

The energetic costs of trunk and distal-limb loading during walking and running in guinea fowl *Numida meleagris*

I. Organismal metabolism and biomechanics

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Accepted 21 March 2006

Summary

We examined the energetic cost of loading the trunk or distal portion of the leg in walking and running guinea fowl (*Numida meleagris*). These different loading regimes were designed to separately influence the energy use by muscles used during the stance and swing phases of the stride. Metabolic rate, estimated from oxygen consumption, was measured while birds locomoted on a motorized treadmill at speeds from 0.5 to 2.0 m s⁻¹, either unloaded, or with a mass equivalent to 23% of their body mass carried on their backs, or with masses equal to approximately 2.5% of their body mass attached to each tarsometatarsal segment. In separate experiments, we also measured the duration of stance and swing in unloaded, trunk-loaded, or limb-loaded birds. In the unloaded and limb-loaded birds, we also calculated the mechanical energy of the tarsometatarsal segment throughout the stride.

Trunk and limb loads caused similar increases in metabolic rate. During trunk loading, the net metabolic rate (gross metabolic rate – resting metabolic rate) increased by 17% above the unloaded value across all speeds. This percentage increase is less than has been found in most studies of humans and other mammals. The economical load carriage of guinea fowl is consistent with predictions based on the relative cost of the stance and swing phases of the stride in this species. However, the

available comparative data and considerations of the factors that determine the cost of carrying extra mass lead us to the conclusion that the cost of load carrying is unlikely to be a reliable indicator of the distribution of energy use in stance and swing. Both loading regimes caused small changes in the swing and/or stance durations, but these changes were less than 10%.

Loading the tarsometatarsal segment increased its segmental energy by 4.1 times and the segmental mechanical power averaged over the stride by 3.8 times. The increases in metabolism associated with limb loading appear to be linked to the increases in mechanical power. The delta efficiency (change in mechanical power divided by the change in metabolic power) of producing this power increased from 11% in walking to approximately 25% in running. Although tarsometatarsal loading was designed to increase the mechanical energy during swing phase, 40% of the increase in segmental energy occurred during late stance. Thus, the increased energy demand of distal limb loading in guinea fowl is predicted to cause increases in energy use by both stance- and swing-phase muscles.

Key words: guinea fowl, *Numida meleagris*, backpack loading, legged locomotion, segmental energy, oxygen consumption, limb loading, swing phase, stance phase, efficiency.

Introduction

One approach to revealing the energetic costs of various mechanical functions during walking and running has been to infer these costs from the effects of changing external loads. For example, application of loads to the trunk has been used to increase the costs of supporting body weight and accelerating body mass (Taylor et al., 1980; Grabowski et al., 2005). In the absence of changes in duty factor or stride frequency, trunk loads should have negligible effects on the cost of swinging the limbs. Conversely, loads applied to the

distal limbs have been used to affect the costs of swinging the limbs with presumably little effect on the energy expended while the foot is in contact with the ground (Martin, 1985; Studel, 1990a; Studel, 1990b).

Despite the seemingly simple effects of these external loading regimes on locomotor biomechanics, making inferences about normal locomotor function from the increases in metabolic rates due to loading may be problematical. The most straightforward use of the results of loading studies is simply the prediction of the exercise energy

metabolism of humans or other animals that normally carry external loads on their body or limbs (Soule and Goldman, 1969; Epstein et al., 1987; Lawrence and Stibbards, 1990; Wickler et al., 2001; Wickler et al., 2004). However, loading studies have also been used to infer the relative costs of weight support and producing the fluctuations in kinetic energy associated with swinging the limbs during normal locomotion, and the conclusions reached are not consistent. For example, the energetic cost of running in humans and several quadrupeds was found to increase by the same percentage as the increase in body weight due to backpack loading (Taylor et al., 1980). These data were taken as evidence that during unloaded running the majority of metabolic energy is expended by muscles exerting force to support body weight during the stance-phase of the stride and that the metabolic cost of swinging the limbs is minimal (see also Taylor, 1985; Taylor, 1994). On the other hand, other investigators have concluded, based on distal limb loading studies, that the cost of swinging the limbs during unloaded running is substantial (Steudel, 1990a; Steudel, 1990b). Also, a considerable number of trunk loading studies, many in walking humans, have shown that the percentage increase in metabolic rate is considerably greater than the percentage increase in body weight (see Discussion) and these data are difficult to incorporate into Taylor's inferences (Taylor et al., 1980). The apparent inconsistencies in the conclusions of these studies may stem from the failure to consider all the underlying assumptions about muscle function that are necessary to connect the change in loading with the increased metabolic cost (see Discussion).

We chose to examine the cost of carrying loads on the trunk and distally on the legs in guinea fowl *Numida meleagris*. Why perform load-carrying studies with a bird? The data on load-carrying collected to date have all been on quadrupeds, with the exception of the numerous studies of humans. Studying a biped has advantages in uncovering the underlying mechanisms that determine the metabolic cost of running because the complication of the differing functions of the forelimbs and hindlimbs in quadrupeds is avoided. The economy of load-carrying may be different in humans and birds. Comparisons of human and ostrich locomotion indicate that ostriches are economical runners compared to humans (Fedak and Seeherman, 1979; Rubenson, 2005). The potential load-carrying ability of terrestrial birds is indicated by the ability of ostriches to run while carrying nearly their own weight in the form of a human rider on their back. Perhaps the most important reason for using guinea fowl is that this model system offers the opportunity to overcome the limitations of past work in this area by comparing alterations in organismal energy use with changes in energy use at the level of individual muscles (Ellerby and Marsh, 2006). Recently, energy use by all the individual leg muscles of guinea fowl during level unloaded running has been analyzed using muscle blood flow as the indicator of muscle metabolic rate (Marsh et al., 2004; Ellerby et al., 2005). Therefore, at the onset of this study we were in the unique position of already knowing the distribution

of energy use between swing and stance. Approximately 25% of the net energy use during walking and running is consumed by muscles active during swing phase (Marsh et al., 2004). We used a combination of metabolic and mechanical measurements in this study to assess the economy of carrying trunk loads and the efficiency of moving loads attached to the distal limbs. The trunk and distal limb loading regimes were expected to differentially influence stance and swing-phase mechanics, respectively, and we examined the extent to which the stride characteristics and segmental energetics were consistent with these predicted differential influences on stance and swing. A companion study (Ellerby and Marsh, 2006) examines the distribution of increased energy use among the individual stance and swing-phase muscles during trunk and distal limb loading.

Materials and methods

Animals

Guinea fowl (*Numida meleagris* L.) were obtained from The Guinea Farm (New Vienna, IA, USA) as hatchlings and cage-reared at the Northeastern University Division of Laboratory Medicine. All procedures with live guinea fowl were conducted under protocols approved by the Northeastern University Institutional Animal Care and Use Committee. At the time of the measurements the birds were between 10 and 14 months old. Birds had *ad libitum* access to food and water and were maintained on a 12 h:12 h light:dark cycle. Body mass was 1.46 ± 0.04 kg (mean \pm s.e.m., $N=6$, range 1.31–1.59 kg; three non-ovulating females and three males).

Training

For 2 months prior to measurements of rates of oxygen consumption (\dot{V}_{O_2}) we trained the birds to run on a motorized treadmill (Trimline 2600, Hebb Industries, Tyler, TX, USA; 120 cm \times 44 cm tread area). During training and subsequent experiments the guinea fowl ran inside a three-sided box with a partial top. The box was open at the back and had a mirror mounted on the front facing the running bird. A duct brought cool air from an air conditioner to one side of the box. Airflow was controlled such that sufficient cool air was allowed to flow into the box to prevent the birds from continuously panting. The training regime consisted of running for approximately 30 min per day, 5 days a week, at speeds ranging from 1.5 to 3.28 m s⁻¹. At the end of the training period all birds could sustain 30 min of exercise at 2.5 m s⁻¹.

Trunk and distal limb loading

A canvas backpack was constructed so that weights could be added to the trunk of the running birds. The pack weighed 32 g and was held in place anteriorly with straps around each wing and posteriorly with a strap running circumferentially around the bird posterior to the sternum (Fig. 1). A lead weight could be attached to the pack with Velcro. The weight consisted of a 5.5 cm wide strip of lead that was shaped so that

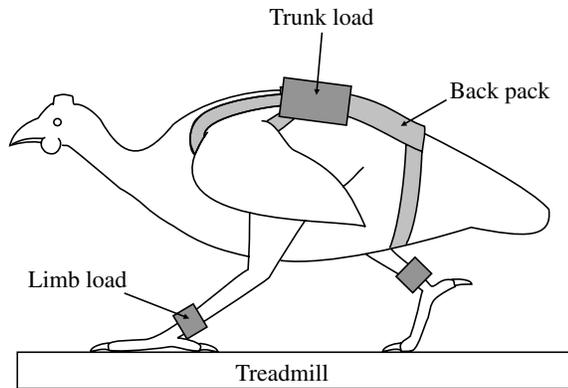


Fig. 1. Approximate position and method of attachment of distal limb and trunk loads. Birds were either limb- or trunk-loaded. Both loading conditions are shown here for illustrative purposes. The limb load was placed near the distal end of the tarsometatarsal segment.

it conformed to the back of the bird and extended approximately 5 cm ventrally along each side of the birds' body. The weight was positioned such that it was approximately above the birds' center of mass. The mass of the load was adjusted for the body mass of the bird. The combined mass of the weight and backpack averaged $22.8 \pm 0.5\%$ (mean \pm s.e.m.) of the individual's body mass.

Distal limb loading was accomplished by taping weights to the tarsometatarsal segment (Fig. 1). Limb weights were constructed from approximately 2 cm wide strips of lead that were wrapped around the distal portion of the tarsometatarsal segments and secured in place with duct tape. A mass of 37 g was attached to each limb. The total mass of the limb weights (74 g) was approximately 5% of the body mass.

Respirometry

Details of the respirometry setup are the same as described previously (Ellerby et al., 2003). Respiratory gases were collected using a flow-through respirometry system with the birds wearing a loose-fitting mask. Excurrent air from the mask passed through a column of DrieriteTM to absorb water and then through a rotameter-type flow meter (factory rated accuracy $\pm 3\%$) with a needle valve on the outlet to control flow. The flow meter calibration was checked using a recording spirometer of known accuracy. The ambient flow rate was set at 83.3 ml s^{-1} and 167 ml s^{-1} for birds at rest and during exercise, respectively. These flow rates kept the excurrent fractional O_2 contents above 0.2. Gas withdrawn for O_2 measurements passed through a column of CO_2 absorbent (AscariteTM) and additional DrieriteTM before measurement of O_2 content using an Amtek S-3A/II O_2 analyzer (AEI Technologies Inc., Naperville, IL, USA). This dual-channel oxygen analyzer was operated in differential mode in which the expired air from the mask was compared with dry, CO_2 -free room air that was pumped continuously through the second cell of the analyzer. Oxygen consumption rates (\dot{V}_{O_2}) in ml s^{-1} was calculated as described previously (Ellerby et al.,

2003) using the appropriate equation for downstream flow (Withers, 1977). Oxygen consumption was converted to rate of energy use in using a conversion factor of $20.1 \text{ W s ml}^{-1} \text{ O}_2$.

Resting metabolic rate was measured while the birds sat in a darkened box on the treadmill. Sufficient time, usually 10–20 min, was allowed for resting metabolic rate to stabilize.

The birds ran at a steady speed until \dot{V}_{O_2} stabilized for at least 1 min. Typically, birds spent 2–4 min at a given speed to assure a stable reading. The time to 100% response of our system was less than 30 s when the flow rate was 167 ml s^{-1} . After the resting \dot{V}_{O_2} measurements, the birds were typically given a 2 min conditioning run at 1.5 m s^{-1} before measuring \dot{V}_{O_2} during walking at 0.5 m s^{-1} . After running at 1.5 m s^{-1} , the \dot{V}_{O_2} at 0.5 m s^{-1} stabilized more quickly than if the walking trial was initiated immediately following the resting measurements. As long as a conditioning run was done, the metabolic rate after 1 min at a given speed accurately reflects the steady state value at that speed.

Initial \dot{V}_{O_2} measurements obtained during load-carrying were high, but decreased on subsequent runs. Approximately three running sessions were needed with either the trunk or limb loads for the birds to become accustomed to the loads and for \dot{V}_{O_2} to stabilize at a given speed.

On a given day, \dot{V}_{O_2} measurements were obtained during unloaded running, and subsequently under one or both of the loading conditions over a range of speeds. The order of the weighted measurements was varied arbitrarily on any given day and unloaded measurements were obtained both before and after the loaded measurements. The order of the measurements did not appear to have any influence on the values obtained. Under all loading conditions, the birds locomoted at 0.5, 1.0 and 1.5 m s^{-1} . Additionally, unloaded birds and birds with limb loads ran at 2.0 m s^{-1} . The speed range and load sizes were chosen to ensure that \dot{V}_{O_2} was always less than the maximum \dot{V}_{O_2} of the birds (Ellerby et al., 2003). For simplicity, 1.0 m s^{-1} is classified as a running speed in most of what follows, but the transition between walking and running has no marked discontinuity in stride kinematics in birds and this speed may be a transitional speed between gaits in guinea fowl (Gatesy, 1999). Following the initial runs to accustom the birds to the loading, 3–5 sets of data were collected for each bird. The mean values for each bird from these sessions were used in the subsequent analyses.

Kinematics and dynamics of normal and loaded strides

For these measurements, we carried out a separate set of running experiments, using the same birds as for the \dot{V}_{O_2} measurements. The guinea fowl ran inside a three-sided box, open at the back, with a mirror mounted on the side facing the running bird. The left side of the box was made of transparent acrylic to enable filming of the running birds. The feathers of the left leg were trimmed so that the distal limb segments could be clearly seen, and the proximal and distal ends of the tarsometatarsal segment were highlighted with white paint. High-speed video was obtained at a frame rate of 500 Hz using a NAC HSAV-1000 video camera (NAC, Tokyo, Japan) for

the running speeds and loading conditions under which \dot{V}_{O_2} measurements were made.

For measurement of swing and stance durations, 8–10 strides were selected for each weighting condition at each speed. Strides were selected during which the birds maintained a steady position on the treadmill. Toe-off and foot-down times were measured to the nearest 2 ms. The mean value of the 8–10 strides was used for further analysis.

To allow calculation of the mechanical energy of the tarsometatarsal segment during running, we measured the center of mass and moment of inertia of this segment both with and without the lead weight added. The birds were sacrificed after a separate series of experiments to determine muscle blood flow (Ellerby and Marsh, 2006). The limbs were frozen and the intact tarsometatarsal segment removed by separating the bones at their articulations. We determined the location of the center of mass of the loaded and unloaded limb segment by using a suspension technique whereby the intersection point from two different suspension positions was taken as the location of the segment's center of mass.

To measure the moment of inertia about the center of mass, the frozen segment was suspended by one end from a stiff steel pin about which it could pivot. The segment was allowed to swing back and forth through an arc about the pivot. We obtained high-speed video at 500 Hz of the swinging segment to determine the period of the oscillation (t) in seconds. This period was used to calculate the moment of inertia (I) about the pivot point in kg m^2 using the following equation derived from the basic mechanics of a pendulum:

$$I = \frac{t^2 mcg}{4\pi^2}, \quad (1)$$

where m is the mass of the tarsometatarsal segment (kg), c is the distance between the center of mass and the axis of suspension (m), and g is the acceleration due to gravity (m s^{-2}). The moment of inertia about the center of mass was then calculated using the parallel axis theorem as:

$$I_0 = I - mc^2. \quad (2)$$

For each individual and speed we selected one stride during steady speed running under the limb-loaded condition and one stride under unloaded conditions for analysis of tarsometatarsal segment mechanical energy. We captured frames of the video at sufficient resolution to obtain approximately 100 data points during the stride (0.004–0.008 ms intervals, depending on speed). Using NIH Image (version 1.63), we hand-digitized the positions of the proximal and distal ends of the tarsometatarsus. The position data were used to calculate the horizontal and vertical coordinates of the center of mass of the tarsometatarsal segment and the angle of this segment with reference to the horizontal (θ_{tm}). The horizontal and vertical coordinates were smoothed using a smoothing interpolation routine in the application Igor Pro (Wavemetrics, Lake Oswego, OR, USA) and differentiated with respect to time to obtain the horizontal (v'_x) and vertical (v'_y) translational

velocities of the segment in the fixed coordinate system of the video field. The values of v'_x were corrected for the speed of the treadmill to obtain the velocity with reference to a fixed point on the belt (v_x). The values of θ_{tm} were smoothed and differentiated to determine the angular velocity of the tarsometatarsal segment (ω). The instantaneous horizontal ($E_{K,x}$) and vertical ($E_{K,y}$) translational and rotational ($E_{K,\text{rot}}$) kinetic energies were calculated as:

$$E_{K,x} = \frac{1}{2}mv_x^2, \quad (3)$$

$$E_{K,y} = \frac{1}{2}mv_y^2, \quad (4)$$

$$E_{K,\text{rot}} = \frac{1}{2}I\phi_{\text{tm}}^2 = \frac{1}{2}I_0\omega^2. \quad (5)$$

We also calculated the gravitational potential energy ($E_g = mgh$) of the tarsometatarsal segment, where h is the height of the center of mass of the tarsometatarsal segment above the tread. The values of $E_{K,x}$, $E_{K,y}$, $E_{K,\text{rot}}$ and E_g were summed at each point in the stride to determine the total instantaneous segmental energy (E_{tm}). The sum of the increases in segmental energy (E_{pos}) over the stride was then determined by summing the positive increments in E_{tm} . The positive mechanical power of the segment \dot{E}_{pos} averaged over the whole stride was calculated by dividing E_{pos} by the stride time.

The segmental mechanical energy term calculated here is not the same as that calculated by Fedak et al. (Fedak et al., 1982) and others, who have partitioned 'external' and 'internal' work. They (Fedak et al., 1982) calculated the kinetic energy with respect to the center of mass, whereas we used a fixed reference point on the ground. Both techniques are useful, but in different contexts. The method of calculating internal work is useful when summing with external work calculated from the force-plate measures of the work done on the center of mass. In this case, the internal work represents work not appearing in the measurement of external work. Our calculation of segmental energy is more useful for examining the temporal distribution of the work used to produce changes in the velocity of the segment. The best example that illustrates this difference is the kinetic energy of the foot. The internal work method calculates a large peak in kinetic energy of the foot during stance when this segment is stationary on the ground, but this is due to changes in the velocity of the center of mass with the respect to the foot, and not due to energy changes in the foot segment.

Statistical analyses

Values are means \pm 1 s.e.m. We carried out statistical analyses using SPSS (Versions 10 and 11 for the Macintosh). ANOVA was used to test for significant differences in the measured values with loading condition and speed as the factors.

Results

Metabolic rate during loading

We found that both running speed (ANOVA, $P < 0.001$) and loading condition (ANOVA, $P < 0.001$) had significant effects on metabolic rate. The relationship between metabolic rate and

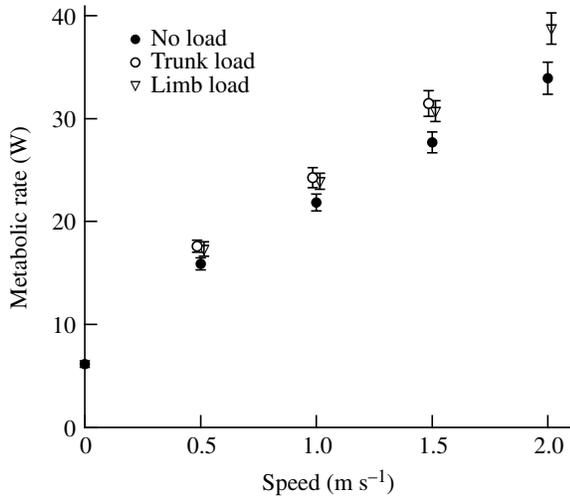


Fig. 2. Metabolic rate (W; see Materials and methods) as a function of treadmill speed in guinea fowl with no load (closed circles), trunk load (open circles) or distal limb load (open triangles). The data were collected at 0.5 m s^{-1} intervals under all conditions, but the loaded data are offset slightly on the speed axis for clarity. Values are means ± 1 s.e.m. ($N=6$).

speed was linear during both trunk-loaded and unloaded running (Fig. 2).

The net metabolic rates during unloaded and trunk-loaded running were calculated by subtracting the value for resting metabolic rate measured with the birds sitting quietly in a darkened box on the treadmill (the zero speed value in Fig. 2).

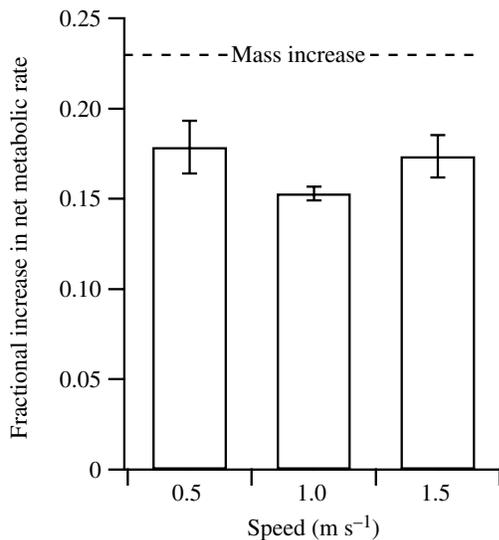


Fig. 3. Fractional increases in net metabolic rate at different speeds in trunk-loaded guinea fowl. Net metabolic rates were calculated by subtracting the resting metabolic rate of the bird sitting quietly in a darkened box on the treadmill from the rates measured at the different speeds. Fractional increases were then calculated by subtracting the unloaded net metabolic rate from the loaded net metabolic rate and dividing by the unloaded net metabolic rate. The broken line indicates the fractional increase in total mass (body mass plus load) produced by loading the trunk. Values are means ± 1 s.e.m. ($N=6$).

The fractional increase in net metabolic rate during trunk loading did not change significantly (ANOVA, $P=0.26$) with speed (Fig. 3). The overall fractional increase across all individuals and speeds was 0.17 ± 0.01 . The mean fractional increase in body mass was 0.23 ± 0.005 . Thus, the increment in net locomotor costs due to trunk loading was 74% of the increment in body mass (Fig. 3).

Distal limb loading, accomplished by loading the tarsometatarsal segments with a total mass equal to approximately 5% of body mass, increased the metabolic rate by a similar amount to the 23% load carried on the trunk (Fig. 2).

Loaded and unloaded kinematics and segment energies

Loading caused small but significant (ANOVA; $P<0.001$) changes in the durations of the stance and swing phases of the stride (Fig. 4). Paired comparisons indicated that trunk loading had no significant effect on swing duration, but caused a significant 4% increase in stance duration (Scheffé test; $P<0.001$). Ankle loading resulted in an approximately 9% increase in both stance and swing durations (Scheffé test; $P<0.03$).

The load on the tarsometatarsal segment increased the segment's mass by 4.3-fold and shifted its center of mass from the approximate midpoint of the segment to 72% of the distance from the proximal to the distal end (Table 1). Despite the large increase in mass, the segment moved in a similar manner during a stride in the loaded and unloaded conditions (Fig. 5).

The energy of the tarsometatarsal segment rose in late stance as it began to accelerate forward due to translation caused by extension of the ankle and flexion of the toe joints. Segment energy continued to rise during the first part of swing as it was

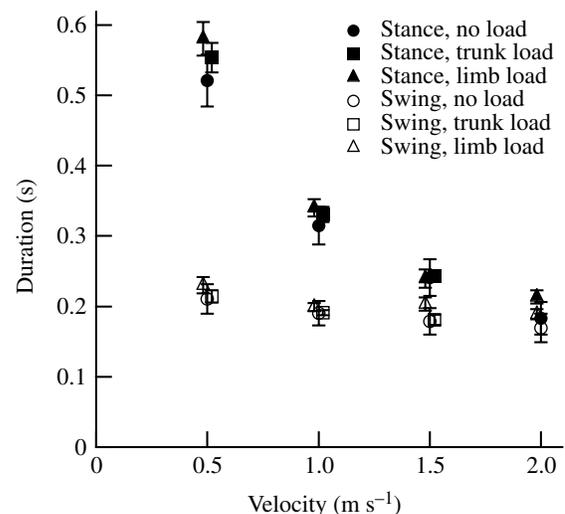


Fig. 4. Mean stance (closed symbols) and swing (open symbols) durations during unloaded (circles), trunk-loaded (squares) and distal limb-loaded (triangles) locomotion. Values are means ± 1 s.e.m. ($N=6$). Closely spaced points are offset slightly on the speed axis for clarity.

Table 1. Physical properties of the unloaded and loaded tarsometatarsal limb segment

	Unloaded	Loaded
Tarsometatarsal segment mass (kg)	0.011±0.001	0.048±0.001
Center of mass location (% of segment length from proximal end)	49.0±0.4	71.8±2.0
Moment of inertia (kg m ²) about center of mass	6.93±0.52×10 ⁻⁶	1.29±0.11×10 ⁻⁵

Values are means ± s.e.m. (N=6).

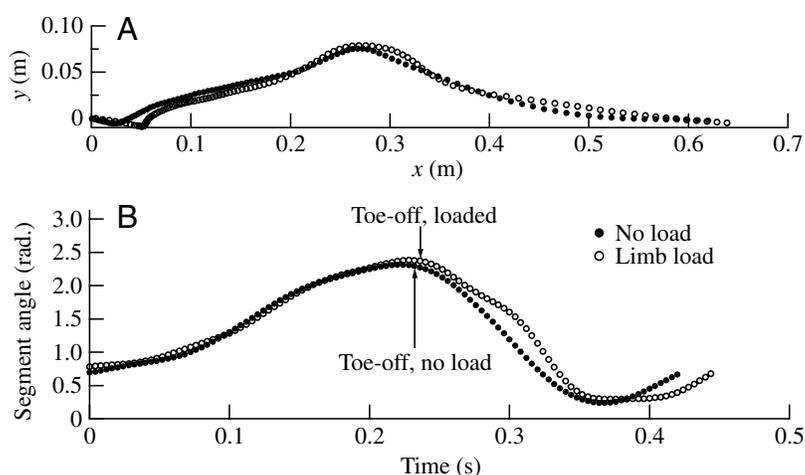


Fig. 5. Horizontal and vertical coordinates of the proximal end of the tarsometatarsal segment (A) and segment angle (B) in a representative bird unloaded (closed symbols) and limb-loaded (open symbols), running at 1.5 m s^{-1} . Horizontal coordinates from the video were corrected for tread speed and thus the total distance moved in A indicates the stride length. Data were collected at 0.004 s intervals from foot-down to the next foot-down.

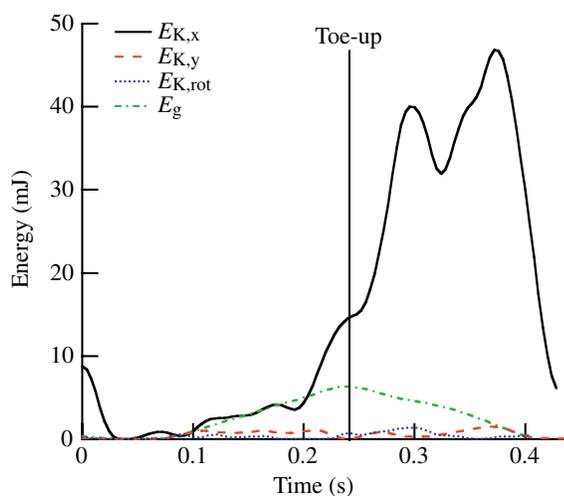


Fig. 6. The components of the energy in a single unloaded tarsometatarsal segment as a function of time during one stride in a representative bird running at 1.5 m s^{-1} . Horizontal ($E_{K,x}$; solid black line), vertical ($E_{K,y}$; broken red line) and rotational ($E_{K,rot}$; dotted blue line) kinetic energies are indicated. The green broken and dotted line indicates the gravitational potential energy (E_g) referenced to zero at the lowest point in the stride. The vertical line indicates the stance swing transition. (Please note that the dip in $E_{K,x}$ shown during in swing phase is representative in that a decrease in this mechanical energy term occurred during mid-swing in 4 of the 5 birds measured. However, the magnitude of the mid-swing decrease in $E_{K,x}$ in the example shown was the largest found.)

moved forward rapidly (Fig. 6). At higher speeds, the energy of the segment was dominated by the horizontal translational energy ($E_{K,x}$). The gravitational potential energy (E_g) remained relatively constant with speed at approximately 6 mJ , and thus was a larger fraction of the total energy at lower speeds. The vertical translational kinetic energy ($E_{K,y}$) and rotational kinetic energies ($E_{K,rot}$) were small fractions of the total energy at all speeds.

The total instantaneous energy of the segment (E_{tm}) was substantially increased by loading the segment (Fig. 7). Most of the increment in E_{tm} was due to the continuous rise in segmental energy in late stance and early swing. We estimated the total positive work done on the segment (E_{pos}) by summing the positive increments in E_{tm} over the stride. The value of E_{pos} for the loaded segment was on average 4.1 times the value for the unloaded segment (Fig. 8A). Under most loaded and unloaded conditions, approximately 60% of the positive work was done during swing and the remaining 40% was due to the rise in segmental energy during late stance (Fig. 8A).

Dividing the total positive work by the stride time provides an estimate of the mechanical power used to move the segment averaged over the entire stride (\dot{E}_{pos}). The value of \dot{E}_{pos} increased by an average of 3.8 times by loading the segment (Fig. 8B). The increase in power is less than the increase in segment energy because the stride duration is slightly longer when the segment is loaded.

The curvilinear relationship of mechanical power as a function of speed was also seen in the increment in metabolic power (Fig. 9). The ratio of the increase in segment mechanical

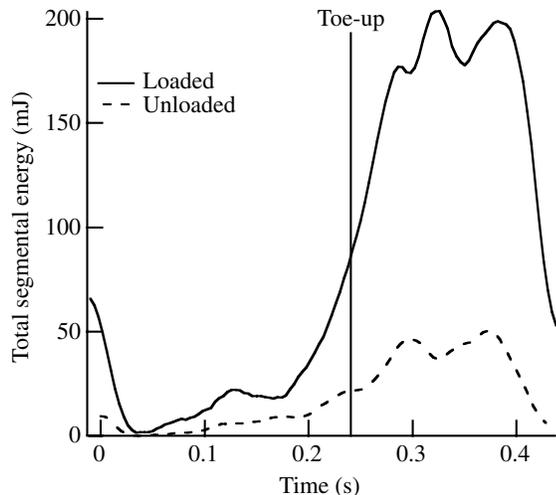


Fig. 7. Total mechanical energy of a single tarsometatarsal segment as a function of time during one stride in a representative bird running at 1.5 m s^{-1} . Broken line, unloaded segmental energy; solid line, loaded segmental energy. The vertical line indicates the stance–swing transition.

power and the increase in metabolic power due to loading provides an estimate of the efficiency of the overall locomotor system in performing the extra work required by the distal limb loading. This estimate of efficiency increased with speed, going from 0.11 at 0.5 m s^{-1} to 0.26 at 2.0 m s^{-1} (Fig. 9).

Discussion

Economy of carrying loads on the trunk

The net metabolic rate of guinea fowl during walking and running increases by 17% for an increase in body mass of 23% across all speeds. In a study of human load-carrying (Griffin et al., 2003), it was suggested that subtracting resting metabolic rate from the total metabolic rate is the most appropriate way to compare differences in loaded and unloaded conditions, a practice also followed in reduced weight studies (Farley and McMahon, 1992) and in recent trunk-loading investigations (Griffin et al., 2003; Grabowski et al., 2005). Our own work on the distribution of blood flow in the guinea fowl suggests that this correction for resting metabolism is appropriate because oxygen delivery to the tissues that are not involved in exercise changes little from rest to exercise (Ellerby et al., 2005).

Our data indicate that walking guinea fowl are economical in carrying trunk loads when compared with most of the data on mammals during walking. The only other bipedal animals on which loading studies have been conducted are humans. Most studies of trunk loading in humans during walking have found that the ratio of the loaded to unloaded net metabolic rate (metabolic ratio) is greater than the ratio of the loaded mass to the unloaded mass (mass ratio, Fig. 10). The major exceptions to the poor economy of carrying loads during walking include two studies of African women carrying loads

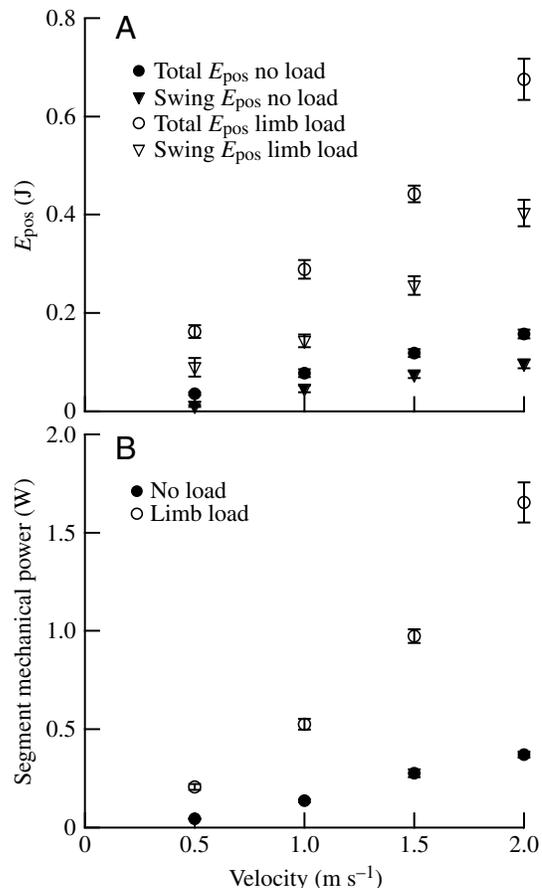


Fig. 8. (A) Mean sum of the positive increments in mechanical energy (E_{pos}) of both tarsometatarsal segments as a function of treadmill speed, in the unloaded (closed symbols) and loaded (open symbols) segments. Circles, total E_{pos} over the whole stride; triangles, E_{pos} for swing phase only. (B) Mean mechanical power of the unloaded (closed circles) and loaded (open circles) tarsometatarsal segments, calculated by dividing total E_{pos} for the stride by the stride duration. Values are means \pm 1 s.e.m. ($N=6$).

on their heads (Maloiy et al., 1986; Jones, 1989), two studies of children carrying moderate backpack loads, and a study of Nepalese porters (Bastien et al., 2005) (Fig. 10). Better mechanical energy recovery by the inverted pendulum mechanism has been suggested as a factor underlying the good economy of load-carrying in African women (Heglund et al., 1995). Jones has also noted (Jones, 1989) that the better-than-average economy of these women depends on their body fat content, with heavier individuals having net ratios similar to the Europeans studied. Why the net metabolic ratios of Nepalese porters carrying very heavy loads are much lower than most of the other values measured during walking (Fig. 10) remains to be explained. With the exception of these data, the net metabolic ratios during human walking increase with increases in the load carried, particularly when loads exceed 50% of the unloaded body mass (Fig. 10A,B). This same trend is evident in the data from large quadrupedal mammals walking with loads on their backs (Fig. 10A,B).

The fractional increase in metabolic rate when guinea fowl run at 1.0 or 1.5 m s⁻¹ with trunk loads is the same as that during walking, and again is lower than the values found in most studies of mammals using running gaits (Fig. 11). The studies that have measured the costs of load carriage in humans during running report lower net metabolic ratios than the

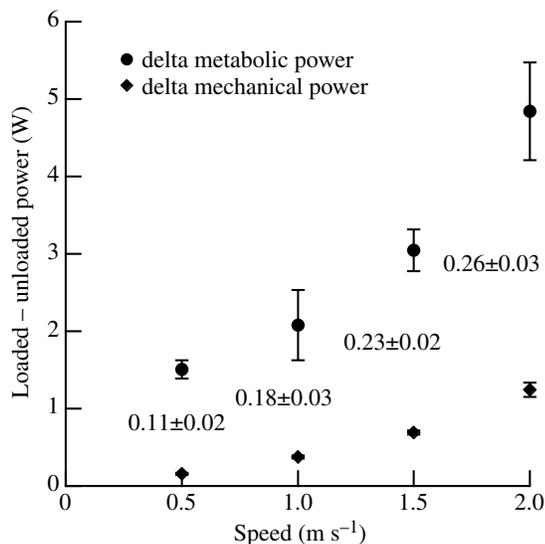
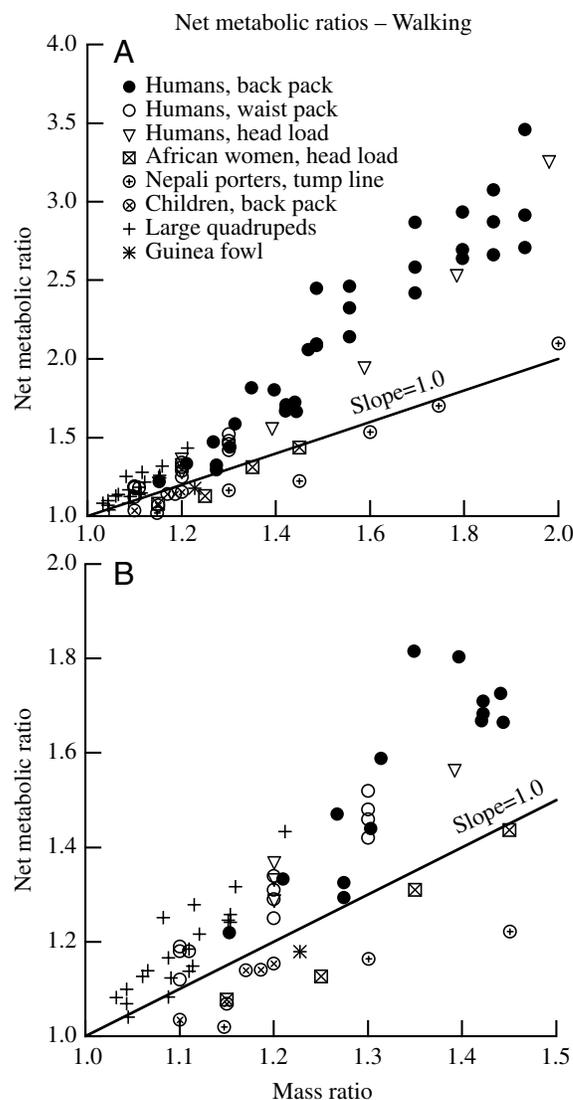


Fig. 9. Mean increments in metabolic (circles) and mechanical (diamonds) power, calculated as loaded power minus unloaded power. Values are means \pm 1 s.e.m. ($N=6$). Numbers between the metabolic and mechanical power indicate the mean delta efficiency (\pm 1 s.e.m.) calculated by dividing the mechanical power increment by the metabolic power increment.

Fig. 10. Mean metabolic response to trunk loading or to head-supported loads in walking mammals and guinea fowl. The ratio of net loaded to net unloaded metabolic rate is plotted as a function of the ratio of loaded (body mass plus load) to unloaded body mass (body mass only). The solid lines with a slope of 1.0 are included for reference. (A) All the data. (B) Measurements in which the mass ratio was less than 1.5 times the unloaded body mass. Solid circles, five human studies with the load applied in back packs (Soule et al., 1978; Pierrynowski et al., 1981; Duggan and Haisman, 1992; Lloyd and Cooke, 2000; Quesada et al., 2000). Open circles, human data for loads carried in a waist pack (Griffin et al., 2003). Open inverted triangles, two studies of human males carrying loads on their heads: American men (Soule and Goldman, 1969); Indian men (Datta et al., 1975). Open squares enclosing x, African women carrying head loads (Jones, 1989). Open circles enclosing +, Nepalese porters carrying loads resting on their backs with a tump line around the head (Bastien et al., 2005) (G. J. Bastien and N. C. Heglund, personal communication). Open circles enclosing x, two studies of children carrying back packs (Hong et al., 2000; Merati et al., 2001). Plus signs, large quadrupeds (horse, Brahman cattle and water buffalo) (Lawrence and Stibbards, 1990). The asterisk indicates the ratio for guinea fowl walking at 0.5 m s⁻¹. Net metabolic rates were calculated as the active metabolic rate minus the resting rate. For human studies in which resting metabolic rate was not given, we used an approximate value of 1.5 W kg⁻¹, which was based on the available data for standing humans in references cited here.

majority of walking studies, but the net metabolic ratios are generally greater than the mass ratios (Fig. 11). As with the walking data, the trend across these studies is for metabolic ratios to approach 1.0 with relatively light loads. Several studies with percentage increases in mass of less than 15% have found net metabolic ratios during running that are lower than the mass ratios (Fig. 11, adult athletes and children). These low fractional increases in metabolic rate could represent random variation because the metabolic changes caused by the small loads approach the resolution of the measurements. However, the better-than-average load-carrying economy could genuinely reflect differences in the physiology or biomechanics of the subjects used in these studies. The individuals studied were generally lean, well-conditioned adult athletes, many of whom ran competitively in middle and long distance events, or were children. Net metabolic ratios calculated from studies of quadrupeds trotting with back loads are also lower than the values from studies of walking quadrupeds, but as with the human studies the fractional increase in metabolic rate is generally slightly



greater than the fractional increase in mass (Fig. 11). The comparative data in Figs 10 and 11 make it clear that guinea fowl carry loads more economically than most mammals, but that some human individuals can carry loads just as economically. Although the most relevant comparisons to our data are from studies of mammals, some invertebrates carry loads with extraordinary economy (Kram, 1996). The underlying causes of this variation in the cost of carrying loads are not clear.

Load-carrying economy and the relative costs of swing and stance

Some previous investigators reasoned that the cost of carrying loads could be used to infer the relative costs of swing and stance (Taylor et al., 1980; Griffin et al., 2003). Loads placed on the trunk should not influence the cost of swinging the limbs when they are off the ground as long as the duty factor does not change appreciably, which appears to be the case for guinea fowl (see Fig. 4) and other animals (Taylor et al., 1980; Griffin et al., 2003). If one assumes that the transport

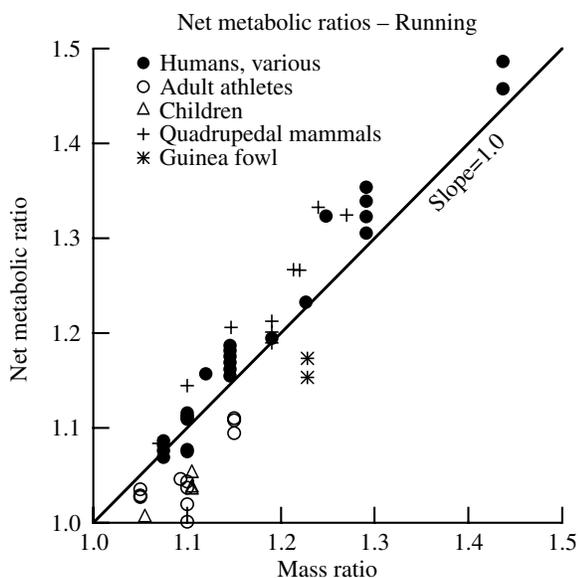


Fig. 11. Mean metabolic response to trunk loading in running mammals and guinea fowl. The solid line with a slope of 1.0 is included for reference. Net metabolic ratios were calculated as in Fig. 10. Solid circles, fit humans (Davies, 1980; Taylor et al., 1982; Epstein et al., 1987; Thorstensson, 1986; Bilzon et al., 2001). Open circles, very well trained adult humans, most of whom competed in distance or middle distance events (Cureton et al., 1978; Cooke et al., 1991; Bourdin et al., 1995). Open triangles, children (Thorstensson, 1986; Cooke et al., 1991; Davies, 1980). Plus signs, quadrupeds ranging in size from rats to horses (Taylor et al., 1980; Wickler et al., 2001) (S. J. Wickler, personal communication). Asterisks, values for guinea fowl running at 1.0 and 1.5 m s⁻¹. For the human studies not providing resting metabolic rates, the resting values were calculated as for the data in Fig. 10. Resting rates for the quadrupeds (Taylor et al., 1980) were calculated as 1.2 times the basal value obtained by entering the body mass (M_b) in the allometric equation, $\dot{E}_{\text{BMR}} = 3.89M_b^{0.76}$ (Peters, 1983).

cost per unit of added mass is the same as the per unit cost of transporting the original body mass, then the increase in metabolic rate can be used to infer the proportion of unloaded cost devoted to stance. For example, if swing phase incurs a significant cost, the metabolic ratio should be less than the mass ratio during trunk loading because the trunk loading is only increasing a portion of the total cost. Conversely, if the costs of swing are negligible, the fractional increase (or decrease) in load should exactly match the fractional increase in mass. This line of reasoning is not affected by the distribution of mechanical functions of the muscles during stance, e.g. the cost of weight support *versus* the cost of work (Chang and Kram, 1999; Donelan et al., 2002; Gottschalk and Kram, 2003), as long as these functions represent similar fractions of the total cost in loaded and unloaded conditions and the mass-specific cost of transporting the extra mass (weight) is the same as the cost of transporting the original body mass. Data showing a match between gross metabolic ratios and mass ratios in various animals during running were taken as evidence in favor of minimal swing costs (Taylor et al., 1980), as were data on net metabolic ratios for human running in simulated reduced gravity (Farley and McMahon, 1992). We will not consider simulated reduced gravity experiments in any detail here because interpreting these experiments is complicated by the reduction in weight, but not mass (Grabowski et al., 2005), and the interaction between the gravitational load the horizontal force during propulsion (Chang et al., 2000; Cavagna et al., 2000).

Following these inferences, the low metabolic ratios of trunk-loaded guinea fowl would be explained by the relatively high swing-phase costs found in this species. Guinea fowl use about a quarter of the total energy use in swing-phase muscles (Marsh et al., 2004). Accepting this line of reasoning would suggest that walking and running birds have much higher swing-phase costs than mammals, despite birds having similar transport costs to mammals (Fedak and Seeherman, 1979; Taylor et al., 1982), and similar increments in total mechanical energy over the stride (Heglund et al., 1982).

However, a number of indications suggest that this seemingly straightforward line of reasoning could lead to misleading conclusions. First, in contrast to the gross metabolic ratios presented in Taylor et al. (Taylor et al., 1980), the net metabolic ratios calculated from this earlier study are actually greater than the mass ratios, as they are for most of the data on both walking and running mammals (Figs 10 and 11). Thus, the cost of transporting a unit of added mass during trunk loading in mammals must be more than the unit cost of transporting the original body mass. This change in mass-specific cost violates the fundamental assumption required to use metabolic ratios to deduce the division of stance and swing costs.

Despite the apparent change in the mass-specific transport costs during loading in mammals, the difference between the mammalian metabolic ratios and those found in guinea fowl might still be taken to suggest that the costs of swing are higher in guinea fowl than in the quadrupedal mammals and humans

studied. However, current evidence suggests that the cost of swinging the limbs is substantial in running humans. Modica and Kram provided a mechanical assist to early swing and found a reduction of up to 20% in net energy cost during running (Modica and Kram, 2005). Electromyographic (EMG) evidence suggests substantial swing-phase muscle activity during human running (Andersson et al., 1997; Prilutsky et al., 1998), and Modica and Kram found a reduction of up to 74% in mean EMG amplitude in the swing active rectus femoris muscle with their swing assist device (Modica and Kram, 2005). Two other swing-phase muscles that they measured, the anterior tibialis and the biceps femoris, did not show reduced mean EMG amplitudes, suggesting that they eliminated only a portion of the swing-phase costs. Gottschall and Kram used a swing assist device during human walking in a more complicated experimental design (Gottschall and Kram, 2005) than that used by Modica and Kram during running (Modica and Kram, 2005). They estimated that the cost of swinging the limb is at least 10% of the net cost of walking. However, the cost is likely higher than this because they found that their swing assist device reduced mean EMG amplitude in the iliopsoas and rectus femoris by at most 26% and 52%, respectively, and mean EMG amplitude remained unchanged or increased in two other swing-phase muscles. Substantial swing-phase costs also have been suggested for human walking by a recent study using a model based on pendulum mechanics combined with energetic measurements (Doke et al., 2005). We conclude that the available evidence suggests that swing-phase costs in humans are of similar magnitude to those in guinea fowl, at least during running, and likely during walking as well. Similar swing-phase costs in the presence of very different net metabolic ratios during trunk loading suggests that factors other than the relative cost of swing are important in determining the relation between the increase in load and the increase in metabolic rate.

We suggest that inferring the relative costs of swing and stance from loading studies is not practical because of the complex determinates of the cost of transporting the additional load. To infer the relative stance-phase costs from the increase in metabolic cost during trunk loading, at least the following assumptions need to be made about the muscles that are responsible for the increase in energy use. (1) The muscles would have to operate with the same mechanical advantage in transporting the added load as they do in transporting the normal body mass. However, the diverse set of muscles active in stance act at different joints and have different mechanical advantages in producing force on the ground. Thus, fulfilling this assumption would likely mean that the distribution of energy use among the stance-phase muscles would have to be the same in the loaded and unloaded conditions. (2) The proportion of different fiber types in the additional volume of muscle activated would have to be the same as that found in the volume of muscles used to support the normal body weight. Recruiting faster fibers would presumably increase the cost of weight support. (3) The muscle volume used to perform any additional work due to the increased mass would have to

operate with the same efficiency as the muscle volume performing work during normal locomotion. (4) During loaded walking, a similar proportion of the work done would have to be conserved *via* the inverted pendulum mechanism as is conserved during normal walking. (5) During loaded running, elastic elements in series with the muscles would have to store and release a similar proportion of the total work as they do during unloaded running.

Fulfilling all of these assumptions seems unlikely in many cases. Depending on the direction of the deviations from these assumptions, the fractional increase in energy use due to trunk loading could be more or less than the value predicted from the relative cost of stance and swing during normal locomotion. Considering just the assumption regarding fiber type usage will suffice to illustrate our point. This assumption seems unlikely to be fulfilled, given the typical mixture of fiber types found in the limb muscles of birds and mammals and the known recruitment order of these fiber types. In a task of increasing intensity, slow fibers are expected to be recruited first followed by faster fibers, both within a muscle (Henneman et al., 1965) and probably among muscles with similar function (Sokoloff et al., 1999). Thus, activating an increasing volume of muscle to support the increased body weight would be hypothesized to require increasing recruitment of faster, less economical fiber types. This hypothesis could help explain the increase in the net metabolic ratios with increasing load found in most human walking studies (Fig. 10). The heavier loads would be expected to recruit greater numbers of faster, less economical fibers.

These considerations lead us to the conclusion that the economical load carriage of guinea fowl compared with mammals cannot be attributed with any certainty to differences in the relative costs of stance and swing. This conclusion is supported by the observation that guinea fowl and humans differ substantially in the economy of load-carrying during running (Fig. 10), despite having a similar proportion of their total energy expenditure devoted to swinging the limbs (Marsh et al., 2004; Modica and Kram, 2005). We suspect that the diversity of load-carrying economies found in humans and other mammals is caused by underlying variation in both biomechanics and physiology, which could include variation in the relative cost of swing and stance. However, using trunk loading to partition the costs of swing and stance does not seem practical, given the large amount of variation due to other causes. Sorting out the underlying causes of differences in load-carrying economy will require knowledge of which muscles are responsible for the increased energy use (Ellerby and Marsh, 2006) and improving knowledge of the relations between biomechanics and energy use.

Increases in metabolic rate due to distal limb loading

The large effects of distal limb loading that we measured in guinea fowl are consistent with data on limb loading in mammals, but the effects of speed on the metabolic increment among these species are less clear. Loading the tarsometatarsal segments in guinea fowl with a total mass equivalent to 5% of

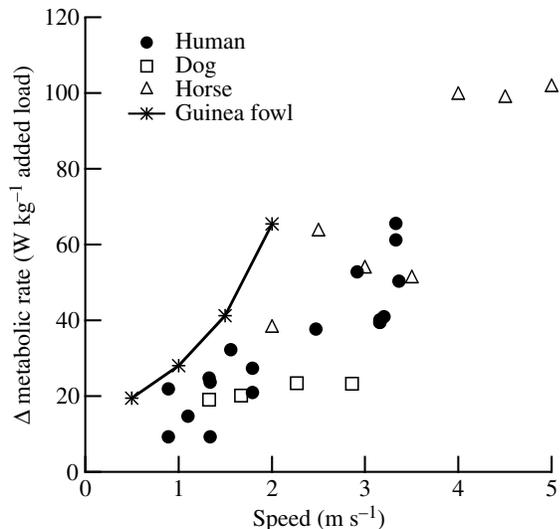


Fig. 12. Increase in metabolic rate due to distal limb loading in walking and running mammals and guinea fowl. The data were calculated by subtracting the loaded metabolic rate from the unloaded metabolic rate and dividing by the mass of the added load. Closed circles, walking and running humans (Soule and Goldman, 1969; Jones et al., 1984; Martin, 1985; Miller and Stamford, 1987; Claremont and Hall, 1988; Bhambhani et al., 1989). Open squares, trotting dogs (Stuedel, 1990a). Open triangles, trotting horses (Wickler et al., 2004). Horse data were calculated from original data provided by S. J. Wickler (personal communication).

body mass increased metabolic rate by an amount comparable to loading the trunk with 23% of body mass. Similar large effects of distal limb loading on metabolic rate have been recorded in humans and two quadrupeds (Martin, 1985; Myers and Stuedel, 1985; Miller and Stamford, 1987; Bhambhani et al., 1989; Stuedel, 1990a; Stuedel, 1990b; Wickler et al., 2004). In guinea fowl, the increment in metabolic cost increases curvilinearly with speed (Fig. 9). The effect of speed on the change in metabolic rate in other animals is difficult to summarize because of large differences among studies in the size of the load and its location on the distal limb, as well as substantial differences in body size among the species studied. One way to collapse the data onto a single plot is to calculate the net added cost of transporting a unit mass of additional limb load (Fig. 12). The data on walking and running humans indicate that the costs of moving a unit mass increases approximately linearly with speed (Fig. 12). However, these data come from different studies using various loads and methods of attaching the load, and thus the exact relation with speed is uncertain. Two quadrupeds, dogs and horses, both show increases with speed in the cost of moving a distal limb load (Fig. 12), but the change with speed in Stuedel's data on dogs (Stuedel, 1990a) is remarkably small.

The comparative data in Fig. 12 and our data on guinea fowl reinforce the idea that the mass of the distal segments of the moving limbs could be an important component of the cost of legged locomotion (Stuedel, 1990b). We do not know the

energy cost of moving the unloaded tarsometatarsal segment in guinea fowl. However, if the cost per mass for moving the combined mass of the two segments (22 g) were similar to the cost of moving the added mass, the metabolic cost of moving this segment would represent approximately 5% of the net metabolic rate during running. The possibility exists that moving the unloaded segment is much less expensive due to energy saving mechanisms that are disrupted by segment loading, but the high cost of swing phase in guinea fowl suggests that this is not the case (Marsh et al., 2004).

Relation of mechanical and metabolic power in distal limb loading

In guinea fowl, the tarsometatarsal segments moved similarly in the unloaded and loaded conditions (Fig. 5). Therefore, the mechanical energy of the segment should have increased by the same ratio as the increase in segment mass, which was about 4.3 times. The actual average increment across all speeds of 4.1 times is close to this predicted value. Because the stride duration was lengthened slightly by distal limb loading, the mechanical power increment averaged over the whole stride, 3.8 times, was less than the increment in mechanical energy.

Loading the distal limb affects stance-phase mechanical energy as well as swing-phase energy. Approximately 40% of the increase in energy occurred during stance and 60% during swing. The significant increase in energy in stance occurs because of the extension of the ankle joint and flexion of the tarsometatarsal-phalangeal joint in late stance, which cause net translation of the tarsometatarsal segment. These joint movements have the effect of accelerating the center of mass of the tarsometatarsal segment forward. Thus, loading the tarsometatarsal segment is predicted to increase energy use by the stance-phase muscles involved in leg extension in late stance as well as the swing-phase muscles (Ellerby and Marsh, 2006). The effect of distal limb loading on stance-phase mechanical work will, of course, depend on the location of the load. The fraction of the segmental acceleration occurring during stance is expected to be higher for more proximal segments and less for more distal segments. In guinea fowl, the distal tarsometatarsus (Fig. 1) is the most distal part of the limb that can be easily loaded and loads on this segment appear to have important influences on stance-phase mechanical work. This location of the load may be analogous to ankle or shank loading in humans (Bhambhani et al., 1989; Royer and Martin, 2005), or loading the dog hindlimb at the level of the metatarsals (Stuedel, 1990a). The loading of the forelimbs of dogs done by Stuedel was more proximal (Stuedel, 1990a). Loads placed on the most distal part of the limb, e.g. the human foot or the hoof of horses (Martin, 1985; Wickler et al., 2004), would be expected to be accelerated almost entirely during swing phase and thus have little effect on stance costs.

Although mechanical energy was measured only for the tarsometatarsal segment, measuring the increase in mechanical energy of this segment due to loading the segment will provide an accurate estimate of the increase in mechanical energy of

the entire body if the other limb segments and the trunk have the same mechanical energy in the loaded and unloaded condition. Studies in humans that have measured the energy of all the limb segments have found that distal limb loading only increases the energy in the loaded segment (Martin, 1985; Royer and Martin, 2005). We did not measure the segmental energy in the other limb segments in this study, but it seems likely that in guinea fowl as well only the energy in the tarsometatarsal segment changed substantially. The trajectories of the proximal end of the tarsometatarsal segment, i.e. the ankle, were similar in the loaded and unloaded conditions at all speeds (Fig. 5). Given that the position of the ankle joint is determined by the combination of hip and knee angles, moving the ankle joint through a similar set of coordinates in loaded and unloaded birds requires the other linked segments of the limb to move similarly under these conditions. If these unloaded segments moved in a similar manner in loaded and unloaded guinea fowl, by necessity their mechanical energies were also similar in loaded and unloaded birds.

Despite our conclusion that the increase in mechanical energy of the tarsometatarsus resulting from its loading is a reasonable estimate of total increase in limb mechanical energy, the approach adopted here cannot discriminate at which joints, or in which muscles, the additional mechanical energy is produced. Changes in the segmental energy of distal segments are due in part to muscles acting directly on the segment, but are also driven by joint reaction forces transferred from adjacent segments (Martin and Cavanagh, 1990; Winter, 1990). Thus, much of the additional mechanical energy of the tarsometatarsus is likely produced by muscles that are distributed throughout the entire limb. Therefore, we would predict that loading the tarsometatarsal segment would cause changes in energy use across many muscles in the leg (Ellerby and Marsh, 2006).

Improving our understanding of the relationship between mechanical and metabolic energetics in distal limb loading will likely benefit from an interaction between more sophisticated biomechanical analyses than those used in the current study and information currently available on the energy use by individual muscles (Ellerby and Marsh, 2006). For example, inverse dynamics analysis can better identify the joints at which mechanical power is produced because it accounts for transfer of energy between adjacent segments (Winter, 1990; Zatsiorsky, 2002). What inverse dynamics studies cannot account for fully is the transfer of energy by two-joint muscles and the effects of co-contraction at joints. However, the distribution of energy use by individual muscles along with EMG data could be used to supplement the inverse dynamics calculations, and aid the implementation of optimization models that are capable of partitioning the mechanical energetics of the limb segments among individual muscles (Anderson and Pandey, 2001; Neptune and Sasaki, 2005).

Given the assumption of equivalent limb trajectories during loaded and unloaded locomotion, the efficiency of performing the extra work due to distal limb loading can be calculated by dividing the increase in mechanical power of the tarsometatarsal

segment by the increase in metabolic rate. The delta efficiencies calculated in this way are apparent mechanical efficiencies and do not necessarily represent muscle efficiencies. The estimated efficiency of producing the extra positive work due to distal limb loading increases with increasing running velocity. At the walking speed of 0.5 m s^{-1} , this measure of efficiency is 11% (Fig. 9). At 1.0 m s^{-1} , which is a transitional speed between gaits (Gatesy, 1999), the efficiency is 18%. When running at 1.5 or 2.0 m s^{-1} , the efficiency is approximately 25%, which approximates the maximum value expected for aerobically functioning muscle. This trend of increasing efficiency with speed has also been found for total joint work during the unloaded swing phase, but the overall efficiencies are lower (J.R. and R.L.M., unpublished).

The high efficiencies of performing the extra positive work during running suggest that the metabolic cost of absorbing work to decelerate the segment at foot-down is not very large. If the cost of absorbing work were substantial, then this cost would have to be removed from the metabolic cost before calculating the efficiency of positive work, which would make the efficiency of the positive work greater than the known efficiency of skeletal muscle. Alternatively, the extra negative work required due to loading could require metabolic energy, but the absorbed work could be returned to do positive work in early stance, thus canceling the cost.

The only other data from which similar calculations of efficiency during distal limb loading can be made are those of Martin (Martin, 1985). Martin reports the segmental energy of the foot during running at 3.33 m s^{-1} in the unloaded condition and when human subjects wore shoes with an added mass of either 0.5 or 1.0 kg distributed equally between the shoes. Martin reports the sum of the absolute values of the positive and negative changes in energy during swing. In human running, almost all the increase and decrease in the segmental energy of the foot occurs during swing, with only a small increase before toe-off (Williams and Cavanagh, 1983). Thus, the positive increments in energy of the foot should be half the values given by Martin, but the values in his table are for a single foot. With these assumptions, the efficiency of moving the extra mass on the foot is approximately 40% under either loading condition. This value clearly exceeds the maximum value expected from skeletal muscle, and some energy saving mechanisms must be used to decrease the metabolic burden of moving the load. One possible explanation of this high delta efficiency of foot loading in human running is the transfer of energy between the limbs (Williams and Cavanagh, 1983). During the flight phase, the decrease in energy of one limb in late swing corresponds in time to the increase in energy in the contralateral limb that has just left the ground. This correspondence suggests that such a transfer could occur but does not prove that it actually does occur. A similar mechanism is not available to guinea fowl running at the speeds used here, because the duty factor is approximately 0.5 at the highest speed, and the negative and positive powers of the contralateral limbs are not in phase.

Conclusions

(1) Fractional increases in metabolic rate during trunk loading in guinea fowl were found to be lower than the values recorded for most mammals. Some data on select groups of humans are similar to the values for guinea fowl. We suggest that the diversity of load-carrying economies in various studies could be caused by a number of underlying biomechanical and physiological factors, and should not be viewed as indicative of the relative costs of swing and stance.

(2) The metabolic cost of distal limb loading in guinea fowl appears to be linked to the increases in the mechanical energy in the loaded segment. The large effect of distal limb loading is consistent with the idea that the mass of the distal segments is an important determinant of the cost of running.

(3) The efficiency of performing the extra positive power to move the loaded segment was approximately 25% at the two highest speeds tested. This value is approximately equal to the maximal value expected for efficiency of skeletal muscle and suggests that either the extra negative work done to decelerate the loaded segment does not require much metabolic energy, or that energy saving mechanisms reduce the total cost of the positive and negative work.

(4) A substantial portion, approximately 40%, of the increase in mechanical energy in the loaded tarsometatarsal segment of guinea fowl occurs during late stance phase. Thus, depending on the location of the load, distal limb loading should not be viewed as influencing only swing-phase costs. Attaching the load to a long segment that undergoes substantial translational acceleration during late stance requires increased stance-phase work as well.

List of symbols

c	distance between the center of mass and the axis of suspension
E_g	instantaneous gravitational potential energy
$E_{K,rot}$	instantaneous rotational kinetic energy
$E_{K,x}, E_{K,y}$	instantaneous vertical, horizontal translational kinetic energy
\dot{E}_{pos}	positive mechanical power of the segment averaged over the whole stride
E_{pos}	sum of the positive increments in segmental energy for the whole stride
E_{tm}	total instantaneous segmental energy
g	acceleration due to gravity
h	height
I	moment of inertia
m	mass
ϕ_{tm}	angle with reference to the horizontal
t	period of the oscillation
\dot{V}_{O_2}	rate of oxygen consumption
v'_x	horizontal velocity referenced to the video field
v_x	horizontal velocity referenced to a fixed point on the treadmill belt
v_y	vertical velocity
ω	angular velocity

This work was supported by NIH grant AR47337 to R.L.M. We are grateful to Karen Bioski and Julia Vasic for their assistance in performing the respirometry experiments and collecting kinematic data. Dr Phillip E. Martin kindly clarified some issues regarding his data (Martin, 1985). Dr Steven J. Wickler provided access to original data, as did Drs Guillaume J. Bastien and Norman C. Heglund, for which we are very grateful.

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