

Performance of guinea fowl *Numida meleagris* during jumping requires storage and release of elastic energy

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Summary

The ability of birds to perform effective jumps may play an important role in predator avoidance and flight initiation. Jumping can provide the vertical acceleration necessary for a rapid takeoff, which may be particularly important for ground-dwelling birds such as phasianids. We hypothesized that by making use of elastic energy storage and release, the leg muscles could provide the large power outputs needed for achieving high velocities after takeoff. We investigated the performance of the leg muscles of the guinea fowl *Numida meleagris* during jumping using kinematic and force-plate analyses. Comparison of the methods indicated that in this species the wings did not supply energy to power takeoff and thus all the work and power came from the leg muscles. Guinea fowl produced a peak vertical force of 5.3 times body weight. Despite having lower muscle-mass-specific power

output in comparison to more specialized jumpers, guinea fowl demonstrated surprisingly good performance by producing muscle-mass-specific work outputs of 45 J kg^{-1} , a value approximately two thirds of the maximal expected value for skeletal muscle. The muscle-mass-specific peak power output during jumping was nearly 800 W kg^{-1} , which is more than twice the peak isotonic power estimated for guinea fowl leg muscles. To account for high power outputs, we concluded that energy has to be stored early in the jumps and released later during peak power production, presumably using mechanisms similar to those found in more specialized jumpers.

Key words: jumping, elastic energy storage, guinea fowl, *Numida meleagris*, power output, work output, takeoff, locomotion, kinematics, force plate, muscle.

Introduction

On first consideration, it may seem odd to study jumping performance in a bird. However, a case can be made that many flying birds need to supplement their locomotor repertoire with effective jumping. The power required for flight is high at low speeds (Rayner, 1979), thus birds face a particular problem in initiating flight because they must accelerate through a range of low speeds to reach their flight speed. Among other reasons, maximizing takeoff performance is important for avoiding predation (Witter et al., 1994) and, thus, rapid vertical acceleration may be particularly important for ground-dwelling birds such as phasianids that rely on fast takeoffs as a means of escape. The power required for flight shortly after takeoff in these birds is very high just to maintain a constant upward velocity after the initial leap into the air, and using the flight muscles to also supply the initial acceleration is probably beyond the power-generating capacity of the flight muscles. For example, during vertical flights immediately following takeoff, the flight muscles of the diminutive blue-breasted quail *Coturnix chinensis* have the highest mass-specific power outputs during cyclical contractions yet recorded (Askew et al., 2001; Askew and Marsh, 2001). Other larger phasianids must also produce very large powers to sustain climbing flights

following takeoff (Tobalaska and Dial, 2000; Askew et al., 2001). Therefore, even though the musculoskeletal system in the legs of these birds may be primarily adapted for walking and running, this system must also provide high power outputs during the leap into the air that allows these animals to become airborne.

Small animals specialized for jumping produce an enormous amount of power to accomplish the task of jumping. For example, during vertical jumping the 0.25 kg primate *Galago senegalensis*, the lesser galago or bush baby, produces a muscle-mass-specific power output in excess of 2400 W kg^{-1} (Hall-Craggs, 1965; Gunther et al., 1991; Aerts, 1998). Small frogs also deliver impressive amounts of power during jumping. Peplowski and Marsh (1997) investigated jumping performance of the Cuban tree frog *Osteopilus septentrionalis* and predicted a peak muscle-mass-specific power output of the hindlimb muscles of over 1600 W kg^{-1} , a value exceeding the power available from the muscles by sevenfold. These extraordinary performances are made possible by power amplification mechanisms involving elastic energy storage and release. These mechanisms allow the animal to temporally redistribute the work done by the muscles and transiently

produce power in excess of that which is available from direct power output by the muscle fibers alone.

Birds have been used in a variety of studies of walking, running and flight, but their jumping performance has received much less scrutiny. Heppner and Anderson (1985) investigated takeoff in the common pigeon *Columba livia* and concluded that leg thrust represented a considerable contribution to forces generated during takeoff. Earls (2002) focused on the kinematics and mechanics of ground takeoff in the European starling *Sturnis vulgaris* and the common quail *Coturnix coturnix*. Her study discussed the evolution of flight in birds and illustrated the key role that jumping plays in takeoff. Using a combination of kinematic and force-plate data, Earls demonstrated that both species of birds performed primarily leg-driven takeoffs; starling leg muscles produce 91% of the total vertical velocity at lift-off and quail leg muscles account for 88% of the total vertical velocity and 100% of the horizontal velocity. Neither of these studies examined whether the measured jumping performance required elastic energy storage and release.

The goal of our study was to examine what mechanisms for enhancing jumping performance are available in a bird specialized for running, the helmeted guinea fowl *Numida meleagris*. We asked whether during jumping these animals rely on the same power amplification mechanisms used by more specialized vertebrate jumpers, such as frogs and some primates. Because the legs of guinea fowl are primarily used during terrestrial locomotion performance, trade-offs may exist in order to achieve adequate performance in both running and jumping. Helmeted guinea fowl were chosen for this study because of their convenient size and ability to be readily trained to jump. Untrained birds were observed to spontaneously jump to heights of up to 1 m. Additionally, their taxonomic relationship to the common quail facilitates comparisons between our data and that obtained by Earls (2002). Guinea fowl are native to West Africa and locomote primarily by running; they seldom fly unless startled and attempting escape (Ayeni, 1982). We hypothesized that the jumping performance of guinea fowl would be sufficient to require prestorage of elastic energy to power maximal jumps.

Materials and methods

Animals

The experimental group consisted of six mature guinea fowl *Numida meleagris* L. approximately 20 months old weighing 1.42 ± 0.10 kg (mean \pm S.E.M.). These birds were obtained as day-old chicks from the Guinea Farm (New Vienna, IA, USA) and were raised in the Division of Laboratory Animal Medicine at Northeastern University. All procedures involving live animals were approved by the Northeastern University Animal Care and Use Committee.

Mass of leg muscles that could power the jump

At the end of the jumping trials, the animals were sacrificed with an overdose of sodium pentobarbital. Within 24 h of

death, all the hindlimb muscles were dissected and weighed. The individual masses were recorded and the sum of the masses of all the muscles (M_m) calculated. For the purposes of calculating muscle-mass-specific work and power we summed the masses of all the muscles that could possibly have contributed to jumping ($M_{m,j}$). We excluded six muscles from this sum because these muscles are anatomically positioned so that they could not produce moments leading to extension at the hip, knee or ankle, or flexion at the toe joint (Hudson, 1959; Gatesy, 1999). These muscles were the ilirotrochanteric medius and cranialis, the tibialis cranialis, the extensor digitorum longus, the iliotibialis cranialis and the anterior portion of the iliofibularis. The iliotibialis cranialis, which is a swing phase muscle in running (Marsh et al., 2004), can produce a knee extensor moment, but the hip flexor moment arm of this muscle is much larger than the knee extensor moment arm. Given that during jumping the amount of hip extension is larger than the amount of knee extension (see Results), the iliotibialis cranialis probably cannot shorten and do positive work in the jump. A similar argument applies to the anterior portion of the iliofibularis, which is another swing phase muscle in running (Marsh et al., 2004). This portion of the iliofibularis has a very small hip extensor moment arm and a large flexor knee flexor moment arm (T. A. Hoogendyk, personal communication).

Training

The goal of our study was to isolate, as much as possible, the jumping performance powered by the leg muscles from contributions of the wings occurring before toe-off. Therefore, we designed a task that involved a nearly vertical jump, with no subsequent phase of powered flight. The jumping regimen consisted of conditioning the birds to jump from a platform up and through the open door of an otherwise enclosed cage. The platform was gradually lowered, thus encouraging the birds to perform higher jumps to reach the cage. Upon completion of each successful jump, the bird was given a food reward of live crickets. This jumping routine was conducted three times per week. The birds' wings were clipped to reduce their contribution to the jump. Because these birds were also used in a study comparing the function of the lateral gastrocnemius in jumping and running, they were also trained to run on a treadmill. The treadmill training regimen for running consisted of having the birds run on a motorized treadmill using the following routine: 5 min at 1.5 m s^{-1} , 10 min at 2.0 m s^{-1} , 3 min at 0.5 m s^{-1} , and 12 min at 2.5 m s^{-1} . This regimen was done three times a week to allow the birds to become accustomed to running steadily on the treadmill. The birds underwent training for jumping and running for a period of 6–8 weeks prior to experimentation.

Jumping procedures

The jumping arena was surrounded by a three-sided clear acrylic box. The lateral sides of the box were 122 cm high and 91 cm long. The side behind the bird was 46 cm high and 66 cm wide. The cage into which the birds jumped was

constructed of wire mesh with dimensions of 56 cm×75 cm×49 cm (width×length×height). The cage was placed on a cart positioned at the open side of the box. The jumping platform was placed on the floor within the acrylic box. The platform was constructed of 2.5 cm thick plywood measuring 30 cm long and 20 cm wide. A 10 cm×10 cm opening along the right side of the platform was made to accommodate a force plate, which was flush with the platform surface. The wooden platform and force plate were raised and lowered by the addition or removal of 5 cm thick cement slabs (46 cm×15 cm). Maximal jumping height attained was 84 cm from the platform to the bottom of the open cage door into which the bird jumped.

The force plate consisted of an aluminum plate (10 cm×10 cm) bolted to a single triaxial quartz force transducer (Model 9067, Kistler, Winterthur, Switzerland) capable of measuring three orthogonal components of a dynamic or quasistatic force. The transducer was pre-stressed between two steel plates. There was low cross talk amongst the channels on the force transducer ($F_z \rightarrow F_x, F_y \leq \pm 1\%$; $F_x \leftrightarrow F_y \leq 3\%$; $F_x, F_y \rightarrow F_z \leq 3\%$) and resonance frequencies ranged from 400 Hz to 800 Hz, depending on the direction of measurement. The transducer was connected to 3, Type 5010, Kistler charge amplifiers. The outputs from the amplifiers were connected to a 16-bit multiplexed A–D converter (PowerLab model 16 sp, ADInstruments, Colorado Springs, CO, USA) interfaced with a Macintosh G4 computer running the application chart from ADInstruments. Data were collected at 2000 Hz. Each force component was calibrated by first zeroing the output and loading the plate uniaxially with a known weight. Weights were chosen to be within the normal range of forces measured in the jumps. Mediolateral forces are not discussed here because, for jumps parallel to the sagittal plane of the animal, the mediolateral force produced by one leg is cancelled by an equal and opposite force produced by the contralateral leg.

Videography

For the measurements reported here, the platform was positioned approximately 84 cm beneath the cage opening. The jumps were video taped from a lateral view at 500 frames s⁻¹ using a high-speed video system (NAC HSV-1000, Simi Valley, CA, USA). Only jumps in which it could be verified that only one foot was on the force platform were analyzed. Verification was done by placing a digital video camera at the rear of the jumping platform to give a clear view of foot placement throughout the jump. Video measurements were synchronized to force measurements using a square-wave signal generated by the PowerLab and recorded on the video fields using a NAC wave inserter.

Birds were prepared for the measurements by trimming feathers where needed and placing a series of markers on the body (Fig. 1). One marker was placed on the back immediately above the hip joint; a second marker was placed at the midpoint between the base of the neck and synsacrum; a third marker was placed on the anterior end of the sternum. The centers of the hip, knee, ankle (tibiotarsal–tarsometatarsal) and toe

(tarsometatarsal–phalangeal) joints were marked with white dots. The tip of digit III was also painted white.

Calculating muscle performance from kinematics

NAC video recordings were played back on a Panasonic AG-1830 VCR capable of field-by-field playback. A series of single fields was captured using a Data Translation video-capture board and analyzed using NIH Image v1.63. Three jumps at a height of 84 cm were analyzed from each animal, resulting in a total of 18 jumps. The following data were obtained: joint angles for the hip, knee, ankle and toe, takeoff velocities, toe-off angle, acceleration, body-mass-specific power output, muscle-mass-specific power output and muscle-mass-specific work output.

The hip, ankle and toe markers were tracked in every frame and used in the joint angle calculations. The position of the knee joint cannot be determined accurately throughout the jump using a surface marker because of movement of the skin, particularly during the pre-jump crouch. However, using the law of cosines, knee angle can be calculated from the distance between the hip and ankle joint centers, assuming constant segment lengths of the femur and tibiotarsus. Femoral and tibiotarsal segment lengths were estimated from average lengths measured from five video fields during which the knee angle was approximately 90°. At this angle, the knee joint marker accurately reflects the joint center. Angles were reported such that extension of the hip, knee and ankle joints and flexion of the toe joint cause an increase in angle (Fig. 1). This convention reflects the expectation that active extension of the hip, knee and ankle joints, and active flexion of the toe joint will contribute to powering the jump. The approximate center of mass was determined by averaging the positions of the sternum and synsacrum markers (Earls, 2002). Tracking the center of mass in this way does not correct for changes in the center of mass due to leg extension (see Results and Discussion).

Kinematically determined performance variables were calculated by tracking the position of the center of mass. Values determined from kinematics are designated by the subscript ki. Vertical and horizontal position data for the center of mass were smoothed using a smoothing spline interpolation in the software application Igor Pro (Wavemetrics, Lake Oswego, OR, USA). Vertical ($\mathbf{V}_{V,ki}$) and horizontal ($\mathbf{V}_{H,ki}$) velocities in m s⁻¹ were obtained by differentiating the smoothed displacement data and vertical ($\mathbf{a}_{V,ki}$) and horizontal ($\mathbf{a}_{H,ki}$) accelerations were obtained by differentiation of the velocity curves. Horizontal force ($\mathbf{F}_{H,ki}$) in N was calculated as $\mathbf{F}_{H,ki} = M_b \mathbf{a}_{H,ki}$; vertical force ($\mathbf{F}_{V,ki}$) in N was calculated as $\mathbf{F}_{V,ki} = M_b \mathbf{a}_{V,ki} + g M_b$ (where M_b is body mass and g is gravitational acceleration). Resultant takeoff velocity ($\mathbf{V}_{res,ki}$) was calculated as the vector sum of the vertical and horizontal velocities: $\mathbf{V}_{res,ki} = \sqrt{(\mathbf{V}_{H,ki})^2 + (\mathbf{V}_{V,ki})^2}$. Horizontal ($\dot{W}_{H,ki}$) and vertical ($\dot{W}_{V,ki}$) muscle-mass-specific powers were calculated as the product of force and velocity divided by $M_{m,j}$: $\dot{W}_{H,ki} = (\mathbf{F}_{H,ki} \mathbf{V}_{H,ki}) / M_{m,j}$ and $\dot{W}_{V,ki} = (F_{V,ki} \mathbf{V}_{V,ki}) / M_{m,j}$. Total muscle-mass-specific power output ($\dot{W}_{sum,ki}$) was calculated as

the sum of $\dot{W}_{H,ki}$ and $\dot{W}_{V,ki}$. Muscle-mass-specific work output ($W_{sum,ki}$) was calculated by integrating $\dot{W}_{sum,ki}$ with respect to time during toe-off. Toe-off angle (θ) was calculated as the arctangent of the slope of the Y coordinates vs the X coordinates at toe-off.

Calculating muscle performance from ground reaction forces

Performance variables calculated from force-plate data are designated by the subscript fp. Performance was also calculated based on horizontal ($F_{H,fp}$) and vertical ($F_{V,fp}$) forces measured using the force plate. The total forces acting on the ground were assumed to be twice the measured single-leg

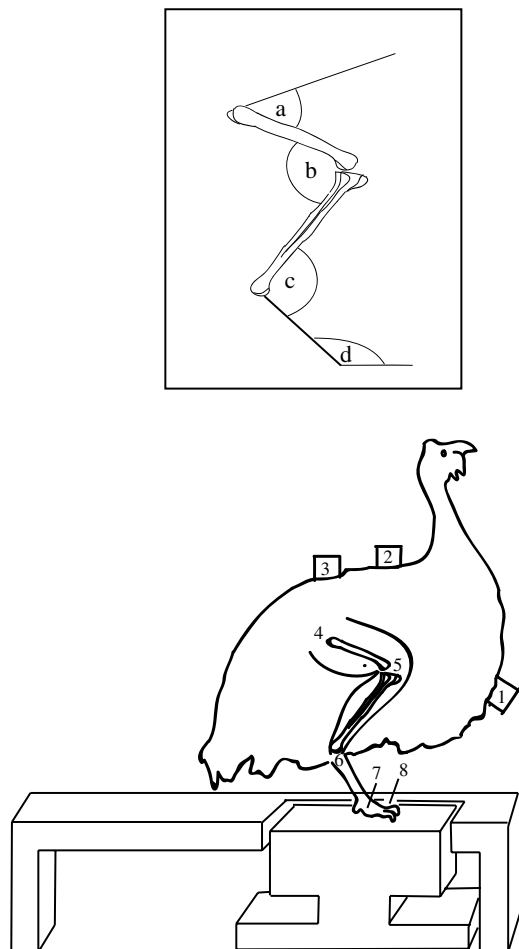


Fig. 1. Diagrammatic view of a guinea fowl standing on the jumping platform. The numbers show the positions marked on each bird. (1) anterior end of sternum; (2) midpoint between synsacrum and base of neck; (3) mid-synsacrum directly above the hip joint; (4) hip joint center; (5) knee joint center; (6) ankle joint center; (7) toe joint center; (8) distal tip of digit III. (Inset) Diagram indicating limb angles. (a) The hip angle was measured between a line parallel to the markers on the back and a line from the hip joint center and the knee joint center; (b) the knee angle was calculated with the law of cosines using constant femur and tibiotarsus segment lengths and the measured distance between the hip and ankle (between a and c); (c) the ankle angle was measured between the tibiotarsus and metatarsus; (d) the toe angle was measured between the tarsometatarsus and digit 3.

forces. Horizontal ($\mathbf{a}_{H,fp}$) and vertical ($\mathbf{a}_{V,fp}$) accelerations were calculated as: $\mathbf{a}_{H,fp} = \mathbf{F}_{H,fp}/M_b$ and $\mathbf{a}_{V,fp} = (\mathbf{F}_{V,fp} - gM_b)/M_b$. Horizontal ($\mathbf{V}_{H,fp}$) and vertical ($\mathbf{V}_{V,fp}$) velocities were calculated by integration of $\mathbf{a}_{H,fp}$ and $\mathbf{a}_{V,fp}$. Integration started at the point at which the center of mass no longer moved downward as determined from the video analysis (Earls, 2002). Muscle-mass-specific vertical ($\dot{W}_{V,fp}$) and horizontal powers ($\dot{W}_{H,fp}$) were calculated by $\dot{W}_{V,fp} = (\mathbf{F}_{V,fp} \mathbf{V}_{V,fp})/M_{m,j}$ and $\dot{W}_{H,fp} = (\mathbf{F}_{H,fp} \mathbf{V}_{H,fp})/M_{m,j}$. Muscle-mass-specific total power

Table 1. Mean mass of leg muscles in guinea fowl

Muscle	Mass (g)	% M_b
Upper thigh muscles		
Ambiens	1.30±0.05	0.09±0.00
Caudofemoralis pars caudalis	2.32±0.12	0.16±0.01
Caudofemoralis pars pelvica	3.95±0.24	0.28±0.02
Femerotibialis medialis and externus	28.42±0.72	2.00±0.04
Femerotibialis internus	4.85±0.18	0.34±0.01
Flexor cruris lateralis pars accessoria	5.72±0.35	0.40±0.02
Flexor cruris lateralis pars pelvica	27.14±1.01	1.90±0.04
Flexor cruris medialis	2.67±0.11	0.19±0.01
Iliofibularis*†	24.01±0.58	1.69±0.04
Iliotibialis cranialis*	21.90±0.72	1.54±0.05
Iliotibialis lateralis pars preacetabularis	7.75±0.36	0.55±0.03
Iliotibialis lateralis pars postacetabularis	37.40±1.80	2.62±0.09
Iliotrochantericus caudalis	17.30±0.40	1.22±0.04
Iliotrochantericus cranialis*	4.84±0.20	0.34±0.02
Iliotrochantericus medius*	0.74±0.05	0.05±0.00
Ischiofemoralis	3.12±0.12	0.22±0.01
Obduratorius medialis	7.07±0.26	0.50±0.02
Puboischiofemoralis lateralis	2.84±0.12	0.20±0.01
Puboischiofemoralis medialis	7.73±0.43	0.54±0.03
Lower leg muscles		
Extensor digitorum longus*	4.11±0.10	0.29±0.00
Superficial digital flexor II	1.62±0.12	0.11±0.01
Superficial digital flexor III	5.59±0.16	0.39±0.01
Other digital flexors	15.38±0.39	1.08±0.03
Flexor digitorum longus and peroneus brevis	8.34±0.22	0.59±0.01
Fibularis longus	15.40±0.52	1.08±0.03
Intermediate gastrocnemius	3.90±0.22	0.27±0.01
Lateral gastrocnemius	20.51±1.35	1.44±0.09
Medial gastrocnemius	21.77±0.88	1.53±0.03
Tibialis cranialis*	15.30±0.37	1.08±0.03
M_m	322.99±8.05	22.69±0.36
$M_{m,j}$	265.50±7.3	18.65±0.31

Values are means ± S.E.M. ($N=6$).

M_b is body mass; M_m is the sum of the masses of all the leg muscles; $M_{m,j}$ is the sum of the masses of the muscles that could possibly power jumping.

*Muscles excluded in calculating $M_{m,j}$.

†For the iliofibularis, approximately 11 g representing the anterior portion of the muscle was excluded from calculation of $M_{m,j}$.

($\dot{W}_{\text{sum,fp}}$) was determined by summing these powers and total work ($W_{\text{sum,fp}}$) calculated by integrating $\dot{W}_{\text{sum,fp}}$ with respect to time.

Statistics

The summary data are presented as means \pm S.E.M. The values reported are based on estimates for each bird representing the mean of 2–4 jumps for a total of 18 jumps. The mean and S.E.M. for jumps presented in the text and Table 2 are based on $N=18$. The total N based on the individual jumps was used because we wanted to compare the two methods used for calculating performance. Paired t -tests were used to examine the differences between data for the same jumps calculated from kinematics and from force-plate data. In order to compare guinea fowl data with the data of Earls (2000), the jumps from each animal were averaged and means \pm S.E.M. calculated using $N=6$.

Results

Leg muscle masses

The total mass of the leg muscles (M_m) was $22.7 \pm 0.36\%$ of body mass (Table 1). The mass of the leg muscles that could be used to power the jump ($M_{m,j}$) was $18.7 \pm 0.30\%$ of body mass (Table 1).

General description of the jump

The jump was preceded by a pre-jump crouching movement characterized by joint flexion (Figs 2, 3). The duration of the crouching movement was quite variable. The mean crouch

duration was 400 ± 69 ms ($N=18$). We defined the jump as beginning with the start of upward movement of the center of mass and ending with the last contact of the toes with the ground (toe-off). The jump duration was much shorter than the crouch duration and was much less variable. The jump had a mean duration of 130 ± 3 ms ($N=18$). The wings remained close to the body throughout the crouch. As the bird lowered itself during the crouch the wings were lowered slightly. When the bird began the jump, the wings began to move away from the body and upwards. The wings continued to extend as the bird continued its upward movement and achieved maximum extension approximately 20 ms prior to toe-off. The wings remained extended as the bird continued to move upwards and they began a downstroke just prior to toe-off.

The pre-jump crouch did not appear to represent a rapid countermovement designed to enhance jumping performance. In a countermovement jump, the potential energy of the body is first converted to kinetic energy, which may be stored as elastic strain energy as the body decelerates at the end of the countermovement. In the guinea fowl jumps, the body was lowered slowly (mean maximum downward vertical velocity = -0.388 m s^{-1}), and the maximum kinetic energy in the downward movement represents only 0.40 J kg^{-1} of leg muscle, or approximately 1% of the work produced in the subsequent jump phase (see Jumping performance).

Joint angles

Joint angles followed a characteristic sequence during jumping (Fig. 3). The timing of the minimum angles reached after crouching was calculated relative to the start of the jump,

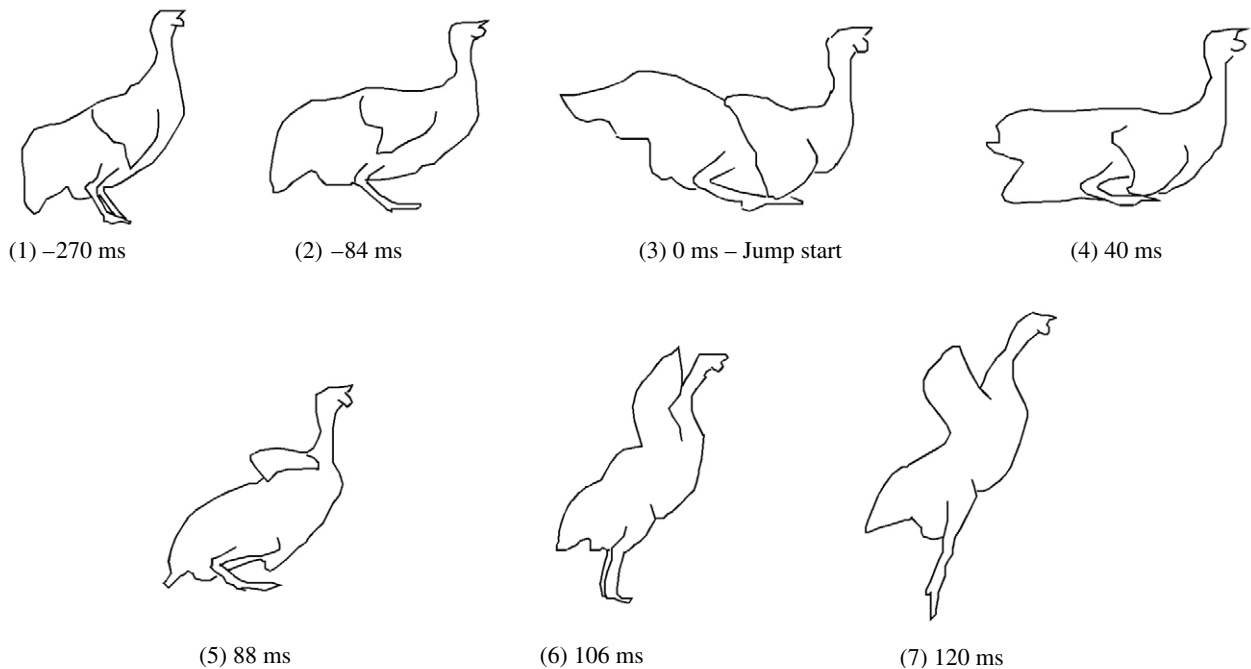


Fig. 2. Bird outlines drawn from video of a typical jump sequence. Time (ms) is relative to the beginning of the jump, defined as when the vertical acceleration became positive. (1) Bird standing upright. (2) Bird lowering itself into a deep pre-jump crouch. (3) Jump start – point of deepest crouch and start of first upward movement when acceleration becomes positive. (4) Beginning of wing upstroke. (5) Middle of wing upstroke. (6) Start of downstroke. (7) Lift-off.

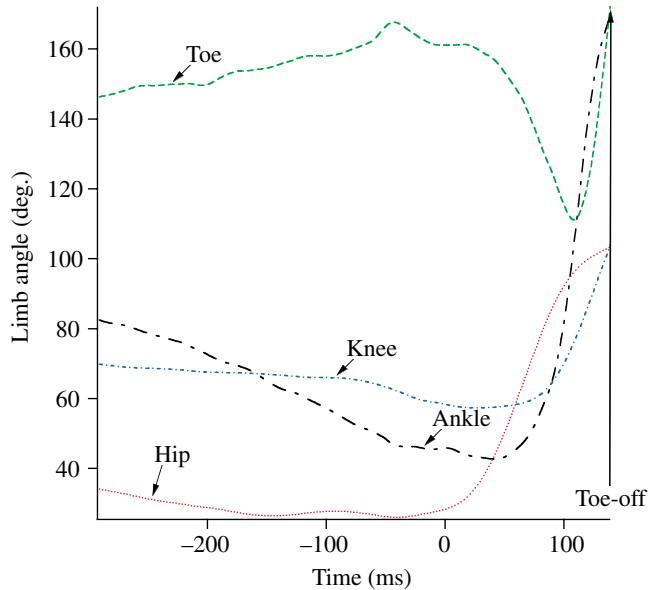


Fig. 3. Limb angles during a representative jump. Red line, hip angle; blue line, knee angle; black line, ankle angle; green line, toe angle.

defined as the time when the vertical accelerations became positive. The hip started with a mean angle of $43.8 \pm 5^\circ$ during standing and gradually flexed throughout the crouch reaching a minimum angle of $30.3 \pm 9^\circ$ at -20 ± 18 ms. From this point the joint gradually extended to a mean of $98 \pm 3^\circ$ at toe-off. The knee joint began at an angle of $64.8 \pm 3^\circ$ and flexed slightly during the crouch, reaching a minimum angle of $54.3 \pm 4^\circ$ occurring at -36 ± 43 ms. The knee reached maximum extension at lift-off at a mean angle $97 \pm 4^\circ$. The ankle started the crouch at an angle of $90 \pm 10^\circ$ and flexed to a minimum angle of $45 \pm 5^\circ$ at 20 ± 12 ms. The ankle joint had the largest angular change during the jump, reaching a maximum of $154 \pm 5^\circ$ at toe-off. The angle measured at the toe joint results in an increase in angle for anatomically defined flexion (see Materials and methods). The toe joint began at an angle of $132 \pm 8^\circ$ and gradually flexed throughout the pre-jump crouch. At the start of the jump, the toe joint begins a rapid extension reaching a minimum of $115 \pm 2^\circ$. Late in the jump the toe started to flex rapidly and reached a maximum angle of $173 \pm 4.77^\circ$ just after toe-off. In general, the beginning of hip extension occurred first or approximately at the same time as the start of knee extension, ankle extension occurred somewhat later and toe flexion occurred last.

Jumping performance

The center of mass of the bird is lowered by 0.09 ± 0.04 m during the pre-jump crouch and subsequently moves upward by 0.25 ± 0.02 m before toe-off (Fig. 4). Maximum vertical and horizontal velocities were achieved just prior to toe-off (Fig. 5). The vertical and horizontal velocities at toe-off were approximately 3.3 m s^{-1} and 1.3 m s^{-1} , respectively yielding a resultant velocity of 3.6 m s^{-1} (Table 2). The peak velocities measured from kinematics and calculated from the force-plate

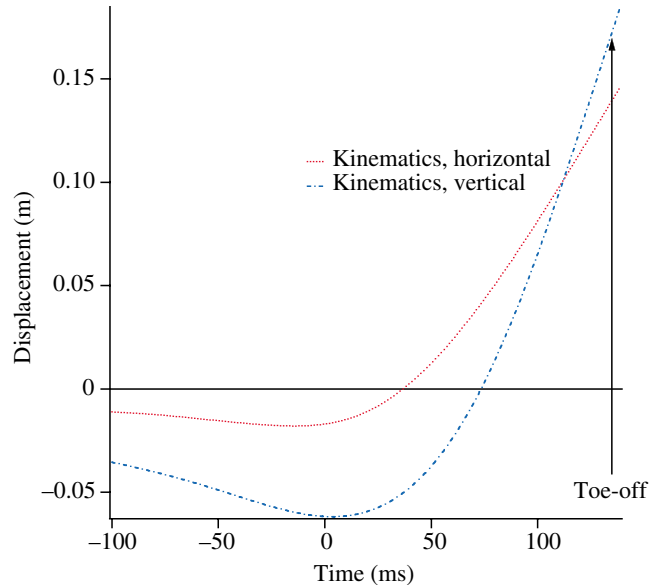


Fig. 4. Horizontal and vertical displacement of the center of mass during a representative jump, based on kinematic data. Zero time is the start of the jump, defined as when the vertical acceleration became positive.

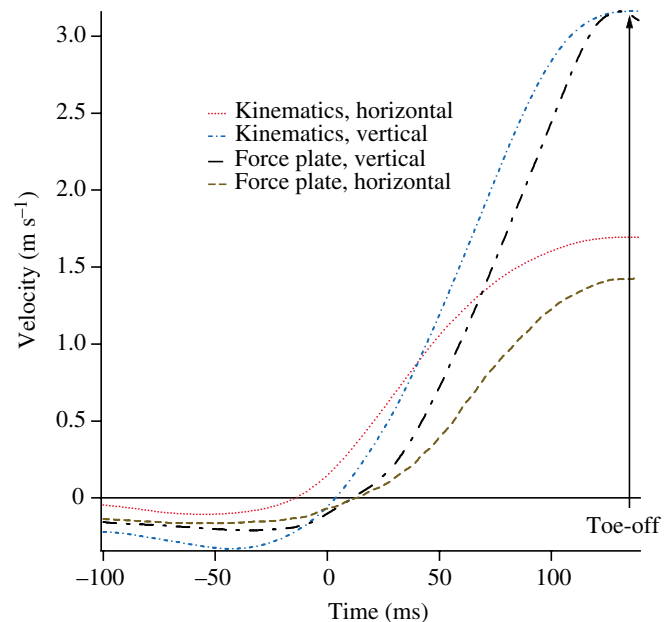


Fig. 5. Velocities during a representative jump, as measured from kinematic and force-plate data. Red line, horizontal velocity measured from kinematics; blue line, vertical velocity measured from kinematics; black line, vertical velocity measured from force plate; brown line, horizontal velocity measured from force-plate data.

data were not significantly different (Table 2). However, the rise in the velocity of the bird's center of mass as measured from the kinematics (using a constant point on the body of the bird) preceded the velocity calculated from the force-plate measurements (Fig. 5).

Table 2. Comparison of jumping performance calculated from kinematic and force-plate data

Variable	Kinematic data	Force-plate data	<i>P</i> *
θ (deg.)	69.3±0.9	70.5±1.5	0.3089
V_v (m s ⁻¹)	3.33±0.05	3.37±0.10	0.6038
H_v (m s ⁻¹)	1.26±0.06	1.19±0.09	0.3079
V_{res} (m s ⁻¹)	3.57±0.05	3.60±0.1	0.7071
F_v ($M_b g$) ⁻¹	5.27±0.9	5.31±0.11	0.6258
F_H ($M_b g$) ⁻¹	1.75±0.13	1.78±0.10	0.7070
Peak \dot{W}_v (W kg ⁻¹)	640.31±16.79	701.56±29.20	0.0177
Peak \dot{W}_H (W kg ⁻¹)	71.98±8.08	76.09±8.74	0.5549
Average \dot{W}_{sum} (W kg ⁻¹)	335.49±13.73	333.17±21.51	0.8915
Peak \dot{W}_{sum} (W kg ⁻¹)	712.29±19.38	777.64±32.97	0.0162
W_{sum} (J kg ⁻¹)	45.02±1.26	44.95±2.43	0.9764

Values are means ± S.E.M., calculated using the individual jumps (*N*=18).

**P*, probability of no difference between the means based on a paired *t*-test.

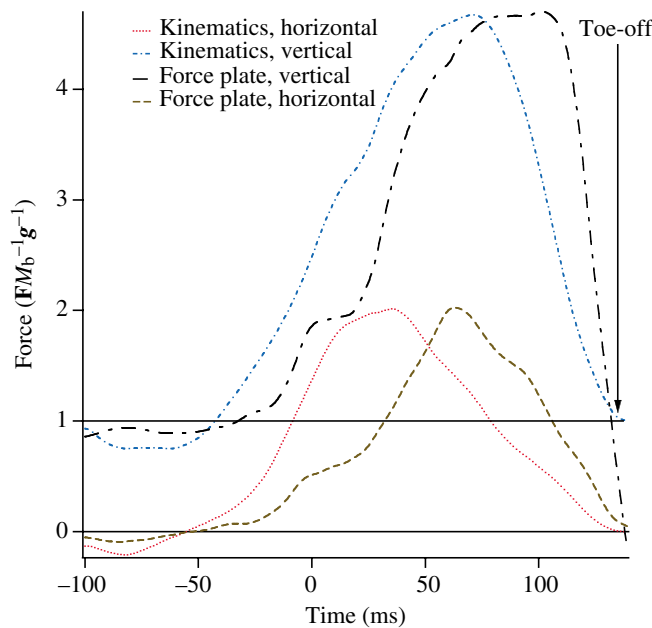


Fig. 6. Force records during a representative jump, as measured from kinematics and measured using the force-plate. Values for force are expressed as multiples of body weight. Red line, horizontal velocity measured from kinematics; blue line, vertical velocity measured from kinematics; black line, vertical velocity measured using the force plate; brown line, horizontal velocity measured using the force plate.

Peak forces calculated from the kinematics were nearly identical to the values recorded from the force plate (Table 2, Fig. 6). Vertical and horizontal forces peaked at approximately 5.3 and 1.8 times body weight, respectively (Table 2).

Muscle-mass-specific power output peaked just prior to toe-off (Fig. 7). The values for peak horizontal power

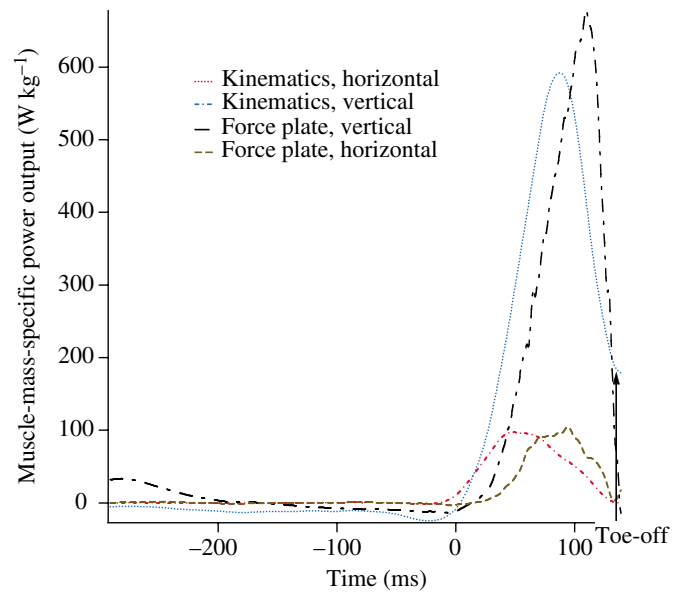


Fig. 7. Muscle-mass-specific horizontal and vertical power outputs during a representative jump, as measured from kinematic and force-plate data. Red line, horizontal velocity measured from kinematics; blue line, vertical velocity measured from kinematics; black line, vertical velocity measured from force plate; brown line, horizontal velocity measured from force plate.

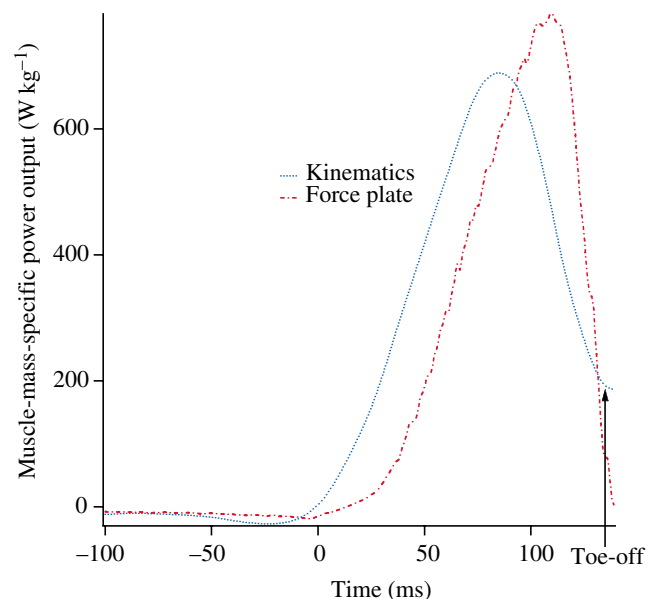


Fig. 8. Muscle-mass-specific total power output during a representative jump, as measured from kinematic and force-plate data.

(76.09±8.74 W kg⁻¹ and 71.98±8.08 W kg⁻¹) calculated by the two methods were similar (Table 2). However, the mean of the peak vertical power calculated from the force-plate data (701.56±29.20 W kg⁻¹) was significantly greater (*P*=0.018) than the peak value calculated from kinematics (640.31±16.79 W kg⁻¹). Because of this difference, the total

muscle-mass-specific peak power was also significantly higher ($P=0.016$) when calculated from the force-plate data (777.64 ± 32.97 W kg⁻¹) than when the kinematic data were used (712.29 ± 19.38 W kg⁻¹) (Fig. 8). The values of muscle-mass-specific power averaged over the entire jump (330 W kg⁻¹) were identical for the two methods and, thus, so was the muscle-mass specific work output (45 J kg⁻¹).

Discussion

Overall jumping performance: the leg muscles are the power source

The goal of our study was to measure the performance during jumping of the leg muscles of the helmeted guinea fowl, a ground dwelling bird specialized for running. Although specialized for running these birds resort to flight in emergency situations. Because flight is used as an escape mechanism, these birds can benefit from a very quick and high-powered jump to initiate flight. Before commencing these studies, we noted that guinea fowl also used jumping to move from the ground to an elevated platform, in the absence of any subsequent flight.

We attempted to design our experiments to exclude any contribution of the flight muscles to the velocity attained at toe-off. We kept the primary and secondary feathers of the birds clipped and trained the birds to jump from a platform to a cage rather than performing a jump followed by a flight. However, the birds did at times flap their wings following the jump. Therefore, we followed Earls (2000) and calculated performance from both kinematic data and force-plate records. Earls (2000) found that in the common quail, the first downstroke of the wings preceded the time at which the toes left the ground. Therefore, the actual toe-off velocity she measured from kinematics was higher than the value she calculated from force-plate data (Table 3). Based on the resultant toe-off velocities reported by Earls (2000), the wings contributed 18% of the kinetic energy present at takeoff.

In contrast to the common quail, the first downstroke of the wings by the guinea fowl in our experiments began almost coincident with or slightly after toe-off. Consequently, the measured velocity of the center of mass at toe-off based on kinematics was the same as that calculated from the ground

reaction forces (Table 2). Therefore, the leg muscles provided all the work required to lift the body weight against gravity and accelerate the bird's mass before toe-off. (These results may have been different if we had examined jumps that preceded a flight.)

Although the work and average power calculated by the two methods were identical (Table 2), the peak power calculated from the force-plate data was significantly higher than the value calculated from the kinematics data (Table 2, Fig. 8). This difference likely results from two factors that both tend to reduce the power calculated from kinematics. First, the smoothing of the position data that was required before the differentiation steps could have resulted in an underestimate of peak power. Second, a consistent temporal offset was observed between force measured from the force plate and that calculated from kinematics. This offset could be due to the method used to estimate the center of mass in the kinematic analysis. In this method, it was assumed that the center of mass was a fixed point on the bird's body throughout the jump (Earls, 2000). The true center of mass is determined by the distribution of the masses of all the body segments and this distribution changes throughout the jump. Leg extension causes the center of mass to move downward and backward relative to the body. The results of this movement of the center of mass, which was not considered in our kinematic analyses, would have been an overestimate of the early acceleration of the center of mass and an underestimate of the acceleration later in the jump. Essentially, the leg segments were initially moving slower than the body but must have caught up late in the jump because the velocities of all segments are equal at takeoff. The fact that the measured peak forces and the power outputs calculated from force-plate data occurred later in the jump than the values calculated from kinematics is consistent with this type of error.

The toe-off velocity of guinea fowl measured by us and the value of Earls (2000) for the common quail (3.6 and 3.9 m s⁻¹, respectively) are consistent with the hypothesis that most or all of the acceleration required for the rapid, steep, escape flights of phasianids is achieved before the birds leave the ground and involves very high work and power outputs by the leg muscles. Horizontal and vertical flight velocities shortly after takeoff have been reported for five species of phasianids (Askew et al.,

Table 3. Comparison of jumping performance in guinea fowl and common quail

	Guinea fowl		Quail*	
	Kinematic data	Force-plate data	Kinematic data	Force-plate data
θ (deg.)	68.60±1.12	69.73±1.22	72.5	69.6
Toe-off V_V (m s ⁻¹)	3.35±0.06	3.35±0.09	3.75±0.06	3.31±0.07
Toe-off V_H (m s ⁻¹)	1.31±0.08	1.23±0.07	1.18±0.10	1.23±0.01
Toe-off V_{res} (m s ⁻¹)	3.61±0.07	3.58±0.09	3.93	3.53
F_V ($M_b g$) ⁻¹	5.25±0.11	5.30±0.19		7.80±0.19
F_H ($M_b g$) ⁻¹	1.82±0.14	1.84±0.13		2.82±0.02

Values for guinea fowl are means ± S.E.M., based on $N=6$.

*Values for quail are taken from Earls (2002).

2001). The resultant flight velocities for these species are all less than 3.3 m s^{-1} except for the value of 4.9 m s^{-1} reported for the very small (44 g) blue-breasted quail. The powers required from the flight muscles of these birds are very high just to maintain upward velocities after takeoff (Askew et al., 2001). Thus, attaining the high rates of vertical acceleration seen in the jump would probably not be possible using the flight muscles alone.

Power amplification by elastic storage and release

How does the level of muscle performance by guinea fowl leg muscles compare with the direct power and work outputs expected from these muscles? To provide a conservative estimate of performance, we assumed that the jumps were powered equally by all the leg muscles capable of producing positive power, based on their anatomically inferred actions (see Materials and methods). Peplowski and Marsh (1997) calculated that vertebrate skeletal muscles used in jumping are likely limited to approximately $60\text{--}70 \text{ J kg}^{-1}$ of work in a single rapid contraction, as occurs during jumping. Guinea fowl, despite their apparent lack of specialization for jumping, produce muscle work outputs of 45 J kg^{-1} , or approximately $2/3$ of the maximal expected value. Although work outputs are expected to be similar among different muscles with similar maximal forces and excursions, the maximal isotonic power expected from a muscle will vary with its maximal shortening velocity and the curvature of the force–velocity relation. Isotonic power outputs are not known for guinea fowl, but Nelson et al. (2004) report values of approximately 320 and 340 W kg^{-1} for two of the large lower leg muscles of turkeys. Adjusting for the expected higher shortening velocity of the smaller guinea fowl gives an estimate of approximately 380 W kg^{-1} for guinea fowl leg muscles. The average power of approximately 330 W kg^{-1} produced by the leg muscles in jumping is within this estimate of the maximum direct power output. However, to satisfy the peak power outputs measured during the jump, the muscles would have to deliver approximately 800 W kg^{-1} , which is clearly beyond their capacities. Elastic energy storage early in the jump and its release during peak power production provides the mechanism to account for the high peak power (Marsh and John-Alder, 1994; Roberts and Marsh, 2003).

The fact that the average power is within the limits of the muscles suggests that the mechanism of the jump may not require much pre-storage of elastic energy before the center of mass starts to move, as is the case in some small jumpers (Bennet-Clark, 1975; Peplowski and Marsh, 1997). Elastic energy storage and release within the jump suggests the operation of an inertial catch mechanism, as described by Roberts and Marsh (2003). In this mechanism an initially poor mechanical advantage in terms of producing ground reaction force, allows muscles to initially shorten and stretch elastic elements, presumably tendons. An improving mechanical advantage later in the jump produces further rapid shortening and also release of the stored elastic energy.

The values we report for the maximal power, nearly 800 W kg^{-1} , and work, approximately 45 J kg^{-1} , from the leg

muscles as a group are likely to be underestimates of the performance of some of the individual muscle–tendon units. All the muscles identified as possibly participating in jumping are unlikely to have contributed equally to the work and power outputs. For example, the parallel-fibered hip and knee extensors that lack significant tendons may not be able to pre-store elastic energy as well as the pinnate muscles with long tendons.

Comparison with more specialized jumpers

How does the jumping performance of guinea fowl compare to that of more specialized jumpers? Some small vertebrate jumpers have truly impressive jumping performances that require substantial storage and release of elastic strain energy. For example, Peplowski and Marsh (1997) estimated that Cuban tree frogs with an average body mass of 13 g produce a peak power exceeding 1600 W kg^{-1} of muscle, about 7 times that available from direct muscle power output. Because even the average power output ($>800 \text{ W kg}^{-1}$) of these small frogs during the jump exceeds the expected muscle power output by a considerable margin, the jumping mechanism likely involves an anatomical catch. An anatomical catch would allow pre-storage of elastic energy before the jump begins, as has been found in insects (Bennet-Clark, 1975). The presence of a substantial period of muscle activity before Cuban tree frogs begin to accelerate has been confirmed with EMG recordings (R. L. Marsh and M. M. Peplowski, unpublished observations). Predicted work outputs for the muscles of these frogs ($\sim 60 \text{ J kg}^{-1}$) are high but within the expected limits for vertebrate muscle. Among mammals, some primates are particularly specialized for jumping. Bush babies *Galago senegalensis*, which weigh about 250 g , perform jumps requiring a peak power output of more than 2400 W kg^{-1} of muscle (Halls-Craggs, 1965; Gunther et al., 1991; Aerts, 1998). Work outputs of these animals probably approach the value of 70 J kg^{-1} suggested as the maximum possible. (These values for power and work depend on assumptions about which muscles are involved in the jump. Muscle masses are given in Grande, 1977). Despite their greater muscle-mass-specific work and power, these primates may be similar to guinea fowl in not pre-storing a lot of energy before the start of the jump. Based the detailed force–plate records published by Gunther et al. (1991), the *Galago* has a substantial period of slow acceleration at the beginning of the jump. Calculations from these records indicate that, although the peak power output of the muscles exceeds 2400 W kg^{-1} , the average power output may be approximately 450 W kg^{-1} . The properties of *Galago* muscles are not known, but very fast lizard muscles can generate an isotonic power of 460 W kg^{-1} at 40°C (Marsh and Bennett, 1985).

The approximately 800 W kg^{-1} of muscle-mass-specific peak power found here during guinea fowl jumping is clearly lower than the values found for these specialized jumpers. However, producing muscle-mass-specific work outputs of 45 J kg^{-1} is a surprisingly good performance for these non-specialized jumpers. Also, in judging the peak power outputs, the larger body size (approximately 1.5 kg) of the guinea fowl relative to the Cuban tree frog and *Galago* should be taken into

consideration. Generally, elastic storage mechanisms are expected to be more important for small animals (Bennet-Clark, 1977; Alexander, 1995). This size effect is seen clearly in the two species of phasianid birds that have been studied. The common quail studied by Earls (2000) achieves a similar leg-powered toe-off velocity, and thus a similar body-mass-specific work output, as that of the guinea fowl, but reaches this velocity in about 2/3 of the time. If these species have similar fractions of their body mass devoted to leg muscles, the expected muscle power outputs of the quail leg muscles would be 1.5 times those of the guinea fowl muscles.

Conclusion

This study has demonstrated that during jumping guinea fowl produce power in excess of the power directly available from their leg muscles. We conclude that elastic storage and recovery of energy in tendons likely provides the mechanism for temporally redistributing the work done by the muscles during jumping. Likely sites for the storage of elastic energy include the tendons of the ankle extensors.

List of symbols

Note: Addition of ki or fp subscript to the abbreviations in the text designates values calculated from kinematic or force-plate data, respectively.

a_H	Horizontal acceleration
a_V	Vertical acceleration
F_H	Horizontal force
F_V	Vertical force
g	Acceleration due to gravity
M_b	Body mass
M_m	Total mass of the leg muscles
$M_{m,j}$	Total mass of the leg muscles that can power jumping
N	Sample size
θ	Toe-off angle
V_H	Horizontal velocity
V_{res}	Resultant velocity
V_V	Vertical velocity
\dot{W}_H	Horizontal muscle-mass-specific power
\dot{W}_{sum}	Total muscle-mass-specific power
W_{sum}	Total muscle-mass-specific work
\dot{W}_V	Vertical muscle-mass-specific power

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