RESEARCH ARTICLE

Mechanical and energetic scaling relationships of running gait through ontogeny in the ostrich (*Struthio camelus*)

Nicola C. Smith* and Alan M. Wilson

Structure and Motion Laboratory, The Royal Veterinary College, University of London, Hatfield AL9 7TA, UK

*Author for correspondence at present address: Kingston University, Kingston-Upon-Thames, Surrey KT1 2EE, UK (nicola.smith@kingston.ac.uk)

SUMMARY

It is unclear whether small animals, with their high stride frequency and crouched posture, or large animals, with more tendinous limbs, are more reliant on storage and return of elastic energy during locomotion. The ostrich has a limb structure that appears to be adapted for high-speed running with long tendons and short muscle fibres. Here we investigate biomechanics of ostrich gait through growth and, with consideration of anatomical data, identify scaling relationships with increasing body size, relating to forces acting on the musculoskeletal structures, effective mechanical advantage (EMA) and mechanical work. Kinematic and kinetic data were collected through growth from running ostriches. Joint moments scaled in a similar way to the pelvic limb segments as a result of consistent posture through growth, such that EMA was independent of body mass. Because no postural change was observed, relative loads applied to musculoskeletal tissues would be predicted to increase during growth, with greater muscle, and hence tendon, load allowing increased potential for elastic energy storage with increasing size. Mass-specific mechanical work per unit distance was independent of body mass, resulting in a small but significant increase in the contribution of elastic energy storage to locomotor economy in larger ostriches.

Key words: biomechanics, economy, gait, locomotion, growth, effective mechanical advantage.

INTRODUCTION

Within a species, running looks relatively similar in small and large individuals and the mechanical demands of stance are similar. An applied vertical ground reaction force (GRF) to support weight imposes a leg length change and horizontal forces as GRF are directed approximately along the leg axis. This phenomenon is summarised by the pervasiveness of the spring mass model as a representation of running gaits (Blickhan, 1989). GRF rises during stance and the leg shortens, with the relationship between the two approximately linear, so the leg behaves as a spring. Whilst muscle fibre can exhibit these force length properties, the metabolic cost would be high and the tendon tends to dominate in the extensor or antigravity muscles of running animals with muscle fibres that are either approximately isometric or slowly shortening to perform work (Roberts et al., 1997; Biewener et al., 1998; Lichtwark and Wilson, 2006). This facilitates the storage of elastic energy to offset the energetic requirements of supporting and redirecting the body weight during stance, improving locomotor efficiency (Cavagna et al., 1977; Heglund et al., 1982). Some previous studies have argued that large animals are less reliant on elastic energy storage because they take fewer steps for a given distance, and have a more upright posture and less joint excursion (Bullimore and Burn, 2005; Taylor, 1994), but larger animals have longer tendons and shorter muscle fibres, which would imply that they are better suited to muscle tendon unit length change occurring in tendon rather than muscle fibres (Biewener, 1998; Reilly et al., 2007; Rubenson et al., 2011; Shadwick, 1990), with a consequence of improved capacity for elastic energy storage.

Variation in body size requires the mechanical design of the musculoskeletal system to change if it is to perform in the same way and be subjected to similar levels of stress under applied loads (Schmidt-Nielsen, 1975). Between species across a large size range, including both mammals and birds, limb bone dimensions have been found to scale close to geometric similarity (Alexander et al., 1977; Biewener, 1983; Maloiy et al., 1979; Olmos et al., 1996) and the GRF has been shown to scale directly proportional to body mass (Alexander and Jayes, 1983; Biewener, 1989; Bullimore and Burn, 2006). Therefore, the stress in the limb bones, and potentially in other tissues of the musculoskeletal system, would be predicted to increase with size proportional to body mass, $M^{0.33}$. The potential for increased stress with increasing body mass has been shown to be avoided in larger species by changes in bone geometry, a more upright limb posture and/or changes in performance. Postural changes with increasing body size can account for maintenance of safety factors between species through realignment of the limb forces with muscles and bones (Biewener, 1989; Biewener, 1990; Bullimore and Burn, 2004). This trend is illustrated by the effective mechanical advantage (EMA), which determines the ratio between the moment arm of the agonist muscle group, r, and the moment arm of the GRF about a specific joint, R. Because the moment created by the GRF at each joint must be balanced by the total moment created by the muscles, for a given GRF, a larger GRF moment arm with no change in muscle moment arm requires the muscles to generate more force, transmitted through any series elastic elements, to balance it. Comparison of small and large species shows that the more crouched posture of smaller animals positions the point of application of force under the foot, and increases the moment arm of the resultant GRF at the limb joint centres. This gives the small animals a greater effective stride length compared with their leg length, but a small EMA. Larger animals tend to have straighter limbs, which aligns the GRF more closely with the limb, giving a smaller GRF moment arm at the joints and

hence requiring less relative muscle force to balance the joints and resulting in a more 'effective' limb. This has been suggested to result in relatively less muscle mass, longer tendons and greater potential for spring savings in larger species of animal (Reilly et al., 2007), anatomical traits that are observed in the largest bird species, the ostrich (Smith et al., 2006), and have been related to its locomotor economy (Alexander et al., 1979; Rubenson et al., 2007; Rubenson et al., 2011). However, previous analysis of kinematic data through growth in this species across a large size range has demonstrated little variation in posture with increasing body size (Smith et al., 2010), which might therefore be expected to result in increased musculoskeletal loads, and hence greater capacity for storage and return of elastic energy as the animals grow. This, in turn, could be expected to affect the locomotor economy of the ostrich through growth.

Comparisons of animals of different sizes have shown how anatomy and morphology change to account for the biomechanical challenges of increased size and permit dynamic similarity across a large size range. Changes in the kinematics and kinetics of ostrich locomotion during ontogeny show trends similar to those found with increasing size between species, allowing many gait parameters to scale close to dynamic similarity (Smith et al., 2010). The similarities of the scaling relationships between different species and within a single species during growth were found to be achievable because of differential scaling of the limb rather than postural changes. However, positive allometry of the limb through growth was also found to lead to small deviations from predicted scaling of some derived parameters, which may suggest altered stresses acting within musculoskeletal tissues, as has been observed in ontogenetic studies of other species (Main and Biewener, 2004; Main and Biewener, 2007). This paper aims to investigate the effect of body size through ontogeny of the ostrich and relates findings to mechanical scaling factors that have been shown to allow maintenance of dynamic similarity, and relative reductions in tissue load, between species with increasing body size. Previously published anatomical data for the ostrich (Smith et al., 2006; Smith et al., 2007) are considered here in combination with kinetic and kinematic data obtained through growth to enable joint moments, muscle forces, EMA and mechanical energy changes to be derived. Scaling of muscle and hence tendon loads are investigated through analysis of the EMA, the interpretation of which is aided through consideration of energetics of running gait and potential for elastic energy storage and return through the spring-like behaviour of the limb. We hypothesise that ontogenetic scaling of joint moments will show positive allometry, consistent with previously reported limb bone scaling in this species (Smith et al., 2010), as a result of maintained limb posture through growth, in contrast to that observed with increasing size between species. Hence, we hypothesise that scaling of EMA will differ from the scaling relationship observed between species, such that the EMA will not change with growth, as suggested by previous analysis of limb postures (Smith et al., 2010). Consequently, we predict that the ontogenetic scaling could result in increased tendon loads, with potential for increased storage and return of elastic energy in the adult birds. We discuss the influence of our reported scaling trends on musculoskeletal loading through growth and consider the implications of our findings in terms of locomotor economy.

MATERIALS AND METHODS
Measurements

Fifteen African black ostriches (*Struthio camelus* var. *domesticus* Linnaeus 1758), eight males and seven females, were used for this study. The ostriches were obtained from a UK ostrich farm (MNS Ostriches, Holsworthy, Devon, UK) and were hand reared from 2 days to 10 months of age, with kinematic and kinetic data collected from 2 weeks to 10 months of age. The ostriches were trained to run at self-selected speeds along a rubber-topped runway with an embedded force plate (9287BA, Kistler Instruments, Hook, Hampshire, UK), sampled at 1000 Hz. Kinematic data were collected at 240 Hz using a four-camera infrared motion analysis system (ProReflex, Qualysis, Gothenburg, Sweden) to detect 3-D positions of reflective markers on palpable bony landmarks defining the joints [hip (femoral trochanter); knee (lateral femoral condyle); intertarsal (ankle) joint (distal tibiotarsus, lateral condyle), tarsometatatarsophalangeal (MTP) joint (distal tarsometatarsus, lateral condyle); third digit, distal interphalangeal (DIP) joint] on the left pelvic limb. Feathers were trimmed and the wings were restrained in a folded position to minimise marker occlusion. Tracked kinematic data were filtered (second order low-pass Butterworth filter, 20 Hz cut off) and processed in MATLAB (The MathWorks, Natick, MA, USA) with the force plate data (low-pass filtered at 25 Hz with a zero-lag fourth-order Butterworth filter). The stance phase was determined from foot contact on the force plate, defined by a threshold value of 20 N for birds of mass over 20 kg and 5 N for birds less than 20 kg, which closely agreed with foot contacts determined from movement of the DIP marker. Kinematic and kinetic data were then integrated with published anatomical data (Smith et al., 2006; Smith et al., 2007) to calculate joint moments, muscle forces, EMA and mechanical energy changes.

Joint moments and EMA

Moment arms of the resultant GRF about each of the joints, R, were defined by the perpendicular distance between the GRF line of action and the estimated joint centre. Joint moments were calculated from the sum of the external joint moment, the inertial joint moment and the gravitational joint moment, with inertial and gravitational moments taking account of all distal segments. Mass, centre of mass and moment of inertia of limb segments were taken from previously published work (Fedak et al., 1982) where data were presented for pelvic limb segments for an 89.5 kg ostrich as proportions of body mass and segment lengths. Mass and moment of inertia values were then scaled with body mass, according to published ontogenetic scaling relationships (Smith et al., 2010).

Total muscle moment arms were calculated from a weighted mean of all the antagonist muscles acting at a joint, such that muscle moment arms were weighted according to physiological cross-sectional area, and hence force-generating capacity (Smith et al., 2006), to give an average moment arm for the total force generation. The EMA was then calculated from the ratio of the total muscle moment arm, r, to the GRF moment arm, R, for each joint and for the total limb, defined by the average of hip, knee, ankle and MTP (Biewener et al., 2004; Biewener, 2005). EMA was calculated as an average value through the stance phase, consistent with previous studies (Biewener et al., 2004; Ren et al., 2010). Muscle moment arms were assumed to scale proportional to limb bone segments (Smith et al., 2010), so measured values from Smith et al. (Smith et al., 2007) were scaled accordingly with body mass, using the published ontogenetic scaling exponents. Muscle force was calculated from joint moments divided by the calculated muscle moment arm, r, for each joint. Because the force applied to a segment by a muscle is transmitted through the tendon, this also gave a value for tendon force.

Mechanical energy

Mechanical energy was calculated from the sum of kinetic and potential energies of the body and the individual limb segments.
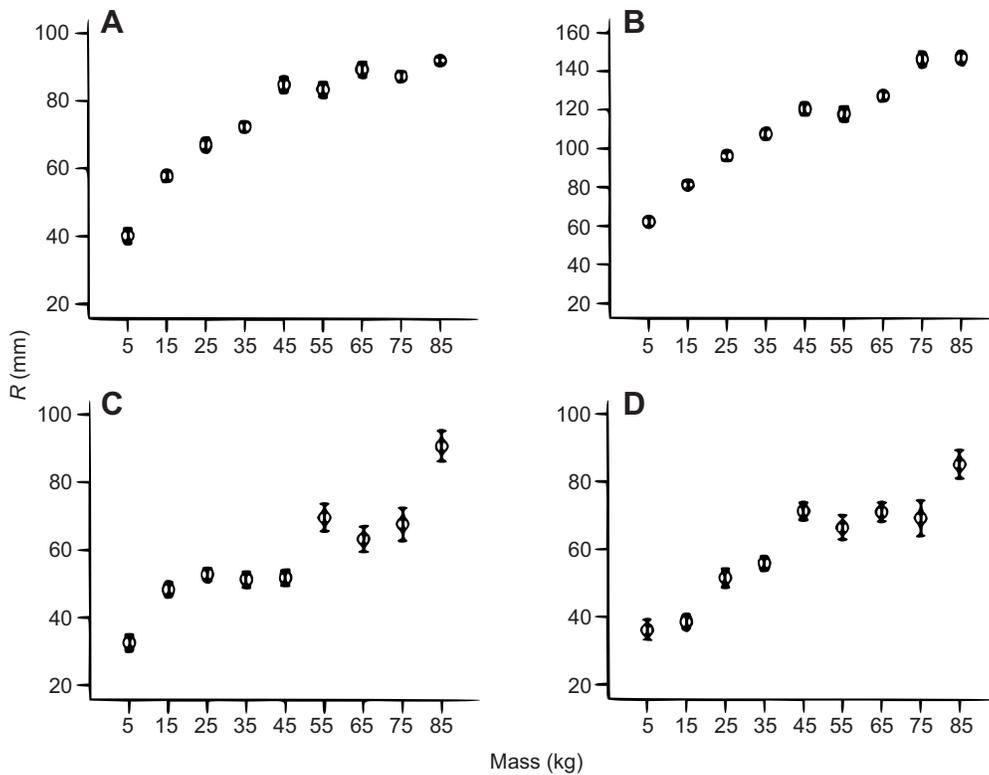
Fig. 1. Moment arm length (*R*) at peak ground reaction force for the (A) tarsometatarsophalangeal (MTP), (B) ankle, (C) knee and (D) hip joints of the left leg with increasing body mass in the ostrich, *Struthio camelus*. Error bars denote ±s.e.m. Regression coefficients of the scaling relationships are given in Table 1.

The calculation of potential energy assumed that movement of the hip marker was representative of centre of mass movement, which although not able to account for lateral roll, trunk movement and visceral movements (Pfau et al., 2006), enabled a consistent, comparable measure throughout the study. Internal energy from movement of the body segments relative to the centre of mass was calculated from the sum of linear and rotational kinetic energies (KE_{int}). Potential energy change of limb segments is small compared with the kinetic energy fluctuation during running (Minetti et al., 1999; Willems et al., 1995) and was therefore not included in the analysis. Elastic potential strain energy (EPE) stored in the limb during loading was calculated as the energy stored in a linear compressed spring, from the GRF and the leg length change, which was determined from the distance between the hip and toe markers at initial contact, the calculated sweep angle and the vertical displacement of the hip (McMahon and Cheng, 1990; Farley et al., 1993; Smith et al., 2010). This analysis models the limb as a lossless linear compression spring and as such neglects any non-linear behaviour or hysteresis within elastic structures. It also assumes the limb to be purely elastic and therefore does not take into account any contribution of negative and positive work of muscles during compression and extension of the limb, although this assumption is supported by evidence of isometric or purely concentric activation of antigravity muscles (Roberts et al., 1997; Lichtwark and Wilson, 2006; Biewener and Daley, 2007).

External work was calculated from the sum of positive increments of the mechanical energy (excluding EPE) and was normalised for body mass and stride length to give the work per kilogram per metre. Internal work was calculated from the sum of positive incremental changes in kinetic energy of each of the limb segments (KE_{int}) of the left limb relative to the estimated centre of mass, the value of which was then doubled to account for similar internal energy changes of the right limb, assuming no energy transfer between the limbs (Willems et al., 1995). Internal work was also normalised as

above and total mechanical work was then calculated from the sum of internal and external work assuming no transfer between the two.

Statistical analysis

Ostriches in the body mass range 3.9 to 108.8 kg were analysed and scaling relationships of each variable with body mass were examined by determining the relevant allometric equations through linear regression analysis of the log-transformed data, taking into account relative speed (Froude number). Significant differences between scaling relationships were ascertained by no overlap of coefficients ± standard error, because when comparing between two coefficients with similar variance, overlap of 95% confidence intervals has been shown to be insensitive, resulting in conservative interpretation (Payton et al., 2003). Data were also analysed in mass groups in 10 kg steps from 5 to 75 kg and a mass group representing >80 kg, due to limited viable trials for the largest groups (95 and 105 kg), with each dependent variable compared between groups using a univariate general linear model with group mass as a fixed factor and relative running speed, defined by Froude number, as a covariate.

RESULTS

Running speed was self-selected by the birds and therefore varied between trials with a mean relative speed, normalised to leg length, at a Froude number of 1.35±0.57 (mean ± s.d.). Mean relative speed was comparable across the size range but there was a tendency towards greater relative running speed in the smaller ostriches.

Joint moments and EMA

The moment arms increased with size at all joints (Fig. 1). Linear regression analysis of the log-transformed data yielded scaling relationships for moment arm lengths of the GRF proportional to $M^{0.39}$, $M^{0.37}$, $M^{0.33}$ and $M^{0.44}$ for the MTP joint, ankle joint, knee

Table 1. Scaling of ground reaction force moment arm length (R) and mass-specific joint moments (Jm) with increasing body mass, M, for regressions of the form: $y=a\log x+\log b$ ($y=bx^a$)

	Scaling exponent (a)	Lower 95% confidence interval	Upper 95% confidence interval	Constant (log b)	R^2
R MTP (m)	0.388	0.354	0.422	1.218	0.59
R ankle (m)	0.369	0.338	0.400	1.407	0.61
R knee (m)	0.333	0.270	0.396	1.197	0.27
R hip (m)	0.436	0.376	0.495	1.027	0.42
Jm MTP (Nm kg^{-1})	0.406	0.374	0.438	−0.498	0.63
Jm ankle (Nm kg^{-1})	0.378	0.348	0.407	−0.306	0.63
Jm knee (Nm kg^{-1})	0.285	0.246	0.324	−0.299	0.40
Jm hip (Nm kg^{-1})	0.369	0.329	0.409	−0.511	0.50

Isometry is defined by a=0.33.
MTP, tarsometatarsophalangeal.

Table 2. Effective mechanical advantage (EMA) at pelvic limb joints (mean data for all age groups) as a mean ± s.d. value through stance (EMA$_{stance}$) and at peak ground reaction force (EMA$_{peak}$)

	EMA$_{stance}$	EMA$_{peak}$
MTP	0.36±0.08	0.39±0.09
Ankle	0.41±0.13	0.29±0.06
Knee	0.43±0.19	0.65±0.29
Hip	0.86±0.40	1.08±0.38
Limb	0.51±0.10	0.59±0.11

joint and hip joint, respectively (where M is body mass; Table 1), such that scaling for all joint moment arms showed slight positive allometry with the exception of the knee joint, for which the scaling exponent was not significantly different from isometry. Joint moments were normalised to body mass to determine the mass-specific joint moment (Nm kg^{-1}) in order to compare peak joint moments through growth. Scaling of the joint moments was found to be similar to the scaling of the GRF moment arm lengths, as GRF scales in direct proportion to body mass (Smith et al., 2010) and effects of inertial and gravitational moments were negligible during stance phase, accounting for less than 1% of total joint moment. Consequently, scaling of peak joint moments proportional to $M^{0.41}$, $M^{0.38}$, $M^{0.29}$ and $M^{0.37}$ were determined for the MTP, ankle, knee and hip joints, respectively (Table 1).

EMA at the MTP and ankle joints was consistent between trials, while EMA at the knee and hip showed greater variability. EMA at each joint varied through stance phase as the weight moved over the limb, but calculations of EMA at peak GRF showed values comparable to the average EMA calculated throughout stance. No significant differences in EMA were found between mass groups for any of the joints or for the limb (Table 2). Scaling relationships determined from linear regression of the log-transformed data showed no correlation between EMA and body mass, with scaling exponents for all variables close to zero (Table 3). Peak muscle force, therefore, increased with body mass at all joints, with the greatest muscle force observed at the ankle joint, consistent with the greatest joint moments. Linear regression of the log-transformed data

showed that, on average, the peak muscle force scaled in proportion to body mass, $M^{1.0}$ (Table 4), although the knee and hip joints showed slight negative and positive allometry, respectively.

Mechanical energy

Internal work of moving the limbs relative to the body was small, with internal kinetic energy of the limb during the swing phase accounting for approximately 4.9% (±1.6%) of the total kinetic energy at the running speeds measured. The greatest component of the total mechanical energy was that of kinetic energy, due to proportionality with the square of velocity, with total kinetic energy (external and internal) accounting for 92% (±3%) of the maximum total mechanical energy. Elastic strain energy was stored in the limb during stance and was therefore out of phase with the kinetic (KE) and potential energy (PE) (Fig. 2). Contribution of the EPE to total mechanical energy (KE + PE + EPE) hence served to reduce the energy change during stance.

All components of mechanical energy increased with size at a rate greater than body mass (Fig. 3). Scaling exponents from linear regression of the log-transformed data are shown in Table 5. Total kinetic energy scaled proportional to body mass, $M^{1.42}$, whilst change in kinetic energy during a stride scaled with a slightly lower exponent of 1.37. Potential energy fluctuation through the stride increased in proportion to body mass, $M^{1.29}$. Storage of elastic energy scaled proportional to $M^{1.44}$, while peak values of maximum total mechanical energy were found to increase with body mass proportional to $M^{1.39}$ for absolute mechanical energy and proportional to $M^{1.36}$ for total mechanical energy change during the stride.

Scaling of mass-specific mechanical work per unit distance [taking into account body mass and stride length; $\propto M^{0.37}$ (Smith et al., 2010)] was found to show negligible scaling with increasing body mass as a result of a small decrease ($\propto M^{-0.08}$) in mass-specific external work and a small increase in mass-specific internal work ($\propto M^{0.05}$) per unit distance travelled. As a result of the divergent scaling of internal and external work, the proportion of total work represented by internal work of moving the limbs was found to increase with body mass proportional to $M^{0.11}$.

Table 3. Scaling exponents of EMA of the limb and limb joints with increasing mass, M, for regressions of the form: $y=a\log x+\log b$ ($y=bx^a$)

	Scaling exponent (a)	Lower 95% confidence interval	Upper 95% confidence interval	Constant (log b)	R^2
MTP	0.003	−0.029	0.036	−0.388	0.30
Ankle	0.029	−0.002	0.061	−0.558	0.06
Knee	0.058	−0.008	0.124	−0.331	0.01
Hip	−0.069	−0.129	-0.010	0.150	0.02
Limb	−0.012	−0.044	0.021	−0.217	0.01

Table 4. Scaling of peak muscle force at each joint with increasing body mass, M, for regressions of the form: $y=a\log x+\log b$ $(y=bx^a)$

	Scaling exponent (a)	Lower 95% confidence interval	Upper 95% confidence interval	Constant (log b)	R^2
MTP muscle force (N)	1.036	1.000	1.073	1.618	0.90
Ankle muscle force (N)	1.001	0.967	1.036	1.797	0.90
Knee muscle force (N)*	0.930	0.867	0.993	1.623	0.76
Hip muscle force (N)*	1.099	1.041	1.157	1.084	0.83

*Significant negative ($a<1.0$) or positive ($a>1.0$) allometry.

DISCUSSION

The way in which the GRFs act on the pelvic limb of the ostrich with increasing body mass during growth and the implications for musculoskeletal loading were investigated by considering joint moments, EMA, muscle forces and mechanical work at submaximal running speeds. Moment arms of the GRF about the joints at maximum GRF increased with increasing body mass, showing positive allometric scaling similar to that of the limb bone segments (Smith et al., 2010). Consequently, peak joint moments scaled in a similar way to the GRF moment arms and values of mass-specific joint moments for the larger mass groups were in the region of published data for humans of similar mass (75.0±5.0 kg) during preferred speed running (Biewener et al., 2004). Because muscle moment arm length has been shown to vary with joint angle for some pelvic limb muscles (Smith et al., 2007), mean moment arm was used in the calculation of EMA in order to be consistent with previous studies (Biewener, 1989; Biewener, 2005; Biewener et al., 2004), and this measurement showed the least variation between individuals. Although it was necessary to estimate the scaling of muscle moment arms, based on the scaling of the limb bones, the effect of this estimate is likely to be small because of maintenance of body posture and hence alignment of the limb bones. Although muscle moment arms may also be influenced by other geometric changes, exponents would not be expected to differ substantially from our estimate, and certainly not sufficiently to enable EMA to scale as between species. It cannot, however, be disregarded that alternative scaling of muscle moment arm might contribute to accommodation of increased joint moments. The greatest EMA was observed at the hip joint, where the muscle moment arms are relatively large and the GRF aligns quite closely with the joint,

resulting in a moment arm ratio close to one. The lowest EMA was that of the ankle, where the cranial positioning of the point of force under the foot maintains the relatively large GRF moment arm, resulting in the large joint moment and muscle force requirements observed at this joint. Anatomical data illustrate the suitability of the musculoskeletal design for this role at the ankle joint, with the ankle extensors having the highest capacity for force generation of all the functional groups and gastrocnemius muscle moment arm length greatest when the limb is extended during stance (Smith et al., 2006; Smith et al., 2007).

EMA of each of the pelvic limb joints, and hence of the limb, was independent of body size during growth, confirming that no significant changes in limb posture, or the way in which the forces align with the limb, are found with increasing mass during growth of ostriches. This is significantly different from the relationship observed with increasing size between quadrupedal mammalian species (Fig. 4), where it has been shown that relative straightening of the limb and the resulting realignment of the GRF accounts for an increase in EMA proportional to $M^{0.27}$ (Biewener, 1989; Biewener, 1990). However, it has previously been suggested that ontogenetic scaling does indeed differ from interspecific scaling in mammalian species, based on measures of anatomical mechanical advantage as an estimate of EMA, which have shown negative allometric scaling (Carrier, 1983; Young, 2005). These findings differ from the ontogenetic scaling observed here for the ostrich, which may be due to the fact that these studies did not consider limb posture or substrate reaction forces, or may be related to inherent functional differences between the species studied. Scaling of EMA in ostriches results in the smallest bird groups having a greater than predicted EMA, and relatively straighter limb posture, for their size, and the largest bird groups having a lower EMA than other mammalian species of comparable size. Ostriches and running humans (Biewener et al., 2004) of similar mass (75±5 kg), however, appear to have comparable EMA of 0.52.

The observed deviation from mammalian scaling for EMA was also found to result in average muscle force scaling in direct proportion to body mass, $M^{1.0}$, whereas between species postural changes and the increase in EMA with size enables a relative reduction in the muscle forces required, such that this has been found to scale proportional to $M^{0.74}$–$M^{0.80}$ (Alexander et al., 1981; Biewener, 1989). However, because the smallest birds benefit from a relatively high EMA, it would be expected that the relative muscle force would be smaller in these younger birds for their size. The increase in relative muscle force with body mass would then result in peak muscle forces proportionally larger in the mature birds than in mammals of similar size. This would be particularly evident for the high force muscles at the ankle and MTP joints, which both scaled directly proportional to $M^{1.0}$. These variations from scaling trends observed between mammal species also prevent the alterations in loading that allow maintenance of safety factors for bone, muscle and tendon stresses across a large size range of different species (Biewener, 1989; Biewener, 1990) and, consequently, it would be
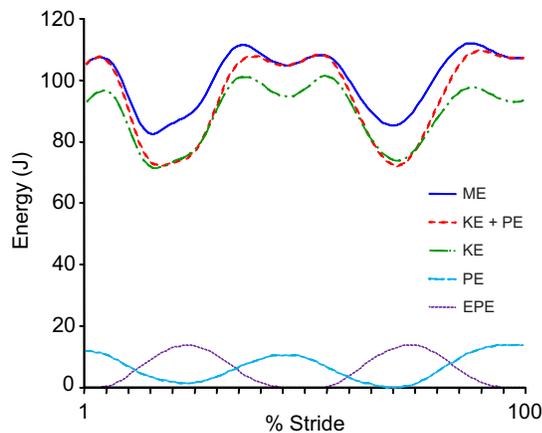

Fig. 2. Mechanical energy changes throughout a stride. Lines indicate total mechanical energy including elastic energy storage (ME), total energy of the centre of mass defined by the sum of kinetic and potential energies (KE + PE), total kinetic energy (KE), potential energy (PE) and elastic potential (strain) energy (EPE). Data are means for a 25 kg ostrich.
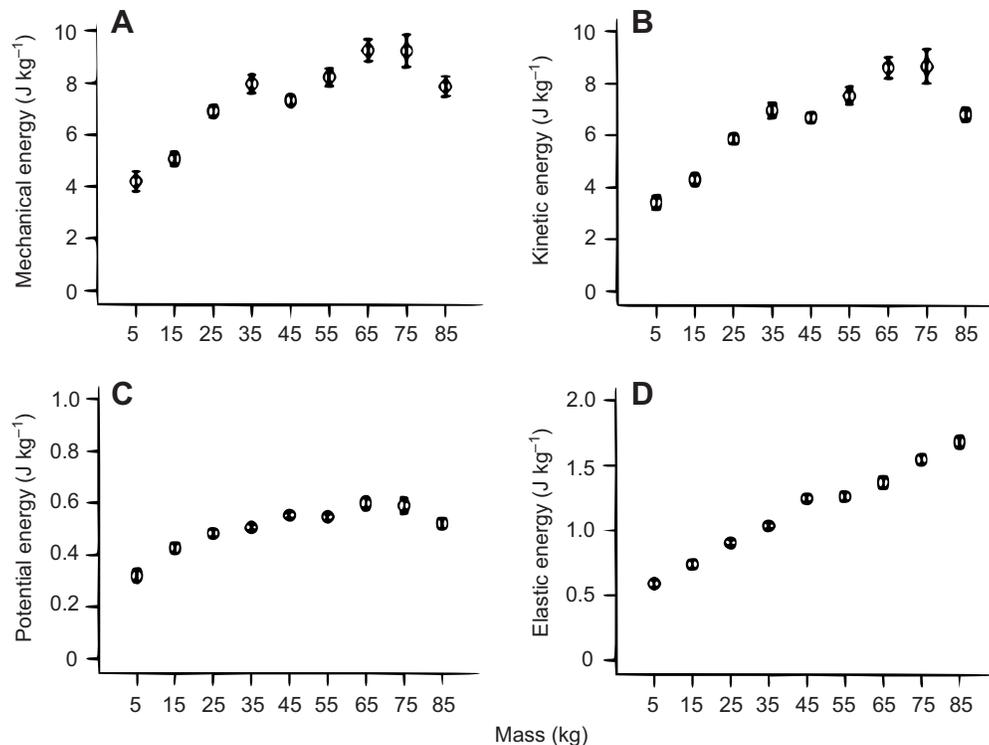
Fig. 3. Relationship between ostrich body mass and (A) peak total mechanical energy, (B) peak kinetic energy, (C) peak potential energy and (D) peak elastic potential energy per unit mass. Error bars denote ±s.e.m. Regression coefficients of the scaling relationships are given in Table 5.

expected that forces applied, relative to body weight, increase during growth. The only joint to show slight negative allometry for muscle force was the knee, although this joint also showed the greatest variation in calculated values (Fig. 1) and offers the greatest risk of error in determination of joint centre due to extensive soft tissue. In contrast, the hip showed slight positive allometry, which suggests even greater relative increases in force requirements at this joint. The relatively high EMA of very young chicks, reducing forces in bones and muscles, suggests that the smallest chicks may have an increased safety factor. This is supported by the finding that bone strain increases during ontogeny in both emus and goats (Main and Biewener, 2004; Main and Biewener, 2007), resulting in a decreased safety factor with increasing body mass. The specific mechanical responses within the tissues are complex, however, with evidence of variation in mechanical properties of tendon during ontogeny (Yamamoto et al., 2004) in comparison with consistent tendon mechanical properties across adult species of different sizes (Pollock and Shadwick, 1994a), which will have implications for the actual stress within the tissues.

The scaling of muscle forces would also be expected to apply to the tendon forces, resulting in relatively higher load in the tendons of larger birds through growth. If cross-sectional area of tendons were to scale as predicted by geometric similarity, proportional to $M^{0.67}$ (Pollock and Shadwick, 1994b; Bullimore and Burn, 2005), or as other limb dimensions during growth, proportional to $M^{0.80}$ (Biewener, 2005), then tendon stress would be predicted to increase with body mass with a scaling exponent between 0.33 and 0.20, respectively. However, analysis of ostrich tendon data across a limited size range (53–105 kg), as reported by Smith et al. (Smith et al., 2006), suggests negative allometric scaling exponents of 0.55 for the combined cross-sectional area of the digital flexor tendons and 0.54 for the cross-sectional area of the large gastrocnemius tendon, implying that such estimates may be conservative, although these data must be interpreted with caution as a more substantial data set is needed. Based on the more conservative estimates of published data, because elastic energy storage per unit volume is proportional to the square of tendon stress, this would also predict an increase in elastic energy storage in the limb during growth, with a scaling exponent between 0.67 and 0.4 for elastic energy stored per unit volume and between 1.67 and 1.4 for elastic energy stored per stride. These scaling estimates for elastic energy storage could also be further increased if slight positive allometry of tendon length

Table 5. Scaling exponents of peak values of mechanical energy components, energy changes during a stride and work per unit distance with increasing body mass, M, for linear regressions of the form: $y = a\log x + \log b$ ($y = bx^a$)

|	Scaling exponent (a)	Lower 95% confidence interval	Upper 95% confidence interval	Constant (log b)	R^2
Total mechanical energy (J)	1.393	1.371	1.416	−0.124	0.98
Kinetic energy (J)	1.415	1.394	1.436	−0.253	0.98
Internal energy (J)	1.329	1.289	1.370	−1.244	0.95
Potential energy (J)	1.293	1.262	1.324	−0.659	0.95
Elastic potential energy (J)	1.440	1.404	1.476	−0.686	0.94
Change in mechanical energy (J)	1.357	1.326	1.388	−0.364	0.96
Change in kinetic energy (J)	1.365	1.328	1.401	−0.521	0.94
Total work (J kg^{-1} m^{-1})	−0.023	−0.051	0.006	0.379	0.15
External work (J kg^{-1} m^{-1})	−0.080	−0.121	−0.039	0.350	0.15
Internal work (J kg^{-1} m^{-1})	0.050	0.010	0.090	−0.408	0.28
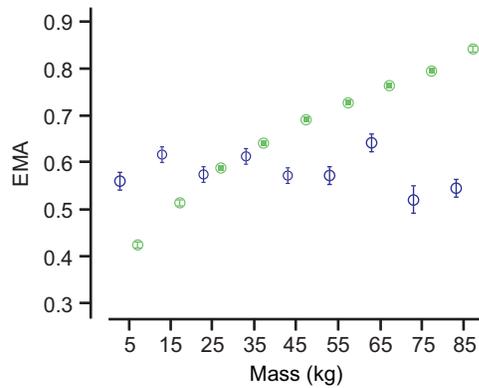
Fig. 4. Measured effective mechanical advantage (EMA) with increasing body mass during growth of ostriches (blue circles) compared with EMA predicted from body mass using the published mammalian relationship from species of different sizes, EMA=0.244$M^{0.274}$ (green squares) (Biewener, 1989; Biewener, 1990). Data are means ± s.e.m.

occurs, consistent with segment length scaling (Smith et al., 2010). Such relationships would indicate that larger ostriches would be able to store proportionally more energy in their tendons than smaller ostriches, as has been suggested between species (Alexander et al., 1981; Bennett and Taylor, 1995; Reilly et al., 2007), and the derived exponents propose a greater increase of elastic storage with mass than the capacity found in quadrupedal mammals [$\propto M^{1.28}$ (Pollock and Shadwick, 1994b)]. Indeed, the preliminary data reported above demonstrate that the proposed theoretical scaling of elastic energy storage per stride could indeed be possible, and in fact exceeded ($\propto M^{1.90}$), for the defined muscle tendon units, which are well designed for this function (Smith et al., 2006; Rubenson et al., 2007). The absolute capacity for energy storage could also be affected by an increase in aponeurosis due to the negative allometry of muscle fibre lengths, which are proportionately shorter in larger animals, that has been identified between species (Pollock and Shadwick, 1994b), assuming this holds true throughout ontogeny in the ostrich. However, all of these estimates assume total transmission of muscle forces to tendons and purely elastic energy storage and return, neglecting response in the toe region, any viscous damping losses or non-linearity of the tendon. In addition, the increased loads applied to the tendons due to the scaling of joint moments is a direct result of increased forces in the muscles, for which it is likely there would be a metabolic cost, reducing the possible energetic benefits of elastic return. There must also be caution in interpretation of elastic storage capacity because of the

unknown ontogenetic material property changes in this species and differences between tendons of specific functional muscles (Allen et al., 2010; Pollock and Shadwick, 1994b; Yamamoto et al., 2004).

In the ostrich, patterns of energy changes during a stride were similar to those observed in other species during symmetrical running gaits (Minetti et al., 1999; Robilliard, 2006). Minimum mechanical energy occurred at midstance, due to minimum potential and kinetic energy. This occurred at the same time as peak limb force and minimum leg length, so elastic potential energy effectively reduces mechanical energy loss through storage and return in the limb during stance (Fig. 2). Mechanical energy changes during a stride were found to scale with a slightly lower exponent than both kinetic and total mechanical energy, and these values are more meaningful in terms of the cost of redirecting and reaccelerating the body during a stride. Kinetic energy changes were found to account for a large proportion of the total energy changes (82.2±6.7%) and the relative decrease of kinetic energy change with increasing body mass (compared with total kinetic energy) resulted in the slight negative scaling of mass-specific external work (per unit distance). Data for the largest bird group suggest a decrease in mechanical energy components and, consequently, work, but this is likely due to the smaller sample size within this group, a more limited data set and reduced bird compliance with the study procedures, resulting in a tendency for slower speed trials and hence a reduction in the kinetic and potential energy. Values of external work for the larger birds (1.69±0.54 J kg^{-1} m^{-1}) were similar to published values for adult ostriches running at low speeds on a treadmill (Rubenson et al., 2004). Slight positive scaling of mass-specific internal work resulted in estimated total work being independent of body mass, with a mean value of 2.7±0.4 J kg^{-1} m^{-1}. However, the differences in scaling of internal and external work resulted in a larger proportion of this total work required to move the limbs relative to the centre of mass in larger birds. Because internal work becomes a greater proportion of total work with increasing speed (Willems et al., 1995), this would be expected to become more significant at higher speeds.

Calculated storage of elastic potential energy, as estimated from the spring limb loading response, increased at a significantly greater rate than the changes in mechanical energy with increasing body mass ($\propto M^{1.44}$). The scaling was within the range suggested by the increase in tendon force previously discussed from scaling of forces and dimensions ($M^{1.40}$–$M^{1.67}$), although closer to the lower value estimated for tendon cross-sectional area scaling with positive allometry, a trend that appears conservative according to provisional data. Estimated values for elastic potential energy increased from peak values of 4.7 to 155.1 J per step from the smallest to the largest
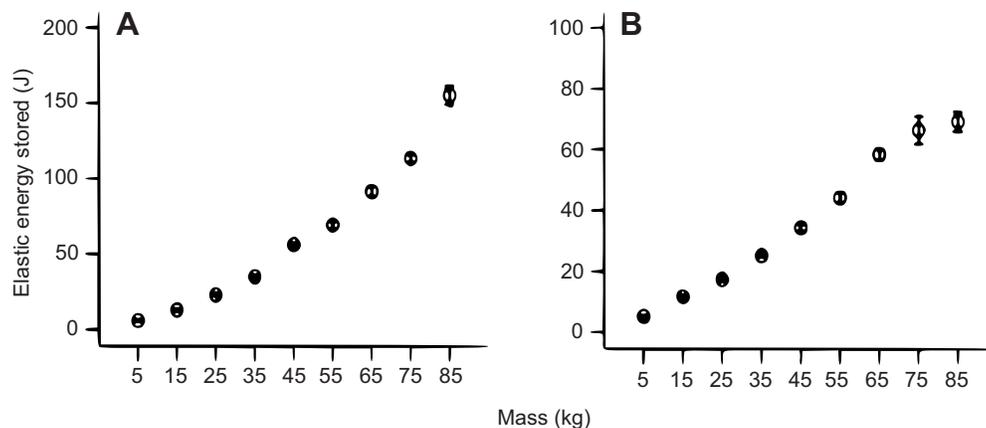

Fig. 5. Maximum elastic energy storage in the ostrich limb during a stride estimated from (A) the integration of instantaneous ground reaction force and geometric leg length and (B) the assumption of the loaded limb as a lossless compression spring.

mass group (Fig. 5A). The value for the 45 kg group was 56 J per step, close to Alexander et al.'s (Alexander et al., 1979) estimate of 60 J for a 41.5 kg ostrich, although it should be noted that this estimate was based on higher speed running (estimated between 12 and 17 m s^{-1}). Estimates of elastic energy storage in the tendons of the digital flexors and gastrocnemius tendon, based on anatomical data (Smith et al., 2006), Young's modulus of tendon of 1.2 GPa (Benedict et al., 1968; Matthews and Ellis, 1968) as used by Alexander et al. (Alexander et al., 1979), and estimates of peak muscle force calculated for the derived joint moments indicate a maximum elastic energy storage of 37 J per step for a 60 kg ostrich at the speeds we studied, comparable with values reported by Rubenson et al. (Rubenson et al., 2011). This is low, however, compared with the value of 69 J for ostriches of this mass, calculated from limb force and instantaneous leg length change. It also assumes no muscle length change, such that contraction occurs to deliver spring-like force length properties in the leg, which although energetically sensible could be challenging for movement control. It is also assumed that all muscle force is transmitted to the tendons with no associated hysteretic losses and neglects the non-linear behaviour demonstrated by the toe region of tendon at low stress. However, capacity for elastic energy storage in the limb is not limited to the long distal tendons and there could be significant capacity for elastic energy storage in proximal tendinous structures, ligaments and muscle aponeurosis (Ettema and Huijing, 1989; Lichtwark and Wilson, 2005; Roberts et al., 1997). Rubenson et al. (Rubenson et al., 2011), in an investigation of economy of running ostriches, identified that the majority of elastic energy storage occurs in the MTP joint, with limited storage in more proximal structures. They did, however, acknowledge that this finding was through analysis of low-speed running (Froude number=0.93) and that different mechanisms might apply at increased running speeds. Examination of Fig. 2 would indicate that storage of even more EPE could be beneficial in reducing the fluctuation of mechanical energy, which may reduce the cost of transport, as has been observed with increasing size between species (Heglund et al., 1982; Kram and Taylor, 1990) and through growth in humans (Frost et al., 2002).

Measured GRFs are consistent with those observed in other species running at similar Froude numbers (Alexander and Jayes, 1983); however, leg length change (ΔL), measured from the distance between the DIP marker and the hip marker through the stride, has a maximum value greater than that estimated by the spring mass model, despite similar scaling with increasing body mass. If ΔL is used to estimate the elastic energy storage in the limb, the scaling relationship with size is similar to that previously calculated ($\propto M^{1.42}$), but absolute values of elastic energy storage in the limb are approximately half of those previously calculated (Fig. 5B), increasing from peak values of 2.5 to 72.9 J from the smallest to the largest mass groups, with a peak value of 44.6 J for an ostrich in the region of 60 kg, close to that calculated to be achievable by elastic energy storage in the digital flexor and gastrocnemius tendons alone for an ostrich of this size. The simplified ΔL measured by the spring mass model is less than the physical length change of the limb, likely because of the non-linear spring behaviour of the limb, which would indicate that the spring mass model does not accurately estimate potential for elastic energy storage in the limb. Therefore, the simple spring mass model may well overestimate the magnitude of elastic energy stored in the limb, as it ignores the potential for muscular contractile element length change contribution during limb compression and extension. This effect is apparent in Fig. 2 because the spring mass model assumes a lossless system so all the reduction in mechanical energy would be expected to be stored and returned in the spring leg. However, because of consistent application of methods across the size range in the present study and the lack of postural variation during stance within increasing size, the scaling trend observed during growth can be considered to be valid.

The proposed increase in elastic energy storage suggested by both the spring mass model and scaling of loads applied to elastic elements confirms an increased contribution of elastic energy storage to locomotor economy with body mass, consistent with the idea of more efficient limb function with increasing size (Alexander, 2005). It appears that elastic energy storage scales at a rate greater than body mass ($M^{1.0}$) and distance travelled during a stride ($M^{0.37}$); therefore, the elastic energy stored per kilogram per metre travelled should also increase with size ($\propto M^{0.07}$, based on conservative estimates). However, mass-specific total work per unit distance (work required to move a unit body mass a unit distance) was confirmed to be independent of body mass (Heglund et al., 1982; Kram and Taylor, 1990), showing potential for a small, but significant increase in locomotor economy due to greater elastic energy storage with increasing body size. Such findings are consistent with Kram and Taylor's (Kram and Taylor, 1990) prediction of metabolic cost of transport decreasing with increasing stance time, as stance time through ontogeny in the ostrich increases proportional to $M^{0.12}$ (Smith et al., 2010). The increased economy with body mass suggested by the estimates of energy storage here, however, is less than the proposed decrease in metabolic cost calculated from contact time, perhaps indicative of an underestimate or alternative contributing factors.

Our findings disagree with those predicted for increasing body mass from scaling of locomotor cost and potential for energy storage, where a decrease in elastic storage with size was determined to be proportional to $M^{-0.19}$ (Bullimore and Burn, 2005). The improved mechanics of the pelvic limb through ontogeny seems ideal for a cursorial species such as the ostrich. Young ostriches have the benefit of parental protection, for the most part negating the need to escape fast-running predators while within the group of chicks (Cooper et al., 2010). The rapid growth rate observed (Smith et al., 2010) coincides with the need for juvenile ostriches to start to fend for themselves in small groups and travel greater distances, allowing adaptation of the limb to improve locomotor performance as they reach the increased athletic demands of adulthood.

Conclusions

During growth, despite many biomechanical parameters scaling close to dynamic similarity, morphological changes that permit maintenance of safety factors within the limb are not observed. As a result, EMA of the limb does not increase with size and therefore the muscle forces required to balance external moments must also increase proportional to body mass, resulting in greater load applied to bones, muscles and tendons. Despite the likely reduction in safety factors of the tissues through growth, there is an apparent benefit in permission of greater storage and return of elastic energy. The trends observed predict an increase in scaling of elastic energy storage per stride with increasing size, which, when normalised for body mass and stride length, predicts an increase in capacity for elastic energy storage in the limb while the mass-specific mechanical work per unit distance is independent of size. The contribution of elastic energy storage to locomotor economy was therefore found to increase during growth in the ostrich. The metabolic cost of transport decreases with size (Frost et al., 2002; Heglund et al., 1982; Kram and Taylor, 1990) and it appears that there is an increased reliance on elastic energy storage in larger cursorial animals through ontogeny.

REFERENCES

Alexander, R. M. (2005). Models and the scaling of energy costs for locomotion. *J. Exp. Biol.* **208**, 1645-1652.

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

Alexander, R. M., Jayes, A. S., Maloiy, G. M. and Wathuta, E. M. (1977). Allometry of the limb bones of mammals from shrews (*Sorex*) to elephant (*Loxodonta*). *J. Zool.* **183**, 291-300.

Alexander, R. M., Maloiy, G. M. O., Njau, R. and Jayes, A. S. (1979). Mechanics of running in the ostrich (*Struthio camelus*). *J. Zool.* **187**, 169-178.

Alexander, R. M., Jayes, A. S., Maloiy, G. M. O. and Wathuta, E. M. (1981). Allometry of the leg muscles of mammals. *J. Zool.* **194**, 539-552.

Allen, V., Elsey, R. M., Jones, N., Wright, J. and Hutchinson, J. R. (2010). Functional specialization and ontogenetic scaling of limb anatomy in *Alligator mississippiensis. J. Anat.* **216**, 423-445.

Benedict, J. V., Walker, L. B. and Harris, E. H. (1968). Stress-strain characteristics and tensile strength of unembalmed human tendon. *J. Biomech.* **1**, 53-63.

Bennett, M. B. and Taylor, G. C. (1995). Scaling of elastic strain energy in kangaroos and the benefits of being big. *Nature* **378**, 56-59.

Biewener, A. A. (1983). Allometry of quadrupedal locomotion: the scaling of duty factor, bone curvature and limb orientation to body size. *J. Exp. Biol.* **105**, 147-171.

Biewener, A. A. (1989). Scaling body support in mammals: limb posture and muscle mechanics. *Science* **245**, 45-48.

Biewener, A. A. (1990). Biomechanics of mammalian terrestrial locomotion. *Science* **250**, 1097-1103.

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

Biewener, A. A. (2005). Biomechanical consequences of scaling. *J. Exp. Biol.* **208**, 1665-1676.

Biewener, A. A. and Daley, M. A. (2007). Unsteady locomotion: integrating muscle function with whole body dynamics and neuromuscular control. *J. Exp. Biol.* **210**, 2949-2960.

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

Biewener, A. A., Farley, C. T., Roberts, T. J. and Temaner, M. (2004). Muscle mechanical advantage of human walking and running: implications for energy cost. *J. Appl. Physiol.* **97**, 2266-2274.

Blickhan, R. (1989). The spring-mass model for running and hopping. *J. Biomech.* **22**, 1217-1227.

Bullimore, S. R. and Burn, J. F. (2004). Distorting limb design for dynamically similar locomotion. *Proc. Biol. Sci.* **271**, 285-289.

Bullimore, S. R. and Burn, J. F. (2005). Scaling of elastic energy storage in mammalian limb tendons: do small mammals really lose out? *Biol. Lett.* **1**, 57-59.

Bullimore, S. R. and Burn, J. F. (2006). Dynamically similar locomotion in horses. *J. Exp. Biol.* **209**, 455-465.

Carrier, D. R. (1983). Postnatal ontogeny of the musculo-skeletal system in the black-tailed jack rabbit (*Lepus californicus*). *J. Zool.* **201**, 27-55.

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

Cooper, R. G., Horbańczuk, J. O., Villegas-Vizcaíno, R., Kennou Sebei, S., Faki Mohammed, A. E. and Mahrose, K. M. A. (2010). Wild ostrich (*Struthio camelus*) ecology and physiology. *Trop. Anim. Health Prod.* **42**, 363-373.

Ettema, G. J. C. and Huijing, P. A. (1989). Properties of the tendinous structures and series elastic component of EDL muscle-tendon complex of the rat. *J. Biomech.* **22**, 1209-1215.

Farley, C. T., Glasheen, J. and McMahon, T. A. (1993). Running springs: speed and animal size. *J. Exp. Biol.* **185**, 71-86.

Fedak, M. A., Heglund, N. C. and Taylor, C. R. (1982). Energetics and mechanics of terrestrial locomotion. II. Kinetic energy changes of the limbs and body as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 23-40.

Frost, G., Bar-Or, O., Dowling, J. and Dyson, K. (2002). Explaining differences in the metabolic cost and efficiency of treadmill locomotion in children. *J. Sports Sci.* **20**, 451-461.

Heglund, N. C., Fedak, M. A., Taylor, C. R. and Cavagna, G. A. (1982). 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.

Kram, R. and Taylor, C. R. (1990). Energetics of running: a new perspective. *Nature* **346**, 265-267.

Lichtwark, G. A. and Wilson, A. M. (2005). Effects of series elasticity and activation conditions on muscle power output and efficiency. *J. Exp. Biol.* **208**, 2845-2853.

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.

Main, R. P. and Biewener, A. A. (2004). Ontogenetic patterns of limb loading, *in vivo* bone strains and growth in the goat radius. *J. Exp. Biol.* **207**, 2577-2588.

Main, R. P. and Biewener, A. A. (2007). Skeletal strain patterns and growth in the emu hindlimb during ontogeny. *J. Exp. Biol.* **210**, 2676-2690.

Maloiy, G. M., Alexander, R. M., Njau, R. and Jayes, A. S. (1979). Allometry of the legs of running birds. *J. Zool.* **187**, 161-167.

Matthews, L. S. and Ellis, D. (1968). Viscoelastic properties of cat tendon: effects of time after death and preservation by freezing. *J. Biomech.* **1**, 65-71.

McMahon, T. A. and Cheng, G. C. (1990). The mechanics of running: how does stiffness couple with speed? *J. Biomech.* **23 Suppl. 1**, 65-78.

Minetti, A. E., Ardigò, L. P., Reinach, E. and Saibene, F. (1999). The relationship between mechanical work and energy expenditure of locomotion in horses. *J. Exp. Biol.* **202**, 2329-2338.

Olmos, M., Casinos, A. and Cubo, J. (1996). Limb allometry in birds. *Ann. Sci. Nat. Zool.* **17**, 39-49.

Payton, M. E., Greenstone, M. H. and Schenker, N. (2003). Overlapping confidence intervals or standard error intervals: what do they mean in terms of statistical significance? *J. Insect Sci.* **3**, 34.

Pfau, T., Witte, T. H. and Wilson, A. M. (2006). Centre of mass movement and mechanical energy fluctuation during gallop locomotion in the thoroughbred racehorse. *J. Exp. Biol.* **209**, 3742-3757.

Pollock, C. M. and Shadwick, R. E. (1994a). Relationship between body mass and biomechanical properties of limb tendons in adult mammals. *Am. J. Physiol.* **266**, R1016-R1021.

Pollock, C. M. and Shadwick, R. E. (1994b). Allometry of muscle, tendon, and elastic energy storage capacity in mammals. *Am. J. Physiol.* **266**, R1022-R1031.

Reilly, S. M., McElroy, E. J. and Biknevicius, A. R. (2007). Posture, gait and the ecological relevance of locomotor costs and energy-saving mechanisms in tetrapods. *Zoology* **110**, 271-289.

Ren, L., Miller, C. E., Lair, R. and Hutchinson, J. R. (2010). Integration of biomechanical compliance, leverage, and power in elephant limbs. *Proc. Natl. Acad. Sci. USA* **107**, 7078-7082.

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.

Robilliard, J. J. (2006). *Mechanical Basis of Locomotion with Spring-like Legs.* PhD dissertation, The Royal Veterinary College, University of London, London, UK.

Rubenson, J., Heliams, D., Lloyd, D. and Fournier, P. (2004). Gait selection in the ostrich: mechanical and metabolic characteristics of walking and running with and without an aerial phase. *Proc. R. Soc. Lond. B* **271**, 1091-1099.

Rubenson, J., Lloyd, D. G., Besier, T. F., Heliams, D. B. and Fournier, P. A. (2007). Running in ostriches (Struthio camelus): three-dimensional joint axes alignment and joint kinematics. *J. Exp. Biol.* **210**, 2548-2562.

Rubenson, J., Lloyd, D. G., Heliams, D. B., Besier, T. F. and Fournier, P. A. (2011). Adaptations for economical bipedal running: the effect of limb structure on three-dimensional joint mechanics. *J. R. Soc. Interface* **8**, 740-755.

Schmidt-Nielsen, K. (1975). Scaling in biology: the consequences of size. *J. Exp. Zool.* **194**, 287-307.

Shadwick, R. E. (1990). Elastic energy storage in tendons: mechanical differences related to function and age. *J. Appl. Physiol.* **68**, 1033-1040.

Smith, N. C., Wilson, A. M., Jespers, K. J. and Payne, R. C. (2006). Muscle architecture and functional anatomy of the pelvic limb of the ostrich (*Struthio camelus*). *J. Anat.* **209**, 765-779.

Smith, N. C., Payne, R. C., Jespers, K. J. and Wilson, A. M. (2007). Muscle moment arms of pelvic limb muscles of the ostrich (*Struthio camelus*). *J. Anat.* **211**, 313-324.

Smith, N. C., Jespers, K. J. and Wilson, A. M. (2010). Ontogenetic scaling of locomotor kinetics and kinematics of the ostrich (*Struthio camelus*). *J. Exp. Biol.* **213**, 1347-1355.

Taylor, C. R. (1994) Relating mechanics and energetic during exercise. In *Comparative Vertebrate Exercise Physiology: Unifying Physiological Principles*, Vol. 38A (ed. J. H. Jones), pp. 181-215. San Diego, CA: Academic Press.

Willems, P. A., Cavagna, G. A. and Heglund, N. C. (1995). External, internal and total work in human locomotion. *J. Exp. Biol.* **198**, 379-393.

Yamamoto, E., Iwanaga, W., Yamamoto, N. and Hayashi, K. (2004). Growth-related changes in the mechanical properties of collagen fascicles from rabbit patellar tendons. *Biorheology* **41**, 1-11.

Young, J. W. (2005). Ontogeny of muscle mechanical advantage in capuchin monkeys (*Cebus albifrons* and *Cebus apella*). *J. Zool.* **267**, 351-362.