

## RESEARCH ARTICLE

# Great power comes at a high (locomotor) cost: the role of muscle fascicle length in the power versus economy performance trade-off

Amanda N. Cooper<sup>1,\*</sup>, William J. McDermott<sup>2</sup>, James C. Martin<sup>3</sup>, Shea O. Dulaney<sup>1</sup> and David R. Carrier<sup>1</sup>

## ABSTRACT

Muscle design constraints preclude simultaneous specialization of the vertebrate locomotor system for explosive and economical force generation. The resulting performance trade-off between power and economy has been attributed primarily to individual differences in muscle fiber type composition. While certainly crucial for performance specialization, fiber type likely interacts with muscle architectural parameters, such as fascicle length, to produce this trade-off. Longer fascicles composed of more serial sarcomeres can achieve faster shortening velocities, allowing for greater power production. Long fascicles likely reduce economy, however, because more energy-consuming contractile units are activated for a given force production. We hypothesized that longer fascicles are associated with both increased power production and locomotor cost. In 11 power-trained and 13 endurance-trained recreational athletes, we measured (1) muscle fascicle length via ultrasound in the gastrocnemius lateralis, gastrocnemius medialis and vastus lateralis, (2) maximal power during cycling and countermovement jumps, and (3) running cost of transport. We estimated muscle fiber type non-invasively based on the pedaling rate at which maximal cycling power occurred. As predicted, longer gastrocnemius muscle fascicles were correlated with greater lower-body power production and cost of transport. Multiple regression analyses revealed that variability in maximal power was explained by fiber type (46% for cycling, 24% for jumping) and average fascicle length (20% for cycling, 13% for jumping), while average fascicle length accounted for 15% of the variation in cost of transport. These results suggest that, at least for certain muscles, fascicle length plays an important role in the power versus economy performance trade-off.

**KEY WORDS:** Cost of transport, Economy, Muscle architecture, Locomotion, Whole-organism performance, Ultrasound

## INTRODUCTION

The life history of an animal places multiple, conflicting demands on the design of its musculoskeletal system. Functional trade-offs are expected to occur because of evolutionary constraints that preclude specialization for more than one performance task. One such trade-off that has captured the interest of comparative and

exercise physiologists is that between powerful bursts of activity (e.g. sprinting, leaping, etc.) and economical locomotion, which allows for travel over longer distances at slower, sustainable speeds. The search for evidence of a trade-off between power- and endurance-based performance has spanned decades and vertebrate taxa. This trade-off has been demonstrated at both the whole-organism level (in fish: Reidy et al., 2000; Langerhans, 2009; Ingley et al., 2016; in frogs: Herrel and Bonneaud, 2012; in lizards: Bennett et al., 1984; Huey et al., 1984; Vanhooydonck et al., 2001; in mammals: Van Damme et al., 2002; Dlugosz et al., 2009; Wilson et al., 2014; van der Zwaard et al., 2018) and the isolated-muscle level (Wilson et al., 2002; Wilson and James, 2004; Vanhooydonck et al., 2014). Given the wealth of evidence supporting the existence of a performance trade-off between muscular power production and economical locomotion, it is surprising that its mechanistic origins have been overwhelmingly attributed to only one aspect of muscle design: muscle fiber type.

Muscular power production is maximized by increasing the force produced by the muscle and/or its shortening velocity. At the level of individual myocytes, these functional parameters are mediated by differences in the relative proportions of three structural elements, with a greater percentage of cellular volume devoted to myofibrils and sarcoplasmic reticulum at the expense of mitochondrial density (Lindstedt et al., 1998). As a consequence of spatial limitations, cellular composition can be optimized exclusively for either explosive or economical force generation. The dichotomous contractile and metabolic profiles of fast- versus slow-twitch muscle fibers are consistent with these conflicting demands on muscle design. Fast-twitch fibers are ideal for power production because of their larger diameters (Martin et al., 1988) and faster shortening velocities (Close, 1972), yet they cannot maintain prolonged locomotor activity because they generate ATP primarily via glycolysis, an anaerobic metabolic pathway that quickly causes fatigue. Conversely, slow-twitch muscle fibers rely to a greater extent on oxidative phosphorylation, a slower, more sustainable process where ATP is generated aerobically (Biewener, 2003). Compared with fast-twitch fibers, slow-twitch fibers are more economical at sustainable walking and running speeds as a result of their ability to perform work more efficiently (Woledge, 1968; Morgan and Proske, 1984). Differences in muscle fiber type between animals specialized for burst and endurance tasks have traditionally been accepted as the definitive explanation for these two extremes of locomotor specialization (e.g. Vanhooydonck et al., 2001; Wilson et al., 2002; Wilson and James, 2004; Herrel and Bonneaud, 2012; Vanhooydonck et al., 2014). Fiber type composition has also been used to explain performance differences in human sprinters and distance runners (Zierath and Hawley, 2004), with sprinters being found to possess more fast-twitch fibers and endurance athletes having a greater percentage of slow-twitch fibers (Gollnick et al., 1972; Costill et al., 1976).

<sup>1</sup>School of Biological Sciences, University of Utah, Salt Lake City, UT 84112, USA.

<sup>2</sup>Sport Science and Research, The Orthopedic Specialty Hospital, Murray, UT 84107, USA. <sup>3</sup>Department of Nutrition and Integrative Physiology, University of Utah, Salt Lake City, UT 84112, USA.

\*Author for correspondence (amanda.cooper@utah.edu)

 A.N.C., 0000-0002-3195-9500

Although muscle fiber type undeniably plays an important role in physiological specialization for performance, it likely interacts with macroscopic muscle traits to limit specialization for locomotor power versus economy (Lieber and Fridén, 2000). Early studies of functional specialization in horses reported that the relatively short fascicles of distal limb muscles were likely ineffective at producing work via shortening, yet ideal for maintaining isometric tension required for effective elastic energy savings (Hermanson and Cobb, 1992; Soffler and Hermanson, 2006). Noting that the most economical mammalian runners possess short muscle fascicles and compliant tendons, Alexander (2000) formally suggested that the structure of the muscle–tendon unit could lead to a trade-off between power production and locomotor economy. Architecturally speaking, maximum muscular power production can be increased by having more contractile units (sarcomeres) placed in series within each muscle fascicle, thereby increasing the contractile length of the muscle and allowing for greater shortening velocity (Biewener, 2003; Kardong, 2009). For example, if two fascicles of different lengths shorten by the same percentage of their resting length, the longer fascicle will shorten a greater absolute distance and, thus, at a greater velocity. The time required for shortening is identical in the two fascicles, but the longer fascicle will have a faster shortening velocity because of its greater excursion distance (Biewener, 2003). Indeed, numerous studies have linked long muscle fascicles with superior power-based performance among human athletes (Abe et al., 2000; Kumagai et al., 2000; Nasirzade et al., 2014; Methenitis et al., 2016; van der Zwaard et al., 2018) and in broader comparisons between different primate species (Huq et al., 2015; O'Neill et al., 2017).

While long muscle fascicles are expected to augment maximal power production, this same design is likely disadvantageous for economical force production during walking and running at sustainable speeds as a result of the simultaneous activation of serial contractile elements along the entire length of a muscle fascicle (Loeb et al., 1987; Lieber and Fridén, 2000). Because each activated serial sarcomere consumes energy, long fascicles of a given cross-sectional area must use more metabolic energy to generate the same amount of force as fascicles composed of fewer serial sarcomeres (Biewener, 2003). Because of this simple functional constraint, specialization of the locomotor muscles for power production via longer fascicles can be expected to have a detrimental effect on locomotor economy. Conversely, it can also be argued that long muscle fascicles improve locomotor economy as a result of their altered force–velocity curve. For a given fascicle shortening velocity, long muscle fascicles can produce more relative force than short fascicles because having more serial sarcomeres decreases the absolute shortening velocity of individual sarcomeres in long fascicles. Thus, for a given amount of force production, a muscle composed of long fascicles may need to recruit a smaller percentage of its total cross-sectional area (i.e. fewer fascicles arranged in parallel), thereby reducing the energy cost of contraction compared with an otherwise identical muscle made of short fascicles. These two opposing consequences of fascicle length both likely influence locomotor economy, but their relative impacts are not understood. The decreased economy of human sprinters compared with distance runners (Weyand et al., 1994) suggests that longer fascicles do decrease economy, because the former group is expected to have longer fascicles.

While results from numerous studies are consistent with a fascicle length-based functional trade-off between power and economy, no study has attempted to simultaneously measure all the variables required to demonstrate and evaluate this hypothesis. Here, we

addressed the relationships between leg muscle fascicle length, fiber type, power and economy in human locomotor specialists: self-identified power and endurance athletes. Using ultrasound imaging, we measured fascicle length in the gastrocnemius lateralis, gastrocnemius medialis and vastus lateralis muscles. We non-invasively estimated fiber type composition using optimal pedaling rate during cycling, which is highly correlated with the percentage of fast-twitch fibers in the vastus lateralis muscle (Hautier et al., 1996). We also collected performance data in the form of maximum power production during stationary cycling and countermovement jumps and cost of transport during level treadmill running. Our final aim consisted of using multiple regression analyses to determine what percentage of the variation in our power and economy measurements can be explained by the individual contributions of fascicle length and fiber type.

We hypothesized that the individuals producing the greatest cycling and jumping power would also be the least economical (i.e. have the highest cost of transport), consistent with a performance trade-off between these two locomotor tasks. We also expected to find a positive correlation between longer muscle fascicles and both metrics of maximal power production as a consequence of the faster fascicle shortening velocities afforded by having more sarcomeres arranged in series. Finally, we predicted that longer fascicles would be associated with higher running costs as a result of more energy-consuming serial sarcomeres being activated for a given amount of force production. These combined results would provide support for our hypothesis that muscle fascicle length is a significant contributor to the power versus economy trade-off.

## MATERIALS AND METHODS

### Participants

Our study population consisted of physically active men aged 19–40 years (mean 27.8±5.0 years; Table 1). In order to maximize (1) the likelihood of identifying a performance trade-off between maximal power production and locomotor economy and (2) the empirical signal of muscle fascicle length, study enrollment was limited to healthy participants who strongly self-identified as specialists for power ( $n=11$ ) or endurance ( $n=13$ ) performance. We did not explicitly quantify individuals' level of experience or participation in power/endurance sports in order to assign them to either category. Instead, we recruited athletes from local sports organizations (CrossFit gyms, running groups, etc.) who self-reported their locomotor performance as being more specialized for power/endurance compared with their peers. Individuals who self-identified as power athletes regularly participated in sports requiring quick bursts of anaerobic performance, such as sprinting, hurdling, volleyball and rugby, whereas self-identified endurance athletes routinely participated in organized distance events such as triathlons, marathons and ultramarathons. Our study population represented a broad range of athletic performance levels for both power- and endurance-based sports, from members of recreational leagues to national and even international competitors. Participants gave their informed consent and all procedures were approved by the University of Utah Internal Review Board (Approval # IRB\_00103134).

### Experimental protocol

The experimental protocol consisted of a series of performance tests measuring maximal-effort lower-body power production and running economy, as well as capturing musculoskeletal ultrasound images and photographs, which were later used to calculate muscle fascicle length and Achilles tendon moment arm, respectively.

**Table 1. Descriptive, performance and morphological variables for self-identified endurance ( $n=13$ ) and power ( $n=11$ ) athletes**

	Endurance	Power
<b>Descriptive measures</b>		
Age (years)	29.4±4.5	26.0±5.1
Mass (kg)	71.7±7.9	85.7±12.9
Height (cm)	180.9±8.4	179.8±7.8
<b>Performance measures</b>		
Cycling		
Peak power (W)	883.6±154.8	1297.9±205.0
OPR (rpm)	114.2±9.7	126.8±12.2
Countermovement jump		
Peak power (W)	2953.0±473.4	4879.1±712.4
Peak force (N)	849.9±431.6	1260.3±307.7
Cost of transport (kcal kg <sup>-1</sup> km <sup>-1</sup> )	0.89±0.09	0.97±0.08 ( $n=7$ )
<b>Morphological measures</b>		
Leg segment length (cm)		
Shank length	42.0±2.8	41.2±2.5
Thigh length	43.6±3.1	44.2±2.5
Total lower limb	87.4±5.9	86.8±3.5
ATMA length (cm)	4.08±0.53	4.11±0.55
Fascicle length (cm)		
GL	7.40±1.71	8.32±1.61
GM	6.06±0.90	6.63±0.92
VL	7.66±0.67	7.91±0.87
Average	7.04±0.88	7.62±0.99

Measurements are given as means±s.d. Cost of transport data for four power athletes were excluded from analyses. Average fascicle length refers to the mean of each individual's GL, GM, and VL fascicle length measurements. OPR, optimal pedaling rate; ATMA, Achilles tendon moment arm; GL, gastrocnemius lateralis; GM, gastrocnemius medialis; VL, vastus lateralis.

Participants were asked to refrain from strenuous exercise for at least 24 h prior to testing. Data collection was scheduled according to participants' availability; as such, we were unable to standardize the time of day that testing occurred for each individual. We controlled for fatigue during performance testing by randomizing the order of trials. Room temperature was maintained between 19 and 22°C (mean±s.d. 20.5±0.8°C).

## Maximal power production

### Inertial load cycling power and optimal pedaling rate

Maximum power production in the lower body was measured via the inertial load method (Martin et al., 1997) on a cycling ergometer. Using this protocol, instantaneous power ( $P_{\text{inst}}$ ) is calculated in a brief exercise bout via the following equation:

$$P_{\text{inst}} = I_{\text{flywheel}} \times \omega_{\text{flywheel}} \times \alpha_{\text{flywheel}}, \quad (1)$$

where  $I_{\text{flywheel}}$  is the known inertia of the flywheel,  $\omega_{\text{flywheel}}$  is the flywheel angular velocity and  $\alpha_{\text{flywheel}}$  is the flywheel angular acceleration. An optical sensor collected flywheel position data, which were spline-smoothed with a Woltring (1986) filter at a cutoff frequency of 8 Hz and then used to calculate flywheel velocity and acceleration. Participants completed a series of three sessions, with each session consisting of three trials. Each subject performed a 5 min warm-up at low intensity prior to the first session to familiarize himself with the cycling ergometer. Sessions two and three were interspersed randomly between other performance tests while participants were still warm. For each trial, participants were verbally encouraged to accelerate maximally for 3–4 s at a time while using the muscles of the arms and torso to remain seated while pedaling. A 2 min resting period was given between trials according to the protocol used by Martin et al. (2000). The greatest value of average power produced over a single crank revolution during the

nine trials was considered that individual's maximum power production. The corresponding optimal pedaling rate was also determined as the pedaling velocity at which maximum power occurred. A strong positive correlation between optimal pedaling rate and the percentage of fast-twitch fibers in the vastus lateralis muscle has been demonstrated previously (Hautier et al., 1996).

### Countermovement jump power and peak force

To facilitate interpretation of our results in a broader, comparative context, we also measured maximal power production during jumping. We chose to have participants perform countermovement versus squat jumps because the former is a better indicator of an individual's capacity for explosive lower-body power production (Markovic et al., 2004), possibly as a result of the increased time for muscle activation afforded by the countermovement motion (Bobbert et al., 1996; Bobbert and Casius, 2005). Maximal-effort countermovement jumps were performed on a force plate (AMTI, Watertown, MA, USA) and sampled at 3000 Hz. Participants were instructed to jump as high as possible while landing in the same position as takeoff with the hands held on the hips for the entire duration of the jump. A total of five jumps were performed, with a rest period of approximately 30 s to 1 min between each jump. We used the ground reaction force time series to calculate the resultant force acting on the athlete's center of mass and power production according to the methods of Linthorne (2001). Maximum countermovement jump power and peak force were respectively defined as the greatest instantaneous power and force an individual produced prior to takeoff across the five jumping trials.

### Locomotor economy

Locomotor economy was measured as the metabolic cost of transport (the amount of energy required to travel a given distance per unit body mass) as subjects ran on a level motorized treadmill (Treadmetrix, Park City, UT, USA). Testing consisted of four running trials at speeds of 7.2, 8.0, 8.9 and 9.7 km h<sup>-1</sup> (4.5, 5.0, 5.5 and 6.0 mph), respectively. Each trial lasted 4 min, and trials were always completed in ascending order with respect to speed (i.e. from the slowest to the fastest running velocity). Rates of oxygen consumption ( $\dot{V}_{\text{O}_2}$ ) and carbon dioxide production ( $\dot{V}_{\text{CO}_2}$ ) were measured on a breath-by-breath basis (1 min<sup>-1</sup>) with a Parvo Medics TrueOne 2400 system (Parvo Medics, Sandy, UT, USA). Metabolic rate (kcal min<sup>-1</sup>) was calculated according to the Weir (1949) formula using mean  $\dot{V}_{\text{O}_2}$  and  $\dot{V}_{\text{CO}_2}$  values during steady-state metabolism, which was considered to occur when a Pearson's correlation analysis indicated no further increase in  $\dot{V}_{\text{O}_2}$  over the span of 1 min ( $P>0.05$ ). We also collected baseline  $\dot{V}_{\text{O}_2}$  and  $\dot{V}_{\text{CO}_2}$  data as participants stood quietly for 5 min prior to testing. Each subject's standing metabolic rate was subsequently subtracted from all running cost measurements to provide the net cost of transport required for locomotion (Cunningham et al., 2010). We then calculated mean mass-specific cost of transport (kcal kg<sup>-1</sup> km<sup>-1</sup>) for each participant by averaging the net costs for all four running trials. Average net cost of transport could not be calculated for the first study participant, a power athlete who completed running trials at different speeds prior to finalization of the running protocol. Locomotor economy data from two additional power athletes were automatically excluded from further analyses for using anaerobic metabolism (respiratory exchange ratio  $\geq 1$ ) and for not achieving metabolic steady state, respectively. Lastly, we chose not to include metabolic cost data from a fourth and final power athlete in our analyses for completing all four trials continuously without stopping to rest between trials. We discuss our rationale for this decision below.

While trial order was the same for all study participants, two protocols were followed with respect to recovery periods between trials. Subjects were given the option to rest as needed between running trials or to complete the trials in one continuous run. Ideally, we would have measured running cost of transport under a set of universal conditions by having all participants complete the four trials either in discrete bouts separated by rest periods or in a continuous fashion without recovery breaks. A previous investigation by Meldrum et al. (1997) employing similar methodology to the present study (four running trials lasting 4 min each) found that running cost did not differ significantly in children when tests were completed in discrete bouts versus continuous increments. However, to our knowledge no studies to date have determined whether this is also true for adults. Running cost could be overestimated at higher speeds with a continuous incremental protocol if prior exercise causes fatigue.

The total number of rest periods used by the each of the 20 self-identified power (P) and endurance (E) athletes whose cost of transport data were included in our analyses fell into one of three categories: no rest (0P:6E), at least one rest between trials (2P:3E) and rest between each trial (5P:4E). While inconsistent recovery periods may have contributed to individual differences in fatigue among our subjects, we do not suspect that they increased the likelihood of falsely rejecting the null hypothesis. If anything, these discrepancies would reduce the empirical signal of fascicle length by creating a disproportionate fatigue bias that increased the cost of locomotion in the endurance athletes.

We predicted *a priori* that a greater proportion of slow-twitch fibers (Gollnick et al., 1972; Costill et al., 1976), in addition to shorter fascicles hypothesized to favor economical force production, of endurance athletes participating in our study would result in these participants exhibiting significantly lower energy costs during running compared with power athletes. We anticipated that such disparities in locomotor performance would be crucial for detecting the empirical signal of fascicle length in a heterogeneous sample of athletes from the general population (so much so that we tried to capture the broadest possible range of the locomotor performance spectrum by restricting study enrollment to individuals who self-identified as exclusively power or endurance specialized). Because a greater proportion of power athletes rested between each trial (71% compared with 31% of endurance athletes), any artificial increases to running cost arising from fatigue would disproportionately affect endurance athletes, thereby reducing the aforementioned disparities in locomotor performance in our study population.

We chose not to analyze locomotor economy data from the single power athlete who ran all four trials continuously because of evidence of fatigue. At  $1.18 \text{ kcal kg}^{-1} \text{ km}^{-1}$ , this subject's cost of transport was the greatest of all study participants, exceeding the mean cost of transport value for the seven remaining power athletes ( $0.97 \pm 0.08 \text{ kcal kg}^{-1} \text{ km}^{-1}$ ; Table 1) by more than two standard deviations. Although the aforementioned differences in muscle fiber type and fascicle length are expected to drive up the running cost of transport in our sample of power athletes, we suspect the markedly higher metabolic cost of this power athlete is a result of fatigue from not resting between trials instead of an accurate measure of his locomotor economy.

### Muscle fascicle length

#### Ultrasound image acquisition

We used B-mode ultrasound (LOGIQ S7, General Electric, Chicago, IL, USA) to measure fascicle length in the

gastrocnemius lateralis (GL), gastrocnemius medialis (GM) and vastus lateralis (VL) muscles. Although ultrasound cannot be used to visualize sarcomeres directly, we expected muscle fascicle length to be proportional to the number of in-series sarcomeres, as there is relatively little variation in the length of individual vertebrate sarcomeres (Biewener, 2003). The mid-muscle bellies of GL, GM and VL were first identified and marked on the dominant leg according to bony anatomical landmarks as described by Murach et al. (2015). A 3.6–12 MHz linear array transducer was placed perpendicular to the skin overlying the muscle of interest, with a coating of gel between the skin and the probe to enhance the transmission of the ultrasound waves. Once placed over the mid-muscle belly, the probe was rotated so that it was parallel with the muscle's deep aponeurosis (longitudinal view). To ensure that muscle length was standardized between participants, measurement of GL and GM was performed with participants lying prone on an examination table. Ankle position was fixed at 90 deg by having participants place the bottom of their overhanging feet against a wall. Measurement of VL occurred while participants stood against a wall while distributing their body mass evenly between both legs. Participants were instructed to relax and remain as still as possible during ultrasound image collection to avoid voluntary shortening of the muscle fascicles.

#### Image analysis

Ultrasound images were analyzed with ImageJ software (National Institutes of Health, Bethesda, MD, USA). Muscle fascicle length was defined as the length of the fascicular trajectory between the deep and superficial aponeuroses. We determined participants' average fascicle length for a given muscle by measuring three separate fascicles in each ultrasound image, with three images used per muscle. Because muscle fascicles of GL, GM and VL often extended beyond the ultrasound image dimensions, fascicle length measurements consisted of direct and estimated portions. First, the entire visible portion of a single fascicle was traced linearly to its end at the image border. Linear extrapolation of the deep and superficial aponeuroses was then performed to estimate the remaining distance between the end of the fascicle and its intersection with a line parallel to the aponeurosis (e.g. Blazevich et al., 2007, 2009b; Erskine et al., 2009; Austin et al., 2010; Csapo et al., 2011; Ema et al., 2013). Ando et al. (2014) have demonstrated that using aponeurosis extrapolation to estimate the length of the non-visible portion of fascicles produces less error in measurements of total VL fascicle length compared with other commonly used methods.

While the majority of study participants had linear fascicles in all three of the examined muscles, the VL muscle fascicles of six power and three endurance athletes exhibited a curvilinear arrangement similar to that documented by Kawakami et al. (1993) in the hypertrophied triceps brachii muscles of highly trained bodybuilders. For the nine individuals with curvilinear VL fascicles, a single fascicle from each of three ultrasound images was measured. We attempted to account for this fascicle curvature in measurements of VL muscle fascicle length by fitting a single cubic Bézier curve to the fascicular trajectory instead of a straight line. Briefly, the shape of a cubic Bézier curve is determined by the relative positions of four points. Two points ( $P_0$  and  $P_3$ ) serve as the endpoints of the curve, while the amount of curvature is specified by adjusting two control points ( $P_1$  and  $P_2$ ). Using the Bézier Curve Tool plugin in ImageJ, the control points were positioned so that the Bézier curve traced the visible portion of the fascicle. An endpoint was placed at the origin of the fascicle from either the superficial or

deep aponeurosis if it was visible within the image dimensions. The curvilinear trajectory of the non-visible portion of the fascicle was estimated by placing one or both endpoints on their respective linear aponeurosis extrapolation lines so that the Bézier curve continued to accurately trace the visible portion of the fascicle.

The intra-rater reliability for fascicle length measurements was assessed via coefficient of variation (CV) as well as intraclass correlation coefficients (ICC) and their 95% confidence intervals (CI). Based on ICC estimates, reliability is considered excellent for GL (CV=4.2%, ICC=0.98, CI=0.97–0.99) and GM (CV=3.1%, ICC=0.98, CI=0.96–0.99), while VL reliability (CV=4.9%, ICC=0.89, CI=0.79–0.95) ranges from good to excellent (Koo and Li, 2016). Because our measurements were obtained in part by estimating the unknown length of non-visible fascicle segments, we quantified the potential error involved in extrapolating the fascicle trajectories beyond the ultrasound image dimensions for (1) each of the three muscles and (2) linear versus curvilinear VL fascicles. As our live study population precluded the use of dissection to verify the actual length of muscle fascicles (e.g. Ando et al., 2014), we tested the efficacy of our extrapolation technique using the known lengths of visible fascicle segments from our existing sample of muscle ultrasound images. We recreated the original conditions for image analysis by first cropping the images to remove a portion of a visible fascicle segment and then using extrapolation to estimate the now unknown segment length. To do this, we re-measured the visible portion of a single fascicle per muscle from the ultrasound images of each participant's GL, GM and VL muscles. This known segment length was then subtracted from our existing measurement of total fascicle length, allowing us to express the original unknown, estimated portion of the fascicle as a percentage of its total length. We cropped the original ultrasound image so as to eliminate a corresponding percentage of the visible fascicle length, which we then re-measured by extrapolating the trajectory of the fascicle to estimate the now unknown segment length. Comparison of our estimated values with the actual visible length of fascicles enabled us to determine the average potential error present in our fascicle length measurements for each muscle, including the two distinct types of fascicle arrangement in VL. Mean error rates for GL and GM were similar at 2.0% and 2.2%, respectively. These values differed significantly from the 4.1% average error across all subjects for VL ( $P=0.021$  for GL;  $P=0.028$  for GM), possibly as a result of a greater average proportion of total fascicle length that extended beyond the original ultrasound image dimensions in VL (36.4%) compared with GL (32.7%) and GM (19.2%). Mean error rates for linear (3.8%) versus curvilinear (4.6%) fascicles in VL were not significantly different from one another ( $P=0.628$ ), suggesting our extrapolation method for estimating fascicle length worked equally well for the two groups.

### Achilles tendon moment arm

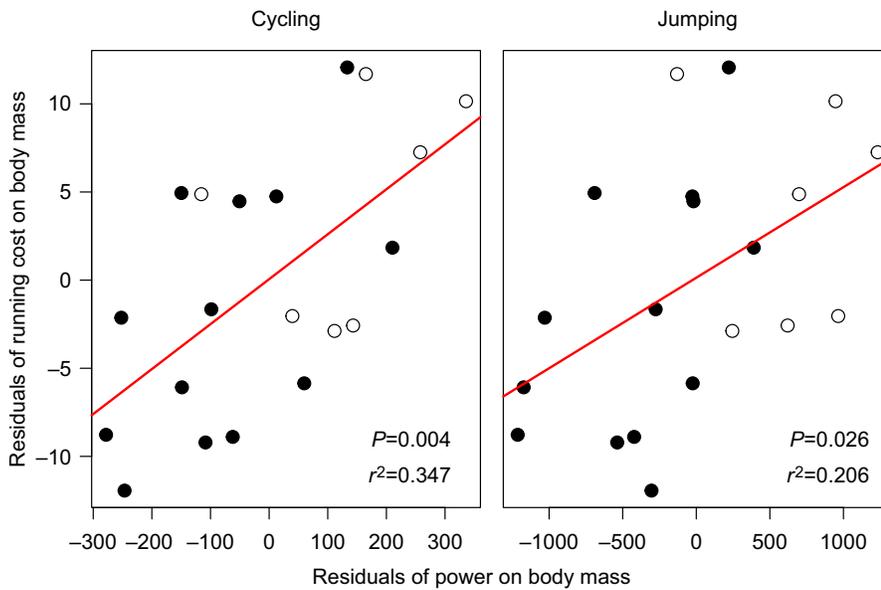
The length of the Achilles tendon moment arm has been shown to influence cost of transport, with shorter moment arms associated with improved running economy (Scholz et al., 2008; Raichlen et al., 2011; Barnes et al., 2014). Lee and Piazza (2009) also report that short moment arms accompany the long plantarflexor muscle fascicles of sprinters. In order to control for individual differences in Achilles tendon moment arm length, we estimated the length of the Achilles tendon moment arm according to the methods of Scholz et al. (2008) and Butler and Dominy (2016). Briefly, the Achilles tendon moment arm is defined as the orthogonal distance from the Achilles tendon line of action to the ankle center of rotation. The approximate center of rotation of the ankle is a line between the most

prominent points of the fibular lateral malleolus and the tibial medial malleolus. In our participants, we marked the most prominent points of the lateral and medial malleoli on the dominant foot, which was then placed flat upon a wooden block with a metric scale on the side while participants sat in a chair. Chair height was adjusted so that the knee joint was flexed at an angle of 90 deg. We then took photographs (Canon EOS Rebel T2i, Tokyo, Japan) of the foot and lower leg while the lateral side of the foot was lined up with the straight edge of the block. This process was repeated for the medial side of the foot. Camera position and focal length were standardized for all photographs so that images were parallel to the sagittal plane. We performed image analysis on the photographs in ImageJ by measuring the orthogonal distance from the posterior aspect of the Achilles tendon to the lateral malleolus. The same process was repeated for images of the medial side of the foot. The lengths of the lateral and medial lines were averaged to calculate the Achilles tendon moment arm length.

### Statistical analyses

All data were tested for normality with Shapiro–Wilk tests prior to analysis. Body mass and peak countermovement jump force values were natural log-transformed to improve normality. Preliminary linear regression analyses showed that running cost ( $\text{kcal km}^{-1}$ ), cycling power (W) and jumping power (W) were significantly correlated with body mass ( $r^2=0.579$ ,  $r^2=0.604$  and  $r^2=0.643$ , respectively; all  $P<0.001$ ); we measured the partial correlations between these variables while controlling for body mass in order to test for the expected performance trade-off between power and locomotor economy in our study population. We then used bivariate linear regression analyses to examine the relationships between muscle fascicle length and peak mass-specific cycling and countermovement jump power and average cost of transport.

We performed a series of stepwise multiple regression analyses in order to examine the relative contributions of muscle force (measured here as peak countermovement jump force) and muscle shortening velocity (muscle fiber type and average fascicle length) to peak mass-specific cycling and countermovement jump power and average cost of transport. Although we did not measure muscle fiber type directly using needle biopsies, Hautier et al. (1996) demonstrated a strong relationship between optimal pedaling rate during cycling and the percentage of fast-twitch muscle fibers present in the vastus lateralis. We included leg length as an additional explanatory variable for cost of transport because of the well-established inverse relationship between running cost and lower limb length (Pontzer, 2007; Steudel-Numbers et al., 2007). We used Pearson product moment correlation coefficients to test for multicollinearity between explanatory variables prior to performing multiple regression analyses. We also used the car package (Fox and Weisberg, 2019) to calculate variance inflation factors (VIFs) for all explanatory variables that were retained in the final regression models (all VIFs  $<2$ ). Final multiple regression models were chosen based on AICc scores, which were calculated with the AICcmodavg package (<https://CRAN.R-project.org/package=AICcmodavg>). Initial models for the three dependent variables contained all explanatory variables and their interaction terms. All three initial models contained no significant interaction terms; thus the final, 'best model' for each of the three dependent variables contained only the explanatory variables that produced the lowest AICc score. Finally, we calculated the partial regression coefficients of explanatory variables in the final models using the relaimpo package (Gromping, 2006). All analyses were performed using the R statistical package (version 3.2.2; <http://www.R-project.org/>).

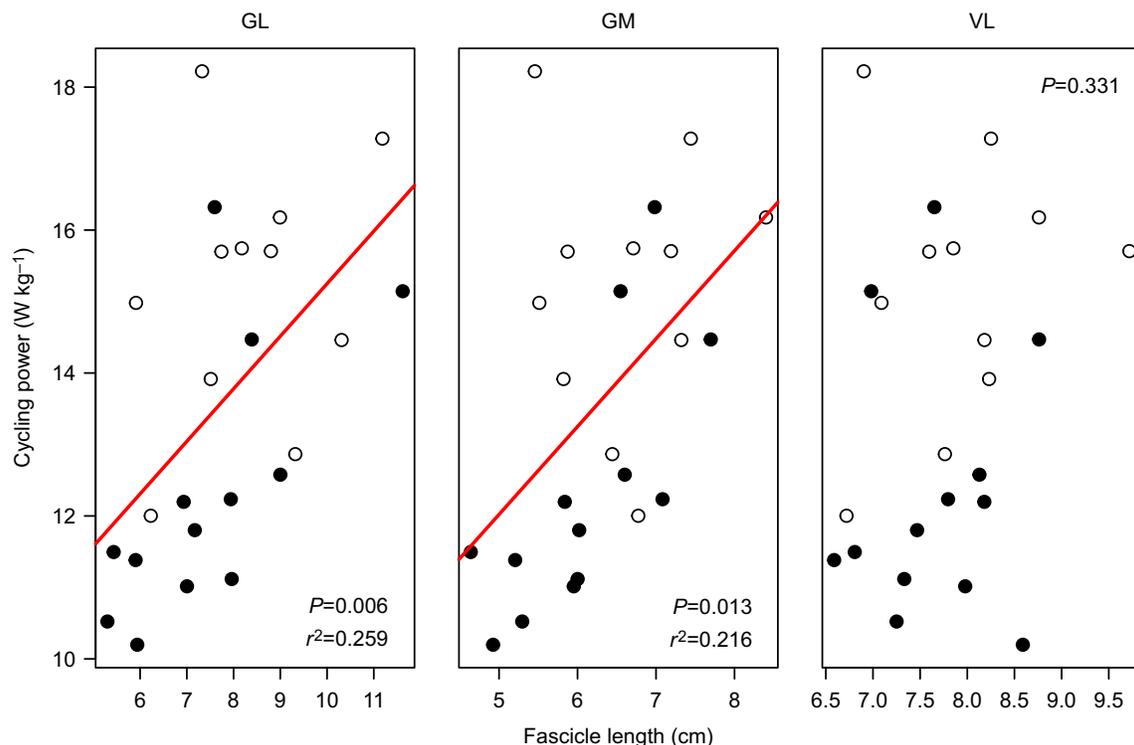


**Fig. 1. Partial correlations between average running cost ( $\text{kcal km}^{-1}$ ) and peak cycling power and countermovement jump power, controlling for body mass. Filled circles, self-identified endurance athletes ( $n=13$ ); open circles, self-identified power athletes ( $n=7$ ).**

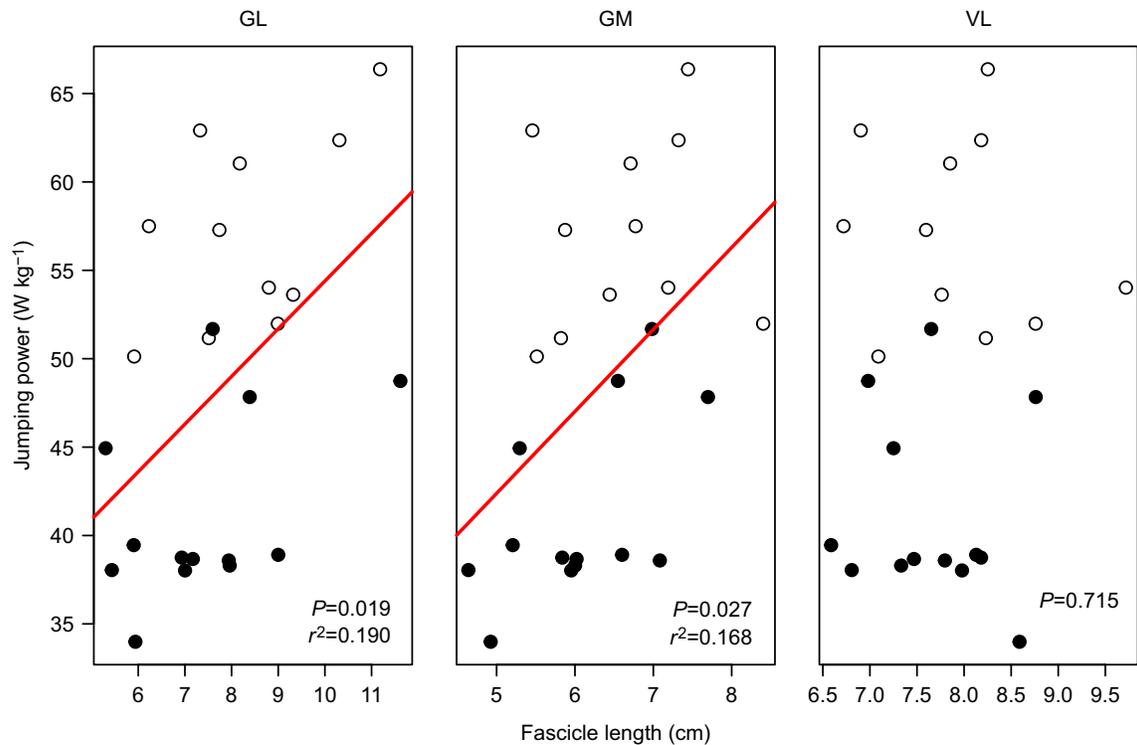
## RESULTS

We successfully identified the expected performance trade-off between locomotor power and economy in our sample of power- and endurance-specialized athletes. When normalizing for body mass, the partial correlations were positive between running cost and maximal power in both cycling ( $r^2=0.347$ ,  $P=0.004$ ) and countermovement jumps ( $r^2=0.206$ ,  $P=0.026$ ), indicating that the most powerful athletes in the study were also the least economical runners (Fig. 1). Our bivariate linear regression analyses revealed that longer GL and GM muscle fascicles were correlated with greater peak mass-specific power in both cycling ( $r^2=0.259$ ,  $P=0.006$  and

$r^2=0.216$ ,  $P=0.013$ , respectively; Fig. 2) and countermovement jumps ( $r^2=0.190$ ,  $P=0.019$  and  $r^2=0.168$ ,  $P=0.027$ , respectively; Fig. 3). VL was not correlated with peak cycling or jumping power ( $P=0.331$  and  $P=0.715$ , respectively; Figs 2 and 3). A significant positive relationship was also found between GL muscle fascicle length and average cost of transport ( $r^2=0.169$ ,  $P=0.041$ ; Fig. 4). No correlations were found between GM or VL fascicle length and cost of transport ( $P=0.195$  and  $P=0.435$ , respectively; Fig. 4). Achilles tendon moment arm length was not significantly correlated with cost of transport ( $P=0.283$ ) or plantarflexor muscle fascicle length ( $P=0.480$  for GL;  $P=0.490$  for GM).



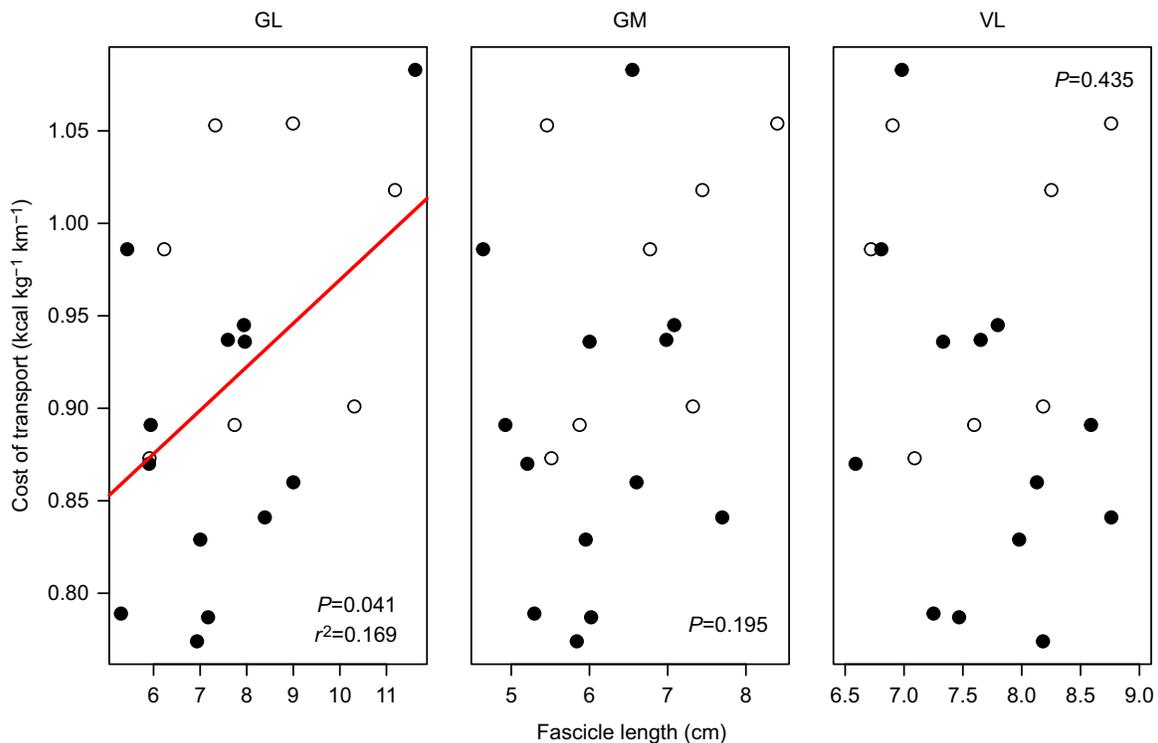
**Fig. 2. Correlations between peak mass-specific cycling power and muscle fascicle length. GL, gastrocnemius lateralis; GM, gastrocnemius medialis; VL, vastus lateralis. Filled circles, self-identified endurance athletes ( $n=13$ ); open circles, self-identified power athletes ( $n=11$ ).**



**Fig. 3. Correlations between peak mass-specific countermovement jump power and muscle fascicle length.** GL, gastrocnemius lateralis; GM, gastrocnemius medialis; VL, vastus lateralis. Filled circles, self-identified endurance athletes ( $n=13$ ); open circles, self-identified power athletes ( $n=11$ ).

We also performed multiple regression analyses to better understand the relative contributions of average muscle fascicle length, muscle fiber type (estimated here as optimal pedaling rate

during cycling) and maximal dynamic lower-body strength (peak countermovement jump force) to peak mass-specific cycling and countermovement jump power and average cost of transport



**Fig. 4. Correlations between average cost of transport and muscle fascicle length.** GL, gastrocnemius lateralis; GM, gastrocnemius medialis; VL, vastus lateralis. Filled circles, self-identified endurance athletes ( $n=13$ ); open circles, self-identified power athletes ( $n=7$ ).

**Table 2. Coefficients of multiple regression models of cycling power, countermovement jump power and cost of transport**

Dependent variable	All independent variables	Independent variables in final model	<i>t</i>	<i>P</i> >   <i>t</i>	Partial <i>r</i> <sup>2</sup>	VIF
Cycling power (W kg <sup>-1</sup> ) ( <i>n</i> =24) Adj. <i>r</i> <sup>2</sup> =0.736; <i>P</i> ≤0.001	Average FL	Average FL	3.386	0.003	0.202	1.057
	OPR	OPR	5.511	<0.001	0.456	1.115
	CMJ force	CMJ force	1.910	0.071	0.113	1.100
CMJ power (W kg <sup>-1</sup> ) ( <i>n</i> =24) Adj. <i>r</i> <sup>2</sup> =0.662; <i>P</i> ≤0.001	Average FL	Average FL	2.278	0.034	0.130	1.057
	OPR	OPR	3.114	0.005	0.242	1.115
	CMJ force	CMJ force	4.026	<0.001	0.333	1.100
Cost of transport (kcal kg <sup>-1</sup> km <sup>-1</sup> ) ( <i>n</i> =20) Adj. <i>r</i> <sup>2</sup> =0.229; <i>P</i> =0.043	LL	LL	-2.201	0.042	0.162	1.053
	Average FL	Average FL	2.125	0.049	0.148	1.053
	OPR				NS	
	CMJ force				NS	

CMJ force was log-transformed in order to achieve normality.

VIF, variance inflation factor; average FL, average fascicle length (cm); LL, leg length (cm); OPR, optimal pedaling rate (rpm) during cycling; CMJ force, peak countermovement jump force (N).

(Table 2). Cycling power ( $r^2=0.736$ ,  $P<0.001$ ) was positively correlated with average fascicle length (partial  $r^2=0.202$ ,  $P=0.003$ ) and optimal pedaling rate (partial  $r^2=0.456$ ,  $P<0.001$ ), with countermovement jump force approaching significance ( $P=0.071$ ). Countermovement jump power ( $r^2=0.662$ ,  $P<0.001$ ) was significantly correlated with average fascicle length (partial  $r^2=0.130$ ,  $P=0.034$ ), optimal pedaling rate (partial  $r^2=0.242$ ,  $P=0.005$ ) and countermovement jump force (partial  $r^2=0.333$ ,  $P<0.001$ ). Average cost of transport ( $r^2=0.229$ ,  $P=0.043$ ) was inversely related to leg length (partial  $r^2=0.162$ ,  $P=0.042$ ) and positively correlated with average fascicle length (partial  $r^2=0.148$ ,  $P=0.049$ ), while optimal pedaling rate and countermovement jump force were excluded from the final model.

## DISCUSSION

Our results are consistent with the hypothesis that, at least for certain muscles, fascicle length plays a significant role in the performance trade-off between power and economy. We found through our bivariate linear regression analyses that longer fascicles in GL and GM are positively correlated with both cycling and jumping power, and that longer GL fascicle length is directly correlated with cost of transport. Multiple regression analyses allowed us to compare the individual contributions of muscle force (peak dynamic countermovement jump force) and muscle shortening velocity (average fascicle length and fiber type) with both mass-specific cycling and countermovement jump peak power. For both power metrics, the final, best-fit models according to AICc scores retained all three explanatory variables. Our analyses revealed that our indirect estimate of fiber type was the single most important contributor to the velocity component of power, explaining approximately twice the variation in both cycling and jumping power compared with fascicle length (46% versus 20% for cycling; 24% versus 13% for jumping, respectively). However, the fact that fascicle length was retained as a significant predictor in both of our power models highlights its importance for maximal power production. Our final multiple regression analysis examined the respective contributions of leg length, fascicle length, fiber type and peak countermovement jump force to average running cost of transport. The final model retained only leg length and fascicle length as significant explanatory variables, with the two factors accounting for almost equal amounts of variation in running cost (16% for leg length; 15% for fascicle length). Thus, our results suggest that the prevalence of muscle fiber type as an explanation for the power versus economy trade-off is absolutely justified (e.g. Vanhooydonck et al., 2001; Wilson et al., 2002; Wilson and James, 2004; Herrel and Bonneaud, 2012; Vanhooydonck et al., 2014), yet

incomplete without the additional component of muscle fascicle length.

The significant relationship we identified between GL and GM fascicle length and peak mass-specific countermovement jump power is in accordance with the prediction that longer fascicles increase maximum power production by shortening at higher velocities. Our findings, including the lack of a relationship between VL fascicle length and jumping power, are supported by previous work linking longer plantarflexor, but not quadriceps, muscle fascicles to countermovement jump performance. Earp et al. (2011) found that GL, but not VL, fascicle length was positively correlated with early countermovement jump rate of force development. This discovery was unexpected, given that longer fascicles are expected to delay early force development because of their greater serial elastic component (Blazevich et al., 2009a) and the increased time required for action potentials to propagate along the length of longer fibers (Methenitis et al., 2019). Earp et al. (2011) argue that the biarticular nature of GL combined with the rapid shortening it experiences as the knee joint flexes during the drop phase preceding a jump may make the faster shortening velocity provided by longer fascicles critical for timely force generation during a countermovement jump. Additionally, longer fascicles in the plantarflexor muscles of the ankle may partially explain why a greater percentage of the total net-work of vertical jumping is accomplished at the ankle versus the knee joint (Robertson and Fleming, 1987).

This pattern also appears to be true for level running: compared with the knee joint, the ankle joint performs a greater percentage of the net positive mechanical work (Roberts and Belliveau, 2005) and produces roughly twice as much positive power (Belli et al., 2002; Farris and Sawicki, 2012). Our hypothesis that muscles with more serial sarcomeres are disadvantageous for economical force production was based in part on the locomotor muscles behaving like springs during running. In humans (Sasaki and Neptune, 2006) and other species (Roberts, 1997; Biewener, 1998; Gregersen et al., 1998), the majority of external work resulting from elastic energy storage and release appears to occur at the more distal joints, such as the ankle. Motor unit recruitment is minimized in the plantarflexors as these muscles contract isometrically for optimum force production according to the force-velocity relationship (Lichtwark and Wilson, 2006). Because isometric force production is not influenced by the number of sarcomeres arranged in series, and because all serial sarcomeres within a muscle fiber are activated when the muscle fiber is turned on, we would expect that a muscle with longer fascicles engaging in non-shortening contractions would be less economical than a muscle with

shorter fibers producing the same amount of force. Our finding that longer GL fascicles are correlated with a greater running cost of transport is consistent with this hypothesis.

### Lack of correlation between VL fascicle length and performance

We were surprised to find that VL fascicle length was not significantly correlated with any performance metric in the present study. This result contrasts with those of previous studies linking longer VL fascicles to superior power-based performance (Abe et al., 2000; Kumagai et al., 2000; Nasirzade et al., 2014; Methenitis et al., 2016; van der Zwaard et al., 2018). One possibility for our null result is that our estimates of VL fascicle length contained more measurement error (4.1%) compared with those for GL and GM (2.0% and 2.2%, respectively) as a result of (1) a greater percentage of total VL fascicle length extending beyond the ultrasound image dimensions (36.4% on average for VL versus 32.7% and 19.2% for GL and GM, respectively) and (2) the fascicular curvature exhibited by nine participants with pronounced VL hypertrophy. Curvilinear fascicle organization may reflect specialization for force production via increased pennation angles (Kawakami et al., 1993). Linear extrapolation performed on ultrasound images of curved fascicles has been shown to produce accurate fascicle length estimates in the biceps femoris muscle (Franchi et al., 2020) and VL (Ando et al., 2014); however, we suspect that the magnitude of VL hypertrophy and, thus, fascicle curvature, was greater in our sample of young male athletes compared with that in the elderly cadavers used in the study of Ando et al. (2014). As such, our estimates of VL fascicle length may not be as accurate as those for GL and GM, despite our attempts to account for fascicle curvature by fitting a Bézier curve to the fascicular trajectory instead of a straight line.

While we cannot rule out the presence of measurement error, our results for VL fascicle length may be valid and could indicate that this muscle behaves differently from GL and GM during maximal-effort cycling and jumping, as well as submaximal running. Previous studies finding no relationships between lower-body power production (during cycling: Kordi et al., 2020; during jumping: Murtagh et al., 2018) and VL fascicle length report highly significant correlations between power and other aspects of muscle architecture, such as quadriceps volume and physiological cross-sectional area. These results suggest that, at least for the knee joint, both peak cycling and jumping power may be best explained by the ability of the quadriceps femoris muscle to generate force. Our results from multiple regression analyses add further support for this observation: peak countermovement force explained more variation in mass-specific peak countermovement jump power than either fascicle length or fiber type alone. Another possibility is that individual differences in neuromuscular coordination determine which muscle properties are most important for explosive power production in the lower body. Methenitis et al. (2016) found that VL fascicle length was a significant predictor of jumping power in only the most experienced power athletes, suggesting that superior 'muscle quality' is advantageous for power production in highly trained individuals with advanced neuromuscular adaptation. Thus, we may not have seen a relationship between VL fascicle length and peak power production in the present study because (1) our mixed study population included endurance-trained participants and (2) we did not control for individual differences in training or years of experience among our sample of 11 power athletes.

Lastly, we may not have seen a relationship between VL fascicle length and cost of transport if this muscle is actively shortening

during running. Not all locomotor muscles behave as economy-maximizing springs specialized for steady-speed running, so our initial hypothesis is over-simplified in that it does not account for complex contractile behavior and energetics. The relationship between fascicle length and the economy of force production is significantly more complicated in such cases of dynamic shortening: based on the altered force-velocity curve of long muscle fibers, it can be argued that fewer fibers may need to be recruited by long-fibered muscles for a given force production (thereby reducing the energy cost) compared with short-fibered muscles. Whether this is true for the VL muscle is uncertain, however, as a recent investigation of *in vivo* VL fascicle length changes during running suggested that this muscle behaves more isometrically than previously thought (Bohm et al., 2018). Such an absence of active shortening in VL during running would nullify any benefits to locomotor economy that may emerge from the contractile dynamics of long fascicles. Future studies could improve our understanding of the relationships between muscle fascicle length, cost of transport and capacity for elastic energy storage by measuring ground reaction forces and joint kinematics to calculate external work while using ultrasonography to track *in vivo* fascicle and tendon excursion during locomotor tasks.

### Muscle fiber type and cost of transport

Our final multiple regression analysis examined the respective contributions of leg length, fascicle length, fiber type and peak countermovement jump force to running cost of transport. To our surprise, fiber type was excluded from the final model as a significant explanatory variable. A greater percentage of fast-twitch fibers in the locomotor muscles is expected to drive up the cost of locomotion, and previous studies have shown that VL fiber type composition is significantly correlated with running cost (Bosco et al., 1987; Hunter et al., 2015). Our final cost of transport model may not have included fiber type because our mixed sample of power and endurance athletes required us to measure average running cost at slow speeds (7.2, 8.0, 8.9 and 9.7 km h<sup>-1</sup>) that the former group could aerobically sustain until reaching metabolic steady state. We suspect these slow speeds overwhelmingly favored slow-twitch muscle fiber recruitment, and that a greater proportion of fast motor units would be activated at higher speeds. Indeed, Kyröläinen et al. (2003) found no relationships between any metric of VL fiber type distribution and running economy at 4.0, 5.0 or 6.0 m s<sup>-1</sup>, which are still well above the speeds used in the present study. Although VL muscle biopsies are commonly used to determine fiber type composition, we chose to non-invasively estimate fiber type as optimal pedaling rate (OPR) during cycling. OPR is strongly correlated with the percentage of fast-twitch VL fibers as determined by muscle biopsy (Hautier et al., 1996), and its high explanatory contributions to both peak mass-specific cycling and jumping power further support its validity in the present study. Despite initial concerns that muscle fascicle length could influence OPR, we found no correlation between OPR and average muscle fascicle length, suggesting that these two variables are independent contributors to muscle shortening velocity. This result is corroborated by studies of mice (Burkholder et al., 1994) and rats (Eng et al., 2008) finding no relationship between the percentage of fast-twitch fibers and hindlimb muscle fascicle length.

### Broader implications and future directions

Our results highlight the importance of muscle fascicle length in anatomical specialization of the locomotor system for either power production or economical transport. This finding has far-reaching

applications, with the potential to address questions about the role of fascicle length in athletic training protocols, the spectrum of human physiques and the interspecific musculoskeletal diversity present among primates. Future investigations of the relationships between fascicle length, performance and morphological diversity should consider the possibility that architectural parameters may not be consistent for all muscles. Such structural variations could indicate a division of labor amongst the locomotor muscles, possibly mitigating costs to whole-body performance imposed by the power versus economy trade-off (Holzman et al., 2011).

Several studies have emphasized the role of fascicle length plasticity in athletic performance, demonstrating that eccentric training is associated with subsequent increases to both maximal power production and fascicle length (Douglas et al., 2017). Given the resultant shifts in joint torque–angle curves (Ferreira et al., 2007) arising from the addition of serial sarcomeres, it is surprisingly unclear whether potentially deleterious rightward shifts in a muscle's length–tension relationship are ameliorated by remodeling of the myotendinous junction. For instance, optimal muscle–tendon unit length may be preserved if new sarcomeres invaginate into the aponeurosis, effectively allowing the tendon to take up the extra slack length.

Beyond its relevance to athletic performance, variation in fascicle length may offer unique insights into our evolutionary history. Differences in fascicle length among human populations and between humans and other apes may be indicative of distinct selective pressures on performance, helping to explain phenotypic diversity among these groups. For instance, differential selection for either muscular power production or economical locomotion may be responsible for expected and observed fascicle length disparities in groups that are dissimilar with respect to subsistence pattern (agriculturalists versus hunter-gatherers foraging over long distances in marginal environments), locomotor mode (a greater reliance on arboreal locomotion in chimpanzees versus terrestrial bipedality in early hominids: Pontzer et al., 2009; O'Neill et al., 2017) and intensity of agonistic male–male contests for access to reproductive resources (polygamous great apes versus monogamous gibbons: Payne et al., 2006; Marchi et al., 2018; Morris et al., 2019).

## Conclusions

In summary, the positive correlations between longer muscle fascicles, peak power in cycling and jumping, and running cost of transport are consistent with the hypothesis that fascicle length plays a significant role in functional specialization of the locomotor muscles for either power- or economy-based performance. The relative importance of fascicle length for maximizing either power or economy appears to be greater for distal versus proximal muscles, and likely varies with the specific locomotor task being performed and the experience level of the individual. With respect to the mechanistic underpinnings of the evolutionary trade-off between muscle power and economy, our results support the conventional explanation of fiber type while providing the first empirical evidence for the long-suspected, additional component of fascicle length. Together, these findings address gaps in our understanding of the specific properties of muscle design that contribute to morphological and functional diversity in the locomotor systems of vertebrates.

## Acknowledgements

We thank the athletes who participated in this study; S. Johnson and J. Walker for the use of and assistance with the ultrasound and respirometry equipment, respectively; and D. Cushman and J. Ruff for helpful discussions.

## Competing interests

The authors declare no competing or financial interests.

## Author contributions

Conceptualization: A.N.C., W.J.M., J.C.M., D.R.C.; Methodology: A.N.C., W.J.M., J.C.M., S.O.D., D.R.C.; Software: A.N.C., W.J.M., J.C.M.; Validation: A.N.C., W.J.M., J.C.M., S.O.D., D.R.C.; Formal analysis: A.N.C.; Investigation: A.N.C., W.J.M., J.C.M., S.O.D., D.R.C.; Resources: W.J.M., J.C.M.; Data curation: A.N.C.; Writing - original draft: A.N.C.; Writing - review & editing: A.N.C., W.J.M., J.C.M., S.O.D., D.R.C.; Visualization: A.N.C.; Supervision: W.J.M., J.C.M., D.R.C.; Project administration: A.N.C., W.J.M., D.R.C.; Funding acquisition: A.N.C., D.R.C.

## Funding

This work was supported by funding from the University of Utah Research Incentive Seed Grant Program to D.R.C.

## References

- Abe, T., Kumagai, K. and Brechue, W. F.** (2000). Fascicle length of leg muscles is greater in sprinters than distance runners. *Med. Sci. Sports Exerc.* **32**, 1125–1129. doi:10.1097/00005768-200006000-00014
- Ando, R., Taniguchi, K., Saito, A., Fujimiya, M., Katayose, M. and Akima, H.** (2014). Validity of fascicle length estimation in the vastus lateralis and vastus intermedius using ultrasonography. *J. Electromyogr. Kines.* **24**, 214–220. doi:10.1016/j.jelekin.2014.01.003
- Alexander, R. McN.** (2000). Optimization of muscles and movement for performance or economy of energy. *Neth. J. Zool.* **50**, 101–112.
- Austin, N., Nilwik, R. and Herzog, W.** (2010). In vivo operational fascicle lengths of vastus lateralis during sub-maximal and maximal cycling. *J. Biomech.* **43**, 2394–2399. doi:10.1016/j.jbiomech.2010.04.016
- Barnes, K. R., McGuigan, M. R. and Kilding, A. E.** (2014). Lower-body determinants of running economy in male and female distance runners. *J. Strength Cond. Res.* **28**, 1289–1297. doi:10.1519/JSC.0000000000000267
- Belli, A., Kyröläinen, H. and Komi, P. V.** (2002). Moment and power of lower limb joints in running. *Int. J. Sports Med.* **23**, 136–141. doi:10.1055/s-2002-20136
- Bennett, A. F., Huey, R. B. and John-Alder, H.** (1984). Physiological correlates of natural activity and locomotor capacity in two species of lacertid lizards. *J. Comp. Physiol. B* **154**, 113–118. doi:10.1007/BF00684134
- Biewener, A. A.** (1998). Muscle function in vivo: a comparison of muscles used for elastic energy savings versus muscles used to generate mechanical power. *Am. Zool.* **38**, 703–717. doi:10.1093/icb/38.4.703
- Biewener, A. A.** (2003). *Animal Locomotion*. Oxford: Oxford University Press.
- Blazevich, A. J., Cannavan, D., Coleman, D. R. and Horne, S.** (2007). Influence of concentric and eccentric resistance training on architectural adaptation in human quadriceps muscles. *J. Appl. Physiol.* **103**, 1565–1575. doi:10.1152/jappphysiol.00578.2007
- Blazevich, A. J., Cannavan, D., Horne, S., Coleman, D. R. and Aagaard, P.** (2009a). Changes in muscle force-length properties affect the early rise of force in vivo. *Muscle Nerve* **39**, 512–520. doi:10.1002/mus.21259
- Blazevich, A. J., Coleman, D. R., Horne, S. and Cannavan, D.** (2009b). Anatomical predictors of maximum isometric and concentric knee extensor moment. *Eur. J. Appl. Physiol.* **105**, 869–878. doi:10.1007/s00421-008-0972-7
- Bobbert, M. F. and Casius, L. J. R.** (2005). Is the effect of a countermovement on jump height due to active state development? *Med. Sci. Sports Exerc.* **37**, 440–446. doi:10.1249/01.MSS.0000155389.34538.97
- Bobbert, M. F., Gerritsen, K. G. M., Litjens, M. C. A. and Van Soest, A. J.** (1996). Why is countermovement jump height greater than squat jump height? *Med. Sci. Sports Exerc.* **28**, 1402–1412. doi:10.1097/00005768-199611000-00009
- Bohm, S., Marzilger, R., Mersmann, F., Santuz, A. and Arampatzis, A.** (2018). Operating length and velocity of human vastus lateralis muscle during walking and running. *Sci. Rep.* **8**, 5066. doi:10.1038/s41598-018-23376-5
- Bosco, C., Montanari, G., Ribacchi, R., Giovenali, P., Latteri, F., Iachelli, G., Faina, M., Colli, R., Dal Monte, A., La Rosa, M. et al.** (1987). Relationship between the efficiency of muscular work during jumping and the energetics of running. *Eur. J. Appl. Physiol. Occup. Physiol.* **56**, 138–143. doi:10.1007/BF00640636
- Burkholder, T. J., Fingado, B., Baron, S. and Lieber, R. L.** (1994). Relationship between muscle fiber types and sizes and muscle architectural properties in the mouse hindlimb. *J. Morphol.* **221**, 177–190. doi:10.1002/jmor.1052210207
- Butler, E. E. and Dominy, N. J.** (2016). Architecture and functional ecology of the human gastrocnemius muscle-tendon unit. *J. Anat.* **228**, 561–568. doi:10.1111/joa.12432
- Close, R. I.** (1972). Dynamic properties of mammalian skeletal muscles. *Physiol. Rev.* **52**, 129–197. doi:10.1152/physrev.1972.52.1.129
- Costill, D. L., Daniels, J., Evans, W., Fink, W., Krahenbuhl, G. and Saltin, B.** (1976). Skeletal muscle enzymes and fiber composition in male and female track athletes. *J. Appl. Physiol.* **40**, 149–154. doi:10.1152/jappphysiol.1976.40.2.149

- Csapo, R., Alegre, L. M. and Baron, R.** (2011). Time kinetics of acute changes in muscle architecture in response to resistance exercise. *J. Sci. Med. Sport*. **14**, 270-274. doi:10.1016/j.jsams.2011.02.003
- Cunningham, C. B., Schilling, N., Anders, C. and Carrier, D. R.** (2010). The influence of foot posture on the cost of transport in humans. *J. Exp. Biol.* **213**, 790-797. doi:10.1242/jeb.038984
- Dlugosz, E. M., Chappell, M. A., McGillivray, D. G., Syme, D. A. and Garland, T., Jr.** (2009). Locomotor trade-offs in mice selectively bred for high voluntary wheel running. *J. Exp. Biol.* **212**, 2612-2618. doi:10.1242/jeb.029058
- Douglas, J., Pearson, S., Ross, A. and McGuigan, M.** (2017). Chronic adaptations to eccentric training: a systematic review. *Sports Med.* **47**, 917-941. doi:10.1007/s40279-016-0628-4
- Earp, J. E., Kraemer, W. J., Cormie, P., Volek, J. S., Maresh, C. M., Joseph, M. and Newton, R. U.** (2011). Influence of muscle-tendon unit structure on rate of force development during the squat, countermovement, and drop jumps. *J. Strength Cond. Res.* **25**, 340-347. doi:10.1519/JSC.0b013e3182052d78
- Ema, R., Wakahara, T., Mogi, Y., Miyamoto, N., Komatsu, T., Kanehisa, H. and Kawakami, Y.** (2013). In vivo measurement of human rectus femoris architecture by ultrasonography: validity and applicability. *Clin. Physiol. Funct. Imaging* **33**, 267-273. doi:10.1111/cpf.12023
- Eng, C. M., Smallwood, L. H., Rainiero, M. P., Lahey, M., Ward, S. R. and Lieber, R. L.** (2008). Scaling of muscle architecture and fiber types in the rat hindlimb. *J. Exp. Biol.* **211**, 2336-2345. doi:10.1242/jeb.017640
- Erskine, R. M., Jones, D. A., Maganaris, C. N. and Degens, H.** (2009). In vivo specific tension of the human quadriceps femoris muscle. *Eur. J. Appl. Physiol.* **106**, 827-838. doi:10.1007/s00421-009-1085-7
- Farris, D. J. and Sawicki, G. S.** (2012). The mechanics and energetics of human walking and running: a joint level perspective. *J. R. Soc. Interface* **9**, 110-118. doi:10.1098/rsif.2011.0182
- Ferreira, G. N. T., Teixeira-Salmela, L. F. and Guimarães, C. Q.** (2007). Gains in flexibility related to measures of muscular performance: impact of flexibility on muscular performance. *Clin. J. Sport Med.* **17**, 276-281. doi:10.1097/JSM.0b013e3180f60b26
- Fox, J. and Weisberg, S.** (2019). *An R Companion to Applied Regression*, 3rd edn. Thousand Oaks: Sage.
- Franchi, M. V., Fitze, D. P., Raiteri, B. J., Hahn, D. and Spörri, J.** (2020). Ultrasound-derived biceps femoris long head fascicle length: extrapolation pitfalls. *Med. Sci. Sports Exerc.* **52**, 233-243. doi:10.1249/MSS.0000000000002123
- Gollnick, P. D., Armstrong, R. B., Saubert, C. W., Piehl, K. and Saltin, B.** (1972). Enzyme activity and fiber composition in skeletal muscle of untrained and trained men. *J. Appl. Physiol.* **33**, 312-319. doi:10.1152/jap.1972.33.3.312
- Gregersen, C. S., Silvertorn, N. A. and Carrier, D. R.** (1998). External work and potential for elastic storage at the limb joints of running dogs. *J. Exp. Biol.* **201**, 3197-3210. doi:10.1242/jeb.201.23.3197
- Gromping, U.** (2006). Relative importance for linear regression in R: the package relaimpo. *J. Stat. Softw.* **17**, 1-27. doi:10.18637/jss.v017.i01
- Hautier, C. A., Linossier, M. T., Belli, A., Lacour, J. R. and Arsac, L. M.** (1996). Optimal velocity for maximal power production in non-isokinetic cycling is related to muscle fibre type composition. *Eur. J. Appl. Physiol. Occup. Physiol.* **74**, 114-118. doi:10.1007/BF00376503
- Hermanson, J. W. and Cobb, M. A.** (1992). Four forearm flexor muscles of the horse, *Equus caballus*: anatomy and histochemistry. *J. Morphol.* **212**, 269-280. doi:10.1002/jmor.1052120306
- Herrel, A. and Bonneaud, C.** (2012). Trade-offs between burst performance and maximal exertion capacity in a wild amphibian, *Xenopus tropicalis*. *J. Exp. Biol.* **215**, 3106-3111. doi:10.1242/jeb.072090
- Holzman, R., Collar, D. C., Mehta, R. S. and Wainwright, P. C.** (2011). Functional complexity can mitigate performance trade-offs. *Am. Nat.* **177**, E69-E83. doi:10.1086/658366
- Huey, R. B., Bennett, A. F., John-Alder, H. and Nagy, K. A.** (1984). Locomotor capacity and foraging behaviour of Kalahari lacertid lizards. *Anim. Behav.* **32**, 41-50. doi:10.1016/S0003-3472(84)80322-X
- Hunter, G. R., McCarthy, J. P., Carter, S. J., Bamman, M. M., Gaddy, E. S., Fisher, G., Katsoulis, K., Plaisance, E. P. and Newcomer, B. R.** (2015). Muscle fiber type, Achilles tendon length, potentiation, and running economy. *J. Strength Cond. Res.* **29**, 1302-1309. doi:10.1519/JSC.0000000000000760
- Huq, E., Wall, C. E. and Taylor, A. B.** (2015). Epaxial muscle fiber architecture favors enhanced excursion and power in the leaper *Galago senegalensis*. *J. Anat.* **227**, 524-540. doi:10.1111/joa.12351
- Ingleby, S. J., Camarillo, H., Willis, H. and Johnson, J. B.** (2016). Repeated evolution of local adaptation in swimming performance: population-level trade-offs between burst and endurance swimming in Brachyraphis freshwater fish. *Biol. J. Linn. Soc.* **119**, 1011-1026. doi:10.1111/bij.12852
- Kardong, K. V.** (2009). *Vertebrates: Comparative Anatomy, Function, and Evolution*, 6th edn. New York: McGraw-Hill.
- Kawakami, Y., Abe, T. and Fukunaga, T.** (1993). Muscle-fiber pennation angles are greater in hypertrophied than in normal muscles. *J. Appl. Physiol.* **74**, 2740-2744. doi:10.1152/jap.1993.74.6.2740
- Koo, T. K. and Li, M. Y.** (2016). A guideline of selecting and reporting intraclass correlation coefficients for reliability research. *J. Chiropr. Med.* **15**, 155-163. doi:10.1016/j.jcm.2016.02.012
- Kordi, M., Folland, J., Goodall, S., Haralabidis, N., Maden-Wilkinson, T., Sarika Patel, T., Leeder, J., Barratt, P. and Howatson, G.** (2020). Mechanical and morphological determinants of peak power output in elite cyclists. *Scand. J. Med. Sci. Sports* **30**, 227-237. doi:10.1111/sms.13570
- Kumagai, K., Abe, T., Brechue, W. F., Ryushi, T., Takano, S. and Mizuno, M.** (2000). Sprint performance is related to muscle fascicle length in male 100-m sprinters. *J. Appl. Physiol.* **88**, 811-816. doi:10.1152/jap.2000.88.3.811
- Kyröläinen, H., Kivelä, R., Koskinen, S., McBride, J., Andersen, J. L., Takala, T., Sipilä, S. and Komi, P. V.** (2003). Interrelationships between muscle structure, muscle strength, and running economy. *Med. Sci. Sports Exerc.* **35**, 45-49. doi:10.1097/00005768-200301000-00008
- Langerhans, R. B.** (2009). Trade-off between steady and unsteady swimming underlies predator-driven divergence in *Gambusia affinis*. *J. Evol. Biol.* **22**, 1057-1075. doi:10.1111/j.1420-9101.2009.01716.x
- Lee, S. S. M. and Piazza, S. J.** (2009). Built for speed: musculoskeletal structure and sprinting ability. *J. Exp. Biol.* **212**, 3700-3707. doi:10.1242/jeb.031096
- Lichtwark, G. A. and Wilson, A. M.** (2006). Interactions between the human gastrocnemius muscle and the Achilles tendon during incline, level and decline locomotion. *J. Exp. Biol.* **209**, 4379-4388. doi:10.1242/jeb.02434
- Lieber, R. L. and Fridén, J.** (2000). Functional and clinical significance of skeletal muscle architecture. *Muscle Nerve* **23**, 1647-1666. doi:10.1002/1097-4598(200011)23:11<1647::AID-MUS1>3.0.CO;2-M
- Lindstedt, S. L., McGlothlin, T., Percy, E. and Pifer, J.** (1998). Task-specific design of skeletal muscle: balancing muscle structural composition. *Comp. Biochem. Physiol. B* **120**, 35-40. doi:10.1016/S0305-0491(98)00021-2
- Linthorne, N. P.** (2001). Analysis of standing vertical jumps using a force platform. *Am. J. Phys.* **69**, 1198-1204. doi:10.1119/1.1397460
- Loeb, G. E., Pratt, C. A., Chanaud, C. M. and Richmond, F. J. R.** (1987). Distribution and innervation of short, interdigitated muscle fibers in parallel-fibered muscles of the cat hindlimb. *J. Morphol.* **191**, 1-15. doi:10.1002/jmor.1051910102
- Marchi, D., Leischner, C. L., Pastor, F. and Hartstone-Rose, A.** (2018). Leg muscle architecture in primates and its correlation with locomotion patterns. *Anat. Rec.* **301**, 515-527. doi:10.1002/ar.23745
- Markovic, G., Dizdhar, D., Jukic, I. and Cardinale, M.** (2004). Reliability and factorial validity of squat and countermovement jump tests. *J. Strength Cond. Res.* **18**, 551-555.
- Martin, T. P., Bodine-Fowler, S., Roy, R. R., Eldred, E. and Edgerton, V. R.** (1988). Metabolic and fiber size properties of cat tibialis anterior motor units. *Am. J. Physiol.* **255**, C43-C50. doi:10.1152/ajpcell.1988.255.1.C43
- Martin, J. C., Wagner, B. M. and Coyle, E. F.** (1997). Inertial-load method determines maximal cycling power in a single exercise bout. *Med. Sci. Sports Exerc.* **29**, 1505-1512. doi:10.1097/00005768-199711000-00018
- Martin, J. C., Diedrich, D. and Coyle, E. F.** (2000). Time course of learning to produce maximum cycling power. *Int. J. Sports Med.* **21**, 485-487. doi:10.1055/s-2000-7415
- Meldrum K. J., Carlson J. S. and Naughton G. A.** (1997). Oxygen uptake during continuous and discrete steady state running. In *Children and Exercise XIX* (ed. N. Armstrong, B. Kirby, J. Welsman), pp. 228-232. New York: E & FN Spon.
- Methenitis, S. K., Zaras, N. D., Spengos, K. M., Stasinaki, A.-N. E., Karampatsos, G. P., Georgiadis, G. V. and Terzis, G. D.** (2016). Role of muscle morphology in jumping, sprinting, and throwing performance in participants with different power training duration experience. *J. Strength Cond. Res.* **30**, 807-817. doi:10.1519/JSC.0000000000001147
- Methenitis, S., Stasinaki, A.-N., Zaras, N., Spengos, K., Karandreas, N. and Terzis, G.** (2019). Intramuscular fibre conduction velocity and muscle fascicle length in human vastus lateralis. *Appl. Physiol. Nutr. Metab.* **44**, 133-138. doi:10.1139/apnm-2018-0081
- Morgan, D. L. and Proske, U.** (1984). Vertebrate slow muscle: its structure, pattern of innervation, and mechanical properties. *Physiol. Rev.* **64**, 103-169. doi:10.1152/physrev.1984.64.1.103
- Morris, J. S., Cunningham, C. B. and Carrier, D. R.** (2019). Sexual dimorphism in postcranial skeletal shape suggests male-biased specialization for physical competition in anthropoid primates. *J. Morphol.* **280**, 731-738. doi:10.1002/jmor.20980
- Murach, K., Greever, C. and Luden, N. D.** (2015). Skeletal muscle architectural adaptations to marathon run training. *Appl. Physiol. Nutr. Metab.* **40**, 99-102. doi:10.1139/apnm-2014-0287
- Murtagh, C. F., Nulty, C., Vanreterghem, J., O'Boyle, A., Morgans, R., Drust, B. and Erskine, R. M.** (2018). The neuromuscular determinants of unilateral jump performance in soccer players are direction-specific. *Int. J. Sports Physiol. Perform.* **13**, 604-611. doi:10.1123/ijsp.2017-0589
- Nasirzade, A., Ehsanbakhsh, A., Ilbeygi, S., Sobhkhiz, A., Argavani, H. and Aliakbari, M.** (2014). Relationship between sprint performance of front crawl swimming and muscle fascicle length in young swimmers. *J. Sports Sci. Med.* **13**, 550-556.

- O'Neill, M. C., Umberger, B. R., Holowka, N. B., Larson, S. G. and Reiser, P. J. (2017). Chimpanzee super strength and human skeletal muscle evolution. *Proc. Natl Acad. Sci. USA* **114**, 7343-7348. doi:10.1073/pnas.1619071114
- Payne, R. C., Crompton, R. H., Isler, K., Savage, R., Vereecke, E. E., Günther, M. M., Thorpe, S. K. S. and D'Août, K. (2006). Morphological analysis of the hindlimb in apes and humans. II. Moment arms. *J. Anat.* **208**, 725-742. doi:10.1111/j.1469-7580.2006.00564.x
- Pontzer H. (2007). Effective limb length and the scaling of locomotor cost in terrestrial animals. *J. Exp. Biol.* **210**, 1752-1761.
- Pontzer, H., Raichlen, D. A. and Sockol, M. D. (2009). The metabolic cost of walking in humans, chimpanzees, and early hominins. *J. Hum. Evol.* **56**, 43-54. doi:10.1016/j.jhevol.2008.09.001
- Raichlen, D. A., Armstrong, H. and Lieberman, D. E. (2011). Calcaneus length determines running economy: implications for endurance running performance in modern humans and Neandertals. *J. Hum. Evol.* **60**, 299-308. doi:10.1016/j.jhevol.2010.11.002
- Reidy, S. P., Kerr, S. R. and Nelson, J. A. (2000). Aerobic and anaerobic swimming performance of individual Atlantic cod. *J. Exp. Biol.* **203**, 347-357. doi:10.1242/jeb.203.2.347
- Roberts, T. J. (1997). Muscular force in running turkeys: the economy of minimizing work. *Science* **275**, 1113-1115. doi:10.1126/science.275.5303.1113
- Roberts, T. J. and Belliveau, R. A. (2005). Sources of mechanical power for uphill running in humans. *J. Exp. Biol.* **208**, 1963-1970. doi:10.1242/jeb.01555
- Robertson, D. G. and Fleming, D. (1987). Kinetics of standing broad and vertical jumping. *Can. J. Sport Sci.* **12**, 19-23.
- Sasaki, K. and Neptune, R. R. (2006). Muscle mechanical work and elastic energy utilization during walking and running near the preferred gait transition speed. *Gait Posture* **23**, 383-390. doi:10.1016/j.gaitpost.2005.05.002
- Scholz, M. N., Bobbert, M. F., Van Soest, A. J., Clark, J. R. and Van Heerden, J. (2008). Running biomechanics: shorter heels, better economy. *J. Exp. Biol.* **211**, 3266-3271. doi:10.1242/jeb.018812
- Soffler, C. and Hermanson, J. W. (2006). Muscular design in the equine interosseus muscle. *J. Morphol.* **267**, 696-704. doi:10.1002/jmor.10433
- Studel-Numbers, K. L., Weaver, T. D. and Wall-Scheffler, C. M. (2007). The evolution of human running: effects of changes in lower-limb length on locomotor economy. *J. Hum. Evol.* **53**, 191-196. doi:10.1016/j.jhevol.2007.04.001
- Van Damme, R., Wilson, R. S., Vanhooydonck, B. and Aerts, P. (2002). Performance constraints in decathletes. *Nature* **415**, 755. doi:10.1038/415755b
- van der Zwaard, S., Weide, G., Levels, K., Eikelboom, M. R. I., Noordhof, D. A., Hofmijster, M. J., van der Laarse, W. J., de Koning, J. J., de Ruiter, C. J. and Jaspers, R. T. (2018). Muscle morphology of the vastus lateralis is strongly related to ergometer performance, sprint capacity and endurance capacity in Olympic rowers. *J. Sports Sci.* **36**, 2111-2120. doi:10.1080/02640414.2018.1439434
- Vanhooydonck, B., Van Damme, R. and Aerts, P. (2001). Speed and stamina trade-off in lacertid lizards. *Evolution* **55**, 1040-1048. doi:10.1554/0014-3820(2001)055[1040:SASTO]2.0.CO;2
- Vanhooydonck, B., James, R. S., Tallis, J., Aerts, P., Tadic, Z., Tolley, K. A., Measey, G. J. and Herrel, A. (2014). Is the whole more than the sum of its parts? Evolutionary trade-offs between burst and sustained locomotion in lacertid lizards. *Proc. R. Soc. B. Biol. Sci.* **281**, 20132677. doi:10.1098/rspb.2013.2677
- Weir, J. B. V. (1949). New methods for calculating metabolic rate with special reference to protein metabolism. *J. Physiol.* **109**, 1-9. doi:10.1113/jphysiol.1949.sp004363
- Weyand, P. G., Cureton, K. J., Conley, D. S., Sloniger, M. A. and Liu, Y. L. (1994). Peak oxygen deficit predicts sprint and middle-distance track performance. *Med. Sci. Sports Exerc.* **26**, 1174-1180. doi:10.1249/00005768-199409000-00016
- Wilson, R. S. and James, R. S. (2004). Constraints on muscular performance: trade-offs between power output and fatigue resistance. *Proc. R. Soc. B Biol. Sci.* **271**, 222-225. doi:10.1098/rsbl.2003.0143
- Wilson, R. S., James, R. S. and Van Damme, R. (2002). Trade-offs between speed and endurance in the frog *Xenopus laevis*: a multi-level approach. *J. Exp. Biol.* **205**, 1145-1152. doi:10.1242/jeb.205.8.1145
- Wilson, R. S., Niehaus, A. C., David, G., Hunter, A. and Smith, M. (2014). Does individual quality mask the detection of performance trade-offs? A test using analyses of human physical performance. *J. Exp. Biol.* **217**, 545-551. doi:10.1242/jeb.092056
- Woledge, R. C. (1968). The energetics of tortoise muscle. *J. Physiol.* **197**, 685-707. doi:10.1113/jphysiol.1968.sp008582
- Woltring, H. J. (1986). A Fortran package for generalized, cross-validated spline smoothing and differentiation. *Adv. Eng. Softw.* **8**, 104-113. doi:10.1016/0141-1195(86)90098-7
- Zierath, J. R. and Hawley, J. A. (2004). Skeletal muscle fiber type: influence on contractile and metabolic properties. *PLoS Biol.* **2**, e348. doi:10.1371/journal.pbio.0020348