

The locomotor kinematics of Asian and African elephants: changes with speed and size

John R. Hutchinson^{1,*}, Delf Schwerda², Daniel J. Famini³, Robert H. I. Dale⁴, Martin S. Fischer² and Rodger Kram⁵

¹*Structure and Motion Laboratory, Department of Veterinary Basic Sciences, The Royal Veterinary College, University of London, Hatfield, Hertfordshire, AL9 7TA, UK,* ²*Institut fuer Spezielle Zoologie und Evolutionsbiologie, mit Phyletischem Museum, Jena, 07743, Germany,* ³*Department of Integrative Biology, University of California, Berkeley, CA 94720-3140, USA,* ⁴*Department of Psychology, Butler University, Indianapolis, IN 46208, USA and* ⁵*Department of Integrative Physiology, University of Colorado, Boulder, CO 80309-0354, USA*

*Author for correspondence (e-mail: jrutch@rvc.ac.uk)

Accepted 13 July 2006

Summary

For centuries, elephant locomotion has been a contentious and confusing challenge for locomotion scientists to understand, not only because of technical difficulties but also because elephant locomotion is in some ways atypical of more familiar quadrupedal gaits. We analyzed the locomotor kinematics of over 2400 strides from 14 African and 48 Asian elephant individuals (body mass 116–4632 kg) freely moving over ground at a 17-fold range of speeds, from slow walking at 0.40 m s⁻¹ to the fastest reliably recorded speed for elephants, 6.8 m s⁻¹. These data reveal that African and Asian elephants have some subtle differences in how size-independent kinematic parameters change with speed. Although elephants use a lateral sequence footfall pattern, like many other quadrupeds, they maintain this footfall pattern at all speeds, shifting toward a 25% phase offset between limbs (singlefoot) as they increase speed. The duty factors of elephants are greater for the forelimbs than for the hindlimbs, so an aerial phase for the hindquarters is reached at slower speeds than for the forequarters. This aerial phase occurs at a Froude number of around 1, matching theoretical predictions. At faster speeds, stance and swing phase durations approach asymptotes, with the duty factor beginning to level off, concurrent with an increase in limb compliance that likely keeps peak forces relatively low. This increase of limb compliance is reflected by increased compression of the hindlimbs. Like other

tetrapods, smaller elephants are relatively more athletic than larger ones, but still move very similarly to adults even at <500 kg. At any particular speed they adopt greater relative stride frequencies and relative stride lengths compared to larger elephants. This extends to near-maximal locomotor performance as well – smaller elephants reach greater Froude numbers and smaller duty factors, hence likely reach relatively greater peak loads on their limbs and produce this force more rapidly. A variety of lines of kinematic evidence support the inference that elephants change their mechanics near a Froude number of 1 (if not at slower speeds), at least to using more compliant limbs, if not spring-like whole-body kinetics. In some ways, elephants move similarly to many other quadrupeds, such as increasing speed mainly by increasing stride frequency (except at fast speeds), and they match scaling predictions for many stride parameters. The main difference from most other animals is that elephants never change their footfall pattern to a gait that uses a whole-body aerial phase. Our large dataset establishes what the normal kinematics of elephant locomotion are, and can also be applied to identify gait abnormalities that may signal musculoskeletal pathologies, a matter of great importance to keepers of captive elephants.

Key words: elephant, Proboscidea, locomotion, biomechanics, speed, gait, scaling.

Introduction

As the largest extant terrestrial animals and as the archetype of ‘graviportal’ animals [large body size with columnar, robust limbs (Coombs, 1978; Gregory, 1912)], elephants provide insight into the biomechanical and physiological constraints that extremely large body size imposes. However, our

understanding of elephant locomotion is impaired by a lack of data and analyses. Anecdotes, qualitative descriptions, lack of rigorous methods and vague data plague this subject. Hence broader inferences based on elephant locomotor data are generally tenuous. For example, this lack of understanding of ‘normal’ elephant locomotion limits the determination of

whether individual elephants are moving abnormally. This hinders early diagnosis of common musculoskeletal pathologies in captive elephants, some of which result in euthanasia (Csuti et al., 2001). Here we describe the kinematics of African bush/savanna (*Loxodonta africana* Blumenbach 1797) and Asian (*Elephas maximus* Linnaeus 1758) elephants using a range of individual sizes and speeds from a large data set. For brevity here, in referring to 'African elephants' we mean only the African bush/savanna elephant (*Loxodonta africana*), not the smaller, possible second African species, the forest elephant (*L. cyclotis* Matschie 1900).

We ask five principal questions.

First, how do the kinematics of elephants change with speed and body size? It is not even agreed what footfall patterns elephants use, let alone how they change with speed or size. Marey and Pagès (Marey and Pagès, 1887) and Muybridge (Muybridge, 1899) were the first to quantitatively describe elephant locomotion, during the dawn of cinematography (Sacks, 2003). Muybridge called the faster walk of an Asian elephant an amble, whereas subsequent authors used a wide variety of terms including rack (Gambaryan, 1974), pace (Webb, 1972), running walk (Howell, 1944), trot (Hildebrand, 1965; Hildebrand, 1966; Hildebrand, 1976) and run (Alexander et al., 1979a; Gambaryan, 1974) for slow- or fast-moving elephants. Hildebrand's useful gait formula for footfall patterns has become favored, so we adopt his terminology here (Hildebrand, 1962; Hildebrand, 1965; Hildebrand, 1966; Hildebrand, 1980; Hildebrand, 1985).

In a previous study we determined that Asian elephants maintain a lateral sequence footfall pattern at all speeds (Hutchinson et al., 2003). There are no comparable kinematic data for African elephants, so it is unclear whether this larger species moves any differently. Here we examine how the footfall pattern changes in elephants of different sizes moving at different speeds, focusing on stride parameters including lengths, times and frequencies. This will provide basic data for more complex studies of elephant locomotor mechanics and comparisons with other species. Furthermore, we examine the kinematics of smaller, younger elephants to resolve whether they truly trot, gallop and/or have an aerial phase.

Second, what is the range of elephant locomotor performance, such as maximal speed, minimal duty factor, and other kinematic parameters? This is not trivial, because elephants are crucial endpoint taxa for understanding the scaling of maximal locomotor performance in animals (e.g. Bakker, 1975; Blanco et al., 2003; Christiansen, 2002; Coombs, 1978; Garland, 1983; Iriarte-Díaz, 2002). Most literature has focused on maximal speeds and is rife with confusion and misinformation. Asian elephants are often claimed to have slower maximal speeds than African elephants (Alexander, 2000; Iriarte-Díaz, 2002; Spinage, 1994). For Asian elephants, Baker (Baker, 1890) was cited by Muybridge (Muybridge, 1899) as observing a maximal speed of 6.7 m s^{-1} (15 mph) and others often quoted this speed or similar values [(Gale, 1974), Sanderson (in Alexander, 2000); 7.0 m s^{-1} (Iriarte-Díaz, 2002); 5.6 m s^{-1} (Paul, 1998)], although the

fastest speed claimed was 8.9 m s^{-1} (Spinage, 1994). Baker's anecdotal speed estimate (Baker, 1890) was confirmed by video analysis of elephants on 'racetracks' (Hutchinson et al., 2003), documenting the fastest verifiable near-maximal speed of Asian elephants at 6.8 m s^{-1} (15 mph). Alexander et al. approximated an Asian elephant's speed in Muybridge (Muybridge, 1899) as 3.8 m s^{-1} but also measured an African elephant's speed as $4\text{--}4.5 \text{ m s}^{-1}$ (Alexander et al., 1979a). African elephants have been stated to move anywhere from this $\sim 4 \text{ m s}^{-1}$ [9 mph (Muybridge, 1899; Alexander and Maloiy, 1989)] to a dubious 13 m s^{-1} [30 mph (Alexander, 2000)]. A speed of 11 m s^{-1} 'charging, across 120 yards' [25 mph (Andrews, 1937) (cited by Garland, 1983; Howell, 1944); similar speedometer estimate claimed (Le Rue, III, 1994)] is often cited, although other studies have used somewhat lower speeds [10 m s^{-1} (Bakker, 1975; Hildebrand and Hurley, 1985); 9.7 m s^{-1} revised estimate (Garland, 1983); 9.5 m s^{-1} (Iriarte-Díaz, 2002)]. We consider African elephant near-maximal speeds to be undocumented, and present new data that point toward a solution of this mystery. In addition, we identify what peak values other stride parameters reach at such speeds, for comparison with other animals.

Third, do detailed kinematic data illuminate whether elephants change gait at any speed (Hutchinson et al., 2003)? What gait(s) elephants use is an important question that bears on the basic principles of why animals use different footfall patterns at different speeds (e.g. Cartmill et al., 2002; Hildebrand, 1976; Hildebrand, 1980; Hildebrand, 1985; Marey and Pagès, 1887; Muybridge, 1899), how much these gaits relate to underlying kinematics and kinetics (e.g. Cavagna et al., 1977; Alexander, 1980; Alexander, 1989; Heglund et al., 1982a; Heglund et al., 1982b; McGeer, 1992; McMahan et al., 1987; Parchman et al., 2003; Raibert, 1990; Riskin et al., 2006) (J. J. Robilliard, T. Pfau and A. Wilson, manuscript submitted for publication), and how size influences locomotor dynamics (e.g. Bertram and Biewener, 1990; Biewener, 1989; Biewener, 1990; Blanco et al., 2003; Farley et al., 1993; Heglund and Taylor, 1988).

Fourth, are there differences in locomotor kinematics between Asian and African elephants? The two lineages of elephants have been separate for at least 6 million years (Thomas et al., 2000) and differ in size, anatomy and habitat, so locomotor differences might exist.

Fifth, how do elephant kinematics compare with those of other animals based on scaling predictions? Even moderately large animals such as horses and rhinos use trotting and galloping footfall patterns in addition to normal walking, yet elephants do not. Perhaps elephants simply follow scaling trends observed in such species but restrict their range of locomotion to just walking, or perhaps their faster locomotion bear more similarity to these faster locomotor modes. Additionally, some horses [as well as primates and other quadrupeds (Cartmill et al., 2002; Schmitt et al., 2006)] such as Icelandic ponies use a footfall pattern (the toelt, or tölt) identical to the lateral sequence footfall pattern of elephants (Biknevicius et al., 2004; Nicodemus and Clayton, 2003; Zips

et al., 2001) (J. J. Robilliard, T. Pfau and A. Wilson, manuscript submitted for publication). We investigated whether the stride parameters of these locomotor modes in horses and elephants differ in any fundamental ways.

Materials and methods

Animals

We collected and analyzed kinematic data from 60 elephants (46 Asian, *Elephas maximus* L., and 14 African, *Loxodonta africana* Blumenbach): four Asian and four African elephants in facilities in California, USA; two African elephants in Indiana, USA; two African elephants in Germany; 42 Asian elephants in Thailand; and two African elephants in England. Vital statistics and housing facilities for each elephant studied are listed in Table 1. As noted in the supplementary information (in Hutchinson et al., 2003), body masses (M_b) had to be estimated for the Thai elephants. All other elephants had known weights from having all four limbs on a truck scale (± 2 kg). The lateral surfaces of the right limb joints (shoulder, elbow, hip and knee in particular) of the elephants were first marked with white tempera paint (surrounded with black paint for added contrast) or (for the four elephants in Europe) with infrared-reflective motion capture markers (Fig. 1). Joint center locations were estimated by palpation and by having elephants flex and extend their joints while multiple observers visually tracked the approximate rotational centers. Additional reference to museum-mounted specimens was made to aid locating skeletal landmarks from surface features. All

experiments with elephants in the UK were done with the approval of The Royal Veterinary College's Ethics and Welfare Committee.

Trials

Similar procedures were used for all trials for all elephants (see Hutchinson et al., 2003; Schwerda, 2003). However, we varied the method of motivation in order to elicit different speeds. Most were led by trainers, but some were either ridden by their mahouts or allowed to move on their own and even chase friendly elephants. For trials at faster speeds, elephants were motivated by a variety of techniques, none inflicting pain or suffering on the elephants, including playful chasing, presence of friendly elephants near the end of the track, food rewards, noisemaking and cheering, and mahout's or trainer's instructions. No behavioral artifacts were observed in how the elephants moved at any particular speed. The elephants moved across level trackways about 30 m in total length. This allowed the animals to accelerate to and decelerate from various speeds as encouraged by the trainers. The total number of trials was 602: 299 for Asian elephants (235 in Thailand) and 303 for African elephants (197 in Germany, 62 in California, 24 in Indiana, and 20 in England). In total about 2400 strides were measured for the 602 trials; these strides were averaged within each trial.

Video acquisition and processing

Similar methods were used for all experiments in the USA, England, Germany and Thailand. The central 10 m of a 30 m

Table 1. Vital statistics for elephants used in this study

Elephant	Facility	Species	Hip height h (m)	Shoulder height (m)	Age (years)	Sex	Body mass (kg)	Maximal u (ms^{-1})	Fr
Tanya	COLCH	African	1.91	2.72	26	F	3512	1.8	0.17
Opal	COLCH	African	2.03	2.70	23	F	3438	1.9	0.18
Amos	HTWT	Asian	1.01		1.5	M	500	3.2	1.03
Liz	SFMW	Asian	1.90		36	F	4373	3.2	0.55
Taj	SFMW	Asian	1.68		60	F	4234	3.7	0.83
Tina	SFMW	Asian	1.68		43	F	3284	1.8	0.20
Malika	SFMW	African	1.68		11	F	1632	3.2	0.62
Misha	SFMW	African	1.93		16	F	3332	4.1	0.89
Tava	SFMW	African	2.10		22	F	3936	3.0	0.44
Tika	SFMW	African	1.75		21	F	4632	3.9	0.89
Kedar	IND	African	0.66	0.98	0.083	M	119	1.8	0.49
Kubwa	IND	African	1.93	2.60	30	F	3365	1.8	0.16
Tombi	IND	African	1.68	2.58	29	F	3265	5.9	2.14
Ajani	IND	African	1.44	2.07	5	M	1681	1.0	0.07
Sophi	IND	African	1.68	2.55	38	F	4358	1.5	0.14
Ivory	IND	African	1.75		24	F	3295	1.5	0.13
Csami	THUR	African	1.18	1.74	5	F	930	4.2	1.52
Seronga	THUR	African	1.28	1.85	6	F	1240	4.8	1.83

COLCH, Colchester Zoo, Stanway, UK; HTWT, Have Trunk Will Travel, Perris, CA, USA; SFMW, Six Flags Marine World Park, Vallejo, CA, USA; IND, Indianapolis Zoo, Indianapolis, IN, USA; THUR, Thüringer Zoo, Ehrfurt, Germany.

For data on 42 Asian elephants see supplementary information (in Hutchinson et al., 2003).

Maximal u is absolute forward velocity (u) across the 10 m track, with the corresponding Froude number (Fr).

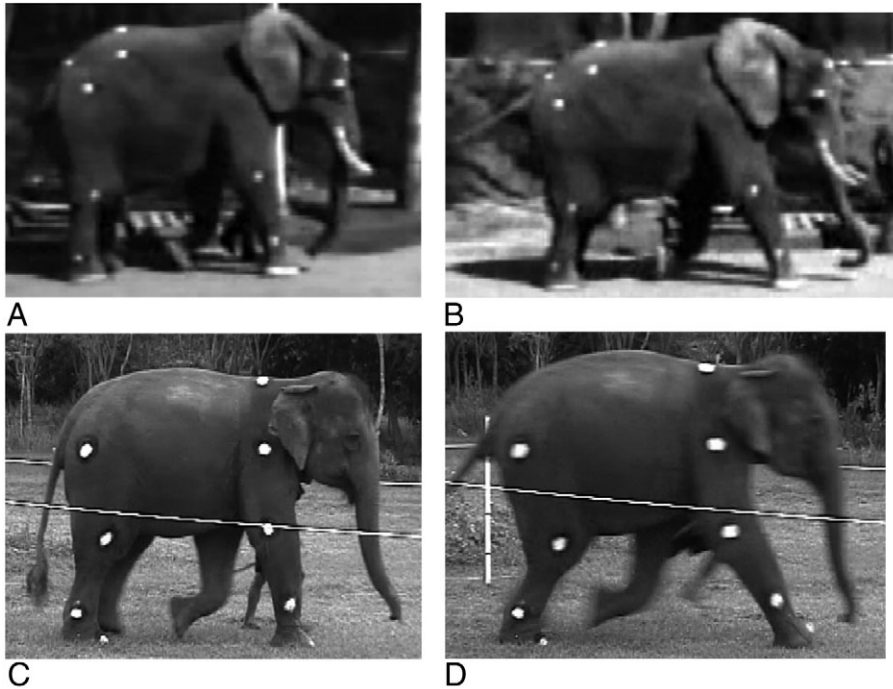


Fig. 1. Mid-stance phase of the right hindlimb, shown in right lateral view for representative slower and faster locomotion of an adult ($h=1.93$ m) African elephant (A, 1.7 m s^{-1} ; B, 4.1 m s^{-1}) and a subadult ($h=1.41$ m) Asian (C, 1.2 m s^{-1} ; D, 5.4 m s^{-1}) elephant. Limb phases were: (A) $P_{lf}=0.15$, $P_{rh}=0.51$, $P_{rf}=0.66$; (B) $P_{lf}=0.23$, $P_{rh}=0.52$, $P_{rf}=0.73$; (C) $P_{lf}=0.18$, $P_{rh}=0.48$, $P_{rf}=0.65$; (D) $P_{lf}=0.22$, $P_{rh}=0.52$, $P_{rf}=0.71$ (compare with Fig. 3). Markers are explained in the text.

track had the field of view of one camera oriented perpendicular to it. Camera image acquisition rates varied: 60 Hz for African elephants in the USA and Thailand, 200 Hz for Asian elephants in California, 120 Hz for African elephants in England, and 50 Hz for African elephants in Germany. The video recordings were encoded with field numbers and manually analyzed to obtain foot touch-down and lift-off events (see below), then digitized in Peak Motus (Peak Performance, Centennial, CO, USA) or SiliconCOACH (Dunedin, New Zealand) software to obtain the positions and displacements of the joint markers. Digitized data were post-processed with Butterworth filtering (fourth order, low pass 6 Hz cut-off frequency). We scaled the video linear dimensions from pixels to meters using the thigh segment length (=hip-to-knee distance) as a scaling factor, when the elephant's right hindlimb was at mid-stance near the center of the 10 m track section. These data allowed us to calculate forward velocities throughout a stride. Additionally, we tracked the vertical motions (in the sagittal plane) of the hip and shoulder joints following Hutchinson et al. (Hutchinson et al., 2003) to examine whether there was a shift in the motion of these joints at any speed that might help discriminate between inverted pendulum-like and spring-like limb function. Hip height (h) from the hip joint to the ground during standing was assumed to equal limb length for related calculations (see below).

Kinematic parameters

For all experiments, as well as velocity (u ; in $m s^{-1}$) we calculated the following kinematic parameters from these data: relative limb phase [P =fraction of a stride that the left fore [P_{lf}], right hind [P_{rh}], and right fore [P_{rf}] foot touch-down follows the left hind foot touch-down at 0.0; (Hildebrand, 1976;

Hildebrand, 1980)], stance and swing durations (t_{st} , t_{sw} ; i.e. stance and swing times or periods), duty factor ($\beta=t_{st}/[t_{st}+t_{sw}]^{-1}$; averaged for all limbs or for respective fore/hindlimb pairs), duty factor fore–hind difference (β_{diff} =forelimb mean β –hindlimb mean β); stride frequencies (F =no. strides s^{-1} , or Hz) and lengths ($L=uF^{-1}$), Froude number ($Fr=u^2/[gh]^{-1}$, where $g=9.81$ m s^{-2}) (Alexander and Jayes, 1983; Alexander, 1989); also non-dimensionalized speed \hat{u} or $Fr^{0.5}$ (e.g. Gatesy and Biewener, 1991) and the vertical displacements of the hip and shoulder joints (see Hutchinson et al., 2003). We normalized our compiled data for body size to obtain relative stride frequencies ($\hat{F}=F[h\cdot g^{-1}]^{0.5}$) and lengths ($\hat{L}=Lh^{-1}$) (Alexander and Jayes, 1983; Gatesy and Biewener, 1991; Hof, 1996).

Christian et al. (Christian et al., 1999) used very similar methods (50 Hz digital video, 30 m track) to obtain footfall patterns for two Asian elephants (their table 1: 19 trials; $h=1.5$ m; $u=0.59$ – 3.86 m s^{-1} ; $Fr=0.024$ – 1.0 ; $\beta=0.57$ – 0.77 ; M_b not reported but assumed equal to our Asian female elephant of identical h : 1300 kg), so we included these data in our analysis for a total of 62 elephants (48 Asian) and 621 trials.

The maximal error of time-related factors for the fastest, smallest elephants (t_{st} 0.196 s) at 60 Hz video sampling was 2 fields or 0.033 s (16.8%); at 200 Hz it was 5.04%. This maximal error is presumably an overestimate by a factor of two or more (see Gatesy and Biewener, 1991), especially for larger or slower elephants ($t_{st}<3$ s). Repeated measures of digitized coordinates by experienced users gave errors of ± 0.1 m s^{-1} for velocities. Horizontal accelerations/decelerations (calculated by double-integrating hip/shoulder position) were typically low across the 10 m track area, <0.2 m s^{-2} (Hutchinson et al., 2003); here we do not use trials with substantial between-stride speed variation.

Assessing when the elephants' feet were on the ground was sometimes difficult as elephants often brought their feet down at very low angles of attack, although there were still discrete heel-strike and toe-off events (Fig. 2), as in other large mammals. We scored video fields as having a foot-on event when the foot had ceased translating forward, and foot-off as when the foot began translating forward and/or upward. This approach is supported by preliminary foot-mounted accelerometer data (J. R. Hutchinson and L. Ren, unpublished data).

Statistical analysis

To check for differences between the relationships of stride parameters with dimensionless speed (\hat{u}) between the African and Asian elephants, we analyzed our data using a general linear model (GLM) in STATISTICA software (StatSoft, Inc., Tulsa, OK, USA), with speed as the independent variable, species as the categorical factor, and stride parameters (normalized for size where necessary, so P_{lf} , P_{rh} , P_{rf} , t_{sw} , t_{st} , β , β_{diff} , \hat{F} and \hat{L}) as the dependent variables. $P < 0.05$ was considered statistically significant. To illustrate the relationships of these normalized stride parameters with speed in our graphs and for comparison with published data for other animals, we applied the best curve fit (based on highest R^2 value). For Reduced Major Axis (RMA or Model II) regressions, we used custom code RMA for Java 1.19 (Bohonak and van der Linde, 2004).

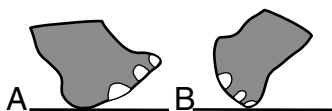


Fig. 2. Typical elephant foot-on (A) and foot-off (B) events. Right hind foot of an African elephant shown in lateral view during slow walking (1.2 m s^{-1} ; $t_{st}=1.5 \text{ s}$).

Results

Stride parameters: size-independent changes with speed

The ranges of parameter values we measured are in Table 2. Equations for any statistically significant correlations of these kinematic parameters (and those of size-dependent parameters) with \hat{u} are in Table 3; the statistical data are in Table 4. The same results were obtained whether data for individual elephants or species were examined.

The relative phasing of elephant forelimb footfalls (P) increased linearly with speed across the measured ranges (Fig. 3), becoming more evenly spaced in time – i.e. from having lateral couplets (Hildebrand, 1976; Hildebrand, 1980) at slower speeds toward a true singlefoot (25% phase offset between all limbs) in lateral sequence at faster speeds. The relative phasing of the right hind footfall (P_{rh}) showed a nearly significant increase with speed ($P=0.055$). In summary, the left front foot hit the ground 20–25% of a stride after the left hind, and was followed 25–30% of a stride later by the right hind, which the right front foot followed by 20–25% of a stride. We observed very few deviations from this pattern (ranges of phases were ± 0.1 from modal values) in our sample of 621 trials; all elephants remained within the boundaries of a lateral sequence footfall pattern, without ever switching to diagonal sequence, trotting, pacing or asymmetrical footfall patterns.

The average all-limb duty factors (β) decreased curvilinearly with speed for all elephants, at Fr around 1 reaching $\beta \sim 0.5$, below which would require aerial phases of some contralateral limbs (Fig. 4A). This decrease of β showed signs of reaching a plateau at $\hat{u} > 1.5$. We never observed anything close to a whole-body aerial phase; elephants had at least one limb firmly contacting the ground at all points during a stride. At least two limbs supported the body at speeds less than $Fr=1$, then there were increasingly long periods of single-leg support at speeds greater than $Fr=1$. At our lowest β of 0.37, a young elephant spent 26% of each stride supported on single limbs.

Table 2. Ranges of kinematic parameter values measured in this study for elephants

Parameter	African elephants			Asian elephants		
	Minimum	Maximum	Range	Minimum	Maximum	Range
u (m s^{-1})	0.40	5.90	5.50	0.47	6.80	6.33
\hat{u}	0.10	1.50	1.40	0.11	1.90	1.79
P_{lf}	0.12	0.26	0.14	0.080	0.31	0.23
P_{rh}	0.41	0.55	0.14	0.38	0.56	0.18
P_{rf}	0.60	0.77	0.17	0.60	0.80	0.20
β	0.44	0.85	0.41	0.37	0.78	0.41
β_{diff}	-0.010	0.070	0.080	-0.050	0.10	0.15
t_{st} (s)	0.26	4.00	3.74	0.20	2.90	2.70
t_{sw} (s)	0.28	0.76	0.48	0.30	0.88	0.58
\hat{L}	0.77	2.60	1.83	0.94	3.00	2.06
\hat{F}	0.090	0.67	0.58	0.12	0.66	0.54
L (m)	0.67	4.40	3.73	1.50	4.50	3.00
F (Hz)	0.21	1.90	1.69	0.26	1.90	1.64

For an explanation of symbols, see List.

Table 3. Least-squares regression equations for the curves that best fit the relationship of kinematic parameters with dimensionless speed (\hat{u}) for Asian and African elephants

Dependent (y-axis)	Independent (x-axis)	Species	a	b	b-RMA	R^2	Curve fit
P_{lf}	\hat{u}	African	0.16	0.043	0.33	0.13	Linear
P_{lf}	\hat{u}	Asian	0.16	0.041	0.12	0.34	Linear
P_{rh}	\hat{u}	African	0.49	0.0088	0.90	0.0098	Linear
P_{rh}	\hat{u}	Asian	0.49	0.010	0.23	0.044	Linear
P_{rf}	\hat{u}	African	0.65	0.042	0.42	0.10	Linear
P_{rf}	\hat{u}	Asian	0.65	0.047	0.15	0.31	Linear
β	\hat{u}	African	0.53	0.32	0.36	0.89	Logarithmic
β	\hat{u}	Asian	0.51	0.32	0.38	0.84	Logarithmic
t_{st}	\hat{u}	African	0.37	-0.93	-1.0	0.91	Power
t_{st}	\hat{u}	Asian	0.40	-0.94	-1.0	0.93	Power
t_{sw}	\hat{u}	African	0.35	-0.34	-0.56	0.61	Power
t_{sw}	\hat{u}	Asian	0.39	-0.37	-0.46	0.81	Power
\hat{L}	\hat{u}	African	2.0	0.35	0.42	0.84	Power
\hat{L}	\hat{u}	Asian	2.1	0.33	0.38	0.86	Power
\hat{F}	\hat{u}	African	0.49	0.65	0.68	0.95	Power
\hat{F}	\hat{u}	Asian	0.48	0.67	0.71	0.95	Power
L	u	African	1.8	0.32	0.73	0.44	Power
L	u	Asian	2.0	0.33	0.54	0.61	Power
F	u	African	0.56	0.68	0.87	0.78	Power
F	u	Asian	0.50	0.67	0.83	0.81	Power

a and b values are for the values in the curve-fit equations; linear: $y=ax+b$, logarithmic: $y=a-b\log x$, power: $y=ax^b$. RMA (Model II) slopes are also indicated (b-RMA column); calculated as (b/R^2) (Sokal and Rohlf, 1995).

For an explanation of symbols, see List.

Contrary to Hildebrand (Hildebrand, 1976) who reported roughly equal duty factors for elephant fore/hindlimbs, average forelimb β values were almost always slightly greater than hindlimb β (respectively, for 93% of African and 91% of Asian elephant trials). β_{diff} was randomly distributed about a mean difference of 0.03 for both species (Fig. 4B) and did not change significantly with dimensionless speed ($P>0.05$). Hence the hindquarters gained its aerial phase at a lower \hat{u} than did the forequarters.

Stance and swing phase durations (t_{st} , t_{sw}) dropped precipitously with increasing speed (Fig. 5A), with strong slopes (especially for t_{st}) at $Fr<1$, then leveled out toward asymptotic values. The decrease of t_{st} with speed was generally three times steeper than t_{sw} (Table 3). The lowest t_{st} values of 0.20 s were reached at $\hat{u}>1.5$, whereas the lowest t_{sw} values of 0.28 s were reached at slower speeds: $\hat{u}\sim 1.0$. Thus minimal stance times were about 71% of minimal swing times.

Relative stride length (\hat{L}) increased curvilinearly with speed (Fig. 5B), showing a slight discontinuity of this slope at around $Fr=1$, with a threefold range of \hat{L} values in both species from slowest to fastest observed speeds. The elephants relied relatively more on increasing relative stride frequency (\hat{F}) to move faster (maximum $\hat{F}=5-8\times$ minimum) than \hat{L} . \hat{F} increased curvilinearly with speed, but with a decreasing relative contribution to speed past $Fr=1$; these fastest speeds were achieved predominantly by increasing relative stride lengths.

Near-maximal locomotor performance

The Asian elephants from Thailand were the fastest of all of the elephants we measured, in absolute and relative terms. The maximal \hat{u} , L , F , \hat{L} and \hat{F} we observed were: 1.8 ($Fr=3.4$), 4.5 m, 1.93 Hz, 3.0 and 0.66, respectively. The minimal β value was 0.37. A large bull Asian elephant (~ 2790 kg) with the fastest absolute speed (6.8 m s $^{-1}$; $Fr=2.8$) and largest absolute L also had the most extreme F , \hat{F} and \hat{L} values for an elephant over 1500 kg: 1.6 Hz, 0.64 and 2.6, respectively. Near-maximal speed did not show an obvious change with size (Fig. 6A), although we lack sufficient data for elephants >4000 kg to see whether the largest elephants cannot reach the same absolute speeds as smaller ones. Even at young ages (~ 2 years), elephants can move as quickly as adults.

In contrast, peak locomotor performance relative to size declined with M_b – the greatest non-dimensionalized stride parameters (and lowest β) listed above were all for smaller elephants. Fig. 6B shows that minimal β (smallest value for each elephant) decreases with M_b . Correspondingly, Fig. 6C supports the inference that maximal absolute stride length increases with M_b , and more convincingly that maximal absolute stride frequency declines with M_b . In Fig. 6A–C, all elephants that did not reach $Fr>0.5$ ($\hat{u}>0.7$) were excluded, as these elephants clearly were not representative proboscidean athletes. The graph does not change markedly if other cut-offs such as $Fr<1.0$ are used.

Elephant hip heights increased near-isometrically with body

Table 4. Results of the general linear model statistical analysis of the relationships of stride parameters with dimensionless speed (\hat{u}) and species

Stride parameter	<i>N</i>	Mean	+0.950	-0.950	<i>F</i> -int	<i>F</i> - <i>u</i>	<i>F</i> -species	<i>P</i> -int	<i>P</i> - <i>u</i>	<i>P</i> -species
P_{lf} (African)	71	0.19	0.18	0.20	2898.54	162.669	0.19	≪0.001	≪0.001	0.66
P_{lf} (Asian)	299	0.19	0.19	0.19						
P_{rh} (African)	83	0.50	0.49	0.51	45901.7	14.22	0.04	≪0.001	0.055	0.83
P_{rh} (Asian)	299	0.50	0.50	0.51						
P_{rf} (African)	68	0.69	0.68	0.70	33836.1	139.01	0.17	≪0.001	≪0.001	0.68
P_{rf} (Asian)	299	0.69	0.69	0.69						
β (African)	282	0.59	0.59	0.60	40104.6	1781.6	38.26	≪0.001	≪0.001	≪0.001
β (Asian)	299	0.57	0.56	0.57						
β_{diff} (African)	82	0.026	0.020	0.031	275.996	23.3014	3.3861	≪0.001	≪0.001	0.067
β_{diff} (Asian)	299	0.031	0.029	0.034						
t_{st} (African)	283	0.68	0.65	0.72	2748.02	707.959	8.024	≪0.001	≪0.001	0.0048
t_{st} (Asian)	299	0.75	0.72	0.79						
t_{sw} (African)	282	0.41	0.40	0.42	8953.77	805.264	129.801	0.00	0.00	0.00
t_{sw} (Asian)	299	0.49	0.48	0.50						
\hat{L} (African)	259	1.8	1.8	1.8	8750.45	3493.72	8.651	≪0.001	≪0.001	0.0034
\hat{L} (Asian)	299	1.8	1.8	1.9						
\hat{F} (African)	259	0.40	0.39	0.40	1702.02	7225.05	12.189	≪0.001	≪0.001	≪0.001
\hat{F} (Asian)	299	0.38	0.38	0.39						

Significant relationships are emphasized in bold.

±95% confidence intervals (+0.950, -0.950) and *F* and *P* values for the intercept (-int), dimensionless speed (-*u*), species (-species) are noted. For an explanation of symbols, see List.

mass (Fig. 6D; slope=0.26); the 95% confidence intervals include the slope expected for a geometric similarity model of scaling (slope=0.33).

Stride parameters: size-dependent factors

Elephants, large and small alike, move in generally similar ways (limb phase, etc). They differ mainly in parameters that would be expected to change with body size: at a given absolute speed smaller elephants use smaller absolute stride lengths and greater absolute stride frequencies (Fig. 7), corresponding to absolutely lower t_{st} and t_{sw} . Likewise, β was lower at any particular absolute speed for smaller elephants. Even the smallest elephants did not use a whole-body aerial phase or change their footfall pattern to a trot, gallop or other pattern dissimilar from adults.

Limb vertical displacement

Like Hutchinson et al. (Hutchinson et al., 2003) we find that, in both species of elephant, at slow speeds the hip and shoulder joints first rise, then fall during their respective stance phases (Fig. 8A), reaching their maximal vertical position at mid-stance. Christian et al. [(Christian et al., 1999) their fig. 2] report similar data (roughly convex arc of hip motion during stance) for an Asian elephant moving at 1.6 m s⁻¹ ($Fr=0.18$; $\beta=0.66$). However, in elephants moving at fast speeds the hips fall, then rise during the stance phase (i.e. are at their minimum vertical position at mid-stance), whereas the shoulders maintain the same rise-fall motion during stance (Fig. 8B). Our larger data sample supports the inference that this change occurs at around a Fr of 1, although with some variation, and is common

to both species. Some elephants showed intermediate patterns (especially with the hip moving down throughout stance) at $Fr>0.5$; of these some even maintained this motion up to $Fr\sim 3$. In all cases, however, maximal vertical displacement of the hip and shoulder joints during the stance phase (from heel strike to maximum) remained relatively small: e.g. in Fig. 8A a mean

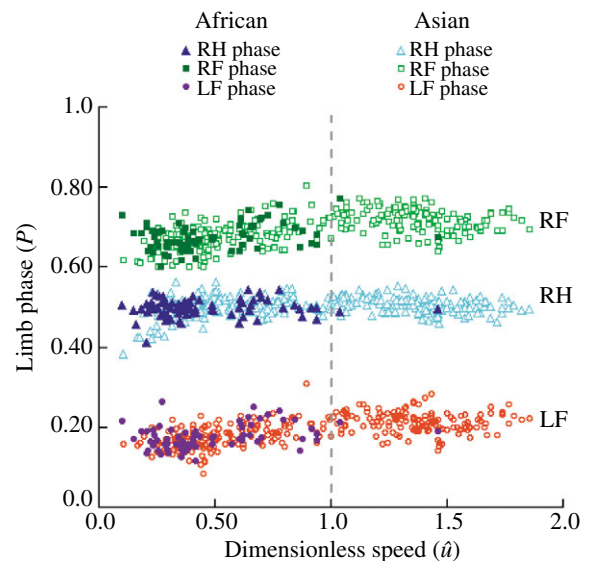


Fig. 3. Relative limb phase (*P*; with left hind foot contact defined as 0.0; others as fraction of a stride following that contact) plotted against dimensionless speed for African (filled symbols) and Asian (open symbols) elephants. Circles, left front (P_{lf}); triangles, right hind (P_{rh}); squares, right front (P_{rf}) feet.

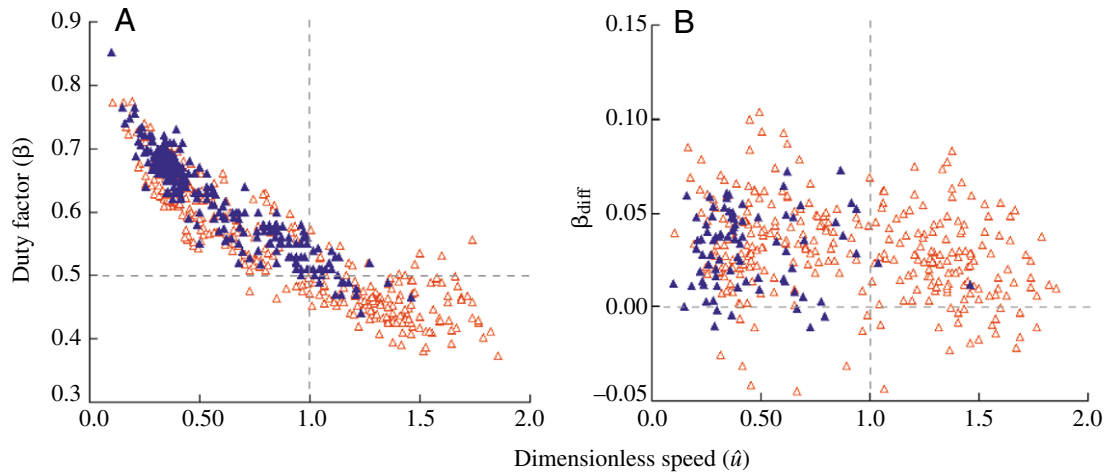


Fig. 4. Duty factor (A) and fore- minus hindlimb duty factor difference (β_{diff} ; B) plotted against dimensionless speed for African (blue; filled triangles) and Asian (red; open triangles) elephants.

increase of 0.12 m for the shoulders and 0.068 m for the hips, or in Fig. 8B an increase of 0.069 m for the shoulders and a decrease of 0.063 m for the hips. These values are only around 4–9% of hip height, which is expected for large animals (e.g. Farley et al., 1993; Schmitt et al., 2006).

The individual shown in Fig. 8 (same one shown in Fig. 1C,D) is fairly typical in that the shift in vertical displacement of the hip (from Fig. 8A to 8B) correlates with a disappearance of the upward movement of the hip that is observed in slower walking during the last half of stance phase. This peak occurs in the swing phase instead (note two peaks in swing phase in Fig. 8B vs one in Fig. 8A). Increased limb flexion during stance (Fig. 1) at fast speeds seems related to this change in hindlimb motion.

Species differences

African and Asian elephants were statistically different in how β , t_{st} , t_{sw} , \hat{L} and \hat{F} changed with dimensionless speed ($P < 0.05$). However, most of these differences were very slight

(compare mean values and 95% confidence intervals in Table 4). At any dimensionless speed, African elephants tended to have larger duty factors with shorter stance and swing times, using slightly greater stride frequencies and smaller stride lengths. The most striking difference was among swing times, which have a mean difference of 0.08 s (~20%) at identical \hat{u} values. However, our analysis strongly indicates that relative limb phases did not change with \hat{u} differently in African and Asian elephants ($P \gg 0.05$), nor did mean forelimb and hindlimb duty factors have statistically significant differences (i.e. β_{diff}) between Asian and African elephants, although there was a trend ($P = 0.067$) (Table 4).

Discussion

What is the range of maximal locomotor performance in elephants?

As maximal speed is strictly speaking a once-in-a-lifetime occurrence for every animal, we cannot consider any speeds

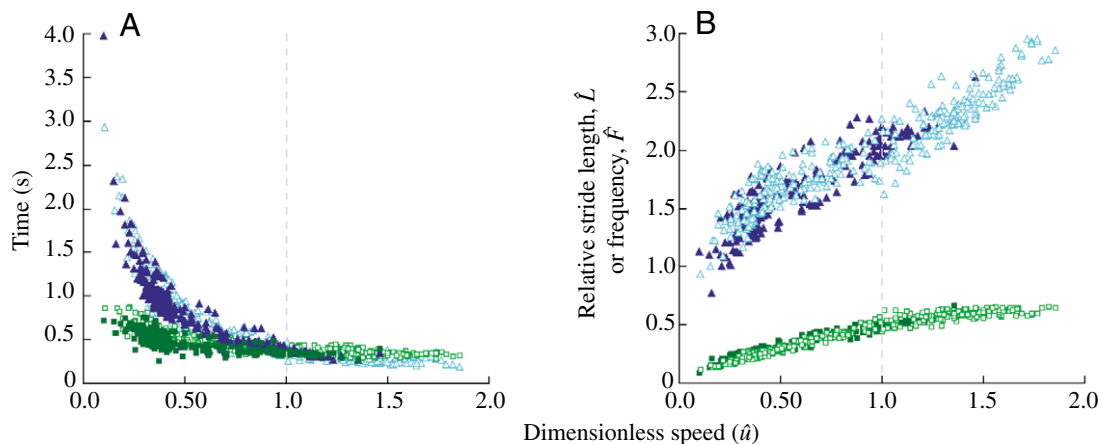


Fig. 5. Stance (blue triangles) and swing (green squares) phase durations (A) and relative stride lengths (triangles) and frequencies (squares) (B) plotted against dimensionless speed for African (filled symbols) and Asian (open symbols) elephants.

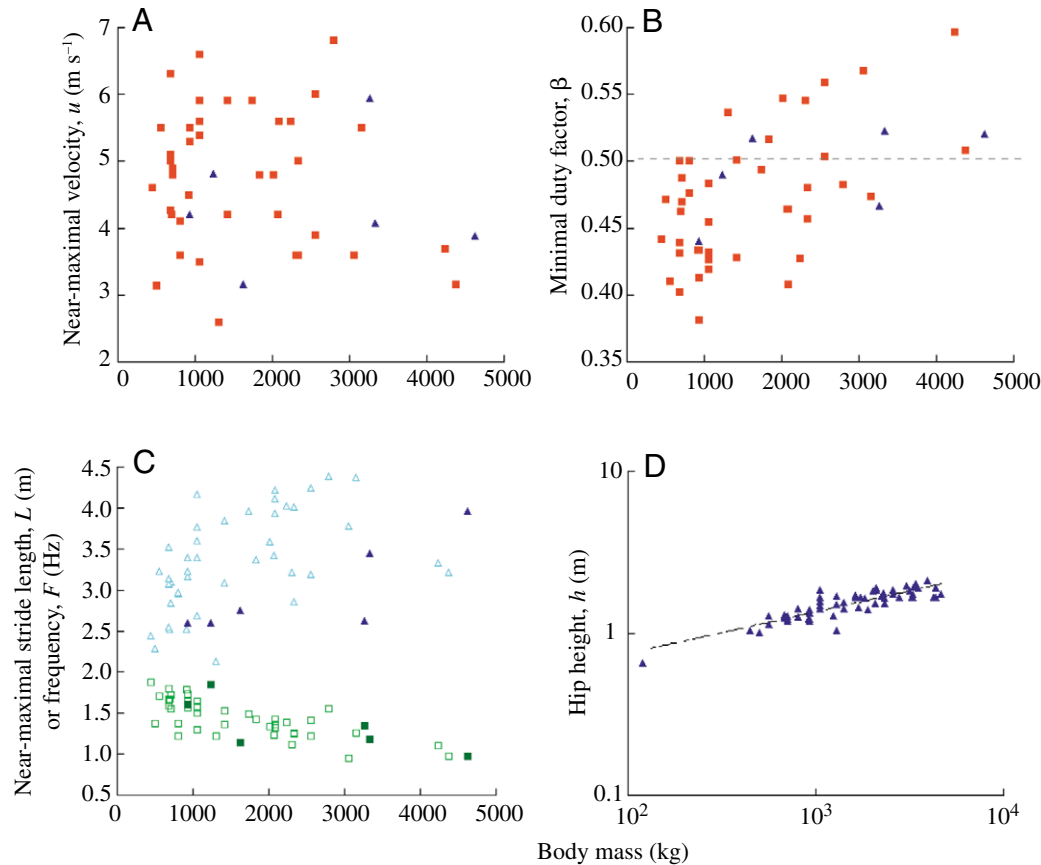


Fig. 6. Relationships of body mass for each individual African (blue triangles) and Asian (red squares) elephant with: near-maximal forward velocity (A), minimum observed duty factor (B), maximum observed stride length (triangles) and frequency (squares) (C; symbols are dark for African, light for Asian), and hip height for all elephants combined (D). Hip height (h) least-squares power curve fit shown: $h=0.23M_b^{0.26}$; $N=60$ [excluding two elephants (from Christian et al., 1999)], $R^2=0.73$; upper/lower 95% confidence intervals 0.26/0.33. This result does not change markedly if the baby elephant outlier is excluded ($h=0.26M_b^{0.24}$; $R^2=0.69$), or if RMA (Model II) regression is used (slope=0.29).

recorded here to be truly maximal. For many of our animals, it was an inescapable conclusion that they were exerting themselves to extreme degrees at faster speeds, but naturally it is impossible to calculate how far from maximal speeds they were (e.g. Losos et al., 2002). However we find it implausible that the Thai elephants in particular were only reaching 50–75% of an alleged 11 m s^{-1} maximal speed. These animals

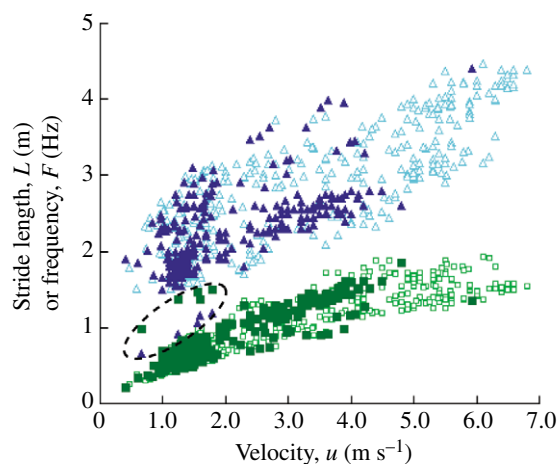


Fig. 7. Relationships of stride length (blue triangles) and stride frequency (green squares) to forward velocity for African (filled symbols) and Asian (open symbols) elephants. Circled data points indicate data for the smallest elephant (African; 116 kg).

were healthy, active and wide-ranging in their daily movements (tourist rides, hauling heavy equipment, etc.). Furthermore, they were ridden/guided by mahouts whom they were trained to obey, and many were ‘elephant hunters’ previously used to chase wild elephants for capture and subsequent domesticity, or were used in elephant races and polo matches. Hence the Thai elephants were trained for speed, unlike zoo-captive elephants that are necessarily selected for passivity, for purposes of space and safety. Considering the relative sizes (<60 kg mahouts, 1000–3000 kg elephants that were ridden) it is doubtful that the riding mahouts affected elephant performance. Additionally, the fastest speeds we recorded are slightly faster than the $\sim 6 \text{ m s}^{-1}$ average speeds for elephant races (J. R. Hutchinson, unpublished). For these reasons, we refer to the fast speeds ($>5\text{--}6 \text{ m s}^{-1}$) of many elephants as ‘near-maximal.’

Three of our 14 African elephant subjects reached $Fr > 1$ and $u > 4 \text{ m s}^{-1}$. One individual that was being chased by another reached a speed of 5.9 m s^{-1} ($Fr=2.1$), which is around the near-maximal speed of many Asian elephant individuals. As African and Asian elephants move very similarly, we doubt reports that African elephants can reach speeds as fast as 11 m s^{-1} (Andrews, 1937; Le Rue, III, 1994) or even $9.5\text{--}9.7 \text{ m s}^{-1}$ (Garland, 1983; Iriarte-Díaz, 2002). Estimating speeds from automobile speedometers or intuition can be extraordinarily inaccurate, particularly because of parallax effects (see Alexander and Maloiy, 1989). We consider

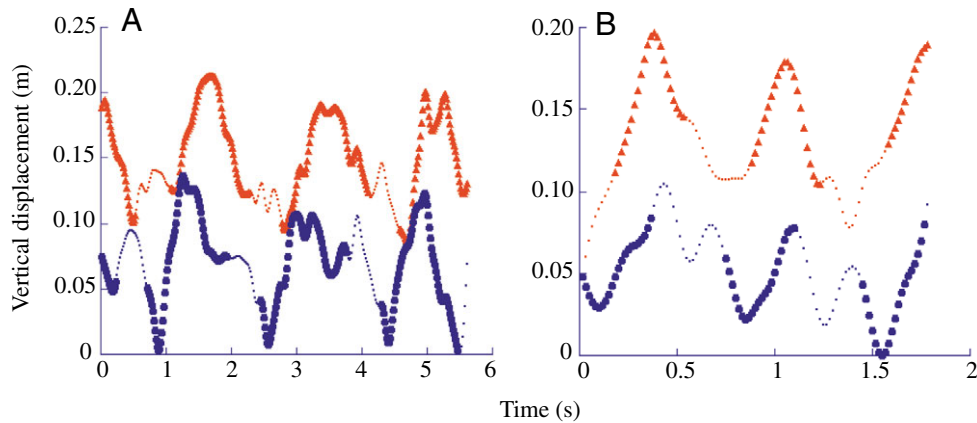


Fig. 8. Vertical displacements (from the lowest point shown) of the right (in lateral view) shoulder (red triangles) and hip (blue circles) joints for a representative Asian elephant ($h=1.41$ m) moving at 1.2 m s^{-1} (in A; ~ 3 strides) and 5.4 m s^{-1} (in B; <2.5 strides), plotted against time. Large symbols indicate motion during the stance phase; small symbols are motion during the swing phase of the respective limb.

$9.5\text{--}11\text{ m s}^{-1}$ speed reports to be exaggerations based upon these errors and the excitement of witnessing a charging wild elephant. Our data (Table 3) allow us to predict that an African bull elephant moving at 11 m s^{-1} (assuming $h=2\text{ m}$; $Fr=6.3$) would have a duty factor of 0.40 (hence still lacking a complete aerial phase), t_{st} and t_{sw} of 0.17 and 0.26 s, respectively (lower than any observed here for juvenile elephants), $\hat{L}=3.5$, $\hat{F}=0.89$, and would be taking 2+ strides of 5+ m length every second. Considering the maximal values we have measured for elephants (above), this is not inconceivable, but stretches credulity. The most reasonable conclusion at present, considering the strong similarities between Asian and African elephant kinematics demonstrated in this study, is that the near maximal speed of African elephants is essentially the same as Asian elephants: $<7\text{ m s}^{-1}$.

The minimal β we observed (0.37) is substantially less than those previously attributed to elephants [0.49+ (Alexander et al., 1979a; Christian et al., 1999; Gambaryan, 1974; Hildebrand, 1980; Hildebrand, 1985)]. Limb bone stresses were estimated during locomotion in an African elephant moving at $\sim 4.5\text{ m s}^{-1}$ ($\beta=0.49$) (Alexander et al., 1979a). Thus maximal bone stresses have probably been underestimated by a factor of 76% (duty factor $0.37/0.49$) or more, especially for smaller elephants that would be experiencing greater relative peak forces. Accurate estimation of such stresses under peak loads depends directly on obtaining near-maximal locomotor performance, particularly as the results have major influence on comparative analyses of scaling, bone strength and speed (e.g. Biewener, 1990; Blanco et al., 2003; Christiansen, 2002).

As minimal β decreases with size, our data hint that very large elephants ($>4000\text{ kg}$) may no longer reach $\beta<0.5$ and hence would lose any aerial phases for the fore- and hindlimb pairs. If elephants change gait (see below), then very large elephants might lose this capacity. Such a phenomenon would be remarkable for terrestrial animals, few of which are known to lose a gait during adulthood because of body size increase.

This identifies a need for more locomotor studies of the largest elephants to test this speculation.

Our data (Fig. 6) show that even small elephants can move as quickly as large elephants; related parameters such as total leg length (Fig. 6D) do not exhibit strong allometry. Near-maximal speed may peak early in life, as would be expected for animals that are especially vulnerable to predation at young ages (Pennycuik, 1975), whereas larger adult elephants presumably have little need for high speed capacity.

Kinematic changes with speed: is there a gait change?

There is no reason to doubt that slow-moving elephants are walking in any sense of the word, but fast-moving elephants pose a challenge for applying many gait definitions. Hutchinson et al. doubted whether fast-moving elephants were merely walking (Hutchinson et al., 2003), but the speed at which any potential gait transition occurred was left open. As they intimated, this issue depends on how one defines or diagnoses a gait: by footfall pattern (Hildebrand, 1966; Hildebrand, 1976; Hildebrand, 1980), presence of an aerial phase or a duty factor <0.5 (Gambaryan, 1974; Hildebrand, 1962; Hildebrand, 1966; Hildebrand, 1976; Hildebrand, 1980; Muybridge, 1899), Froude number (Alexander and Jayes, 1983), pendular/bouncing body or limb dynamics (Cavagna et al., 1977; Farley et al., 1993; Heglund et al., 1982a; Heglund et al., 1982b; McGeer, 1992; Parchman et al., 2003), or discontinuities in locomotor parameters (Alexander, 1989; Gatesy, 1999; Gatesy and Biewener, 1991). We favor a biomechanical definition, but here explore how these definitions agree and disagree in identifying a potential gait transition in elephants (Table 5).

The elephants only used lateral sequence (with lateral couplets or singlefoot) footfall patterns; no change of footfall pattern to another mode such as pacing or trotting was observed. Hildebrand stated that elephants use a 'slow trot' at lower speeds (Hildebrand, 1965; Hildebrand, 1966; Hildebrand, 1976) but we did not observe this in 62 elephants;

Table 5. Results of the application of different gait definitions to the question: do elephants only walk at their fastest speeds?

Criterion	Reference	Only walk?
Froude number <1 or <0.5	(Alexander and Jayes, 1983)	No, no
Walking footfall pattern	(Hildebrand, 1976)	Yes
Duty factor >0.5	(Hildebrand, 1976)	No
No whole body aerial phase (or limb pairs)	(Hildebrand, 1976)	Yes (no)
Continuous stride parameters across all speeds	(Alexander, 1989; Gatesy, 1999)	No
Pendular shoulder/hip motion in stance phase	(McMahon et al., 1987)	Yes/no
Speed close to metabolic optimum	(Hoyt and Taylor, 1981)	No
Inverted pendulum-like center of mass mechanical energy pattern	(Cavagna et al., 1977)	?

it is conceivable that this pattern might be used under unusual conditions. Hence a strict footfall sequence-based definition would not classify elephants as having any gait transition. Regardless, it is not only young elephants that use these lateral sequence footfall patterns (Hildebrand, 1985). We observed similar locomotion in elephants as large as 4632 kg.

As speed increased, elephants moved away from having forefoot contacts ~15% of a stride after the ipsilateral hindfoot contacts toward 25% phasing. According to the quadrupedal walking model (Griffin et al., 2004), the phasing at slow walking (present in dogs) keeps pendulum-like energy recovery high when combined with higher forelimb impulses [expected for elephants that support ~60% of their body weight on their forelimbs, like most mammals (e.g. Alexander et al., 1979a); J.R.H., unpublished observations]. The shift toward evenly offset footfalls in faster-moving elephants may thus be additional evidence of a mechanical transition.

Elephants never have a whole-body aerial phase so in a classical sense they do not run. Yet numerous studies have shown that an aerial phase is not a *sine qua non* of bouncing (i.e. running) gaits (Clark and Alexander, 1975; Gatesy and Biewener, 1991; McMahon et al., 1987; Parchman et al., 2003; Robilliard et al., 2006; Rubenson et al., 2004). Additionally, an aerial phase for one rather than both fore/hindlimb pairs may impart enough limb compression for a transition to bouncing mechanics. At around $Fr > 1$ ($\beta < 0.5$), elephant fore- or hindlimb pairs attain their own aerial phases, so the dynamics of their fore/hind quarters could biomechanically be running. Considering that β_{diff} tended to remain positive (~0.03), assuming a $\beta = 0.5$ boundary between walking and running (Cartmill et al., 2002; Hildebrand, 1976; Hildebrand, 1980) would give one (just using the mean duty factor β) or two (fore- and hindlimb) potential gait transition points, which is problematic.

Using our duty factor and limb phase data we can determine when each left-right limb pair (fore/hind) gained its own aerial phase, and at what speed elephants should have an aerial phase in their locomotion, if they move appreciably faster than observed speeds. An aerial phase must occur in any quadruped if β falls below 0.25, because four feet cannot be spaced out more evenly than relative limb phases of 0.0, 0.25, 0.50 and 0.75. If β were less than the longest gap between foot falls, then there would be an aerial phase for the whole body. The longest gap was always between a hind foot contact and the

contact of the diagonal fore foot. Hence it is either ($P_{th} - P_{lf}$) or ($P_{lh} - P_{rf}$); fortunately these quantities are equal, so either suffices. Substituting 1.0 for P_{lh} (same as 0.0), and plotting these data against \hat{u} (Fig. 9), we find that at slow speeds the decrease of β required in order to have a whole-body aerial phase is greater than at fast speeds. This is not surprising as slower speeds involve greater β (Fig. 4), and the possibility of an aerial phase is not a concern at most P values. At fast speeds, however, β would need to be only ~0.1 less for an aerial phase to occur. As β decreased less steeply with increasing speed (especially past $Fr \sim 2$), we infer that this pattern helps prevent the attainment of an aerial phase in elephants. This conclusion holds whether one considers the mean β or β for individual limbs.

How elephants actively or passively control this pattern, or why a whole-body aerial phase is never used even in small elephants, remains unknown. One potential mechanism used by fast-moving elephants is a decrease of limb stiffness at greater \hat{u} and smaller β values. This is supported by the increase of hindlimb compression at $\hat{u} > 1$, evidenced by increased hip and knee flexion [Fig. 1D (see McMahon et al., 1987)]. This could lengthen t_{st} and keep β values greater [and rates of force application smaller (Hoyt et al., 2000)] than they would be if β decreased linearly with dimensionless speed. In the latter case, elephants would be more likely to attain whole-body aerial phases, and attendant increases in peak vertical ground reaction forces and/or potentially injurious limb vibrations (e.g. McMahon et al., 1987).

Most animals change gait at $Fr \sim 0.4-0.6$ (Ahlborn and Blake, 2002; Alexander and Jayes, 1983; Gatesy and Biewener, 1991), and theoretically a shift must occur at $Fr \sim 1$ (Alexander and Maloiy, 1989; Usherwood, 2005). On these grounds elephants, which routinely attain $Fr > 0.6$ or even $Fr > 2.5$ [where most quadrupeds switch from trotting to galloping (Alexander and Jayes, 1983)], should change gait at some point. Elephants show no diagnostic kinematic characteristics of running at $Fr \sim 0.5$, but at $Fr > 1$ (see above) exhibit an increasingly compliant hindlimb and an aerial phase for the hindquarters, followed by an aerial phase for the forequarters at slightly faster speeds.

Additionally, like Hutchinson et al. (Hutchinson et al., 2003) we find kinematic evidence that the hindlimbs of elephants are generally less pendular (in terms of rigidity) in their stance phase motions than the forelimbs, indicating that

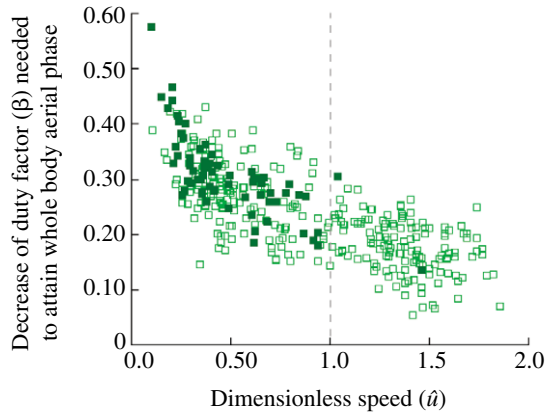


Fig. 9. Duty factor minus right forelimb relative limb phase (P_{rf}) (see Discussion) required to have an aerial phase for the entire body, plotted against dimensionless speed for African (filled symbols) and Asian (open symbols) elephants. A value of 0 or less would require a whole-body aerial phase.

limb function may differ among these limbs, particularly at moderately fast speeds. Gambaryan supposed that the motion of the center of mass of the body was horizontal [(Gambaryan, 1974) p. 169]. Yet he depicted [(Gambaryan, 1974) fig. 117] the vertical displacements of the limb joints of a ‘fast walking’ (unknown speed) elephant as having inverted pendulum-like scapular (presumably comparable to shoulder) motion. Unusually, the same elephant also had a hip joint that raised vertically throughout stance. This is similar to some patterns in elephants that we measured at intermediate speeds ($Fr \sim 1$); also for an elephant ‘running’ at unknown speed (Marey and Pagès, 1887).

Elephants show some subtle discontinuities in how their stride parameters change with speed. Such discontinuities can be viewed as evidence for a gait shift (Alexander, 1989; Gatesy, 1999). In particular, stride lengths and frequencies showed a noticeable change of slope close to $Fr=1$, and possibly $Fr \sim 0.3$ as well (Fig. 5B, Fig. 7). Additionally, the gradual shift toward more evenly spread P values coincided with a shortening of t_{sw} toward a minimum of 0.28 s. As β never dropped below 0.37, there may be some overlap (about 10% of a stride) required for elephants to comfortably shift weight-bearing from one limb to another (Hildebrand, 1965; Hildebrand, 1966). Avoiding ipsilateral limb interference is another likely explanation for this limb phase shift (Gambaryan, 1974; Hildebrand, 1966; Hildebrand, 1976; Hildebrand, 1980). Interestingly, at $\hat{u} > 1$, values of t_{st} and t_{sw} approached asymptotic values (Fig. 5A). Thus at their fastest speeds, the elephants were not taking much faster steps, and were not using a whole-body aerial phase, so some other mechanism to extend stride length was used to increase velocity. Altered angular excursions of the limb joints are a likely candidate (Hildebrand, 1984; Schwerda, 2003; Usherwood, 2005). Our findings are consistent with the observation of Christian et al. that elephants change speed largely by decreasing swing times and increasing stride frequency (Christian et al., 1999), which helps to keep stance

times large and peak limb forces small. Yet at fast speeds, increased limb displacement (or compliance) may contribute to stride length and speed increases, as swing time and stride frequency, respectively, approach their minimum and maximum values.

The minimal metabolic cost of transport for three mid-sized African elephants (~ 1500 kg) was at 1.0 m s^{-1} (Langman et al., 1995). If elephants do not change gait, they should face high energetic costs at their maximal speed, which is almost seven times the energetic optimum. The latter would be rather unusual compared to other animals. Changing gait would allow them to reach a second minimal metabolic cost of transport (e.g. Hoyt and Taylor, 1981). Elephants do not habitually use speeds anywhere near their maximum. One reason may be energetic.

Like Hutchinson et al. (Hutchinson et al., 2003) we still consider it prudent to avoid characterizing fast-moving elephants as truly running (i.e. as having bouncing kinetics of the whole-body center of mass) until kinetic force platform data are available. Even the classical dichotomy between pendular walking and springy running gaits may be blurred in, or overly simplistic for, animals like elephants that use widely out-of-phase limb motions at fast speeds or change kinematic parameters smoothly with increasing speed (e.g. Ahn et al., 2004; Clark and Alexander, 1975; Gatesy and Biewener, 1991; Parchman et al., 2003; Riskin et al., 2006; Rubenson et al., 2004) (J. J. Robilliard, T. Pfau and A. Wilson, manuscript submitted for publication). Regardless, elephants seem to change their limb, and possibly body, mechanics near a Froude number of 1, although a shift at a lower Fr cannot be ruled out as the kinematic patterns are almost a continuum.

Do Asian and African elephants have different kinematics?

Although we found statistically significant differences in all but relative limb phases and fore- minus hindlimb duty factors, we doubt that these differences have tremendous biological significance. The differences in absolute terms are all quite small and our sample was not ideally representative (or random) for African elephants (14 individuals vs 48 Asian). Because African and Asian elephants share a common ancestry with extinct mammoths (*Mammuthus* spp.) as members of the Elephantidae (Krause et al., 2006; Thomas et al., 2000), we expect that mammoths and other extinct elephantids moved similarly to extant elephants, except where there are major size, shape or other mechanically relevant differences. We expect that even dwarf insular forms, if morphologically similar to baby elephants, would have moved similarly. This is because small baby elephants only differ in their relative locomotor abilities compared to large adults; they do not use drastically different kinematics. This common elephantid pattern of locomotion provides a baseline from which evolutionary changes within Proboscidea can be reconstructed backwards toward the much smaller, probably semi-aquatic distant ancestors of all elephants, or to infer how strange proboscideans such as mastodons and deinotheres may have stood and moved.

Comparison with other animals

Elephant locomotor kinematics have many patterns in common with typical tetrapods, especially larger quadrupeds, such as increasing velocity primarily by increasing stride frequency until a near-maximal stride frequency is reached (at around the walk–run transition in other animals), then relying relatively more on increasing stride length (Pennycuick, 1975; Heglund and Taylor, 1988). Additionally, size seems to influence their locomotion in ways similar to other animals: smaller elephants have relatively greater locomotor performance such as greater near-maximal relative stride lengths (Hoyt et al., 2000; Pennycuick, 1975) and frequencies or Froude numbers, and smaller minimal duty factors. Elephants use relative stride lengths and duty factors that are expected (Table 6) for corresponding Fr in smaller animals (Alexander, 1977; Alexander and Jayes, 1983), and likewise use stride frequencies that are expected for their body mass (Heglund et al., 1974) or for animals galloping at maximal observed speed (Heglund and Taylor, 1988). Hence despite

their obvious non-geometric similarity with other quadrupedal mammals, especially cursorial ones (Christiansen, 2002; Coombs, 1978; Gregory, 1912), elephants tend to meet many predictions of dynamic similarity theory. At their faster speeds, elephant stride parameters likewise match those of running quadrupeds (Alexander and Jayes, 1983; Heglund and Taylor, 1988). This adds credence to our inference that elephants are not simply walking at their near-maximal speeds (Table 5).

However, elephants also display some kinematic patterns that are unusual for terrestrial quadrupeds (Table 6). They reach absolute stride lengths and near-maximal speeds that are smaller than predicted for their size (Heglund and Taylor, 1988). Although elephants can reach moderate speeds, they do not change their footfall patterns, so this is another striking feature in which they violate expectations from dynamic similarity theory.

A comparison of elephants with the second heaviest land mammals, rhinoceroses, reveals important differences in locomotor function whose underlying mechanical and

Table 6. *Elephant locomotor kinematics compared with scaling data from other animals*

Dependent variable	Independent variable	At x value of	Predicted value	Actual value	Ratio	a	b	Reference
Relative stride length								
Walk	Fr	0.067	1.0	1.2	0.80	2.4	0.34	1
Run	Fr	1.0	1.9	2.0	0.95	1.9	0.40	1
Run; non-cursorial	Fr	1.0	2.7	2.0	1.4	2.7	0.28	1
Forelimb duty factor								
Walk	Fr	0.067	0.76	0.91	0.83	0.52	-0.14	1
Run	Fr	1.0	0.52	0.53	0.98	0.52	-0.28	1
Hindlimb duty factor								
Walk	Fr	0.067	0.83	0.88	0.94	0.51	-0.18	1
Run	Fr	1.0	0.53	0.51	1.0	0.53	-0.28	1
Stride frequency (Hz)	M_b (kg)	560	1.8	1.8	1.0	4.48	-0.14	2
Stride length (m)	M_b (kg)	560	3.9	3.1	1.3	0.35	0.38	2
Velocity ($m\ s^{-1}$)	M_b (kg)	560	7.0	6.8	1.03	1.53	0.24	2
Stride frequency (Hz)	M_b (kg)	2790	1.5	1.5	0.98	4.48	-0.14	2
Stride length (m)	M_b (kg)	2790	7.1	4.2	1.70	0.35	0.38	2
Velocity ($m\ s^{-1}$)	M_b (kg)	2790	10.3	6.8	1.51	1.53	0.24	2
Relative stride length	\hat{u}	1.0	2.3	2.0	1.2	2.3	0.60	3
Relative stride length	\hat{u}	1.7	3.2	2.6	1.2	2.3	0.60	3
Stride frequency (Hz): maximal speed	M_b (kg)	560	1.7	1.8	0.94	4.7	0.162	4
Stride frequency (Hz): maximal speed	M_b (kg)	2790	1.3	1.5	0.87	4.7	0.162	4
Minimal trotting velocity	M_b (kg)	560	2.9	3.3	0.86	0.593	0.249	4
Minimal trotting velocity ($m\ s^{-1}$)	M_b (kg)	2790	4.3	4.1	1.1	0.593	0.249	4
Maximal speed ($m\ s^{-1}$)	M_b (kg)	560	10.25	6.8	1.51	17	-0.08	5
Maximal speed ($m\ s^{-1}$)	M_b (kg)	2790	9.01	6.8	1.33	17	-0.08	5
Maximal stride frequency (Hz)	M_b (kg)	560	2.21	1.7	1.30	6.9	-0.18	5
Maximal stride frequency (Hz)	M_b (kg)	2790	1.65	1.3	1.27	6.9	-0.18	5
Minimal hindlimb duty factor	M_b (kg)	560	0.27	0.40	0.67	0.11	0.14	5
Minimal hindlimb duty factor	M_b (kg)	2790	0.33	0.49	0.68	0.11	0.14	5

The dependent (y) and independent (x) variables are listed along with the independent value used to predict the y value, the actual y value used by elephants (from least-squares equations in Table 3), the ratio of the predicted/actual y values, and the ‘predicted value’ scaling equations used (in $y=ax^b$). References for the ‘predicted value’ equations used are: ¹(Alexander and Jayes, 1983); ²(Heglund et al., 1974); ³(Alexander, 1977); ⁴(Heglund and Taylor, 1988); ⁵(Alexander et al., 1977).

Body mass values used are estimates for representative juvenile (560 kg) and adult (2790 kg) individuals.

anatomical explanations remain poorly understood. For example, unlike elephants, rhinoceroses can trot and gallop, reaching $Fr > 3$ (Alexander and Jayes, 1983; Alexander and Pond, 1992). This underscores the great difference between these animals: size differences aside, rhinoceros locomotion is fairly typical for cursorial quadrupeds in general (Alexander and Jayes, 1983) whereas elephants move somewhat differently and are more limited in their range of locomotor performance (near-maximal speed in particular; as above). Differences in limb proportions and other anatomical parameters help explain some of these differences (Christiansen, 2002; Coombs, 1978; Paul, 1998), but not all. Differential scaling [discontinuously stronger allometry at larger sizes (Bertram and Biewener, 1990; Christiansen, 2002; Iriarte and Díaz, 2002)] is likely a major factor underlying these differences. Unlike elephants, rhinoceroses scale with strong positive allometry [following static stress similarity (Bertram and Biewener, 1990)], which would facilitate relatively greater locomotor performance (Alexander et al., 1979a,b; Alexander and Pond, 1992).

Elephants are the exemplar of living animals with graviportal limb design, whereas horses are among the largest living animals with very cursorial limb design. Despite these major anatomical differences, some horses use footfall patterns that are very similar to elephants: the ‘running walk’ or tölt [(Biknevicius et al., 2004; Zips et al., 2001); J. J. Robilliard, T. Pfau and A. Wilson, manuscript submitted for publication]. Do these horses that maintain singlefoot with lateral sequence footfall patterns across a wide speed range move the same as elephants? Indeed there are striking similarities. Both taxa show a fairly smooth change of stride parameters (although with some subtle discontinuities) with speed across the boundary of $Fr=1$ [$\sim 3 \text{ m s}^{-1}$ (Biknevicius et al., 2004); J. J. Robilliard, T. Pfau and A. Wilson, manuscript submitted for publication]. Both reach small duty factors while avoiding a whole-body aerial phase, yet increasing limb compliance. Finally, both taxa rely mainly on linear increases of stride length to increase speed, particularly at faster speeds where stride frequency reaches a plateau (Biknevicius et al., 2004). However, differences are also evident: unlike elephants, tölting horses have greater hindlimb than forelimb duty factors and stance times (Biknevicius et al., 2004) (J. J. Robilliard, T. Pfau and A. Wilson, manuscript submitted for publication), occasionally attain aerial phases [albeit at greater Fr than measured for elephants (Zips et al., 2001; Biknevicius et al., 2004)], and do not seem to have consistent changes of relative forelimb phase with speed (Zips et al., 2001). This divergence of fore- and hindlimb mechanics inferred for horses and elephants may be even more commonplace among animals – for example, some cows have been shown to have strongly different ground reaction force profiles for their fore- and hindlimbs (Scott, 1988). Slow normal walking and slow tölting in horses have quite different kinematics (J. J. Robilliard, T. Pfau and A. Wilson, manuscript submitted for publication), whereas elephants increase speed from a slow walk to faster locomotion more smoothly. Additionally, although comparable data are limited, elephants seem to reach smaller duty factors

($\beta=0.37$ at $Fr=3.4$) than horses at greater Fr [$\beta=0.41$ at $Fr=4.5$ (Biknevicius et al., 2004)]. Hence it would be premature to infer that the horses and elephants have very similar center of mass or limb dynamics, particularly as the linkage between limb compliance (i.e. spring-like limb function) and center of mass movement (i.e. spring-mass whole-body mechanics) is complex (Ahn et al., 2004; Alexander, 1980; Griffin et al., 2004). Yet the noted similarities underscore the underlying physical mechanisms that are presumably common to many animals that maintain lateral sequence gaits at fast speeds (Alexander, 1980; Hildebrand, 1976).

Conclusions

We have shown how elephant kinematics are related to size, speed and species, yet many general kinematic patterns are maintained across all of these spectra. Most stride parameters change smoothly with increasing speed in both species of extant elephants regardless of size – there is no discrete transition where many parameters change in tandem. Yet we find evidence that limb mechanics (e.g. hindlimb compression, aerial phases for contralateral limb pairs) change near a Froude number of 1, suggesting at least more compliant hindlimb function. Although force platform data on center of mass dynamics are needed, our kinematic data are vital for an integrative solution to the mystery of how elephant locomotor dynamics change with speed. Larger or smaller elephants do not use different maximal speeds, but smaller elephants have higher relative locomotor performance like other animals, and very large elephants may even lose the capacity to exceed Froude numbers of 1 or use more compliant limb mechanics. Compared with other quadrupeds, elephants are unusual in maintaining a lateral sequence ‘walk’ at fast speeds, but remarkably other stride parameters match expectations for dynamic similarity. Our kinematic data are useful not only for understanding how elephants move, but as we have established ‘normal’ kinematic patterns (e.g. Figs 3–5, 7), our data are also useful for identifying abnormal outlier (e.g. pathological) locomotor patterns in elephants, which could aid early identification of musculoskeletal disorders in captive elephants.

List of symbols

β	duty factor
β_{diff}	duty factor fore–hind difference
F	stride frequency
\hat{F}	relative stride frequency
Fr	Froude number
g	acceleration due to gravity
h	hip height
L	stride length
\hat{L}	relative stride length
M_b	body mass
P	relative limb phase (left fore [P_{lf}], right hind [P_{rh}], and right fore [P_{rf}])
t_{st}	stance phase duration (i.e. stance time)

t_{sw}	swing phase duration (i.e. stance time)
u	forward velocity
\hat{u}	dimensionless speed ($Fr^{0.5}$)

We thank the many elephant handlers, keepers and managers/advisors we have worked with, including David Hagan and staff at Indianapolis Zoo, Anthony Tropeano and staff at Colchester Zoo, Dave Blasko and Steve Johnson (Six Flags Marine World), Gary and Kari Johnson (Have Trunk Will Travel), and Richard Lair (Thai Elephant Institute). Richard Lair deserves special thanks for his dedicated support of our Thailand research and for sharing his vast knowledge of elephants, including elephant races and elephant-friendly motivational techniques. We give heartfelt thanks to the elephants we've studied, from Misha to Amos, to Nong Pop and Nong Big, and all others. We also thank the Polypedal Lab at the University of California for usage of digitizing equipment. J.R.H. thanks Hinnah Rehman for her dedicated data analysis, supplemented by help from Kirsten Patrick and Alice Yao. Karin Jespers was instrumental in many technical aspects of the UK work. We also thank the many funding sources that supported this work from 1998–2006. J.R.H. thanks the *Journal of Experimental Biology* for a Travelling Fellowship awarded in 2000, the National Science Foundation for a Research Fellowship in Biological Informatics awarded in 2001, the BBSRC for New Investigator research grant number BB/C516844/1 awarded in 2005, and the Departments of Integrative Biology (University of California) and Veterinary Basic Sciences (The Royal Veterinary College) for financial support. D.J.F. appreciates funding from the University of California URA Program and summer stipend. Helpful comments on early aspects of this work and drafts of this manuscript are appreciated from the Berkeley Biomechanics Seminar, the Stanford Neuromuscular Biomechanics Lab, and the Structure and Motion Lab. We also appreciate similarly helpful comments on this research from Norman Heglund, Charlotte Miller, Lei Ren, James Usherwood, Sarah Williams, Alan Wilson, and two anonymous reviewers.

References

- Ahlborn, B. K. and Blake, R. W. (2002). Walking and running at resonance. *Zoology* **105**, 165–174.
- Ahn, A., Furrow, E. and Biewener, A. A. (2004). Walking and running in the red-legged running frog, *Kassina maculata*. *J. Exp. Biol.* **207**, 399–410.
- Alexander, R. McN. (1977). Allometry of the limbs of antelopes (Bovidae). *J. Zool.* **183**, 125–146.
- Alexander, R. McN. (1980). Optimum walking techniques for quadrupeds and bipeds. *J. Zool.* **192**, 97–117.
- Alexander, R. McN. (1989). Optimization and gaits in the locomotion of vertebrates. *Physiol. Rev.* **69**, 1199–1227.
- Alexander, R. McN. and Jayes, A. S. (1983). A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *J. Zool.* **201**, 135–152.
- Alexander, R. McN. and Maloiy, G. M. O. (1989). Locomotion of African mammals. *Symp. Zool. Soc. Lond.* **61**, 163–180.
- Alexander, R., McN. and Pond, C. M. (1992). Locomotion and bone strength of the White Rhinoceros, *Ceratotherium simum*. *J. Zool.* **227**, 63–69.
- Alexander, R. McN., Langman, V. A. and Jayes, A. S. (1977). Fast locomotion of some African ungulates. *J. Zool.* **183**, 291–300.
- Alexander, R. McN., Maloiy, G. M. O., Hunter, B., Jayes, A. S. and Nturi, J. (1979a). Mechanical stresses in fast locomotion of buffalo (*Syncerus caffer*) and elephant (*Loxodonta africana*). *J. Zool.* **189**, 135–144.
- Alexander, R. McN., Jayes, A. S., Maloiy, G. M. O. and Wathuta, E. M. (1979b). Allometry of the limb bones of mammals from shrews (*Sorex*) to elephant (*Loxodonta*). *J. Zool.* **187**, 305–314.
- Alexander, S. (2000). *The Astonishing Elephant*. New York: Random House.
- Andrews, R. C. (1937). Wings win. *Nat. Hist.* October **1937**, 559–568.
- Baker, S. W. (1890). *Wild Beasts and Their Ways*, Vol. 2. New York: Macmillan.
- Bakker, R. T. (1975). Experimental and fossil evidence for the evolution of tetrapod bioenergetics. In *Perspectives of Biophysical Ecology* (ed. D. M. Gates and R. B. Schmerl), pp. 365–399. New York: Springer Verlag.
- Bertram, J. E. A. and Biewener, A. A. (1990). Differential scaling of the long bones in the terrestrial Carnivora and other mammals. *J. Morphol.* **204**, 157–169.
- Biewener, A. A. (1989). Scaling body support in mammals: limb posture and muscle mechanics. *Science* **245**, 45–48.
- Biewener, A. A. (1990). Biomechanics of mammalian terrestrial locomotion. *Science* **250**, 1097–1103.
- Biknevicius, A. R., Mullineaux, D. R. and Clayton, H. M. (2004). Ground reaction forces and limb function in töltting Icelandic horses. *Equine Vet. J.* **36**, 743–747.
- Blanco, R. E., Gambini, R. and Farina, R. A. (2003). Mechanical model for the theoretical determination of maximum running speed in mammals. *J. Theor. Biol.* **222**, 117–125.
- Bohonak, A. J. and van der Linde, K. (2004). RMA: software for Reduced Major Axis regression. Java version. Website: <http://www.kimvdlinde.com/professional/rma.html>.
- Cartmill, M., Lemelin, P. and Schmitt, D. (2002). Support polygons and symmetrical gaits in mammals. *Zool. J. Linn. Soc.* **136**, 401–420.
- Cavagna, G. A., Heglund, N. C. and Taylor, C. R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **233**, R243–R261.
- Cavagna, G. A., Franzetti, P., Heglund, N. C. and Willems, P. (1988). The determinants of the step frequency in running, trotting and hopping in man and other vertebrates. *J. Physiol.* **399**, 81–92.
- Christian, A., Müller, R. H. G., Christian, G. and Preuschoft, H. (1999). Limb swinging in elephants and giraffes and implications for the reconstruction of limb movements and speed estimates in large dinosaurs. *Mitt. Mus. Nat. Berl. Geowiss. Reihe* **2**, 81–90.
- Christiansen, P. (2002). Locomotion in terrestrial mammals: the influence of body mass, limb length and bone proportions on speed. *Zool. J. Linn. Soc.* **136**, 685–714.
- Clark, J. and Alexander, R. McN. (1975). Mechanics of running by quail (*Coturnix*). *J. Zool.* **176**, 87–113.
- Coombs, W. P. (1978). Theoretical aspects of cursorial adaptations in dinosaurs. *Q. Rev. Biol.* **53**, 393–415.
- Csuti, B. A., Sargent, E. L. and Bechert, U. S. (ed.) (2001). *The Elephant's Foot: Care and Prevention of Foot Conditions in Captive Asian and African Elephants*. Ames: Iowa State Press.
- Farley, C. T., Glasheen, J. and McMahon, T. A. (1993). Running springs: speed and animal size. *J. Exp. Biol.* **185**, 71–86.
- Gale, U. T. (1974). *Burmese Timber Elephant*. Rangoon, India: Trade Corporation.
- Gambaryan, P. P. (1974). *How Mammals Run*. New York: John Wiley & Sons.
- Garland, T. G. (1983). The relation between maximal running speed and body mass in terrestrial mammals. *J. Zool.* **199**, 157–170.
- Gatesy, S. M. (1999). Guineafowl hind limb function. I: Cineradiographic analysis and speed effects. *J. Morphol.* **240**, 115–125.
- Gatesy, S. M. and Biewener, A. A. (1991). Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *J. Zool.* **224**, 127–147.
- Gregory, W. K. (1912). Notes on the principles of quadrupedal locomotion and the mechanisms of the limbs in hoofed animals. *Ann. NY Acad. Sci.* **22**, 267–292.
- Griffin, T. M., Main, R. P. and Farley, C. T. (2004). Biomechanics of quadrupedal walking: how do four-legged animals achieve pendulum-like mechanics? *J. Exp. Biol.* **207**, 3545–3558.
- Heglund, N. C. and Taylor, C. R. (1988). Speed, stride frequency and energy cost per stride: how do they change with body size and gait? *J. Exp. Biol.* **138**, 301–318.
- Heglund, N. C., Taylor, C. R. and McMahon, T. A. (1974). Scaling stride frequency and gait to animal size: mice to horses. *Science* **186**, 1112–1113.
- Heglund, N. C., Cavagna, G. A. and Taylor, C. R. (1982a). Energetics and

- mechanics of terrestrial locomotion III: Energy changes of the centre of mass as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 41-56.
- Heglund, N. C., Cavagna, G. A. and Taylor, C. R.** (1982b). Energetics and mechanics of terrestrial locomotion IV: Total energy changes as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 57-66.
- Hildebrand, M.** (1962). Walking, running, and jumping. *Am. Zool.* **2**, 151-155.
- Hildebrand, M.** (1965). Symmetrical gaits of horses. *Science* **191**, 701-708.
- Hildebrand, M.** (1966). Analysis of the symmetrical gaits of tetrapods. *Folia Biotheor.* **6**, 9-22.
- Hildebrand, M.** (1976). Analysis of tetrapod gaits: general considerations and symmetrical gaits. In *Neural Control of Locomotion* (ed. P. S. G. Stein and D. G. Smart), pp. 203-236. New York: Plenum Press.
- Hildebrand, M.** (1980). The adaptive significance of tetrapod gait selection. *Am. Zool.* **20**, 255-267.
- Hildebrand, M.** (1984). Rotations of the leg segments of three fast-running cursors and an elephant. *J. Mammal.* **65**, 718-720.
- Hildebrand, M.** (1985). Walking and running. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble and K. F. Liem), pp. 38-57. Cambridge: Harvard University Press.
- Hildebrand, M. and Hurley, J. P.** (1985). Energy of the oscillating legs of a fast-moving cheetah, pronghorn, jackrabbit, and elephant. *J. Morphol.* **184**, 23-31.
- Hof, A. L.** (1996). Scaling gait data to body size. *Gait Posture* **4**, 222-223.
- Hoyt, D. F. and Taylor, C. R.** (1981). Gait and the energetics of locomotion in horses. *Nature* **292**, 239-240.
- Hoyt, D. F., Wickler, S. J. and Cogger, E. A.** (2000). Time of contact and step length: the effect of limb length, running speed, load carrying and incline. *J. Exp. Biol.* **203**, 221-227.
- Howell, A. B.** (1944). *Speed in Animals: Their Specialization for Running and Leaping*. Chicago: University of Chicago Press.
- Hutchinson, J. R., Famini, D., Lair, R. and Kram, R.** (2003). Biomechanics: are fast-moving elephants really running? *Nature* **422**, 493-494.
- Iriarte-Díaz, J.** (2002). Differential scaling of locomotor performance in small and large terrestrial mammals. *J. Exp. Biol.* **205**, 2897-2908.
- Krause, J., Dear, P. H., Pollack, J. L., Slatkin, M., Spriggs, H., Barnes, I., Lister, A. M., Ebersberger, I., Paabo, S. and Hoffreiter, M.** (2006). Multiplex amplification of the mammoth mitochondrial genome and the evolution of Elephantidae. *Nature* **439**, 724-727.
- Langman, V. A., Roberts, T. J., Black, J., Maloiy, G. M. O., Heglund, N. C., Weber, J.-M., Kram, R. and Taylor, C. R.** (1995). Moving cheaply: energetics of walking in the African Elephant. *J. Exp. Biol.* **198**, 629-632.
- Le Rue, L., III** (1993). *A Portrait of the Animal World*. New York: Todtri Productions.
- Losos, J. B., Creer, D. A. and Schulte, J. A., II** (2002). Cautionary comments on the measurement of maximum locomotor capabilities. *J. Zool.* **258**, 57-61.
- Marey, E. J. and Pagès, C.** (1887). Locomotion comparée: mouvement du membre pelvien chez l'homme, l'éléphant et le cheval. *C. R. Acad. Sci.* **105**, 149-156.
- McGeer, T.** (1992). Principles of walking and running. In *Advances in Comparative and Environmental Physiology: Mechanics of Animal Locomotion* (ed. R. McN. Alexander), pp. 133-139. Berlin: Springer-Verlag.
- McMahon, T. A., Valiant, G. and Frederick, E. C.** (1987). Groucho running. *J. Appl. Physiol.* **62**, 2326-2337.
- Muybridge, E.** (1899). *Animals in Motion*. New York: Dover.
- Nicodemus, M. C. and Clayton, H. M.** (2003). Temporal variables of four-beat, stepping gaits of gaited horses. *Appl. Anim. Behav. Sci.* **80**, 133-142.
- Parchman, A. J., Reilly, S. M. and Biknevičius, A. R.** (2003). Whole-body mechanics and gaits in the gray short-tailed opossum *Monodelphis domestica*: integrating patterns of locomotion in a semi-erect mammal. *J. Exp. Biol.* **206**, 1379-1388.
- Paul, G. S.** (1998). Limb design, function and running performance in ostrich-mimics and tyrannosaurs. *Gaia* **15**, 257-270.
- Pennycuik, C. J.** (1975). On the running of the gnu (*Connochaetes taurinus*) and other animals. *J. Exp. Biol.* **63**, 775-799.
- Raibert, M. H.** (1990). Trotting, pacing and bounding by a quadruped robot. *J. Biomech.* **23** suppl. 1, 79-98.
- Riskin, D. K., Parsons, S., Schutt, W. A., Jr, Carter, G. G. and Hermanson, J. W.** (2006). Terrestrial locomotion of the New Zealand short-tailed bat *Mystacina tuberculata* and the common vampire bat *Desmodus rotundus*. *J. Exp. Biol.* **209**, 1725-1736.
- Rubenson, J., Heliams, D. B., Lloyd, D. G. and Fournier, P. A.** (2004). Gait selection in the ostrich: mechanical and metabolic characteristics of walking and running with and without an aerial phase. *Proc. R. Soc. Lond. B Biol. Sci.* **271**, 1091-1099.
- Sacks, O.** (2003). Early work on elephant gait not to be forgotten. *Nature* **423**, 221.
- Schmitt, D., Cartmill, M., Griffin, T. M., Hanna, J. B. and Lemelin, P.** (2006). The adaptive value of ambling gaits in primates and other mammals. *J. Exp. Biol.* **209**, 2042-2049.
- Schwerda, D.** (2003). Analyse kinematischer parameter der lokomotion von *Loxodonta africana* (Proboscidea: Elephantidae). Diplomarbeit, Friedrich-Schiller-Universität Jena, Germany.
- Scott, G. B.** (1988). Studies of the gait of Friesian heifer cattle. *Vet. Rec.* **123**, 245-248.
- Sokal, R. R. and Rohlf, F. J.** (1995). *Biometry: The Principles and Practice of Statistics in Biological Research* (3rd edn). New York: W. H. Freeman.
- Spinage, C. A.** (1994). *Elephants*. London: T&AD Poyser Natural History.
- Thomas, M. G., Hagelberg, E., Jones, H. B., Yang, Z. and Lister, A. M.** (2000). Molecular and morphological evidence on the phylogeny of the Elephantidae. *Proc. R. Soc. Lond. B Biol. Sci.* **267**, 2493-2500.
- Usherwood, J. R.** (2005). Why not walk faster? *Biol. Lett.* **1**, 338-341.
- Webb, S. D.** (1972). Locomotor evolution in camels. *Forma et Functio* **5**, 99-112.
- Zips, S., Peham, C., Scheidl, M., Licka, T. and Girtler, D.** (2001). Motion pattern of the toelt of Icelandic horses at different speeds. *Equine Vet. J.* **33**, 109-111.