The three-dimensional locomotor dynamics of African (Loxodonta africana) and Asian (Elephas maximus) elephants reveal a smooth gait transition at moderate speed

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We examined whether elephants shift to using bouncing (i.e. running) mechanics at any speed. To do this, we measured the three-dimensional centre of mass (CM) motions and torso rotations of African and Asian elephants using a novel multisensor method. Hundreds of continuous stride cycles were recorded in the field. African and Asian elephants moved very similarly. Near the mechanically and metabolically optimal speed (a Froude number (Fr) of 0.09), an inverted pendulum mechanism predominated. With increasing speed, the locomotor dynamics quickly but continuously became less like vaulting and more like bouncing. Our mechanical energy analysis of the CM suggests that at a surprisingly slow speed (approx. 2.2 m s\(^{-1}\), Fr 0.25), the hindlimbs exhibited bouncing, not vaulting, mechanics during weight support. We infer that a gait transition happens at this relatively slow speed: elephants begin using their compliant hindlimbs like pogo sticks to some extent to drive the body, bouncing over their relatively stiff, vaulting forelimbs. Hence, they are not as rigid limbed as typically characterized for graviportal animals, and use regular walking as well as at least one form of running gait.

Keywords: elephant; Proboscidea; locomotion; biomechanics; dynamics; gait

1. INTRODUCTION

As the epitome of graviportal animals (Gregory 1912; Gray 1968; Coombs 1978), elephants possess pillar-like legs for supporting their massive body weight (exceeding 7000 kg in some animals; Wood 1972; Christiansen 2004). Even at moderately fast speeds, elephants hold their legs relatively straight when on the ground, with estimated strain levels in lower leg bones similar to those of much smaller running animals (Alexander 1977; Alexander et al. 1979; Rubin & Lanyon 1984; Biewener & Taylor 1986). But do these fairly straight, although not necessarily completely columnar, limbs obviate the ability to use the limbs in a compliant, bouncing fashion? Elephants are a superb model system to gain insight into how musculoskeletal design is a compromise with the biomechanical and physiological constraints that extremely large body size imposes, and to test if, when, how and why locomotor abilities become lost at large size. Here we develop a new inertial sensor-based method to estimate the rigidness/compliance of elephant limbs, by quantifying centre of mass (CM) motions in locomotion, which are key indicators of limb/body compliance (Farley et al. 1993; Biknevicius et al. 2006).

Elephants are unusual not only in their enormous size, but also in their special locomotor pattern (Hutchinson et al. 2003, 2006). Elephants do not normally trot or gallop, even as juveniles, but they can move smoothly to fairly fast speeds (approx. 6.8 m s\(^{-1}\)) without changing their lateral sequence footfall pattern (Hutchinson et al. 2003). Their locomotor pattern at their faster speeds is atypical of most familiar quadrupedal animals (Muybridge 1899; Gambaryan 1974; Hildebrand 1985). Fast moving elephants exceed Froude numbers (Fr, where Fr=velocity\(^2\)\times(gravitational acceleration\times hip height\(^{-1}\)) of 1.0, even reaching Fr 3.4 (Hutchinson et al. 2003), speeds at which most other quadrupedal mammals gallop (Alexander & Jayes 1983). Across their entire speed range, elephants constantly keep at least one foot on the ground; they never change their footfall pattern to one that uses a whole-body aerial phase (Hutchinson et al. 2003, 2006).

The kinematics of slow moving elephants fall nicely into the definition of walking from all aspects, but fast moving elephants pose a challenge for applying many gait definitions. This issue hinges on how one defines a gait...
the fundamental understanding of elephant locomotion. (Hutchinson et al. 2005) may be used at moderate to near-maximal speeds; Cavagna and other stride parameters are now available, providing potential gait transition occurred was left open, although it was concluded that near a dimensionless speed of 1.0 (equal to Fr$^{-0.5}$, 1.0) elephants probably were running, in the mechanical sense of the term.

It is generally accepted that at least two fundamental mechanisms are employed by animals to modulate their energy costs in terrestrial locomotion (Cavagna et al. 1977; Heglund et al. 1982a,b; McGeer 1992; Farley et al. 1993; Minetti 2000; Ruina et al. 2005). Inverted pendulum-like movement of the body’s CM during slower locomotion is characterized by exchange of potential and kinetic energies associated with conservation of mechanical energy via a vaulting mechanism (Cavagna et al. 1977; McGeer 1992; Biewener 2006; Biknevicius & Reilly 2006). During running, trotting, hopping or Groucho (compliant) walking/running, kinetic and potential energies fluctuate in phase, but energy is conserved to some extent as the body bounces on somewhat elastic legs (Cavagna et al. 1977; McMahon et al. 1987; Farley et al. 1993). Despite their massive body weights and ponderous motions, elephants are the most economical living land animals, moving very cheaply at their normal walking speed in terms of metabolic cost of transport (J kg$^{-1}$m$^{-1}$; African elephant data from Langman et al. 1995). Hence, some-energy-saving mechanism (very likely pendulum-like walking; although elastic mechanisms may contribute even in walking, e.g. Geyer et al. 2006) must be utilized by elephants at their energetically optimal speed. However, as speed increases, elephants should change their locomotor pattern at least in a biomechanical sense, as inverted pendulum-like walking (i.e. vaulting) becomes more and more expensive in terms of metabolic cost (Hoy & Taylor 1981; Farley & Taylor 1991), and even impossible at faster speeds (Usherwood 2005). Although basic information on football patterns and other stride parameters are now available, providing hints that a bouncing gait (i.e. running in a biomechanical sense; Cavagna et al. 1977; Farley et al. 1993; Ruina et al. 2005) may be used at moderate to near-maximal speeds (Hutchinson et al. 2003, 2006), there are still wide gaps in the fundamental understanding of elephant locomotion.

The major objective of this study is to quantify the three-dimensional locomotor dynamics of Asian (Elephas maximus Linnaeus 1758) and African (Loxodonta africana Blumenbach 1797) elephants. We aim to test whether bouncing limb or CM mechanics are used at any speed (i.e. do elephants run?), or if all observable speeds in elephants comprise only standard vaulting mechanics (do they only walk?). Here we separate limb and CM mechanics, as the possibility remains that elephant limbs do not function identically (Hutchinson et al. 2006) and at some speeds vaulting whole-body CM mechanics still could involve spring-like functioning of some limbs. We also sought to identify whether there were any major kinetic differences between Asian and African elephants, as their kinematics are very similar (Hutchinson et al. 2006) but it is not impossible that there would be underlying kinetic differences.

We developed a novel multiple inertial sensor method, following Pfau et al. (2005, 2006), incorporating three-dimensional accelerometers and gyroscopes to measure the three-dimensional body CM dynamics and the torso rotations of several elephants (here we use the term ‘torso’ to refer to the limbless body, rather than ‘trunk’, which in the case of elephants may confuse readers, or ‘body’, which we only use to refer to the whole body with all four limbs included). Hundreds of continuous strides were recorded as the elephants moved freely outside in open fields at a range of speeds (0.5–3.5 m s$^{-1}$). We calculated the three-dimensional CM velocities and vertical displacements in each stride and we determined the potential energy, translational and rotational kinetic energies at different speeds. We also investigated the mechanical energy transductions in all the strides, and examined the possible gait pattern changes across the speed range.

2. METHODS

2.1. Animal measurements

Five healthy adult elephants were used in this study: two Asian elephants from Woburn Safari Park (Bedfordshire, UK) and three African elephants from West Midlands Safari Park (West Midlands, UK). Prior to testing, we used flexible measuring tape to record elephant hip and shoulder heights, and hip–hip, shoulder–shoulder and hip–shoulder distances. All elephants had known body masses ($m_b$) from placing all four limbs on a truck scale ($\pm$ 2 kg). The vital data for each elephant used in this study are listed in Table 1.

Table 1. Vital data for elephants used in this study. (Woburn: Woburn Safari Park, Bedfordshire, UK; WMSP: West Midlands Safari Park, West Midlands, UK. ‘Shoulder’ height was measured from the top of the scapula, not the glenohumeral joint, as typical for elephant studies.)

<table>
<thead>
<tr>
<th>Elephant</th>
<th>Facility</th>
<th>Species</th>
<th>Sex</th>
<th>Age (years)</th>
<th>Weight (kg)</th>
<th>Hip height (m)</th>
<th>Shoulder height (m)</th>
</tr>
</thead>
<tbody>
<tr>
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<td>Woburn</td>
<td>Asian</td>
<td>F</td>
<td>14</td>
<td>3000</td>
<td>1.97</td>
<td>2.46</td>
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<tr>
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<td>Woburn</td>
<td>Asian</td>
<td>F</td>
<td>12</td>
<td>2840</td>
<td>2.08</td>
<td>2.42</td>
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<tr>
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<td>African</td>
<td>F</td>
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<td>2780</td>
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</tr>
<tr>
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<td>WMSP</td>
<td>African</td>
<td>M</td>
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<td>3230</td>
<td>2.03</td>
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</tr>
<tr>
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<td>African</td>
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<td>1.84</td>
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Each elephant was equipped with two miniature integrated inertial sensors (MT9, Xsens, Enschede, Netherlands), two foot-mounted accelerometers (ADXL150, Analogue Devices, Norwood, MA, USA), and one stand-alone Global Positioning System (GPS) device (BTGPS II, EMTAC Technology, USA; figure 1). Each inertial sensor unit, incorporating a three-dimensional accelerometer, a three-dimensional gyroscope and three magnetometers, provided three-dimensional translational accelerations, rates of gyration, and orientation data for their point of attachment to the torso (Xsens, Enschede, Netherlands). The two inertial sensors were mounted on specially designed attachment pads and firmly attached to the elephant’s torso, with one over the spinous processes of the thoracic vertebrae on the caudal border of the scapula, and the other over the spinous processes of the caudalmost lumbar vertebrae just on the dorsal peak of the hindquarters. The sensor data were recorded at a sample rate of 256 Hz and transmitted to two data loggers (Anticyclone Systems, Surrey, UK), which were mounted on the elephant using an elastic strap around the mid-torso. The GPS unit was mounted securely on the dorsal peak of the torso strap, and recorded 1 Hz data of heading speed, latitudinal and longitudinal position and universal time.

Prior to the trials, an inertial sensor was located on the ground surface, aligned with the trackway to record a trackway coordinate system (figure 2). Thereafter, the inertial sensors and foot accelerometers were synchronized at the beginning of the trials, and the universal time was recorded simultaneously to allow synchronization of the GPS data with the inertial sensor data.

Foot touchdowns and lift-offs for the two right limbs were determined by measuring foot acceleration using two uni-axis accelerometers (ADXL150, Analogue Devices, Norwood, MA, USA; Witte et al. 2004). The accelerometers were mounted on the dorsal side of the toenail of each middle toe using melted glue, with their sensitive axis along the proximal-distal direction. The signals were logged to two data loggers (customized MP3 recorders) and recorded at a sample rate of 44.1 kHz (Parsons & Wilson 2006). Each data logger was mounted on the lateral aspect of the distal ulna/fibula on the right limbs using elastic bandages.

The elephants moved along level trackways of approximately 30 m (Woburn Safari Park) and approximately 25 m (West Midlands Safari Park) lengths at various speeds. This allowed the animals to accelerate or decelerate to and from even their fastest speeds. They were led by trainers in most trials (no difference was seen between led and not led). At fast speeds, they were also motivated by food rewards and trainer’s requests. The sensors and recording system are lightweight and completely body mounted, so the elephants moved untethered and negligibly weighted. No behavioural artefacts were observed in how the elephants moved at any particular speed. The entire trial period normally lasted approximately 70 min, and the entire range of speed of the elephants was covered. Inertial sensor, foot accelerometer and GPS data were collected continuously. A total of 153 trials were recorded: 42 for Asian elephants (Woburn Safari Park) and 111 for African elephants (West Midlands Safari Park).

2.2. Multiple sensor method

It was previously demonstrated that using just one of the inertial sensors, the three-dimensional displacement of a horse’s body CM can be captured with accuracy comparable to optical motion capture systems (Qualisys AB, Svedalen, Sweden) during trotting at up to 9.0 m s^{-1} (Plaau et al. 2005). In this study, we use an improved new sensor method to estimate the body CM acceleration, by combining the data from multiple inertial sensors attached at different positions of the animal body, similar to Hayes et al. (1983) and van den...
Bogert et al. (1996). A major advantage of using multiple sensors is that it provides an optimal estimation of the body CM acceleration by combining the motion data of different parts of the body, rather than only one particular part (Morris 1973; Hayes et al. 1983; van den Bogert et al. 1996). As the fore and hindquarters move differently in walking due to the limb phase differences, the body CM motion is a combination of both fore and hindquarter motions (Griffin et al. 2004). Therefore, a multiple sensor method using both fore and hindquarter sensors is more suitable in this study.

In addition to an earth-fixed and sensor-fixed coordinate system inherently defined in the inertial sensors (Xsens, Enschede, Netherlands), a local (body-fixed) coordinate system fixed on the animal body was defined (figure 2). The origin lay at the whole-body CM of the animal, with the $x$-axis pointing in the horizontal (cranial) direction, the $y$-axis pointing left and the $z$-axis pointing dorsally. When an inertial sensor is attached to the animal at a known position $r$ with respect to the body CM (the position of the inertial sensor relative to the body CM was determined using a three-dimensional geometric elephant model and the measured dimensional data; see details below), it generates the following linear acceleration vector (in the sensor-fixed coordinate system),

$$a = a_c + g + \omega \times (\omega \times r) + \alpha \times r,$$

where $a_c$ is the translational acceleration vector of the animal’s body CM; $g$ is the gravitational acceleration vector; $\omega$ is the angular velocity vector measured by the gyroscopes expressed in the sensor-fixed coordinate system; and $\alpha$ is the angular acceleration vector.

When signals from $n$ inertial sensors attached to the animal body are recorded, $n$ of these equations lead to a linear simultaneous equation with two unknown kinematic variables ($a_c, \alpha$). The Moore–Penrose pseudoinverse method (Campbell & Meyer 1991) was used to solve the equation. When the system is over-determined ($n > 2$), the redundancy of the inertial sensor is used to improve the accuracy. The calculation was initially conducted in a sensor-fixed coordinate system, and finally the derived results ($a_c, \alpha$) were converted into the body-fixed coordinate system of the animal. In contrast to multiple sensor methods using only accelerometer data (Kane et al. 1974; Hayes et al. 1983; van den Bogert et al. 1996), which need iterative runs of nonlinear solvers and a good initial guess, this method provides a linear closed-loop solution to estimate the whole-body CM acceleration without requiring differentiation and integration.

2.3. Data analysis

GPS data were downloaded from the GPS device using CRUX II GPS software (EMTAC Technology, USA). Speed data were extracted for each second using custom software in MATLAB (Mathworks, Natick, MA, USA). The foot accelerometer data were also processed using custom MATLAB software. The data were first resampled to the sample rate of the inertial sensors, and then the foot touchdown and lift-off timings were identified manually based on the accelerometer signals (Witte et al. 2004). Figure 3 shows a trace of resampled foot accelerometer signal with determined touchdowns and lift-offs for the right forelimb of an African elephant walking at approximately $1.3 \text{ m s}^{-1}$ (in contrast to...
horses (Witte et al. 2004), the touchdown peak signal of elephants is much lower than that of lift-off, presumably due to their large, soft foot pads). The GPS data were synchronized with the accelerometer data based on the universal time recorded. We averaged the GPS speed data within each gait cycle to calculate the average locomotor speed of that stride based on foot-on and foot-off timings.

Our multiple sensor method was implemented in MATLAB (Mathworks, Natick, MA, USA) to process the inertial sensor data. The sensor signal data first were segmented into each stride based on the touchdown and lift-off events determined from the foot accelerometer data. Next, the data were filtered using a low-pass, zero-lag fourth-order Butterworth digital filter with a cut-off frequency of 10 Hz. The body-fixed coordinate systems of the elephants were defined for each stride based on the average progression direction in the stride and the vertical axis of the trackway coordinate system. Thereafter, the multiple sensor algorithm was used to derive the three-dimensional body CM accelerations and angular accelerations from the filtered signal data of the two inertial sensors. The calculation was initially conducted in the sensor-fixed coordinate system of the forequarters’ inertial sensor, and finally the derived results were converted into the body-fixed coordinate system of the elephants. The linear acceleration and heading direction data were examined stride by stride, and all accelerating, decelerating and turning strides were discarded. We used the averaged horizontal acceleration in a stride to identify acceleration and deceleration cycles. A threshold of ±10% of peak horizontal acceleration was used to discard the accelerating and decelerating cycles. The heading direction recorded by the magnetometers on the forequarters was used to find straight moving strides, where a threshold of ±20° was used.

In the multiple sensor algorithm, knowledge of the whole-body CM position of the elephants is required to determine the relative position of each inertial sensor. However, there are no empirical body CM position data for elephants based on direct cadaver measurements. In this study, the body CM positions were determined based on a three-dimensional geometric elephant model (including all four limbs and other appendages) using validated three-dimensional graphics software (figure 4), which uses interactive deformable B-spline solids to estimate the inertial parameters for animal body segments (Hutchinson et al. 2007). The initial three-dimensional model was originally constructed based on an Asian elephant (based on a graphical artist’s representation). For each elephant, the body size and shape of the model was scaled in different directions according to the dimensional values measured for the individual elephants (hip and shoulder heights, hip-hip, shoulder–shoulder and hip–shoulder lengths), and sculpted to conform well to photos of the individuals (including minor differences in Asian versus African elephant body shape). The body mass, body CM position and inertial tensor around the CM (J) were calculated using isotropic material with a density of 1000 kg m⁻³. The inertial product components were very small, and hence were neglected. Therefore, the three principal axes of the inertia tensor coincided with the axes of the animal body-fixed coordinate system, and the inertial tensors were defined by three principal components (Ixx, Iyy, Izz).

Table 2 lists the inertial parameters for each elephant. We found the inertial sensor positions with respect to the body CM by moving a reference point interactively in the three-dimensional software environment, and simultaneously referring to multiple photos (taken from different views) of standing elephants mounted with sensors in the trials.

Energy analysis was conducted in each stride to assess the mechanical energy fluctuations, mechanical work and power required to move the CM and rotate the animal’s body (Cavagna & Keneko 1977; Cavagna et al. 1977). Total mechanical energy E_m comprises two components: potential energy \( E_p = m_0 g z \) and kinetic energy \( E_k = E_{kx} + E_{ky} \), where \( z \) is the vertical position of the body CM and \( E_{kx} \) and \( E_{ky} \) are the translational and rotational kinetic energies, respectively, defined as \( E_{kx} = (1/2) m_0 (v_x^2 + v_y^2) \) and \( E_{ky} = (1/2) \omega \cdot (J \cdot \omega) \). CM acceleration data were numerically integrated to calculate the CM velocity \( v \). The average locomotor speed in a stride was used as the integration constant for horizontal speed, and the average vertical and lateral speeds were assumed as zero. The derived vertical velocity was then integrated to calculate the vertical displacement of the CM, \( z \), using zero as the integration constant. The total mechanical power provided by the limbs to maintain the energy fluctuations of the elephant’s body was defined as the time derivative of the total mechanical energy \( P_m = (dE_m)/dt \). Like \( E_m \), it is the instantaneous sum of two terms, \( P_p = (dE_p)/dt \) and \( P_k = (dE_k)/dt \), defined as \( P_p = m_0 g z \) and \( P_k = m_0 \omega \cdot (\omega \cdot J \cdot \omega) + \omega \cdot (J \cdot \omega) / 2 \).

To quantitatively estimate the theoretical energy saving due to the transfer between potential and kinetic energies for inverted pendulum-like walking, percentage energy recovery was calculated in each stride as (Cavagna et al. 1977; Heglund et al. 1982a,b)

\[
C_s = \frac{\Delta E_p + \Delta E_k - \Delta E_w}{\Delta E_p + \Delta E_k},
\]

where \( \Delta E_p \) is the sum of the positive increment of \( E_p \); \( \Delta E_k \) is the sum of the positive increment of \( E_k \); and \( \Delta E_w \) is the sum of the negative increment of \( E_w \).
is the sum of the positive changes in total mechanical energy $E_m$ (the rotational kinetic energy $E_{kr}$ was removed from $E_m$ when calculating the energy recovery). The phase shift angle between the potential and kinetic energies of the CM (representing how far out of phase they are) was also calculated for each stride, with $180^\circ$ being totally out of phase (i.e. ideal vaulting) and $0^\circ$ being exactly in phase (i.e. ideal bouncing). If there were two small kinetic energy peaks in a step (typical for slower motion), the midway point of the two peaks was used to define the phase angle, by representing the general phase relationship between the kinetic and potential energy fluctuations (similar results were obtained using the minimum kinetic energy and maximum potential energy as in Griffin et al. 2004a). The relative magnitude of the kinetic energy fluctuation with respect to the potential energy fluctuation was also calculated.

### 3. RESULTS

We collected 876 strides of valid data for the 153 trials and show representative time trace curves of an African elephant moving at 1.37 (figure 5) and 3.07 m s$^{-1}$ (figure 6). We confirmed that all representative traces shown were broadly consistent among trials and individuals. Both horizontal ($\omega_x$) and lateral ($\omega_y$) CM accelerations fluctuated around zero. The horizontal acceleration exhibited a typical sinusoidal pattern at all speeds in each step. The lateral component was of small amplitude and greater variability than the other directions, especially during faster locomotion. The vertical CM acceleration $\omega_z$ fluctuated around gravitational acceleration (9.8 m s$^{-2}$) with two or three small peaks in each step. The fluctuation amplitude of vertical acceleration was approximately 3 m s$^{-2}$ at 1.37 m s$^{-1}$, and increased only moderately to 7 m s$^{-2}$ at 3.07 m s$^{-1}$. Both the horizontal and vertical CM accelerations at slow speeds broadly matched previous force plate and modelling data for slowly walking dogs and other quadrupeds (Cavagna et al. 1977; Griffin et al. 2004a; Usherwood et al. 2007). The torso angular velocities (roll $\omega_x$, yaw or heading $\omega_y$ and pitch $\omega_z$) all oscillated cyclically around zero with small amplitude, and increased only slightly when speed increased to 3.07 m s$^{-1}$. Similar to angular velocity, the angular accelerations ($\alpha_x$, $\alpha_y$, $\alpha_z$) also fluctuated periodically around zero in each stride. However, they increased markedly when speed increased.

Represented average curves of translational kinetic energy ($E_{kt}$), total kinetic energy ($E_{kt}+E_{kr}$), potential energy ($E_p$) and mechanical energy ($E_m$) of an African elephant moving at 1.37 and 3.07 m s$^{-1}$ are shown in figures 7 and 8 (corresponding to figures 5 and 6). At slower speeds, the rotational kinetic energy ($E_{kr}$) due to torso rotations only accounted for very small amount of the total kinetic energy, even at moderate speed (3.07 m s$^{-1}$). Although the inertia tensors of elephants are very large due to the massive body mass and size, the torso angular velocities were relatively small. The total kinetic energy showed a two-peaked pattern per stride, reaching its minima in the forelimb mid-stance phase and its maxima in the forelimb double support phase. The potential energy also showed a two-peaked pattern that was almost out of phase with kinetic energy, reaching minima around forelimb touchdown and maxima between mid-stance of the supporting hindlimb and mid-stance of the supporting forelimb. These potential and kinetic energy patterns in a stride closely match the trends from previous force plate and modelling data for walking dogs and other quadrupeds at slow and normal speeds (Cavagna et al. 1977; Griffin et al. 2004a; Usherwood et al. 2007). Although the mechanical energy fluctuations were small throughout most of the stride, there were still some distinct mechanical energy changes (energy inputs and losses), especially as the CM raised towards its highest position.

When speed increased to 3.07 m s$^{-1}$ (figure 8), the potential energy showed a similar pattern to slow speeds, but its greatest magnitude shifted closer to the timing of the contralateral hindlimb touchdown. The total kinetic energy increased markedly due to the speed increase, and was dominated by translational kinetic energy. In contrast to the 2.24 times slower speed shown, the relative magnitude of the kinetic energy with respect to potential energy increased more than three times, from 126 to 410%. However, unlike at slower speeds, the kinetic energy became more in-phase with potential energy at faster speeds, reaching its maxima shortly after the lift-off of each forelimb, during the late stance phase of the contralateral hindlimb.

The estimated vertical CM displacements (figure 9; corresponding to figures 7 and 8) had very similar patterns at slower and faster speeds, showing two peaks in a stride. There were no striking changes in the fluctuation amplitude of the vertical CM displacements when speed increased from 1.37 to 3.07 m s$^{-1}$; the fluctuation ranges were approximately 30 mm in both cases. However, as was the case for potential energy, the timing of the maximum vertical displacement moved towards the contralateral hindlimb touchdown when speed increased.

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**Table 2. Estimated inertial parameters for elephants used in this study. ($I_{xx}$, $I_{yy}$, $I_{zz}$: three principal components of whole-body inertial moment around the CM.)**

<table>
<thead>
<tr>
<th>elephant</th>
<th>measured mass (kg)</th>
<th>estimated mass (kg)</th>
<th>estimation error (%)</th>
<th>$I_{xx}$ (kg m$^2$)</th>
<th>$I_{yy}$ (kg m$^2$)</th>
<th>$I_{zz}$ (kg m$^2$)</th>
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<tr>
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At slower speeds, the total CM mechanical power was of small amplitude (figure 9). The elephants used alternating periods of double and triple limb support at the speeds shown. During the early part of triple limb support (just after a hindlimb touchdown, when both hindlimbs and the contralateral forelimb were on the ground), the mechanical power exhibited only very small fluctuations. This is consistent with the inference that an inverted pendulum mechanism is very effective during this period in elephants. Just before each forelimb’s touchdown, there was a burst of positive power, presumably to reduce the touchdown collisional losses.

Figure 5. Representative time traces of (a) three-dimensional CM accelerations, (b) torso angular velocities and (c) angular accelerations of an African elephant (2780 kg) moving at 1.37 m s$^{-1}$, with approximately 4.5 continuous steady strides. RH and RF (above) show foot touchdown and lift-off events from the accelerometer data.
and hence save energy (Kuo 2002; Ruina et al. 2005; Usherwood et al. 2007). This positive power continued until slightly before the next forelimb lift-off, raising the elephant’s CM to its highest position presumably via the trailing forelimb’s push-off. Thereafter, the mechanical power became slightly negative, probably due to the simultaneous positive and negative work of the ipsilateral forelimb and hindlimb (Donelan et al. 2002). After the contralateral hindlimb landed on the ground, the animal passed into its next triple support phase.

At faster speeds, the pattern of CM mechanical power totally changed, even though the footfall pattern remained almost identical. This change was not sudden, but was rather continuous across the range of speeds.
Figure 7. Representative time histories of translational kinetic energy $E_{kt}$, total kinetic energy $E_{kt} + E_{kr}$, potential energy $E_p$ and total mechanical energy $E_m$ in a stride cycle of an African elephant (2780 kg) moving at 1.37 m s$^{-1}$ (Fr 0.093), averaged for four continuous strides (corresponding to figure 4). Left limb touchdowns and lift-offs were estimated by assuming a half stride phase difference between right and left limbs (Hutchinson et al. 2006).

Figure 8. Representative time histories of translational kinetic energy $E_{kt}$, total kinetic energy $E_{kt} + E_{kr}$, potential energy $E_p$ and total mechanical energy $E_m$ in a stride cycle of an African elephant (2780 kg) moving at 3.07 m s$^{-1}$ (Fr 0.47), averaged for two continuous strides (corresponding to figure 5).
observed. There were two large negative power bursts and two large positive bursts per stride. The mechanical energy losses occurred in early hindlimb stance and were recovered near the hindlimb mid-stance phases. In contrast to slower speeds, the positive power burst continued after the contralateral forelimb left the ground, when only the ipsilateral forelimb and hindlimb were in stance.

Very similar to the African elephants described above, the total kinetic energy and potential energy of Asian elephants (figures 10 and 11) during a stride were also almost out of phase at around their metabolically optimal speed, with phase shift angles approximately 145°–165°, very close to the 150°–170° of African elephants (figures 7 and 8). When speed increased to 2.41 m s\(^{-1}\), this phase relationship changed to more in-phase. The vertical CM displacement also showed a two-peaked pattern at both speeds, with its maximum position being between mid-stance of the supporting hindlimb and mid-stance of the supporting forelimb at slower speeds, and moving towards the contralateral hindlimb touchdown when speed increased. It showed no particular change in its fluctuation amplitude with increasing speed, which was approximately 28–35 mm, very similar to 30–38 mm of African elephants (figure 9). The total mechanical power pattern was likewise very similar to African elephants, showing spring-like power bursts associated with the hindlimbs at moderately fast speeds, unlike slow speeds (figure 12).

To quantify the transduction between potential and kinetic energies, we calculated the mechanical energy recovery (§2) for all elephants across their entire speed range (figure 13a). The associated phase shift angle between the potential and kinetic energies at different speeds is shown in figure 13b. The energy recovery reached its maximum of approximately 0.35–0.50 at a dimensionless speed (Fr\(0.5\)) of 0.30. The corresponding phase angle was approximately 160° (140°–180°), i.e. the potential and kinetic energies were almost out of phase. With increasing speed, the energy recovery decreased gradually, associated with simultaneous decreases of phase angle. Interestingly, both energy recovery and phase shift angle appear to have levelled off after a dimensionless speed of approximately 0.50 (Fr 0.25), with values approaching energy recovery of 0.10 (0.06–0.15) and phase angle of 90° (70°–110°). When the speed was slower than normal, both energy recovery and phase angle decreased.

4. DISCUSSION

In this study, we have quantified the three-dimensional locomotor dynamics of African and Asian elephants using a novel multisensor method incorporating three-dimensional accelerometers and three-dimensional gyroscopes. Our methodology has some advantages over standard force platform analysis (also see Pfau et al. 2005, 2006): animal locomotion can be studied in open-field environments and across any ground surface; data collection is continuous (the sensors go where the animal goes) without being restricted to smaller plate areas; the equipment is reasonably inexpensive and requires little set-up time or maintenance, and runs on self-contained batteries; and three-dimensional body motion is measured allowing for internal work calculations. However, the technique involves errors (e.g. skin motion artefacts) and signal noises, only estimates rather than directly measures locomotor mechanics (e.g. ground reaction forces) and requires estimation of the CM position of the animal. But if caution is taken to deal with (and examine with sensitivity analysis) these errors and noises, this kinematics-based method can still produce good results compared with methods based on force transducers (e.g. force plates). For example, Bobbert et al. (1991) used a very simple motion analysis marker system, and successfully predicted the ground impact peak during human running with less than 10% error compared with force plate data. Ladin & Wu (1991) successfully estimated the forces exerted on a pivot joint using only one triaxial accelerometer. The results matched well with the measured forces using an instrumented array of strain gauges in the pivot joint. Van den Bogert et al. (1996) found that four triaxial accelerometers attached on the torso reasonably reproduced the patterns of force plate data for human walking and running. Bobbert et al.

Figure 9. Representative averaged time histories of vertical CM displacement and total mechanical power in a stride cycle of an African elephant (2780 kg) moving at (a) 1.37 m s\(^{-1}\) (Fr 0.093) and (b) 3.07 m s\(^{-1}\) (Fr 0.47) (corresponding to figures 4 and 5). Elephant pictures modified from Gambaryan (1974).
Figure 10. Representative time histories of translational kinetic energy $E_{kt}$, total kinetic energy $E_{kt}+E_{kr}$, potential energy $E_p$ and total mechanical energy $E_m$ in a stride cycle of an Asian elephant (3000 kg) moving at 1.56 m s$^{-1}$ (Fr 0.12), averaged for three continuous strides (cf. figure 7).

Figure 11. Representative time histories of translational kinetic energy $E_{kt}$, total kinetic energy $E_{kt}+E_{kr}$, potential energy $E_p$ and total mechanical energy $E_m$ in a stride cycle of an Asian elephant (3000 kg) moving at 2.41 m s$^{-1}$ (Fr 0.30), averaged for two continuous strides (cf. figure 8).
(2007) successfully calculated the vertical ground reaction forces on individual limbs of horses based only on some marker kinematics data. The estimated forces concurred with the measured force plate data. The current method does not directly account for the motions of the limbs and head, although our three-dimensional CM model (figure 4) included these appendages. However, the ratios of elephant’s limb and head/neck masses to the whole body mass are moderate; overall they are close to those of horses (6–9% of body mass per limb for horses and elephants; 9.5% body mass for head/neck for horses, approx. 15% for elephants; Shoshani et al. 1982; Buchner et al. 1997; also supported by our three-dimensional CM model’s data). In addition, as the elephant’s touchdown and lift-off angles are small, and change only slightly with increasing speed (our unpublished limb motion data (2006)), the effect of limb motion on CM estimation would be small. Additionally, according to our observations based on video data (e.g. Hutchinson et al. 2006), the motions of the head and forequarters largely move out of phase, which may cancel each other’s motions out to some extent. Hence, we are confident that the errors induced by neglecting the head and limb motions in our method will be small (see also van den Bogert et al. 1996; Pfau et al. 2005, 2006) and should not change the major trends. These assumptions are validated by using multi-segment kinematic data (see electronic supplementary material).

Our results show that, like stride parameters (Hutchinson et al. 2006), the CM motions of African and Asian elephants are qualitatively quite similar. The body CM of both species reached its highest position around forelimb mid-stance with small fluctuation amplitudes (around 3 cm), and increased slightly with increasing speed. This vertical CM displacement was of very small amplitude; however, it is consistent with our previous kinematic data. The peak vertical displacement of the hip and shoulder skin markers at any speed is very small (generally less than 0.10 m, often less than 0.05 m; Hutchinson et al. 2006). As these displacements are out of phase to some extent even at moderately fast speed (Hutchinson et al. 2003, 2006), this may further flatten the CM vertical displacement pattern. Gambaryan (1974) reached comparable conclusions independently, inferring a rather horizontal CM path. Furthermore, this fluctuation amplitude is comparable to that of toltting horses (Biknevicius et al. 2006) based on force plate data, which is approximately 1.2 cm (less than 1% of limb length, even lower than the approx. 1.5% of hip height relative peak displacement values in our elephants). However, our inertial sensor processing may slightly reduce the CM displacement, as the digital filtering process (see §2) will remove some signals when reducing the noise (Winter 1990). Yet this is inevitable for all motion analysis methods even the multiple camera system (Winter 1990; Pfau et al. 2005) as the noises, e.g. skin movements, are in a similar

Figure 12. Representative averaged time histories of vertical CM displacement and total mechanical power in a stride cycle of an Asian elephant (3000 kg) moving at (a) 1.56 m s$^{-1}$ (Fr 0.12) and (b) 2.41 m s$^{-1}$ (Fr 0.30) (cf. figure 9). Elephant pictures modified from Gambaryan (1974).

Figure 13. (a) Mechanical energy recovery and (b) phase shift angle between potential energy and kinetic energies plotted against dimensionless speed ($Fr^{0.5}$) for African (open symbols) and Asian (filled symbols) elephants.

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band as the useful motion signals. As we have chosen a well-validated and publicly recognized digital filtering method (Winter et al. 1974; Winter 1990), this reduction should be minimized.

Like kinematic patterns, the kinetics of African and Asian elephants are also quite similar. The body CM kinetic and potential energies of both species of elephants have out-of-phase relationships at their energetically optimal speed around a dimensionless (relative) speed of 0.30 (Fr 0.09, approx. 1.3 m s\(^{-1}\); figures 7 and 10), as mechanical energy recovery reaches its maximum (figure 13a). This coincides with the observation that elephants’ metabolic cost of transport (J kg\(^{-1}\) m\(^{-1}\)) is minimal at their normal moving speed (Langman et al. 1995), consistent with the inference that they may use a passive inverted pendulum (and perhaps some elastic; Geyer et al. 2006) mechanism(s) to conserve energy at their optimal speed, like most other terrestrial animals (Cavagna et al. 1977; Blickhan & Full 1993; Farley & Ko 1997; Ahn et al. 2004; Rubenson et al. 2004; Biewener 2006; Biknevicius & Reilly 2006). Their maximal energy recovery may appear to be lower than that of typical walking quadrupeds (approx. 60–75%; Cavagna et al. 1977; Griffin et al. 2004a; Usherwood et al. 2007), but this may be explained by their relatively smaller vertical CM displacement, which leads to small potential energy fluctuations. This will reduce the transduction between the potential and kinetic energies when they are out of phase, and hence result in small energy recovery. A similar pattern was observed in tilting horses (Biknevicius et al. 2006). Additionally, at normal moving speed (approx. Fr 0.10), the elephants’ potential energy fluctuations reach their maxima between mid-stance of the supporting hindlimb and mid-stance of the supporting forelimb, which is very similar to the findings of previous studies of quadrupedal walking in which the limbs were modelled as rigid struts (Griffin et al. 2004a; Usherwood et al. 2007). This indicates that probably both the supporting forelimbs and the hindlimbs use vaulting mechanics during normal walking, as expected. However, in any case, we urge caution in overinterpreting our recovery values relative to other animals (or relative to energetic costs in elephants), as some errors inevitably are involved in our method, and along with other factors (including the assumptions of the recovery method itself) this renders comparison of recovery magnitudes among species far from straightforward.

At slower than normal speeds, the metabolic cost of transport increases (Langman et al. 1995) with decreasing mechanical energy recovery (figure 13a), which is consistent with previous force plate and modelling measurements of other quadrupeds (Cavagna et al. 1977; Griffin et al. 2004a; Usherwood et al. 2007). This may explain why elephants do not habitually move very slowly (indeed it is difficult to convince them to maintain very slow speeds), as their energy-conserving mechanisms may be less effective in this speed range.

At higher than normal speeds, the energy recovery decreased gradually (figure 13a), associated with simultaneous decreases of phase angle (figure 13b), suggesting less vaulting and increased bouncing mechanics for the limbs. Both energy recovery and phase shift angle levelled off after a dimensionless speed of approximately 0.50 (approx. 2.2 m s\(^{-1}\)); the patterns are strikingly reminiscent of a very different animal using a ‘grounded run’ (i.e. no whole-body aerial phase but bouncing mechanics): ostriches (Rubenson et al. 2004). Associated with the mechanical power patterns and the vertical CM displacements (figures 9 and 12), these data bolster the hypothesis that a gait transition may happen at this relatively slow speed. But were all or just some limbs using bouncing mechanics?

Our mechanical power analysis found that elephants use a spring-like power burst pattern at moderate speeds (greater than 2.2 m s\(^{-1}\), Fr ≥0.25), which is more associated with the hindlimbs. After hindlimb touchdown, as the contralateral shoulder joint is rolling down from its highest position, the hindlimb should generate a braking force as in a typical quadrupeds, absorbing mechanical energies in early stance phase, then presumably generating propulsive power, probably from middle to late stance, to push the body CM over the ipsilateral forelimb. After the contralateral forelimb left the ground, when only the ipsilateral forelimb and hindlimb were in stance, the forelimb should produce a braking force in its early stance (as in a typical quadruped); however, the total CM power was of large positive value at this time, which means that the stance hindlimb should have produced a larger propulsive power to counteract the braking forelimb and push the body CM. This indicates that the propulsion was probably contributed mainly by the hindlimbs. The whole-body CM displacement is more closely associated with the stance forelimb motion, reaching its maximum around forelimb mid-stance. As the elephant’s body CM is closer to the forelimbs (Thompson 1917; Henderson 2006; this study), and the forelimbs remain very straight during the stance phase (Hutchinson et al. 2003, 2006), this indicates that the forelimbs most likely still use vaulting mechanics even at faster speeds. Although the vertical CM displacement showed a similar two-peaked pattern at both slower and faster speeds, its highest position moved towards the contralateral hindlimb touchdown as speed increased. As the forelimb remained fairly straight, this phase shift indicates that the hindlimb probably compressed at least during its early stance phase, as the CM vertical displacement of a bounding hindlimb should peak at touchdown whereas a vaulting hindlimb should reach its highest position in its mid-stance. Therefore, a vaulting hindlimb would make the CM maximum vertical displacement point shift away from the contralateral hindlimb touchdown, which is contradictory to our data (figures 9 and 12).

Therefore, it is reasonable to hypothesize that when speed increased, the elephant’s locomotor pattern changed smoothly from a fairly stiff-limbed vaulting gait to a more bouncing gait. Beyond a dimensionless speed of 0.50 (approx. 2.2 m s\(^{-1}\)), the hindlimbs exhibited some bouncing mechanics that we infer helped to push the elephant’s body CM over their
strut-like vaulting forelimbs. However, this mechanism differs from other quadrupedal bouncing gaits at medium speeds, e.g. trotting or pacing. The potential and kinetic energies were not exactly in phase, and there were still some interchanges between potential and kinetic energies, presumably related to the more straightened forelimbs (e.g. Hutchinson et al. 2006).

The mechanical energy analysis conducted in this study is mainly about the whole-body CM, rather than individual limbs. Our hypothesis of hindlimb-powered bouncing is mainly inferred from the whole-body CM dynamics and the footfall timings. The forelimbs are probably also involved to drive the body CM in addition to the hindlimb bouncing to some extent (which cannot be determined here), e.g. contralateral forelimb push-off around each hindlimb’s mid-stance. Although some speculations are involved, this is the explanation that is most consistent with all available lines of evidence. Indeed, the rather slow speed gait transition revealed by this study concurs with previous results from kinematics: at moderately rapid speeds, the shoulder motion in stance phase still resembles walking, moving upwards and then downwards, whereas the hip motion is characteristic of running, moving downwards and then upwards (Hutchinson et al. 2003, 2006). Additionally, our conclusions are also consistent with stride parameter studies on African and Asian elephants. The regression slopes of stance phase duration, swing phase duration and relative stride length versus speed all show slight changes (discontinuities) before and after dimensionless speed 0.50 (greater than 2.2 m s\(^{-1}\), Fr > 0.25; Hutchinson et al. 2006).

In a classical kinematic sense, elephants do not run (Hildebrand 1985; Hutchinson et al. 2003, 2006). However, this does not mean that they do not use any bouncing mechanism (Hutchinson et al. 2003, 2006; also see Biewener 2006; Biknevicius & Reilly 2006). Our mechanical energy analysis suggests that elephants probably use a special locomotor pattern at moderate speeds (greater than 2.2 m s\(^{-1}\), Fr \(\geq\) 0.25), characterized by vaulting forelimb and probably bouncing hindlimb mechanics. These locomotor dynamics, combining vaulting and bouncing mechanics, are similar to those seen in cantering/galloping (Cavagna et al. 1977; Minetti 2000; Pfau et al. 2006) and ‘intermediate gaits’ (Ahn et al. 2004; Biknevicius & Reilly 2006).

The fastest speed recorded in this study for the captive elephants is 3.5 m s\(^{-1}\) (Fr \(\leq\) 0.56), which is slower than the near-maximal speed of more athletic elephants (6.8 m s\(^{-1}\), Fr \(\leq\) 3.4). What happens when speed increases? Is there another gait transition as elephants approach their near-maximal speed? Previous studies on elephant stride parameters inferred that elephants must change their gait pattern by a dimensionless speed (or Fr) of 1.0 (Hutchinson et al. 2006). Near Fr 1.0, an elephant’s forelimbs and hindlimbs attain their own separate aerial phases, so their fore and hindquarters could biomechanically be running. Those studies also found that at least the hindlimbs showed increasingly compliant motion. Although the forelimbs surely have some compliance, they still should be appreciably stiffer than the hindlimbs, as the shoulder joint retains its highest vertical position in forelimb mid-stance even at near-maximal speed (Hutchinson et al. 2003, 2006). However, we can only determine what the gait of fast moving elephants is when whole-body dynamics data at faster speeds are available.

Although athletic elephants can attain speeds over Fr 1.0 and as quick as Fr 3.4 (Hutchinson et al. 2003), we hypothesize that they change their locomotor pattern to a hindlimb bouncing gait at much slower, moderate speeds. This is surprisingly less than the medium gait transition speed of most other animals (e.g. from walking to running or trotting), which is usually Fr 0.4–0.6 (Alexander & Hayes 1983; Usherwood 2005). However, the elephant gait transition at Fr \(\approx\) 0.25 is very close to the walk–trot gait transition speed (approx. 0.3; Alexander & Hayes 1983; J.R.H. 2006, unpublished data) of white rhinoceroses (Ceratotherium simum), the second largest land animals. Unlike elephants, rhinoceroses can trot and gallop (Alexander & Hayes 1983; Alexander & Pond 1992), which is typical of less gravitoportal quadrupeds. Furthermore, horses switch to trotting at slightly low Froude numbers as well (approx. 0.35; Griffin et al. 2004b), suggesting that this is a common pattern for larger quadrupedal mammals, although more data are needed to further test how broadly this trend applies. Why might large mammals change their gait at relatively slower speeds (Fr < 0.40)? We speculate that this may be because more compliant limb mechanics can attenuate transient impact forces on the feet (McMahon 1985; McMahon et al. 1987; Blickhan 1989), and hence reduce the risk of limb injury incurred by the massive body weight. In addition, bouncing limb mechanics helps to modulate vertical CM oscillations (Biknevicius et al. 2006; Schmitt et al. 2006), which may be particularly critical for the locomotor stability (and efficiency) of large quadrupeds.

The lateral sequence single-foot pattern used by elephants has been observed at slow walking speeds in a broad range of mammals (Muybridge 1899; Gambaryan 1974; Hildebrand 1985). But few species retain this footfall pattern into faster speeds, including elephants and horses (Hutchinson et al. 2003, 2006; Biknevicius et al. 2004, 2006; Schmitt et al. 2006). Some gaited horses, such as the Icelandic horse (tölt) and the Paso Fino horse (classic fino, paso largo), can move quite rapidly using the single footfall pattern without changing to trotting or galloping (Biknevicius et al. 2004, 2006), which is very similar to the kinematics of elephants. However, in a biomechanical sense, the tölt of Icelandic horses is a running (i.e. bouncing) gait (Biknevicius et al. 2006). Töltting Icelandic horses have an almost in-phase kinetic and potential energy relationship with a phase shift angle much less than 90\(^\circ\) (often less than 45\(^\circ\)), and the body CM is at its lowest position during the forelimb mid-stance (Biknevicius et al. 2006). These are all typical features of a purely running gait. It remains to be seen whether past Fr \(\sim\) 1.0 elephants move in this fashion.

Elephants at moderate speed move rather unlike töltting in that they seem to have a combined vaulting and bouncing gait. Although the quadrupedal walking of many mammals is to some extent driven by the hindlimbs (Manter 1938; Demes et al. 1994; Gregersen...
et al. 1998), we infer that elephants feature extreme specialization of the forelimbs as stiff supportive struts, whereas the hindlimbs act as bouncing motors. This mechanism may provide biomechanical advantages for the largest land animals during natural locomotion. The bouncing of the stance limbs may provide some energetic benefits for these animals by reducing muscular work when they move fast, similar to the energy-saving mechanisms found in other bouncing gaits (Alexander 1988, 1991; Farley et al. 1993). However, a more crouched, bouncing hindlimb should cause a reduced effective mechanical advantage of extensor muscles and a consequent increase of muscle force production, which could be a trade-off for this elastic energy-saving mechanism (Biewener et al. 2004). Furthermore, the evenly spaced single-foot pattern (Hildebrand 1976, 1985; Hutchinson et al. 2006) provides superior stability at faster speeds because the supporting base is normally larger and the simultaneous counteractions of forelimb and hindlimb throughout the stride help to preserve body stability along the direction of progression (Manter 1938; Hildebrand 1976, 1985; Winter 1990; Donelan et al. 2002). Thus, at medium speeds elephants may take advantage of both spring mass and inverted pendulum mechanisms while retaining superior body stability typically only associated with slower gaits.

Finally, our analysis defies the classic dogma that elephants do not run in any sense because they are either too large or have overly rigid, inflexible limbs that prevent bouncing (Alexander & Pond 1992; Paul 1998). It is conceivable that other parts of elephants (e.g. the head or internal organs) contribute some bouncing, but our data support the hypothesis that at least the hindlimbs bounce at moderate-to-high speeds. As Gambaryan (1974) also noted, elephants have extraordinarily rigid bodies; hence, we expect that our assumption that the body is effectively rigid is more justifiable for them than for most other animals. The second gait of elephants could be called an amble, intermediate gait or run (Muybridge 1899; Gambaryan 1974; Alexander et al. 1979; Ahn et al. 2004; Schmitt et al. 2006), and raises the question of whether gaits may be better defined by individual limb dynamics (e.g. vaulting or bouncing of particular limbs) rather than whole-body CM dynamics (Biewener 2006; Biknevicius & Reilly 2006). However, we caution that the kinematic (Hutchinson et al. 2003, 2006) and kinetic (this study; especially figure 13) changes as elephants increase in speed are fairly continuous, perhaps involving a more gradual and subtle gait transition that blurs the distinction between seemingly discrete gaits (also see Ruina et al. 2005; Geyer et al. 2006). Although this strays dangerously into semantic issues, the shift from vaulting to bouncing hindlimb mechanics we have inferred from slow to fast speeds in elephants is a major change of locomotor function that was not suspected or as thoroughly demonstrated in previous studies, and hence we view it as a distinct gait. We expect that other aspects of prevailing locomotor paradigms about large ‘graviportal’ mammals and the biomechanical constraints that large size imposes on locomotor capabilities will need further revision as additional empirical data on their locomotor mechanics become available.

All experiments with elephants were conducted with the approval of the Royal Veterinary College’s Ethics and Welfare Committee.

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