

Biomechanics of locomotion in Asian elephants

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SUMMARY

Elephants are the biggest living terrestrial animal, weighing up to five tons and measuring up to three metres at the withers. These exceptional dimensions provide certain advantages (e.g. the mass-specific energetic cost of locomotion is decreased) but also disadvantages (e.g. forces are proportional to body volume while supportive tissue strength depends on their cross-sectional area, which makes elephants relatively more fragile than smaller animals). In order to understand better how body size affects gait mechanics the movement of the centre of mass (COM) of 34 Asian elephants (*Elephas maximus*) was studied over their entire speed range of 0.4–5.0 m s⁻¹ with force platforms. The mass-specific mechanical work required to maintain the movements of the COM per unit distance is ~0.2 J kg⁻¹ m⁻¹ (about 1/3 of the average of other animals ranging in size from a 35 g kangaroo rat to a 70 kg human). At low speeds this work is reduced by a pendulum-like exchange between the kinetic and potential energies of the COM, with a maximum energy exchange of ~60% at 1.4 m s⁻¹. At high speeds, elephants use a bouncing mechanism with little exchange between kinetic and potential energies of the COM, although without an aerial phase. Elephants increase speed while reducing the vertical oscillation of the COM from about 3 cm to 1 cm.

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

INTRODUCTION

Most animals use two fundamental mechanisms to minimise the metabolic cost of legged locomotion (Cavagna et al., 1977; Farley et al., 1993; Heglund et al., 1982a; Heglund et al., 1982b). At lower speeds of progression, the kinetic and potential energies of the centre of mass of the body (COM) are out-of-phase, like in a pendulum. This pendulum mechanism allows potential energy to be transformed into kinetic energy, and *vice versa*. As a result, the muscular work done to move the COM relative to the surroundings (i.e. the external work, W_{ext}) is reduced. At higher speeds, the kinetic and potential energies of the COM oscillate in-phase, like in a bouncing ball. As a consequence, the energy fluctuations of the COM, and thus W_{ext} , increase, but part of the work comes from elastic energy stored and recovered from the muscle–tendon units, resulting in reduced energy expenditure (Cavagna et al., 1964; Farley et al., 1993).

In most species, a transition speed exists at which the animal switches from the pendular mechanism of walking to the bouncing mechanism of trotting and running (Heglund and Taylor, 1988). At this speed, many variables show a discontinuity, e.g. the mass-specific W_{ext} per unit distance and the rate at which W_{ext} changes with speed increase dramatically (Cavagna et al., 1977; Heglund et al., 1982a; Heglund et al., 1982b; Minetti et al., 1999; Willems et al., 1995). The switch in gait also noticeably influences other variables such as the footfall pattern, the limb phase (the time interval between two successive limb touchdowns) and the duty factor (the fraction of a stride during which a limb is in contact with the ground) (Hildebrand, 1977; Hildebrand, 1980; Schmitt et al., 2006). Furthermore, in most cases the presence of a whole-body aerial phase appears when the animal starts to bounce (Biewener, 2006; Biknevicius and Reilly, 2006), and this results in a marked increase in vertical peak force (Biewener, 2006; Biknevicius et al., 2006; Bobbert et al., 2007). Apart from a few exceptions – such as the

Elegant-crested Tinamou (Hancock et al., 2007), the giant Galapagos tortoise (Zani et al., 2005) and the alligator (Willey et al., 2004) – the kinematics (e.g. the presence or absence of an aerial phase) and the kinetics (e.g. the presence of either a pendular or a bouncing mechanism) lead to the same definition of gait (Biewener, 2006; Biknevicius and Reilly, 2006; Schmitt et al., 2006).

In slow-moving elephants, both kinematic and kinetic variables fall nicely into the definition of a walk (Hutchinson et al., 2006; Ren and Hutchinson, 2008). On the contrary, when elephants move fast, the kinematic and kinetic variables often result in contradictory definitions of gait: some indicating a walk and some indicating a trot. According to Hutchinson et al., at high speeds of progression, the elephant's forelimbs walk while the hindlimbs trot (Hutchinson et al., 2003). Furthermore, at high speeds, the duty factor is <0.5, which is normally a trot characteristic, but there is no aerial phase, which is normally a walk characteristic (Hutchinson et al., 2006).

In addition, no transition speed seems to exist in elephants. Step length and step frequency increase continuously as an elephant progresses from its slowest to its fastest speeds (Hutchinson et al., 2006). The footfall pattern does not change with increasing speed; elephants move smoothly to their fastest speeds without changing their footfall sequence, and their limb phase remains nearly constant (Hildebrand, 1980; Hildebrand, 1984; Hutchinson et al., 2006; Muybridge, 1893). Thus, based upon these kinematic data, it seems that elephants do not shift from a walk to a trot or gallop, as seen in most other animals. Despite the lack of a clear gait transition, Hutchinson et al. doubt whether elephants only walk throughout their speed range, and suggest that elephants probably run at moderate and high speeds (Hutchinson et al., 2003; Hutchinson et al., 2006; Ren and Hutchinson, 2008).

As Gray observed more than 60 years ago, 'a complete and accurate picture of all the forces acting on the body (...) is essential

for analysing and understanding the physiological properties of a locomotory mechanism' (Gray, 1944). Therefore, a force platform that measures the ground reaction forces under the limbs of an elephant during locomotion was built. For the first time, the gait of an elephant moving at different speeds could be analysed from the movements of the COM of the body.

MATERIALS AND METHODS

Measurement of the ground reaction forces

The forces exerted by the ground on the feet of an elephant were measured by means of a 2 m × 8 m force platform mounted at ground level in the middle of a 50 m track. The platform consisted of 16 1 m × 1 m plates. Each plate was composed of a steel frame, four 3-axis force transducers and an aluminium plate surface. The force transducers consisted of strain-gage instrumented spring blades, somewhat similar in principle to those described by Heglund (Heglund, 1981). Each force plate weighed 270 kg and was capable of measuring forces up to 60 kN at a maximal resolution of 1.8 N with a linear response within 1% of the measured value. The plates had a natural frequency of 300 Hz. Crosstalk between the three axes of a force plate was less than 1% of the applied force, independent of the point of application of the force.

Each plate contained its own data acquisition system. The transducer signals were amplified, low-pass filtered (4-pole Bessel filter with a -3 dB cut-off frequency of 200 Hz) and digitized by a 16-bit analog-to-digital converter at 50–100 Hz, depending upon running speed. The 50 Hz sample rate was used for the lower speeds (0.38–1.56 m s⁻¹), and the 100 Hz sample rate was used for the higher speeds (0.51–4.97 m s⁻¹). The plates were connected to a PC *via* TCP/IP over Ethernet. The amplifier gain, analog-to-digital converter data acquisition, zero-offset and Ethernet interface were all controlled by an embedded micro-controller (Rabbit Semiconductor, Davis, CA, USA). The signals from the 16 plates were summed digitally on the PC in order to obtain the vertical, forward and lateral components of the ground reaction force (top three panels Fig. 1). Calculations and data processing were performed using custom software (LABVIEW 7.1, National Instruments, Austin, TX, USA).

Calculation of the mechanical work done to move the COM

The mechanical work done during each step to lift and accelerate the COM, W_{ext} , was calculated using a procedure similar to that described in detail by Cavagna (Cavagna, 1975) and Willems et al. (Willems et al., 1995). This procedure is only briefly described here.

Because air resistance is negligible at the speeds studied, the acceleration of the COM in the vertical (a_v), forward (a_f) and lateral (a_l) directions can be calculated as:

$$a_v = F_v - P_b / M_b, \quad (1)$$

$$a_f = F_f / M_b, \quad (2)$$

and

$$a_l = F_l / M_b, \quad (3)$$

where F_v , F_f and F_l are, respectively, the vertical, forward and lateral components of the ground reaction forces, P_b is the body weight and M_b the body mass.

Because the animal is moving on the level, the average vertical force (\bar{F}_v) over an integral number of steps should be equal to the P_b , and Eqn 1 can therefore be rewritten as:

$$a_v = F_v - \bar{F}_v / M_b. \quad (4)$$

To avoid errors due to the determination of P_b , a_v was computed from Eqn 4 instead of Eqn 1. In our experiments, the difference between F_v and P_b was $1.36 \pm 3.07\%$ (mean \pm s.d., $N=392$) of P_b .

The accelerations a_v , a_f and a_l were integrated, using the trapezoidal rule, to determine the velocity changes in the three directions. To obtain the instantaneous velocity of the COM in the vertical (V_v), forward (V_f) and lateral (V_l) directions (panels 4, 5 and 6 in Fig. 1), the integration constants were evaluated as follows. The integration constant of V_v was set so that the average vertical velocity of the COM is nil over a complete number of steps on the assumption that, when moving over level terrain, the height of the COM is the same at the beginning and at the end of the step(s) analysed. The integration constant of V_f was calculated on the assumption that the average forward velocity of the COM (\bar{V}_f) was equal to the average velocity of the elephant's forehead as measured by means of photocells placed at each end of the platform. The integration constant of V_l was set so that the average lateral velocity of the COM is nil over a stride, on the assumption that the lateral position of the COM relative to the force platform was the same at the beginning and the end of the stride. V_l was measured only in trials involving a complete stride. The vertical displacement (S_v) of the COM over one step cycle was then computed by integration of V_v (panel 7 in Fig. 1).

Only steps during which the animal was moving at a constant average velocity were retained for analysis. For this reason, steps were selected only if the difference between the forward speed at the beginning and at the end of the selected steps was no greater than 3% of the average speed of progression (except at speeds lower than 0.83 m s⁻¹, where it never exceeded 12%). As explained above, the average vertical force over a complete number of steps should be equal to body weight. If two successive steps (i.e. an entire stride) met the selection criteria, then both were retained and the lateral work, as well as the vertical and forward work, could be determined. Because the work due to the lateral movement of the COM was small, no selection criteria were applied to the lateral velocity.

The potential energy of the COM was calculated as $E_p = M_b g S_v$, where g is the gravitational acceleration. The kinetic energy of the COM due to its vertical (V_v), forward (V_f) and lateral (V_l) velocities was calculated as: $E_{kv} = M_b V_v^2 / 2$, $E_{kf} = M_b V_f^2 / 2$ and $E_{kl} = M_b V_l^2 / 2$, respectively. The mechanical energy of the COM was calculated as:

$$E_{\text{com}} = E_p + E_{kv} + E_{kf} + E_{kl} = E_p + E_k, \quad (5)$$

where E_k is the kinetic energy of the COM.

The increments in $E_p + E_{kv}$, E_{kf} , E_{kl} and E_{com} represent, respectively, the positive work done against gravity (W_v), the positive work done to accelerate the COM forwards (W_f), the positive work done to accelerate the COM laterally (W_l) and the positive work done to maintain the motion of the COM (W_{ext}). In this study, the selection of a complete step or stride was made from easily distinguishable repeatable events such as the maximal or minimal peaks in vertical or horizontal velocities of the COM.

Percentage recovery

The relative amount of energy recovered (%R) by the pendular exchange between the kinetic and potential energies of the COM can be calculated as:

$$\%R = 100 \frac{(W_v + W_f + W_l) - W_{\text{ext}}}{(W_v + W_f + W_l)}. \quad (6)$$

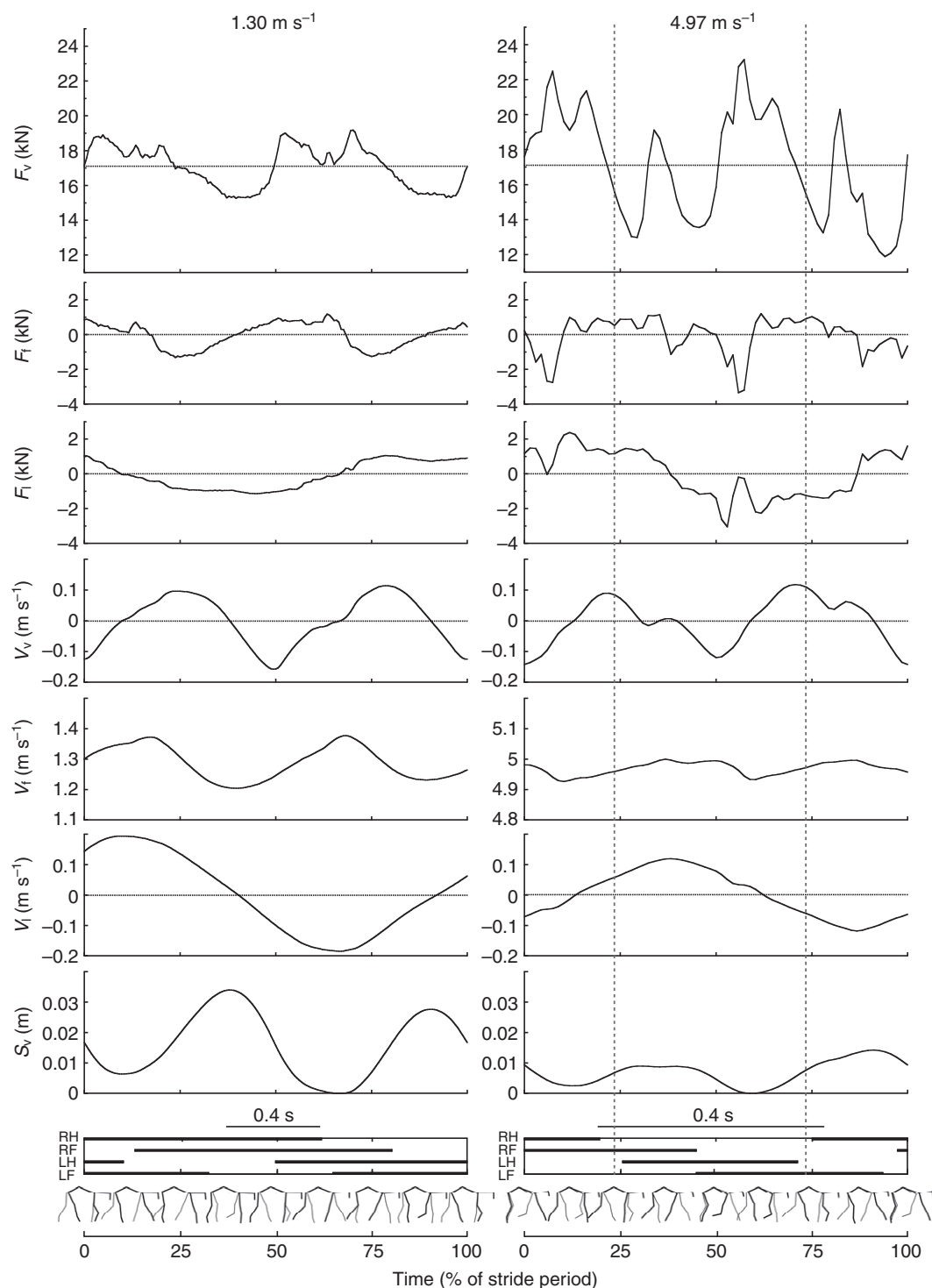


Fig. 1. Illustration of the analysis starting from force records and finishing with the vertical displacement of the centre of mass (COM) of a 1740 kg elephant during one stride of locomotion. The left curves show a walking speed (1.30 m s^{-1}) and right curves show the fastest speed obtained (4.97 m s^{-1}). Both strides start on the maxima of the vertical downward speed of the COM. The three top curves show the vertical (F_v), forward (F_f) and lateral (F_l) forces during a stride. The horizontal force is positive when the push against the platform is directed backward, causing an acceleration of the COM. The next three curves show the vertical (V_v), forward (V_f) and lateral (V_l) velocities obtained from the integration of the ground reaction forces, as described in the Materials and methods. The bottom curves show the vertical displacement (S_v) of the COM obtained from the integration of the vertical velocity. The lower panel shows the footfall pattern during the stride period, and the stick figures show the position of the limb segments every 12.5% of the stride period. Thick lines indicate the position of the right (camera side) segments of the animal. The mechanical energy traces shown in Fig. 4 are calculated from the velocity and vertical displacement represented in this figure, i.e. for the same trials. The vertical dotted lines on the right side represent the period of the step described in detail in Fig. 7. RH, RF, LH, LF, respectively, for right hind, right fore, left hind and left forelimb contact period.

Measurement of the footfall pattern

In order to match the force-time curves with the footfall pattern (bottom of Fig. 1), the movements of the elephants were recorded by means of a high-speed video camera (BASLER A501k, Ahrensburg, Germany, resolution 1280×1024 pixels, aperture time 3 ms). The camera was placed 15.3 m to the side of the plate surface, and its field encompassed about $12 \text{ m} \times 4 \text{ m}$. Images were recorded at 50–100 Hz, depending upon running speed. The 50 Hz image rate was used for the lower speeds (0.38 – 1.58 m s^{-1}), and the 100 Hz image rate was used for the higher speeds (0.53 – 4.97 m s^{-1}). Camera images were synchronised with the force

traces by matching a foot-down event on the film with the same event on the force records.

In this study a stride is defined as the period of time necessary for a limb to complete a cycle, e.g. right hind foot strike to right hind foot strike. A step is one half of a stride, which, in our example, would be from right hind foot strike to left hind foot strike.

Step frequency and stride length

Step frequency (f) was computed by dividing the number of steps selected by their duration. The stride length (L) was obtained by dividing \bar{V}_f by the stride frequency. In order to take into account

Table 1. Individual data for elephants used in this study

Elephant	Sex	Age (years)	Body mass M_b (kg)	Mass on the front legs (% M_b)	Hip height (m)	Maximal velocity (m s^{-1})	Fr
Add	M	8	2515	57.4	1.64	2.04	0.70
Boonmii	F	43	3376		1.79	2.80	1.43
Boonteung	M	45	3819	58.6	1.69	0.88	0.13
Gaew	M	5	1740	59.4	1.52	4.97	3.83
Jai	M	27	3218		1.82	1.39	0.36
Janpui	M	36	3259		1.72	2.52	1.11
Jojo	M	13	3000	59.3	1.77	4.51	3.67
Kampaeng	M	37	3221		1.66	2.25	0.86
Kangluay	M	9	1956	62.1	1.61	1.81	0.54
Kumlha	M	58	3125	60.2	1.84	1.31	0.32
Lookgob	M	10	2977	61.6	1.89	0.99	0.19
Lookkhang	F	12	2635	62.2	1.72	4.61	3.73
Monkol	M	29	3147		1.8	1.11	0.23
Phajan	M	45	3869	61.2	1.83	2.06	0.79
Pong	M	7	2274		1.59	2.64	1.13
Prajuab	F	24	3061	58.8	1.70	2.42	1.01
Prame	M	43	3218	59.5	1.84	1.68	0.53
Pratida	F	11	2617		1.69	2.02	0.70
Prayao	M	24	4001		1.86	2.58	1.26
Prayoungkeart	F	3	872		1.22	3.33	1.38
Samai	M	16	3085		1.74	1.41	0.35
Satit	M	29	3525		1.89	1.98	0.76
Somboon	M	53	3131	59.7	1.70	1.34	0.31
Somchai	M	7	1504	58.1	1.57	1.97	0.62
Srisiam	M	6	1258	63.3	1.32	4.85	3.17
Tadaeng	M	36	3543	62.8	1.71	0.82	0.12
Tantawan	F	47	3636		1.70	1.29	0.29
Tao	M	7	1893	64.7	1.58	1.72	0.48
Thong	M	53	2994	62.3	1.82	1.07	0.21
Umpang	F	8	1641	59.6	1.32	3.58	1.72
Wanalee	F	8	2072	63.2	1.51	4.32	2.87
Wangjao	F	45	3102		1.58	1.72	0.48
Wassana	M	48	3078	62.6	1.8	1.13	0.23
Yai	M	48	3034	58.9	1.72	1.23	0.27
Means		26.5	2805	60.6	1.68	2.25	1.05
s.d.		17.9	778	2.0	0.16	1.21	1.10

Maximal forward velocity and the corresponding Froude number (Fr) are presented for comparison with the literature. The means and standard deviations (s.d.) are given below the columns.

the difference in body size, f and L were normalised using the dimensionless step frequency (f_{sn}) and dimensionless stride length (L_n):

$$f_{sn} = f \sqrt{\frac{h}{g}}, \quad (7)$$

$$L_n = L / h, \quad (8)$$

where h is the limb length in metres (Alexander and Jayes, 1983; Hof, 1996). Limb length was assumed to be equal to the distance between the hip joint and the ground during standing. As will become clear, step frequency (as opposed to stride frequency) is used for comparison with the natural frequency of oscillation, and stride length (as opposed to step length) is used to describe a complete locomotory cycle and for comparisons with the literature.

Animals and experimental procedure

Experiments were performed at the Thai Elephant Conservation Centre near Lampang (Northern Thailand) and were approved both by the Ethics Committee of the Faculty of Medicine of the UCL and the Forest and Industry Organization (FIO) in Thailand.

Data were collected on 34 Asian elephants (*Elephas maximus* L.). The P_b was measured three times, by means of the force platform (samples of 4 s at 250 Hz), and averaged. The P_b of the 34 elephants

ranged from 0.9 tons to 4.0 tons. The standing antero-posterior repartition of the weight was measured in 21 elephants by placing the elephant's forequarters and hindquarters on separate force plates. Morphological parameters and antero-posterior repartition of the weight are presented in Table 1.

The elephants moved at different speeds across the force platform. In most cases, the elephant's keeper or 'mahout' was sitting on the back of the elephant. Because the weight of the mahout represented 1–5% of the weight of the elephant, the weight of the mahout was assumed to have no influence on the elephant's locomotion.

The elephants were given the opportunity to become familiar with the force platform before data acquisition was started. At the start of data acquisition, the elephant was allowed to move at its freely chosen speed. Then, for each successive trial, the mahout encouraged the elephant to go slightly faster (in steps of about 0.28 m s^{-1}), up to the maximal speed. At the highest speeds, the elephants were motivated by the mahout's instructions, playful chasing and/or food rewards at the end of the track. The low speed trials, down to the slowest speeds attained, were acquired at the end of the data acquisition.

A total of 310 steps and 82 strides were obtained at steady speeds, ranging from 0.38 m s^{-1} to 4.97 m s^{-1} . Data were grouped in 0.28 m s^{-1} speed classes regardless of the number of data recorded on each animal. Typically, 1–2 trials per animal were recorded in each speed

class, between the lowest and the highest speeds attained for that animal. For most of the variables presented in the paper [f , $F_{v\max}$ (maximum vertical force), $F_{v\min}$ (minimum vertical force), S_v , F_v , W_f , W_v and W_{ext}], a check was done to avoid errors due to the fact that the data were not completely independent (pseudo-replication). The data of each elephant were averaged in each speed class and a two-way analysis of variance (ANOVA) was performed between the raw data and the averaged data. The effect of speed on each of these variables was not statistically different between the two situations ($P>0.55$). For this reason, the curves presented in this study were fitted through all of the data obtained, and the averages in each speed class were computed regardless of the animals on which the data were measured.

RESULTS

Stride parameters

Over the speed range studied, the step frequency increases nearly 5 times (Fig. 2) whereas the stride length increases ~ 2.5 times (Fig. 3A): f_{sn} increases from ~ 0.25 at 0.4 m s^{-1} to ~ 1.15 at 4.7 m s^{-1} , and L_n increases from ~ 0.9 at 0.4 m s^{-1} to ~ 2.2 at 4.7 m s^{-1} . Over the whole speed range, f_{sn} increases linearly whereas L_n increases more at slow speeds than at high speeds. These observations show that

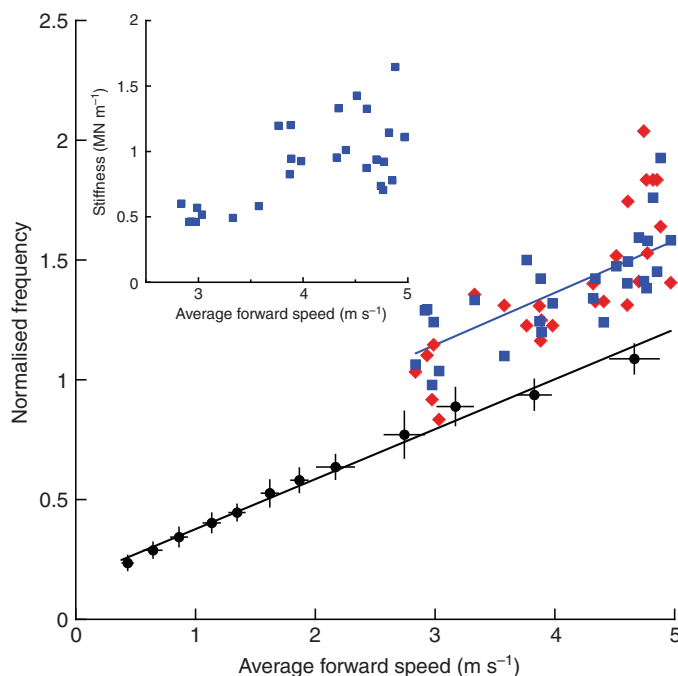


Fig. 2. The normalised step frequency calculated from Eqn 7 (f_{sn} , black circles) and the natural frequency of the elastic system calculated from Eqn 9 (f_n , blue squares) and from Eqn 10 (f_h , red diamonds) as a function of the average forward speed \bar{V}_f . Over the entire speed range the step frequency increases ~ 5 -fold. The bouncing mechanism occurs from 2.80 m s^{-1} to 4.97 m s^{-1} , and consequently f_n and f_h were measured over this speed range. Lines are linear least-square curve fits: $f_{sn}=0.17+0.21 \bar{V}_f$ and $f_n=0.49+0.21 \bar{V}_f$. Because f_n and f_h show a good match, at least during the part of a step when the F_v is greater than body weight, the elephant is using a bouncing mechanism at its natural frequency. Symbols and bars are means \pm s.d. The speed classes are in m s^{-1} , and number of points averaged (N) are: 0–0.5 (8), 0.5–0.75 (57), 0.75–1 (70), 1–1.25 (78), 1.25–1.5 (45), 1.5–1.75 (46), 1.75–2 (25), 2–2.5 (25), 2.5–3 (15), 3–3.5 (3), 3.5–4 (6), 4–5 (14). Insert. The blue squares in the insert show the stiffness determined from the F_v vs S_v relationship shown in Fig. 7.

below $\sim 1.8 \text{ m s}^{-1}$, the animal increases its speed of progression both by lengthening the stride and increasing the stride frequency. At $\sim 1.8 \text{ m s}^{-1}$, the limb excursion angle appears to attain a maximum, limiting the distance travelled during the contact phase of any foot. As a consequence, further increases in speed are mainly due to an increase in stride frequency (Cavagna et al., 1988), but also in part due to a continued increase in the distance travelled during the swing phase of any foot (L_n minus L_f or L_h in Fig. 3A).

Below $\sim 1.8 \text{ m s}^{-1}$, the increase in L_n can be explained by an increase both in the distance travelled by the COM while the fore (L_f) or hind (L_h) limbs are on the ground (Fig. 3A, open triangles and open circles, respectively) and in the distance travelled between the ipsilateral hind and fore foot touchdowns (Fig. 3A, open squares). This observation is illustrated in the two upper panels of Fig. 3B, which show the distance travelled by the COM while each limb is on the ground. It can be seen that between the speeds of 0.62 m s^{-1} and 1.35 m s^{-1} both the length travelled during the contact phase and during the swing phase are increased.

Above $\sim 1.8 \text{ m s}^{-1}$, the limb excursion angle appears to approach a maximum, limiting the distance travelled during the support (L_h and L_f reach a constant value of ~ 1). As a consequence, further increases in step length occur by increasing the distance travelled between the ipsilateral hind and fore foot touchdowns (Fig. 3A, open squares). This phenomenon is illustrated in the two lower panels of Fig. 3B. Between the speeds of 1.87 m s^{-1} and 4.72 m s^{-1} the length of contact of any limb does not change whereas the stride length increases by 33% due to the increase in the distance between the limb-supports.

Energy curves and related foot events

Typical energy curves of the COM and the footfall pattern of an elephant moving at an intermediate speed (1.30 m s^{-1} , left column) and at the fastest speed attained (4.97 m s^{-1} , right column) are shown in Fig. 4. The E_{kf} , E_{kl} and E_{kv} curves are the mechanical energy of the COM due to, respectively, its forward, lateral and vertical velocities. At all speeds, the variations of the total kinetic energy of the COM (E_k) are mainly due to the changes in E_{kf} . Indeed, as can be easily seen in Fig. 4, the variations of the E_{kv} and E_{kl} curves represent a small fraction of the variations of E_{kf} .

The total energy of the COM (E_{com}) is the sum of its potential (E_p) and kinetic (E_k) energy at each instant. At 1.30 m s^{-1} , the variations of E_{com} are smaller than those of either the E_p or the E_k curves. Because E_p and E_k are out-of-phase, an increase in one tends to be cancelled by a decrease in the other, resulting in smaller changes in the sum. This energy exchange mechanism is similar to what occurs in a pendulum (Cavagna et al., 1976; Cavagna et al., 1977).

On the contrary, at 4.97 m s^{-1} , the variations in E_{com} are about equal to the sum of the amplitudes of the E_p and the E_k curves. Because E_p and E_k are in-phase, only a small amount of energy transfer occurs between E_p and E_k . This mechanism is similar to what occurs in a bouncing ball (Cavagna et al., 1976; Cavagna et al., 1977; Cavagna et al., 1988).

In terms of their footfall pattern, elephants always use a lateral sequence, i.e. the hindlimb on one side is always followed by the forelimb on the same side (Muybridge, 1893; Hildebrand, 1980; Hildebrand, 1984; Hutchinson et al., 2006). This footfall pattern is shown in Figs 3 and 4. As speed increases, the average number of feet on the ground falls from three at 0.62 m s^{-1} to just less than two at 4.97 m s^{-1} .

In both the left and right panels of Fig. 4 the strides are delimited at the moment of the maximum downward vertical velocity of the COM. Due to a difference in phase shift of the E_p and the E_k curves

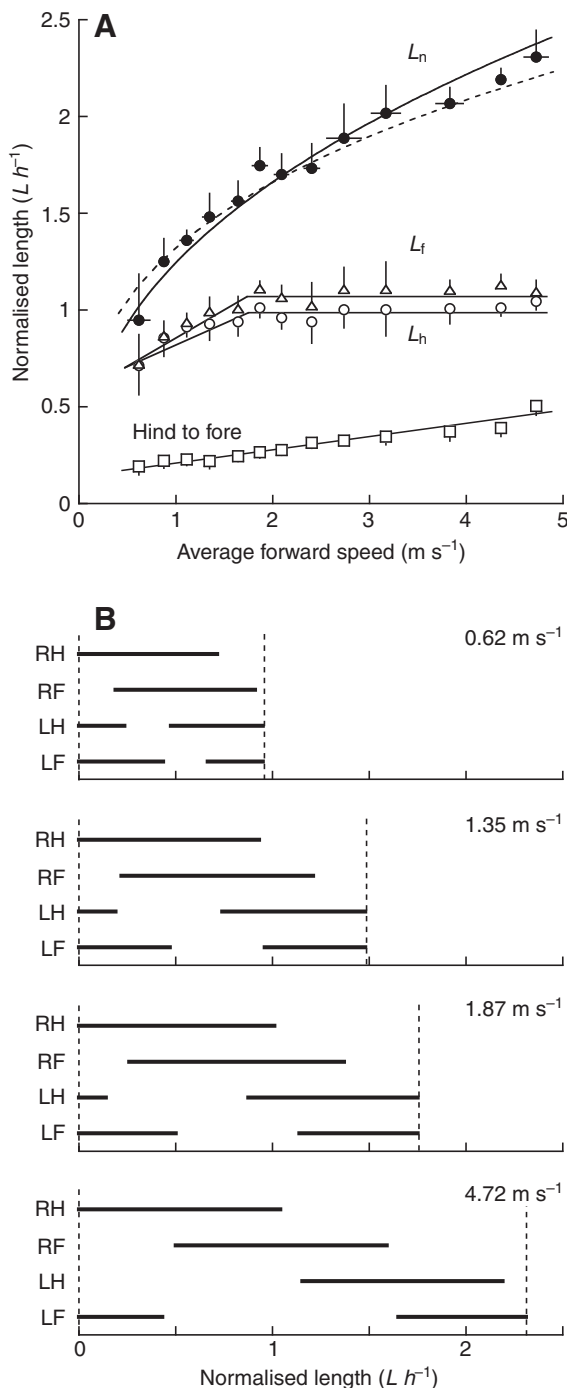


Fig. 3. (A) Normalised stride length (L_n , filled circles) increases curvilinearly with speed, increasing ~3-fold over the entire speed range. At low speed the increase in L_n is due to an increase in the forward distance travelled by the centre of mass (COM) during the forelimb (L_f , open triangles) and the hindlimb (L_h , open circles) support periods. As speed increases above $1.8 m s^{-1}$, the distance travelled during the support periods shows a plateau, indicating that the excursion angle of the hip and shoulder joints has reached a maximum. Further increases in stride length can thus be explained by the continuous increase in the forward distance travelled between ipsilateral hind and fore foot touchdowns (hind to fore length). This is also illustrated by the limb contact periods during a stride for four different speeds shown in (B) (RH, RF, LH, LF, respectively, for right hind, right fore, left hind and left forelimb contact period). The stride length measured from force platform measurements matches with previous video studies in Asian and African elephants [broken line (Hutchinson et al., 2006)]. These authors used dimensionless speed [computed as $V_t(gh)^{-0.5}$], their speeds were converted to $m s^{-1}$ using a leg length of 1.7 m. Symbols and bars are means \pm s.d. The speed classes in $m s^{-1}$, and number of points averaged (N) are: 0–0.75 (12), 0.75–1 (6), 1–1.25 (14), 1.25–1.5 (9), 1.5–1.75 (12), 1.75–2 (7), 2–2.25 (14), 2.25–2.5 (6), 2.5–3 (12), 3–3.5 (3), 3.5–4 (6), 4–4.5 (3), 4.5–5 (9).

Mechanical work done to move the COM relative to the surroundings

The mass-specific mechanical work done to move the COM a unit distance is presented as a function of the speed of progression in Fig. 5A,B. Fig. 5C presents the percentage of energy recovered through the pendulum-like transformation of kinetic into potential energy, and *vice versa* (%R).

The work done to sustain the lateral movements of the COM (W_l) represents less than 9% of W_{ext} at low speeds and diminishes to zero at high speeds. At low speeds, W_v , the work done to move the COM upwards (red triangles in Fig. 5A) is greater than W_f , the work done to accelerate the COM forwards (green circles, Fig. 5A). As speed increases, W_v decreases and W_f increases. Thus, at intermediate speeds (around $1.30 m s^{-1}$), W_f is about equal to W_v ($\sim 0.18 J kg^{-1} m^{-1}$), and at the high speeds W_f is greater than W_v . The decrease in W_v is due to a diminution of the vertical displacement of the COM (from 0.03 m to 0.01 m through the range of speeds, Fig. 6B), and the increase in W_f is due to a higher absolute forward velocity and an increase in the stride length (Fig. 3A), resulting in larger changes in the kinetic energy of forward motion.

At all speeds, the mass-specific external work per unit distance (W_{ext}) is less than the sum of W_f and W_v due to an exchange between kinetic and potential energy. The amount of energy recovered (%R) through this pendulum-like mechanism reaches an average maximum of ~60% at $\sim 1.40 m s^{-1}$ (Fig. 5C). This speed corresponds approximately to the 'optimal' speed ($\sim 1.55 m s^{-1}$) at which W_{ext} shows a minimum of $\sim 0.16 J kg^{-1} m^{-1}$ (Fig. 5B). The external work increases at higher and lower speeds as the %R decreases down to as low as 10%.

Vertical force and vertical displacement

The maximum (F_{vmax}) and minimum (F_{vmin}) vertical force divided by P_b is shown as a function of speed in Fig. 6A; when moving on the level, the average vertical force over an integral number of steps must be $1 P_b$. F_{vmax}/P_b increases with speed up to a maximum of ~ 1.4 at high speed. Although F_{vmin}/P_b decreases with increasing speed, even at the fastest speed measured, an elephant is not even close to achieving an aerial phase, as the minimum vertical force is still 0.7 (Fig. 6A).

The vertical displacement of the COM over one step (S_v) is shown as a function of speed in Fig. 6B. The S_v shows a maximum of

as speed increases, the synchronisation between the movements of the COM and the footfall pattern is modified. For example, at both speeds, the right hind (RH) heel strikes the ground when the COM accelerates forwards (i.e. when E_k increases). At $1.30 m s^{-1}$, this event occurs at 0% of the stride period when the COM is moving downwards (i.e. when E_p decreases). The RH and right front (RF) footfall sequence occurs thus during the lower part of the vertical displacement of the COM. On the contrary, at $4.97 m s^{-1}$, the RH heel strikes the ground at 75% of the stride when the COM is moving upwards (i.e. when E_p increases). The RH and RF footfall sequence occurs thus during the upper part of the trajectory of the COM.

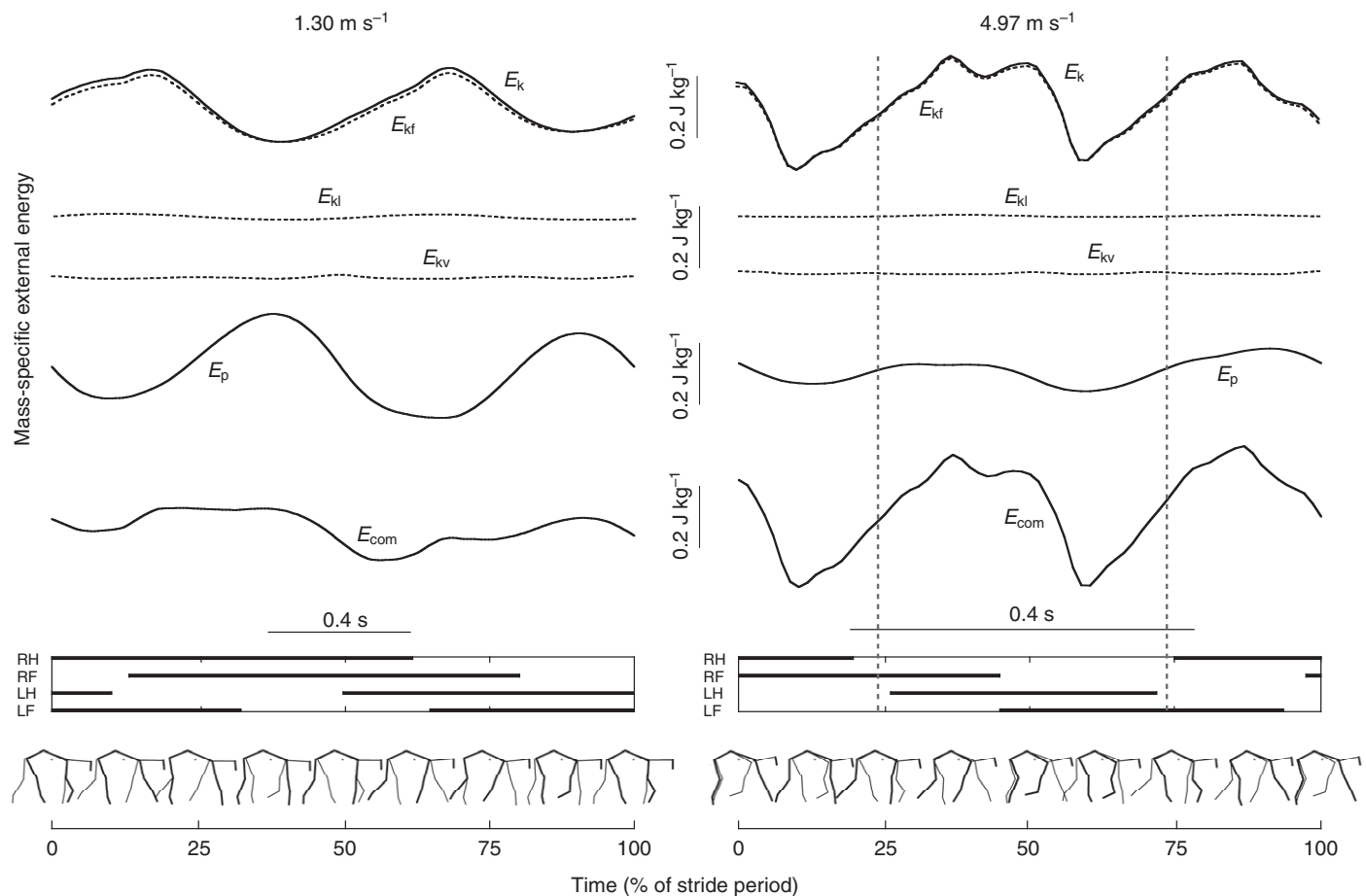


Fig. 4. Typical traces of the mass-specific mechanical energy of the centre of mass (COM) of a 1740 kg elephant during one stride of locomotion. The left curves show a normal walking speed (1.30 m s^{-1}) and right curves show the fastest speed obtained (4.97 m s^{-1}). Both strides start on the maximum of vertical downward speed of the COM. The lower panel shows the footfall pattern during the stride period and the stick figures show the position of the limb segments every 12.5% of the stride period. Thick lines indicate the position of the right (camera side) segments of the animal. RH, RF, LH, LF, respectively, for right hind, right fore, left hind and left forelimb contact period. The upper curves show the forward kinetic energy (E_{kf} , dotted lines) and total kinetic energy (E_k , solid lines) of the COM. The second and third curves show the lateral and vertical kinetic energy (E_{kl} and E_{kv} , respectively, in dotted lines). Next is the potential energy curve (E_p , solid curve), and the bottom curve shows the total energy of the COM (E_{com}). The E_p curve reaches its highest point around 40% and 90% of the stride period, when the elephant stands firmly on its ipsilateral pair of limbs. The pendulum mechanism is clearly seen in the left column as the E_p and E_k curves are out-of-phase and largely cancel out. Consequently the E_{com} curve varies less than the E_p and E_k curves (Cavagna et al., 1976). At high speeds (right column) the E_p and E_k curves are in-phase and consequently add rather than cancel out. The vertical movement of the COM is mainly determined by the forelimb acting like a compliant spring (see E_p and E_k curves around 10% and 60% of the stride period, for further details see Fig. 7).

$<0.03 \text{ m}$ at $\sim 1.5 \text{ m s}^{-1}$, then decreases rapidly and remains just $\sim 0.01 \text{ m}$ from 2 m s^{-1} to 5 m s^{-1} .

Natural frequency of a bouncing system

At speeds above 2.8 m s^{-1} , the E_p and the E_k curves fluctuate in-phase (Fig. 4, right panels) and the %R becomes smaller than 20% (Fig. 5C), suggesting that the COM behaves like a mass oscillating on a spring or like a bouncing ball. In order to assess this mechanism, the vertical component of the ground reaction force (F_v) was plotted as a function of the vertical displacement of the COM (S_v), and the normalised natural frequency of the system (f_n) was compared with the normalised step frequency (f_{sn}) (Cavagna et al., 1988). A typical trace of the F_v vs S_v relationship during one step obtained at 4.97 m s^{-1} is presented in Fig. 7, upper panel.

During the loading of the hindlimb (i.e. from A to B in Fig. 7), the contralateral forelimb is on the ground. During this phase, the vertical force (F_v) increases from $\sim 13 \text{ kN}$ to $\sim 19 \text{ kN}$ while the height

of the COM remains constant or increases slightly ($\sim 0.001 \text{ m}$). Therefore, during this phase the diagonal pair of limbs acts like a rigid, non-compliant system.

During the loading of the front limb (i.e. LF from C to D in Fig. 7), the ipsilateral hindlimb (LH) is on the ground. The vertical force F_v increases from $\sim 13 \text{ kN}$ to $\sim 23 \text{ kN}$ while the height of the COM decreases. During this phase, the relationship between S_v and F_v is nearly linear and the system acts as a compliant spring and mass. The slope of the straight line drawn from heel strike (Fig. 7, point C) to the maximal load on the forelimb (point D) can be considered to represent the whole-body vertical stiffness (k , expressed in N m^{-1}). The normalised natural frequency of the spring-mass system over which the body bounces (f_n) was calculated by:

$$f_n = \frac{1}{2\pi} \sqrt{\frac{k}{M_b}} \sqrt{\frac{h}{g}}, \quad (9)$$

where kM_b^{-1} is the mass-specific vertical stiffness, and the normalisation factor is the same as for Eqn 7.

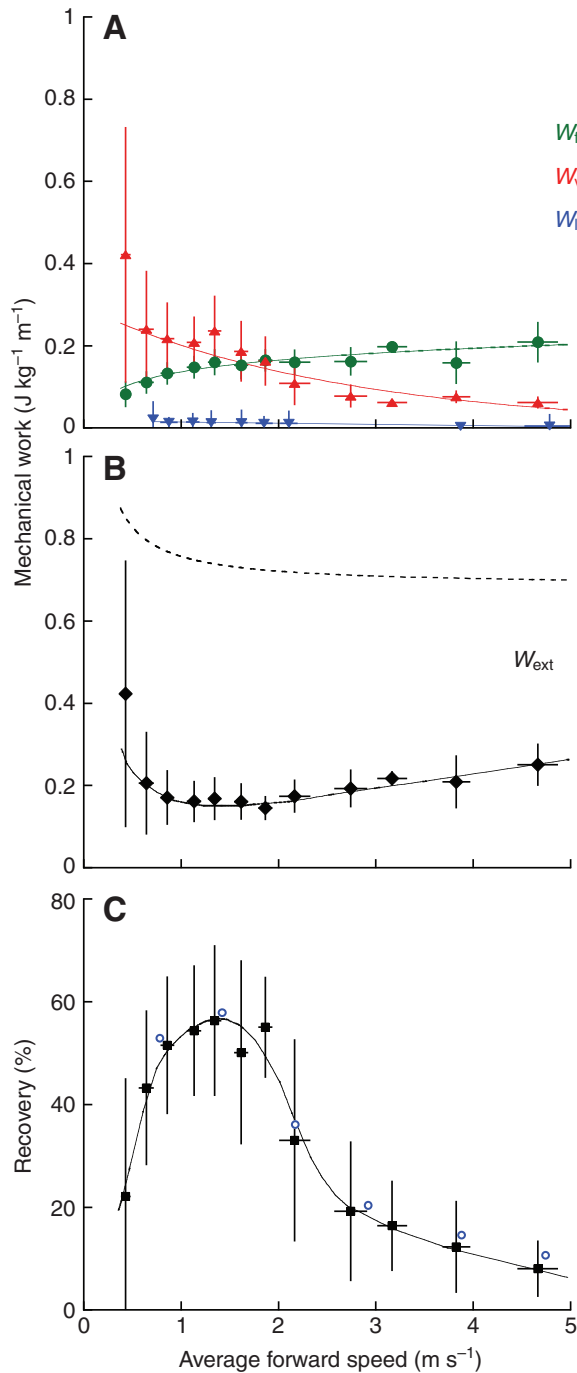


Fig. 5. The recovery and the mass-specific mechanical work done to move the center of mass (COM) per unit distance as a function of speed. (A) The forward kinetic work (W_f , green circles) increases while the vertical potential work (W_v , red triangles) decreases as speed increases; the two curves cross at ~ 1.6 m s⁻¹. The lateral kinetic work (W_l , blue triangles) remains very low at all speeds measured. (B) The mass-specific external work (W_{ext}) varies little with increasing speed, and shows a slight minimum at ~ 1.6 m s⁻¹. The W_{ext} value is smaller than the sum of W_f and W_v , which is due to the pendular transfer of kinetic energy (E_k) into potential energy (E_p), and *vice versa*. The broken line represents the average W_{ext} for all other animals, taken from Heglund et al. (Heglund et al., 1982a). (C) The percentage recovery (%R, Eqn 6) represents the amount of energy transferred from E_k into E_p . %R shows an inverted U-shaped curve with an average maximal value of $\sim 60\%$ at an optimal speed of 1.4 m s⁻¹. Circles represent %R values for individual trials shown in Fig. 10. Other details are similar to Fig. 2.

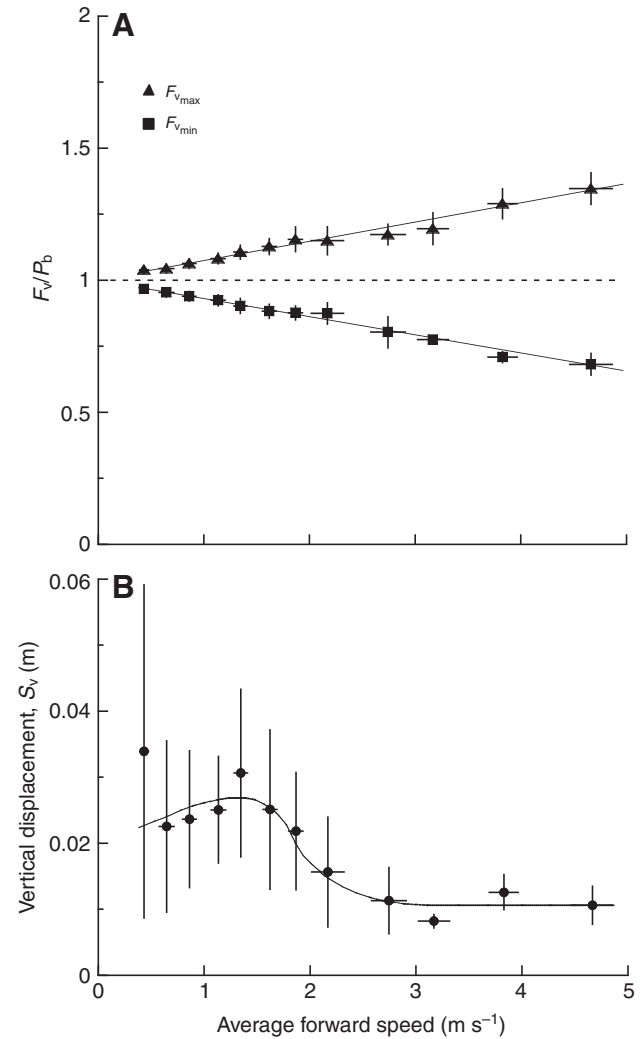


Fig. 6. (A) The evolution of the minimum (F_{vmin} , squares) and maximum (F_{vmax} , triangles) vertical force divided by body weight (P_b) as a function of speed. F_{vmin} decreases but no aerial period is achieved at the fastest speed, moreover the minimal vertical force is still $0.7 P_b$ at that speed. F_{vmax} increases with speed up to a maximum of $\sim 1.4 P_b$ at high speed. These small oscillations in vertical forces are related to very small vertical displacements of the centre of mass (COM) over a step, shown in (B). Other details are similar to Fig. 2.

The comparison of the natural frequency f_n (blue squares) to the step frequency f_{sn} (black circles) at speeds above 2.8 m s⁻¹ is shown in Fig. 2. The f_{sn} increases with speed, as does f_n , although f_n is ~ 30 to 50% greater than f_{sn} , depending upon the speed.

When a mass oscillates on a spring in contact with the ground, the half-cycle (t_h) during which the vertical force is greater than body weight corresponds to one half of the period of the oscillating system. During a step of an elephant moving at high speed, the duration of t_h corresponds to the fraction of the period C–D–A (Fig. 7), during which F_v is greater than body weight. The corresponding frequency f_h can be calculated by:

$$f_h = \frac{1}{2} \frac{1}{t_h} \sqrt{\frac{h}{g}} \quad (10)$$

Fig. 2 shows that f_h (red diamonds) matches f_n (blue squares).

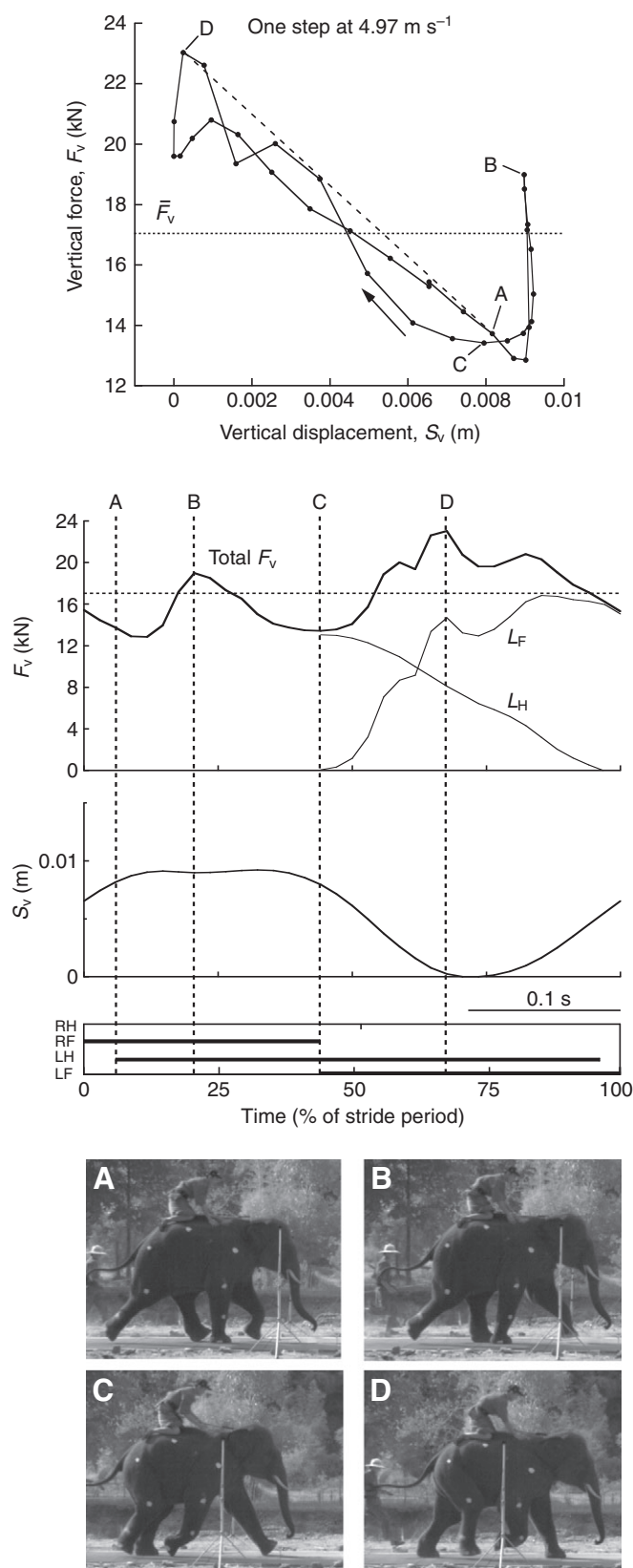


Fig. 7. A typical curve of vertical ground reaction force (F_v) plotted as a function of the vertical displacement of the COM (S_v) during one step (same trial as shown in Fig. 1, right panel and in Fig. 4, right panel). The letters indicate: A, hindlimb touchdown; B, hindlimb maximal load; C, forelimb touchdown; D, forelimb loading. Hindlimb loading (from A to B) results in a moderate F_v increase and a small S_v increase, which makes the system very rigid during that period of the step. Forelimb loading (from C to D) results in a large F_v increase and S_v decreases, which is typical of a spring-mass system. The stiffness of the model was computed as the slope of the line from C to D, i.e. during the loading phase of the forelimb (broken line). The average vertical force (\bar{F}_v) over the step period is represented by the horizontal dotted line. The middle panels show the same variables as a function of time, along with the single foot force recordings for the left front foot (L_F) and left hind foot (L_H). The bottom panels show images of the elephant at instants A, B, C and D.

mechanisms involved in elephant locomotion, how they change with speed and how they are adapted to the unique size of elephants.

Changes in stride length and stride frequency with speed

The forward displacement of the COM during a foot contact increases with speed up to a speed of $\sim 1.8 \text{ m s}^{-1}$, after which the displacement during the support is constant, indicating that the excursion angles of the fore and hindlimbs have reached a limit (open triangles and circles, respectively, in Fig. 3A). The stride length, however, continues to increase with speed (closed circles) because the distance travelled between successive foot contacts increases (e.g. the distance travelled between RH contact and RF contact in Fig. 3B, which is shown as open squares in Fig. 3A), even though the contact displacement remains constant. In other words, the limb support periods become more asynchronous with increasing speed. In fact, as easily seen in Fig. 3B, the average number of feet on the ground decreases from 3.2 at 0.62 m s^{-1} to 1.6 at 4.72 m s^{-1} .

While acknowledging the danger in extrapolation, it is interesting to compare the elephant's speed and step frequency with the speed and step frequency predicted from the allometric equations of Heglund and Taylor (Heglund and Taylor, 1988), which were based upon measurements in 16 quadrupedal species from mice to horses. Our fastest elephant weighed about two tons and achieved a maximum speed of 4.97 m s^{-1} at a step frequency of 3 Hz. According to the equations of Heglund and Taylor, a speed of 4.97 m s^{-1} would correspond to only a slow trot for a two-ton quadruped; and a step frequency of 3 Hz would be higher than the maximum predicted step frequency for an animal of that size at any speed.

The stride length and frequency measured in this study are in accordance with previous results reported by Hutchinson et al. (Hutchinson et al., 2006), which includes Asian and African elephants (L_n obtained by these authors is represented by the broken line in Fig. 3A). The observed limb phase is also in agreement [compare, for example, our Fig. 3B with fig. 3 of Hutchinson et al. (Hutchinson et al., 2006)].

Elephants do walk

Elephants walk very well; they are able to match the best walking performance of any other biped or quadruped observed to date with the exception of the African women carrying head-supported loads (Cavagna et al., 2002; Heglund et al., 1995). For example, Fig. 5C presents the amount of energy recovered by the exchange between kinetic and potential energies as a function of speed. At intermediate walking speeds (i.e. around 1.4 m s^{-1}), this pendulum-like mechanism allows the recovery of $\sim 60\%$ of the energy necessary to move the COM relative to the surroundings. The speed where the recovery

DISCUSSION

In this study, the gait of elephants was analysed for the first time from the movements of the COM recorded by means of a force platform. This analysis allows a better understanding of the

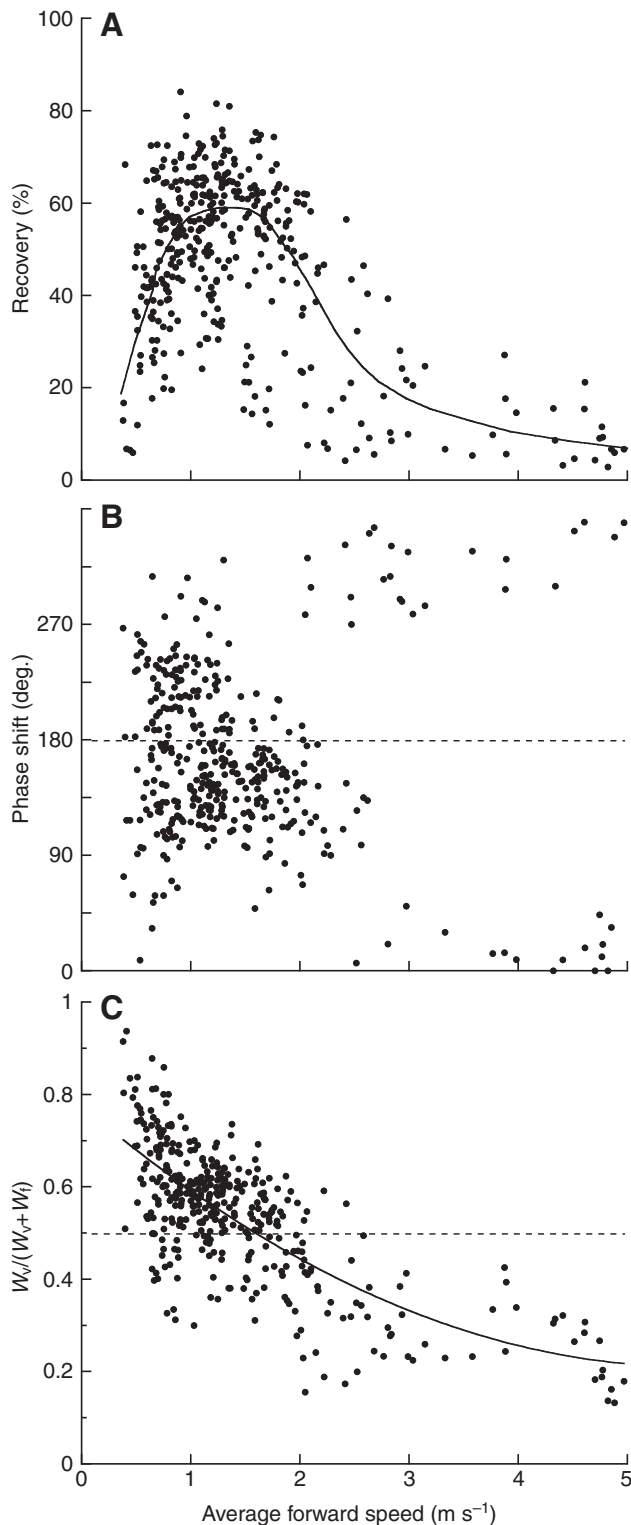


Fig. 8. The percentage recovery (%*R*) (A), phase shift between minima of kinetic energy (*E_k*) and potential energy (*E_p*) (B) and relative amplitude of work done to accelerate the centre of mass (COM) forwards (*W_t*) and positive work done against gravity (*W_v*) (C) as a function of speed. The phase shift shows an average value of ~180 deg. at low and intermediate speeds, which is typical of an inverted-pendulum walk. At the highest speed, energy curves are almost completely in-phase (~10 deg.), which is typical of a bouncing mechanism. The $W_v/(W_v+W_t)$ ratio decreases from ~0.7 to ~0.2 with increasing speed, averaging about 0.6 at the speed where %*R* is maximum.

is maximal roughly corresponds to the 'optimal' speed at which the W_{ext} is minimal (Fig. 5B).

The pendulum mechanism depends on three parameters (Cavagna et al., 1976): (1) the phase shift between *E_p* and *E_k*, (2) the relative amplitude of the *E_p* and *E_k* curves, and (3) the shape of the *E_p* and *E_k* curves. In the case of %*R*=100, the *E_p* and *E_k* curves must be mirror images. The first two parameters are compared with the %*R* as a function of speed in Fig. 8. The %*R* is a maximum at the speed where the phase shift between the kinetic and potential energy is 180 deg. (Fig. 8B) and the potential and kinetic energy are about equal (Fig. 8C).

Transition speed between walk and run

At slow and intermediate speeds, the kinetic and potential energies of the COM of the elephants are out-of-phase, as in a pendulum (Fig. 4, left); while at high speeds, the kinetic and potential energies of the COM of the elephants are in-phase, as in a spring-mass system (Fig. 4, right). This is the same as seen in almost all bipeds and quadrupeds, where out-of-phase speeds are walks and in-phase speeds are runs. However, in most bipeds and quadrupeds the step frequency and the mass-specific muscular work done per unit distance (W_{ext}) present a discontinuity at the speed the animal switches from one gait to the other: a walk-trot or walk-run transition is observed in horses (Biknevicius et al., 2006; Bobbert et al., 2007), in humans (Nilsson and Thorstensson, 1989; Willems et al., 1995) and in other animals (Ahn et al., 2004; Biewener, 2006; Cavagna et al., 1977; Heglund et al., 1982a; Rubenson et al., 2004).

Notably in elephants, over the whole speed range studied, no discontinuity can be seen in the step frequency (Fig. 2), stride length (Fig. 3A), %*R* (Fig. 5C), W_{ext} (Fig. 5B), minimum and maximum vertical force (Fig. 6A) or the vertical displacement of the COM (Fig. 6B), suggesting that either elephants do not switch from one gait to another (i.e. they use one gait only) or the transition is smoother than expected.

The kinetic and potential energy curves of the COM during one representative step at six different speeds from 0.78 m s⁻¹ to 4.76 m s⁻¹ are shown in Fig. 9 (the corresponding points on the %*R* curve are shown as open circles in Fig. 5C). The ordinate is normalised to 1.0 *E_k* and the abscissa to 360 deg. per step. At the lowest speed the *E_p* curve is much larger than the *E_k* curve, the two curves are out-of-phase and the %*R* is less than the maximum. The second speed is close to the optimal speed for a walk; although the *E_p* curve is somewhat larger than the *E_k* curve, the two are out-of-phase, and the recovery is 57%. As speed is increased, the *E_p* amplitude decreases continuously relative to the *E_k*, and by the moderate speed of 2.93 m s⁻¹ the *E_p* is half the *E_k* curve, the two are in-phase, and the %*R* is already reduced to 21%.

Do elephants run?

In running in terrestrial animals, the motion of the COM can be compared with the movement of a spring-mass system bouncing on the ground (Cavagna et al., 1988); during the contact phase, the relationship between the vertical ground reaction force (*F_v*) and the vertical movement (*S_v*) of the COM is rather linear and the slope of this line corresponds to the overall stiffness of the bouncing system (Cavagna et al., 1988).

In elephants moving faster than 2.8 m s⁻¹, the *F_v* vs *S_v* relationship can be divided into a rigid part and a compliant part. During the rigid part, corresponding to the loading of the hindlimb (A–B–C in all panels of Fig. 7), *F_v* increases while the height of the COM remains constant or increases slightly. In this part of the step the body acts as a rigid, non-compliant system.

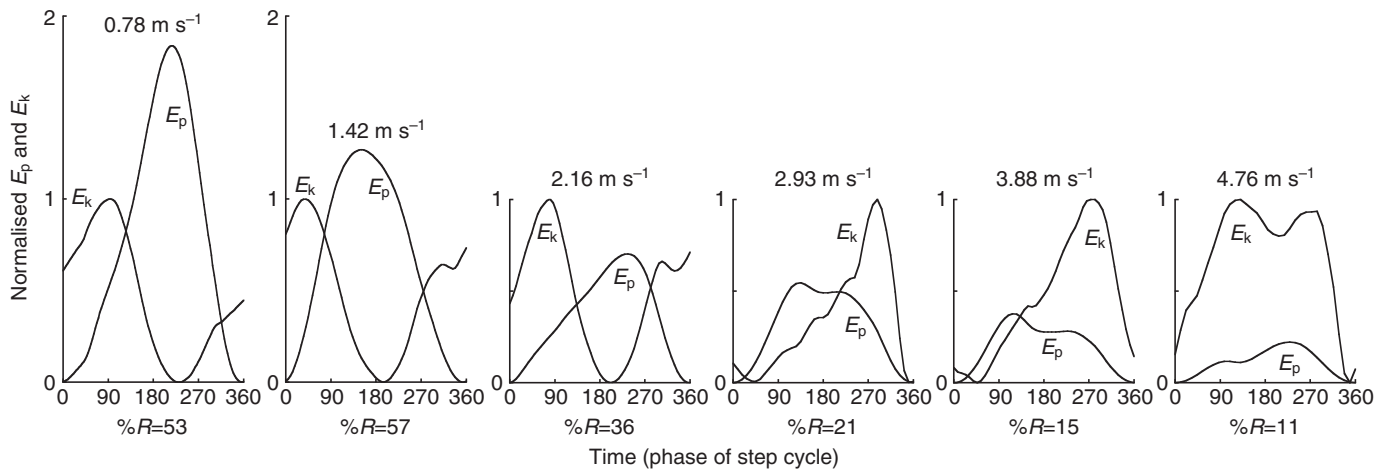


Fig. 9. Representative traces of the normalised potential (E_p) and kinetic energies (E_k) during a step at six different speeds. Both curves are normalised to an E_k value of 1. These traces are considered as typical, in terms of relative amplitude and phase shift, because their corresponding percentage recovery (% R) values are close to the mean values (these traces are represented as open circles in Fig. 5C), and the speed interval is similar throughout the six panels. As speed increases, the relative amplitude of E_p curve decreases and the phase shift between E_k and E_p curves decreases, resulting in a decreasing % R .

During the compliant part of the step, corresponding to the loading of the forelimb (C–D–A in all panels of Fig. 7), F_v increases while the height of the COM decreases. In this part of the step the body acts as a compliant bouncing system; the F_v vs S_v relationship is nearly linear, and the natural frequency of the body's bouncing system (f_n) can be calculated from the slope of the broken line in Fig. 7, upper panel, using Eqn 9.

In a spring–mass system oscillating at its natural frequency, one half cycle is the time it takes for the system to go from its equilibrium (or resting) condition, to an extreme position, back to the equilibrium condition. Because one body weight is the equilibrium force for the body's bouncing system, one half cycle corresponds to the time it takes the F_v to go from body weight (shown as the horizontal dotted lines at 17 kN in Fig. 7), to maximum vertical force, back to body weight. This period has been measured and converted to the half cycle natural frequency, f_h (Eqn 10).

The f_n (blue line in Fig. 2) is ~50% greater than the measured step frequency f_{sn} (black line). However, there is a good match between f_n and f_h (blue squares and red diamonds, respectively). This indicates that, during the loading of the forelimb, the system is indeed acting like a spring–mass system oscillating around M_b . The difference between f_n (or f_h) and f_{sn} can thus be explained by the fact that, out of this half period, the movements of the COM do not correspond to a compliant spring–mass system. Additionally, note that the fraction of the step during which the system acts like a spring–mass system is achieved by the forelimbs, which support almost 2/3 of the body weight both dynamically and statically (e.g. the antero-posterior repartition of the weight shown in Table 1).

At high speed, the vertical movements of the COM of the elephant seem to indicate that the bouncing mechanism is not used during the whole step. Indeed, this mechanism is only used during the lower part of vertical oscillation of the COM, corresponding to the lower part of the potential energy curve (Fig. 4, right). During this phase, the elephant is loading its forelimb (when the COM descends) and unloading its forelimb (when the COM ascends) and the system acts like a mass bouncing on a spring. However, to maintain the muscles and bone stress relatively low, the vertical force oscillates only between ~0.7 P_b and ~1.3 P_b (Fig. 6A).

During the upper part of the oscillation of the COM, when an aerial phase is present in other running animals, the system is very rigid. In fact, during this phase, the elephant is loading its hindlimb (when the COM ascends a little) and unloading its hindlimb (when the COM descends a little) and the system acts more similarly to the walking gait, explaining why the % R does not decrease to nearly zero as in other running animals.

Thus, at high speeds, the elephant uses a rigid mechanism during the support of contralateral limbs, and a compliant mechanism similar to that of running during the support of ipsilateral limbs. This is seen clearly in Fig. 7; during the A–B–C phase the weight is being shifted from the right side to the left side while the system is rigid (S_v is nearly constant). During the C–D phase the COM descends while the F_v increases, and during the D–A phase the COM ascends while the F_v decreases, like the bounce of a spring–mass system.

Minimising W_{ext} relative to other animals

The most striking finding is that the mass-specific work necessary to maintain the movements of the COM is nearly independent of speed and only ~0.2 J kg⁻¹ m⁻¹ (Fig. 5B), only about 1/3 that seen in other animals (broken line in Fig. 5B) (Heglund et al., 1982a; Heglund et al., 1982b). This is most easily explained by the fact that the elephants adopt a step frequency much higher than would be predicted for animals of their size. As has been shown by Cavagna and Franzetti (Cavagna and Franzetti, 1986) for walking, and Cavagna et al. (Cavagna et al., 1991) for running, when the step frequency is increased at a given speed, the external work is decreased. In effect, when the step frequency is increased at a given speed, the COM enjoys a 'smoother ride'; the vertical displacement of the COM is decreased and the forward decelerations/accelerations of the COM are also decreased.

In addition to the increased step frequency, elephants further smooth the ride by maximising the number of feet on the ground and increasing the asynchronicity of their support phases. This is most easily seen in Fig. 3. For the most part, at the lowest speed the elephant has three and sometimes four feet on the ground at the same time, and the swing phases are taken one-at-a-time. As speed is increased, at first the length of contact of each foot increases (up to a maximum, attained at 1.8 m s⁻¹) in order to maximise the average

number of feet on the ground. At the highest speed the hind-to-fore distance increases relative to the normalised step length, increasing the hind-to-fore phase angle to 78 deg. and fore-to-hind phase angle to 102 deg. (because the gait is symmetrical, the hind-to-hind or fore-to-fore phase is 180 deg. in the elephants), approaching to the most asynchronous value of 90 deg., which gives the smoothest ride for any given duty factor or average number of feet on the ground.

Because of the smooth ride, the vertical force oscillates less than in other animals (Cavagna et al., 1988). At slow speed, the maximal vertical force represents less than $1.05P_b$. When speed increases, the maximal F_v increases but this increase is rather small as compared with other species. At the highest speed, the maximal F_v observed in elephants represents less than $1.5P_b$. For comparison, this force reaches $4P_b$ in kangaroo hopping at about the same speed (Cavagna et al., 1988).

When an animal moves with an aerial phase, the minimum of F_v goes to zero. In elephants, this minimal force never approaches zero. It represents more than $0.95P_b$ at low speeds and $\sim 0.7P_b$ at the highest speeds. Note that the minimal value of $\sim 0.7P_b$ observed in our study is quite different from the minimum value of 3 ms^{-2} ($0.3g$) at a speed of 3 ms^{-1} measured by Ren and Hutchinson (Ren and Hutchinson, 2008) using motion sensors attached to the back of the elephants.

The small range over which the vertical force varies results in relative small vertical displacement of the COM, which decreases with increasing speed from 0.03 m at low speeds to 0.01 m at high speeds. This range is about the same as observed in 5–20 kg dogs trotting (Cavagna et al., 1988). The value observed at low speed is similar to the 33 mm measurement of Ren and Hutchinson (Ren and Hutchinson, 2008) at 1.37 ms^{-1} , but these authors find that the S_v increases rather than decreases with running speed, arriving at a value nearly four times higher than the value shown in Fig. 6B at top speed. This discrepancy could be due to many different factors such as limb-mass errors, segment position errors and above all integration errors due to changes in the orientation of the accelerometers in the gravitational field.

The whole body vertical stiffness in the elephants moving at speeds greater than 3 ms^{-1} (inset of Fig. 2) was calculated from the slope of the F_v vs S_v curve as shown in Fig. 7. In order to compare the stiffness of the elephants with that of other animals in the literature (Cavagna et al., 1988; Heglund et al., 1982a), F_v was divided by body weight and S_v was divided by limb length. Without taking speed into account, the resulting dimensionless stiffness ranged from 30 to 65. The value for the elephants at 4 ms^{-1} is about 60. This shows that the small S_v observed in the elephants at high speed is not due to the fact that they have an unusually high stiffness but rather because they minimise the oscillations in the F_v .

LIST OF ABBREVIATIONS

a_v, a_f, a_l	acceleration of the COM in the vertical, forward and lateral directions, respectively
COM	centre of mass
E_{com}	total mechanical energy of the COM, $E_{\text{com}} = E_p + E_{kv} + E_{kf} + E_{kl} = E_p + E_k$
E_k	kinetic energy of the COM
E_{kv}, E_{kf}, E_{kl}	kinetic energy of the vertical, forward and lateral motions of the COM, respectively
E_p	potential energy of the COM
f	step frequency
f_h	normalised step frequency measured from the above-body-weight contact period
f_n	normalised natural frequency of a spring-mass model
f_{sn}	normalised step frequency
\bar{F}_v	average vertical force over an integral number of steps

F_v, F_f, F_l	vertical, forward and lateral components of the ground reaction forces, respectively
$F_{v\text{max}}, F_{v\text{min}}$	maximum and minimum vertical forces, respectively
g	gravitational acceleration
h	limb length
L	stride length
L_f, L_h	normalised forward distance travelled by the COM while, respectively, the fore or hindlimb is on the ground
L_n	normalised stride length
M_b	body mass
P_b	body weight
%R	relative amount of energy recovered by the pendular exchange between the kinetic and potential energies of the COM
S_v	vertical displacement of the COM over one step cycle
t_h	half cycle period
V_v, V_f, V_l	the instantaneous velocity of the COM in the vertical, forward and lateral directions, respectively
\bar{V}_f	average forward speed
W_{ext}	positive work done to maintain the movement of the COM, W_{ext} is the sum of the increments in E_{com} over an integral number of steps
W_f	positive work done to accelerate the COM forwards, W_f is the sum of the increments in E_{kf} over an integral number of steps
W_l	positive work done to accelerate the COM laterally, W_l is the sum of the increments in E_{kl} over an integral number of strides
W_v	positive work done against gravity, W_v is the sum of the increments in $E_p + E_{kv}$ over an integral number of steps

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