Mechanical power output during running accelerations in wild turkeys

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Summary

We tested the hypothesis that the hindlimb muscles of wild turkeys (*Meleagris gallopavo*) can produce maximal power during running accelerations. The mechanical power developed during single running steps was calculated from force-plate and high-speed video measurements as turkeys accelerated over a trackway. Steady-speed running steps and accelerations were compared to determine how turkeys alter their running mechanics from a low-power to a high-power gait. During maximal accelerations, turkeys eliminated two features of running mechanics that are characteristic of steady-speed running: (i) they produced purely propulsive horizontal ground reaction forces, with no braking forces, and (ii) they produced purely positive work during stance, with no decrease in the mechanical energy of the body during the step. The braking and propulsive forces ordinarily developed during steady-speed running are important for balance because they align the ground reaction force vector with the center of mass. Increases in acceleration in turkeys correlated with decreases in the angle of limb protraction at toe-down and increases in the angle of limb retraction at toe-off. These kinematic changes allow turkeys to maintain the alignment of the center of mass and ground reaction force vector during accelerations when large propulsive forces result in a forward-directed ground reaction force. During the highest accelerations, turkeys produced exclusively positive mechanical power. The measured power output during acceleration divided by the total hindlimb muscle mass yielded estimates of peak instantaneous power output in excess of $400\,\mathrm{W\,kg^{-1}}$ hindlimb muscle mass. This value exceeds estimates of peak instantaneous power output of turkey muscle fibers. The mean power developed during the entire stance phase increased from approximately zero during steady-speed runs to more than $150\,\mathrm{W\,kg^{-1}}$ muscle during the highest accelerations. The high power outputs observed during accelerations suggest that elastic energy storage and recovery may redistribute muscle power during acceleration. Elastic mechanisms may expand the functional range of muscle contractile elements in running animals by allowing muscles to vary their mechanical function from force-producing struts during steady-speed running to power-producing motors during acceleration.

Key words: locomotion, muscle, work, power, bird, running, turkey, *Meleagris gallopavo*.

Introduction

What limits the maximal locomotor performance of a running animal? Skeletal muscle is the ultimate source of power for movement, yet the connection between muscle contractile properties and locomotor performance is not always clear. For example, many different muscle properties have been investigated or proposed as possible limits to top running speed, including muscle power output (Hill, 1950; Swoap et al., 1993), the magnitude of force production (Weyand et al., 2000), stiffness (Farley, 1997), shortening velocity (Marsh, 1988) and the rate of activation or deactivation (Marsh, 1988, 1990). The difficulty in establishing the link between muscle properties and performance during steady-speed running results in part from uncertainty as to what mechanical function muscle contractile units perform.

During running, muscle–tendon units operate like springs, storing and recovering mechanical energy as the limbs flex and extend with each step (Alexander, 1988; Alexander and Bennet-Clark, 1977; McMahon and Cheng, 1990). Some of this cyclical work is done by muscle contractile elements that absorb work as they are actively stretched and produce work as they shorten. However, most of the spring-like function of the limb could be performed by the passive stretch and recoil of tendons because steady-speed running on level ground involves no net change in the average mechanical energy of the body. Elastic mechanisms can allow muscle contractile elements to operate as near-isometric struts, developing force without shortening or producing significant power (Roberts et al., 1997; Biewener and Roberts, 2000; Dickinson et al., 2000). The spring-like function of muscle–tendon units allows for economic force development by minimizing muscular work.

The mechanical function of muscles during acceleration must differ fundamentally from their function during steady-

speed running. The work done to increase the kinetic energy of the body with each step in an accelerating animal must be performed by contraction of skeletal muscle because passive elastic mechanisms cannot perform net work (i.e. they can only store and recover energy, they cannot increase the net mechanical energy of the body). An animal's ability to accelerate quickly may be critical for avoiding predation or for capturing prey (Elliott et al., 1977; Huey and Hertz, 1983), and selection for acceleration has probably been an important factor shaping the design of the musculoskeletal system. Therefore, it might be expected that, during the highest accelerations, all available muscle would be recruited to operate at maximal power output. However, there is little information available to test this idea.

We sought to determine the power developed by the hindlimb musculature during acceleration in running turkeys. The study was motivated by the question: Can a muscular system that effectively minimizes muscular power during steady-speed running also act to maximize muscular power for acceleration? Because the spring-like function of muscle–tendon units during steady-speed running differs fundamentally from the motor-like function required during acceleration, we also investigated how turkeys alter some of the mechanical features that are characteristic of a bouncing gait but unfavorable or impossible for an animal accelerating effectively.

First, we examined how turkeys alter horizontal propulsive forces to produce accelerations without losing their balance. The propulsive and braking components of the horizontal (fore–aft) ground reaction force developed during steady-speed running are important for balance because they maintain the alignment of the resultant ground reaction force with the center of mass of the body (Clark and Alexander, 1975). To increase speed, a runner must produce a net propulsive force impulse either by reducing braking forces or by increasing accelerative forces, or both. Humans appear to be able to produce purely accelerative forces during the first one or two steps of acceleration in a sprint (Cavagna et al., 1971) by leaning forward to position the center of mass in line with the forward-oriented ground reaction force (Harland and Steele, 1997). The posture of running birds makes this kind of adjustment unlikely, and it is unclear how birds might eliminate braking forces and still maintain balance. To determine how turkeys maintain balance while increasing propulsive horizontal forces during accelerations, we measured limb kinematics and ground reaction forces over a range of accelerations.

We also examined the pattern of mechanical energy changes of the body during a step to determine whether turkeys could generate exclusively positive work during a single step of an acceleration. Steady-speed running involves negative work; the kinetic and potential energies of the body decrease as the limb compresses in the first half of the step. Acceleration will be maximized if these mechanical energy losses are minimized. Any loss of energy from the body requires muscle–tendon units to absorb energy and reduces the time available during ground contact for positive work production by muscles. It is unclear whether the natural compliance and spring-like behavior (McMahon and Cheng, 1990; Farley et al., 1993) of the limbs of runners might make this energy absorption phase difficult to eliminate. We measured the pattern of change in mechanical energy of the body during a step to determine whether turkeys could completely eliminate negative work done on the body.

Many of the features of the mechanics of gait and muscle function appear to be common among vertebrate runners (Close, 1972; Cavagna et al., 1977; Dickinson et al., 2000). We used wild turkeys to investigate muscle function during acceleration because they are able runners and have served as a useful model for investigating the energetics and mechanics of muscle function during locomotion (Roberts et al., 1997, 1998). We measured the mechanical power output developed during a single step as turkeys accelerated over a force plate. To estimate the muscle-mass-specific power output of the entire hindlimb musculature, we measured total hindlimb muscle mass. We hypothesized that, despite the potential constraints imposed by the spring-like properties of the limbs, turkeys would develop power outputs during maximal accelerations that were near the limit expected for full recruitment of their hindlimb extensor muscles.

Materials and methods
Animals and running protocol

Five adult eastern wild turkeys *Meleagris gallopavo* L. were obtained from a local breeder. Two males and three females were used in this study. The mean body mass of the animals was 3.08 ± 0.27 kg (mean ± S.D.). Animals were housed in a large indoor enclosure at approximately 20 °C and fed food and water *ad libitum*.

Turkeys were trained to run along a 10 m track way. The runway was covered with a rubber surface 3 mm thick. For running trials, animals were positioned 0–2 m from the force plate, and ground reaction force and video were recorded as the animals accelerated. Only a small subset of the recorded runs could be included for analysis. To calculate the power output of a single limb, it was necessary to limit the analysis to runs in which only one foot contacted the force plate, and this contact had to be preceded and followed by an aerial phase (i.e. there could be no double-support period). In practice, this meant that the steps that could be analyzed were typically the second or third footfall of an acceleration. To minimize the effects of variation in speed, only accelerations in which the mean speed was between 1.75 and 2.25 m s^{-1} were analyzed. This speed range was chosen in part because it was difficult to elicit accelerations at higher speeds. Studies of sprinting humans suggest that maximal powers are developed within the first steps of an acceleration (Cavagna et al., 1971), but it is possible that turkeys develop higher power outputs than those measured at the speeds used in the present study.

Video analysis

Movements in the sagittal plane were recorded from a high-speed video camera (Redlake Motionscope 1000) operating at

250 Hz. Joint centers of rotation were marked with reflective tape (3M; 70610WS). The location of the hip was determined from a marker glued to the back at a known distance from the acetabulum. Another back marker located anterior to the first was used to determine the angle of the body. Video recordings were digitized to a Macintosh computer with a Scion LG-3 video capture card. The locations of the joint centers of rotation and back markers were determined using a custom-designed macro written for NIH Object-Image (a version of NIH Image adapted by Norbert Vischer; http://simon.bio.uva.nl/object-image.html) and smoothed in the program Igor (Wavemetrics) using a cubic spline interpolation (smoothing factor 1, s.D.=0.001 m).

Video data were used to determine limb protraction and retraction angle, the rotation of the body during stance and the initial velocities of the body for force-plate integrations. Protraction and retraction angle were calculated as the angle from vertical of a line drawn from the hip to the tarsometatarsal/phalangeal joint (Gatesy and Biewener, 1991). Protraction angle was measured at toe-down, and retraction angle was measured at toe-off. Two markers along the back were used to determine the angle of the back relative to the horizontal.

Mechanical energy and power

Force-plate (Kistler 9233a) measurements were used to determine the mechanical energy changes of the center of mass during single footfalls. Force-plate signals were acquired to computer with a 12-bit A/D board (National Instruments PCI-MIO-16E-1) using Labview software. Force signals were acquired at 1000 Hz and filtered in software with a bi-directional low-pass Butterworth filter with a cut-off frequency of 100 Hz. The start of video recording and force acquisition was triggered from an external signal to allow for synchronization of the two signals.

Changes in potential and kinetic energy during the contact period were calculated from the integrated vertical and horizontal forces (Cavagna, 1975). Integration of the horizontal forces allows determination of the change in horizontal kinetic energy during stance, and vertical force integration allows calculation of changes in potential and vertical kinetic energy. The sum of horizontal kinetic, vertical kinetic and gravitational potential energies gives the total mechanical energy change of the center of mass during the contact phase. Differentiation of the change in energy with respect to time yields the instantaneous power during foot contact. The mean rate of acceleration during the step was measured from the mean horizontal force divided by the mass of the animal.

In addition to the ground reaction forces, calculation of the energy changes of the body during a step requires a measure of the initial velocities of the center of mass. The horizontal and vertical positions of the hip were digitized for approximately 10 frames prior to toe-down, and these position data were differentiated with respect to time to estimate the velocity of the center of mass at the time of toe-down. Rotation

of the body may cause some error in estimating center of mass velocity from the velocity of the hip. Estimates of the rotation of the body at toe-down indicate that this error would be less than $0.2 \, \mathrm{m \, s^{-1}}$ for the initial vertical velocity and negligible for the initial horizontal velocity. A sensitivity analysis indicated that error in the initial velocity of the body had the largest effect on the calculated value for peak instantaneous power, and this error was less than 10 % of the calculated value.

Muscle-mass-specific power output was determined from the center of mass power and the total extensor muscle mass of the limb. The total limb extensor muscle mass of a single limb of three birds was determined by weighing each muscle. The muscle-mass-specific measures of work and power were calculated by dividing the estimates of the mechanical energy changes of the center of mass by the total hindlimb muscle mass. The resulting value gives the mean muscle power per unit hindlimb muscle mass necessary to power the measured changes in mechanical energy of the body.

It was assumed that the mean power output during stance represents the power developed by muscle contractile elements. Although elastic elements influence instantaneous power output at any given time during a muscle contraction, they cannot perform net work. Therefore, the mean power developed during a muscle contraction must be developed by muscle contractile elements. We assumed that significant elastic energy is not stored during the swing phase and recovered during stance.

Statistical analyses

Least-squares linear regression was used to determine the effect of acceleration on variables of interest. It was determined by analysis of covariance (ANCOVA) that there was no significant effect of individual bird on any of the values measured. Therefore, data for individuals were pooled for least-squares regressions.

Results
Rate of acceleration

The highest rates of acceleration measured during a single stance period exceeded $5 \, \mathrm{m \, s^{-2}}$ (Fig. 1). At the running speeds studied, this corresponded to an increase in speed of approximately $1 \, \mathrm{m \, s^{-1}}$ during a single step. There was no significant correlation between running speed and acceleration for the runs analyzed (r^2=0.004, P=0.66). The 49 runs analyzed were obtained from more than 500 trials in which animals produced a range of accelerations. Thus, although it is impossible to be certain that maximal-effort accelerations were elicited, it seems likely that the highest accelerations recorded represent at least near-maximal effort.

Ground reaction forces and balance

Turkeys accelerated by both decreasing the braking component of the horizontal ground reaction force and increasing the propulsive force. This is illustrated by the representative plots of ground reaction force during a single
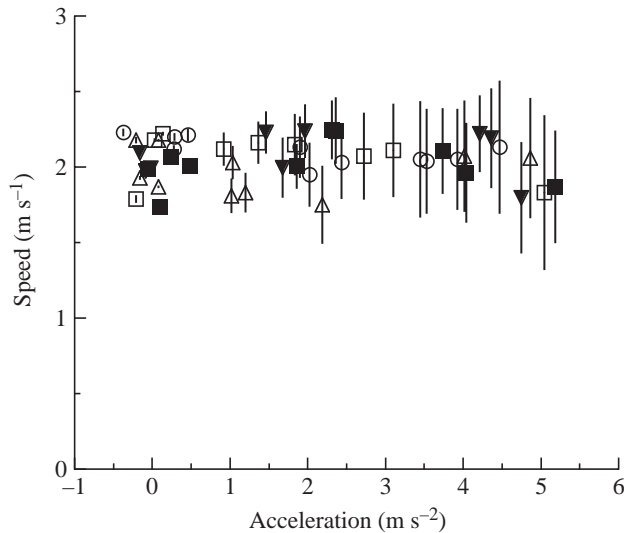
Fig. 1. The mean velocities (symbols) and the velocity change from toe-down to toe-off (vertical lines) for each acceleration analyzed. The highest accelerations corresponded to a change of nearly $1\,\mathrm{m\,s^{-1}}$ in the speed of the center of mass during a single footfall. Mean running speed was independent of acceleration for the runs analyzed.

forces; peak propulsive horizontal forces were more than 40 % of peak vertical force during the fastest accelerations (Fig. 3B).

Increases in horizontal propulsive forces were associated with a more anteriorly oriented resultant ground reaction force vector (Figs 2, 3C). During steady-speed running, the ground reaction force is posteriorly oriented during the first half of the step and anteriorly oriented during the second half, such that the average orientation of the ground reaction force is vertical (Fig. 2A). Limb protraction and retraction angles mirror this pattern, and the average position of the limb during stance is vertical. If the limb posture observed during steady-speed running were maintained during accelerations, the anteriorly oriented ground reaction force would lead to excessive pitching of the body about a transverse axis. We found that in accelerating turkeys alignment between the center of mass and the ground reaction force was maintained in part by changes in limb kinematics. Turkeys decreased limb protraction angle and increased limb retraction angle as their rate of acceleration increased (Figs 2, 4A,B). These changes tended to position the center of mass more anterior to the point of force application and therefore helped maintain the alignment between the center of mass and the more anteriorly oriented ground reaction force during accelerations. On average, increases in limb retraction angle equaled decreases in limb protraction angle, resulting in no change in the total angle swept by the limb during stance ($P=0.67$). Changes in limb angle helped to maintain alignment between the center of mass and the ground reaction force, and there was no significant change in the net body rotation during the contact phase as a function of acceleration (Fig. 4C).

Mechanical power output

Turkeys increased power output for acceleration by decreasing the negative power developed by the hindlimbs and

stance phase in a steady-speed run (Fig. 2A) and a high acceleration (Fig. 2B). Peak horizontal forces during steady-speed runs (acceleration approximately zero) were approximately 10 % of peak vertical force, a value typical for running animals (Cavagna et al., 1977). During the highest accelerations, turkeys produced peak propulsive forces exceeding one body weight and braking forces at or near zero (Fig. 3A). Peak vertical forces also increased with acceleration (Fig. 3A). Horizontal forces increased more than vertical

Fig. 2. Representative force traces and kinematic diagrams for a steady-speed run (A) and a high acceleration (B). High accelerations involved high peak propulsive horizontal forces (dotted lines), no braking horizontal forces and a delay in vertical force (solid line) development. The insets in the force graphs represent the mean orientation of the ground reaction force vector during stance. The turkey diagrams illustrate the changes in limb angle during acceleration that help to maintain the alignment between the forward-oriented ground reaction force (bold arrow) and the center of mass.
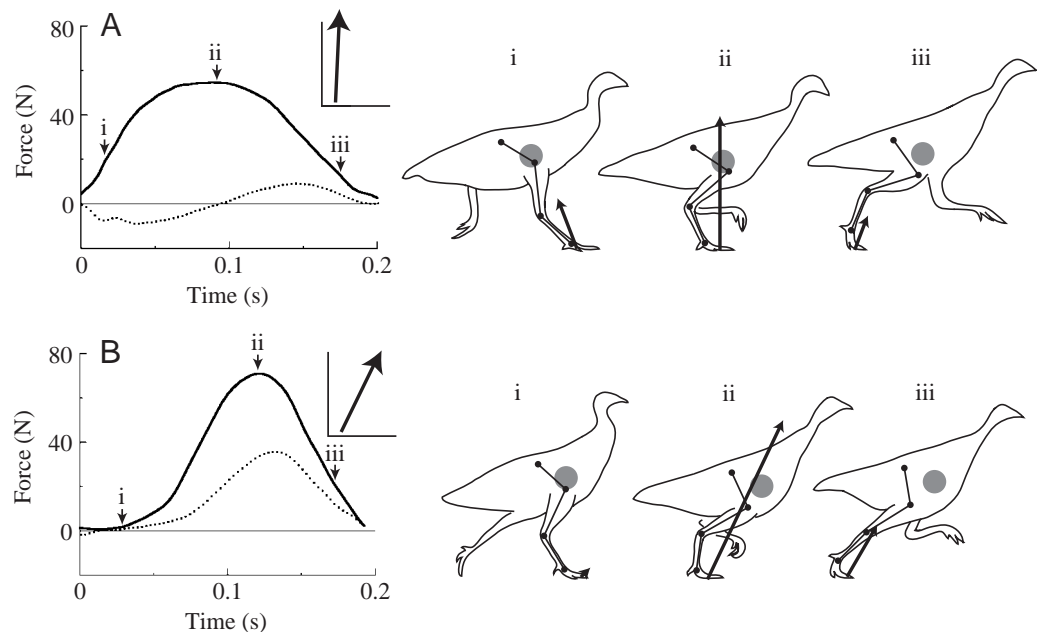
These diagrams were traced from video frames at the times indicated by arrows on the force graphs. The gray shaded circle represents the approximate location of the animal's center of mass.
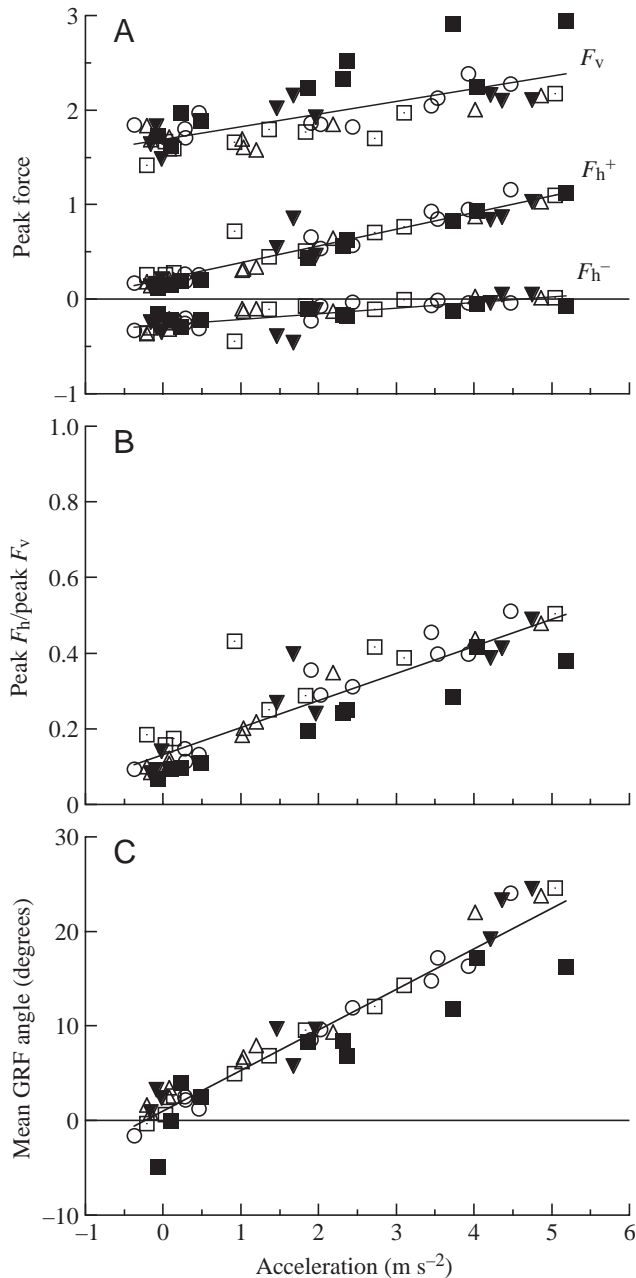
Fig. 3. Peak horizontal propulsive ground reaction force F_h^+ and peak vertical force F_v increased with acceleration, while negative horizontal forces F_h^- decreased (A). Force is given as a proportion of body weight. The peak propulsive horizontal force, as a fraction of peak vertical force, increased with acceleration (B). The mean angle of the resultant ground reaction force (GFR) from vertical, averaged over the stride, increased with acceleration (C). Linear regressions (N=49) are shown for F_v (y=0.13x+1.69, r^2=0.52, P<0.01), F_h^+ (y=0.18x+0.207, r^2=0.91, P<0.01), F_h^- (y=0.06x–0.27, r^2=0.61, P<0.01), F_h/F_v (y=0.071x+0.132, r^2=0.81, P<0.01) and ground reaction force angle (y=4.28x+1.03, r^2=0.91, P<0.01).
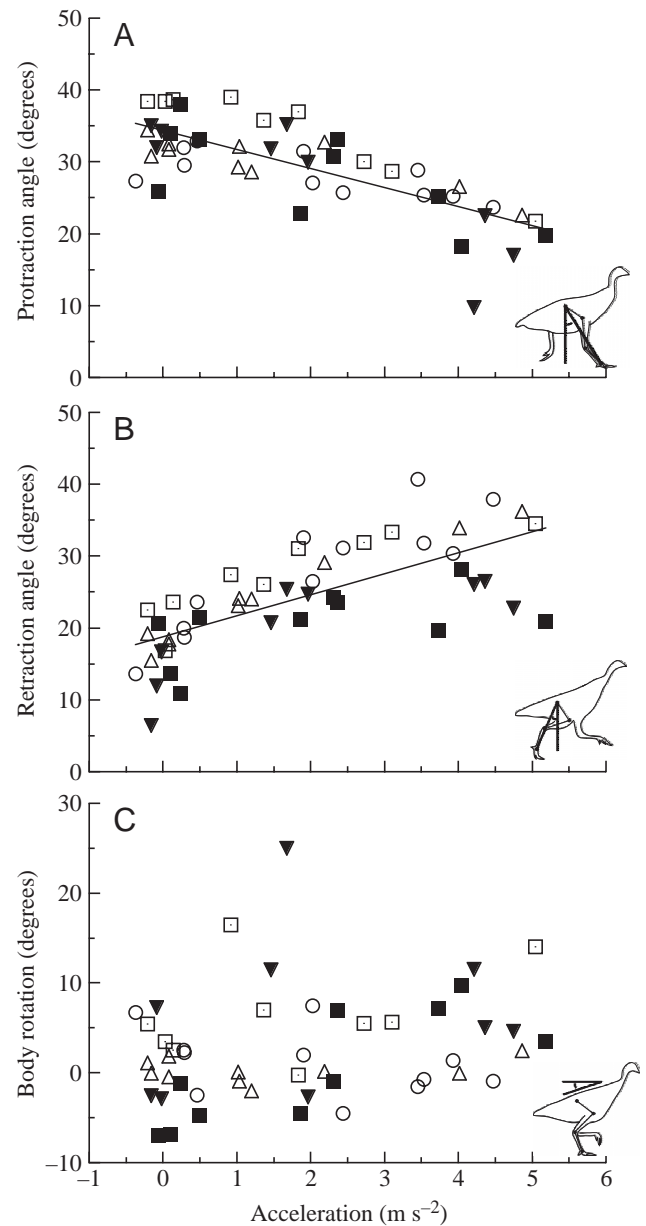

Fig. 4. Increasing acceleration correlated with a decrease in hindlimb protraction angle (A) and an increase in retraction angle (B). The net pitch of the body (the angle at toe-off minus the angle at toe-down) did not change significantly (y=0.84x+1.15, r^2=0.06, P=0.10) with increasing acceleration (C). Linear regressions (N=49) are shown for protraction angle (y=2.64x+34.36, r^2=0.55, P<0.01) and retraction angle (y=2.92x+18.74, r^2=0.49, P<0.01).

increasing the positive power (Fig. 5). The power profiles during accelerations were asymmetrical, peak power outputs occurred late in the stance phase. The area under the negative region of the curves represents energy absorbed by

muscle–tendon units (negative work), while the area under the positive region of the vertical axis is the positive work done by the muscle–tendon. As expected, negative and positive work at steady running speeds were approximately equal, resulting in negligible net work (Fig. 5).

Most of the increase in the net muscle work performed during accelerations resulted from an increase in the positive work done by muscles (Fig. 6). A decrease in the mechanical energy loss of the center of mass (negative work) also
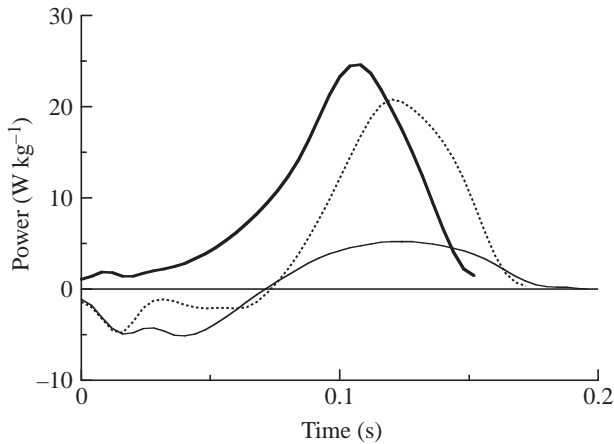
Fig. 5. Body-mass-specific power output profiles for a steady-speed run (thin solid line), a moderate acceleration (dotted line) and a high acceleration (thick solid line). The mean accelerations for these runs were 0.1 m s^{-2} (steady), 2.4 m s^{-2} (moderate) and 4.7 m s^{-2} (high).
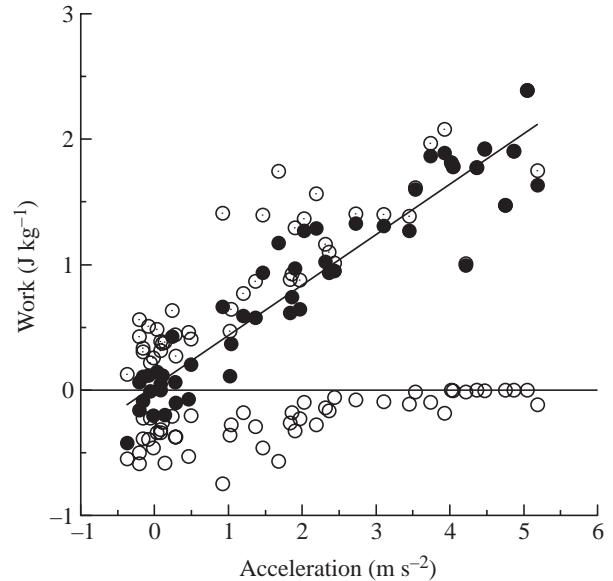

Fig. 6. Body-mass-specific work done per step as a function of acceleration. Net work (filled circles) increased as a result of both an increase in positive work (dotted circles) and a decrease in negative work (open circles). For the fastest accelerations, only positive work was performed. All birds are represented by the same symbol for clarity. The linear regression (N=49) is shown for net work (y=0.402x+0.034, r^2=0.89, P<0.01).

contributed to the increase in net work with acceleration. During the highest accelerations, the total mechanical energy of the body showed no period of decrease, and only positive work was performed.

Muscle-mass-specific mechanical power and work

The hindlimb muscle mass potentially available to power accelerations was measured from turkeys of similar age and condition to those used for the running experiments. The total mass of all hindlimb muscle (including hip, knee, ankle and phalangeal extensors and flexors) was 7.7 ±0.3 % of body mass for one limb (N=3 animals, mean ± S.D.).

The power and work produced per unit limb muscle mass was remarkably high during high accelerations. Fig. 7 shows the peak instantaneous power output of the muscle–tendon units of the hindlimb, calculated from total hindlimb extensor muscle mass and the body center of mass power. Peak muscle-mass-specific power outputs increased with increasing acceleration. The highest measured peak power outputs exceeded 400 W kg^{-1} muscle mass. The mean power produced during the stance phase also increased with increasing acceleration, with the highest values exceeding 150 W kg^{-1} muscle. This measure gives a conservative estimate of muscle–tendon power output because it assumes complete activation of all muscles, which is unlikely during our measurements.

Discussion
Muscle power output during acceleration

Do muscles generally operate at their highest power outputs during locomotion? Sprinting at maximal speed involves high rates of metabolic power consumption and might be expected to elicit muscle power outputs exceeding those observed during acceleration. However, during steady-speed running, the mechanical energy absorbed in the first half of the step is nearly

equal to the energy produced in the second half of the step, resulting in a mean power output close to zero. Very high instantaneous mechanical power outputs occur at the highest running speed during a maximal sprint in humans, but estimates of the contribution of elastic energy storage and recovery in a sprint suggest that the power output from muscle contractile elements at a top running speed of 8 m s^{-1} is less than the power developed in the initial push-off (Cavagna et al., 1971). Elastic energy storage and recovery may allow muscle contractile elements to operate primarily as near-isometric struts even at the fastest running speeds. Thus, at the level of the contractile elements, steady-speed running might be characterized as a low-power gait. Studies of running lizards support this idea: *Coleonyx variegatus* and *Eumeces skiltonianus* develop 3.9 times as much positive mechanical power running at their top speed on an incline compared with their maximal running speed on the level (Farley, 1997). Direct measurements of muscle force and power *in vivo* have demonstrated that animals can run or hop at high speeds with active muscles that produce high forces but little mechanical power (Biewener et al., 1998b; Roberts et al., 1997).

Do turkey muscles operate at high power outputs during accelerations? A few direct measurements of muscle power output *in vivo* in locomotor systems that should be specialized for power production provide a source of comparison. Swimming and flying both require high muscle power outputs to overcome drag. Direct measurements of *in vivo* muscle function in swimming scallops (Marsh et al., 1992) and flying pigeons (Biewener et al., 1998a) reveal muscle power outputs
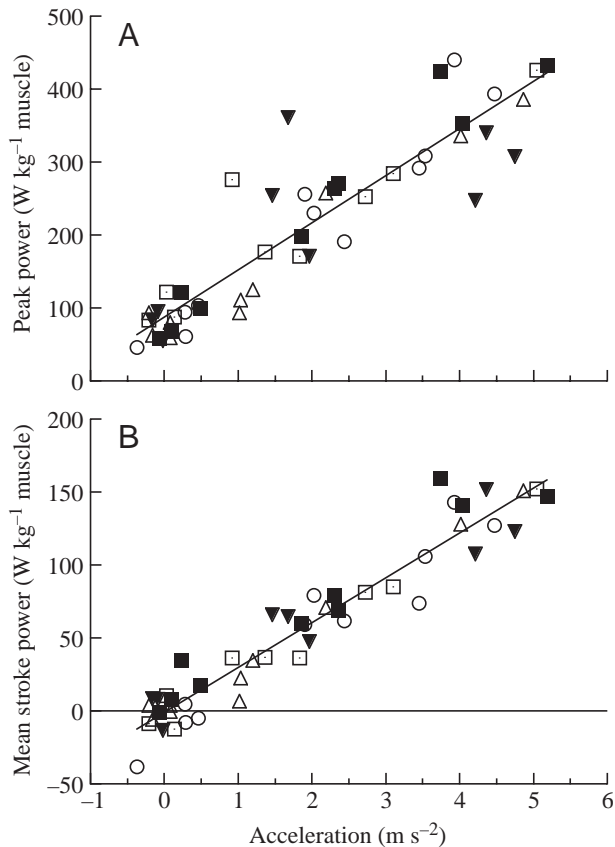
Fig. 7. Peak instantaneous muscle power produced per unit muscle mass increased with increasing acceleration (A). The power averaged over the entire stance period, the mean stroke power, increased with increasing acceleration (B). Muscle-mass-specific powers were calculated by assuming that all hindlimb extensors contributed to the power applied to the center of mass. Linear regressions (N=49) are shown for peak power output (y=64.7x+87.5, r^2=0.84, P<0.01) and mean stroke power (y=30.8x–1.1, r^2=0.93, P<0.01).

that are similar to those observed for the hindlimb musculature of turkeys during acceleration (to eliminate the effects of duty cycle, Table 1 compares only the power developed during muscle contraction, or stroke power). Estimates of power developed during take-off in quail indicate substantially higher power outputs (Askew et al., 2001). Differences between pigeon and quail power output in Table 1 are due in part to submaximal power outputs required during steady-speed, level flight; kinematic studies suggest that muscle power outputs during take-off can be twice those measured for level flight (Dial and Biewener, 1993). Power outputs for turkey hindlimbs are also much lower than estimated values for quail pectoralis.

Differences in contractile properties probably explain some of the variation in power output. Quail pectoralis is composed of fast glycolytic fibers and can power flight for only brief bursts. The hindlimb musculature of galliforms is capable of powering sustained running and contains a mixture of fiber types (Talesara and Goldspink, 1978). Measurements of the contractile properties of the gastrocnemius of wild turkeys (F. E. Nelson and T. J. Roberts, unpublished observations) indicate peak isotonic power outputs similar to those measured for fast oxidative muscles in mice (372.4 W kg^{-1} for mouse extensor digitorum longus; Askew and Marsh, 1997) and lower than the sustained mean power output observed in quail (Askew et al., 2001).

The peak instantaneous values for hindlimb muscle mass power output during high accelerations in turkeys exceeded 400 W kg^{-1}. The high instantaneous power output suggests an elastic contribution to power output late in stance phase. Even if the intrinsic power-generating capacity of the turkey hindlimb musculature exceeds 400 W kg^{-1}, is it likely that some muscle–tendon units must produce instantaneous power outputs in excess of muscle capacity during maximal accelerations. The measured values for muscle-mass-specific power output are calculated on the basis of the assumption that all hindlimb skeletal muscles actively produce power during acceleration, because it is difficult to eliminate definitively any given muscle from some potential contribution to power output

Table 1. In vivo *stroke power and work output for cyclical muscle contractions during locomotion*

Muscle(s)	Activity	Stroke power (W kg^{-1})	Stroke work (J kg^{-1})	Reference
Scallop adductor	Swimming	120	20	Marsh et al. (1992)
Pigeon pectoralis	Flying (steady-speed)	130	10	Biewener et al. (1998a)
Quail pectoralis	Flying (take-off)	560	17.7	Askew et al. (2001)
Turkey hindlimb extensors	Acceleration	150	26	This study

Values presented are per unit muscle mass.

Scallop values are calculated from values for the first cycle in a swim of *Chlamys hastata*, 62 W kg^{-1}, and a reported stroke time of 51% of the cycle. Pigeon (*Columba livia*) values are calculated from the reported power output during steady flight, 70 W kg^{-1}, and the fraction of the wingbeat cycle spent in downstroke, 0.63. Quail (*Coturnix Chinensis*) power output is calculated from the mean power reported for a complete wingbeat cycle in take-off (390 W kg^{-1}) and the fraction of the wingbeat cycle spent in downstroke, 0.70.

during accelerations. However, it is likely that some muscles cannot contribute. For example, flexors of the ankle and hip are unlikely to produce significant power output during the stance phase of acceleration because these joints do not undergo significant flexion. Muscles involved primarily in adduction or abduction of the limb may also be less likely to contribute to powering forward locomotion. The present study also underestimated mechanical power output because the work necessary to accelerate the mass of the limbs during the step and the work associated with co-contraction of muscle antagonists were not estimated. These components of work are expected to be small relative to the work required to accelerate the body but would require some muscle power output during acceleration.

Ground reaction forces produced during acceleration.

One of the features of a bouncing gait that allows muscle–tendon units to operate economically as springs is the pattern of braking and propulsive horizontal ground reaction forces developed in each step. Horizontal forces produced during a steady-speed running step actually increase the work muscle–tendon units must do (Clark and Alexander, 1975), but they improve muscle mechanical advantage, reduce the muscle force required to support body weight (Chang and Kram, 1999; Full et al., 1991) and contribute to balance by limiting body pitching (Clark and Alexander, 1975). The importance of maintaining the alignment of the ground reaction force and center of mass is illustrated by the observation that humans running in reduced gravity reduce their horizontal forces in proportion to the reduced vertical force to maintain a similar ground reaction force angle (Chang and Kram, 1999).

To accelerate, an animal must produce forward-oriented ground reaction forces while still maintaining balance and reasonable joint moments. A turkey running with the limb kinematics observed during a steady-speed run and the ground reaction force observed during a high acceleration would experience a mean moment about the center of mass of $9\,N\,m$ that would tend to pitch the body about a transverse axis. This moment would result in $300°$ of body rotation in $200\,ms$, approximately the time of one step (based on an estimated body moment of inertia of $0.035\,kg\,m^2$). Thus, in the absence of a mechanism to maintain the alignment of the ground reaction force and the center of mass, the propulsive forces produced by an accelerating turkey would be sufficient to produce nearly a full backward rotation of the body in a single contact period.

Interestingly, examples from three studies of acceleration reveal three different mechanisms for maintaining alignment between the ground reaction force and the center of mass during accelerations. To maintain alignment between the center of mass and ground reaction force, an accelerating runner must either position its center of mass more anteriorly (relative to steady-speed running) or position the point of force application more posteriorly. Human runners rely primarily on the first of these options, leaning forward during the accelerative portion of a sprint to position the center of mass

anterior of the foot and in line with the forward-oriented ground reaction force vector (Harland and Steele, 1997). In contrast, dogs accelerate during a trot by redistributing vertical force between the fore- and hindlimbs to position the mean origin (center of pressure) of the ground reaction force more posteriorly (Lee et al., 1999).

Some of these mechanisms are unavailable to running birds because their center of pressure is constrained to the area of their foot and their center of mass is positioned anterior to their hip during normal running. Instead, during an acceleration, turkeys alter their angle of limb retraction and protraction to keep the center of mass anterior to the foot during most of the step. Changes in the pattern of force development also contribute to the alignment of the center of mass and ground reaction force during acceleration. An increase in the magnitude of the vertical force means that the angle from vertical of the ground reaction force for any given propulsive force is smaller. Also, during accelerations, the development of the vertical ground reaction force is delayed with respect to the time of foot contact so that the body is positioned more anteriorly by the time significant force is developed (Fig. 2). These mechanisms allow turkeys to produce the high propulsive forces needed in an acceleration without losing balance.

How quickly can turkeys accelerate?

There is little information available to estimate how quickly animals can accelerate to top speed. Our measurements are based only on power outputs during single footfalls near one running speed, but they can provide a first estimate of the time it would take a turkey to accelerate to top speed, assuming that they maintain the same power output across their entire speed range. At a top speed of $7\,m\,s^{-1}$ (based on our own observations of free-running turkeys), a turkey's kinetic energy is $24.5\,J\,kg^{-1}$ body mass. The maximum stroke power measured here of $11.5\,W\,kg^{-1}$ body mass suggests that the animal would be able to accelerate to this top speed in just over $2\,s$ (assuming a duty factor of 0.5). If we assume a mean stride frequency of $2.5\,Hz$ (Gatesy and Biewener, 1991), the animal would reach maximum speed in approximately four strides.

Elastic energy storage and recovery during accelerations

What role does elastic energy storage and recovery play in accelerations? Two features of the power profile suggest that redistribution of muscle power by storage and recovery of strain energy in elastic elements is important during powerful accelerations. First, values for peak instantaneous power output of the entire hindlimb musculature during the highest accelerations exceed $400\,W\,kg^{-1}$. Although recent data suggest very high power-generating capacity in pectoralis muscle of galliform birds (as high as $400\,W\,kg^{-1}$ sustained power), it is likely that the very high power output measured during turkey accelerations results in part from the amplification of muscle power by the recoil of elastic elements late in the step. Second, our estimates of the high mean stroke power developed during the step indicate that the muscle contractile units must operate

at a relatively constant, high power output during the entire step (Fig. 7B). Given the very low power applied to the body during the first half of the step (Fig. 5), a high mean muscle power output is possible only if, during this time, muscle power is applied to the stretch of elastic elements rather than to increasing the mechanical energy of the body. The asymmetric power profile is consistent with the idea that muscle shortening directly stretches elastic elements to store elastic strain energy in the first half of the step. Then, during the second half of the step, both muscle power and released elastic power are applied to the body.

A similar mechanism of elastic energy redistribution of muscle power has been suggested for specialized jumpers, frogs (Marsh and John-Alder, 1994) and galagos (Aerts, 1997). Jumping humans also use store and recover muscle work as tendon strain energy during squat jumps; modeling suggests that tendons store and recover nearly the same amount of energy in a squat jump and a counter-movement jump (Anderson and Pandy, 1993), and elastic energy recovery in the second half of a jump enhances muscle–tendon shortening velocity and power output (Bobbert, 2001; Kurokawa et al., 2001). The similarity between the power profiles for jumping animals and accelerating turkeys suggests that the redistribution of muscle power by elastic mechanisms may be generally important for muscle-powered accelerations in vertebrates.

Why store and recover muscle work in elastic elements during an acceleration? The most obvious explanation is that, by necessity, tendons must stretch and recoil whenever muscular force is produced. The difference between steady-speed running and acceleration appears to be the source of the stored elastic strain energy. During steady-speed running, some of the mechanical energy of the body is converted into elastic strain energy as the body slows and lowers during the first half of the step. During maximal accelerations in turkeys, there is no decline in the total mechanical energy of the body, and stored elastic strain energy must be supplied directly from active shortening of muscle fibers. Although this redistribution may result simply from the fact that elastic storage and recovery cannot be avoided, it seems likely that elastic energy storage and recovery may actually enhance muscular power production during accelerations. Redistribution of muscle power may facilitate the dramatic change in muscle fiber shortening necessary as muscles transition between the strut-like function of muscle contractile elements during steady-speed running and the power-producing motor-like function during acceleration. Because muscle shortening is applied to tendon stretch rather than to movements of the body, this mechanism may allow an uncoupling of body movement and muscle movements necessary to produce high muscle power outputs.

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