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DYNAMICS OF MALLARD (*ANAS PLATYRHYNCHOS*) GASTROCNEMIUS FUNCTION DURING SWIMMING *VERSUS* TERRESTRIAL LOCOMOTION

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Summary

This study investigates how the contractile function of a muscle may be modulated to accommodate changes in locomotor mode and differences in the physical environment. *In vivo* recordings of lateral gastrocnemius (LG) activation, force development (measured using tendon buckle transducers) and length change (measured using sonomicrometry) were obtained from mallard ducks (*Anas platyrhynchos*) as they swam at steady speeds in a water tank and walked or ran on land. LG force recordings were compared with combined lateral and medial gastrocnemius (MG) muscle–tendon force recordings obtained from the contralateral limb, allowing force development by the MG to be estimated relative to that of the LG. Although similar stresses were calculated to act in the LG and MG muscles during terrestrial locomotion (126 and 115 kPa, respectively), stresses were considerably greater in the LG compared with the MG during swimming (62 *versus* 34 kPa, respectively). During both steady swimming and terrestrial locomotion, the LG developed force while shortening over a considerable range of its length (swimming 23.6 % *versus* terrestrial 37.4 %). Activation of the muscle occurred near the end of passive lengthening during the recovery stroke, just prior to muscle shortening. As a result, the muscle generated broad positive work loops during both locomotor modes. LG work during swimming (4.8 J kg^{-1}) averaged 37 % of the work performed during terrestrial locomotion (13.1 J kg^{-1}), consistent with the twofold greater force and 58 % greater strain of the muscle during walking and running. Because limb cycle frequency was similar for the two locomotor modes (swimming 2.65 *versus* terrestrial 2.61 Hz), differences in power output (swimming 12.6 W kg^{-1} *versus* terrestrial 32.4 W kg^{-1}) largely reflected difference in work per cycle. Tendon elastic energy savings was a small fraction (<5 %) of the work performed by the muscle, consistent with a fiber–tendon design of these two muscles that favors muscle work to produce limb movement with little tendon strain. These results are consistent with a higher cost of terrestrial locomotion in ducks compared with other, more cursorial birds that may operate their muscles more economically and achieve greater tendon elastic savings.

Key words: muscle–tendon force, sonomicrometry, muscle work, power, stress, duck, mallard, *Anas platyrhynchos*.

Introduction

Animals must regularly modulate their locomotor behavior when altering direction, changing speed and gait or moving over uneven land. Indeed, requirements for changes in locomotor behavior may be most extreme for those species that must move through different environments, as when moving over the land *versus* when swimming (Biewener and Gillis, 1999). In the present study, we examine the hypothesis that broad-based changes in locomotor function associated with changes in environment are mediated by changes in the contractile behavior of key locomotor muscles. We test this hypothesis by investigating the mechanical function of the gastrocnemius muscle of mallard ducks (*Anas platyrhynchos*) during terrestrial *versus* aquatic locomotion. Past work on swimming (Butler et al., 1988; Prange and Schmidt-Nielsen, 1970) and terrestrial locomotion (Bech and Nomoto, 1982; Grubb, 1982) in mallards has examined their energetic, cardiovascular and respiratory function, as well as the swimming hydrodynamics of ducklings (Clark and Fish, 1994; Aigeldinger and Fish, 1995), but has not considered changes in musculoskeletal performance across these two locomotor modes.

During swimming, it seems likely that the medial and lateral gastrocnemius muscles of mallards function primarily to perform work for hydrodynamic propulsion. In contrast, during terrestrial locomotion and particularly during running, we hypothesize that the mallard gastrocnemius generates force more economically by shortening less and performing less work. In their classical experiments on the heat production of

muscle, Fenn (Fenn, 1924) and Hill (Hill, 1938) originally demonstrated that muscles liberate less energy when they contract isometrically than when they shorten (liberating additional shortening heat). Hence, not only can muscles generate greater force under isometric conditions, they consume less energy doing so. Because muscles develop even greater force when they are actively lengthened (Abbott and Aubert, 1952; Harry et al., 1990; Katz, 1939), their force economy is enhanced further if they are actively stretched, in addition to doing little work. It has been argued that the ability to generate force economically is important to the design and function of muscle–tendon systems during terrestrial locomotion (Taylor, 1994; Roberts et al., 1997; Biewener, 1998a; Biewener and Roberts, 2000).

In their study of the wild turkey (*Meleagris gallapavo*) lateral gastrocnemius (LG), Roberts et al. (Roberts et al., 1997) showed that, during level running, the LG performs little shortening work. Instead, its function was interpreted as providing economical force generation for weight support during running, while facilitating elastic energy recovery from the non-ossified portions of its tendon. A similar, yet more extreme, pattern of economical force generation has also been observed in the hind-leg muscles of hopping tammar wallabies (*Macropus eugenii*). These muscles develop force during isometric or lengthening contractions, with tendon elastic energy recovery exceeding muscle work by more than 20-fold (Biewener and Baudinette, 1995; Biewener et al., 1998b). The hopping of wallabies and running of turkeys represent bouncing gaits that favor muscle force economy and tendon elastic savings to reduce energy cost and are consistent with recent evidence that the energy cost of terrestrial locomotion is determined largely by the rate of force generation and magnitude of force that muscles must generate to support an animal's weight (Kram and Taylor, 1990), rather than by the amount of work they perform to move the limbs and body (Heglund et al., 1982b).

The contractile function of a muscle is also probably influenced by its architecture and that of its tendon. Short-fibered pinnate muscles with long slender tendons are better suited for force economy and tendon elastic savings than longer, parallel-fibered muscles that lack a tendon (Biewener, 1998a). In contrast, longer parallel-fibered muscles may provide improved control of overall length and movement (Ker et al., 1988; Gans and Gaunt, 1992; Biewener and Roberts, 2000). Because of this, muscle–tendon architecture may constrain the contractile performance of a muscle, requiring modulation of recruitment among different limb muscles to accommodate changes in locomotor environment (Biewener and Gillis, 1999). Nevertheless, in their study of the turkey LG, Roberts et al. (Roberts et al., 1997) found evidence that the LG shortened more and contributed increased work during incline running. In the present study, we ask whether the medial (MG) and lateral (LG) gastrocnemius of mallard ducks modulate their contractile function during swimming *versus* when moving on land.

A preliminary report of these results has appeared previously in a review of muscle function under variable locomotor conditions (Biewener and Gillis, 1999). In the present paper, we include more extensive analysis of the dynamics of the force–length contractile properties of these muscles in relation to agonist motor recruitment, in terms of muscle and tendon stress, and provide a comparison of kinematic *versus* sonometric measurements of muscle–tendon length change.

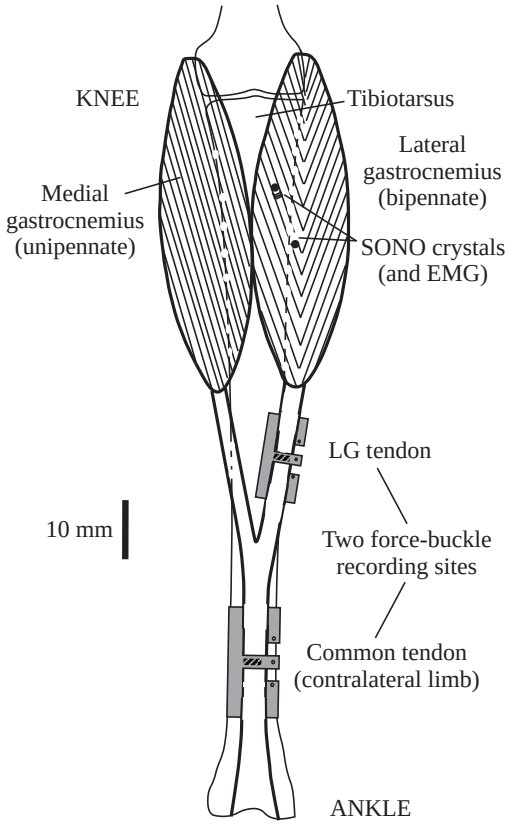
Materials and methods

Animals, training and video recording

Six adult (four male and two female) mallards (*Anas platyrhynchos*) averaging 1.05±0.12 kg body mass (mean ± S.E.M.) were obtained under Illinois Permit NH-97.0370 and US Federal Permit 827908 from a licensed commercial animal dealer. The animals were trained to swim voluntarily in a large tank of still water and to run or walk over a concrete runway 6 m long. The tank measured 1 m wide × 1.5 m high × 25 m long and was filled to a depth of 0.5 m (of which a 10 m section was used to swim the ducks). For terrestrial recordings, the animals were chased or gently prodded to walk or run down the runway. The animals were videotaped in lateral view using a Panasonic AG-450 S-VHS camera equipped with a 10× zoom lens set to obtain a video field approximately 1 m wide. Video recordings of animals made prior to surgical implantation of the transducers demonstrated no significant changes in limb kinematics (limb frequency, ground contact time, angle and angular velocity of the ankle joint) obtained during subsequent experimental recordings of swimming and walking. The video tapes were analyzed at a resolution of 60 fields s^{-1} using a Panasonic 1760 S-VHS tape deck in jog-shuttle mode. Video fields were digitized by a frame-grabber board following time-base correction (IDEN model IVT-7) and analyzed using MTv video digitizing software (DataCrunch, Inc.). The mean speed of each animal was assessed by quantifying the distance that the animal traveled over a known time while moving in the camera's field of view (typically this spanned two cycles during running and 3–4 cycles during swimming).

Surgery

After training and obtaining pre-operative video recordings of swimming and terrestrial locomotion, the animals were anesthetized (sodium pentobarbitol, 20 mg kg^{-1} intravenously, supplemented with methoxyflurane gas administered *via* a mask) and prepared for sterile surgery to implant the sonomicrometry crystals, tendon force buckles and electromyographic (EMG) electrodes. Small incisions were made over the synsacrum and the hip to pass the electrodes and transducers subcutaneously from the animal's back to the implantation sites. The lateral gastrocnemius and its tendon were exposed by making an incision over the lateral aspect of the right leg. Small 0.7 mm sonomicrometry crystals (Sonometrics, Inc.) with 42 gauge wire leads were then inserted 9–12 mm apart along the axis of the muscle's fibers into small openings made with sharp-pointed scissors at a site approximately half-way up the muscle's belly (Fig. 1). These



(Posterior view, right leg)

Fig. 1. Anatomy of the medial and lateral gastrocnemius muscles and their tendons in the mallard hindlimb, illustrating the sites where tendon buckle force transducers were implanted. Isolated forces, fiber length changes measured *via* sonomicrometry (SONO) and electromyographic (EMG) activity were measured for the lateral gastrocnemius (LG) of one limb, and combined medial gastrocnemius (MG) and LG forces were obtained from the common gastrocnemius tendon of the contralateral limb.

openings were sutured using 5-0 gauge silk after aligning the crystals to achieve maximum signal strength. A fine-wire (0.1 mm diameter, California Fine Wire, Inc.) silver bipolar EMG hook electrode (0.5 mm bared tips with 1 mm spacing) was implanted immediately adjacent to the site of the sonomicrometry crystals and secured using 5-0 gauge silk in fascia near its exit point from the muscle. In mallards, the medial and lateral heads of the gastrocnemius muscle (MG and LG, respectively) have distinct tendons that run separately for approximately 15–18 mm before joining to form a common tendon. A small intermediate slip of the gastrocnemius (measuring less than 4 % of the muscles' combined mass) also attaches *via* the MG head. Otherwise, no other muscle contributes force *via* the muscles' common tendon (birds lack a soleus muscle, and the plantaris muscle acts *via* its own tendon). This anatomical arrangement allowed us to implant a small tendon buckle on the LG tendon just distal to the muscle's aponeurosis, but proximal to where it merges with the MG tendon. A larger buckle transducer was implanted on the contralateral (left side) muscles' common tendon by making a lateral incision over the tendon. This allowed us to record isolated forces generated by the LG muscle of one limb, which could be compared with combined MG and LG forces measured by the common tendon force buckle implanted on the opposite limb. By subtracting LG forces from those recorded for the MG and LG combined, we could thus estimate MG force for a particular locomotor activity. Although this approach does not provide a direct recording of the temporal pattern of force development of the MG muscle operating as an agonist to the LG within the same limb, it does allow us to assess the relative distribution of force recruited between these two muscle agonists. The buckle force transducers were constructed from 1.0 mm thick stainless steel in an 'E'-shaped design, with a strain gauge (type FLK-2-11, Tokyo Sokki Kenkyujo, Ltd) mounted on the middle arm to record muscle–tendon force (Biewener et al., 1998b). After all the transducers and electrodes had been implanted, the skin incisions were sutured using 3-0 gauge silk.

The small epoxy-mounted connector (Microtech, Inc.), to which the lead wires were soldered and insulated, was secured to connective tissue overlying the synsacrum and sealed against the skin opening using 3-0 gauge silk suture and silicone adhesive.

Sonomicrometry

The use of sonomicrometry to record muscle length changes assumes a constant velocity of sound propagation through the muscle when it is both active and relaxed. Previous work indicates that this is the case (Hatta et al., 1988) and that 1540 m s^{-1} represents a reliable value to use for vertebrate skeletal muscle (Goldman and Richards, 1954). Because the sound pulse used to detect the distance between a pair of crystals travels at a faster velocity through the epoxy lens overlying the piezoelectric crystals, this introduces an offset error (an underestimate) in the length measurements. For the Sonometrics 0.7 mm crystals used in the study, this was determined to be 0.32 mm on the basis of direct measurements of crystals mounted to a digital caliper made by manipulating the crystals in a water bath. This distance was added as an offset to the recorded length measurements before determining fascicle strain and overall fascicle length change. Measurements of overall muscle length change also assume that measurements of fascicle strain (or fractional length change) obtained between the recording crystals are representative of the fascicle as a whole as well as of other activated fascicles within the muscle. The fractional length change of the muscle's fascicles measured in the region of the crystals was determined by recording the length changes obtained between the crystals (ΔL) and dividing by the resting distance between the crystals recorded when the animal was anesthetized (L_{rest}). The mean total fascicle length change of the whole muscle was then calculated on the basis of the mean fascicle length of the muscle (L_f) multiplied by the fractional length change or strain measured by the crystals ($=L_f \times \Delta L/L_{rest}$).

The sites of crystal implantation relative to the fascicle axis

were confirmed *via post-mortem* dissection. In all cases for which data are reported, the crystals were found to be aligned within 0–6° to the fascicle axis, so errors resulting from misalignment [=1−cos(angle)] were judged to be insignificant. EMG recordings immediately adjacent to the sonomicrometry crystals provided confirmation that the region of muscle length change was actively recruited during the locomotor behaviors studied. Because muscle fibers in intact, whole muscles are invested in, and mechanically linked by, the connective tissue surrounding them (Purslow, 1989; Trotter and Purslow, 1992; Trotter et al., 1992), the force and length changes of activated fibers are probably transmitted throughout a broader region of the muscle *via* their connective tissue matrix. Consequently, differential recruitment of muscle fibers in the regions of the implanted crystals is not considered problematic to tracking fascicle length changes associated with locally activated fibers.

Experimental recordings and buckle force calibration

Animals were allowed to recover overnight from the surgery, and experimental recordings were made during the following 2 days. Recordings were made *via* a light-weight 12 m shielded cable, which was grounded to the animal's skin by means of a small clip. The cable was connected at the other end to a strain gauge bridge amplifier (Vishay 2120, Micromeasurements), EMG amplifiers (Grass, P-511) and a Triton 120.2 sonomicrometry amplifier. The outputs of each of these amplifiers were sampled by an A/D converter (Axon Instruments) at 2000 Hz and stored on a computer for subsequent analysis. Several trials of swimming and terrestrial gait were obtained during each recording session.

Following completion of the recordings, each animal was killed by an overdose of sodium pentobarbitol (100 mg kg^{-1}, intravenously). The common and LG tendon buckles were then calibrated *in situ* by cutting free the distal end of each tendon, tying the tendon's end to a force transducer using 0 gauge silk suture, and freezing the suture in place on the tendon by slowly pouring liquid nitrogen over the tied end. A small plastic dam was used to prevent the tendon from freezing in the region where the buckle transducer was attached. Tension, sufficient to exceed the maximum output recorded from the buckle transducer during *in vivo* recordings, was then applied to the tendon *via* the force transducer in a series of 4–5 loading cycles. A dynamic calibration of force was obtained using the least-squares linear regression fits to both the rise and fall of buckle output *versus* applied force. In all cases, regressions had r^2>0.996, with the differences in slope (hysteresis) for the rise *versus* fall in force being less than 2%. These calibration slopes were averaged to obtain a calibration for each buckle transducer. No visible sign of damage to the tendons was observed after removal of the buckle transducers.

Morphological measurements

Measurements of the lateral and medial gastrocnemius wet mass and mean fascicle length (based on 8–10 separate measurements obtained for varying regions of each muscle, using metric digital calipers) were used to determine muscle fiber cross-sectional area (assuming a muscle density of 1060 kg m^{-3}) (Table 1). Measurements of tendon mass and length were used to determine tendon cross-sectional area, assuming a tendon density of 1120 kg m^{-3} (Ker, 1981).

Table 1. *Muscle and tendon data*

	Mass (g)	Length (mm)	Area (mm^2)
Muscle (*N*=6)			
Lateral gastrocnemius	4.13±0.66	24.2±4.0	150±46
Medial gastrocnemius	3.91±0.47	28.7±3.5	124±19
Tendon (*N*=6)			
Lateral gastrocnemius		57.9±6.2	1.24±0.23
Medial gastrocnemius		52.5±6.0	1.12±0.21
Common		56.1±5.4	2.48±0.32

Length data correspond to the mean fiber length of the muscle or to total tendon length; common tendon measurements are for the contralateral limb.

Values are means ± S.D.

Data sampling and statistical analyses

Comparisons between locomotor modes were based on two-way analyses of variance (ANOVAs) run on samples from all animals for which satisfactory data were obtained, using individuals and locomotor mode (swim *versus* terrestrial) as random and fixed treatment effects, respectively. In general, sample sizes of *N*=17–21 were obtained for five individuals for each locomotor mode. Unless otherwise noted, values are presented as means ± S.E.M.

Results

Swimming

The ducks swam using a narrow range of speeds (0.3–0.6 m s^{-1}) and cycle frequencies that ranged from 1.4 to 3.6 Hz, averaging 2.65±0.2 Hz (*N*=6 individuals, 24 trials). To move at a faster rate (as for escape), the ducks propelled themselves over the water using their wings in rapid rowing strokes. During swimming, force generation by the lateral gastrocnemius (LG) was coincident with the period of muscle shortening (Figs 2A, 3). Peak forces developed by the LG averaged 9.8±1.4 N (*N*=5 individuals, 103 cycles), contributing 67±8% of the total force (14.6±1.7 N) developed by the medial (MG) and lateral gastrocnemius to extend the ankle for hydrodynamic propulsion *via* the foot. Oscillatory length changes of the muscle during swimming were regular and fairly symmetrical, with shortening representing 55±2% and lengthening 45±3% of the cycle (*N*=6 individuals, 114 cycles). Activation of the muscle (based on EMG recordings) occurred just prior (4±1 ms) to the onset of muscle shortening, continuing through 70±4% of force development and muscle shortening (*N*=4 individuals, 80 cycles).

LG shortening and force development occurred synchronously with extension of the ankle joint from 50 to

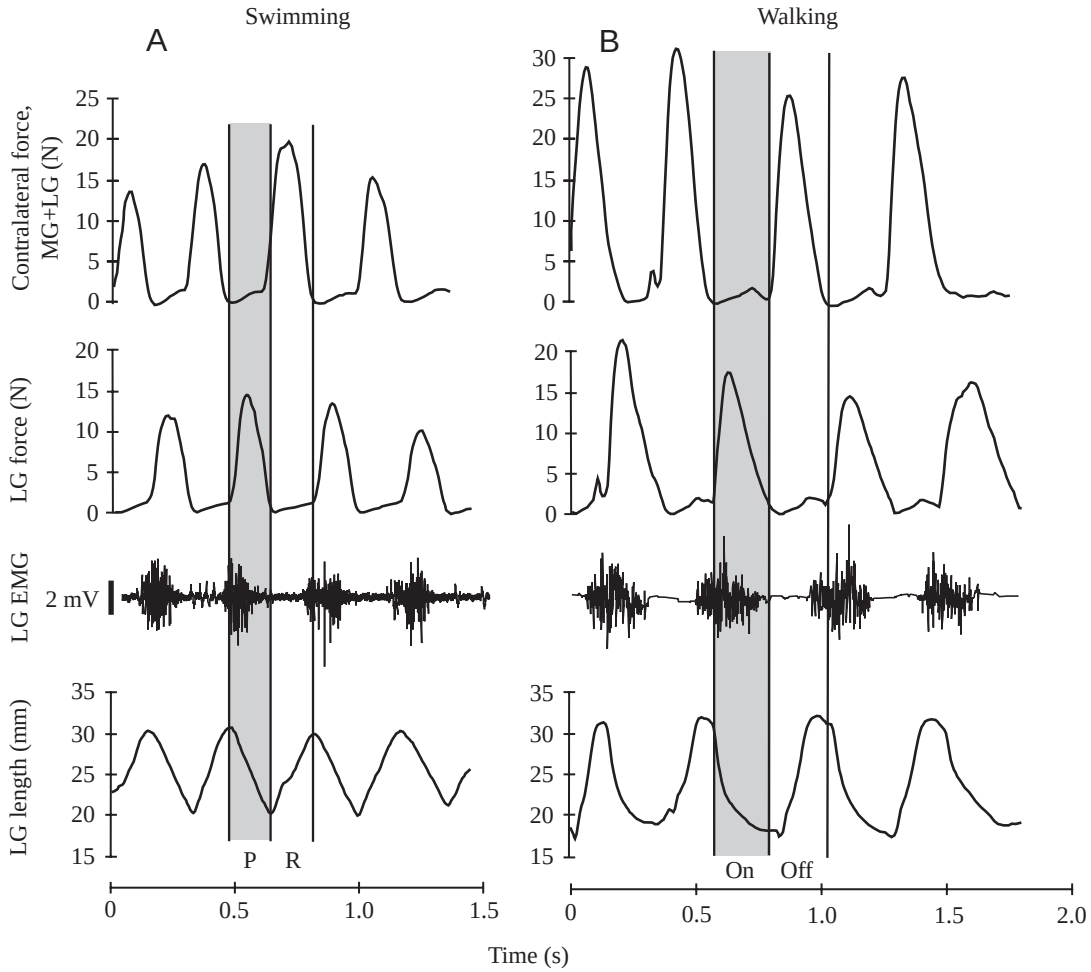


Fig. 2. Representative recordings of muscle force, lateral gastrocnemius (LG) length change and electromyographic (EMG) activity during (A) swimming at 0.40 m s^{-1} and (B) terrestrial locomotion at 0.93 m s^{-1}. Because measurements were obtained from contralateral limbs, the combined recording of the medial gastrocnemius (MG) and LG muscle force is out of phase with the force, length change and EMG recorded for the LG alone. 'P' and 'R' correspond to the propulsive and recovery phases of the swimming cycle for which isolated LG forces and length changes were obtained. Similarly 'On' and 'Off' correspond to the stance and swing phases of the locomotor cycle during walking.

140 ° during the propulsive stroke of the swimming cycle. However, the ankle reached full extension well before (37±4 ms, *N*=5 individuals, 10 cycles) the muscle finished shortening (Fig. 3). Subsequent LG shortening during ankle flexion late in the propulsive stroke, therefore, reflects knee extension during this phase of the locomotor cycle. In general, however, the knee underwent considerably smaller angular excursions (15–20 °) than the ankle joint (angular excursion 70–90 °), reflecting the importance of ankle extension *versus* knee flexion to propulsive movements of the foot during swimming.

Terrestrial locomotion

Recordings were obtained for animals moving at speeds that ranged from 0.3 to 1.7 m s^{-1}. Over this speed range, limb cycle frequencies varied from 1.7 to 3.8 Hz, averaging 2.61±0.4 Hz (*N*=6 individuals, 24 trials), nearly the same (*P*>0.25) as during swimming. We pooled all terrestrial runs into a single sample because our main goal was to compare muscle function across a change in locomotor mode. In general, it is difficult to determine whether birds are walking or running solely on the basis of limb kinematics and relative limb support times (Gatesy and Biewener, 1991). One possible basis for distinguishing walking from running gaits is to determine an animal's Froude number ($=v^2/\boldsymbol{g}l$, where v is forward velocity, $\boldsymbol{g}$ is the gravitational acceleration constant and l is hip height). According to Alexander and Jayes (Alexander and Jayes, 1983), terrestrial animals change gait from a walk to a run at a Froude number in the range 0.6–1.0. This would correspond to a speed of between 1.0 and 1.3 m s^{-1} for the mallards in our study (given a mean hip height at mid-stance of 0.173 m). Thus, it is likely that our terrestrial recordings included both walking and running gaits. Using 1.2 m s^{-1} to distinguish walks from runs indicates that our sample comprised 70 walking cycles (73 %) and 26 running cycles.

As for swimming, LG force generation occurred coincident with muscle shortening during terrestrial locomotion (Figs 2B, 4). Peak forces developed by the LG averaged 20.2±3.2 N

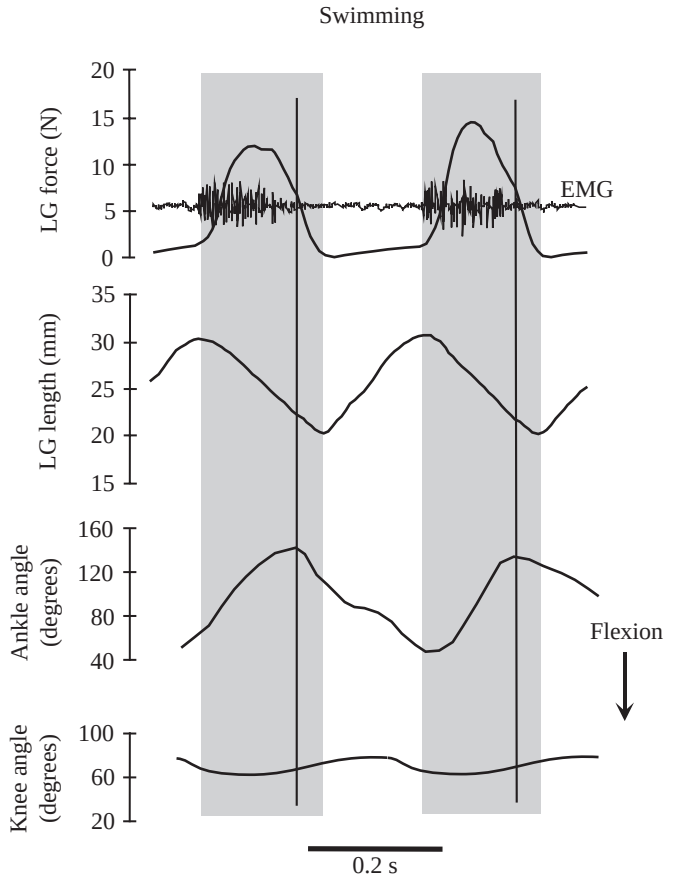


Fig. 3. Expanded recordings of lateral gastrocnemius (LG) force, electromyographic (EMG) activity and length, together with angular changes of the ankle and knee, during two cycles of swimming. The shaded regions depict the propulsive phase of each cycle. The vertical lines depict the timing of maximum ankle extension relative to muscle force, fascicle length change and knee excursion during each cycle. Similar patterns were obtained for the other animals.

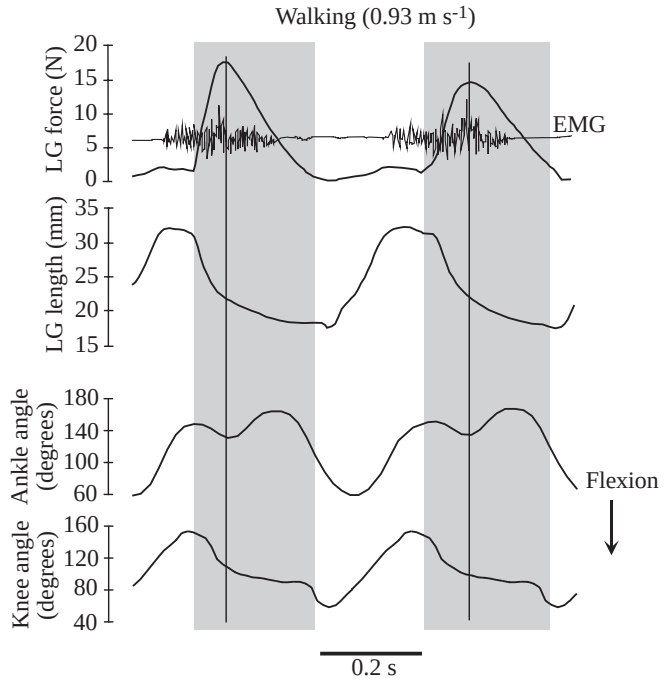


Fig. 4. Expanded recordings of lateral gastrocnemius (LG) force, electromyographic (EMG) activity and length, together with angular changes of the ankle and knee, during two cycles of terrestrial locomotion. The shaded regions depict the limb support phase of each cycle. The vertical lines depict the timing of maximum force relative to fascicle length change and ankle and knee joint excursions during each cycle. Similar patterns were obtained for the other animals.

(*N*=5 individuals, 96 cycles) over the full range of recorded speeds. Overall, the LG developed 59±10 % of the combined force (34.4±4.1 N) of the MG and LG during terrestrial locomotion. During walking and running, length changes of the muscle were more irregular in pattern within each cycle compared with the fairly symmetrical oscillation observed during swimming. Rapid lengthening of the muscle was observed during the swing phase of the limb, with a decelerated pattern of shortening during the support phase. As was observed for swimming, activation of the muscle during terrestrial locomotion occurred just prior (5±1 ms) to the onset of muscle shortening and continued through 65±5 % (*N*=4 individuals, 65 cycles) of force development and muscle shortening. The decline in muscle force both prior to EMG offset and subsequently probably reflects a shortening- and work-induced deactivation of the muscle (Edman, 1975; Josephson and Stokes, 1999).

At the beginning of support, the ankle initially flexed, stretching the gastrocnemius muscle–tendon unit (Fig. 4); however, during this time, the knee also flexed, offsetting the tendency for muscle–tendon stretch due to ankle flexion. Nevertheless, the early rapid shortening shown by the LG fascicles suggests that some of this shortening also probably occurs to take up slack by stretch of the series elastic compliance of the muscle's tendon and aponeurosis. Ankle flexion continued until peak force was developed in the LG muscle–tendon unit, at which time the ankle began to extend. At this time, the LG fascicles continued to shorten, but at a slower rate. This was reflected by the subsequent ankle extension, with limited knee flexion, until late (70–75 %) in limb support. At the end of support, the ankle and knee both exhibited a final, brief period of flexion, during which the LG fascicles remained nearly isometric, suggesting that flexion of these joints was driven by contraction of more proximal muscles of the limb.

Muscle work and power

Graphs of *in vivo* muscle force *versus* length change exhibited counterclockwise work loops indicative of the positive work performed by the lateral gastrocnemius during both swimming and terrestrial locomotion (Fig. 5). The work loops shown in Fig. 5A,B are derived from the cycles shown in Fig. 2. For each locomotor mode, the work loops were broad, indicating large muscle length changes. As noted above, muscle shortening occurred as the muscle began to develop

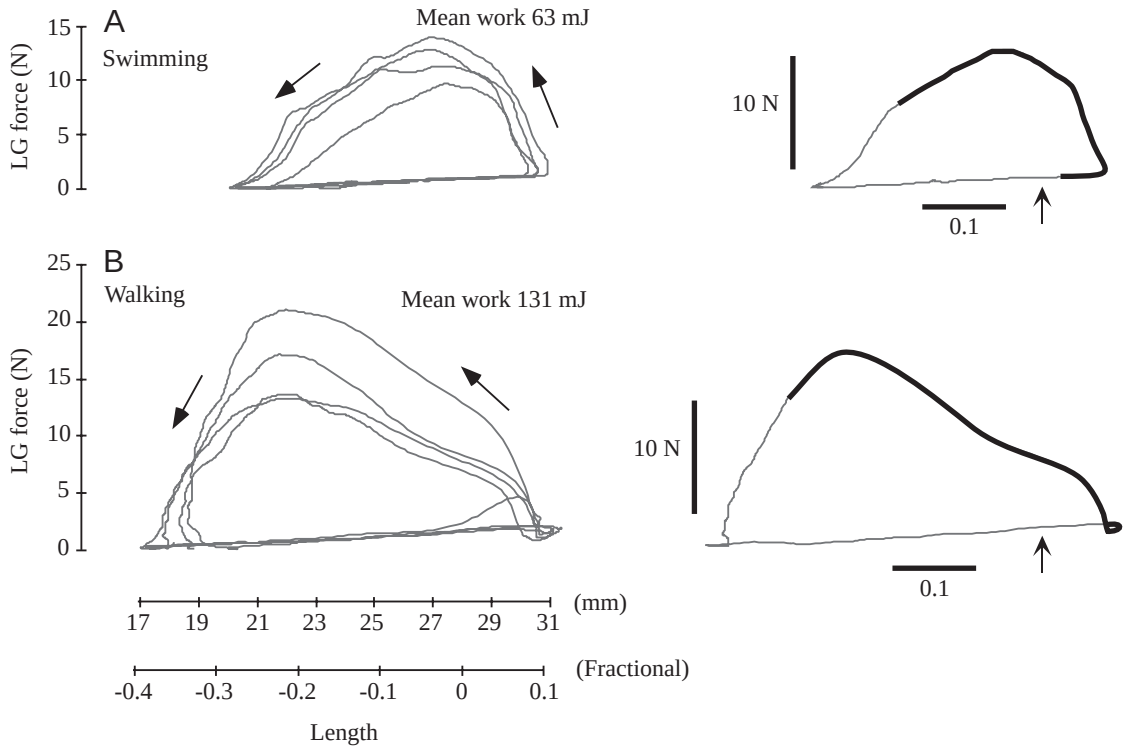


Fig. 5. *In vivo* work loops of the lateral gastrocnemius (LG) muscle for four consecutive cycles during (A) swimming and (B) terrestrial locomotion. These cycles correspond to the same cycles shown in Fig. 2 for each locomotor mode. Although the cycles during terrestrial locomotion represent the animal walking at an average speed of 0.93 m s^{-1}, it is likely that the animal was slowing down, given that the first three cycles exhibited progressively diminished levels of muscle force development. Similar work loop patterns were found over the full range of terrestrial walking and running speeds observed. Arrows indicate the direction of the loops. On the right is shown the third work loop for each locomotor mode, with the bold portion of the loop depicting the period during which electromyographic activity of the muscle was recorded. The scale bar shows a fractional length change of 0.1.

force and continued throughout the entire period of force generation. During swimming, force rose more rapidly during initial shortening and then declined as the muscle continued to shorten after reaching peak force. During terrestrial locomotion, the rise in muscle force was generally less steep than during swimming, but force remained high and near the peak magnitude achieved over much of the shortening period. The muscle then relaxed rapidly during the final phase of shortening. The work loops shown in Fig. 5B probably represent a sequence of strides during which the animal was slowing down because progressively lower forces were recorded over the first three cycles. In general, similar patterns of force, length change and, hence, work loop shape were recorded for walking and running cycles. Because the muscle was lengthened only after relaxing to near zero force, little or no energy was absorbed (‘negative work’) in either locomotor mode during this phase of the cycle.

The broad work loop patterns of the LG reflect activation of the muscle just prior to the start of shortening during both locomotor modes (Fig. 5). This enabled the muscle to develop force rapidly as it began to shorten. Activation of the muscle lasted for 65–70 % of the shortening duration of both locomotor modes, allowing the muscle to sustain substantial force over nearly the entire period of shortening.

Total muscle shortening strain averaged 0.236±0.042 (N=5 individuals, 103 cycles) during swimming and 0.374±0.077 (N=5 individuals, 96 cycles) during terrestrial locomotion (Fig. 6A). For both locomotor modes, the muscle was passively lengthened beyond its resting length (swimming strain, +0.061±0.010; terrestrial locomotion strain, +0.136±0.023) before being activated to develop force while shortening (net shortening strain during swimming, –0.175±0.044; during terrestrial locomotion, –0.238±0.016). Both total muscle strain ($F_{1,4}$=9.01) and lengthening muscle strain ($F_{1,4}$=7.88) were significantly greater (P<0.05) during walking and running than during swimming.

Because the LG shortened 58 % more (Fig. 6A) and developed 106 % greater force (Fig. 6B) during walking and running, the work performed by the LG during terrestrial locomotion (13.1±3.5 J kg^{-1}) averaged 2.7 times more ($F_{1,4}$=14.61, P<0.025) than that produced during swimming (4.8±1.6 J kg^{-1}; Fig. 6C). Combining muscle work with cycle frequency gives the steady power output of the muscle. Because cycle frequency was similar (P>0.25) during swimming (2.65 Hz) and terrestrial locomotion (2.61 Hz), differences in power output by the LG largely reflected differences in work per cycle observed between the two locomotor modes. Consequently, LG power output during

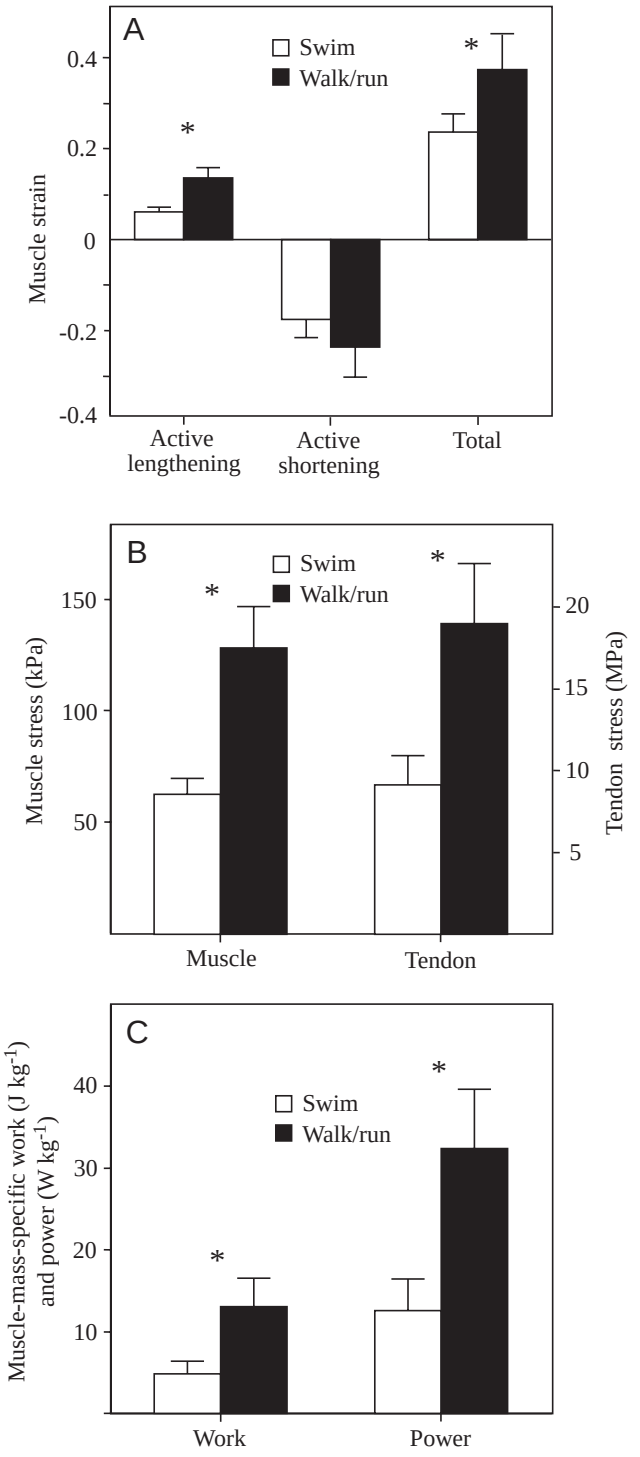


Fig. 6. Histograms comparing (A) fascicle lengthening strain, shortening strain (relative to rest) and total strain (absolute shortening strain from maximum to minimum length), (B) muscle and tendon stress and (C) muscle-mass-specific work and power output for the lateral gastrocnemius during swimming *versus* terrestrial locomotion. Values are means + S.E.M. An asterisk denotes a statistically significant difference between locomotor modes based on the results of two-way ANOVA. N=5 individuals, 103 cycles for swimming and N=5 individuals, 96 cycles for terrestrial locomotion.

swimming (12.6±3.9 W kg^{-1} muscle, N=5 individuals, 103 cycles) was much less ($F_{1,4}$=17.34, P<0.025) than during terrestrial locomotion (32.4±7.3 W kg^{-1} muscle, N=5 individuals, 96 cycles).

Comparison of lateral and medial gastrocnemius muscle and tendon stresses

Calculated values of muscle stress in the medial and lateral heads of the gastrocnemius (based on the differences in force recorded for the combined muscles of the contralateral limb *versus* the isolated recordings of the LG) showed that during terrestrial locomotion similar ($F_{1,4}$=0.61, P>0.25; N=5 individuals, 96 cycles) stresses acted within both agonist components, averaging 125.6±10.5 kPa in the LG and 114.82±11.2 kPa in the MG. Hence, forces developed by each muscle component were matched to the average difference in their fiber cross-sectional areas. However, during swimming, LG and MG forces were not similarly matched, with peak stresses in the LG (62.1±7.3 kPa) significantly exceeding ($F_{1,4}$=13.61, P<0.025; N=5 individuals, 103 cycles) those developed in the MG (33.9±6.1 kPa). Because higher forces were developed by the LG during terrestrial locomotion, stresses in the muscle's tendon were also twofold greater (18.3±3.7 MPa; $F_{1,4}$=14.16, P<0.025) than during swimming (9.1±1.7 MPa; Fig. 6B).

Because of its '**J**'-shaped stress–strain curve, vertebrate tendon has a much lower stiffness at low stresses than at higher stresses (>20 MPa) where the slope (elastic modulus) of its stress–strain curve is more uniform. For the stresses that we calculated to act in the mallard LG tendon during swimming and terrestrial locomotion, the tendon's elastic modulus probably varies from 0.35 to 0.70 GPa (Ker, 1981; Shadwick, 1990). For this range of modulus, assuming an 8 % loss due to hysteresis but neglecting the tendon's non-linear behavior, we estimate elastic storage to be only approximately 3–5 mJ during swimming and 16–20 mJ at the fastest terrestrial speeds recorded. Hence, tendon elastic savings constituted only 3–5 % of the work performed by the LG.

Discussion

Mallard gastrocnemius function in relation to locomotor mode

In contrast to our hypothesis, we found that the lateral gastrocnemius of mallards functions similarly during swimming and terrestrial locomotion. In both locomotor modes, the muscle shortens over a considerable range of its length while developing force to perform substantial positive work. Shortening and power generation are expected for swimming, in which hydrodynamic propulsion *via* the animal's webbed feet is achieved primarily by extension of the ankle joints. However, rather than shortening less during terrestrial locomotion to favor more economical force generation, the lateral gastrocnemius maintained a similar pattern of length change relative to its activation and force development. In fact, the muscle shortened over a significantly greater length range

during the terrestrial gait. This probably included both walking and running; however, our analysis of running depended on an estimate of the Froude number and represented a much smaller sample than our recordings of walking. In contrast, the lateral gastrocnemius muscles of running wild turkeys (Roberts et al., 1997) and hopping tammar wallabies (Biewener et al., 1998b) operate under nearly isometric conditions, or undergo active stretch, to develop force economically and facilitate elastic energy savings in their tendons.

The cycle frequencies used by the ducks during voluntary swimming and terrestrial locomotion were quite similar. This would be expected if the muscles were operating at shortening velocities (resulting in limb frequencies) optimal for maximum efficiency and/or power production. In any event, the similar frequencies observed across locomotor modes strengthen the basis for comparing muscle performance in relation to force and length change for these two activities. It seems likely that cycle frequency is also limited by the hydrodynamics of surface swimming, which limits the ducks' speed range. This is because faster swimming by paddling at the water surface is constrained by the inefficiency and cost needed to overcome the bow wave created by the body (Vogel, 1994). Whereas adult mallards use their wings to propel themselves across the water surface at faster speeds, smaller ducklings generate more vertical force with their feet (in addition to thrust) to elevate themselves out of the water, which enables them to reduce drag by hydroplaning over the surface at faster speeds (Aigeldinger and Fish, 1995). Certainly, the forces and work performance that we observed during steady unforced swimming were far lower than those that the animals' hind-limb muscles are capable of producing. The relatively high cost of swimming at the water surface in mallards, and in a variety of other animals (Fish, 1984; Prange and Schmidt-Nielsen, 1970; Williams, 1983), is consistent with their low propulsive efficiencies (Fish, 1984). This presumably limits the useful performance range of the leg muscles to power surface swimming. The extent to which limb frequency and muscle shortening velocity are modulated and can be increased for faster speed swimming and faster speed running requires further study.

Muscle work versus *force economy in relation to tendon elastic savings and locomotor cost*

Whereas turkeys and wallabies have evolved the capacity for high-speed running and economical hopping, mallards appear to be limited in their ability to move economically and at high speeds over ground. Previous studies of the energetic cost of locomotion during walking in mallard and Pekin ducks *Anas plaryrhynchos domesticus* (Bech and Nomoto, 1982; Grubb, 1982) suggest that these ducks incur a cost of transport (the energy consumed per distance traveled) that is as much as four times that predicted for an avian biped or mammalian quadruped of similar size (Fedak and Seeherman, 1979). It may not be surprising, therefore, that the lateral gastrocnemius does not generate forces under energetically economical (near-isometric) conditions (Fenn, 1924; Hill, 1938) during terrestrial locomotion at any speed.

For many animals, running and hopping represent high-speed bouncing gaits (Alexander, 1984; Cavagna et al., 1977) in which near-isometric or stretch/shorten contractile behavior of limb muscles would be expected to favor reduced metabolic energy expenditure by means of elastic energy savings and increased muscle force economy. Under these conditions, the amount of elastic strain energy stored and recovered in the muscle's tendon would be expected to exceed the amount of work performed by the muscle. In wallabies, tendon elastic energy exceeded muscle work by an average of 20-fold (Biewener et al., 1998b), and for the turkey LG this was found to be 2.5-fold (Roberts et al., 1997). In a study of cat walking and trotting (Prilutsky et al., 1996), elastic energy recovery from the tendons of agonist ankle extensors (soleus, gastrocnemius and plantaris muscles) was found to contribute 14–50 % of the total work generated by the muscle–tendon units. Surprisingly, tendon elastic energy contributions to muscle–tendon work were found to decrease in two of the three muscles (soleus and gastrocnemius) as the cats increased speed and changed gait. On the basis of whole-body mechanics (Alexander, 1984; Cavagna et al., 1977), elastic savings would be expected to increase with speed, particularly at a trot. In contrast, because of the low to moderate stresses operating in the mallard LG tendon compared with the large amount of work performed by the muscle, tendon elastic energy recovery represented only a small fraction (<5 %) of muscle work during terrestrial locomotion.

The uniform behavior of the mallard lateral gastrocnemius observed here may reflect, to some extent, the fairly limited range of speeds (0.3–1.7 $m\,s^{-1}$) that we were able to record during the terrestrial gait, in which the majority of trials were walks. While this may indicate a limited locomotor capacity of mallards on land, recordings obtained for a running gait at faster speeds are needed to confirm whether the contractile behavior of the LG is limited to the extent reported here. Use of a treadmill, or a longer trackway and force-platform-based mechanical work measurements, would favor a greater range of speed and probably provide better confirmation of a running gait than we were able to achieve in the present experiments. At the same time, it would also be informative to examine the contractile function of turkey or other galliform leg muscles during walking in comparison with running to determine whether a pattern of isometric behavior is maintained or modulated as a function of a change in gait.

Even so, it seems likely that morphological features adaptive to swimming, such as webbed feet, shorter hind limbs and a broad pelvis, underlie the inability of mallards to achieve an energetically favorable gait that reduces muscle work and economizes force generation. Whether or not other hind-limb muscles of ducks, and galliforms, function similarly to the gastrocnemius by performing substantial work during terrestrial locomotion remains to be examined, but available energetic data (Bech and Nomoto, 1982; Grubb, 1982) suggest that the cost of force generation by locomotor muscles generally within the duck hind limb is high during terrestrial locomotion. Compared with the cursorial gaits of animals that

move their limbs mainly in a parasagittal plane and minimize lateral and vertical oscillations of their body's center of mass (Cavagna et al., 1977; Heglund et al., 1982a), the waddling of mallards and other ducks would appear to involve greater lateral sway and rotation of the animal's body over the supporting limb. This presumably requires greater muscle work and incurs a higher energy cost.

Comparison of muscle in vivo *work dynamics among species*

In contrast to the near-isometric or active-stretch behavior of the leg muscles of wallabies and turkeys, the extensive shortening (25–40 % of resting length) of the mallard lateral gastrocnemius to perform work is similar to that observed in the pectoralis muscle of a variety of birds during flight (Biewener et al., 1998a; Tobalske and Dial, 2000; Williamson et al., 2001) and to that of certain hind-limb muscles in anurans during jumping and swimming (Lutz and Rome, 1994; Olson and Marsh, 1998; Gillis and Biewener, 2000). *In vivo* measurements of muscle length change indicate that the fascicles of these muscles often shorten over a considerable range of their length (20–40 %), often much greater than the length range traditionally believed to yield optimal force output for a muscle operating near the plateau of its force–length curve (e.g. Gordon et al., 1966; McMahon, 1984). However, in the case of the avian pectoralis and the mallard gastrocnemius, diminished force-generating ability due to non-optimal myofilament overlap is probably mitigated by the fact that these muscles are lengthened beyond their resting length before shortening over such a substantial range. In the mallard LG, lengthening prior to force development averaged 6 % during swimming and 14 % during terrestrial locomotion, so that subsequent shortening past rest length was 18 % and 24 %, respectively, corresponding to a total shortening strain of 23 % and 37 %. This pattern of length change relative to resting length is similar to that of the pigeon (*Columba livia*) pectoralis (Biewener et al., 1998a), in which initial lengthening prior to force development was 20 %, allowing the muscle to shorten by as much as 32–38 % and resulting in a net shortening of 12–18 % below resting length. In both these studies, however, the active force–length properties of the muscle were not evaluated, limiting interpretations of where the muscles operate on their force–length curve. Future work that establishes this will provide important evidence of whether these muscles operate on the ascending and plateau regions of their force–length curve, which is believed to favor stable contractile function (McMahon, 1984; Morgan, 1990). Finally, it seems likely that the decline in LG force prior to the end of neural activation, and subsequently during the remainder of the propulsive phase of the stride, reflects a shortening-induced (Edman, 1975) and/or work-induced (Josephson and Stokes, 1999) force depression or deactivation of the muscle. Such a depression of muscle force is important to allow the muscle to become fully relaxed prior to being re-lengthened by muscle antagonists.

Consistent with the pattern of extensive shortening during force development, stresses developed within the mallard LG during swimming (mean 61 kPa) and terrestrial locomotion (mean 127 kPa) are more similar in magnitude to those observed in the pigeon pectoralis during flight (54–76 kPa; Dial and Biewener, 1993) than to the much higher stresses observed in wallabies during hopping (227–262 kPa; Biewener and Baudinette, 1995) or kangaroo rats (*Dipodomys spectabilis*) during jumping (90–350 kPa; Biewener and Blickhan, 1988). In the latter two cases, the muscles developed force while being actively stretched, enhancing the peak magnitude of force generated. Correspondingly, stresses developed in the mallard LG tendon were also fairly low (swimming 9 MPa; walking/running 18 MPa), consistent with the tendon's limited elastic energy recovery.

In their study of muscle–tendon design, Ker et al. (Ker et al., 1988) define a fiber length factor (FLF) as the ratio of a muscle's fiber length to the extension of its tendon that occurs when the muscle generates maximal force (in their analysis, this was estimated as peak isometric force on the basis of measurements of muscle fiber cross-sectional area). According to their model, FLF values greater than 4 are found in muscles with thick tendons that produce limb movements with little tendon strain, while FLF values less than 2 are characteristic of muscles designed to generate high tendon stresses for elastic energy storage. According to the model of Ker et al. (Ker et al., 1988), it seems clear that that the mallard LG and MG muscles and tendons are not well designed for elastic energy savings. Even if the muscles developed a peak isometric force of 250 kPa, well above the levels observed during terrestrial locomotion, peak tendon stresses would reach only 30 MPa, corresponding to a strain of approximately 3 % and a total tendon extension of approximately 3.3 mm. The fiber lengths of these two muscles (Table 1) indicate an FLF of approximately 7–9. For the maximum tendon stresses that we recorded during terrestrial locomotion (18 MPa), the FLFs of these two muscles are even greater (12–15). Hence, the results of the present study are consistent with the model of Ker et al. (Ker et al., 1988), indicating a muscle–tendon design that is much better suited to producing limb movement *via* muscle work with little tendon strain.

In addition to swimming and terrestrial locomotion, mallards also use their legs for propulsive thrust during take-off. It seems possible that muscle–tendon forces developed during the jumping phase of flight take-off may be considerably higher than those achieved during steady-speed terrestrial locomotion, in which case the design of the hind-leg muscles and tendons of anseriforms and other water birds may be influenced by performance requirements for flight take-off, in addition to steady swimming and terrestrial locomotion. Nevertheless, even for this activity, muscle work and power would be expected to be far more important than effective elastic energy storage in the tendons.

Muscle stress and agonist muscle recruitment

An attractive feature of the mallard hind limb as a model system for examining motor recruitment in relation to locomotor function is that the forces generated by the medial

and lateral heads of the gastrocnemius can be recorded independently. A common assumption made in many biomechanical and neural control studies of muscle force generation based on joint moment analysis (e.g. Alexander, 1974; Biewener, 1983; Biewener, 1998b; Herzog and Leonard, 1991) is that agonist muscles develop force in proportion to their fiber cross-sectional area; in other words, that muscles operate with equal stress to control the moment at a joint. The results obtained here show that, while this may be a reasonable assumption under certain circumstances (nearly equal stresses were developed in the MG and LG during terrestrial locomotion), under other conditions it may not be the case (quite different stresses were measured for the MG and LG during swimming). Our previous work on wallaby hind-leg muscles (Biewener and Baudinette, 1995) also indicates that substantial variation in agonist muscle stress (up to 30 %) can occur during steady-speed hopping, in which the flexor digitorum longus muscle was found to develop significantly lower stresses than the gastrocnemius and plantaris muscles at any given speed. Similarly, studies of *in vivo* muscle forces developed by cat ankle extensors (Herzog et al., 1993; Walmsley et al., 1978) suggest that these muscles also develop different stresses during locomotion at different speeds and inclines. Whereas the cat soleus (a slow oxidative muscle) is recruited at slow walking speeds and its force production is maintained uniformly over different speeds and gradients, the gastrocnemius and plantaris modulate force generation with respect to speed and gradient. Future studies of muscle recruitment and function under non-steady as well as steady-state conditions are needed to explore this issue more broadly. In the case of mallards, comparison of the force–length behavior of the mallard MG with the LG will also enable a determination of whether these two muscle components exhibit the same contractile behavior across a change in locomotor mode.

Animals must accommodate a range of variable conditions when moving through their natural environment. This probably entails the modulation of muscle recruitment (Gillis and Biewener, 2000) and/or contractile function on a stride-to-stride basis or over a number of strides within a given locomotor behavior. The capacity of muscles to alter their contractile function, modulating the timing and amount of shortening and, thus, the amount of force developed and work performed, is therefore an important issue to address. Direct muscle force and length recordings provide an opportunity to accomplish this for key locomotor muscles of certain species. Early results show that some muscles may be able to alter their contractile behavior (Roberts et al., 1997), while others, such as the mallard LG observed here, may have a more limited capacity. Future studies examining a broader number of locomotor conditions (incline, gait and acceleration) in other species and for other muscles will help to provide much needed insight into the structure–function relationships of muscle–tendon systems and how motor function is modulated to enable animals to adjust to the variable conditions typical of their natural environment.

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References

Abbott, B. C. and Aubert, X. M. (1952). The force exerted by active striated muscle during and after change in length. *J. Physiol., Lond.* **117**, 77–86.

Aigledinger, T. L. and Fish, F. E. (1995). Hydroplaning by ducklings: overcoming limitations to swimming at the water surface. *J. Exp. Biol.* **198**, 1567–1574.

Alexander, R. McN. (1974). The mechanics of a dog jumping (*Canis familiaris*). *J. Zool., Lond.* **173**, 549–573.

Alexander, R. McN. (1984). The gaits of bipedal and quadrupedal animals. *J. Robotics Res.* **3**, 49–59.

Alexander, R. McN. and Jayes, A. S. (1983). A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *J. Zool., Lond.* **201**, 135–152.

Bech, C. and Nomoto, S. (1982). Cardiovascular changes associated with treadmill running in the Pekin duck. *J. Exp. Biol.* **97**, 345–358.

Biewener, A. A. (1983). Locomotory stresses in the limb bones of two small mammals: the ground squirrel and chipmunk. *J. Exp. Biol.* **103**, 135–154.

Biewener, A. A. (1998a). Muscle function *in vivo*: the design of muscles used as springs *versus* muscles used to generate mechanical power. *Am. Zool.* **38**, 703–717.

Biewener, A. A. (1998b). Muscle–tendon stresses and elastic energy storage during locomotion in the horse. *Comp. Biochem. Physiol.* B **120**, 73–87.

Biewener, A. A. and Baudinette, R. V. (1995). *In vivo* muscle force and elastic energy storage during steady-speed hopping of tammar wallabies (*Macropus eugenii*). *J. Exp. Biol.* **198**, 1829–1841.

Biewener, A. A. and Blickhan, R. (1988). Kangaroo rat locomotion: design for elastic energy storage or acceleration? *J. Exp. Biol.* **140**, 243–255.

Biewener, A. A., Corning, W. R. and Tobalske, B. T. (1998a). *In vivo* pectoralis muscle force–length behavior during level flight in pigeons (*Columba livia*). *J. Exp. Biol.* **201**, 3293–3307.

Biewener, A. A. and Gillis, G. B. (1999). Dynamics of muscle function during locomotion: accommodating variable conditions. *J. Exp. Biol.* **202**, 3387–3403.

Biewener, A. A., Konieczynski, D. D. and Baudinette, R. V. (1998b). *In vivo* muscle force–length behavior during steady-speed hopping in tammar wallabies. *J. Exp. Biol.* **201**, 1681–1694.

Biewener, A. A. and Roberts, T. J. (2000). Muscle and tendon contributions to force, work and elastic energy savings: a comparative perspective. *Exerc. Sport Sci. Rev.* **28**, 99–107.

Butler, P. J., Turner, D. L., Al-Wassia, A. and Bevan, R. M. (1988). Regional distribution of blood flow during swimming in the tufted duck (*Aythya fuligula*). *J. Exp. Biol.* **135**, 461–472.

Cavagna, G. A., Heglund, N. C. and Taylor, C. R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditures. *Am. J. Physiol.* **233**, R243–R261.

Clark, B. D. and Fish, F. E. (1994). Scaling of the locomotory apparatus and paddling rhythm in swimming mallard ducklings (*Anas platyrhynchos*): test of a resonance model. *J. Exp. Zool.* **270**, 245–254.

Dial, K. P. and Biewener, A. A. (1993). Pectoralis muscle force and power output during different modes of flight in pigeons (*Columba livia*). *J. Exp. Biol.* **176**, 31–54.

Edman, K. A. P. (1975). Mechanical deactivation induced by active shortening in isolated muscle fibres of the frog. *J. Physiol., Lond.* **246**, 255–275.

Fedak, M. A. and Seeherman, H. J. (1979). Reappraisal of energetics of locomotion shows identical cost in bipeds and quadrupeds including ostrich and horse. *Nature* **282**, 713–716.

Fenn, W. O. (1924). The relation between the work performed and the energy liberated in muscular contraction. *J. Physiol., Lond.* **58**, 373–395.

Fish, F. E. (1984). Mechanics, power output and efficiency of the swimming muskrat (*Ondatra zibethicus*). *J. Exp. Biol.* **110**, 183–201.
Gans, C. and Gaunt, A. S. (1992). Muscle architecture and control demands. *Brain Behav. Evol.* **40**, 70–81.
Gatesy, S. M. and Biewener, A. A. (1991). Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *J. Zool., Lond.* **224**, 127–147.
Gillis, G. B. and Biewener, A. A. (2000). Musculoskeletal mechanisms for accommodating locomotion in different environments: hindlimb extensor muscle function during hopping and swimming in the toad (*Bufo marinus*). *J. Exp. Biol.* **203**, 3547–3563.
Goldman, D. E. and Richards, J. (1954). Measurements of high-frequency sound velocity in mammalian soft tissue. *J. Acoust. Soc. Am.* **26**, 981–983.
Gordon, A. M., Huxley, A. F. and Julian, F. J. (1966). The variation in isometric tension with sarcomere length in vertebrate muscle fibers. *J. Physiol., Lond.* **184**, 170–192.
Grubb, B. R. (1982). Cardiac output and stroke volume in exercising ducks and pigeons. *J. Appl. Physiol.* **53**, 207–211.
Harry, J. D., Ward, A., Hegland, N. C., Morgan, D. L. and McMahon, T. A. (1990). Cross-bridge cycling theories cannot explain high-speed lengthening behavior in muscle. *Biophys. J.* **57**, 201–208.
Hatta, I., Sugi, H. and Tamura, Y. (1988). Stiffness changes in frog skeletal muscle during contraction recorded using ultrasonic waves. *J. Physiol., Lond.* **403**, 193–209.
Heglund, N. C., Cavagna, G. A. and Taylor, C. R. (1982a). Energetics and mechanics of terrestrial locomotion. III. Energy changes of the centre of mass as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **79**, 41–56.
Heglund, N. C., Fedak, M. A., Taylor, C. R. and Cavagna, G. A. (1982b). Energetics and mechanics of terrestrial locomotion. IV. Total mechanical energy changes as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 57–66.
Herzog, W. and Leonard, T. R. (1991). Validation of optimization models that estimate the forces exerted by synergistic muscles. *J. Biomech.* **24**, 31–39.
Herzog, W., Leonard, T. R. and Guimaraes, A. C. S. (1993). Forces in gastrocnemius, soleus and plantaris muscles for the freely moving cat. *J. Biomech.* **26**, 945–953.
Hill, A. V. (1938). The heat of shortening and the dynamic constants of muscle. *Proc. R. Soc. Lond. B* **126**, 136–195.
Josephson, R. K. and Stokes, D. R. (1999). Work-dependent deactivation of crustacean muscle. *J. Exp. Biol.* **202**, 2551–2565.
Katz, B. (1939). The relation between force and speed in muscular contraction. *J. Physiol., Lond.* **96**, 45–64.
Ker, R. F. (1981). Dynamic tensile properties of the plantaris tendon of sheep (*Ovis aries*). *J. Exp. Biol.* **93**, 283–302.
Ker, R. F., Alexander, R. McN. and Bennett, M. B. (1988). Why are mammalian tendons so thick? *J. Zool., Lond.* **216**, 309–324.
Kram, R. and Taylor, C. R. (1990). Energetics of running: a new perspective. *Nature* **346**, 265–267.
Lutz, G. J. and Rome, L. C. (1994). Built for jumping: the design of the frog muscular system. *Science* **263**, 370–372.
McMahon, T. A. (1984). *Muscles, Reflexes and Locomotion*. Princeton, NJ: Princeton University Press.
Morgan, D. L. (1990). New insights into the behavior of muscle during active lengthening. *Biophys. J.* **57**, 209–221.
Olson, J. M. and Marsh, R. L. (1998). Activation patterns and length changes in hindlimb muscles of the bullfrog *Rana catesbeiana* during jumping. *J. Exp. Biol.* **201**, 2763–2777.
Prange, H. D. and Schmidt-Nielsen, K. (1970). The metabolic cost of swimming in ducks. *J. Exp. Biol.* **53**, 763–777.
Prilutsky, B. I., Herzon, W., Leonard, T. R. and Allinger, T. L. (1996). The role of the muscle belly and tendon of soleus, gastrocnemius, and plantaris in mechanical energy absorption and generation during cat locomotion. *J. Biomech.* **29**, 417–434.
Purslow, P. P. N. (1989). Strain-induced reorientation of an intramuscular connective tissue network: implications for passive muscle elasticity. *J. Biomech.* **22**, 21–32.
Roberts, T. J., Marsh, R. L., Weyand, P. G. and Taylor, C. R. (1997). Muscular force in running turkeys: the economy of minimizing work. *Science* **275**, 1113–1115.
Shadwick, R. E. (1990). Elastic energy storage in tendons: mechanical differences related to function and age. *J. Appl. Physiol.* **68**, 1033–1040.
Taylor, C. R. (1994). Relating mechanics and energetics during exercise. *Adv. Vet. Sci. Comp. Med.* **38**A, 181–215.
Tobalske, B. W. and Dial, K. P. (2000). Effects of body size on takeoff flight performance in the Phasianidae (Aves). *J. Exp. Biol.* **203**, 3319–3332.
Trotter, J. A. and Purslow, P. P. (1992). Functional morphology of the endomysium in series fibered muscles. *J. Morph.* **212**, 109–122.
Trotter, J. A., Salgado, J. D., Ozbaysal, R. and Gaunt, A. S. (1992). The composite structure of quail pectoralis muscle. *J. Morph.* **212**, 27–35.
Vogel, S. (1994). *Life in Moving Fluids. The Physical Biology of Flow*. Princeton, NJ: Princeton University Press.
Walmsley, B., Hodgson, J. A. and Burke, R. E. (1978). Forces produced by medial gastrocnemius and soleus muscles during locomotion in freely moving cats. *J. Neurophysiol.* **41**, 1203–1216.
Williams, T. M. (1983). Locomotion in the North American mink, a semi-aquatic mammal. I. Swimming energetics and body drag. *J. Exp. Biol.* **103**, 155–168.
Williamson, M. R., Dial, K. P. and Biewener, A. A. (2001). Pectoralis muscle performance during ascending and slow level flight in mallards (*Anas platyrhynchos*). *J. Exp. Biol.* **204**, 495–507.