ENERGETICS OF BIPEDAL RUNNING

II. LIMB DESIGN AND RUNNING MECHANICS

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Summary

Compared with quadrupeds, bipedal runners of the same weight have longer legs, take longer steps and can presumably use slower, more economical muscle fibers. One might predict that bipedal running is less expensive, but it is not. We hypothesized that bipeds recruit a larger volume of muscle to support their weight, eliminating the potential economy of longer legs and slower steps. To test our hypothesis, we calculated the relative volume of muscle needed to support body weight over a stride in small dogs (*Canis familiaris*) and wild turkeys (*Meleagris gallopavo*) of the same weight. First, we confirmed that turkeys and dogs use approximately the same amount of energy to run at the same speed, and found that turkeys take 1.8-fold longer steps. Higher muscle forces and/or longer muscle fibers would require a greater volume of active muscle, since muscle volume is proportional to the product of force and fascicle length. We measured both mean fascicle length and mean mechanical advantage for limb extensor muscles. Turkeys generated approximately the same total muscle force to support their weight during running and used muscle fascicles that are on average 2.1 times as long as in dogs, thus requiring a 2.5-fold greater active muscle volume. The greater volume appears to offset the economy of slower rates of force generation, supporting our hypothesis and providing a simple explanation for why it costs the same to run on two and four legs.

Key words: locomotion, energetics, muscle, dog, *Canis familiaris*, turkey, *Meleagris gallopavo*.

Introduction

Animals use more metabolic energy the faster they run and, on a mass-specific basis, small animals use more energy than do larger ones (Taylor *et al.* 1970). It has been hypothesized that the differences in the energy cost of running that occur with speed and body size result from the increased energy cost of generating muscular force with faster muscle fibers (Taylor *et al.* 1980; Heglund *et al.* 1982; Taylor, 1985; Kram and Taylor, 1990; Rome, 1992). Among quadrupeds and small bipedal hoppers, the energy cost of locomotion decreases in proportion to the time available to generate force, measured as the time for which the foot is in contact with the ground (Kram and Taylor, 1990). Bipedal runners have longer legs, longer times available to generate force with each step and should presumably be able to use slower, more economical muscle fibers than quadrupeds (Roberts *et al.* 1998), yet their energy consumption is the same (Fedak and Seeherman, 1979; Roberts *et al.* 1998). In the present study, we seek to determine whether differences in the volume of muscle required to generate force might explain why bipedal runners use more energy for a given rate of force generation.

The rate at which a running animal's muscles consume metabolic energy is determined by the total volume of muscle that must be active to support the body and maintain movement and by the rate at which a unit volume of muscle uses energy. Experiments in which animals were trained to carry weights while running suggest that much of the active muscle acts to provide support for the body. When rats, dogs, humans and horses run with weighted backpacks, their energy consumption increases in direct proportion to the supported load (Taylor *et al.* 1980). Up to a load equivalent to 27 % of body mass, stride frequency and time of foot contact do not change, but the mean force that must be produced against the ground increases in direct proportion to the load. Glycogen depletion studies in rats show that the cross-sectional area of muscle showing glycogen loss also increases in direct proportion to the supported load (Armstrong and Taylor, 1982), indicating that the increase in energy consumption with loading results from an increase in active muscle volume to provide more force.

The muscle force that a running animal must produce to provide support is determined not only by its body weight but also by the design of its limbs. Differences in the mechanical advantage with which limb muscles operate through the

skeletal lever system result in large differences in the muscular force required to support the body (Gray, 1968; Smith and Savage, 1956). Biewener (1989) has demonstrated that limb mechanical advantage changes in a regular way with animal size; the crouched posture of small animals increases the moment of the ground reaction force about the joints and reduces their muscle mechanical advantage relative to larger animals with more upright postures. Among quadrupedal mammals, the mass-specific muscle force required to support the body scales according to $M_b^{-0.26}$, where M_b is the body mass (Biewener, 1989). On average, a 30 g mouse must produce 10 times as much muscle force as a 300 kg pony to produce 1 N of force against the ground. If the active muscle fibers produce the same force per unit cross-sectional area, the mouse must recruit 10 times the cross-sectional area of muscle to support each newton of body weight.

The total volume of muscle necessary to support the body is equal to the product of the cross-sectional area and the fascicle length of the active muscle. Longer muscle fascicles produce the same force per unit cross-sectional area, but a larger volume of muscle is activated for each newton of force produced. Small quadrupeds have relatively shorter muscle fibers than large quadrupeds, proportional to $M_b^{0.26}$ (Alexander et al. 1981; mean of exponents for all muscle groups for non-hoppers). From large to small quadrupeds, the increase in cross-sectional area of muscle required to support the body weight during running, proportional to $M_b^{-0.26}$, is offset by a decrease in the relative lengths of the muscle fibers, proportional to $M_b^{0.26}$, such that the volume of muscle required per unit body weight is constant across size in quadrupedal mammals (Biewener, 1989; Kram and Taylor, 1990).

It has been suggested that differences in muscle mechanical advantage and active muscle volume might explain the variation in the energy cost of generating force during locomotion in insects that have markedly different limb postures (Full et al. 1990). Humans use more energy when they run in a crouched posture ('Groucho running') because of the poor mechanical advantage and increased muscle recruitment at the knee (McMahon et al. 1987). To determine the influence of muscle mechanical advantage and fiber length on running energetics in bipeds and quadrupeds, we compared dogs and turkeys of the same size. On average, bipedal runners use 1.7 times as much metabolic energy as quadrupeds for a given rate of force generation (Roberts et al. 1998). We hypothesized that this difference resulted from a greater volume of active muscle necessary to generate force in bipedal runners. We tested two possible causes of an increased active muscle volume: (1) a poorer muscle mechanical advantage for force production, and (2) a longer fascicle length of the active muscles.

Materials and methods
Animals

Three adult wild turkeys (*Meleagris gallopavo* L.) (two female and one male; mass 5.3±2.3 kg; mean ± S.D.) and three adult dogs (*Canis familiaris* L.; breed, Teacup terrier) (two males and one female; mass 4.5±1.0 kg) were purchased from USDA-approved breeders. These particular species were chosen because they have approximately the same body weight and they perform well on the treadmill. The animals were fed commercial bird and dog diets *ad libitum* and were housed in large indoor/outdoor pens.

Metabolic energy consumption

The energetic and kinematic data for turkeys are presented in Roberts *et al.* (1998). All energetic and kinematic measurements were made while the animals ran on a variable-speed treadmill. We selected speeds within the range of comfortable trotting speeds for the dog and running speeds for the turkey. All animals were trained for 20 min a day, 3 days a week for at least 6 weeks before measurements were made.

The rate of oxygen consumption ($\dot{V}_{O_2}$) was determined using an open-circuit indirect calorimetry system (Fedak *et al.* 1981). Animals wore loose-fitting masks through which air was metered at constant rates. A small sample of the collected gas was removed, dried, scrubbed for CO_2 and measured for O_2 content with a Beckman F3 oxygen analyzer. Calibration with a known flow rate of nitrogen allowed calculation of $\dot{V}_{O_2}$ (Fedak *et al.* 1981). The system was found to be accurate to within ±2 %.

The rate of O_2 consumption was measured continuously during each trial. We used measurements taken after a steady-state level of $\dot{V}_{O_2}$ had been maintained for 5 min or more. Several measurements were made on different days and averaged. We used an energy equivalent of 20.1 J ml^{-1} O_2 to convert measurements of oxygen consumption to energy consumption (Blaxter, 1989). $\dot{E}_{metab}$ for a given running speed was defined as the metabolic rate minus the zero-speed (*y* intercept) rate. The cost coefficient was determined according to equation 1. The cost of transport was defined as the slope of the least-squares linear regression of $\dot{E}_{metab}W_b^{-1}$ against speed.

Kinematic measurements

Time of foot contact (t_c) was measured from high-speed video recordings of treadmill running. Animals were recorded using a NAC 200 high-speed video camera operating at 200 fields s^{-1}. Time of contact was determined by counting the number of fields during which the foot was in contact with the treadmill belt. Measurements were taken for each foot and averaged. Ten strides were analyzed for each animal at each running speed.

Overview of muscle force and length measurements

Fig. 1 summarizes schematically the method for calculating the effect of muscle force and fascicle length on the volume of active muscle required to support body weight during running. This calculation is based on two variables: (1) the extensor muscle force required to balance the ground reaction force moments at each joint and (2) the mean muscle fascicle length. Measurements of the fascicle lengths (*l*) and muscle moment arms (*r*) of individual muscles are averaged to calculate a composite extensor muscle for each joint, with a mean fascicle
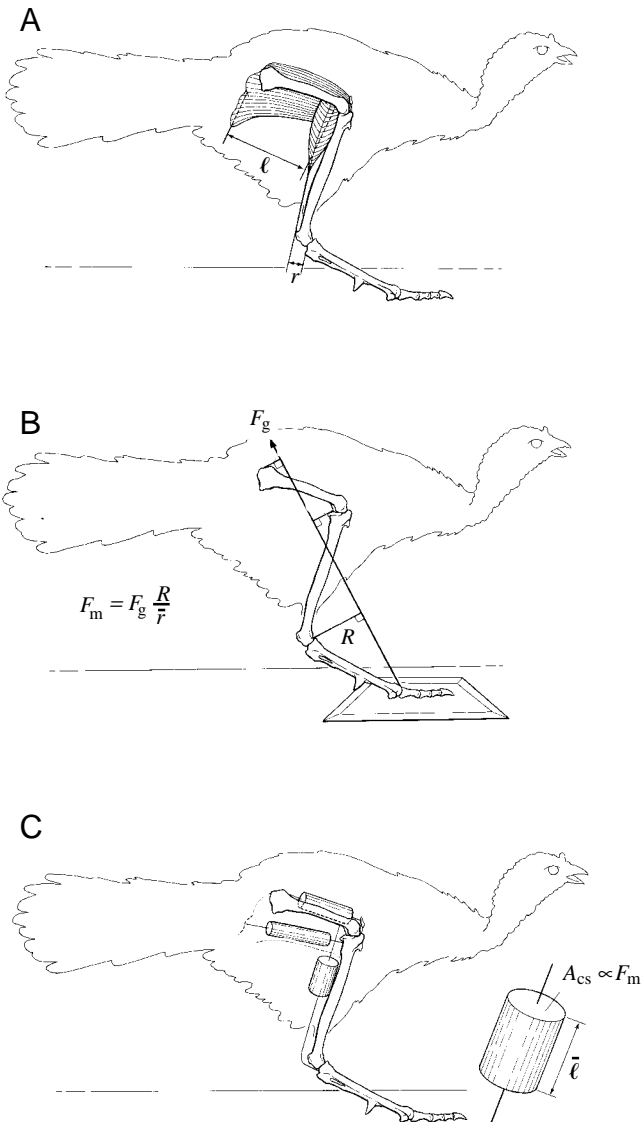
Fig. 1. A diagram of the logic and summary of the methods for estimating active muscle volume. Measurements of the fascicle length *l* and moment arm *r* of each extensor are combined to give a characteristic mean fascicle length ($\bar{l}$) and mean moment arm ($\bar{r}$) for a composite extensor at each joint (A,C). The muscle moments required to produce ground reaction forces F_g are measured from force plate recordings and video analysis and used to calculate *R*, the ground reaction force moment arm, and F_m, the mean muscle force at each joint (B). The volume of active muscle is represented as a cylinder with a cross-sectional area A_{cs} proportional to the measured force, F_m, and a length equal to the mean fascicle length, $\bar{l}$ (C).

length and moment arm (Fig. 1A). Muscle moment arm values are combined with joint moments measured by video and force plate analysis (Fig. 1B) to calculate the muscle force F_m required to support body weight at each joint. The volume of active muscle is represented as a cylinder having a cross-sectional area A_{cs} that is proportional to the muscle force F_m at the joint and a length that is equal to the mean fascicle length ($\bar{l}$) of the extensors at the joint (Fig. 1C).

Anatomical measurements

Anatomical measurements were taken from three limbs of two turkeys and three front and three hind limbs from two dogs. To take advantage of cadaver material available from other experiments, two of the animals dissected were not the same individuals used for the running measurements, but they were similar in weight and condition.

Muscle fascicle length (*l*), pinnation angle (θ), moment arm (*r*) and mass (*m*) of each of the extensors were measured at the ankle, knee and hip for the turkey and dog, as well as the wrist, elbow and shoulder of the dog. The intertarsal joint of the turkey is referred to as the ankle for ease of comparison. Measurements were made on muscles that act primarily as extensors. Proposed function determined from anatomy (Raikow, 1985; Gatesy, 1989; Miller *et al.* 1979; George and Berger, 1966) as well as electromyography measurements of muscle activity during stance (Gatesy, 1989; Tokuriki, 1973; Goslow *et al.* 1981) were used to determine which muscles to include (see Table 1). Two-joint muscles were included only if the extensor moment arm was greater than the flexor moment arm. Anatomical measurements were similar in method to those described by Alexander (1974). Muscle moment arms were determined by measuring the perpendicular distance from the line of action of each muscle to the center of rotation of the joint. The joints were held at approximately the joint angle observed at mid-stride for muscle moment arm and length measurements. For muscles with a variable fascicle length, a mean value was determined from several measurements. For pinnate muscles, the fascicle length was determined after the muscle had been dissected away and bisected with a sharp scalpel. Muscle fiber pinnation angle was determined using a protractor or small goniometer.

Calculation of composite muscle variables

Because the relative contribution of individual muscles to the sum moment at a joint cannot be determined from external measurements, it is necessary to determine a mean muscle fascicle length and moment arm for each joint. We calculated a composite fascicle length ($\bar{l}$) and moment arm ($\bar{r}$) for each joint from the mean of the extensors at each joint, weighted by cross-sectional area (Biewener, 1989). This provided a measure weighted to the capacity of each muscle to generate force.

The physiological cross-sectional area of each of the muscles at a joint was calculated according to the following equation:

$$A_{cs} = \frac{m\cos\theta}{\rho l} , \tag{1}$$

where A_{cs} is the cross-sectional area in cm^2, *m* is muscle mass in g, ρ is the density of muscle in g cm^{-3}, θ is the pinnation angle in degrees, and *l* is the muscle fascicle length in cm. A density for muscle of 1.06 g cm^{-3} was used (Mendez and Keys, 1960).

The fascicle length for the composite muscle ($\bar{l}$) was

determined by dividing the sum of the muscle volumes by the sum of the cross-sectional areas:

$$\bar{l} = \frac{\sum(m/\rho)}{\sum A_{cs}} \; . \tag{2}$$

This is equivalent to a weighted (by cross-sectional area) mean muscle fascicle length. The mean muscle moment arm ($\bar{r}$) for each joint was also a weighted mean based on the cross-sectional area of each muscle:

$$\bar{r} = \frac{(r_1 A_{cs,1} + r_2 A_{cs,2} + ... + r_n A_{cs,n})}{\sum A_{cs}} \; . \tag{3}$$

These variables describe a composite muscle at each joint with a characteristic mean fascicle length and muscle moment arm (Biewener, 1989). The composite mean values are presented in Table 1. These mean values were used for all calculations of force and active muscle volume. Small corrections in anatomical values for body mass were made by assuming that length scaled according to $M_b^{0.33}$. The variation in anatomical measurements was not included in subsequent calculations of muscle force and active fascicle length.

Force measurements

We assumed that the contributions of lateral ground reaction forces and inertial forces required to accelerate the limbs were small relative to the horizontal and vertical ground reaction forces (Clark and Alexander, 1975; Pandy *et al.* 1988). Measurement of ground reaction force moment at each joint requires measurements of the position of the center of rotation of the joint, the point of force application and the direction and magnitude of the resultant ground reaction force. The position was recorded using high-speed video, and force measurements were carried out using a Kistler model 9261A force plate mounted midway along a 15 m track.

The running speed along the track was recorded as the animal broke photocell beams from three photocells located 1 m apart. Three criteria were necessary for a run to be analyzed further. First, the animal had to run at the appropriate speed. We chose speeds that were close to the preferred speeds of the animals (a 2.0 m s⁻¹ trot for dogs, 3.5 m s⁻¹ for turkeys) and only accepted runs within 0.2 m s⁻¹ of this speed. Second, the animal had to run at a steady speed with little acceleration or deceleration. The horizontal force was integrated during the foot contact time, and only those runs in which the integrated accelerative and decelerative forces (i.e. impulse) differed by less than 25 % were accepted as steady-speed runs. This results in a net change in speed per stride of less than 0.1 m s⁻¹. The third criterion was that the turkey should land with one foot only on the plate; the dog had to land with the front foot and then the hind foot on the same side of the body in the same run. This condition was necessary in order to resolve the ground reaction forces for individual limbs.

Two channels of vertical (summed front and back of the force plate) and one channel of summed horizontal components of force were recorded using a Kistler 9261A force plate. The

Table 1. *Mean muscle mass, moment arm and fascicle length for composite joint extensors for the turkey and dog*

	Muscle mass (g)	Moment arm, $\bar{r}$ (cm)	Fascicle length, $\bar{l}$ (cm)
Turkey			
Hip	118.7±5.0	3.54±0.16	6.80±0.58
Knee	36.9±1.0	2.09±0.60	3.05±0.21
Ankle	130.8±9.6	1.17±0.09	2.38±0.37
Dog			
Hip	63.8±2.1	1.34±0.04	4.61±0.52
Knee	20.5±1.69	1.24±0.56	2.29±0.43
Ankle	20.2±1.2	1.20±0.12	1.41±0.16
Shoulder	13.9±0.3	1.01±0.06	1.80±0.75
Elbow	19.0±2.0	1.37±0.20	3.11±0.32
Wrist	11.3±1.2	0.61±0.07	0.68±0.05

Values are means ± 1 S.D. (*N*=3).

Turkey muscles: hip; iliotibialis lateralis*, iliofibularis, flexor cruris lateralis, flexor cruris medialis, pubo-ischio-femoralis, ischiofemoralis; knee; femorotibialis externus and medius; ankle; gastrocnemius, fibularis longus*, flexor hallucis longus, flexor digitorum longus, flexor perforatus II&III, flexor perforans et. perforatus II&III.

Dog muscles: hip; gluteus medius, gluteus superficialis, biceps femoris, semimembranosus; knee; vastus lateralis, vastus medialis, vastus intermedius; ankle; gastrocnemius, plantaris, deep digital flexors; shoulder, supraspinatus; elbow, triceps medialis and lateralis; wrist, deep digital flexors, superficial digital flexors, flexor carpi ulnaris, flexor carpi radialis.

*Only those heads that extend the joint were included.

signal was collected on an Apple Macintosh computer after analog-to-digital conversion on a National Instruments board (no. NB MIO 16H). The force data, along with one channel of photocell output and a synchronization channel, were collected using a National Instruments Labview program. Data collection was triggered when the animal broke the first photocell beam. Force data were sampled at 1000 Hz and filtered in software with a Chebyshev low-pass filter with a cut-off frequency of 60 Hz. The point of force application was determined by the relative outputs of the vertical channels in the front and back of the force plate. The force plate was calibrated for force and position daily using a known mass.

Joint centers of rotation were determined by marking each joint and video-taping the animal running across the force plate. Images were digitized (Quickcapture frame-grabbing board) and analyzed using NIH Image software. Force and video measurements were synchronized using a light-emitting diode triggered by the photocells and recorded on video.

A spot of white latex paint was applied to the skin overlying the approximate joint centers, using bony landmarks to aid in locating the center of rotation. For turkeys, only the ankle could be marked with paint. The wing obstructed the view of the hip, and knee movement occurred independently of skin movement. These joint positions were determined with the aid

of a small marker on the back over the hip, the ankle marker and measured leg segment lengths. In an immobile bird, the distance from the ankle to the center of rotation of the knee was determined. A line of this length was drawn on the digitized image from the ankle marker following the middle of the tibiotarsal muscle mass to locate the knee center of rotation. The same strategy was used to determine the position of the hip from the position of the knee, using the marker glued to the back of the animal just above the hip as a guide. Because there is virtually no movement of the skin on the back, this marker was fixed relative to the acetabulum, thus providing a good indicator of the position of the center of rotation of the hip.

High-speed X-ray cine film was used to check the accuracy of joint markers in both the dogs and the turkeys (Siemens cineoradiographic apparatus with an Eclair GV16 camera). We placed radio-opaque markers on the skin and filmed the animals running on a treadmill. We could visualize the center of rotation of the joint directly with the X-ray film and observe how reliably our external markers indicated the joint axis. The largest error in joint marking occurred at the most proximal joints and was less than 0.5 cm.

Muscle force at each joint was determined using the following equation:

$$F_\mathrm{m} = F_\mathrm{g}\,\frac{R}{\bar{r}}\ ,\qquad (4)$$

where F_m is muscle force (in N), F_g is the ground reaction force (in N), R is the perpendicular distance from the line of action of the ground reaction force to the axis of rotation of the joint (in cm), and $\bar{r}$ is the mean muscle moment arm (in cm), as described above (Biewener, 1989). Ground reaction force was determined from the force output recorded from the force plate. The ground reaction force moment arm, R, was determined from the position of the joint and the position and direction of the ground force, as determined from force plate and video measurements.

The total muscle force also included a component of force contributed by two-joint muscles that extended one joint but also flexed another. For example, if the gastrocnemius muscle is active to extend the ankle, it will also produce a small flexion moment about the knee that must be balanced by knee extensors. The muscle flexor moments produced by two-joint muscles were calculated from the flexor moment arm and the force required to balance ground-reaction-based extensor forces, assuming that force was distributed equally (by cross-sectional area) across all joint extensors. In both dogs and turkeys, muscle flexion moments from two-joint hip and ankle extensors increased the extensor force required at the knee by approximately 60 % over the force required to balance ground reaction forces only. The extensor force required to balance these antagonist muscle forces was less than 2 % of the total extensor force required in the limb in dogs and less than 9 % in turkeys. It was assumed that any other forces due to co-contraction of antagonist flexor muscles were negligible. This assumption is supported by the close agreement between

muscle forces measured directly by force buckles and the forces calculated from force-plate measurements in the ankle extensors of hopping kangaroo rats *Dipodomys merriami* (Biewener *et al.* 1988).

Active muscle force and fascicle length

To compare dogs and turkeys, we calculated the muscle force required per unit ground reaction force. This was performed by dividing the muscle force integrated over the time period of support, $\int F_\mathrm{m}$, by the integrated ground reaction force, $\int F_\mathrm{g}$. Averaged over time, a running animal must produce one body weight of force against the ground. Therefore, the ratio $\int F_\mathrm{m}/\int F_\mathrm{g}$ is a measure of the muscle force, averaged over time, that must be produced to support body weight. If the mechanical advantage does not change with running speed, as has been demonstrated for quadrupeds (Biewener, 1989), this ratio will be independent of speed or duty factor. The sum of limb extensor forces that must be produced to generate 1 N of force on the ground ($\int F_\mathrm{sum}/\int F_\mathrm{g}$) was obtained by summing the mean force at each joint for a stride. For the hind limb:

$$\frac{\int F_\mathrm{sum}}{\int F_\mathrm{g}} = \frac{\int F_\mathrm{m,ankle} + \int F_\mathrm{m,knee} + \int F_\mathrm{m,hip}}{\int F_\mathrm{g}}\ .\qquad (5)$$

For the dogs, the sum of the forces for all six joints was divided by the sum of the ground reaction forces for the hind limb and fore limb.

The 'active fascicle length' (L_act) is a mean of fascicle length for the whole animal, weighted at each joint according to how much force is produced at that joint. For the hind limb, this calculation was:

$$L_\mathrm{act} = \frac{\int F_\mathrm{m,ankle}\bar{l}_\mathrm{ankle} + \int F_\mathrm{m,knee}\bar{l}_\mathrm{knee} + \int F_\mathrm{m,hip}\bar{l}_\mathrm{hip}}{\int F_\mathrm{sum}}\ .\qquad (6)$$

L_act for quadrupeds was calculated using the same method for all six joints. The mean is weighted by force in order to provide an estimate of the mean length of the active muscle fascicles. If all muscle fibers operate with the same stress, then the volume of active muscle necessary per unit body weight during running will be proportional to the product of $\int F_\mathrm{sum}/\int F_\mathrm{g}$ and L_act.

Results
Energetics and kinematics of running

The energetic costs of running were similar in trotting dogs and running turkeys (Fig. 2). The speed range of these gaits overlapped between 1.5 and 2.0 m s^{-1}. At these two speeds, the measured metabolic rate was approximately 15 % higher for turkeys, but this difference was not significant (two-tailed *t*-test, $P=0.09$).

The slope of the relationship between mass-specific energy cost ($\dot{E}_\mathrm{metab}W_\mathrm{b}^{-1}$) and running speed is the 'cost of transport' ($E_\mathrm{trans}W_\mathrm{b}^{-1}$). It represents the amount of energy used by the muscles to move a unit body mass a unit distance. The cost of transport was not significantly different for dogs and turkeys

Table 2. *Hip height at mid stride, step length, time of foot contact, cost of transport and cost coefficient for dogs and turkeys*

	Hip height (cm)	Step length (cm)	Time of contact, t_c (s)	Cost of transport, $E_{trans}W_b^{-1}$ (J N^{-1} m^{-1})	Cost coefficient, c (J N^{-1})
Turkey	35.8±2.0	55.3±4.7	0.259±0.017	0.63±0.03	0.349±0.015
Dog	22.6±0.9	26.9±1.0	0.141±0.005	0.68±0.02	0.183±0.018
P	0.004	0.002	0.003	0.322	0.003
Turkey:dog	1.6	2.0	1.8	0.9	1.9

$E_{trans}W_b^{-1}$ is the slope ±95 % confidence intervals of the least-squares regression of $\dot{E}_{metab}W_b^{-1}$ on running speed (see Fig. 2).

All other values are means ± S.E.M. ($N=3$).

All values are means for all speeds, except t_c which is for 2.0 m s^{-1}.

P values are given for two-tailed *t*-tests.

(Table 2). Transport cost changes in a regular way with body mass, and the values for the dog and turkey given in Table 2 are close to the values predicted for their size (Taylor *et al.* 1982).

Turkeys took longer steps than did dogs running at the same speed (Table 2). Step length, equal to the product of running speed and time of contact, was twice as long for turkeys. This is explained by the long tibiotarsal and tarsometatarsal bones of the turkeys, giving them almost twice the leg length and a 1.6-fold greater hip height at mid-stance than dogs (Table 2). The longer steps of the turkeys meant that each foot was in contact with the ground 1.8 times longer than the feet of the dogs. A longer foot contact time provides more time to generate force and presumably allows the turkeys to use slower, more economical muscle fibers.

Both bipeds and quadrupeds show a direct relationship between the energy cost of running and the time course of force generation, and the ratio between these two is described by the cost coefficient, c, according to the following equation:

$$\dot{E}_{metab}W_b^{-1} = \frac{c}{t_c} \tag{7}$$

(Kram and Taylor, 1990). The cost coefficient for turkeys was 1.9 times greater than that measured for dogs (Table 2), consistent with differences between other bipedal and quadrupedal runners (Roberts *et al.* 1998).

Muscle force

The muscle force required to support weight is determined by the magnitude of the ground reaction force and the mechanical advantage of the muscle. Changes in the ground reaction force moment arm, R, that occur during a step result in a pattern of muscle force that does not necessarily parallel changes in the ground reaction force with time (Fig. 3). For example, hip extensors in the turkey experience their peak forces early in the step, while the knee extensor force is maximal later in the step, after the peak ground reaction force. The ground reaction force can also act to extend a joint, indicating an opposing flexor muscle force. These moments were small relative to the moments that required extensor muscle force and were recorded as zero extensor force. The total integrated flexion moment summed for all joints was less than 8 % of the total extensor moment in dogs and less than 2 % in turkeys.

Biewener (1989) defined the effective mechanical advantage (EMA) as the mean mechanical advantage, $\bar{r}/R$, of the limb extensors averaged over a step. We calculated the EMA over the period of the stride when the measured muscle force was greater than 25 % of the measured maximum muscle force (Biewener, 1989). The EMA of the turkey hind limb, 0.451±0.052 (mean ± S.E.M.), was not significantly different from that of the dog hind limb, 0.652±0.089 ($P=0.12$, two-tailed *t*-test), or the dog fore limb, 0.298±0.025 ($P=0.06$, two-tailed *t*-test). The scaling of EMA across body mass for a number of species of mammals (Biewener, 1989) predicts an EMA of 0.337 for the fore limb and 0.385 for the hind limb for a mammal of the same body mass as the dogs in the present study. There are no comparable values published for birds.
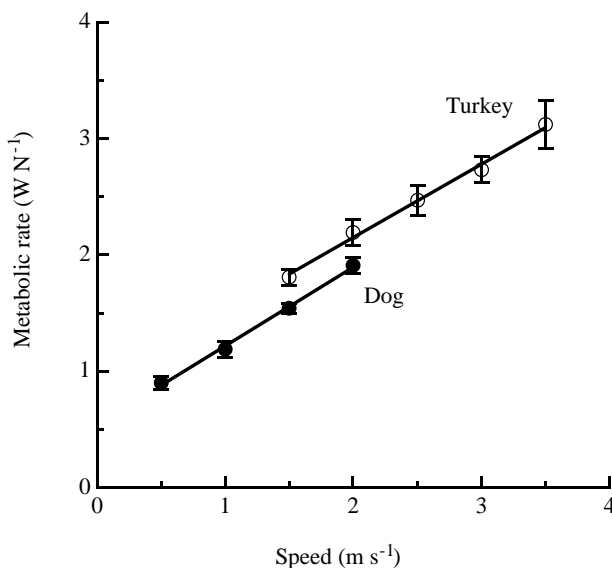

Fig. 2. Metabolic rate ($\dot{E}_{metab}W_b^{-1}$) *versus* speed in turkeys and dogs. The slope of the line gives the cost of transport, $E_{trans}W_b^{-1}$, and was not significantly different for the dog and turkey. Values are means ± S.E.M. ($N=3$), and lines are least-squares regressions. Regression equations: turkey, $y=0.63x+0.884$, $r^2=0.993$, $P<0.001$; dog, $y=0.68x+0.539$, $r^2=0.997$, $P=0.001$.
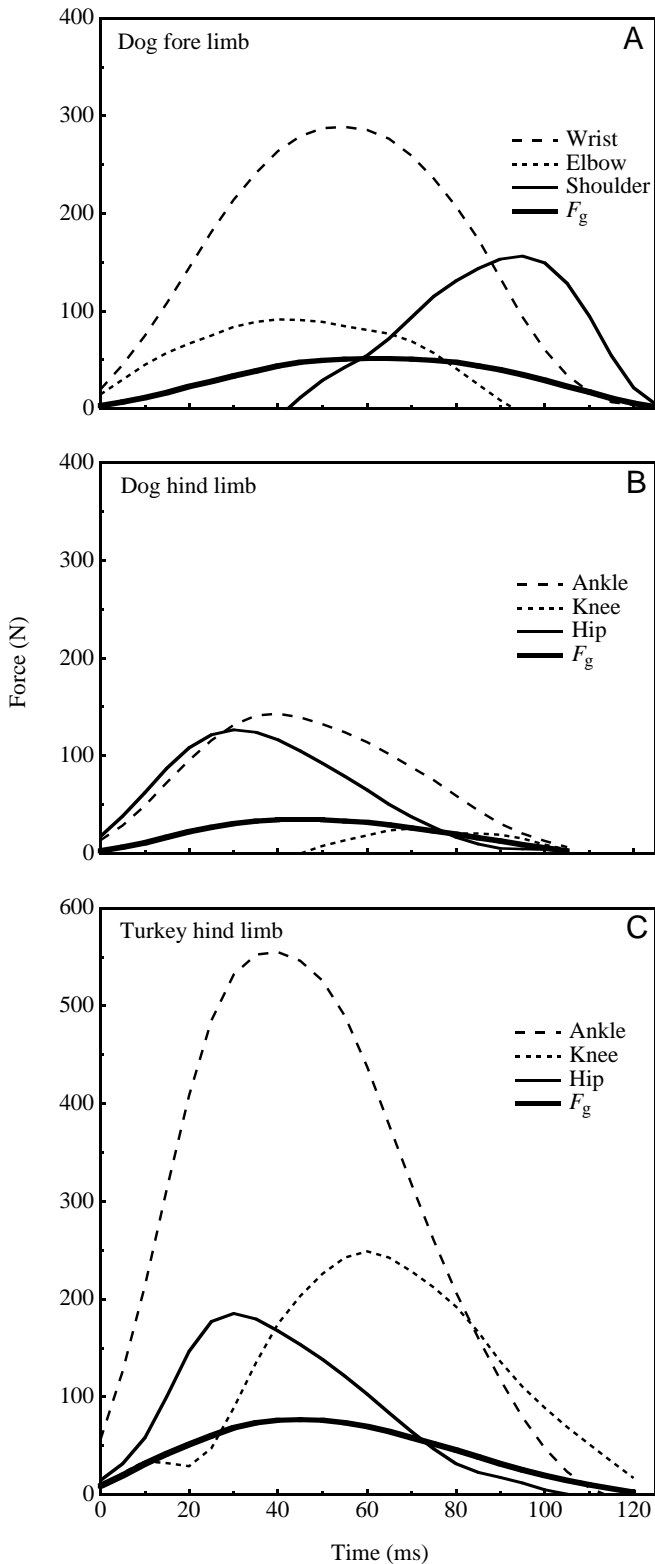
Fig. 3. Muscle forces at the ankle, knee and hip and ground reaction forces F_g for a representative stride for a dog fore (A) and hind limb (B) and a turkey (C). The area under each individual muscle force *versus* time curve represents the impulse, $\int F_m$, produced at that joint.

The EMA expresses the mean of the ground reaction force produced per unit muscle force for all of the extensors and is useful for comparing the mechanical design of the limbs of different animals. For the purposes of an energetic comparison, however, we required a measure of muscle force that could be summed for all joints and that included the entire force-generating period. We divided the integrated muscle force, $\int F_m$ (the area under the muscle force curve in Fig. 3), at each joint by the integrated ground reaction force, $\int F_g$ (the area under the ground reaction force curve in Fig. 3). This gives a measure of the amount of muscle force required at each joint to produce 1 N of ground reaction force (Fig. 4). In both turkeys and dogs, the highest muscle forces occurred at the distal joints. When all joints were included, the muscle force required to support each newton of body weight, $\int F_{sum}/\int F_g$, was 9.8±0.8 for turkeys compared with 8.0±0.6 (mean ± s.e.m.) for dogs. This 1.2-fold difference was not significant (*P*=0.15, two-tailed *t*-test) (Fig. 4).

Active muscle

Running turkeys used a greater muscle volume to generate a unit of force than dogs (*P*=0.003, two-tailed *t*-test) because of their longer muscle fascicles (Fig. 5). If we assume that the dog and turkey muscles produce the same force per active cross-sectional area of muscle, the product of mean muscle force and fascicle length is proportional to the volume of active muscle (Figs 1, 5). Thus, the turkey uses 2.5 times the active limb muscle volume to generate each unit of ground reaction force as the dog (*P*=0.003, two-tailed *t*-test). Much of this difference can be explained by the high forces and relatively long fascicles in the ankle of the turkey. The volume of muscle required to support weight at the ankle of the turkey was at least as much as that used for all the joints of the front and hind limb combined in the dog. The was due to both high muscle forces (Fig. 4) and long fascicles at the ankle in turkeys (Table 1). The
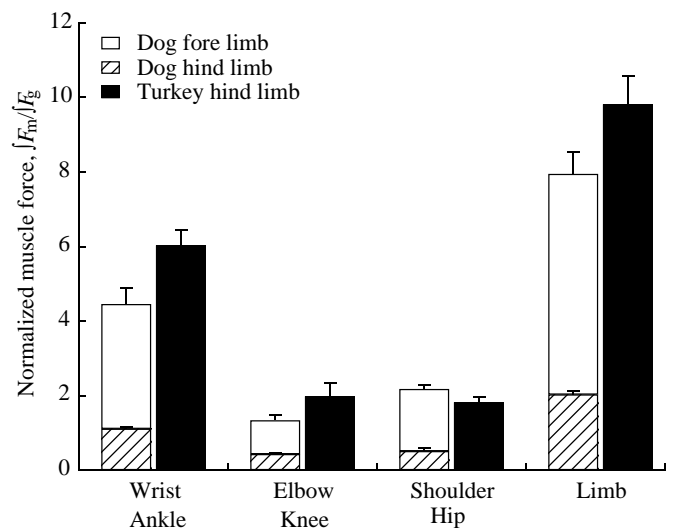

Fig. 4. Muscle force F_m required per unit ground reaction force F_g. Values for dogs are calculated by dividing the muscle impulse $\int F_m$ at a given joint by the total ground reaction force impulse $\int F_g$ for both front and hind limbs. Values are means + s.e.m. (*N*=3).
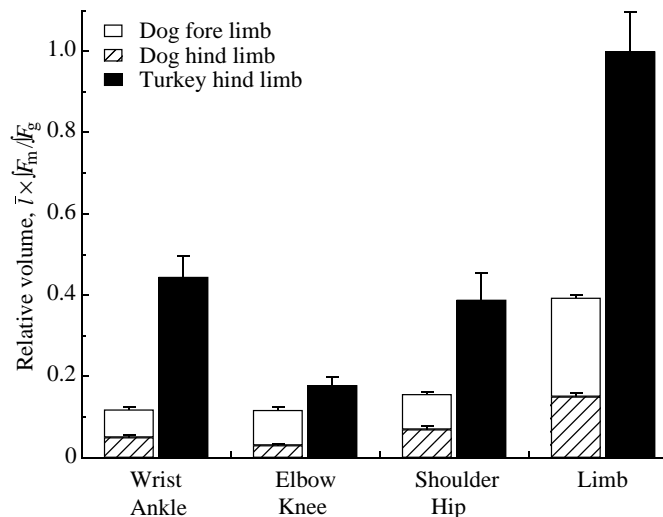
Fig. 5. The product of muscle force per unit ground reaction force ($\int F_{\mathrm{m}}/\int F_{\mathrm{g}}$) and fascicle length ($\bar{l}$), which is proportional to the recruited muscle volume necessary to support body weight for each joint in the turkey and dog. Values are means + S.E.M. (N=3).

difference in distribution of active muscle volume in dogs and turkeys was reflected in the distribution of total extensor muscle mass (Table 1). For example, the total extensor mass available at the ankle of the turkey is more than four times the combined muscle mass at the wrist and ankle of the dog.

The energy cost of generating force

The limb extensor muscles of the turkey have much longer fascicles than those of a similarly sized dog (Table 1). To determine a fascicle length that is relevant to the energetic cost of generating force, we have calculated an 'active fascicle length', L_{act}, which is the mean fascicle length at each joint weighted by the muscle force produced at that joint (Fig. 6B). This should provide a measure of the mean length of the active muscles. For example, very long fascicles of the extensor muscles that act about a particular joint would not contribute to the active fascicle length if no force is generated (see equation 6). The active fascicle length for the turkey was 3.3±0.4 cm, 2.1 times greater than the value of 1.6±0.1 cm for the dog (mean ± S.E.M., P=0.01, two-tailed t-test). Turkeys use muscles that are, on average, 2.1 times longer while producing similar muscle forces, providing an explanation for their 1.9-fold greater cost coefficient (Fig. 6; Table 2).

Discussion

Limb design and the energy cost of running

We started with the hypothesis that running bipeds use more muscle to run than do quadrupeds, to explain why their longer legs and slower rates of force generation do not result in a lower energy cost. Our data indicate that the longer muscle fascicles of the turkey require them to recruit more than twice the volume of limb muscle as a running dog to support their body weight. This helps explain the higher cost coefficient of
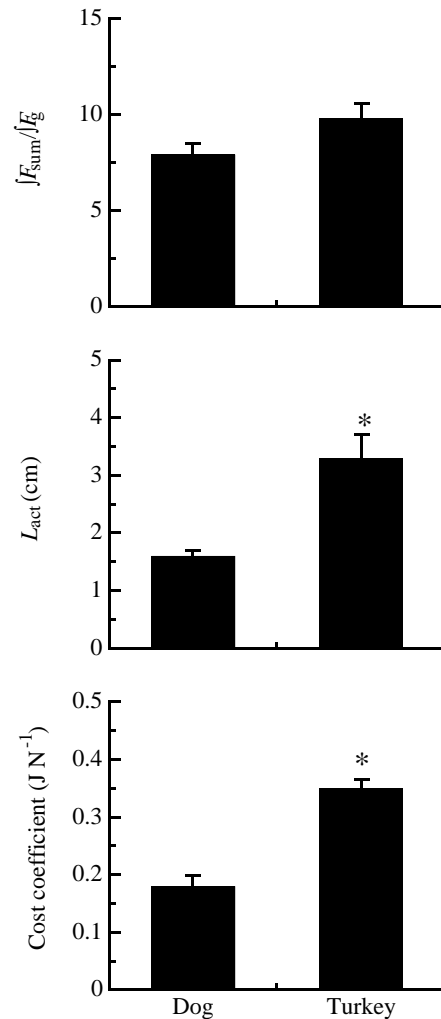

Fig. 6. The muscle force required to support 1 N of body weight for all joints combined ($\int F_{\mathrm{sum}}/\int F_{\mathrm{g}}$) (A), the mean active fascicle length (L_{act}) for the whole limb weighted by the force produced (B) and the mean cost coefficient (C) for the dog hind and fore limbs (combined) and for the turkey. Values are means + S.E.M. (N=3). An asterisk denotes a significant difference (two-tailed t-test, P<0.05) between values for the dog and turkey.

running bipeds compared with quadrupeds and provides a link between limb design and running energetics.

Previous studies have suggested that differences in mechanical advantage or fascicle length can influence the metabolic cost of running (Biewener, 1990; Full $et\ al.$ 1990; McMahon $et\ al.$ 1987). Our study presents a quantitative method for evaluating the effect of limb design on running energetics and extends previous models of the energy cost of running (Taylor, 1985; Kram and Taylor, 1990). The rate of energy consumption $\dot{E}_{\mathrm{metab}}$ of a contracting muscle can be expressed by the following equation:

$$\dot{E}_{\mathrm{metab,muscle}} = (LF/\sigma)\dot{E}_{\mathrm{muscle}}, \qquad (8)$$

where F is muscle force (N), L is fiber length (cm) and σ is the force per unit cross-sectional area of active muscle (N cm^{-2}).

The total volume of muscle active to generate force is a cylinder with a length L and a cross section F/σ. $\dot{E}_{\mathrm{muscle}}$ (W cm^{-3}) is the rate at which each unit volume of muscle uses energy. The volume-specific rate of energy consumption is greater in faster muscles, because faster muscles have higher rates of cross-bridge cycling and higher activation costs (Barany, 1967; Rall, 1985). Running animals must use faster muscles with higher rates of cross-bridge cycling to develop force more rapidly when they take faster steps. If the rate of cross-bridge cycling is directly proportional to the rate of force development, $1/t_c$, then:

$$\dot{E}_{\mathrm{muscle}} = 1/t_c \times k, \tag{9}$$

where k is a constant. In the present study, we measured a total muscle force necessary to support body weight, $W_b \int F_{\mathrm{sum}} / \int F_g$, and a mean fascicle length of the active muscles, L_{act}. Substituting these and equation 9 into equation 8 gives a description of the energetics of muscle contraction in a running animal:

$$\dot{E}_{\mathrm{metab}} = \left(L_{\mathrm{act}} \frac{\int F_{\mathrm{sum}}}{\int F_g} W_b \frac{1}{\sigma} \right) \frac{1}{t_c} k. \tag{10}$$

The turkey uses the same amount of energy as the dog running at the same speed, but it has a $1/t_c$ that is slightly more than half that of the dog. According to equation 10, the turkey should use approximately twice the volume of muscle to support its body. Our results suggest that turkeys required 2.5 times the volume of active limb muscle to support their body weight, assuming that turkeys and dogs produce the same force per unit cross-sectional area of muscle (σ). This difference in active muscle volume helps to explain why the long legs and slower rates of force development of the turkey do not reduce their energy cost.

Estimating active muscle volume – assumptions and limitations

Our approach estimates the relative volume of active muscle only for extensors of the limbs. We could not estimate the muscle forces involved in stabilizing the trunk, head and neck. Microsphere measurements in miniature swine *Sus scrofa* indicate that non-limb muscles receive less than 20% of the total blood flow to muscle during treadmill exercise (Armstrong *et al.* 1987), suggesting that the energy cost of fueling non-limb muscles is considerably less than that required for limb muscles. The muscular effort required in the non-limb muscles of running bipeds may be even lower than for quadrupeds. Thus, our estimate of active limb muscle volume may overestimate the difference in total active muscle volume between dogs and turkeys.

A critical assumption of our approach is that the force produced per unit cross-sectional area of active muscle, σ, is equivalent in running dogs and turkeys. This stress is determined by the force-generating capability of the muscle, P_0, and the relative shortening velocity, V/V_{max}, at which it operates. Few studies of isolated avian muscle have been performed, but *in situ* measurements suggest that the maximum

force-generating capacity is within the range of published values for mammals (Biewener *et al.* 1992). Large differences in active muscle stress occur when muscles operate at different V/V_{max} in order to perform different tasks. Muscles contracting at an intermediate shortening velocity, where high power outputs are produced, generate only approximately one-third of the force generated during an isometric contraction (Hill, 1938). Elastic energy storage and recovery in tendons can reduce the energy cost of running by allowing muscles to operate nearly isometrically to produce a high active muscle stress and reduce the volume of muscle required to support the body (Roberts *et al.* 1997). For both bipedal and quadrupedal runners, the mechanical energy fluctuations of the body and limbs are unrelated to changes in metabolic energy consumption across animal size and speed (Heglund *et al.* 1982), and level running at a constant speed requires little net mechanical work. It seems likely that muscles operate on average close to isometrically in both dogs and turkeys, allowing similar force per unit cross-sectional area of active muscles.

Mechanics of support in bipedal and quadrupedal limbs

Quadrupedal and bipedal runners show similarities in the mechanics of movement of the body and limbs (Cavagna *et al.* 1977; Gatesy and Biewener, 1991). Our results show that turkey limbs also have a mechanical advantage that is similar to that predicted for quadrupedal hind limbs (Biewener, 1989). However, there is a marked difference in the mass distribution in the limb between dogs and turkeys that may reflect different strategies for support and power production by limb muscles. Both dogs and turkeys generate their highest forces at the joints with the shortest muscle fibers. This is consistent with the suggestion that shorter muscle fibers can be used to provide more economical force. However, the turkey requires a much greater active muscle volume at the ankle, because it has longer muscle fascicles at that joint, nearly four times as long as the fascicles at the wrist of the dog. This difference may reflect the specialization of distal muscles of the quadruped for force production compared with muscles that produce the mechanical power necessary to accelerate, run uphill or jump. Turkey ankle muscles provide force nearly isometrically during level locomotion, but they also shorten considerably and generate power during uphill running (Roberts *et al.* 1997). Dogs generate the power for a jump in proximal muscles, using the muscles of the ankle and the wrist only to provide support (Alexander, 1974). While quadruped limbs have a characteristic taper, the muscle mass of the ankle extensors in turkeys is almost as large as the extensor mass at the hip and knee combined. This gross morphological difference may reflect fundamental differences in the way that mammalian and avian hind limbs operate to produce mechanical power for locomotion.

Our results suggest that bipedal turkeys require a greater volume of active muscle than quadrupedal terriers when they run, primarily because they have longer muscle fascicles. The difference in active fascicle length measured between dogs and turkeys was approximately the same as the difference in leg length, but this outcome was not inevitable; very long-legged

birds do not have proportionately long muscle fascicles (Bennett, 1996). The longer legs of the turkey allow it to use slower, more economical fibers, but having longer fascicles means that more muscle must be active. This appears to explain the similar energy cost of running in the biped and quadruped.

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