Locomotion Efficiency of Elephants: Mechanical work and energetics

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Abstract

Understanding how large terrestrial animals manage the energetic demands of locomotion remains a major question in biomechanics. While smaller animals have been well studied, data on species exceeding one tone are scarce, making it difficult to evaluate whether principles derived from small and medium-sized species hold at the upper limits of body size. In this study, we examined the mechanical work of locomotion in 27 Asian elephants (872 - 4000 kg) across a large range of speed of progression. We quantified the internal work required to move the limbs relative to the whole-body centre of mass (*COM*) and combined it with external work to estimate total mechanical cost. Our results show that elephants devote a surprisingly large proportion of total mechanical work - up to ~75% at higher speeds - to move the limbs. This highlights the importance of internal limb dynamics in shaping the energetic profile of large quadrupeds. Using published metabolic cost values for elephants, we estimate that their muscular efficiency during locomotion ranges between ~30 and 45%, values that fall within the range reported for other large mammals such as horses and humans. Together, these findings offer the first detailed breakdown of internal and external mechanical work in elephant locomotion and provide novel insights into how extreme body size influences the partitioning of mechanical work. This study contributes new data essential for understanding locomotor energetics at the upper limits of terrestrial animal mass.

Introduction

Terrestrial movement energetics and its relationship with size have captivated biologists for more than 50 years (Clemente and Dick, 2023). One major question is related to the quest of biological invariants, trying to explain and predict the evolution of the cost of locomotion. In 1982, Taylor et al. measured the net metabolic cost of transport (E_{metab}, in J kg^{-1} m^{-1}) of mammals and birds with a body mass range of 0.01 to 260 kg (Taylor et al., 1982). They found that the mass-specific E_{metab} was roughly inversely proportional to the cube root of the body mass (M_b), *i.e.* $E_{metab} \propto M_b^{-0.32}$. The same relationship was later found in reptiles, amphibians and arthropods weighing less than 10 g (Full et al., 1989).

According to the above relation, since the elephant is the biggest living terrestrial animal, it should also be the most economical. Langman et al. (Langman et al., 1995; Langman et al., 2012) confirmed this hypothesis. They measured the energy expenditure during locomotion of African elephants weighing about 3.5 tons. These authors found that elephants present the lowest mass-specific metabolic cost of terrestrial locomotion ever measured: the addition of animals with a 12-fold increase in body mass over the largest animal measured by Taylor et al. (1982) produced an allometric relationship for mammals ranging from 7g to 3.5 tons ($E_{metab} \propto M_b^{-0.27}$). In other words, the mass-specific cost per unit distance of an elephant is ~1/40 of the cost of a mouse.

It is commonly accepted that the main factor determining the energy expenditure of terrestrial locomotion is the mechanical work done by the animal to travel along the land (Heglund, 2004; Peyré-Tartaruga et al., 2021). During legged locomotion, the limbs (i) support and propel the body by exerting forces against the ground and (ii) oscillate forwards to be 'reset' each step. For this reason, the muscular work of locomotion falls naturally into two parts: (i) the work required to maintain the movements of the centre of mass (*COM*) relative to the surroundings (defined as external work, W_{ext}) and (ii) the work required to maintain the movements the body segments relative to the *COM* (defined as internal work, W_{int}). The total mechanical work (W_{tot}) done during locomotion is then best computed as the sum of W_{ext} and W_{int} (Dewolf et al., 2019a; Mesquita et al., 2023; Willems et al., 1995).

In the early eighties, Heglund and his colleagues publishes a series of four papers, in which they measured W_{int}, W_{ext} and W_{tot} in different species of birds and mammals with a body mass ranging from 0.01 to 260 kg (Fedak et al., 1982; Heglund et al., 1982a; Taylor et al., 1982). They found that the mass specific mechanical work that muscles perform to swing the limbs forward and backward and raise and lower the *COM* does not vary with size. Extrapolating the metabolic and mechanical cost of locomotion from scaling trends observed in smaller mammals to an animal the size of an elephant leads to the paradoxical conclusion that, beyond ~1500 kg, mechanical work would exceed metabolic energy input - an outcome that violates conservation of energy and highlights the need for direct measurements in large animals (see Heglund et al., 1982).

Two papers evaluated the mechanical work in elephants (Genin et al., 2010; Ren et al., 2010), considering the work required to move the *COM* whereas the second one considered an individual limb method (inverse dynamics). However, neither of them considered the cost of moving the body segments relative to the *COM* (W_{int}). Although W_{int} represents a significant fraction of W_{tot} during steady state level locomotion, particularly at high speeds (Hill, 1950), its impact on the total energy demand during elephant's locomotion is still unknown. Taylor et al. (Taylor et al., 1974) found that, despite large differences in limb mass, the energetic cost of running in cheetahs, gazelles, and goats of about the same total body mass and limb length was nearly identical over a wide range of speeds, suggesting that most of the energy expended in running might not be used to accelerate and decelerate the limbs. Furthermore, in their attempt to find a unifying hypothesis to explain simply the cost of locomotion, Kram and Taylor assumed that the cost of swinging the limbs back and forth was negligible (Kram and Taylor, 1990). More recently, however, Marsh et al. (Marsh et al., 2004) found that the metabolic cost of moving the limbs in guinea fowl was far from negligible, comprising 25% of total energy expenditure, while the cost of generating force to support the body during the stance phase accounts for 75% of the total. Compared with smaller animals, elephants have heavy and bulky legs, which together increase the inertia of the limbs. Thus, the elephant is an extreme case which may highlight the importance of W_{int} on W_{tot} during terrestrial locomotion.

Hildebrand and Hurley (1985) studied elephants at near their maximal speed and found that large oscillations in the kinetic energy of the limbs occur both during

stance and swing phase of the limb. Unfortunately, a large amount of information is missing from this study (weight of the animals, the energy curves are not normalised, unknown running speed, no evolution of the energy at different speeds, no description of the determination of the position of the *COM* for each segment, unknown reference point for energy fluctuations, the head and torso segment are not considered, and so on), making comparisons to this study impossible.

Furthermore, elephants move with a high step frequency compared to other large animals at the same speed. Genin et al. (2010) have observed that the highest speed of an elephant corresponds to a slow trot for a 2-ton quadruped, while the step frequency adopted is higher than the maximum predicted step frequency for an animal of that size, even at a top speed gallop. In humans, walking or running at a given speed with a higher step frequency requires less W_{ext} but more W_{int} (Cavagna et al., 1988; Cavagna et al., 1991; Dewolf et al., 2016; Mesquita et al., 2023). Since at a given speed elephants are moving with higher step frequency than other large animals, the relative contribution of W_{int} to W_{tot} could also be modified.

In this study, the kinetic energy of the body segments relative to the *COM* in Asian elephants is measured. The internal work is calculated from these energy curves, and together with the measurements of the external work (Genin et al., 2010), a complete figure of the total mechanical work is presented and compared to the individual limb methods in Ren et al. (2010). Finally, the total muscular work measured in this study is compared with the metabolic cost measured by Langman et al. (Langman et al., 1995; Langman et al., 2012), to estimate the efficiency of positive work production during elephant locomotion. Work, cost and efficiency will be compared to allometric predictions, opening new directions for re-examining the comparative mechanical costs of terrestrial locomotion and revising classical scaling theories about locomotor costs and efficiency.

Materials and Methods

The internal work, W_{int}, was measured on 27 Asian elephants (*Elephas maximus*), at the Thai Elephant Conservation Centre, near Lampang in Northern Thailand. Experiments were approved by the Ethic Committee of the Faculty of Medicine of the UCLouvain and by the Forest and Industry Organization in Thailand.

The body mass (M_b) of the elephants ranged from 1.3 to 4 tons. Morphological values for each elephant are listed in Table 1. In most cases, a mahout representing 1-5% of the weight of the elephant rode on the elephant; we assumed the mahout had no influence on movements of the elephant's limbs.

Elephants moved at different speeds along a 50 m-long track. Measurements of W_{int} were realized simultaneously with the measurement of the external work, W_{ext}. The external work was evaluated by means of a 2 x 8 m force-platform mounted at ground level in the middle of the track. The method to compute W_{ext} from the ground reaction forces (GRF) and the results obtained on W_{ext}, were presented in Genin et al. (2010). In brief, the velocity and displacement of the *COM*, required to measure W_{ext}, were computed from 3D ground reaction forces. The fore-aft, lateral, and vertical accelerations of the *COM* were calculated by dividing the corresponding GRF components (F_f, F_l, and F_v-BW) by body mass. Note that BW (i.e. body weight) was assessed by having the elephant stand still on the force plate (Dewolf et al., 2021). The three components of the *COM*-acceleration were then numerically time-integrated to obtain the three components of the *COM*-velocity. In turn, the time-integration of the vertical velocity resulted in the vertical displacement of the *COM*. External positive mechanical work (W_{ext}) over each stride was obtained by adding up the positive increments of the total energy of the *COM*, i.e. of the sum of its kinetic plus potential energies.

Before data acquisition, elephants walked a few times back and forth on the track to become familiar with the experimental set-up. At the beginning of the data acquisition, the elephant moved at their freely chosen speed. During the next trials, the mahout encouraged the elephant to go slightly faster, up to the maximal speed. At the highest speeds, elephants were motivated by playful chasing or by food rewards at the end of the track. The data acquisition ended with the trials at the slowest speeds. During all the trials, the average speed of the elephants was measured by means of two pairs of photocells placed at each end of the force-platform and adjusted at the level of the elephant's forehead.

Measurements of the limb movements

The movements of the limb segments of the elephants were recorded using a high-speed digital camera A501k Basler® (Vision Technologies, Ahrensburg, Germany). The resolution of the camera was 1280 x 1024 pixels and the aperture time of the objective was 3 ms. According to the speed of progression, images were sampled at a rate of 50-100 frames s^{-1}. The camera was positioned perpendicular to the middle of the 8 m long force-plate, 15.3 m to the side and 1.15 m above the plate surface on one side of the track. The field of the camera encompassed about 12 x 4 m and its centre pointed roughly at the centre of the torso of an elephant that would stand in the middle of the force plate.

The body of the elephant was divided into 14 rigid segments: two hindfeet, two shanks, two thighs, one torso, two upper arms, two forearms, two forefeet and one head. The limb segments on one flank of the elephant were delimited by white dots painted at the level of the lateral surface of the joints (Fig. 1). The marker painted in the middle of the torso also allowed evaluating the movements of the hip and the shoulder relative to that marker. In most cases, elephants moved from right to left in respect to the camera field. Therefore, elephants were mainly painted on their left flank (only in a few cases, the right flank of the elephants was filmed). For the sake of uniformity, in most cases, we "flipped" the images to show the elephants moving from left to right, so that the direction of progression corresponded to the reading direction, and we defined "right" side to be the side facing the camera.

The coordinates of the markers in the fore-aft and vertical directions were measured each frame using Lynxzone software (Arsalis, Glabais, Belgium). Displacements in the lateral direction were ignored. The images were calibrated using the dimensions of the force-platform. The error due to parallax on the distances and angles measured at the centre of the image compared to that measured at the side of the image represents less than 3% of the measurement. In order to minimise this error, measurements were realised only on strides recorded close to the centre of the image. Strides were delimited by the "right" hind-limb touchdown. For each elephant, one stride was selected and analysed in each speed class of 0.28 $m \cdot s^{-1}$, covering the entire range of speeds recorded for that individual.

Calculation of the internal energy W_{int} due to velocity changes relative to the COM

The internal work (W_{int}) done to move the body segments relative to the *COM* was evaluated from their translational and rotational kinetic energy, using a procedure similar to that described in detail in Willems et al. (1995). Only translational and rotational movements taking place in the sagittal plane were considered.

The angle made by each segment with the horizontal was calculated each frame from the coordinates of the markers. The angle-time curves were smoothed using a spline function (Matlab®, Mathworks, Natick, MA, USA). A 'stick elephant' was then reconstructed from these angles and from the segment lengths. The segment lengths were measured on a frame taken in the middle of the stance phase for each limb. The distances between the torso marker and the hip and shoulder markers were measured on each frame to account for the movements of the hip and the shoulder relative to the torso (these distance *vs* time curves were smoothed using a spline function). The positions of the body segments hidden from the camera were reconstructed on the assumption that the movements of the segments on the hidden side of the body during a half stride were equal to those of the camera side during the other half stride (Dewolf et al., 2018).

The position of the centre of mass of each segment and the moment of inertia relative to the centre of mass were calculated for each limb segment (Table S1), assuming each segment had the shape of a truncated cone with a uniform mass distribution (see Supplementary Materials). For the head and torso segments, the position of the centre of mass and the moment of inertia about the centre of mass (Table S1) were calculated assuming that the head had the shape of a sphere and the torso the shape of a cylinder, with a uniform mass distribution. The length and the circumference at the proximal and distal end of each segment were measured on the elephants previous to the experiments. The proximal circumference of the thigh and the upper arm could not be measured on all elephants and were then set to 1.5 times the distal circumference of these segments; this ratio was approximated from measurements made on pictures and from data obtained on dissected segments by Hutchinson (unpublished data). Similarly, the diameter of the sphere representing the head was measured on pictures and was estimated as 14% of the torso length. The segment masses (and the circumference of the torso) were estimated using volumes (and volumetric mass) reconstructed from scans and using the data of Ren and Hutchinson (Ren and Hutchinson, 2008).

The horizontal and vertical position (X, Y) of the *COM* of the elephant was computed each frame by:

$$X = \frac{1}{M_b}\sum_{i=1}^{n} m_i x_i \quad \text{and} \quad Y = \frac{1}{M_b}\sum_{i=1}^{n} m_i y_i \qquad (1)$$

where M_b is the mass of the animal, m_i, x_i, y_i are the mass, the horizontal, and the vertical position of the centre of mass of the i*th* segments and n= 14 (Fig. 1). Its position relative to the *COM* was computed as the difference between the absolute coordinates of the segments and those of the *COM.*

The angular velocity of each segment was calculated from the derivative of its angle *versus* time relationship. The relative linear velocity of each segment was calculated from the time-derivative of the coordinates of its centre of mass relative to the *COM*. At each instant, the kinetic energy ($E_{k,int}^{i}$) of the ith segment was calculated as the sum of its translational and rotational energy:

$$E_{k,int}^{i} = \frac{1}{2} m_i (V_{f,i}^2 + V_{v,i}^2 + K_i^2 \omega_i^2), \qquad (2)$$

where m_i and K_i are the mass and radius of gyration of the ith segment, $V_{f,i}$ and $V_{v,i}$ are the horizontal and vertical velocity of its centre of mass relative to the *COM* and ω_i is its angular velocity.

The energy-time curve of each hindlimb and forelimb was obtained by summing the $E_{k,int}^{i}$-time curves of each of its segments. This procedure allowed energy transfer between the segments of the same limb.

Assessment of the pendulum-like energy transfer between kinetic and potential energy of the limbs

As discussed by Willems et al. (1995), gravity may help the movement of the limb relative to the *COM* by a pendulum-like transfer between gravitational potential and kinetic energy or *vice versa*. To account for this possible energy transfer, we extended the classical internal work calculation to include the "internal" potential energy ($E_{p,int}^{i}$) of each segment relative to the *COM*. Note that, by definition, the sum of all the segmental E_p relative to the *COM* across all segments is zero at any instant. For each body segment, $E_{p,int}^{i}$ was computed as the product of segment weight by the difference in vertical position between the segment's centre of mass and the *COM*. The instantaneous internal energy of each segment relative to the *COM* was calculated as

$E^i_{k,int} + E^i_{p,int}$. The energy-time curve of each hindlimb and forelimb was obtained by summing the $\left(E^i_{k,int} + E^i_{p,int}\right)$-time curves of each of its segments. In addition, computing $E^i_{p,int}$ of each body segment allows us to assess the pendulum-like energy exchanges - that could be important during the swing periods of the limbs (Fig. S1).

Computation of the internal work and of the total mechanical work

The work done to move a hindlimb (W^{hl}_{int}), a forelimb (W^{fl}_{int}), the head (W^{he}_{int}) and the torso (W^{to}_{int}) relative to the *COM* was obtained by summing the increments of the respective energy-time curves. The increments were considered to represent work actually done by the muscles only if the time between two successive maxima was greater than 10‑80 ms, depending on the speed of progression. The total internal work (W_{int}) was computed as:

$$W_{int} = 2\,W^{hl}_{int} + 2\,W^{fl}_{int} + W^{he}_{int} + W^{to}_{int}. \quad (3)$$

Two previous studies (Cavagna and Kaneko, 1977; Willems et al., 1995) showed that the most accurate computation of the internal work was to include only energy transfers between segments within a limb, and to exclude transfers between segments of two different limbs. In this study, we used this method to calculate W_{int}. In other words, equation (3) allows energy transfers within the limbs but excludes transfers between the limbs, torso and/or head (Dewolf et al., 2019a; Schepens et al., 2004; Willems et al., 1995).

To assess the maximum influence of other possible, if unlikely, energy transfers on the value of the internal work, complementary computations of the internal work were made: (i) excluding any energy transfer ($W_{int,\,max}$), resulting in a maximum limit for the measure of internal work; (ii) including all energy transfers, including transfers across the torso ($W_{int,\,min}$), representing the minimum value for W_{int}, and (iii) considering the possible pendulum-like energy exchange into the limbs ($W_{int,\,trans}$). The $W_{int,\,max}$ was computed by summing the positive increments of the $E^i_{k,int}$-time curves of the 14 segments, while $W_{int,\,min}$ was obtained by summing the 14 segments $E^i_{k,int}$-time curves and then measuring the positive increments of the single resulting energy curve. The $W_{int,\,trans}$ was calculated as W_{int} but including the gravitational potential energy of the hindlimbs and forelimbs relative to the body COM in equation (2).

Computation of the total mechanical work

The stride/step selection was not made synchronously between W_{int} and W_{ext}: a stride for internal work measurement was made between two successive 'right' hindlimb touchdowns, and the selection of a stride/step for external work was made between peaks of velocity of the *COM* (see methods in Genin et al. (2010) for more details). Consequently, the total work (Eq. 4) was not computed point by point but by summing the average curves of W_{int} and W_{ext}.

Results

Internal energy of the body segments

The E_{int} *versus* time curves of the limb-segments (Fig. 2) are consistent with previously published data (Hildebrand and Hurley, 1985). The mass of the hindfoot and forefoot each represent less than 1% of M_b whereas the shank and the forearm are around 2% of M_b. Nevertheless, the amplitudes of their internal energy curves are similar because the hind and forefeet have a higher speed relative to the *COM* than the shanks and forearms. Note also that, despite the heavier mass of the thighs and upper arms (about 5% of M_b), the amplitudes of their internal energy curves are smaller than the more distal limb segments because they have a lower speed relative to the *COM*.

Over one stride, the internal energy of the limbs presents two maxima, one when the limbs are moving forwards and a second when the limbs are moving backwards, relative to the *COM* (Fig. 3). As the torso and head move once upwards and once downwards with each step, their energy-time curves show four maxima during the stride. The amplitude of the internal energy-time curves of the limbs are much greater than those of the torso and the head.

At low speeds, the period when a limb is moving backwards relative to the *COM* (~contact phase) is longer than the period when it is moving forwards (~swing phase). Consequently, its velocity and its internal energy are smaller when the limb moves backwards than when it swings forwards (Fig. 3 left). When speed increases, the relative contact period of each limb is reduced and consequently, the energy variations of the limbs during the contact phase and during the swing phase are about equal (Fig. 3 right).

Internal work done to move the limbs relative to the COM

The mass-specific internal work per unit distance (J kg^{-1} m^{-1}) done to move the 14 segments relative to the *COM* (W_{int}) increases with speed (Fig. 4): from ~0.1 J kg^{-1} m^{-1} at the lowest speeds to ~0.7 J kg^{-1} m^{-1} at the highest speeds. As speed increases, both the step length and the step frequency increase (see Figs. 1 & 2 in Genin et al., (2010)). Consequently, the speed of the limb segments relative to the *COM* and thus the work W_{int}^{hl}+W_{int}^{fl} becomes more important (Fig. 4A, green and red symbols).

In addition, as speed increases the fraction of W_{int} due to limb movements (W_{int}^{hl}+W_{int}^{fl}) increases. Although the mass of the four limbs is less than 30% of M_b, the work done to move these segments represents ~80% of W_{int} at 0.5 m s^{-1} and ~95% at 5.0 m s^{-1} (Fig. 4B). This is due to the relative decrease in the work done to bob the head (W_{int}^{he}), which decreases from ~15% of W_{int} at low speeds to about 10% of W_{int} at the highest speed. At all speeds the work done to move the torso represents less than 5% of the W_{int}, even though the mass of the torso represents ~55% of M_b.

Inter- and intra- segment energy transfer

In this paper, we consider that when the internal kinetic energy of a limb, or the head or the torso increases, it is because the muscle-tendon units have performed positive work to accelerate the segment(s). As for human locomotion (Willems et al., 1995), this procedure assumes energy transfer between the segments of a same limb, but not between limbs, torso and head. In other words, we consider that passive energy transfer occurs if segment A of a limb gains energy while segment B of the same limb loses energy. However, in certain cases, the muscles of segment A could perform positive work while the muscles of segment B are performing negative work. In this case, W_{int} would be underestimated. In other situations, it could be that energy transfers exist between limbs via the torso or between the torso and the limbs or even between the torso and the head, in which case W_{int} would be overestimated.

The minimum ($W_{int, min}$) and maximum ($W_{int, max}$) limits of W_{int} were computed respectively (1) by assuming complete energy transfer among all body segments and

(2) by assuming no energy transfer between these. Fig. 5A presents the influence of energy transfers on the amplitude of W_{int}, $W_{int,\,min}$ and $W_{int,\,max}$ as a function of speed in absolute value (Fig. 5A) and in relative values (Fig. 5B). The difference between W_{int} and $W_{int,\,max}$ represents less than 10% of $W_{int,\,max}$. However, considering complete energy transfer reduces W_{int} by 30 to 60%.

Pendular energy transfer between kinetic and potential energy of the limbs

As pointed by Cavagna and Kaneko (1977), gravity may help the movement of the limb relative to the *COM* by a pendulum-like transduction between potential gravitational energy and kinetic energy. Such a transduction could significantly influence the internal work estimations in quadrupedal locomotion (Fig. 5C). Willems et al. (1995) previously reported that including segmental 'internal' potential energy in internal work calculations during human gait modified the results by less than 5%. In elephants, we observe a similar outcome: including 'internal' segmental potential energy ($E^{i}_{p,int}$, see Methods) altered the limb work by only ~3-5% (Fig. 5C). This limited effect is due to partial passive energy exchange within the limbs, consistent with pendular dynamics during swing. We quantified this by estimating the fraction of energy attributable to passive pendular exchange: approximately 25% of the energy can be recovered through passive pendulum-like exchange for both hindlimbs and forelimbs at low speeds (Fig. S1). These findings suggest that although some passive exchanges may occur, their impact on total internal work remains modest, even in quadruped. Therefore, the total internal work in quadrupeds can be estimated from the kinetic energy only.

Discussion

The internal work (W_{int}) as measured in this study includes only the work done to accelerate the body segments relative to the *COM*. There are many other types of internal work; in fact, internal work is sufficiently complex that it is easier to define what it is not. Internal work is not any of the work done against the environment, such as work done against the resistance of air or done to move the substrate under the feet (Dewolf et al., 2019b; Lejeune et al., 1998; Mesquita et al., 2024; Pugh, 1971); neither is internal work any of the work done to lift or accelerate the *COM* on slopes (Dewolf et al., 2016; Dewolf et al., 2017; Gomeñuka et al., 2016; Minetti et al., 1993) - these

are all external work. However, internal work is all the rest of the work done during locomotion. For example, not counted in this study, internal work is the work done to pump air, blood, and calcium; it is the work done by one muscle against another during antagonistic contractions; it is the work done by one leg against another during a step phase involving multiple foot contacts (Bastien et al., 2003). In short, it is all the work done that does not result in a displacement of the *COM*, or against the environment.

Some of these other types of internal work are not insignificant. For example, the work done by one limb against another during ground contact was not included here (Bastien et al., 2003; Schepens et al., 2004). Also in elephants, limbs generated or absorbed a substantial amount of simultaneous positive and negative power during double or triple support (Ren et al., 2010). However, in their 'individual limb methods' analysis, Ren et al. (2010) summed the power curve of all limbs, allowing transfer between them (Fig. 6A). Such transfer of energy may allow a potential compression and rebound of each limb during the stance (and thus a potential elastic energy storage and release), without increasing the vertical displacement of the *COM* (and thus W_{ext}) (Lambert et al., 2010; Ren et al., 2010). This is made possible by rotation of the torso (Fig. 6B), which increases until about 2 m s^{-1} and decreases at higher speeds.

Recently, it has been shown that the mechanical energy fluctuations due to soft tissue energy dissipation (heel pad and foot arch compressions, visceral sway, cartilage and intervertebral disc compressions etc.) can also affect the mechanical work production in locomotion (Dewolf et al., 2024; Riddick and Kuo, 2016; Riddick and Kuo, 2022; Zelik and Kuo, 2010). During walking, the body's soft tissues deform and dissipate a fraction of the mechanical energy (negative mechanical work) that must be actively replaced by the muscles to maintain a constant speed (positive mechanical work) (Riddick and Kuo, 2022). The energy dissipated by the soft tissues can be estimated by comparing different methods used to calculate the mechanical energy output of the body (Dewolf et al., 2024; Riddick and Kuo, 2022; Zelik and Kuo, 2010). The discrepancy between our mechanical work measurements and the data published by Ren et al. (2010) may partly be due to soft tissue vibration, increasing with speed (Fig. 6A), as in human running (Riddick and Kuo, 2016). In any case, the work done to move the body segments relative to the *COM* is by far the greatest single type of internal work during legged terrestrial locomotion.

Maximum and minimum limits of internal work

Cavagna and Kaneko (1977) measured the mechanical work required to move the limbs relative to the *COM* in human walking and running and discussed the different possibilities of energy transfer between different segments of the body. Willems et al. (1995) have done the most detailed analysis to date on the possibility of energy transfers between segments as well as between the segments and the *COM* of the whole body. The upper line in Fig. 5B (squares) shows that allowing energy transfers between the segments within the limb reduces W_{int} independently of speed by no more than 10%, a result like that found in human walking or running (1995). On the other hand, allowing any energy transfers between all 14 of the body segments (open triangles) would result in a W_{int} reduction of up to 60% at intermediate and fast speeds, which is twice the maximum reduction found in humans (1995). Such a difference in maximum W_{int} reduction ($W_{int, min}$, in Fig. 5B) between elephants and humans can be explained in part by the shift of ~20% in the stride phase between ipsilateral limb touchdowns (see Fig. 2 of Genin et al., (2010)), which is the possible occasion of large amounts of energy transfer. In contrast, the human ipsilateral upper and lower limbs oscillate almost simultaneously in opposite directions, but upper and lower limb energy curves increase and decrease together (note that kinetic energy is independent of the direction of the speed). This results in smaller possible energy transfers between limbs across the torso and limits the decrease of $W_{int, min}$ to ~30% relative to $W_{int, max}$ in humans (see Fig. 1, 7 and 8 in Willems et al., (1995)).

While the $W_{int, min}$ represents the arithmetic minimum limit to the internal work done during elephant locomotion, we do not consider this limit to be realistic for the following reasons. First, there is no anatomical structure for transferring kinetic energy, for example from the forefoot to the hindfoot. Second, although kinetic energy is a scalar and therefore increases with increases in both positive and negative segment velocity changes relative to the *COM*, clearly kinetic energy transfers cannot occur between two segments which both undergo velocity changes in the same direction, as happens often in segments of ipsilateral limbs during elephant locomotion. Thus, we consider the most correct solution is to allow energy transfers (where possible) within limbs but not between limbs, as has been done previously (Willems et al., 1995); all the discussion that follows is predicated upon this assumption.

Internal, external work and total work

The total muscle and tendon work required to maintain the energy fluctuations of the body during steady-state locomotion can be computed as:

$$W_{tot} = W_{ext} + W_{int}, \quad (4)$$

where W_{ext} is the mechanical work necessary to maintain the motion of the *COM* of the whole-body during locomotion (*e.g.* in humans (Cavagna et al., 1976; Dewolf et al., 2016; Dewolf et al., 2017); in non-human animals (Cavagna and Kaneko, 1977; Genin et al., 2010; Heglund et al., 1982a)), and W_{int} is the mechanical work necessary to maintain the movements of the body segments relative to the *COM* (Dewolf et al., 2019a; Heglund et al., 1982a; Mesquita et al., 2023; Willems et al., 1995). It has been shown in humans that energy transfers between W_{ext} and W_{int} are quite small (Willems et al., 1995), and we have assumed in Eq. 4 that any similar transfers in elephants are negligible.

Fig. 7 shows the efficiency (panel A) and the total (panel B), external (panel C) mass ‑specific internal (panel D) work in elephants as compared to horses walking and trotting (Minetti et al., 1999). The W_{ext} is almost independent of the speed, whereas W_{int} increases curvilinearly with speed. The curve fit of W_{tot} (in J kg^{-1} m^{-1}) versus speed (V_f in m s^{-1}) is a quadratic function:

$$W_{tot} = 0.249 + 0.081\ V_f + 0.016\ V_f^2. \quad (5)$$

The ratio of W_{int} to W_{ext} shows their relative importance as a function of speed. In most animals, the ratio is considerably less than 1 at low speeds. However, since the W_{ext} remains roughly constant while W_{int} increases exponentially with speed, the ratio often approaches 2 at high speeds. Notably, this ratio attains values up to 3:1 in fast-moving elephants, a much higher ratio than seen in cursorial animals. Even humans, who attain much higher speeds than elephants, only reach a ratio of ~2:1 (Willems et al., 1995). The high W_{int}:W_{ext} ratio in elephants is a result of heavy legs, a heavy head, an unusually high step frequency, and a relatively low W_{ext} (Genin et al., 2010). In humans, at any given speed a high step frequency increases W_{int} and decreases W_{ext} (Cavagna et al., 1988; Mesquita et al., 2023).

The walk-trot gait transition in a horse shows a clear difference in the work value and the slope of the work as a function of speed, for internal, external and total work. These changes are typical indicators (amongst others) of a change in gait and can be observed in most species (Fedak et al., 1982; Heglund et al., 1982a; Heglund et al., 1982b). In contrast, internal, external and total work in elephants show a continuous evolution throughout their entire range of speed, suggesting that the gait transition is smoother than observed in other animals (Hutchinson et al., 2006).

Efficiency of positive work during elephant locomotion

Efficiency is one of the fundamental properties of any 'energy transducer', i.e. something that converts energy from one form to another. During locomotion, all animals convert metabolic energy into mechanical work. In this case, the efficiency is the ratio between the mechanical work performed and the metabolic energy consumed during locomotion. Efficiency has no units since both the numerator and the denominator have units of energy (or power). The main conceptual difficulty of determining the efficiency of animal locomotion comes from the definition of the work done during constant average speed level locomotion. In this study, we have taken the approach of many before us and have indirectly measured the net positive work done by the muscle-tendon units. The use of the term 'muscle-tendon unit' implicitly acknowledges that part of this positive work may have been done by tendons and other elastic structures. Any increase in the total kinetic and gravitational potential energy of the body is assumed to be due to positive muscular work (in reality, part of it could come from the energy stored in elastic structures); any decrease in the total kinetic and gravitational potential energy of the body is assumed to be lost mainly as heat (in reality, part of it could be stored in elastic structures).

To a lesser extent, metabolic energy consumption also presents conceptual problems. Although it is generally agreed that steady-state oxygen consumption is a good measure of energy input to a subject, much of animal locomotion occurs at speeds that are not steady state. Furthermore, there is the question of whether the basal, resting or standing metabolism (or nothing) should be subtracted from the steady-state value when calculating the energy expenditure of locomotion.

The net metabolic energy expenditure of locomotion (i.e. the energy expenditure during locomotion minus energy expenditure during standing) has been

508 measured in a previous study (Langman et al., 1995) in three young African elephants
509 (average mass 1542 kg) at speeds up to 2.5 m s^{-1}, and is shown in Fig. 7B (thick dotted
510 line), along with data from horses for comparison to the next-largest animal with
511 comparable data (thin dotted lines, in Minetti et al., (1999)). Although our work
512 measurements were conducted on Asian elephants, various studies have shown no
513 differences between African and Asian elephants in kinematic parameters (Hutchinson
514 et al., 2006; Ren and Hutchinson, 2008) or energy changes of the *COM* as measured by
515 motion sensors (Ren and Hutchinson, 2008).

516 The efficiency is shown in Fig. 7A for both elephant gait and horse walk and
517 trot. In both animals, efficiency is computed as the ratio between total mechanical work
518 and the net metabolic cost. In elephants, efficiency was calculated over the speed range
519 for which metabolic data was available (up to 2.5 $m \cdot s^{-1}$). Efficiency as a function of
520 velocity shows an inverted U-shaped curve with a peak of ~45% at 1.2 $m \cdot s^{-1}$. Here, we
521 define locomotor efficiency as the ratio of total mechanical work (internal + external)
522 to net metabolic cost. As addressed in Heglund and Cavagna (1987), it should not be
523 confused with isolated muscle efficiency, which refers specifically to the conversion of
524 metabolic energy into positive mechanical work by contractile elements and typically
525 peaks around 25% (Hill, 1964). While 45% may appear high in comparison, it is
526 consistent with values reported in other large mammals, such as horses, where
527 locomotor efficiency can exceed 70% during trotting (Minetti et al., 1999). Such values
528 reflect the contribution of favourable whole-body dynamics (Willems et al., 1995),
529 including passive elastic recoil (Mantovani et al., 2001) and energy transfer
530 mechanisms (Cavagna et al., 1988), rather than an increase in muscle contractile
531 efficiency.

532 Notably, the peak occurs near the speed at which the pendular mechanism of
533 walking is optimal (as reflected by the percent recovery in Genin et al. (2010), Fig. 4A),
534 and where external mechanical work is minimal (Cavagna and Kaneko, 1977). We also
535 acknowledge that our calculation of efficiency may be slightly biased due to
536 unmeasured sources of metabolic cost not included in our mechanical work estimates -
537 such as isometric force production, joint friction, or muscle co-contraction - which
538 nonetheless consume energy. A peak locomotion efficiency of ~45% in elephants
539 compare favourably with that observed in horses (Fig. 7A) and in humans (Cavagna et

al., 1977; Willems et al., 1995), supporting the view that elephants are biomechanically well-adapted for energy-efficient walking at low speeds.

Mechanical work and body size

In the early '80s, Taylor's group at Harvard's Concord Field Station published a series of papers on the mechanical work and metabolic cost of locomotion in animals of different sizes. They concluded that the mass-specific metabolic power ($\dot{E}_{\mathrm{metab}}$, in W kg^{-1}) increased linearly with the speed of progression. However, at a given speed, $\dot{E}_{\mathrm{metab}}$ decreased with body size over a 4-orders of magnitude size range from 0.01 to 260 kg (Taylor et al., 1982). In comparison, the mass-specific total mechanical power ($\dot{W}_{\mathrm{tot}}$, calculated in the same manner as in this study, in W kg^{-1}) increased curvilinearly with speed of progression but appeared to be independent of body size over a 3-orders of magnitude size range from 0.043 to 70 kg (Fedak et al., 1982; Heglund et al., 1982b; Heglund et al., 1982a).

This led to some speculation in the literature involving extrapolation of the mechanical power data to animals the size of adult elephants, with the conclusion that the two lines cross at a body size of about 2 tons (Alexander, 2005). In other words, extrapolating from animals less than 70 Kg to animals larger than 2 tons leads to the unlikely muscular efficiency calculation of more than 100%. Although this value is not impossible given the way the mechanical power is measured (as noted above, all work done by elastic structures is attributed to the muscles), it would require that very large animals be extremely 'bouncy' – not a characteristic normally attributed to adult elephants (Kram and Taylor, 1990; Taylor, 1985).

Since the original Harvard studies, metabolic data on very large animals have become available, and the up to 3500 kg elephants (Langman et al., 1995; Langman et al., 2012) show a reasonably good fit to an extrapolation of the allometric equation of Taylor et al. (Taylor et al., 1982). The current study provides the first data on very large animals that can be compared to the total mechanical work and efficiency measurements of the Harvard studies (Heglund et al., 1982a). It is not surprising that the allometric equation of Heglund et al. (1982a) relating total mechanical power output to body size, based upon just 5 species and a limited size range, cannot be used to accurately predict power outputs for animals that are ~50 times larger than the animals

measured. The mechanical power data of Minetti et al. (1999) on horses supports this conclusion as well. Unfortunately, the too-high mechanical power predictions have led to erroneous conclusions of very high efficiency in large animals (Alexander, 2005; Full et al., 1989). In fact, the measured efficiency in elephant locomotion is quite like that in much smaller horses (Fig. 7A) and humans.

In conclusion, our findings contribute to resolving long-standing ambiguities in the scaling of locomotor energetics by providing direct mechanical data from one of the largest extant terrestrial animals. Our study provides the first comprehensive quantification of the total mechanical work in elephants, revealing that a substantial portion of this work - especially at higher speeds - is dedicated to moving the limbs relative to the centre of mass.

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Figure legends

Figure 1 *top* - Marker placements on one side of a representative elephant's skeleton with skin contour in greyed background. These markers were used to determine the position of the segments. Joint centre positions were estimated by palpation and by movements of flexing-extending limbs. A pair of markers defined a segment. Picture from Shoshani, (1992) *bottom* - a picture of an elephant standing. The blue open dots represent the marker displacement relative to the centre of mass (black and white dot) during one stride. Note that the proboscis was not considered in this study.

Figure 2 Typical traces of mass-specific kinetic energy curves of segments within the "right" hind and fore limbs due to their velocity relative to the *COM* during one stride, for an elephant of 1740 kg. Curves start and stop on successive touchdowns of the "right" hindlimb (i.e. the limb facing the camera). Left panels are for a regular walking speed (1.3 m s^{-1}) and right panels are for the fastest speed obtained (4.97 m s^{-1}). The top panels are for the segments of the "right" hindlimb, and the panels just below are for the segments of the "right" forelimb. The total kinetic energy of the limb (black curve) is the sum of the kinetic energy of the distal (red), intermediate (blue) and proximal (green) segments within the limb. The third line of panels indicates the footfall pattern of the elephant. The bottom panel shows stick elephants illustrating the position of the limbs every 12.5% of the stride cycle (the side facing the camera is black and the other side in grey). At intermediate speed, the kinetic energy remains low when the limb is on the ground, and large oscillations occur during the swing of the limb. Hind and fore energy curves are not in phase due to the limb phase of ~18% at that speed (Hutchinsn et al., 2006). At high speed, large oscillations of the kinetic energy occur during both stance and swing phases of the limb. Hind and forelimb energy curves are out of phase due to the limb phase of ~23% (Genin et al., 2010). Note that for both speeds and both limbs, the small distal segment of the limb accounts for the largest part

of the fluctuations of the energy curve of the total limb. A different scale is used between left and right panels to draw attention to the influence of each segment on the limb energy curve.

Figure 3 Effect of speed on typical traces of mass-specific kinetic energy curves of the limbs (internal energy), the torso and the head due to their velocity relative to the *COM* during one stride. From top to bottom: kinetic energy *vs.* time of the hindlimbs, forelimbs, torso and head. Thick continuous lines indicate the kinetic energy of the limbs facing the camera. Energy curves for the opposite side (interrupted lines) are similar, as the movements of this side are reconstructed from the movements facing the camera, shifted by 180° of a stride period (see Methods for more details). Energy oscillations of the limbs increase greatly between intermediate and high speed. Internal energy of the torso and the head segments (55 and 16% of M_b respectively) is negligible at intermediate speed, whereas the energy of the head segment shows larger oscillations at maximal speed. This illustrates the importance of the head segment in our model.

Figure 4. (A) Effect of speed of progression on the mass-specific positive work per unit-distance associated with the kinetic energy changes due to the movement of all the body segments relative to the *COM* (W_{int}, black squares), computed as the sum of the internal positive work of the two hindlimbs (W_{int}^{hl}, red triangle) and the two forelimbs (W_{int}^{fl}, green diamond), the torso (W_{int}^{to}, black triangles) and the head (W_{int}^{he}, blue circles). Lines are second order polynomial curve fits. (B) The internal work due to hindlimbs and forelimbs, the head and the torso as a fraction of the total internal work. W_{int}^{hl} and W_{int}^{fl} each account for ~40-45% of $W_{int.}$. The internal work due to the movements of the head, W_{int}^{he}, accounts for ~14% of W_{int} and is mainly due to the vertical movements of the head relative to the *COM* (the horizontal distance between the *COM* and the head doesn't change much). The W_{int}^{to} accounted for less than 5% at all speeds of progression.

Figure 5. Schematic representations of hypothetical energy exchanges during walking are shown at the top of the graph. (A) Effect of energy transfer on the mass-specific internal work per unit distance. The initial values for internal work (W_{int}, from Fig. 4, black squares) include energy transfer between segments within a limb, but not between segments of two different limbs, nor between limbs and the torso and head. To assess

the effect of energy transfers, the internal work excluding any energy transfer ($W_{\text{int, max}}$, open circles) and including energy transfer across all the segments ($W_{\text{int, min}}$, black triangles) are plotted as a function of speed. (B) W_{int} (white squares) and $W_{\text{int, min}}$ (black triangle) expressed as a fraction of the upper limit for internal work, $W_{\text{int, max}}$. Including energy transfer between the segments within each limb in our calculation on elephants reduces W_{int} independently of speed by no more than 10%. Assuming energy transfer between all the segments within each limb, the head and torso results in a reduction of W_{int} by up to 70% at intermediate and fast speeds. (C) Internal work of the limbs as a function of speed of progression. The black and white squares represent hindlimb and forelimb internal work ($E_{k,int}^{i}$) calculated without accounting for potential energy ($E_{p,int}^{i}$) of the segments relative to the *COM* (same from Fig. 4). The dashed lines show internal work ($E_{k,int}^{i} + E_{p,int}^{i} E_{k,int}^{i}$) for each limb. Solid and dashed lines are second-order polynomial fits across the data. The small difference (less than 5%) between the two curves shows that considering the potential energy relative to the *COM* does not change much the value of the internal work.

Figure 6. (A) Comparison of total mechanical work estimated by two different approaches. The first method (black squares) represents the sum of external and internal mechanical work, where external work was derived from ground reaction force measurements (Genin et al., 2010) and internal work was calculated from segmental kinematics as described in this study. The second method (open circles) shows total joint work computed from the sum of hindlimb and forelimb joint powers obtained through inverse dynamics (Ren et al., 2010). Both methods are expressed as total positive work per unit mass and unit distance across a range of speeds of progression. (B) Oscillation of the torso (trunk segment) during one stride cycle, represented as a function of speeds of progression. The vertical axis shows the standard deviation of torso angle evolution over the cycle, averaged across individuals. An increase in oscillation amplitude is observed up to approximately 2.0 $m \cdot s^{-1}$, suggesting a change in dynamic movement of the torso near the potential walk-to-bounce-like gait transition (consistent with the data of Ren et al., 2008).

Figure 7. (A) Locomotor efficiency, computed as the ratio between total mechanical work (W_{tot}) and net metabolic cost, plotted as a function of speed of progression. The

efficiency curve for elephants (thick solid line) shows an inverted U-shape with a peak of ~45% around 1.24 $m \cdot s^{-1}$. Efficiency curves for horses during walking and trotting are shown for comparison (thin solid lines). (B) Mass-specific total mechanical work per unit distance (W_{tot}), computed as the sum of external and internal work ($W_{tot} = W_{ext} + W_{int}$). Thick solid lines represent elephant locomotion; thin solid lines indicate horses walking (W) and trotting (T). Dotted lines represent net metabolic cost of transport in elephants and horses, showing U-shaped curves. (C) External mechanical work per unit distance (W_{ext}) as a function of speed. In elephants (thick lines), W_{ext} follows a U-shaped curve, with a minimum at intermediate speeds of progression. Horses show distinct patterns for walking and trotting (thin lines), with a noticeable discontinuity across the gait transition. (D) Internal mechanical work per unit distance (W_{int}). In elephants (thick lines), W_{int} is higher than W_{ext} except at the lowest speeds and increases steadily with speed. In horses, internal work differs sharply between walking and trotting gaits (thin lines). Each line type is consistent across panels: thick lines indicate elephants, and thin lines indicate horses (walk and trot). The figure highlights key differences in mechanical work patterns and efficiency between species and gaits.

Figure S1. Passive exchange of mechanical energy during limb swing in elephants. The percentage of energy exchanged passively between potential and kinetic forms during limb swing is plotted against average forward speed for both hindlimbs (green) and forelimbs (red). Data points represent individual stride cycles. Curves show locally weighted smoothing trends for each limb. Passive pendular exchange remains relatively stable in the hindlimbs across speeds (~25%), while it decreases notably with speed in the forelimbs. This analysis quantifies the contribution of pendular dynamics to internal work during swing and supports the limited impact of unmeasured gravitational energy fluctuations on total mechanical work.

847 # Tables

848

849 Table 1. Individual data for elephants used in this study. Maximal forward velocity for
850 each elephant and the corresponding Froude number are presented for comparison with
851 the literature.

852

Elephant	Sex	Age (yrs)	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	2.8	1.43
Gaew	M	5	1740	59.4	1.52	4.97	3.83
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
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	1.7	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
Satit	M	29	3525		1.89	1.98	0.76
Somboon	M	53	3131	59.7	1.7	1.34	0.31
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		1.7	1.29	0.29
Tao	M	7	1893	64.7	1.58	1.72	0.48
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
	Yaï	M	48	3034	58.9	1.72	1.23	0.27
	Mean		27.4	2849	60.9	1.68	2.42	1.2
	SD		17.7	712	2	0.15	1.24	1.2

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