 (0.06)	0.29 (0.09)
B	Female adult	11/20	4.23 (0.78)	4.16 (0.75)	0.39 (0.14)	0.37 (0.12)
C	Female adult	11/10	3.54 (0.59)	3.51 (0.64)	0.23 (0.09)	0.22 (0.06)
D	Male juvenile	28/32	4.06 (0.60)	4.43 (0.76)*	0.36 (0.13)	0.36 (0.09)
E	Male juvenile	5/5	3.81 (0.46)	3.45 (0.59)	0.25 (0.06)	0.24 (0.06)
Sumatra						
F	Male subadult	15/15	3.95 (0.74)	4.21 (0.42)	0.30 (0.10)	0.30 (0.06)
G+	Female adult	5/6	3.29 (0.65)	3.90 (0.43)	0.22 (0.11)	0.27 (0.08)
H+	Female adult	17/16	3.16 (0.60)	3.13 (0.48)	0.21 (0.05)	0.19 (0.02)
I+	Female adult	5/5	3.64 (0.41)	3.93 (0.29)	0.29 (0.07)	0.27 (0.03)
J+	Female adult	15/15	3.19 (0.68)	3.73 (0.83)	0.23 (0.06)	0.27 (0.08)
K	Female adult	4/6	3.58 (0.29)	4.14 (0.53)	0.30 (0.08)	0.30 (0.10)
L	Female adult	19/17	3.94 (0.85)	3.79 (0.88)	0.26 (0.09)	0.22 (0.06)
M	Male adolescent	21/18	3.94 (0.85)	3.98 (0.88)	0.26 (0.09)	0.26 (0.10)
N	Indet. juvenile	2/1	2.96 (0.60)	5.78	0.23 (0.05)	0.35
O	Male adult	10/8	3.87 (0.72)	4.19 (0.61)	0.20 (0.08)	0.21 (0.04)
P	Male subadult	4/4	4.54 (0.53)	4.75 (0.26)	0.31 (0.09)	0.28 (0.04)
Q	Female adult	3/3	3.90 (0.95)	2.93 (0.62)	0.14 (0.05)	0.10 (0.01)
Q+	Female adult	11/13	3.51 (0.64)	3.32 (0.85)	0.14 (0.06)	0.14 (0.06)
Extended-elbow vertical climbing						
H+	Female adult	10/10	3.59 (0.55)	3.53 (0.43)	0.24 (0.05)	0.24 (0.04)
K	Female adult	7/7	3.13 (0.26)	3.21 (0.24)	0.22 (0.03)	0.23 (0.03)
Groups						
Flexed-elbow vertical climbing						
Adult females (B, C, K, L)		45/53	3.69 (0.80)	3.92 (0.78)	0.29 (0.12)	0.29 (0.11)
Mothers (G+, H+, I+, J+)		42/42	3.24 (0.61)	3.55 (0.68)*	0.23 (0.07)	0.24 (0.07)
Wild mother (Q)		14/16	3.59 (0.70)	3.25 (0.81)	0.14 (0.05)	0.13 (0.05)
Adult male (O)		10/8	3.87 (0.72)	4.19 (0.61)	0.20 (0.08)	0.21 (0.04)
Subadult males (A, F, P)		29/30	4.07 (0.70)	4.28 (0.57)	0.29 (0.09)	0.29 (0.07)
Adolescent male (M)		21/18	3.94 (0.85)	3.98 (0.88)	0.26 (0.09)	0.26 (0.10)
Juveniles (D, E, N)		35/38	3.96 (0.63)	4.34 (0.83)*	0.34 (0.13)	0.34 (0.09)
Captive (A, B, C)		32/41	3.94 (0.73)	4.01 (0.77)	0.30 (0.12)	0.31 (0.11)
Rehabilitant (F, G, H, I, J, K, L)		80/80	3.45 (0.74)	3.77 (0.72)*	0.25 (0.09)	0.25 (0.07)
Wild (O, P, Q)		28/28	3.83 (0.74)	3.73 (0.90)	0.19 (0.09)	0.18 (0.07)
Extended-elbow vertical climbing						
Adult females (H+, K)		17/17	3.40 (0.50)	3.40 (0.39)	0.24 (0.04)	0.24 (0.04)

Relative stride length is obtained by dividing stride length by lower leg length. Normalised climbing speed is calculated as the square root of the Froude number. Values represent means, with s.d. given in parentheses. + signifies an adult female carrying an infant. Asterisks mark statistically significant differences between fore- and hindlimbs: * $P<0.05$ (unpaired *t*-tests).

groups most often used a diagonal sequence/diagonal couplets gait, but females that carried an infant used trot more, whereas single females preferred a diagonal sequence/single limb gait.

Discussion

Variation in vertical climbing within sex/age and locality groups

Testing for significant differences within groups indicates that the most variable parameter is speed. Individual variation in speed may be partly influenced by the behavioural context of the vertical climbing sequences, although efforts were made to only select sequences for analysis that appeared to be

relaxed and unhindered. Differences within the wild group were mostly between the wild adult female (Q) and the males from Bukit Lawang. It should be noted that the behaviour of the wild males at Bukit Lawang differed substantially from the rehabilitants at the same site. They did not visit for food but, in both cases, had arrived whilst in consort with rehabilitant females in oestrus. They maintained some distance from the feeding platform and occasionally gave distress calls ('kiss squeaked'). Consequently, although these individuals were in an unnatural environment, their behaviour was substantially more characteristic of wild individuals than of rehabilitants. However, the adult female (Q) remains the only truly wild individual, in a wild environment, in this study.

Table 8. Parameter values for the linear regressions between relative stride length of the hindlimbs and normalised speed for vertical climbing in *Pongo p. abelii*

Individual	Age/sex	N	Log (relative stride length)			
			Slope (a)	Intercept (b)	r ²	P value of slope
Individuals						
Jersey Zoo						
A	Male subadult	10	0.49 (0.21)	0.88 (0.12)	0.413	0.045
B	Female adult	11	0.34 (0.16)	0.76 (0.07)	0.342	0.059
C	Female adult	11	0.30 (0.12)	0.74 (0.08)	0.405	0.035
D	Male juvenile	28	0.30 (0.08)	0.74 (0.04)	0.379	<0.001
E	Male juvenile	5	0.39 (0.16)	0.81 (0.10)	0.658	0.096
Sumatra						
F	Male subadult	15	0.48 (0.05)	0.85 (0.03)	0.854	<0.001
G+	Female adult	5	0.23 (0.20)	0.67 (0.15)	0.309	0.330
H+	Female adult	17	0.47 (0.20)	0.81 (9,14)	0.272	0.032
I+	Female adult	5	0.22 (0.26)	0.68 (0.14)	0.201	0.449
J+	Female adult	15	0.59 (0.12)	0.88 (0.08)	0.655	<0.001
K	Female adult	4	0.28 (0.09)	0.70 (0.05)	0.834	0.087
L	Female adult	19	0.35 (0.13)	0.75 (0.08)	0.303	0.015
M	Male adolescent	21	0.26 (0.14)	0.75 (0.09)	0.153	0.080
N	Indet. juvenile	–				
O	Male adult	10	0.46 (0.07)	0.91 (0.05)	0.860	<0.001
P	Male subadult	4	0.40 (0.07)	0.86 (0.04)	0.942	0.030
Q	Female adult	–				
Q+	Female adult	11	0.16 (0.16)	0.68 (0.14)	0.106	0.329
Extended-elbow vertical climbing						
H+	Female adult	10	0.67 (0.19)	0.96 (0.12)	0.854	0.008
K	Female adult	7	0.59 (0.17)	0.88 (0.11)	0.709	0.017
Groups						
Flexed-elbow vertical climbing						
Adult females (B, C, K, L)		45	0.34 (0.06)	0.75 (0.04)	0.403	<0.001
Mothers (G+, H+, I+, J+)		42	0.43 (0.08)	0.79 (0.05)	0.419	<0.001
Wild mother (Q)		14	0.25 (0.14)	0.77 (0.13)	0.204	0.105
Adult male (O)		10	0.46 (0.07)	0.91 (0.05)	0.860	<0.001
Subadult males (A, F, P)		29	0.48 (0.06)	0.87 (0.04)	0.698	<0.001
Adolescent male (M)		21	0.27 (0.15)	0.75 (0.09)	0.157	0.075
Juveniles (D, E, N)		35	0.34 (0.06)	0.76 (0.03)	0.460	<0.001
Captive (A, B, C)		32	0.33 (0.07)	0.77 (0.04)	0.456	<0.001
Rehabilitant (F, G, H, I, J, K, L)		80	0.43 (0.05)	0.80 (0.03)	0.476	<0.001
Wild (O, P, Q)		28	0.32 (0.06)	0.83 (0.05)	0.555	<0.001
Extended-elbow vertical climbing						
Adult females (H+, K)		17	0.71 (0.14)	0.98 (0.09)	0.644	<0.001

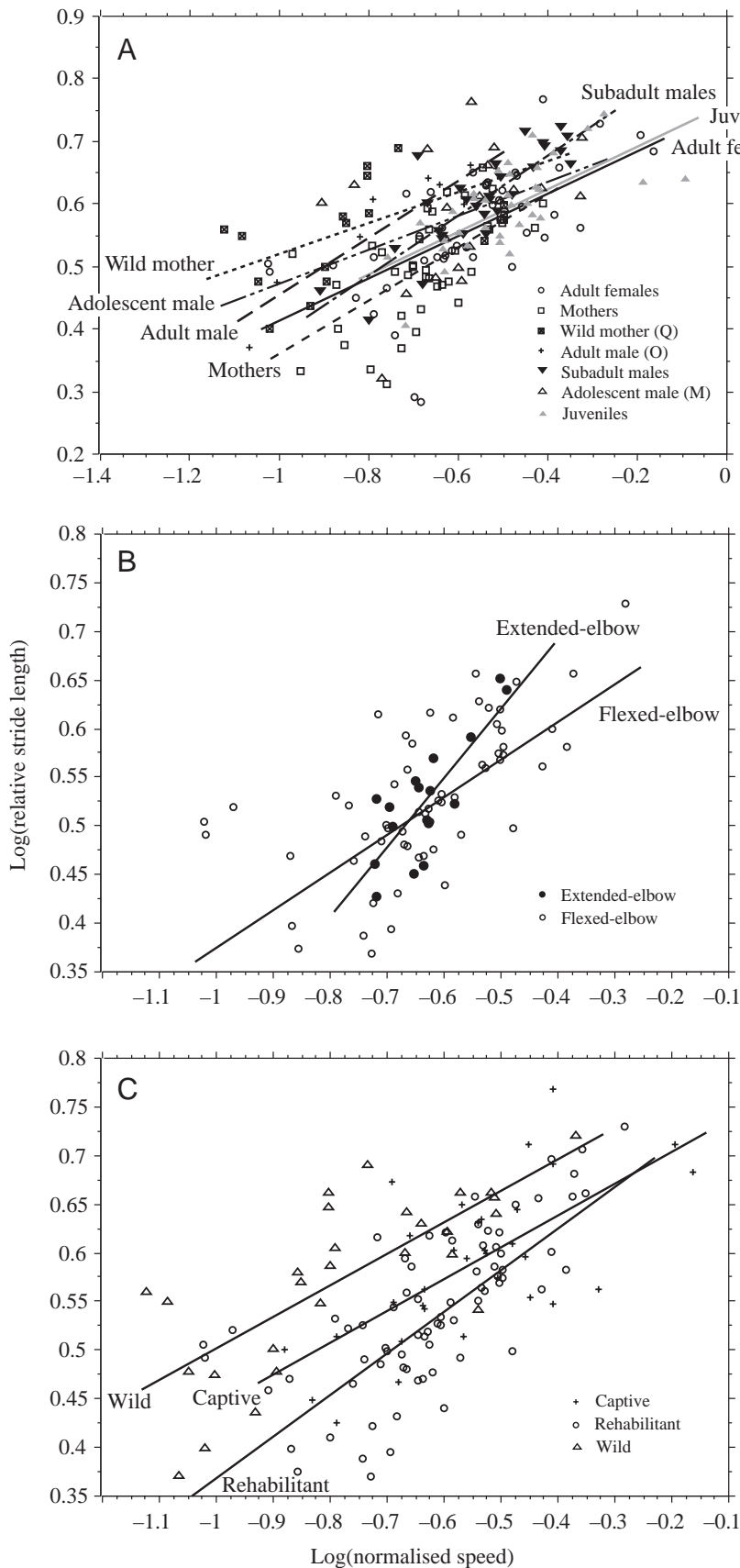


Fig. 2. Regression of relative stride length versus normalised speed in vertically climbing orang-utans. (A) Different sex/age groups; (B) flexed-elbow versus extended-elbow climbing of adult females at Bukit Lawang; and (C) captive versus rehabilitant versus wild adult or subadult individuals.

Differences in vertical climbing between wild, rehabilitant and captive orang-utans

As a general rule, gait parameters of vertically climbing orang-utans are remarkably similar between wild, rehabilitated and captive subjects from Bukit Lawang, Ketambe and Jersey Zoo. Comparison is complicated by the limited number of observations of wild individuals and the fact that the groups are not balanced in terms of sex and age classes. However, some differences between the climbing of zoo animals and that of orang-utans in Sumatra are apparent: cycle duration is much longer, and normalised speed is lower, for the wild orang-utans than for the rehabilitants, and even more so compared with the zoo animals (Table 4). Thus, no deficiencies in the ability to climb, which would be revealed by a somewhat unstable or asymmetric gait or a higher duty factor, could be detected in the rehabilitant orang-utans compared with wild animals. As our study subjects were already rehabilitated to a certain extent, roaming freely through the forest and only visiting feeding platforms, the differences in locomotor fitness compared with wild individuals may not be substantial and may indicate that orang-utans are able to adapt well to a locomotor repertoire that includes a significant climbing component from one dominated by terrestrial quadrupedalism. However, all observations of climbing in rehabilitants were obtained at the feeding platform, on substrates that the animals were very familiar with, and are thus not directly comparable to the locomotion of wild animals on unknown substrates.

The studied zoo animals climb even faster and take longer strides than do rehabilitant orang-utans, indicating that their confined living conditions did not significantly impair their climbing ability. This may be partly due to the fact that the captive subjects were not overweight. An influence of different motivations for climbing is less likely, as in all cases climbing was motivated mainly by the wish to gain access to food. Ultimately, it would be interesting to compare the locomotion of reintroduced ex-captives before and after their release or to study the locomotion of rehabilitant orang-utans at regular time intervals.

Table 9. Comparison of speed modulation in vertical climbing of *Pongo p. abelii*

Comparison	d.f.	Slopes		y-intercepts	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Adult females vs mothers	83	0.684	0.411	2.009	0.160
Mothers vs wild mother (Q)	52	1.416	0.240	23.18	<0.001
Subadult males vs adult females	70	1.756	0.189	5.474	0.022
Adult male (O) vs subadult males	35	0.063	0.804	10.98	0.002
Juveniles vs adult females	77	<0.001	0.999	0.154	0.696
Adolescent male (M) vs juveniles	52	0.231	0.633	1.188	0.281
Subadult males vs juveniles	60	2.464	0.122	8.193	0.006
Adolescent male (M) vs subadult males	46	2.095	0.155	0.085	0.772
Captive vs rehabilitant	108	1.284	0.260	4.666	0.033
Captive vs wild	56	0.003	0.958	10.30	0.002
Rehabilitant vs wild	104	1.696	0.196	41.89	<0.001
Infant-carrying vs single adult females (Bukit Lawang)	61	0.461	0.500	0.191	0.664
Extended-elbow vs flexed-elbow of adult females (Bukit Lawang)	78	1.637	0.205	0.261	0.611

F-statistics and *P*-values denote the significance of differences between the slopes and the y-intercepts of the linear regressions given in Table 8 (analysis of covariance). d.f., degrees of freedom.

Another possible explanation for the differences in gait parameters observed between the animals of different locations would be that wild individuals climb more cautiously than do rehabilitant and captive orang-utans. A more cautious locomotion would show in slower speed, but, as the animals would physically be able to climb faster, the other gait parameters can be expected to remain unchanged (i.e. a steady, symmetrical gait with a similar duty factor, as in fact was observed in the wild subjects of this study). It seems likely that zoo animals are so familiar with the climbing structures in their enclosure that the need for caution is reduced. They simply know from experience that the ropes will not break. Wild orang-utans, on the other hand, inhabit large tracts of rainforest and may climb a specific tree or liana only once in their lifetime. Moreover, in the forest canopy, seemingly robust substrates may break under the animal's body weight, and orang-utans were frequently observed to test the strength of substrates before placing body weight on them. As a consequence, it is beneficial for wild individuals to move cautiously. Rehabilitant orang-utans are also familiar with their environment, particularly at the feeding platform, where the present observations were made. Accordingly, the gait parameters of rehabilitant orang-utans lie in-between those of wild and captive animals.

Captive orang-utans were found to have a larger degree of humeral head torsion than wild animals (Sarmiento, 1985), which could be explained by the fact that the former devote a considerable amount of time to quadrupedal walking on the ground (Larson, 1988). This morphological feature may be related to the degree of humeral abduction during climbing, which remains to be investigated in a three-dimensional analysis of the joint angle kinematics. Such kinematic and musculoskeletal modifications in captive animals compared

with wild subjects indicate that studying the locomotion of wild primates in undisturbed surroundings must remain the ultimate aim of researchers if meaningful biomechanical data are required.

Extended-elbow versus flexed-elbow vertical climbing

The characteristics of vertical climbing on different substrates by adult female *Pongo p. abelii* at Bukit Lawang were compared. As only two climbing sequences on large-diameter trees in Bukit Lawang were observed, the following conclusions must be regarded as preliminary. A diagonal sequence/single limb gait was preferred, and trot was not employed during extended-elbow vertical climbing. The main difference between flexed- and extended-elbow vertical climbing, however, was found in the relative duration of the support phase, or duty factor, which was higher in extended-elbow climbing. The mean number of supporting limbs was larger than three during extended-elbow vertical climbing. At the same speed of locomotion, the duty factor is an indicator of the effort that a subject exerts relative to its physical ability or fitness (Murray et al., 1969; Isler, 2002a). It follows that extended-elbow vertical climbing is more demanding than climbing a liana or a small-diameter tree and quantifies the results of Thorpe et al. (submitted), who showed that wild individuals revealed a strong preference for climbing single and multiple substrates of less than 10 cm in diameter. Cant (1992) also noted this preference when he observed wild orang-utans entering the crowns of large fruiting trees, not by climbing the trunks with extended elbows but by utilising adjacent, small, vertical lianas. The same pattern of a higher duty factor can be observed in the vertical climbing of adult male gorillas compared with adult females or juvenile gorillas (Isler, 2002a).

Nevertheless, mean cycle duration and relative stride length did not differ between flexed-elbow and extended-elbow vertical climbing of female orang-utans. Apart from the data presented here, gait parameters of extended-elbow vertical climbing are available only for spider monkeys (*Ateles fusciceps robustus*; Isler, 2003). They belong to a group of South American primates that exhibit adaptations to suspensory locomotion and are convergent to hominoids in many morphological traits of the postcranium, although their arms are not nearly as elongated as in orang-utans. In spider monkeys, cycle duration was found to be shorter, i.e. the step frequency was higher, and the stride length was shorter during extended-elbow vertical climbing on a large-diameter tree than during flexed-elbow vertical climbing on a rope or thin tree (Isler, 2003). Thus, it seems that the differences between climbing on different substrates are more pronounced in *Ateles* than in orang-utans, and this may suggest that climbing a large-diameter vertical substrate is more demanding for spider monkeys than for orang-utans. Thus, climbing on a large-diameter vertical substrate may indeed be of adaptive significance for the evolution of elongated arms, as biomechanical considerations suggest (e.g. Cartmill, 1974; Fleagle et al., 1981; Preuschoft, 1990; Stern et al., 1977). However, to test this conclusion it would be necessary to investigate the 3-D kinematics and kinetics of extended-elbow vertical climbing in the two species.

Infant-carrying

Gait parameters of flexed-elbow climbing in adult female *Pongo p. abelii* at Bukit Lawang were very similar between individuals carrying an infant and those climbing alone. Thus, the climbing kinematics of female orang-utans do not seem to be overly influenced by the additional load of a clinging infant. This may be due to the small size of the observed infants and may change later in development. A longitudinal study would be beneficial for the understanding of the energetic costs of infant carrying in primates.

Age and sex differences

Sex differences in the gait parameters of vertically climbing *Pongo p. abelii* are surprisingly small, given that the sexual dimorphism in body mass of adult orang-utans is extreme (Morbeck and Zihlman, 1988). Duty factor, relative stride length, dimensionless speed and laterality of limb cycles do not differ between the sexes. Only cycle duration is significantly longer in the adult male than in adult females. However, as only one adult male was observed, these results should be interpreted with caution. Subadult males resemble adult females in all gait characteristics studied. Thorpe et al. (submitted) conducted a log-linear analysis of the likely influences on orang-utan locomotion. They also found that frequencies of vertical climbing did not differ substantially between the sexes and, contrary to classic geometric predictions, the age/sex category of the individual has only limited influence on overall locomotor repertoire. They proposed that this in part reflected the presence of arboreal

pathways, which individuals of all age/sex categories attempt to follow.

Juvenile orang-utans exhibit a shorter cycle duration than adults, subadults or adolescents and a lower duty factor than adults and subadults (see Fig. 1). The laterality of hindlimb cycles is also higher in juveniles than in adults, although this is largely due to an increased frequency of lateral couplets gait patterns in juvenile male D from Jersey Zoo (Table 5). Stride length and speed do not differ between juvenile and adult orang-utans if they are normalised against lower leg length. In a study of 3-D joint angles during flexed-elbow vertical climbing in captive orang-utans (Isler, 2003), it was shown that the range of motion of all joints was reduced in the juvenile individual: the shoulder and elbow joints were less flexed and the knee and hip joints were less extended than in the adult orang-utans. This reduced range of motion of the major limb joints in the juvenile orang-utan yields a larger distance of the body centre of gravity from the substrate.

Consequently, whilst previous studies have shown that the frequency of vertical climbing does not differ substantially between individuals of a different age, the present study indicates that the kinematics of locomotion do differ. This reflects the fact that, due to metabolic differences and the allometric relationship of muscle dimensions to body mass, climbing is energetically relatively more expensive for larger animals (Cartmill, 1972, 1974; Cartmill and Milton, 1977; Taylor et al., 1972). Since metabolic rates per unit body mass vary inversely with body mass, the increase in oxygen consumption demanded by vertical locomotion represents a much larger fraction of resting metabolism in large animals than in small ones (Taylor et al., 1972). Thus, juveniles are expected to climb more easily than adult animals of the same species, which is corroborated by the observed differences in gait parameters during flexed-elbow vertical climbing.

However, as a considerable amount of variability between individuals as well as between different trials of the same individual was found in the present study, it must be emphasised that it is crucial to include a sufficient number of individuals and trials in studies on orang-utan locomotion, allowing extraction of reliable information through statistical analysis of the kinematic data. In particular, further analysis would indicate whether the results for the wild adult female (Q) are an outlier or truly representative of the vertical climbing of wild adult females.

Comparison with vertical climbing kinematics in other primates

Gait parameters of other hominoid primates are shown in Table 10. Orang-utans are peculiar in exhibiting an extremely long cycle duration and longer strides during vertical climbing than other primates (Hirasaki et al., 2000; Isler, 2002a, 2003). At any given dimensionless speed, the relative stride length of orang-utans is the longest of all primates studied by Isler (2003), i.e. gorillas (*Gorilla gorilla gorilla*), bonobos (*Pan paniscus*), gibbons (*Hylobates concolor gabriellae* and *H. c. leucogenys*), spider monkeys (*Ateles fusciceps robustus*) and

Table 10. Comparison of hindlimb gait parameters in flexed-elbow vertical climbing of hominoids

	<i>Pongo pygmaeus abelii</i>	<i>Gorilla gorilla gorilla</i>	<i>Pan paniscus</i>	<i>Hylobates leucogenys/gabriellae</i>
Number of individuals	>17	5	9	5
Number of leg cycles	282	583	522	637
Cycle duration (s)	2.44 (1.00)	1.32 (0.44)	1.25 (0.49)	1.01 (0.39)
Duty factor (%)	71.6 (8.8)	70.6 (9.0)	64.6 (10.4)	62.1 (13.5)
Laterality of footfalls (%)	16.5 (11.8)	13.9 (8.6)	15.5 (11.8)	24.5 (14.3)
Relative stride length	3.73 (0.76)	3.13 (0.59)	3.06 (0.85)	4.88 (1.01)
Normalised speed	0.27 (0.11)	0.44 (0.15)	0.48 (0.30)	0.72 (0.23)

Values represent means, with s.d. given in parentheses. Data from Isler (2003).

woolly monkeys (*Lagothrix lagotricha*). Together with woolly monkeys and gorillas, orang-utans exhibit the highest percentages of quadrupedal support, and thus also a large mean number of supporting limbs and a high duty factor, when compared with other apes. These characteristics can be explained by the peculiarities of orang-utan locomotion and their corresponding morphological adaptations: orang-utans are the largest extant canopy-dwelling animals (Cant, 1987), and adult males sometimes crash to the ground when a substrate breaks (Delgado and van Schaik, 2000), which explains why they aim to distribute their body weight on various substrates and move slowly to test the strength of their holds. Their limb joints are highly mobile due to the demands placed upon them by orthograde scrambling and bridging (Morbeck and Zihlman, 1988; Tuttle and Cortright, 1988). Accordingly, the range of motion of the major limb joints during vertical climbing was found to be larger in orang-utans than in African apes (Isler, 2003). Shoulder and elbow joints are more extended at hand contact, and, in the hindlimb, the foot is more elevated relative to the position of the hip joint than in African apes, thus further increasing stride length. However, such mobility is achieved at a cost. Large strides require forces to be exerted throughout a large range of joint positions. Thus, muscles are primarily designed for mobility and velocity of shortening rather than for the production of large forces, and joints are not robust enough to withstand high impact forces at sudden speed changes. As a result, orang-utans achieve only low climbing speeds. The same can be seen in other relatively slow primates, such as slow and slender lorises (*Loris tardigradus*; Demes and Jungers, 1989; Sellers, 1996). Additionally, the large body size of orang-utans disproportionately increases the forces acting on the joints. Thus, the slow and cautious movements of orang-utans may not be an expression of their character or purely a result of cautiousness but rather a biomechanical necessity reflecting a compromise between large body mass and enhanced joint mobility.

Conclusions

In conclusion, our results show that the gait parameters of wild, rehabilitant and captive orang-utans are reasonably similar, despite very different environments. Nevertheless,

there are a few significant differences between individuals from the different localities. Cycle duration is longer and normalised speed is lower for the wild orang-utans than for the rehabilitants and captives, reflecting the complexity of, and lack of an individual's familiarity with, the wild environment in comparison with that of the feeding platform and zoos. As a result, wild orang-utans climb more cautiously than the other locality groups. However, as the wild sample consisted of only three individuals, these results need to be corroborated by further analysis. Sex/age differences in the gait parameters of climbing orang-utans are small, although juveniles in general exhibited a shorter cycle duration and lower duty factor than other groups, reflecting the advantage of their lower body mass. Extended-elbow vertical climbing is primarily characterised by a higher duty factor than flexed-elbow climbing, indicating that the former is an energetically more demanding form of locomotion. No significant differences were found in the spatio-temporal parameters of adult females compared with mothers, indicating that clinging infants do not influence climbing kinematics. In comparison with other primates, orang-utans exhibit a longer cycle duration, longer strides but lower climbing speed, reflecting a compromise between the demands of a large body mass and extreme joint mobility.

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