

## Task-dependent force sharing between muscle synergists during locomotion in turkeys

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### SUMMARY

**At most joints, there is a redundancy of muscle function. For any given movement, there are a wide range of possible solutions to the problem of how force is shared among muscle synergists. A better understanding of how force is shared among muscle synergists can provide insight into the mechanics and control of movement. We examined force sharing in the gastrocnemius of wild turkeys (*Meleagris gallopavo*), using strain gauges bonded to bony tendons. Force was measured separately in the lateral (LG) and medial (MG) heads of the gastrocnemius, to evaluate force sharing. We also used inverse dynamics to determine the total force required during swing phase. To determine whether the pattern of force sharing varied depending on the mechanical task, we used running speed (1 to 3.5 m s<sup>-1</sup>) and limb loading (30 and 60 g added tarsometatarsal mass) to vary the force required at the intertarsal joint. We found that the distribution of force between these two heads varied depending on the phase of the stride cycle. During stance, force was shared in near equal amounts between the two heads and this distribution was unaffected by changes in running speed or limb load. During swing phase, however, there was no force sharing. Force was produced only in the lateral head, and this force was not significantly different from the total force required, as calculated from inverse dynamics. Thus, the LG produced all of the force required for limb extension during swing. This change in the pattern of force sharing between stance and swing supports the theory that force sharing between muscle synergists is task-dependent.**

Key words: force sharing, running, bird.

### INTRODUCTION

Any walker or runner must develop muscular force at each of its limb joints to overcome inertia and resist gravity. The joint moment resulting from these muscle forces can be measured relatively easily using standard biomechanical techniques (Bresler and Frankel, 1950; Robertson and Winter, 1980). It is difficult, however, to determine the relative contribution of individual muscles to a given joint moment (Raikova, 1992; Zajac and Gordon, 1989). The difficulty results from the fact that multiple muscles are capable of contributing to most joint actions. For example, in humans eight different muscles are capable of contributing to extensor moments at the ankle. The redundancy of function of muscle synergists means that there are many different possible solutions to the problem of how force is distributed among individual muscles during movement (Loeb, 1985; Prilutsky, 2000; Raikova, 1992). Our understanding of how muscle synergists share force has important implications for models of locomotor energetics (Roberts et al., 1998a; Roberts et al., 1998b), mechanics (Alexander, 1974; Biewener et al., 1981; Thorpe et al., 1998) and motor control (Higginson et al., 2006; Prilutsky, 2000).

Several different models have been developed to predict the distribution of force among muscle synergists during movement (reviewed in Crowninshield and Brand, 1981; Herzog and Leonard, 1991; Herzog, 1996). One of the simplest models predicts that force is distributed among muscles according to their capacity to develop force, as measured by their physiological cross-sectional area (Crowninshield, 1978). More complex models have been developed to incorporate the dynamic behavior of muscles during locomotion and the influence of muscle properties on the capacity of each

synergist to develop force (Pedotti et al., 1978), or to include the effect of muscle fiber type and fatigue susceptibility of different muscle heads on force distribution (Dul et al., 1984). Empirical measurements of force production in muscle synergists (Akima et al., 2002; Biewener and Baudinette, 1995; Biewener and Corning, 2001; Fagg et al., 2002; Herzog and Leonard, 1991; Kaya et al., 2003; Stokes and Gardner-Morse, 2001) do not consistently support any of these models. This lack of consistent agreement between empirical measurements and theoretical predictions has led several researchers to suggest there may not be one model of force sharing for all musculoskeletal tasks. Instead, it has been suggested that force distribution may be task-dependent (Loeb, 1985; Prilutsky, 2000; Raikova, 1992).

We investigated how force is shared between two heads of the gastrocnemius muscle in wild turkeys (*Meleagris gallopavo*). This system is particularly well suited to investigate the action of synergistic muscles. The lateral (LG) and medial (MG) heads of the gastrocnemius muscle have independent origins, but share a common tendon of insertion that acts to extend the intertarsal (ankle) joint. The distal tendons of the LG and MG are separate before merging at approximately the point of transition from bony to soft tendon. Thus, we could bond strain gauges to the separate bony tendons of the LG and MG to measure force output from each head independently. The LG has an action during stance and swing phase, producing small forces during rapid muscle length changes during swing, and high forces during small length changes during stance (Roberts et al., 1997). Measurements of force production in the MG allowed us to determine how it shares force production with the LG

during both the stance and swing phase of locomotion. We also used inverse dynamics to calculate the total force required during swing, to determine the relative fraction of the total force required supplied by each muscle head.

To determine whether force sharing varies with whole muscle force output, we measured muscle force output across a range of walking and running speeds, and with weights added to the limbs. We anticipated that stance phase force would increase with speed, because increased running speed is associated with increased ground reaction forces, and previous energetic studies showed energy use increased in these two muscles with speed in guinea fowl (Ellerby et al., 2005). We also expected muscle force would increase in both heads with speed during swing, because decreased duration of swing time should require more rapid accelerations and decelerations of the swinging limb. Increases in the mass that must be accelerated should also increase the force required, thus we predicted that the addition of limb weights would also increase the force produced during swing in both muscles.

## MATERIALS AND METHODS

### Animals, muscles instrumented and training protocol

Six adult female Eastern wild turkeys *Meleagris gallopavo* L. were obtained from a breeder (Reedsport, OR, USA) and housed in an outdoor enclosure at Oregon State University. A diet of Game Bird Flight Conditioner (Purina-Mills, Inc., St Louis, MO, USA) and water were provided *ad libitum*. The mean body mass of the birds was  $4.2 \pm 1.0$  kg ( $\pm$  s.d.). The mean mass of the lateral gastrocnemius (LG) muscle was  $21.6 \pm 4.5$  g ( $\pm$  s.d.), and the medial gastrocnemius (MG) muscle was  $30.7 \pm 7.1$  g ( $\pm$  s.d.).

The avian gastrocnemius consists of three heads in most species (George and Berger, 1966; Baumel, 1993). The MG is the largest of the three heads, with two sites of origin: a fleshy one on the proximomedial portion of tibiotarsus and the second on the patellar tendon. The MG inserts *via* a common tendon with the lateral head on the proximal end of the tarsometatarsus. In turkeys, as in several other genera of birds, the tendons for the medial and lateral heads are separate (Hudson et al., 1959) and only join just before the tendon crosses the intertarsal joint. Here, we refer to the intertarsal joint as the ankle for ease of reference. The lateral head is the next largest and originates from a short tendon attached to the external condyle of the femur. The intermediate head is by far the smallest of the three heads. It has a fleshy origin on the internal condyle of the femur and inserts *via* a tendon onto the medial head about a third of the way down the tibiotarsus. A comprehensive anatomical description of these muscles is given by several other authors (Ellerby and Marsh, 2006; Gangl et al., 2004; Gatesy, 1999; Hudson et al., 1959).

The gastrocnemius acts to extend the ankle, but its action at the knee is more complex. The lateral head acts as a knee flexor (Ellerby et al., 2005; Gatesy, 1999; Smith et al., 2007). The medial head appears to have little action at the knee, with the possible exception of a small extensor moment developed by the small portion of the muscle originating on the patellar tendon (Ellerby and Marsh, 2006; Smith et al., 2007). We measured a moment arm of zero at the knee when the MG was only detached from its point of insertion. The action of the intermediate head may be knee flexion and ankle extension, but in order to perform this action it needs to act through the medial head it inserts on.

The training protocol used was similar to that used by Gabaldon and coworkers (Gabaldon et al., 2004). Turkeys ran on a level treadmill for 10–20 min day<sup>-1</sup>, 4–5 days a week, for about 4–6 weeks. Speeds were varied over the course of a training session.

Animals were also trained over the course of 3–5 weeks to run with weights added to their limbs. On separate days, turkeys were subjected to one of three limb-loading regimes: unloaded, 30 g or 60 g weights. The 30 or 60 g weights were attached to the limbs just proximal to the tarsometatarsal–phalangeal joint. At the end of training all birds could run at 2 m s<sup>-1</sup> for 20 min. All training and research was conducted in accordance with Oregon State University Institutional Animal Care and Use Committee and federal and institutional guidelines.

### Surgery

Animals were induced and maintained on inhaled isoflurane anesthesia with a sterile environment maintained throughout all surgical procedures. Strain gauges (Type FLK-1-11, Tokyo Sokki Kenkyujo Co., Ltd, Tokyo, Japan) were attached to both the superficial and deep aspect of the calcified tendon for both the lateral and medial gastrocnemius muscle after the tendons were scraped and degreased with chloroform. The strain gauge wires were routed subcutaneously from each muscle to a small skin incision near the middle of the synsacrum. The incision was closed and small electrical connectors (Microtech, Inc., Boothwyn, PA, USA) were secured to the skin with 3-0 silk suture. Animals were given an injection of buprenorphine and allowed to recover from surgery for 24–48 h before treadmill running experiments.

### Running experiments

Gastrocnemius muscle forces were measured as the birds ran with and without limb weights on a level treadmill. The birds were first run without limb weights over a range of speeds, from 1 to 3.5 m s<sup>-1</sup>. For limb-loading experiments, 30 or 60 g lead weights were secured with tape to the limb segment just proximal to the tarsometatarsal–phalangeal joint. Ten seconds of data were collected for each run. Birds remained on the treadmill at slow walking speeds between speed changes and were allowed to rest on a stopped treadmill as needed. Force signals were collected at 4000 Hz with a Macintosh G3 computer using a 12-bit A/D converter (PCI-MIO-16-1, National Instruments, Austin, TX, USA) controlled by the software program IGOR Pro (WaveMetrics, Inc., Lake Oswego, OR, USA). The tendon strain signals were amplified using a strain gauge conditioner (model 2120, Vishay Measurements Group, Raleigh, NC, USA) before being collected by the computer. Data were synchronized with 2-D high-speed video, which was recorded at 250 frames s<sup>-1</sup> (Redlake Imaging MotionScope 1000S, Morgan Hill, CA, USA) in the sagittal plane. To ensure that there were no changes in strain gauge signals or running behavior over the course of the experiment, we compared force measurements taken at 2 m s<sup>-1</sup> at the beginning of the experiment with measurements taken at the same speed at the completion of the experiment.

### Kinematics

The timing of footfall and the positions of the ankle and metatarsal–phalangeal joint were determined directly from video recordings. The video recorded from the Redlake camera was transferred to a computer through NIH ObjectImage software. This transferred video was then digitized using a custom program (written by Ty Hedrick, DLT Data Viewer 2, <http://www.unc.edu/~thedrick/>) operating in MatLab 7.0 (The Mathworks, Inc.). All of the digitized coordinates for each bird were converted from pixels to m by determining the pixel distance between the ankle and tarsometatarsal–phalangeal joints and comparing this to the known distance in m. This conversion was done for each sequence from a single frame during movement. After

this conversion a smoothing spline (smoothing factor 1, s.d. 0.001–0.003 m) was fit to the data using the software IGOR Pro (Wavemetrics, Inc.) to remove random noise. This smoothed data was used to locate the limb segment and also to calculate the segment angles. Segment angles were differentiated twice to obtain joint angular accelerations.

### Inverse dynamics

Two-dimensional sagittal plane inverse dynamics was used to determine the moment required at the ankle joint during swing phase (Bresler and Frankel, 1950; Robertson and Winter, 1980). The joint moment was expressed by the following equation:

$$M_p = I_0\alpha + (m_s\mathbf{a}_x)\mathbf{r}_x + (m_s\mathbf{a}_y + m_s\mathbf{g})\mathbf{r}_y, \quad (1)$$

where  $M_p$  is the moment at the proximal joint (ankle joint),  $I_0$  is the moment of inertia of the combined tarsometatarsus and phalanges about the center of mass,  $\alpha$  is the angular acceleration of the tarsometatarsus and phalanges,  $m_s$  is the mass of the tarsometatarsus and foot limb segment,  $\mathbf{a}_x$  is the acceleration of the center of mass in the  $x$  direction (fore–aft),  $\mathbf{r}_x$  is the distance from the ankle to the center of mass in the  $y$  direction (vertical),  $\mathbf{a}_y$  is the acceleration of the center of mass in the  $y$  direction (vertical),  $\mathbf{g}$  is the gravitational constant, and  $\mathbf{r}_y$  is the distance from the ankle to the center of mass in the  $x$  direction (fore–aft).

The mass, position of the center of mass and inertia of the tarsometatarsus and phalanges were determined empirically. The tarsometatarsus and phalanges limb segment was severed from the rest of the limb at the ankle joint in a frozen limb. The segment was weighed, and the position of the center of mass (COM) was determined by balancing the segment on a plastic straight edge (Fedak et al., 1982). For the segments measured in this study the average position of the COM was  $7.78 \pm 0.54$  cm (mean  $\pm$  s.d.) from the ankle joint for six birds. Average segment mass was  $52.37 \pm 14.29$  g (mean  $\pm$  s.d.).

The moment of inertia about the tarsometatarsus and phalanges limb segment center of mass was determined by measuring the natural period of oscillation of the segment. The segment was mounted near its proximal end to a stiff steel rod that provided a pivot. The segment was released at a small angle from vertical to swing in an arc in the sagittal plane. The time of five swings was recorded. This procedure was repeated five times for the limb segment, and also for the limb segment with weights attached in the same location as during running measurements. The average of all five trials was used to calculate the average period of swing for each bird's tarsometatarsus and phalanges limb segment. This period was used to calculate the moment of inertia ( $I$ ) about the pivot point in  $\text{kg m}^2$  using the following equation derived from the basic mechanics of a physical pendulum:

$$I = t^2 m_s d g / 4\pi^2, \quad (2)$$

where  $t$  is the period of one swing (s),  $m_s$  is the mass of the limb segment (in kg),  $d$  is the distance from the segment center of mass to the point of rotation, and  $\mathbf{g}$  is the gravitational constant ( $\text{m s}^{-2}$ ). The moment of inertia about the centre of mass ( $I_0$ ) of the segment was calculated using the parallel axis theorem:

$$I_0 = I - m_s d^2. \quad (3)$$

### Muscle moment arm

Inverse dynamics measurements of joint moment were used to calculate the force that would be required from the gastrocnemius muscle to produce the motion observed during swing. The required

muscle force was calculated from the joint moment (Eqn 1) divided by the LG muscle moment arm.

The moment arm of the gastrocnemius muscle about the ankle joint was determined post-mortem by the tendon travel method (Lutz and Rome, 1996). The apparatus and technique used to relate muscle length change to joint angle were modified versions of those used by Lutz and Rome (Lutz and Rome, 1996). Joint angles were measured with a goniometer and the displacements of the tendon were measured with a ruler. The moment arm ( $r$ ) of a muscle about a given joint was calculated as:

$$r = \Delta l / \Delta \theta, \quad (4)$$

where  $\Delta l$  is the length change of the muscle (in m) and  $\Delta \theta$  is the joint angle change (in rad). The slope of a regression line fit to a plot of muscle length change vs joint angle determined the moment arm of the gastrocnemius muscle about the knee and ankle joint. Moment arm measurements using this technique corroborated earlier measurements using a different technique (Roberts et al., 1998a).

### In situ calibration of muscle force

Tendon strains measured using strain gauges were calibrated to muscle force *in situ* at the end of running experiments according to techniques described by Gabaldon and coworkers (Gabaldon et al., 2004). The procedure involved electrically stimulating the muscle *via* the sciatic nerve while simultaneously measuring whole muscle force and tendon strain. The slope of a regression line fit to the linear portion of the tendon strain and muscle force data, between muscle forces of 0 and 200 N, was used to calibrate tendon strain to muscle force. The birds were kept under deep anesthesia with isoflurane gas during the experiments and body temperature was maintained at 38–40°C.

### Muscle cross-sectional area

Muscle fiber length, angle of pennation and muscle mass were measured *post-mortem* from excised muscle to determine the cross-sectional area of the lateral and medial head of the gastrocnemius muscles. Fiber length was measured with a pair of calipers between the beginning of a fiber at the origin of the muscle and its insertion onto the muscle's superficial aponeurosis. The pennation angle was determined on longitudinally bisected muscles with a goniometer. Physiological cross-sectional area (PCSA) was calculated as:

$$\text{PCSA} = m_m \cos \theta / l \rho, \quad (5)$$

where  $m_m$  is the mass of the muscle,  $\theta$  is the angle of pennation,  $l$  is the fiber length, and  $\rho$  is the density of muscle (Gans, 1982; Powell et al., 1984).

### Force variables

The simple repeatable pattern of the ankle joint moment allowed the force required from the gastrocnemius for joint extension to be characterized by three variables: maximum force, time to maximum force and impulse. These three variables were determined from inverse dynamics during swing only and are referred to as the required maximum force for extension ( $F_{m,r}$ ), required impulse for extension ( $I_r$ ), and time to required maximum force ( $T_{m,r}$ ). All three variables were used to compare muscular forces required and muscular forces produced for joint extension during swing, since the possibility of a timing difference between required and produced force could exist. The muscular force variables are referred to as: maximum force produced ( $F_{m,LG}$  or  $F_{m,MG}$ ), impulse produced ( $I_{LG}$  or  $I_{MG}$ ), and time to maximum force produced ( $T_{m,LG}$  or  $T_{m,MG}$ ). We used the same variables to describe force production during stance in the lateral and medial head of the gastrocnemius with the

Table 1. Effects of speed\* and added weights† on kinematic variables

Variable	Speed			Weight		
	d.f.	F	P	d.f.	F	P
Kinematics						
Swing duration	2,10	2.637	NS	2,10	16.645	0.001
Stride duration	2,10	219.740	0.001	2,10	0.578	NS
Duty factor	2,10	80.347	0.001	2,10	4.021	NS
Tarsometatarsus-foot limb segment movements during swing						
Angular excursion	2,10	5.875	0.021	2,10	4.389	0.034
Horizontal excursion	2,10	0.01	NS	2,10	0.007	NS
Vertical excursion	2,10	0.039	NS	2,10	4.575	0.039

\*Speeds: 1, 1.5 and 2 m s<sup>-1</sup>.

†Added weights: 0, 30 and 60 g.

Three-way mixed model ANOVA on variables during swing. NS, not significant ( $P>0.05$ ).

addition of a variable for the time to the end of force production ( $T_{e,LG}$  or  $T_{e,MG}$ ).

### Statistics

Balanced data sets suitable for analysis of variance (ANOVA) were obtained for six birds for joint forces, five birds for muscle forces from the lateral head of the gastrocnemius, and four birds for the muscle forces from the medial head of the gastrocnemius. Some descriptive statistics are provided for trials at speeds where all birds did not perform. All ANOVAs were restricted to speeds of 1 m s<sup>-1</sup>, 1.5 m s<sup>-1</sup> and 2 m s<sup>-1</sup> and three weighting conditions, 0 g, 30 g and 60 g, where all birds did perform. The measurements used in all ANOVAs were from 4 strides per individual per speed per weight. A three-way mixed model ANOVA, for which speed ( $N=3$ ) and weight ( $N=3$ ) were fixed factors and individual ( $N=4, 5$  or 6) was a random factor, were performed in the statistics program SPSS version 14.0. Multiple observations per individual were accounted for by calculating the  $F$ -ratio for the main effect of speed as the mean square for speed divided by the mean square for the speed  $\times$  individual interaction term (Zar, 1999). Similarly, the  $F$ -ratio for the main effect of weight was the mean square for slope divided by the mean square for weight  $\times$  individual interaction term. The  $F$ -ratio for the interaction effect of weight and speed was the mean square for weight  $\times$  speed divided by the mean square for the speed  $\times$  weight  $\times$  individual interaction. The criterion for statistical significance was  $P<0.05$ . *A priori* power analysis showed these statistical tests with  $N=6$  have a power of 0.90 or greater.

The minimal detectable difference in peak force with limb loading,  $\delta$ , was calculated as:

$$\delta = \sqrt{2k's^2\phi^2/n'}, \quad (6)$$

[from p. 263 (Zar, 1999)] where  $k'$  is the number of limb-loading conditions,  $s^2$  is the mean square remainder term from the ANOVA table of our predicted changes with limb-loading,  $\phi$  is from the power curves in Zar (Zar, 1999) and  $n'$  is the degrees of freedom of the remainder term. For our mixed-model (type III) ANOVA the following numbers were used in the power tables  $v_1=2$  and  $v_2=20$ ,  $\alpha=0.05$ , and power=0.90.

All comparisons of force measurements were made in a series of  $t$ -tests. Paired  $t$ -tests were used to compare the required forces ( $F_{m,r}$ ,  $I_r$ ,  $T_{m,r}$ ) to the muscular force produced by the lateral ( $F_{m,LG}$ ,  $I_{LG}$ ,  $T_{m,LG}$ ) and medial ( $F_{m,MG}$ ,  $I_{MG}$ ,  $T_{m,MG}$ ) head of the gastrocnemius within the same stride.

The amount of force sharing between the two heads of the gastrocnemius was determined with reduced major axis

regressions (RMA). Independent RMA regressions were run for peak force production and impulse during swing and stance using the computer program RMA (Bohanak and van der Linde, 2004). The data for these regressions were taken from the four strides for each speed and weight condition in the three birds we had simultaneous measurements of force in the lateral and medial head.  $t$ -tests were used to test whether the slope was different from predicted values of 1 and 1.12 for optimizations models where force is shared equally or in proportion to physiological cross-sectional area (reviewed in Crowninshield and Brand, 1981; Herzog and Leonard, 1991; Herzog, 1996). For our system a ratio of 1.12 may also support the minimum fatigue optimization model (Dul et al., 1984), since there is no difference in fiber type distribution between the LG and MG in other terrestrial birds (Patak and Baldwin, 1993).

Measured and predicted results are presented as the mean  $\pm$  1 standard error (s.e.m.). Unless stated otherwise, the mean values for each speed and weight combination presented for descriptive purposes were calculated so each individual was weighted equally. Depending on the particular speed and weight, mean values were from different numbers of individuals ( $N_i$ ).

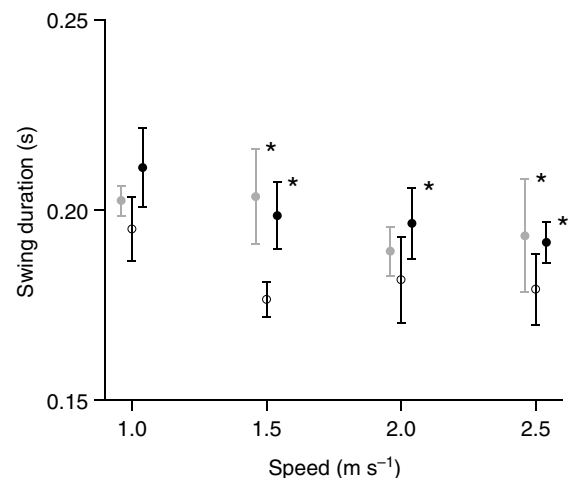


Fig. 1. Swing duration for unloaded (open circles) running and for running with added limb weights of 30 g (solid gray circles) and 60 g (solid black circles). Values significantly different ( $P<0.05$ ) from the unloaded value at each speed are indicated with an asterisk. The symbols for swing duration with limb weights of 30 g and 60 g are offset from their measured speed to the right and left, respectively.

Table 2. Effects of locomotor speed\* and added weights† on required force and force produced in the lateral head of the gastrocnemius during swing

Variable	Speed				Weight			
	d.f.	<i>F</i>	<i>P</i>	$\delta$	d.f.	<i>F</i>	<i>P</i>	$\delta$
$F_{m,r}$	2,10	6.233	0.017	7.53	2,10	2.506	NS	7.53
$T_{m,r}$	2,10	0.473	NS		2,10	1.820	NS	
$I_r$	2,10	9.311	0.005	0.56	2,10	3.077	NS	0.56
$F_{m,LG}$	2,8	2.380	NS		2,8	1.381	NS	
$T_{m,LG}$	2,8	0.116	NS		2,8	13.86	0.003	
$I_{LG}$	2,8	2.798	NS		2,8	0.71	NS	

\*Speeds: 1, 1.5 and 2 m s<sup>-1</sup>.

†Added weights: 0, 30 and 60 g.

Three-way mixed model ANOVA on variables during swing. NS, not significant ( $P>0.05$ ).

## RESULTS

### Kinematics

The time spent to swing the limb was significantly affected by both locomotor speed and limb weight. Swing duration decreased as speed increased ( $P<0.01$ ; Table 1; Fig. 1). With the addition of limb weights, swing duration increased ( $P<0.01$ ; Table 1) for all, but the slowest speed (Fig. 1). Stride duration similarly decreased significantly with increases in locomotory speed ( $P<0.001$ ; Table 1) and increased significantly with increased weight ( $P<0.01$ ; Table 1). Duty factor increased significantly with increased speed ( $P>0.001$ ; Table 1), and ranged from  $0.70\pm 0.02$  at 1 m s<sup>-1</sup> to  $0.53\pm 0.02$  at 3.5 m s<sup>-1</sup>. However, duty factor did not change with added weight ( $P>0.05$ ; Table 1).

### Ankle joint moments and forces

The force that would be required from the gastrocnemius to produce the measured joint moment ( $F_{m,r}$ ) was calculated from the measured joint moment (from inverse dynamics) and the muscle moment arm. The force ( $F_{m,r}$ ) and impulse ( $I_r$ ) required significantly increased with speed ( $P<0.005$ ; Table 2), but did not change ( $P>0.15$ ; Table 2) with the addition of limb weights within a given speed (Fig. 2). The time to peak required force ( $T_{m,r}$ ) did not change with running speed, but did increase with added mass ( $P<0.013$ ; Table 2).

### Muscle forces

The lateral head of the gastrocnemius produced all of the extensor force required during swing phase for all speed and weighting

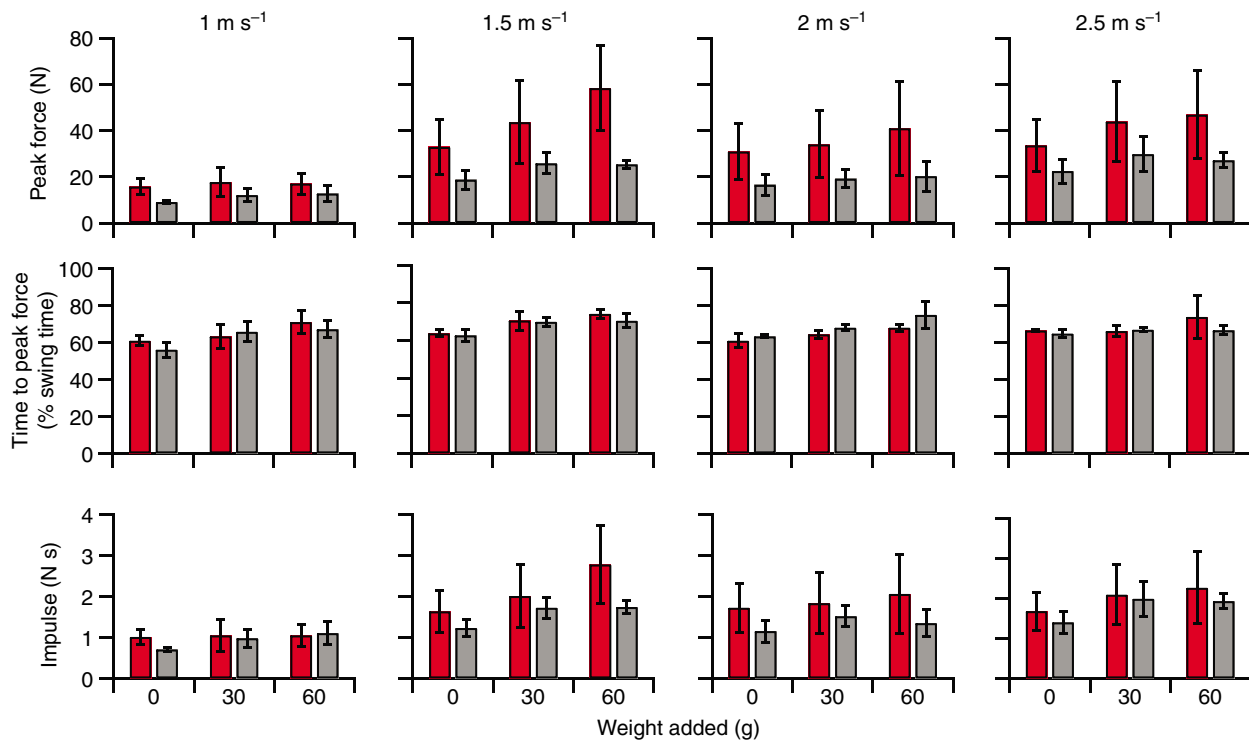


Fig. 2. Values of peak force, time to peak force and impulse produced by the lateral head of the gastrocnemius (red bars) during swing phase were not different from the values required to generate the extension moment at the ankle joint (gray bars) across speed and weighting conditions. The force and impulse required did not change with added mass ( $P>0.09$ ) and were not significantly different ( $P>0.31$ ) than the force produced by the LG. For speeds 1–2 m s<sup>-1</sup>,  $N_i=5$  for all variables; for 2.5 m s<sup>-1</sup>,  $N_i=4$  for all variables.

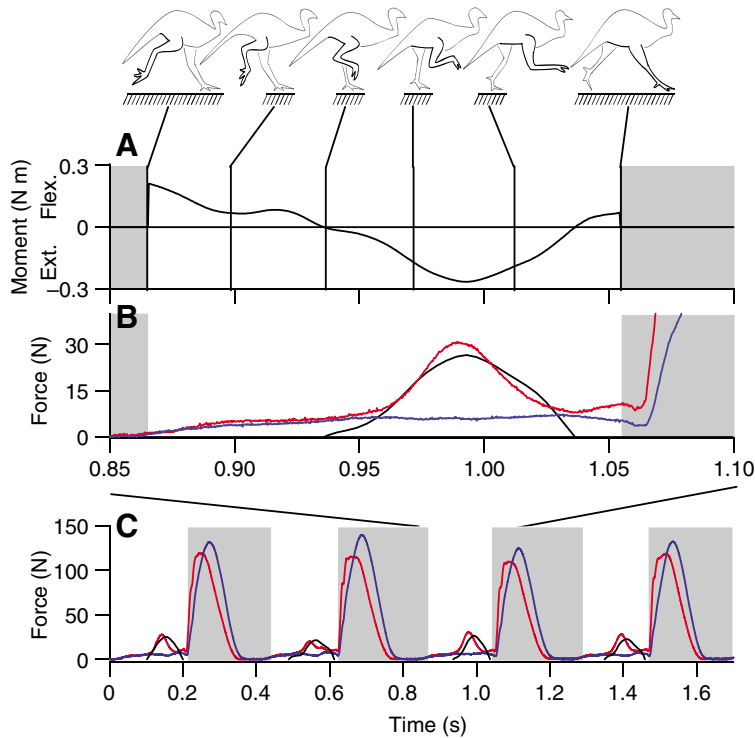


Fig. 3. A representative trace of joint moments (A) and forces (B,C) developed by the MG (blue lines) and LG (red lines) for the right limb of a turkey running at  $2 \text{ m s}^{-1}$ . A positive then negative joint moment is required at the ankle joint during swing as the joint flexes and extends. The black line (B,C) is the force required from the gastrocnemius, calculated from the moment measured by inverse dynamics and the muscle moment arm. Only forces during swing phase were calculated from inverse dynamics (required force). The muscular force required to produce the measured joint extension moment is closely matched by the force produced by the lateral head of the gastrocnemius, while the medial head produces almost no force. The exclusive force production by the LG ends at the beginning of stance (gray shaded region in C).

conditions. The magnitudes of all three variables characterizing force production ( $F_{m,LG}$ ,  $I_{LG}$ ,  $T_{m,LG}$ ) in the lateral head were not significantly different from the magnitudes of the same three variables characterizing the force required for extension ( $F_{m,r}$ ,  $I_r$ ,  $T_{m,r}$ ) at any speed or weight condition ( $P > 0.31$ , Fig. 2). The MG did not contribute significantly to force production during swing. Both measurements of force produced in the medial head ( $F_{m,MG}$  and  $I_{MG}$ ) were less than the  $F_{m,r}$  and  $I_r$  (Fig. 3) and not significantly different from zero ( $P < 0.05$ ).

Although the lateral head of the gastrocnemius was the sole producer of force during swing, force was shared between the two gastrocnemius heads during stance. In both muscles, the maximum force produced during stance increased significantly across speed ( $P < 0.02$ ; Table 3; Fig. 4). However, the impulse produced did not change in either head across speed ( $P > 0.54$ ; Table 3). The time to maximum force occurs later in stance for both heads with speed

( $P < 0.01$ ; Table 3; Fig. 4), while only the lateral head produced force for a longer duration with increases in speed ( $P < 0.01$ ; Table 3).

Contrary to expectations, force production in lateral head of the gastrocnemius was not significantly affected by the addition of weights ( $P > 0.05$ ).

To evaluate force sharing, we performed a reduced major axis (RMA) regression of MG peak force against LG peak force and MG average force against LG average force. Regressions were performed separately for stance and swing phase forces. The data for the reduced major axis regressions were pooled from each speed and weight condition. A slope of 1.0 for swing or stance would indicate equal force production in the two heads of the muscle. Alternatively a slope of 1.12 would indicate that force was produced in proportion to the cross-sectional area of the two heads of the muscle. The slope of the RMA regression for peak force values measured during swing was significant but low ( $P < 0.05$ , slope =  $-0.04$ ,  $R^2 = 0.04$ , Fig. 5B). Similarly, the RMA regression for average force produced during swing has a significant slope, but is also less than 1 or 1.12 ( $P < 0.05$ , slope =  $0.15$ ,  $R^2 = 0.09$ ). Thus, the lateral and medial head do not share force production equally or in proportion to their cross-sectional areas during swing. In stance phase, RMA regressions of MG vs LG maximum force has a significant slope ( $P < 0.05$ , slope =  $0.99$ ,  $R^2 = 0.73$ , Fig. 5A). This slope is significantly ( $P < 0.05$ ) less than 1.12, but not different from 1. Similarly, the slope of the RMA regression for average force production during stance is significantly less than 1.12 ( $P < 0.05$ , slope =  $0.88$ ,  $R^2 = 0.77$ ), but not different from 1. Therefore force is shared equally between the MG and LG during the stance phase of locomotion.

## DISCUSSION

### Force sharing in the medial and lateral gastrocnemius

Contrary to our expectation that the lateral and medial heads of the gastrocnemius would share force equally, we found that the degree

Table 3. Effects of locomotor speed\* and added weights† on the force produced in the lateral and medial head of the gastrocnemius during stance

Variable	Speed			Weight		
	d.f.	F	P	d.f.	F	P
$F_{m,LG}$	2,8	6.036	0.025	2,8	3.677	NS
$T_{m,LG}$	2,8	9.301	0.008	2,8	1.889	NS
$T_{e,LG}$	2,8	8.787	0.010	2,8	1.224	NS
$I_{LG}$	2,8	0.650	NS	2,8	5.714	0.029
$F_{m,MG}$	2,6	7.997	0.02	2,6	1.919	NS
$T_{m,MG}$	2,6	20.960	0.002	2,6	0.289	NS
$T_{e,MG}$	2,6	1.784		2,6	0.243	
$I_{MG}$	2,6	0.362		2,6	2.192	

\*Speeds: 1, 1.5 and  $2 \text{ m s}^{-1}$ .

†Added weights: 0, 30 and 60 g.

Three-way mixed model ANOVA on variables during stance. NS, not significant ( $P > 0.05$ ).

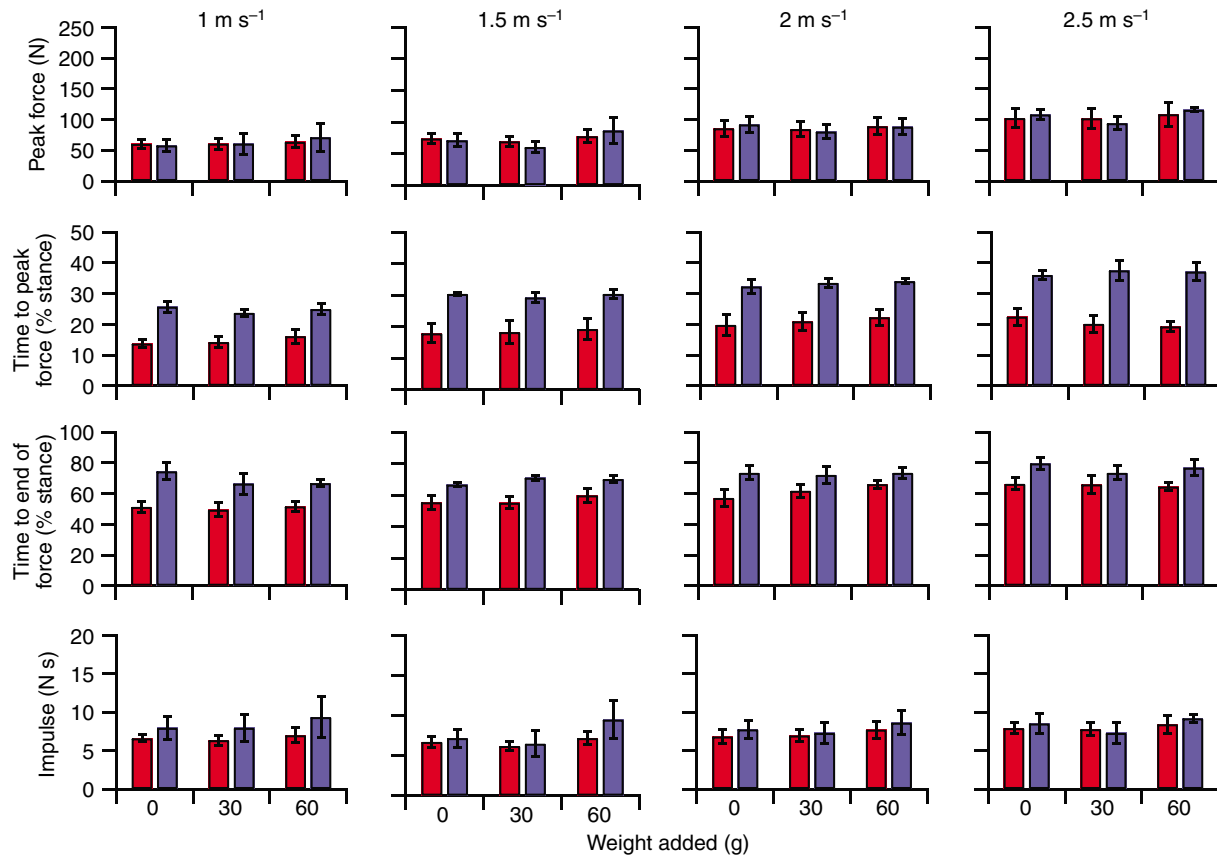


Fig. 4. An equal amount of force is produced in the two heads of the gastrocnemius during stance. Peak force significantly ( $P < 0.05$ ) increases in both the lateral head (red) and the medial head (blue) with speed. With increasing speed, the time of peak force occurs consistently later in the medial head. Other timing variables were unchanged across changes in mass and speed. For speeds 1–2  $\text{m s}^{-1}$ ,  $N=5$  for LG and  $N=4$  for MG variables. For 2.5  $\text{m s}^{-1}$ ,  $N=4$  for LG variables and  $N=3$  for MG variables.

of force sharing varied with the phase of the stride cycle. During swing phase, the LG produced all of the force required to extend the distal limb segment. Force sharing during stance was as predicted, with approximately equal force production in the two heads of the gastrocnemius. The fact that force sharing is variable between two heads of the same muscle within a single stride challenges simple rules for how force is shared between muscle synergists.

Several models have been proposed to predict the distribution of force among muscle synergists. Pedotti and coworkers (Pedotti et al., 1978) proposed that the distribution of force between synergists at a joint was a function of each muscle's capacity for force production, which was in turn a function of each muscle's contractile properties and instantaneous velocity and length. Dul and coworkers (Dul et al., 1984) proposed that a muscle's susceptibility to fatigue was an important factor in determining force sharing among synergists, so that muscles with a higher percentage of oxidative fibers will bear a greater fraction of the total force required from synergists. A rigorous test of these models requires information about contractile properties, length, velocity during contraction and fiber type of the muscles. This information is not available from our study. However, both of these models predict that some degree of force sharing should occur between muscle synergists during force development. We find that the LG and MG in turkeys share force during stance, but force during swing is developed exclusively by the LG. These results indicate

that force sharing, even within a single locomotor cycle, can be quite flexible.

One of the simplest models of muscle force sharing is that force is distributed among muscle synergists at a joint in proportion to each muscle's cross-sectional area (Crowinshield, 1978). This model is supported by some measurements of muscle forces, but often it is not. Force buckle measurements for the medial and lateral gastrocnemius of ducks showed that nearly equal stresses were developed during terrestrial locomotion, but during swimming the stress in the LG was approximately twice that of the MG (Biewener and Corning, 2001). Hopping wallabies develop similar stresses in their lateral gastrocnemius and plantaris muscles, but slightly lower values in the flexor digitorum longus (Biewener and Buadinette, 1995). Perhaps the best-known example of unequal force sharing among muscle synergists comes from force buckle measurements of forces during locomotion in the cat soleus and medial head of the gastrocnemius (Hodgson, 1983; Kaya et al., 2003; Walmsley et al., 1978; Whiting et al., 1984), soleus and gastrocnemius (Prilutsky et al., 1994), and soleus, gastrocnemius and plantaris (Herzog and Leonard, 1991; Herzog et al., 1993; Herzog et al., 1994; Prilutsky et al., 1996; Prilutsky et al., 1997). The soleus produces relatively high forces at slow walking speeds, while the gastrocnemius produces low forces at low speeds. With increases in speed, the force output of the gastrocnemius increases steadily while there is little change in the force output of the soleus. Thus, the degree of force sharing between these two muscles is speed dependent. It is

generally accepted that this pattern reflects the more postural role of the slow-fibered soleus relative to the faster fibered gastrocnemius.

During the stance phase, the force output of the medial and lateral heads of the gastrocnemius in locomoting turkeys is shared equally. The cross-sectional area of the MG is 12% larger than the LG. Therefore, similar stress models of force sharing predict the MG should produce 1.12 or more times the force of the LG (reviewed in Herzog and Leonard, 1991). The slopes of the reduced major axis regressions for maximum force and average force during stance are close to, but significantly below 1.12, so our data do not strictly support any of these models. It is also unlikely that our data support the minimum fatigue model of force sharing (Dul et al., 1984), since the fiber type composition of these two heads is most likely similar. The medial and lateral gastrocnemius of another bird that moves on the ground, the emu (*Dromaius novaehollandiae*), are both composed primarily of fast glycolytic and fast oxidative glycolytic muscle fibers (Patak and Baldwin, 1993). Our preliminary analyses of turkey (data not shown) confirm this fiber type composition. However, our force data in the LG and MG do show equal sharing of force between the synergists.

Our results for force production during swing phase show no sharing of force between the two heads of the gastrocnemius. The MG does not appear to contribute any of the force required during

swing; the force developed in the medial head is not different from zero. Our observation that the force developed in the LG is equal to the force required at the ankle joint, as measured by inverse dynamics, indicates that it is likely that there is no force sharing among any of the muscles capable of extending the ankle joint during swing phase. Swing phase forces are produced exclusively by the lateral head of the gastrocnemius. These results challenge current models of force sharing, because all models predict some amount of force sharing among synergists. The pattern of force production in the turkey MG and LG also indicate that the pattern of motor recruitment can vary between muscles even within a single locomotor cycle.

The difference in force production between the MG and LG during swing may be related to their differing functions at the knee. The heads share a common insertion but their origins are different. As a result, only the LG has an action as a flexor at the knee (Ellerby and Marsh, 2006). The period of rapid extension at the ankle during late swing corresponds to a period of rapid extension at the knee. Thus, it is possible that some of the power for ankle extension during swing is transferred from knee extensors *via* the biarticular LG. It has been proposed that energy transfer *via* biarticular muscles can improve locomotor economy (Aleshinsky, 1986). The fact that the LG is capable of transferring power and the MG is not may explain, in part, the observation that the LG is the sole source of muscle force at the ankle during swing.

#### Changes in required muscular force with speed and added mass

We expected both increases in speed and increases in effective limb mass to result in increases in muscle force. Stance phase peak force increased with speed in both muscles. Swing phase peak force in the LG increased with running speed, as swing duration decreased and higher forces had to be developed to accelerate the foot more rapidly. These increases in force are consistent with previous measurements of increased work to swing the limbs with increased speed (Cavagna and Kaneko, 1977; Fedak et al., 1982; Marsh et al., 2006; Steudel, 1990b).

Contrary to expectations, increases in effective limb mass by the addition of weights did not result in a significant increase in force. Both the force required to swing the limb, as measured by inverse dynamics, and the force developed by the LG, did not change significantly with added limb weights. This is surprising because, given equivalent accelerations, an increase in the moment of inertia of the limb segment should result in a proportional increase in the moment required at the joint. Other studies have demonstrated an increase in segment mechanical power (Marsh et al., 2006; Martin, 1985; Martin and Cavanagh, 1990; Royer and Martin, 2005), and metabolic cost (Bhambhani et al., 1989; Ellerby and Marsh, 2006; Martin, 1985; Soule and Goldman, 1969; Steudel, 1990a; Wickler et al., 2004) with limb loading, consistent with an increase in demand for muscle force and power.

The observation that the required muscle force did not change with limb loading is surprising. The expected change in required muscle force can be calculated by substituting values for weighted limbs into the inverse dynamics data obtained during unloaded running. The addition of 60 g weights to the tarsometatarsus-foot limb segment increases the limb segment's moment of inertia of  $73.18 \pm 14.10\%$  from the unweighted condition. This increase in the moment of inertia of the tarsometatarsus-foot limb segment would increase the peak moment required at the ankle by 80%, if there were no changes in kinematics from the weighted to unweighted condition. If this force were provided by the gastrocnemius, it would translate to an increase from the  $14.02 \pm 2.24$  N measured in the

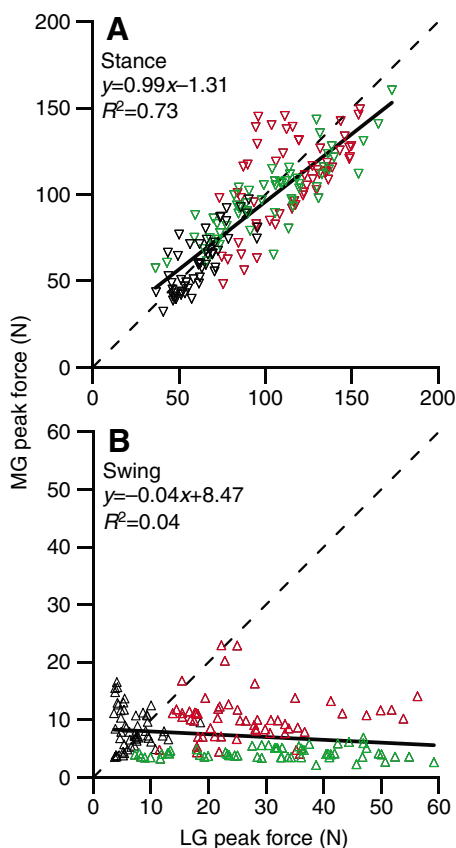


Fig. 5. Reduced major axis regressions of MG peak force against LG peak forces shows that for all speed and loading conditions, forces in the LG and MG are similar during stance phase (A), but not during swing phase (B). Black triangles, bird 1; red triangles, bird 2; green triangles, bird 3. The slopes of both regression lines through the pooled data of all three birds were significant ( $P < 0.05$ ). Solid lines, slopes for measured data; broken line, hypothetical slope=1.0.



unloaded condition to  $25.65 \pm 4.54$  N required for the loaded condition. A power analysis indicates that our statistical analysis is capable of resolving a 53% change in required muscle force, thus this expected change in required muscle force is well within our ability to detect statistically. Thus, it seems that significant alterations in the kinematics of swing are important for reducing the peak muscular forces required during limb-loaded conditions.

Two kinematic changes with limb loading help compensate for increases in limb mass and inertia with limb loading, and reduce the peak muscular force required. First, the duration of swing increases significantly ( $P < 0.01$ ) with the addition of limb weights. Other studies have also shown an increase in swing duration (Marsh et al., 2006; Royer and Martin, 2005) or total stride duration (Martin, 1985; Ropret et al., 1998; Royer and Martin, 2005; Steudel, 1990a) with limb loading. Second, the angular excursion significantly ( $P < 0.05$ ) decreases a small amount (from  $0.82 \pm 0.17$  to  $0.73 \pm 0.12$  rad) with the addition of limb weights. The smaller angular excursion combined with the longer duration of swing act together to decrease the angular acceleration of the limb segment with added limb weight. This reduction in acceleration likely explains the lack of a significant increase in the joint moment that would otherwise be expected with the addition of external weights.

### SUMMARY

The two heads of the gastrocnemius share force differently during stance and swing phase. Across a wide range of speed and loading conditions, the LG and MG produce approximately the same force during stance, while the LG alone produces the force required during swing. The very different patterns of force sharing between heads of a single muscle and within a single stride suggest the force sharing among muscle synergists may be task-dependent and quite variable.

### LIST OF SYMBOLS AND ABBREVIATIONS

$a_x, a_y$	acceleration of the center of mass in the $x, y$ direction
COM	center of mass
$d$	distance from the segment center of mass to the point of rotation
$F_{m, LG}, F_{m, MG}$	maximum force produced by the LG, MG
$F_{m, r}$	required maximum force
$g$	acceleration due to gravity
$I, I_0$	moment of inertia of the combined tarsometatarsus and phalanges about the pivot point, center of mass
$I_{LG}, I_{MG}$	impulse produced by the LG, MG
$I_r$	required impulse
$k'$	number of limb-loading conditions
$l$	muscle fiber length
LG	lateral head of the gastrocnemius muscle
MG	medial head of the gastrocnemius muscle
$m_m, m_s$	mass of the muscle, tarsometatarsus and foot limb segment
$M_p$	moment at the proximal joint
$n'$	number of individuals
$N_i$	number of individuals
PCSA	physiological cross-sectional area
$r$	moment arm of muscle about a given joint
RMA	reduced major axis
$r_x, r_y$	distance from the ankle to the center of mass in the $x, y$ direction
$s^2$	mean square remainder term
$t$	time
$T_{e, LG}, T_{e, MG}$	time to the end of force production
$T_{m, LG}, T_{m, MG}$	time to maximum force produced in the LG, MG
$T_{m, r}$	time to required maximum force
$\alpha$	angular acceleration of the tarsometatarsus and phalanges
$\delta$	minimal detectable difference with limb-loading
$\Delta l$	change in muscle length

$\Delta\theta$	change in joint angle
$\theta$	angle of pennation
$\rho$	density of muscle
$\phi$	desired power level

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