

ENERGETICS AND MECHANICS OF TERRESTRIAL LOCOMOTION

III. ENERGY CHANGES OF THE CENTRE OF MASS AS A FUNCTION OF SPEED AND BODY SIZE IN BIRDS AND MAMMALS

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SUMMARY

This is the third in a series of four papers examining the link between the energetics and mechanics of terrestrial locomotion. It reports measurements of the mechanical work required ($E_{CM, tot}$) to lift and reaccelerate an animal's centre of mass within each step as a function of speed and body size during level, constant average speed locomotion. A force platform was used in this study to measure $E_{CM, tot}$ for small bipeds, quadrupeds and hoppers. We have already published similar data from large animals. The total power required to lift and reaccelerate the centre of mass ($\dot{E}_{CM, tot}$) increased nearly linearly with speed for all the animals. Expressed in mass-specific terms, it was independent of body size and could be expressed by a simple equation:

$$\dot{E}_{CM, tot}/M_b = 0.685 v_g + 0.072$$

where $\dot{E}_{CM, tot}/M_b$ has the units of $W \text{ kg}^{-1}$ and v_g is speed in m s^{-1} .

Walking involves the same pendulum-like mechanism in small animals as has been described in humans and large animals. Also, running, trotting and hopping produce similar curves of $\dot{E}_{CM, tot}$ as a function of time during a stride for both the small and large animals. Galloping, however, appears to be different in small and large animals. In small animals the front legs are used mainly for braking, while the back legs are used to reaccelerate the centre of mass within a stride. In large animals the front and hind legs serve to both brake and reaccelerate the animal; this difference in mechanics is significant in that it does not allow the utilization of elastic energy in the legs of small animals, but does in the legs of large animals.

INTRODUCTION

The first paper in this series demonstrates two very general relationships about energetic cost of terrestrial locomotion in birds and mammals: (1) metabolic power increases nearly linearly with speed over a wide range of speeds; and (2) the cost to move a gram of body mass a given distance decreases as a regular function of in-

creasing body mass (e.g. a 30 g quail uses approximately 13 times as much energy to move each gram of its body a given distance as a 100 kg ostrich or pony). The second paper quantifies the kinetic energy changes of the limbs and body relative to the centre of mass as a function of speed and body mass. It shows that the mechanical power required to maintain these changes in kinetic energy increases as the 1.55 power of speed and is independent of body size.

This third paper considers a second component of the mechanical work required to sustain a constant average speed along the ground: the work required to lift and reaccelerate the centre of mass within a step, $E_{CM, tot}$. Locomotion at a constant average speed consists of a series of cycles (steps) during which the potential and kinetic energy of the centre of mass oscillates as the centre of mass rises, falls, accelerates and decelerates. These oscillations in energy have been measured over a wide range of speeds in man (Fenn, 1930; Elftman, 1940; Cavagna, Saibene & Margaria, 1963, 1964; Cavagna, Thys & Zamboni, 1976); in one step of a cat (Manter, 1938); in one step of a quail (Clark & Alexander, 1975); and in two hops of a wallaby (Alexander & Vernon, 1975). They have been found to constitute an important part of the mechanical work of locomotion in all these studies.

More than five years ago we began studies designed to find out how $\dot{E}_{CM, tot}$ varied as a function of speed and body mass. Our investigation had to be broken into two parts because the tool for measuring $\dot{E}_{CM, tot}$, a force platform, can only be used for a limited size range of animals. The first part of the study was carried out using a force platform that had originally been built for humans in Milan, Italy. It was suitable for studies of animals ranging in body mass from 3 to 100 kg. We studied $\dot{E}_{CM, tot}$ as a function of speed for a diversity of bipeds, quadrupeds and hoppers that fell within this size range (Cavagna, Heglund & Taylor, 1977). Then we designed and built a force platform that was suitable for small animals ranging in body mass from 30 g to 3 kg. This paper reports the experiments relating $\dot{E}_{CM, tot}$ and speed for small bipeds, quadrupeds and hoppers. We then utilize the data for $\dot{E}_{CM, tot}$ as a function of speed for both the small animals and the large animals to find out how it varies as a function of body mass.

MATERIALS AND METHODS

Experimental approach

We utilized two force platforms (one for animals greater than 3 kg and one for animals less than 3 kg) to quantify the vertical displacement and the horizontal and vertical speed changes of the animal's centre of mass as it moved along the ground at a constant average speed. The force platform measured the force exerted on the ground and resolved it into vertical and horizontal components. These forces were integrated to obtain horizontal and vertical velocities. The forces and velocities were recorded on a strip chart recorder. The velocity records were used to decide whether a particular experiment was acceptable for analysis of the energy changes of the centre of mass; we included only experiments where the animals moved at a constant average speed across the platform. Our criteria for inclusion of an experiment were: (1) records included one or more complete strides; (2) the sum of the increases in velocity (as measured by the integrators) was within 25% of the sum of the decreases

in velocity in both the horizontal and vertical directions for an integral number of strides; and (3) no drift in the integrators during the period of analysis. For a typical chipmunk stride at 2.1 m s^{-1} , our 25% limit amounted to a forward speed change of less than 1.5% of the average forward speed.

For experiments that met our criteria, we carried out a second integration of the vertical forces to give the vertical displacement of the centre of mass. Then kinetic and gravitational energy changes of the centre of mass within a stride were calculated from the velocities and the displacement. Cavagna (1975) has described this technique in detail.

Theoretically, it might be possible to calculate the displacements and the speed changes of the centre of mass using the film analysis technique described in the previous paper. Practically, however, these displacements and speed changes were too small to be resolved accurately with the filming technique. For example, the centre of mass of a 170 g quail running at 2.6 m s^{-1} typically went up and down only 7 mm and decelerated (and reaccelerated) only 0.07 m s^{-1} within each step.

The mechanical work required to lift and reaccelerate the centre of mass was first measured as a function of speed of locomotion for individual animals. Then we used the equations relating the work necessary to accelerate and lift the centre of mass and speed to develop an equation which described how this work changed with body mass. Finally, we compared the equations for metabolic energy consumed with the work required to sustain a constant average speed of the centre of mass.

Animals

Two species of small bipedal runners, two species of small quadrupedal runners and two species of small bipedal hoppers were trained to run across the small force platform while we measured mechanical energy changes of their centre of mass. Measurements from two large bipedal runners, three large quadrupedal runners and two large bipedal hoppers had already been obtained on the large force plate, and these data have been reported (Cavagna *et al.* 1977).

We selected species in this study for which metabolic rate had been measured as a function of speed (see the first paper of this series) and which extended the range of body mass as much as was feasible. The bipedal runners included two 42–44 g Chinese painted quail (*Excalfactoria chinensis*) and three 150–180 g bobwhite quail (*Colinus virginianus*). Measurements had been made on the large plate for turkeys, rhea and humans, giving us a 2000-fold range in body mass for bipedal runners. The quadrupedal runners included two 80–100 g chipmunks (*Tamias striatus*) and one 190 g ground squirrel (*Spermophilus tridecemlineatus*). Measurements had been made on the large force plate for monkeys, dogs and ram, giving us a 1600-fold range in body mass for quadrupedal runners. The bipedal hoppers included one 37 g kangaroo rat (*Dipodomys merriami*) and three 100–140 g kangaroo rats (*Dipodomys spectabilis*). Measurements had been made on the large force plate for spring hares and kangaroos, giving us a size range 600-fold for bipedal hoppers.

Force measurement

In order to obtain measurements from small animals we constructed a smaller force platform suitable for measurements from animals ranging in body mass from 30 g to 3 kg. The small platform consisted of twelve mechanically distinct plates placed end to end in the middle of an 11 m runway. Each plate consisted of an aluminium honeycomb-panel surface (25 × 25 cm) with a sensing element at each corner. Each sensing element consisted of adjacent spring blades, one horizontal and one vertical, that were instrumented with metal-foil strain-gauges. The horizontally oriented spring blade was sensitive only to the vertical forces and the vertically oriented spring blade was sensitive only to the horizontal forces. Cross talk between the vertical and horizontal outputs of the force plate was less than 5% in the worst case. The output of any particular plate was independent of where on the plate surface the force was exerted to within 3%. The output of the platform was linear to within 1.5% over the range of forces measured in these experiments. The natural frequency of oscillation of an unloaded plate was 170 Hz. The design of this force platform has been described in detail elsewhere (Heglund, 1979, 1981).

Velocity of the centre of mass

The horizontal force, and the vertical force minus the body weight, were each integrated (using an LM 208 op-amp with a 0.3 s R-C constant) to obtain continuous recordings of the velocity changes of the centre of mass. These recordings were entered directly into a microcomputer at 2 ms intervals using a 12-bit analog-digital converter. The remainder of these procedures were carried out by the microcomputer; complete schematics of the electronics and listings of the programs utilized in this analysis have been given elsewhere (Heglund, 1979).

In order to calculate the absolute vertical and horizontal velocity of the centre of mass, the constants of integration have to be evaluated. The integration constant for the vertical velocity was taken to be zero over an integral number of strides, that is, we assume that the height of the centre of mass was the same at the beginning and end of the strides that were analysed. The integration constant for the horizontal velocity is the average running speed during the period of integration. The average speed was measured by placing two photocells along the path of the force platform; the first photocell turned the integrators on and the second photocell turned the integrators off. The computer then calculated the integration constant (average speed) from the distance between the photocells and the time the integrators were on. The system was calibrated daily for each animal.

Kinetic and gravitational potential energy of the centre of mass

The kinetic energy due to the horizontal component of the velocity of the centre of mass (E_H) was calculated as a function of time ($KE = \frac{1}{2}M_b \cdot v^2$, where v is the horizontal velocity of the centre of mass). The vertical velocity of the centre of mass was integrated to obtain the vertical displacement of the centre of mass as a function of time. Multiplying the vertical displacement by the animal's body mass and the acceleration of gravity ($\Delta PE = M_b g \Delta h$) gave the gravitational energy changes of the centre of mass as a function of time. The instantaneous sum of the changes in potential

energy and the kinetic energy due to the vertical component of the velocity of the centre of mass gives the total changes in energy due to vertical position or movements of the centre of mass (ΔE_V).

Total energy of the centre of mass, $E_{CM, tot}$

The total energy of the centre of mass, $E_{CM, tot}$, was calculated as a function of time by summing the kinetic and gravitational potential energies of the centre of mass at the 2 ms intervals.

The mechanical power required to maintain potential and kinetic energy of the centre of mass constant over a stride, $\dot{E}_{CM, tot}$

The average rate of increase in the total energy of the centre of mass, $\dot{E}_{CM, tot}$, was calculated by summing the increments in the $E_{CM, tot}$ curve over an integral number of strides and dividing by the time interval of those strides. This power had to be supplied by the muscles and tendons of the animal.

$\dot{E}_{CM, tot}$ as a function of speed

The procedure outlined above was repeated for 7–38 speeds in each animal. The function relating $\dot{E}_{CM, tot}$ to speed was then calculated by linear regression analysis.

$\dot{E}_{CM, tot}$ as a function of body size

We used the equations relating $\dot{E}_{CM, tot}$ to speed for the individual animals from this and the previous study (Cavagna *et al.* 1977) to develop an equation relating $\dot{E}_{CM, tot}$ to body mass.

RESULTS

Force, velocity and energy of centre of mass within a step

Walk. The small quails (30 and 200 g) utilized the same walking mechanism as we had observed in larger animals (Cavagna *et al.* 1977) and humans (Cavagna *et al.* 1976). Fig. 1 shows force, velocity and energy records for a typical walking step of the quail. The changes in gravitational potential energy and kinetic energy due to the forward velocity of the animal are out of phase. Thus the decrease in kinetic energy that occurs as the animal slows during one part of the step is stored in gravitational potential energy as the centre of mass rises. This stored potential energy is recovered subsequently in the step as the animal reaccelerates and the centre of mass falls. This energy-saving mechanism is similar to an inverted pendulum or an egg rolling end over end.

Fig. 2 gives a quantitative measure of the energy savings resulting from this pendulum mechanism. As much as 75% of the energy changes that would have occurred had there been no transfer were recovered by this pendulum mechanism. Percentage recovery was calculated using the following equation:

$$\% \text{ recovery} = \frac{(\Sigma + \Delta E_H) + (\Sigma + \Delta E_V) - (\Sigma + \Delta E_{CM, tot})}{(\Sigma + \Delta E_H) + (\Sigma + \Delta E_V)} \times 100 \quad (1)$$

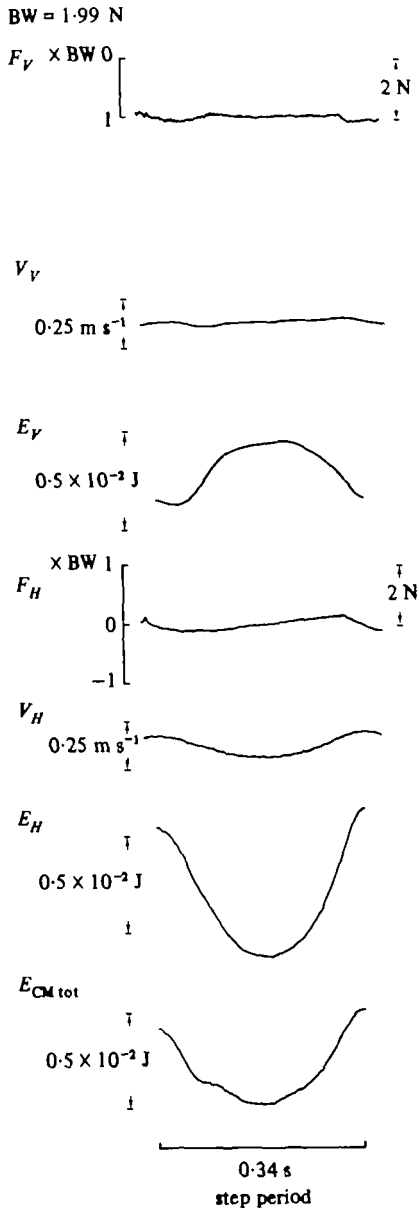


Fig. 1. *Walk*. One step of a 203 g (body weight = 1.99 N) bobwhite quail walking at 0.25 m s^{-1} is analysed according to the procedure outlined in the text. The top curve, F_V , is the vertical force exerted by the animal on the force platform. The second curve is the vertical velocity change of the centre of mass, V_V , obtained by analog integration of the vertical force minus the animal's body weight. The third curve, E_V , is the sum of the kinetic energy of the centre of mass due to V_V plus the changes in potential energy of the centre of mass; the potential energy changes are calculated by integrating the vertical velocity. The fourth curve, F_H , is the forward-aft horizontal force exerted by the animal on the force platform. The fifth curve, V_H , is the horizontal velocity change of the centre of mass, obtained by analogically integrating the horizontal force. The sixth curve, E_H , is the kinetic energy of the centre of mass due to its horizontal velocity, calculated from V_H and the average forward speed of the animal (as measured by photocells, see text). The bottom curve, $E_{\text{CM, tot}}$ is the total energy change of the centre of mass of the quail, obtained by summing at each instant the E_V and E_H curves. Note that since the changes in E_V and E_H are out of phase, they tend to cancel when they are summed, resulting in smaller changes in $E_{\text{CM, tot}}$. $\dot{E}_{\text{CM, tot}}$ is calculated by summing all the increments in the E_{tot} curve and dividing by the step period; the increments in the E_{tot} curve are due to work done by the muscles and tendons.

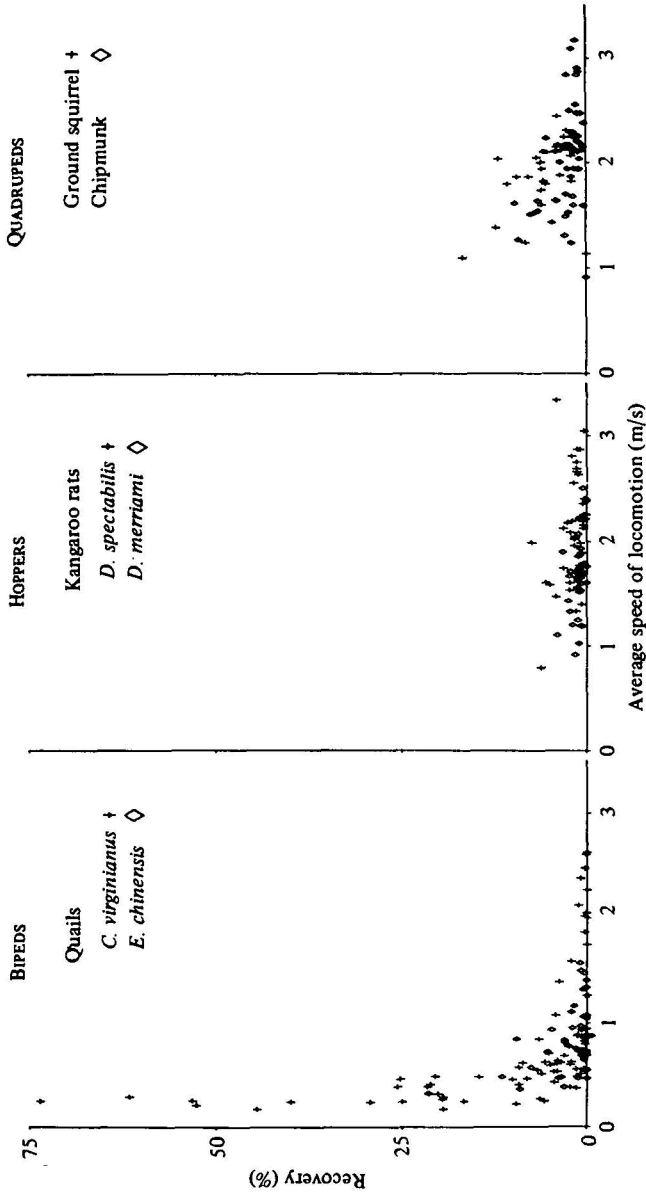


Fig. 2. Percentage recovery as a function of average speed of locomotion for small bipeds, hoppers and quadrupeds. Percentage recovery is the amount of energy that is transferred between the potential energy of the centre of mass and the kinetic energy due to the forward velocity of the centre of mass, expressed as a percentage of the energy changes that would have occurred had there been no transfer. Percentage recovery was high in walking quail, nearly zero in running quail and hopping kangaroo rats, and small in galloping ground squirrel and chipmunk.

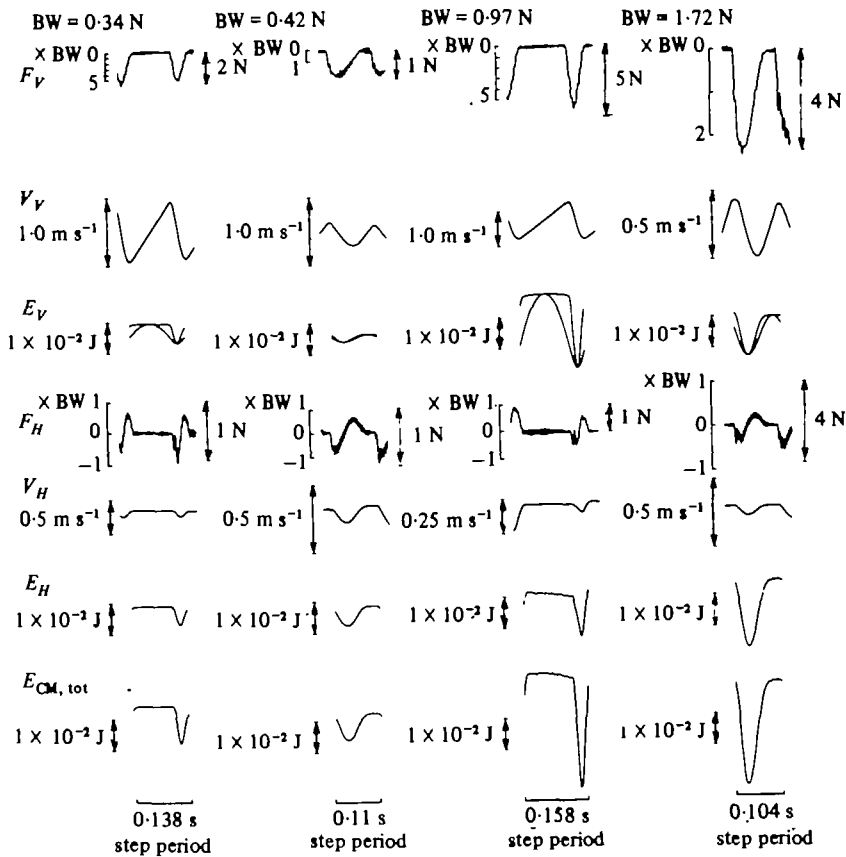


Fig. 3. Typical force, velocity and energy curves for the run or hop gait for small bipeds. The left column is one hop of a 35 g (body weight = 0.34 N) kangaroo rat hopping at 1.76 m s⁻¹; the second column is one step of a 43 g (body weight = 0.42 N) painted quail running at 1.04 m s⁻¹; the third column is one hop of a 99 g (body weight = 0.97 N) kangaroo rat hopping at 2.12 m s⁻¹; and the right column is one step of a 176 g (body weight = 1.72 N) bobwhite quail running at 1.75 m s⁻¹. The top row, F_v , is the vertical component of the resultant force exerted by the animal on the force platform; the peak vertical force was about 5–6 times body weight for the hopper, and 2–3 times body weight for the runners. The second row, V_v , is the vertical velocity of the centre of mass of the animal; this velocity goes from negative to positive as the animal's centre of mass goes up and down. The slope of the V_v curve during free fall (when the $F_v = 0$) is equal to the acceleration of gravity, 9.8 m s⁻². The third row, E_v , comprises two curves: the lower curve is the gravitational potential energy of the centre of mass; the upper curve is the sum of the gravitational potential energy of the centre of mass plus the kinetic energy of the centre of mass due to its vertical velocity. The two curves are equal twice during each stride: when the vertical velocity is zero because the centre of mass has just stopped going up before starting to go down; and when the vertical velocity is zero because the centre of mass has just stopped going down before starting back up. The top curve can be thought of as the total vertical energy of the centre of mass; note that it is constant during the aerial phase because gravitational potential energy is converted to kinetic energy during free fall. The fourth row, F_h , is the forward–aft horizontal component of the resultant force exerted by the animal on the force platform. There is initially a decelerating force as the animal lands with its leg(s) extended in front; this is followed immediately by an accelerating force as it subsequently takes off. The fifth row, V_h , is the horizontal velocity changes of the centre of mass; the horizontal velocity is constant during the aerial phase (air resistance is neglected), decreases upon landing and increases again during take-off. The sixth row, E_h , is the kinetic energy of the centre of mass due to the horizontal velocity changes. The seventh row, $E_{CM, tot}$, is the total energy of the centre of mass of the animal as

where $\Sigma + \Delta E_H$ is the sum of the positive increments in energy in the horizontal direction, $\Sigma + \Delta E_V$ is the sum of the positive increments in energy in the vertical direction and $\Sigma + \Delta E_{CM, tot}$ is the sum of the positive increments in total energy of the centre of mass that occur during a step. Percentage recovery in both quail falls rapidly with increasing speed to near zero at 1 m s^{-1} . We were unable to train the chipmunk and ground squirrel to walk at the very low speeds necessary for the small animals to have an appreciable transfer of energy.

Run or hop. The small bipeds (quails) and hoppers (kangaroo rats) utilized a run or hop gait at speeds above 1 m s^{-1} similar to the gaits observed in larger animals (Cavagna *et al.* 1977) and humans (Cavagna *et al.* 1976). Fig. 3 gives force, velocity and energy records for a typical run or hop step for a 35 g kangaroo rat, a 43 g quail, a 99 g kangaroo rat and a 176 g quail. The changes in gravitational potential energy and kinetic energy due to the forward velocity of the animal are in phase. Thus the decrease in kinetic energy as the animal slows within a stride occurs almost simultaneously with the decrease in gravitational potential energy as the animal's centre of mass falls and little exchange can occur (Fig. 2).

The shape of mechanical energy curves are similar for a run, trot and hop, regardless of size of the animal or its mode of locomotion. The magnitude of the energy changes and the stride frequency, however, do change with body size. For example, $E_{CM, tot}$ during the step of a human running at a moderate speed is 80 J, and about 2.5 steps are taken each second. $E_{CM, tot}$ for a step of a bobwhite quail running at a moderate speed, by contrast, is only $4.5 \text{ J} \times 10^{-2}$ and the quail takes 9.5 steps each second. We were unable to train the chipmunk and ground squirrel to move across the platform slowly enough to obtain good records for the trotting gait.

Gallop. The small quadrupeds (chipmunk and ground squirrel) galloped across the force platform over a wide range of speeds ($1-3 \text{ m s}^{-1}$). The force, velocity and energy tracings obtained from these animals during a gallop (Fig. 4) are different from those we obtained from large animals (Cavagna *et al.* 1977). In each stride, the front legs decelerate the animal causing its kinetic energy to fall, and the rear legs reaccelerate the animal, causing its kinetic energy to increase. In the larger animals, both front and back legs decelerated and immediately reaccelerated the animal. Also, there was a significant transfer between gravitational potential energy and kinetic energy during the low-speed gallops of the larger animals, but not in the chipmunk and ground squirrel (Fig. 2).

Energy changes of the centre of mass as a function of speed

Mass specific powers (W kg^{-1}) are plotted as a function of average speed in Fig. 5. Mass specific energy changes per unit time obtained from the vertical forces, \dot{E}_V/M_b , and horizontal forces, \dot{E}_H/M_b , and the total energy changes of the centre of mass,

a function of time; it is the instantaneous sum of the E_V and E_H curves. Note that since the E_V and E_H curves are in phase, there is little opportunity for energy transfer between them, and consequently the percentage recovery is very low in these gaits, as shown in Fig. 2. The sum of the increases in the $E_{CM, tot}$ curve divided by the step period gives $\dot{E}_{CM, tot}$, the average mechanical power required to maintain the observed oscillations in energy of the centre of mass.

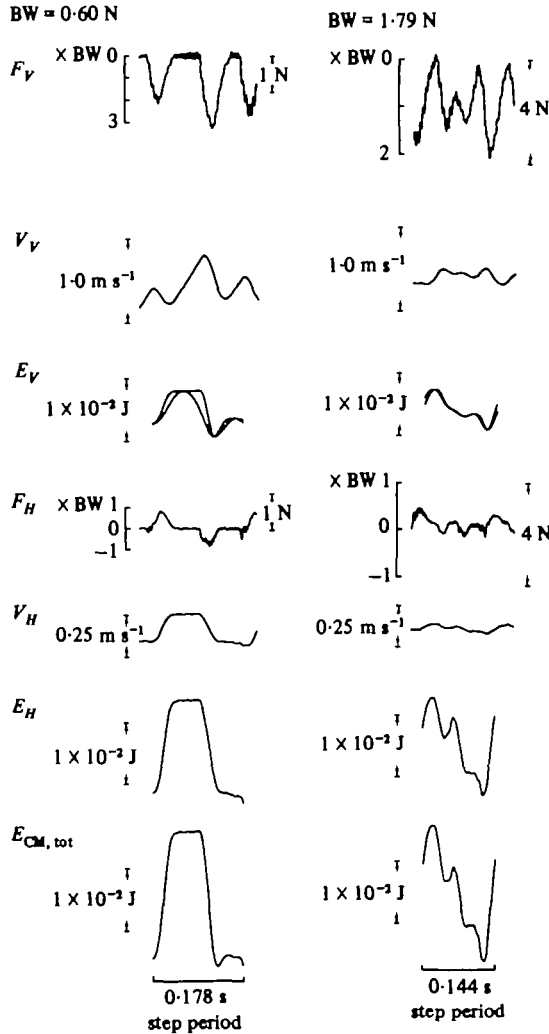


Fig. 4. Typical force, velocity and energy curves for one stride of a 61 g chipmunk (body weight = 0.6 N) galloping at 1.43 m s^{-1} (left column) and a 182 g ground squirrel (body weight = 1.79 N) galloping at 1.6 m s^{-1} (right column). Indications are the same as for Figs 1 and 3. The $E_{\text{CM, tot}}$ curve for the chipmunk reproducibly showed two aerial phases; one occurring at the highest $E_{\text{CM, tot}}$ achieved during the stride, and the other occurring at near the lowest. In the stride illustrated, the galloping chipmunk took off with a large upward and forward push of the rear legs (note the large increase in F_V and E_H) resulting in the large increase in $E_{\text{CM, tot}}$. $E_{\text{CM, tot}}$ remains constant during the aerial phase, then decreases sharply when the animal lands on its front legs; this energy is absorbed in the muscles and tendons of the body. The front legs then give only a small forward push, resulting in only a slight increase in $E_{\text{CM, tot}}$, before the next aerial phase. Most of the energy absorbed in the front legs therefore must be dissipated as heat and then generated *de novo* by the rear legs as the cycle is repeated. However, if any of the energy absorbed by the animal during the large decrease in $E_{\text{CM, tot}}$ is stored in the muscles and tendons of the trunk, the animal may be able to recover this elastic strain energy as useful work during the subsequent simultaneous push of the rear legs and extension of the spine as the cycle is repeated. Careful analysis of the ground squirrel tracings shows that a similar situation exists; namely, primarily energy absorption by the front legs with very little positive work done by them as they push off, followed by an aerial phase, a small amount of energy absorption by the rear legs, and then a large amount of work done. The correspondence between the energy curves and footfall patterns of the animals was determined using film analysis.

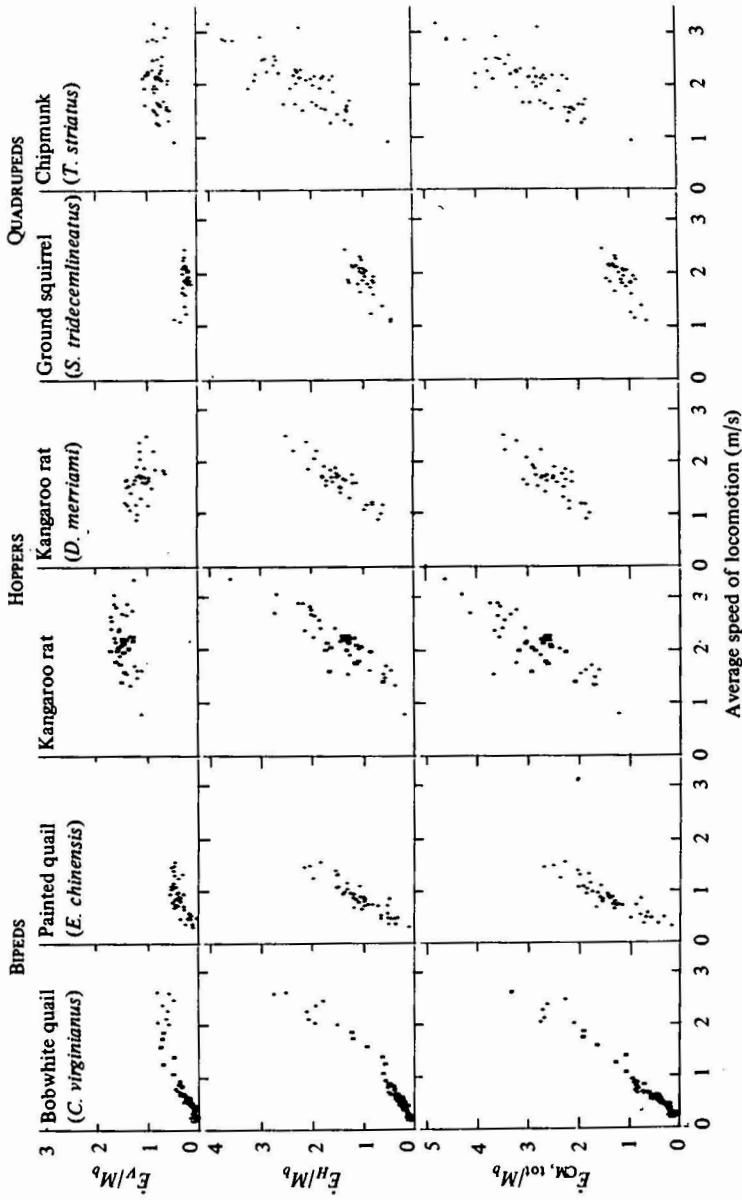


Fig. 5. The mass-specific mechanical power required to maintain the oscillations in energy of the centre of mass as a function of speed in six species of small animals. The top row, \dot{E}_v/M_b , is the average power required to maintain the oscillations in gravitational potential energy of the centre of mass. The second row, \dot{E}_H/M_b , is the average power required to maintain the oscillations in kinetic energy due to horizontal velocity changes of the centre of mass within a stride. The bottom row, $\dot{E}_{CM,tot}/M_b$, is the average power required to maintain the oscillations in the total kinetic and potential energy of the centre of mass. These values were calculated by summing the increments in the E_v , E_H and E_{tot} (Figs. 1, 3, 4) over an integral number of strides and dividing by the duration of the stride and body mass.

Table. 1. The equations: $\dot{E}_{CM, tot}/M_b = \text{slope} \cdot v_0 + Y\text{-intercept}$ represents the sum of the increments in the total energy of the centre of mass per unit time over an integral number of strides ($\dot{E}_{CM, tot}$) divided by body mass (kg) as a function of speed (in m s^{-1}) for 15 species ranging in body mass from 35 g to 73 kg. The slope and intercept values were calculated by linear regression of the data in Fig. 5, or were taken from the literature. Average values were calculated from the slope and intercept values presented in the table.

Animal	N	M_b (kg)	$\dot{E}_{CM, tot}/M_b =$ slope $\cdot v_0 + Y\text{-intercept}$		r^2	Speed ranges	
			Slope ($\text{J m}^{-1} \text{kg}^{-1}$)	Y-intercept (W kg^{-1})		v_0 min (m s^{-1})	v_0 max (m s^{-1})
Kangaroo rat	1	0.035	0.947	0.951	0.64	0.91	2.5
Painted quail	2	0.042	1.68	-0.053	0.84	0.32	1.57
Chipmunk	2	0.098	1.28	0.235	0.64	0.91	3.16
Kangaroo rat	3	0.112	1.32	0.007	0.81	0.79	3.33
Bobwhite	4	0.175	1.57	-0.372	0.80	0.17	2.63
Ground squirrel	1	0.186	0.470	0.21	0.54	1.1	2.45
Spring hare*	1	2.5	0.392	0.282	0.85	1.9	6.67
Monkey*	2	3.6	0.513	-2.03	—	1.4	6.11
Dog†	1	5.0	0.279	-0.7	—	1.0	7.2
Turkey*	2	7.0	0.398	-0.450	0.91	1.9	5.0
Dog†	1	17.0	0.243	0.0	—	1.5	9.4
Kangaroo*	2	20.5	0.438	0.804	0.95	2.1	7.78
Rhea*	1	22.5	0.279	0.422	0.82	1.8	5.0
Human‡	10	70	0.330	0.657	0.94	1.4	8.89
Ram*	2	73	0.136	1.112	0.39	1.1	3.47
Average			0.685	0.072			
Standard deviation			± 0.525	± 0.777			

* Data from Cavagna *et al.* 1977.

† Data recalculated from Cavagna *et al.* 1977 to include all gaits in each animal.

‡ Data from Cavagna *et al.* 1976.

$\dot{E}_{CM, tot}/M_b$, are plotted separately in Fig. 5. The divisions into vertical and horizontal power terms are useful in evaluating the relative amount of energy required to account for the height and speed changes of the centre of mass.

During a walk (walks were obtained only for the two quails), the vertical and horizontal power increased with increasing walking speed and are approximately equal in magnitude. This allows the relatively large transfer between kinetic and gravitational potential energy observed in Fig. 2. This is similar to what was observed in large animals and man during a walk (Cavagna *et al.* 1977; Cavagna *et al.* 1976). Because the details of the transfer have been discussed in these papers, we will not repeat them here.

During a run or hop and a gallop, the vertical power remained nearly constant over the entire range of speed, while the horizontal power increased. The magnitude of the vertical power was much greater in both the large and small hopping animals than in the running and galloping animals (Cavagna *et al.* 1977).

Total power required to lift and reaccelerate the centre of mass ($\dot{E}_{CM, tot}$) increased nearly linearly with speed for all of the animals in this study (Fig. 5), as it had for the larger animals in our previous study (Cavagna *et al.* 1977). The linear increase in tot

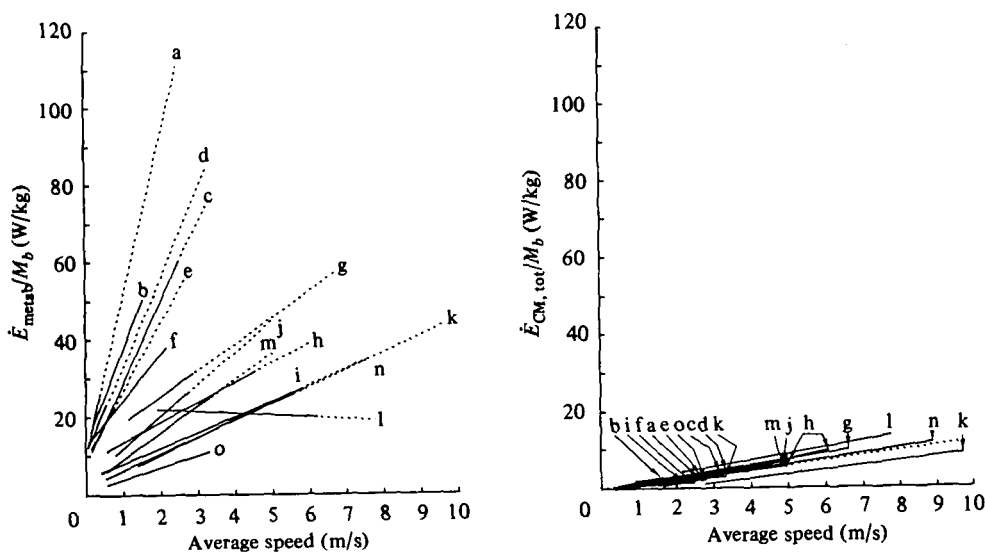


Fig. 6. Mass-specific metabolic rate, $\dot{E}_{\text{metab}}/M_b$, and mass-specific rate at which mechanical energy is required to reaccelerate and lift the centre of mass, $\dot{E}_{\text{CM,tot}}/M_b$ are plotted as a function of speed. $\dot{E}_{\text{metab}}/M_b$ decreases dramatically with increasing body size while $\dot{E}_{\text{CM,tot}}/M_b$ does not change in any regular way with body size. The dotted extensions of the $\dot{E}_{\text{metab}}/M_b$ lines refer to extrapolated data; the dotted $\dot{E}_{\text{CM,tot}}$ line is the average line as given in Equation 3 in the text. The animals are: a, 35 g Merriam's kangaroo rat; b, 42 g painted quail; c, 90 g chipmunk; d, 105 g kangaroo rat; e, 178 g bobwhite quail; f, 190 g ground squirrel; g, 2.5 kg spring hare; h, 3.6 kg monkey; i, 5.0 kg dog; j, 7.0 kg turkey; k, 17.5 kg dog; l, 20.5 kg kangaroo; m, 22.5 kg rhea; n, 70 kg human; o, 75 kg ram. Human data from Cavagna & Kaneko (1977).

power with speed makes it possible to express the relationship between total power and speed for each animal by a linear equation of the form:

$$\dot{E}_{\text{CM,tot}}/M_b = \text{slope} \cdot \text{speed} + \text{Y-intercept} \quad (2)$$

In Table 1 we have included the values for slope and Y-intercept (calculated using the method of least squares) together with the speed range over which measurements were made and the coefficient of determination for the linear regression (r^2) for both the small animals in this study and the large animals in our previous study (Cavagna *et al.* 1977).

Energetic cost for lifting and reaccelerating the centre of mass as a function of body mass

There are two components of the mechanical power expended to lift and reaccelerate the centre of mass (as there were with oxygen consumption): an extrapolated zero speed power (the Y-intercept) and an incremental power (the slope) (see equation 2). Both terms are constant for an individual animal because the relationship between $\dot{E}_{\text{CM,tot}}/M_b$ and speed is linear. Both terms are independent of body mass because the slope of the function relating each term of the equation to body mass is not significantly different from zero. Both the metabolic energy consumed ($\dot{E}_{\text{metab}}/M_b$) and $\dot{E}_{\text{CM,tot}}/M_b$ are plotted as a function of speed in Fig. 6. This figure clearly demon-

strates that the relationship between $\dot{E}_{\text{metab}}/M_b$ and speed changes dramatically with body size, while the relationship between $\dot{E}_{\text{CM, tot}}/M_b$ and speed does not.

We have obtained a single equation relating $\dot{E}_{\text{CM, tot}}/M_b$ and speed for all the animals by averaging the values for the Y-intercept and slope:

$$\dot{E}_{\text{CM, tot}}/M_b = 0.685 \cdot v_g + 0.072 \quad (3)$$

where $\dot{E}_{\text{CM, tot}}/M_b$ has the units W kg^{-1} and v_g is in m s^{-1} . The standard deviations for the terms are given in Table 1.

DISCUSSION

Force, velocity and energy of the centre of mass within a step

Our data show that quail, like some large animals, utilize a pendulum-like energy conservation mechanism during a walk. Up to 70% of the energy is exchanged between kinetic and gravitational potential energy within a step. This is the same magnitude of exchange that was found in humans (Cavagna *et al.* 1976) and large animals (Cavagna *et al.* 1977). However, it was extremely difficult to obtain good walking records from small animals, and we were never able to obtain them from the chipmunks and ground squirrels. At slow speeds, small animals normally moved in a series of short bursts, alternating with stops, rather than at a constant speed.

During a run or hop small animals exhibit force and velocity patterns similar to those we observed for large animals. However, one major difference exists. At high speeds dogs, kangaroos and humans stored energy as elastic strain energy in the muscles and tendons when they landed and recovered some of this energy when they took off. This was demonstrated because the magnitude of energy changes of the centre of mass was greater than the metabolic energy consumed by the muscles (assuming muscles convert energy stored in carbohydrates, fats and proteins into work at a 25% efficiency). In the small animals, however, one could account for all of $\dot{E}_{\text{CM, tot}}/M_b$ with muscular efficiencies of less than 25%. Recent studies by Biewener, Alexander & Heglund (1981) show that the tendons of small kangaroo rats are relatively thicker than those of large kangaroos, and are too stiff to store large amounts of elastic energy. It seems possible, therefore, that large animals are able to utilize an elastic storage mechanism during a run or hop, but that small animals are not. This matter certainly merits more investigation.

The gallop of the small quadrupeds was quite different from the gallop of the large quadrupeds (Cavagna *et al.* 1977). The small animals landed on their front legs, decelerating the body, and then, after an interval (aerial phase), reaccelerated their body with their hind legs. In the larger animals, both front and hind limbs alternately decelerated and then reaccelerated the body during a stride. This means that elastic storage and recovery within the tendons and muscles of the limb would be possible for large animals but not for small animals. However, small animals did exhibit enormous spinal flexion during a gallop, and it might be possible for them to store energy elastically in the muscles and tendons of the back as the animal landed on its front limbs which could be recovered as it pushed off from its hind limbs. In addition, the large animals were capable of alternately storing and recovering significant

amounts of forward kinetic energy in gravitational potential energy at slow galloping speeds. Small animals do not appear to be able to utilize this energy-saving mechanism in a gallop.

Energetic cost for lifting and reaccelerating the centre of mass as a function of speed and body mass

$\dot{E}_{CM, tot}$ like \dot{E}_{metab} , increases nearly linearly with speed. Thus, $\dot{E}_{CM, tot}$ might provide an explanation of the linear increase in \dot{E}_{metab} for individual animals if it were the major component of mechanical work performed by the animal's muscles. However, at the highest speeds achieved by the large animals, the rate at which muscles and tendons must supply energy to accelerate the limbs and body relative to the centre of mass, $\dot{E}'_{KE, tot}$ becomes equal to or greater than $\dot{E}_{CM, tot}$ and cannot be ignored (see Fedak, Heglund & Taylor, 1982). For this reason, consideration of the explanation of the linear increase in \dot{E}_{metab} is left to the following paper when total mechanical energy is calculated. The relationship between $\dot{E}_{CM, tot}$ as a function of speed is nearly independent of body size as predicted by Alexander's mathematical models of running (Alexander, 1977; Alexander, Jayes & Ker, 1980). The increase in amplitude of the oscillations in energy of the centre of mass during a step with increasing body size appears to be nearly exactly compensated by a decrease in step frequency. Thus $\dot{E}_{CM, tot}/M_b$ does not help to explain the 10 to 15-fold changes in \dot{E}_{metab}/M_b with body size observed in the first paper of this series.

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