The Journal of Experimental Biology **198**, 629–632 (1995)
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MOVING CHEAPLY: ENERGETICS OF WALKING IN THE AFRICAN ELEPHANT

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Accepted 4 November 1994

Summary

Large animals have a much better fuel economy than small ones, both when they rest and when they run. At rest, each gram of tissue of the largest land animal, the African elephant, consumes metabolic energy at 1/20 the rate of a mouse; using existing allometric relationships, we calculate that it should be able to carry 1 g of its tissue (or a load) for 1 km at 1/40 the cost for a mouse. These relationships between energetics and size are so consistent that they have been characterized as biological laws. The elephant has massive legs and lumbers along awkwardly, suggesting that it might expend more energy to move about than other animals. We find, however, that its energetic cost of locomotion is predicted remarkably well by the allometric relationships and is the lowest recorded for any living land animal.

Key words: locomotion, metabolic rate, allometry, elephant, energetics, walking.

Introduction

African elephants are the largest living land animals; a large adult male weighs as much as 6000 kg (six metric tonnes). They are the classic example of a graviportal animal, possessing massive pillar-like legs for supporting their weight (Gray, 1968). They walk or amble rather than run. At a fast walk, the strains in their limb bones reach levels similar to those in a horse at a fast gallop, with a similar safety factor to failure (Alexander *et al.* 1979; Biewener and Taylor, 1986).

Fuel economy normally improves with increasing size. The metabolic energy cost of moving each kilogram over 1 m decreases with body mass to the power -0.316 (Taylor *et al.* 1982) and, on the basis of its size, the elephant ought to be the most fuel-efficient living land animal. However, we felt that it might pay an energetic price for its massive legs and lumbering gait. Functional anatomists have argued convincingly that cursorial animals are efficient runners with limbs designed for running economically (Howell, 1944), while graviportal animals are at the opposite end of the continuum of limb design. It takes energy to accelerate and decelerate the limbs alternately during each stride and, although the amount is small in walking humans (Cavagna and Kanekeo, 1977) and in most birds and mammals at walking speeds (Fedak *et al.* 1982), the moments of inertia of an elephant leg are orders of magnitude greater. Swinging its limbs could involve a substantial cost and, if so, the elephant will be an exception to the allometric rule.

Elephants are not sedentary animals, and there are clear ecological advantages and selection pressures for a high fuel economy. They travel long distances (483–644 km; 300–400 miles) during their seasonal migrations (Sikes, 1971) and may sustain a constant speed for 3–4 h at a time, covering up to 16 km (Guy, 1976). It would clearly be advantageous for them to move cheaply. We measured the energetics of walking elephants to determine whether they moved as cheaply as predicted by the allometric relationship (Taylor *et al.* 1982) or whether they paid an energetic price for their massive legs and lumbering gait.

Materials and methods

We measured the oxygen consumption of three young African elephants (mean mass 1542 kg). They were trained by their keepers at Zoo Atlanta, Georgia, USA, to wear a loose-fitting mask (which enclosed both trunk and mouth) while standing quietly and while following a motorized golf cart (Fig. 1). The mask was connected to a pump mounted on the

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Fig. 1. One of the young male elephants wearing a mask.

cart and air was metered through it at 100 l s^{-1}. A constant walking speed (measured with a calibrated electronic speedometer) was maintained for 10 min on a level circuit. During the last 3 min, a small sample of the flow was collected in a 200 l Douglas bag. This was analyzed for oxygen concentration with a paramagnetic oxygen analyzer (Taylor Servomex OA272). The entire system was calibrated by metering nitrogen into the mask (Fedak *et al.* 1981) and the accuracy was better than ±2 %. The rate of energy expenditure was calculated from the rate of oxygen consumption using an energetic equivalent of 20.1 J ml^{-1} O_2.

We calculated total cost of transport for walking elephants, the energy (J) expended in moving 1 kg over 1 m, by dividing the mass-specific metabolic rate by speed. We also calculated the net cost of transport to estimate the oxygen consumption of the active muscles during walking. This involves subtracting the oxygen consumption of the elephants as they stood quietly from the walking cost before dividing by speed.

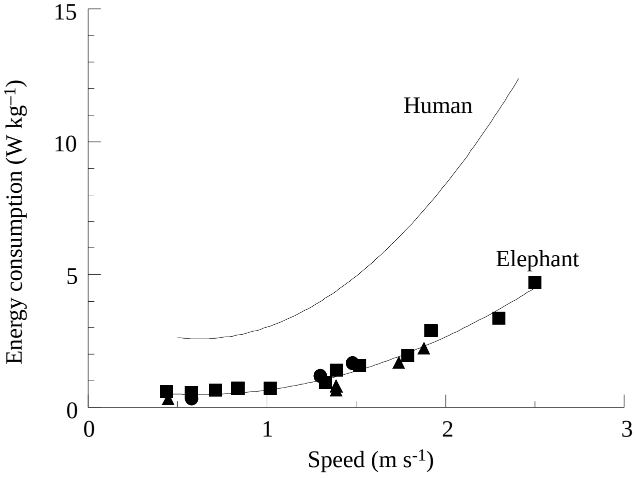

Fig. 2. Energy consumption of walking elephants increased curvilinearly with speed in the same way as in walking humans (Margaria, 1938). The different symbols represent different individuals. Rate of energy consumption was calculated from rate of oxygen consumption using an energetic equivalent of 20.1 J ml^{-1} O_2.

Results

The mean rate of energy expenditure of standing elephants was 0.915±0.068 W kg^{-1} (S.E.M.). This value is similar to that reported by Benedict (1938) more than 50 years ago. Oxygen consumption of walking elephants increased curvilinearly with speed, in a manner similar to that of walking humans (Fig. 2). Oxygen consumption increased fourfold as speed increased from 0.4 to 2.5 m s^{-1}, the fastest speed that the elephants maintained for 10 min.

The net cost of transport was lowest (0.78 J kg^{-1} m^{-1}) at about 1.0 m s^{-1} (Fig. 3), approximately the same speed as in walking humans (Margaria, 1938), and increased both at slower and faster speeds. If we consider total cost of transport, the picture is quite different. It is highest at the slowest walking speed (about 3.2 J kg^{-1} m^{-1} at 0.44 m s^{-1}) and lowest at the fastest walking speed (1.6 J kg^{-1} m^{-1}). The difference between net and total cost is due to the effect of resting metabolism; it is a large fraction of the total metabolism at the slowest speed (more than 60 %) and decreases to less than 25 % at the fastest speed.

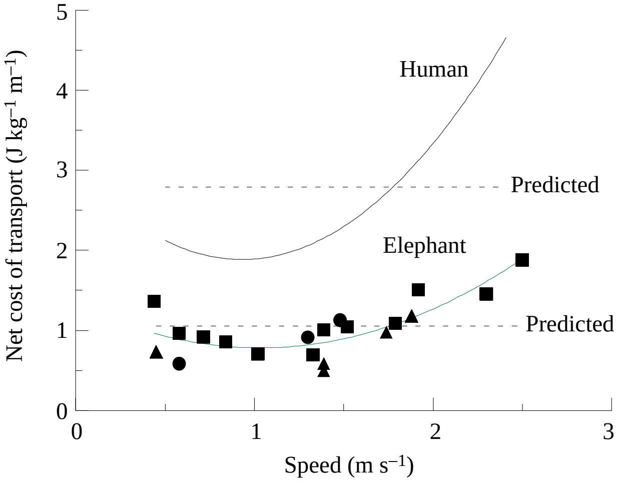

Fig. 3. Net energetic cost of walking in elephants reached a minimum value at about 1.0 m s^{-1}, just as it does for walking humans (Margaria, 1938). Energetic cost was calculated by dividing net rate of energy consumption (walking rate minus standing rate) by walking speed, providing a measure of the amount of energy used by the elephant to transport 1 kg of body mass for 1 m. The different symbols indicate different individuals. The minimum cost for the three elephants (mean mass 1542 kg) was 0.78 J kg^{-1} m^{-1} (calculated using a least-squares second-order polynomial fit of the data), very close to the value predicted for an animal of this size using the allometric equations (Taylor *et al.* 1982). Dotted lines represent minimum costs calculated for humans and elephants (see Fig. 4 legend for equation). Energetic cost increased rapidly with walking speed at speeds above the minimum.

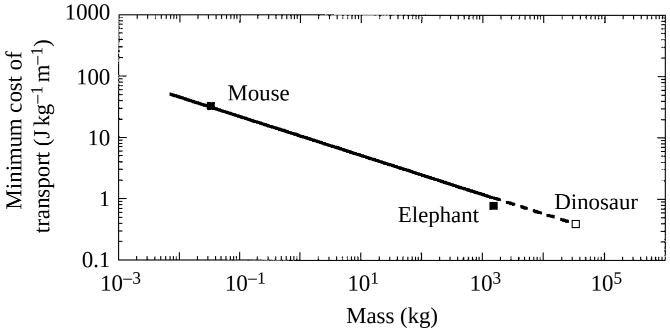

Fig. 4. Minimum cost of transport (in J kg^{-1} m^{-1}) is plotted against body mass (M_b in kg) on logarithmic coordinates. The solid line is the allometric relationship relating minimum cost of walking, running, trotting, galloping and/or hopping to mass on the basis of data from 90 species of birds and mammals spanning a range of body mass from a 7 g pygmy mouse to a 260 kg zebu steer (Taylor *et al.* 1982). This relationship, $\mathrm{COT_{tot}}=10.7M_b^{-0.316}$, where $\mathrm{COT_{tot}}$ is total cost of transport, predicts the minimum cost observed for walking elephants remarkably well (1.05 *versus* 0.78 J kg^{-1} m^{-1}). Full and Tu (1991) found that including measurements from reptiles, amphibians, crustaceans, insects and myriapods with the measurements from birds and mammals gave an almost identical allometric relationship, $\mathrm{COT_{tot}}=10.8M_b^{-0.32}$. Therefore, it seems likely that the relationship probably also held for the largest land animals that ever inhabited the earth, dinosaurs that weighing 34 000 kg (34 metric tonnes). The dashed line is extended to include these animals.

Discussion

How does the minimum cost of walking in the elephant compare with the minimum costs of walking, running and galloping in other animals? Within each gait (walk, run, trot, gallop), energy cost is minimized over a narrow range of speeds (Alexander, 1989). Horses trained to trot at speeds at which they would normally walk or gallop use much more energy than they would at their preferred gait (Hoyt and Taylor, 1981). Wildebeest, zebras and gazelles migrating across the African plains use narrow ranges of speeds within each gait (Pennycuick, 1975), presumably also minimizing cost. In horses, wildebeest and most other animals, the minimum energetic cost is the same regardless of gait (Taylor *et al.* 1982; Hoyt and Taylor, 1981). The minimum cost of walking in elephants can be calculated using a simple allometric equation derived from measurements in more than 90 species of birds and mammals (Taylor *et al.* 1982). The calculated value for elephants is 1.05 J kg^{-1} m^{-1}, slightly higher than our measured value of 0.78 J kg^{-1} m^{-1}, but it falls within the 95 % confidence limits of the regression line (Fig. 4). Furthermore, this relationship, $\mathrm{COT_{tot}}=10.7M_b^{-0.32}$, where $\mathrm{COT_{tot}}$ is the minimum total cost of transport and M_b is body mass, is not altered by including our values for elephants in the regression. Full and Tu (1991) found that including measurements from reptiles, amphibians, crustaceans, insects and myriapods with the measurements from birds and mammals gave the identical allometric relationship, $\mathrm{COT_{tot}}=10.8M_b^{-0.32}$. Therefore, it seems likely that this relationship is very general and probably holds even for the largest land animals that ever inhabited the earth, dinosaurs, which weighed 34 000 kg. The dashed line in Fig. 4 extends the regression to include these animals.

Two simple parameters seem to play a primary role in setting the rate at which the muscles of running animals use energy: the time available to apply force to the ground by each foot, and the forces the muscles have to generate to support the body weight (Kram and Taylor, 1990; Taylor, 1994). Longer legs and longer steps allow slower rates of force application and the use of slower, more economical, muscles. We have not been able to develop the same simple relationship between time of force application and cost for walking as we have for running (Taylor, 1994).

In the past, land dinosaurs existed that weighed up to ten times as much as elephants. Alexander (1989) has calculated their speeds from fossilized footprints. He found that most of these tracks were made at speeds of about 1 m s^{-1} and that none was made at a speed above 2.2 m s^{-1}. Large dinosaurs probably moved at these slow speeds for the same mechanical reasons as elephants and, like elephants, they were probably able to move cheaply, following the allometric rules. It seems likely that these were the fuel economy champions of all time, with a minimum cost of locomotion 1/90 that of a mouse and 1/1300 that of an ant. Selection pressures other than fuel economy have obviously determined evolutionary success, since ants are one of the most successful living animal groups and dinosaurs are extinct.

This work was supported by US NIH grant 2RO1 AR18140, the Atlanta/Fulton County Zoo and Friends of Zoo Atlanta.

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