Biomechanical Modeling and Sensitivity Analysis of Bipedal Running Ability. I. Extant Taxa

John R. Hutchinson*

Biomechanical Engineering Division, Stanford University, Stanford, California 94305-4038

ABSTRACT I used a simple mathematical model of the inverse dynamics of locomotion to estimate the minimum muscle masses required to maintain quasi-static equilibrium about the four main limb joints at mid-stance of fast running. Models of 10 extant taxa (a human, a kangaroo, two lizards, an alligator, and five birds) were analyzed in various bipedal poses to examine how anatomy, size, limb orientation, and other model parameters influence running ability. I examined how the muscle masses required for fast running compare to the muscle masses that are actually able to exert moments about the hip, knee, ankle, and toe joints, to see how support ability varies across the limb. I discuss the assumptions and limitations of the models, using sensitivity analysis to see how widely the results differed with feasible parameter input values. Even with a wide range of input values, the models validated the analysis procedure. Animals that are known to run bipedally were calculated as able to preserve quasi-static equilibrium about their hindlimb joints at mid-stance, whereas non-bipedal runners (iguanas and alligators) were recognized as having too little muscle mass to run quickly in bipedal poses. Thus, this modeling approach should be reliable for reconstructing running ability in extinct bipeds such as nonavian dinosaurs. The models also elucidated how key features are important for bipedal running capacity, such as limb orientation, muscle moment arms, muscle fascicle lengths, and body size. None of the animals modeled had extensor muscle masses acting about any one joint that were 7% or more of their body mass, which provides a reasonable limit for how much muscle mass is normally apportioned within a limb to act about a particular joint. The models consistently showed that a key biomechanical limit on running ability is the capacity of ankle extensors to generate sufficiently large joint moments. Additionally, the analysis reveals how large ratite birds remain excellent runners despite their larger size; they have apomorphically large extensor muscles with relatively high effective mechanical advantage. Finally, I reconstructed the evolution of running ability in the clade Reptilia, showing that the ancestors of extant birds likely were quite capable runners, even though they had already reduced key hip extensors such as M. caudofemoralis longus. J. Morphol. 262:421–440, 2004.

KEY WORDS: biomechanics; biped; bird; computer model; locomotion; maximum speed; running; size

What limits maximum running velocity? Although velocity is ultimately the product of stride length and stride frequency, other factors determine those two parameters in a very complex fashion (Koechling and Raibert, 1988; McGeer, 1990; Gatesy and Biewener, 1991; Gatesy, 1999a; Irschick and Jayne, 1999; Roberts and Scales, 2002). A mathematical model developed by Hutchinson and Garcia (2002) used inverse dynamics to estimate the minimum active muscle mass required to balance the moments (torques, or rotational forces) incurred about the joints of a single leg during fast running in *Tyrannosaurus* and other animals. The study by Hutchinson and Garcia (2002) was not sufficiently complex to model most other dynamic parameters that are thought to influence maximum running performance, such as minimum swing time (Pratt, 2000), minimum ground contact time (Farley, 1997; Weyand et al., 2000), maximum leg stiffness (McMahon et al., 1987; McMahon and Cheng, 1990; Farley et al., 1993; Farley, 1997; Ahlborn and Blake, 2002), maximum muscle contraction velocity and fiber type (Gans and DeVree, 1987; Rome et al., 1988; Williams et al., 1997; Medler, 2002), metabolic power output (Jones and Lindstedt, 1993; Weyand et al., 1999), musculoskeletal mechanical power output (Hill, 1950; Ingen Schenau et al., 1994; but see Farley, 1997; Weyand et al., 2000; Roberts and Scales, 2002), bone strength (Biewener, 1983, 1989, 1990; Christiansen, 1998; Iriarte-Díaz, 2002), or limb proportions (Coombs, 1978; Christiansen, 2002). However, muscle-tendon units must produce the forces that are needed for an activity (such as running at maximum speed) as a minimum requirement—if the forces are too low, then the activity will either be impossible to generate or the limb will collapse. The mechanical limit posed by the extensor muscle mass is complementary to the study by Weyand et al. (2000; also Chang et al., 2000), who showed that maximum ground reaction force provides a primary mechanical limit to running speed, as ground reac-

Contract grant sponsor: National Science Foundation.

*Current address and correspondence to: J. R. Hutchinson, Structure and Motion Laboratory, The Royal Veterinary College, University of London, Hatfield, Herts AL9 7TA, UK. E-mail: jrhutch@rvc.ac.uk

Published online in
Wiley InterScience (www.interscience.wiley.com)
DOI: 10.1002/jmor.10241

tion force must mainly be produced by muscles in moving animals. Other factors might limit running speed even further, but this approach provides a logical baseline for examining the limits of running ability. In particular, it is of interest how various biomechanical parameters such as limb orientation, muscle moment arms and fascicle lengths, segment dimensions, and size pose mechanical limits on running ability, why the limits on running ability differ in animals, and how those limits evolved.

This study is the first part of a two-part study that follows up on the analysis begun by Hutchinson and Garcia (2002). My aims are to explain the modeling procedure and its assumptions and limitations, discuss how the models reveal some of the biomechanical limits on running speed in extant taxa and validate the analysis, and reconstruct how running evolved on the line to crown group birds. Like Hutchinson and Garcia (2002), the modeling method is essentially identical to that used by Roberts et al. (1998, fig. 1 therein), and the quasi-static equilibrium requirement used in the analysis is a standard assumption in many other experimental and theoretical studies (e.g., Clark and Alexander, 1975; Alexander et al., 1979; Biewener, 1989; Roberts, 2001). Unlike Hutchinson and Garcia (2002), I focus here on how different joints (as opposed to joints averaged across a whole limb) might enable or limit fast running. The limb of a runner cannot support a more extreme activity than its weakest joint can sustain. Might proximal muscles, which are typically larger than distal muscles, be more able to sustain fast running than muscles that act about more distal joints, and hence might distal joint extensor muscles impose the most severe limits on supporting the body during fast running? Such a "division of labor" from proximal (work modulation) to distal (force generation and elastic rebound) limb muscles is an important focus of recent experimental analyses (e.g., Biewener and Roberts, 2000; Roberts, 2001; Biewener et al., 2004). I examine this question with models of 10 extant taxa, whereas Hutchinson and Garcia (2002) only briefly examined three extant taxa. Importantly, Hutchinson and Garcia (2002) did not model birds larger than a chicken, whereas this study examines how some larger birds (e.g., emus and ostriches) are able to remain competent runners despite their size. A second study (Hutchinson, 2004) will examine extinct taxa, especially theropod (carnivorous) dinosaurs such as *Tyrannosaurus*, to check the conclusions of Hutchinson and Garcia (2002) and investigate how support capability might have varied across the limb of extinct bipeds, especially larger ones.

MATERIALS AND METHODS

I used 10 biomechanical models (analyzed similarly to Hutchinson and Garcia, 2002, except where noted below) of various extant animals in bipedal poses to gauge how the extensor muscle masses needed to support the body on one hindlimb differed across the individual limb joints, and how those muscle masses compared with the actual masses present in the intact animal. Not all of these taxa were habitual bipeds; two quadrupeds (*Alligator, Iguana*) that do not run bipedally were included for negative validation, because my analysis should show that they cannot run fast bipedally. A human was modeled because humans are bipedal and medium in body size, sharing some striking similarities to and differences from birds, the only other habitually striding bipeds (Gatesy and Biewener, 1991; Hutchinson and Gatesy, 2000). Additionally, human locomotor mechanics and anatomy have been well studied, so abundant experimental data are available to verify the validity of my model results. A juvenile red kangaroo (*Macropus rufus*) was likewise modeled because many studies on macropodid anatomy and biomechanics have been published (e.g., Cavagna et al., 1977; Farley et al., 1993; Bennett and Taylor, 1995; Biewener et al., 2004), including sufficient data to model one specimen (Alexander and Vernon, 1975). This allowed comparison of the mechanics of a hopping biped to striding bipeds.

I chose to study *Iguana, Basiliscus*, and *Alligator* because the hindlimb morphology of iguanians and crocodylians is generally similar to most other nonavian Reptilia (e.g., Hutchinson, 2002), and thus these three taxa were expected to provide reasonable examples of how limb design in conventional reptiles relates to bipedal running performance. In addition, iguanians and crocodylians are successively closer extant outgroups to theropod dinosaurs, allowing phylogenetic comparison with extinct bipeds (Hutchinson, 2004). Finally, although *Basiliscus* and some *Iguana* individuals are known to run bipedally, iguanians and crocodylians (and presumably many of their extinct saurian relatives) are less specialized for a habitually bipedal, running lifestyle than other taxa I modeled, such as birds. Therefore, these models were also a baseline comparison that might identify features important even for intermittent bipedalism. The *Iguana iguana* specimen was an adult, which are able to run bipedally (Blob and Biewener, 2001), albeit relatively slowly and less frequently than smaller juveniles or species (Snyder, 1962; pers. obs.), whereas the adult *Basiliscus vittatus* specimen (California Academy of Sciences specimen CAS 73529) was presumably a capable bipedal runner, like most individuals of that species (Snyder, 1949). The juvenile *Alligator mississippiensis* specimen I dissected was presumably not a fast bipedal runner, like other extant crocodylians.

The five bird taxa (tinamou [*Eudromia elegans*], chicken [*Gallus gallus*], turkey [*Dromaius novaehollandiae*], emu [*Meleagris gallopavo*], and ostrich [*Struthio camelus*]) span a range of size, morphology, phylogeny, and ecology, but are all relatively rapid bipedal runners. Because birds are the descendants of theropod dinosaurs (Gauthier, 1986), the models allowed me to compare "typical" running birds to models of their extinct relatives (Hutchinson, 2004). Data available on locomotor function in other birds (Clark and Alexander, 1975; Gatesy and Biewener, 1991; Gatesy, 1999a; Reilly, 2000; Roberts, 2001) could be compared with my analysis to check the validity of the model. Additionally, because the five taxa are relatively basal in the bird crown clade Neornithes (or Aves; Cracraft and Clarke, 2001), I used them to assess the ancestral running mechanics of extant birds for comparison to other bipeds.

MatLab Models

Musculoskeletal data were collected to build a 2D model of a biped standing on its right leg, in order to calculate the positions of the centers of mass of the body segments in different poses. I entered these data into a computer model to construct a free-body diagram (e.g., Biewener and Full, 1992), explained in "Biomechanical model of one-legged stance," below. I used MatLab software (MathWorks, Natick, MA; v. 6.5, 2002), assisted by Mariano Garcia, who wrote the original code for the MatLab model. This model estimated the moments acting about the hindlimb joints during standing on the right leg. These moments were later used

TABLE 1. Dimensions of biomechanical models used for this analysis

Dimension	Non-birds					Birds				
Masses (kg)	*Homo*	*Macropus*	*Basiliscus*	*Iguana*	*Alligator*	*Eudromia*	*Gallus*	*Meleagris*	*Dromaius*	*Struthio*
m_{body}	71.0	6.6	0.191	4.04	5.91	0.406	2.89	3.70	27.2	65.3
thigh	8.81	0.812	0.0150	0.213	0.130	0.0183	0.223	0.189	3.54	6.50
shank	3.51	0.297	0.0055	0.0636	0.0663	0.0141	0.181	0.135	3.19	4.40
metatarsus	1.20	0.0726	0.0024	0.0185	0.0386	0.00349	0.0426	0.0250	0.471	0.861
foot	0.205	----	0.0021	0.0122	0.0518	0.00171	0.0221	0.0172	0.222	0.483
trunk	57.3	2.12	0.166	3.73	5.62	0.368	2.42	3.33	19.8	53.1
Lengths (m)										
thigh	0.401	0.297	0.049	0.088	0.081	0.051	0.085	0.084	0.180	0.205
shank	0.430	0.584	0.053	0.089	0.087	0.083	0.13	0.15	0.408	0.465
metatarsus	0.163	0.323	0.027	0.056	0.050	0.051	0.085	0.12	0.276	0.416
foot	0.0750	0.150	0.037	0.072	0.053	0.034	0.089	0.074	0.149	0.237
trunk	0.846	1.3	0.65	1.4	1.4	0.24	0.40	0.44	0.770	0.710
CM position (m)										
thigh	0.229	0.225	0.030	0.035	0.049	0.028	0.045	0.048	0.14	0.095
shank	0.244	0.360	0.027	0.042	0.042	0.044	0.075	0.10	0.31	0.29
metatarsus	0.100	0.0122	0.018	0.022	0.024	0.016	0.044	0.061	0.090	0.21
trunk	0.402	0.157	0.039	0.082	0.12	0.042	0.070	0.044	0.080	0.087

Masses, lengths, and center of mass (CM) positions (expressed along the long axis of the bone, from the distal end in the limb segments or cranially from the hip joint in the trunk segment) for each segment incorporated, from dissections of a single individual per taxon.

(see Muscle Masses, below) to calculate how large the muscles needed to be to exert those moments during fast running, and then compared to how large the muscles actually were in the animals I studied. This method is almost identical to that used by Roberts et al. (1998, fig. 1 therein). The MatLab data collection and modeling consisted of three steps.

Body segment dimensions. I measured the lengths of the body segments ("trunk" [body from snout to tail tip]; thigh [femur]; shank [tibiotarsus]; metatarsus, and foot [along the third digit]). The joint centers of rotation were estimated by dissection and radiography following Alexander (1977) and Biewener and Full (1992). All data are shown in Table 1. I measured the masses of dissected body segments with an electronic balance and estimated the locations of the segmental centers of mass (CM) along the segment longitudinal axes by balancing (Alexander et al., 1979; Maloiy et al., 1979). The left leg mass was included in the trunk mass, so the final value of the trunk segment mass that I used in the MatLab model was equal to m_{body} minus the mass of the right limb, not both limbs, as the left leg still would require support during single-legged stance. For simplicity, the trunk CM position was calculated with the left leg detached; the mass of the left leg was added to the trunk mass without changing the trunk CM position (which would have required additional assumptions about the joint angles of the left leg during the swing phase, and had little effect on the trunk CM position anyway because of the proximity of the left leg to the CM). The CM position of each segment was only expressed along the x-axis (longitudinal; or craniocaudal for the trunk). Displacing the trunk CM ventrally would only have increased the net moments about the limb joints slightly if the pelvis was pitched upward.

Limb orientation. The joint angles entered (Fig. 1) were the sagittal plane angles about the joint centers, including: pelvic pitch (angle of the trunk segment to the horizontal), hip (angle between the trunk and thigh segment axes on the cranial side), knee (angle between the thigh and shank axes on the caudal side), ankle (angle between the shank and metatarsal axes on the

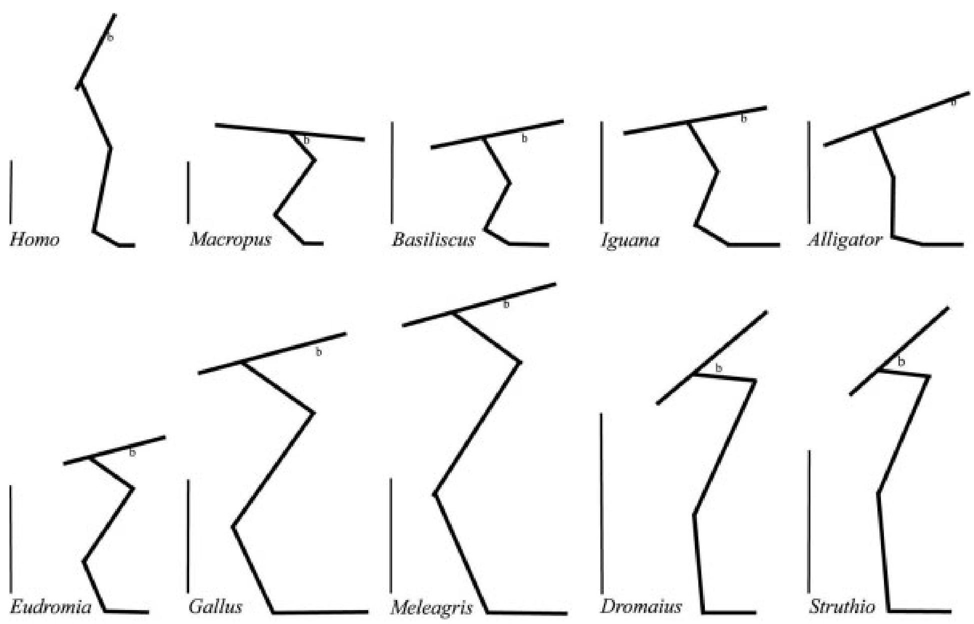

Fig. 1. Images of MatLab models showing the initial poses used in the biomechanical analysis (models numbered "_1"). All are images from the right side of the body in lateral view, showing single-limb support. Depicted trunk lengths had no influence on the analysis. "b" indicates the location of the entire body CM. The vertical scale bars are 0.5 m for the largest bipeds (*Homo, Macropus, Dromaius, Struthio*) and 0.1 m for the others. See Table 4 for the exact joint angles used.

cranial side), and toe (angle between the metatarsal and foot axes on the caudal side). See, for example, Gatesy (1991, 1999a), Hutchinson and Gatesy (2000), and Hutchinson and Garcia (2002) for how these angles are defined. The foot segment was constrained to be completely fixed to the ground, oriented horizontally. Once the joint angles were entered, the model calculated the position of the total body center of mass (CM; trunk segment plus all limb segments) in (x,y) coordinates. All models depicted the right side of the body in lateral view, so the positive x-direction was cranial; positive y-direction was dorsal. I used limb joint angles for mid-stance of running.

The human model used anatomical parameters from Anderson (1999). Kinematic data came from Novacheck (1998), including the mid-stance joint angles from sprinting at 3.9 m s^{-1}, which are similar to angles from "elite sprinting" at 9.0 m s^{-1}, for which insufficient kinematic data are available in Novacheck (1998). The kangaroo model used data from Alexander and Vernon (1975) on anatomical parameters (scaled to their "Kangaroo A" from other specimens) and mid-stance joint angles for a kangaroo hopping at 6.2 m s^{-1}. Unlike the other models, this model considered hopping, with both limbs in mid-stance and hence only one-half body mass supported on the right limb.

Alligator is not known to stand, walk, or run bipedally. To represent *Alligator* as a biped in the model for the purposes of this analysis, I entered a set of joint angles that: 1) my manipulations of fresh material showed the joints would allow; 2) kept the whole body CM over the foot; and 3) were extended so as to align the ground reaction force with the limb, lowering the moment arms of the ground reaction force (Biewener, 1989; Carrier et al., 1994; Chang et al., 2000; Roberts and Scales, 2002); a conservative and realistic assumption. Using published joint angles for *Alligator* from Gatesy (1991), Reilly and Elias (1998), or Blob and Biewener (2001) was deemed inappropriate because these joint angles are from slowly moving quadrupedal alligators. When I tried entering these angles into the MatLab model, the CM was far cranial to the foot, and hence maintaining static equilibrium would be impossible in those poses.

Similar joint angles (Fig. 1) were input for *Iguana* and *Basiliscus* (based on Snyder, 1949, fig. 1 therein, sequence 10; also Hsieh, 2003). Unfortunately, rigorously measured kinematics for the latter two species during terrestrial bipedalism remain unavailable, so estimation was necessary. This assumption was later tested with sensitivity analysis of joint angles. Entering published joint angles for much smaller bipedal lizards with different body segment proportions (Irschick and Jayne, 1999) resulted in unstable models, with the CM far cranial to the foot. For both lizards, the trunk segment was treated as one rigid segment, whereas extant lizards can pitch their trunk and tail at different angles (Snyder, 1949; Irschick and Jayne, 1999). More complex models could test how much this would change the body CM position.

The joint angles for the *Gallus* and *Meleagris* models were taken from Gatesy's (1999a) data for *Numida*, using the approximate angles of the joints at mid-stance of running at 3.0 m s^{-1}. Unfortunately, accurate joint angle data for birds running at very high speeds are unavailable. *Numida, Meleagris*, and *Gallus* are closely related as galliform birds which all have grossly similar locomotor morphology and kinematics (Muir et al., 1996; Reilly, 2000; Roberts, 2001). No kinematic data are published for the tinamou *Eudromia*, so I entered the same joint angles as for the galliform birds. Joint angles for the *Struthio* model and *Dromaius* model were taken from Alexander et al. (1979), at ~12 m s^{-1}. This assumes similar joint angles in both taxa, which are closely related and similar in locomotor morphology (Gatesy and Biewener, 1991). Because some uncertainty exists for all limb orientations modeled, I conduct sensitivity analyses of these limb orientations later.

Biomechanical model of one-legged stance. I first had the MatLab model checked if the limb orientation could be maintained in static equilibrium (whole body CM over the foot segment), assuming sufficient muscular capacity. I then used a free-body diagram (e.g., Nordin and Frankel, 1989) in the model to calculate the moments about each joint. Figure 2 shows how these moments were computed. My procedures were equivalent to calculating the moments of the ground reaction force (GRF) as well as the gravitational moments of the body segments (sensu Nordin and Frankel, 1989; Biewener and Full, 1992; localized at the segmental CM). However, instead of proceeding from the GRF at the foot up to the hip joint (as in Biewener, 1989, and similar studies), neglecting the gravitational moments of body segments, the model calculated moments from the hip down to the toe (e.g., Nordin and Frankel, 1989). Either approach is appropriate; I merely found this approach to be computationally simpler in the model. This is mainly because the trunk CM position was known, whereas I did not initially assume a precise location of the center of pressure at the foot (i.e., where the GRF would be acting through); required in a "toe up" free body diagram. Instead, I generally (but not strictly) favored poses that placed the whole body CM over or almost over a line perpendicular to the middle of the foot segment, as appropriate for mid-stance of locomotion. Hence for simplicity, I avoided potential complications caused by incorporating dorsi/plantarflexion of the interphalangeal joints (e.g., Alexander et al., 1979), which would shift the relative center of pressure and is certainly worthy of investigation in more complex models. Inertial dynamic effects from motion of the body segments were excluded, so the analysis was quasi-static rather than fully dynamic. During quiet standing, this is certainly appropriate, and I discuss later how this quasi-static analysis can be extrapolated to mid-stance of locomotion.

A glossary of symbols used in the following equations is in Appendix E. As Figure 2 shows, the net muscle moment about any joint (M_{musc}) required to maintain quasi-static equilibrium in the model was equal to the summed weight of all body segments above that joint (F_{func}) times the moment arm of that summed weight (R; which is the perpendicular distance from the CM of all segments above the joint to the joint center):

$$M_{musc} = F_{func} \cdot R \tag{1}$$

The M_{musc} was calculated for all four limb joints of each animal in each pose modeled. The value of the F_{func} depended on the activity being executed by the modeled animal (during quiet one-legged standing it would be equal to body weight), whereas the value of R depended on the limb orientation at that instant: if the CM location was far cranial or caudal to the joint center, R (and hence M_{musc}) would be large. Therefore, the limb orientation entered into the model was very important, because a more crouched limb orientation would generally increase R about each joint (Biewener, 1983, 1989, 1990; Hutchinson and Garcia, 2002). The MatLab model only calculated the F_{func} magnitude incurred by one supportive leg during quiet standing, which was equal to body weight (W). Body weight is the body mass (m_{body}) times the acceleration due to gravity (g), so the M_{musc} in the MatLab model was derived from Eq. 1 as:

$$M_{musc} = m_{body} \cdot g \cdot R \tag{2}$$

This M_{musc} value was the only output parameter taken directly from the MatLab model for use in the calculation of muscle masses in the next section. The sign of M_{musc} (and all other moments used in this study) follows the "right-hand rule" convention of mechanics: a moment is positive if it acts to rotate a joint counterclockwise (in sagittal view of the right side of the body) and negative if it incurs clockwise rotation. M_{musc} was a negative (extensor) moment about all joints except the knee, acting to decrease the joint angles. About the knee joint (see Fig. 2), the orientation of M_{musc} depended on the relative position of the CM, and hence depended on the limb orientation. If the CM was caudal to the knee (e.g., when the limb joints were strongly flexed), M_{musc} was an extensor moment (but its sign was positive). The converse was true if the CM was cranial to the knee (e.g., if the limb joints were strongly extended). In the next section, I explain how the muscle mass required to produce these moments was estimated.

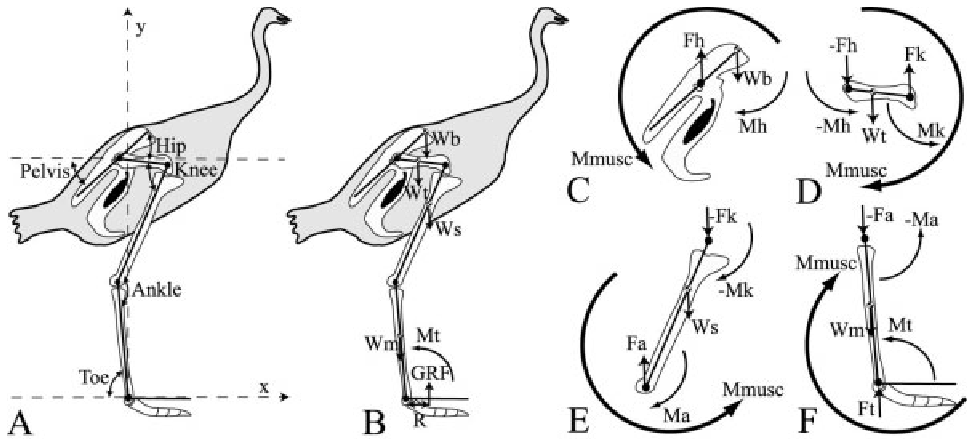

Fig. 2. Schematic explanation of the MatLab model procedure to obtain the value of M_{musc} for this analysis (also see Hutchinson and Garcia, 2002). The skeletal illustration of an ostrich was modified from Paul (1988), showing the model in right lateral view as in Figure 1. The precise pitch of the pelvis and trunk at mid-stance in fast-runing ostriches is not well known; it was varied from this pitched-up position to a more horizontal orientation. **A:** The joint angles for the pelvis, hip, knee, ankle, and toe are shown. The pelvis angle was simply the part of the hip angle relative to the horizontal and hence was redundant. The toe joint was the origin of the (x,y)-coordinate space, and the foot was simplified to a single line. **B:** Segment weights for the trunk, thigh, shank, and metatarsus segment are shown (Wb, Wt, Ws, and Wm, respectively). Notice that because the segment weights are behind the trunk CM, the whole body CM will be displaced to lie caudal to the trunk CM. The ground reaction force (GRF) at the foot (passing through the whole body CM) and its moment arm about the toe (R) were used to calculate the toe joint moment (Mt) that digital flexor muscles needed to support (see **F**). **C–F:** The net extensor muscle moments (M_{musc}) about the limb joints were calculated from proximal to distal joints in the MatLab model. These moments were later multiplied by a factor G to simulate the larger moments incurred during running vs. unipodal standing. The free body diagrams shown are for calculating M_{musc} about the hip (**C**), knee (**D**), ankle (**E**), and toe (**F**) joints. See, for example, Nordin and Frankel (1989) for how they were constructed. Factors shown that were used to calculate the M_{musc} values (which were then used to calculate minimum muscle masses, m_i) are the joint contact forces (Fh, Fk, Fa, Ft), segment weights (as in **B**), and joint moments (from gravity, opposed by extensor muscles) (Mh, Mk, Ma, Mt).

Muscle Masses

The next step in my analysis was calculating how much muscle mass would be required to produce the M_{musc} calculated in the MatLab model. As a conservative approach to find the minimum muscle mass required to produce M_{musc}, I calculated the maximum moment that extensor muscles could generate and equated that with M_{musc}. The maximum moment that the muscles acting about a given joint can exert during isometric contraction (M_{max}) is equal to the maximum isometric force (F_{max}) that these muscles can exert times their moment arm (r). In my equations, I represented all of the muscles acting about a joint as one muscle with a mean value of F_{max} and r. This involved the conventional assumption that active muscles typically operate at similar stresses, exerting forces in proportion to their physiological cross-sectional areas (Taylor, 1985; Perry et al., 1988; Biewener, 1989, 1990; Thorpe et al., 1998; Roberts, 2001):

$$M_{max} = F_{max} \cdot r \quad (3)$$

It is important to recognize that the moment arm (r) of the muscles acting about a given joint depends on the limb orientation, becoming relatively larger as the limb orientation becomes more crouched and the line of action of the muscles is moved further from the joint center (Biewener, 1983, 1989, 1990; Carrier et al., 1994). This was especially the case for the hip and knee muscles, many of which clearly had large and variable moment arms about these joints, but was less critical for the ankle and toe joints, which might have had less variable muscle moment arms because most of the muscles act almost parallel to the long axis of the bones.

The maximum isometric force (F_{max}) of the muscles acting about a given joint is the product of the physiological cross-sectional area (A_{phys}; Calow and Alexander, 1973; Alexander and Vernon, 1975; Gans and DeVree, 1987) of the muscles and the force per unit area, or isometric stress within the muscles (σ):

$$F_{max} = A_{phys} \cdot \sigma \quad (4)$$

Gans and DeVree (1987; also see Biewener and Full, 1992) explained how A_{phys} is equal to the volume (V) of the muscle times the cosine of the mean pennation angle of the muscle fascicles (θ), divided by the mean length of the muscle fascicles (L; which occasionally consist of more than one fiber but typically can be assumed to be equivalent to fiber length; Zajac, 1989). The derivation of this formula is explained in more detail in Appendix A.

$$A_{phys} = (V \cdot \cos\theta)/L \quad (5)$$

Equations 3–5 were combined to solve for the maximum moment that a certain volume of muscle could generate about a joint. The volume of a muscle is equal to the muscle mass (m_{musc}) divided by the muscle density (d), so the maximum moment that a given mass of muscle could generate about a joint is:

$$M_{max} = (m_{musc} \cdot \cos\theta \cdot \sigma \cdot r)/(L \cdot d) \quad (6)$$

Next, I assumed that the net muscle moment (M_{musc}) required at any instant was equal to a factor of relative recruitment of the muscle mass (c; ranging from 0 to 1, for 0 to 100% activation of the muscle fibers) times the maximum moment that the muscles could exert (M_{max}). I then solved for M_{musc}:

$$M_{musc} = (m_{musc} \cdot c \cdot \cos\theta \cdot \sigma \cdot r)/(L \cdot d) \quad (7)$$

During any particular activity, the m_{musc} acting about any one joint is a certain fraction of body mass (m_{body}), which was expressed as a percentage, termed m_i. The factor m_i is important because it standardizes comparisons of muscle mass among taxa of different body masses. I then solved for m_i, the percentage of body mass that would be required as actively contracting muscles

TABLE 2. Values of G (as units of peak vertical ground reaction force per unit body weight) at mid-stance for various animals from experimental studies

Animal	Ref.	m_{body} (kg)	G	Velocity ($m\ s^{-1}$)	Gait
Bennett's wallaby	1	10.5	2.47	2.7	hop
bobwhite quail	2	0.203	1.10	0.3	walk
bobwhite quail	2	0.176	2.40	1.75	run
chipmunk	3	0.09	4.02	2.4	gallop
greyhound	4	27.8	4.54	7.6	gallop
horse	5	132	2.44	4.1	trot
human	6	71	1.58	4.0	Groucho run
human	7	81	3.87	6.5	run
Japanese quail	8	0.095	1.50	0.5	run
macaque	9	3.6	3.89	5.8	gallop
painted quail	2	0.043	2.40	1.0	run
red kangaroo	1	6.6	2.93	6.2	hop
rhea	9	22.5	1.33	1.0	walk
rhea	9	22.5	2.67	4.7	run
springhare	9	2.5	3.00	4.3	hop
turkey	9	7	2.86	3.8	run
white sheep	9	60	2.92	3.5	gallop

Slower speeds are included for comparison. For bipeds, values are for a single hindlimb. For quadrupeds, values are combined for one forelimb and hindlimb. Note that most studies excluded body segment gravitational forces and focused only on the vertical GRF. Blank spaces indicate unreported data. References in the "Ref" column are: 1, Alexander and Vernon (1975); 2, Heglund et al. (1982); 3, Biewener (1983); 4, Bryant et al. (1987); 5, Farley and Taylor (1991); 6, McMahon et al. (1987); 7, Arampatzis et al. (1999); 8, Clark and Alexander (1975); and 9, Cavagna et al. (1977).

to maintain static equilibrium about any joint *i*, in a particular limb orientation:

$$m_i = (100 \cdot M_{musc} \cdot L \cdot d)/(\cos\theta \cdot \sigma \cdot c \cdot r \cdot m_{body}) \quad (8)$$

To estimate the M_{musc} required about the joints at mid-stance of running, when only one limb is supporting the body and the peak GRF is much greater than body weight (Table 2; Alexander, 1977; Taylor, 1985; Biewener, 1983, 1989, 1990), I introduced a "relative activity factor," G, which represented the magnitude of the F_{func} (and M_{musc}) with respect to body weight (W) for one-legged stance during any activity (Appendix B). Factor G is equivalent to the GRF multiplier of body weight commonly cited in dynamic studies of locomotion. It could be varied to represent changes of the F_{func} (Eq. 1) during different activities as compared with one-legged standing. I reformulated Eq. 8 to express M_{musc} as a function of body mass (Eq. 2). This procedure further aids comparisons among taxa of different sizes. It also removes the potentially confounding effects of m_{body} from the analysis. Body mass is an unknown parameter for extinct taxa and thus it is desirable to remove it (Hutchinson, 2004). No matter what m_{body} value I entered for a particular animal, the m_i was calculated the same:

$$m_i = (100 \cdot G \cdot g \cdot R \cdot L \cdot d)/(\cos\theta \cdot \sigma \cdot c \cdot r) \quad (9)$$

To review, in Eq. 9, G is the "relative activity factor" from the MatLab model, g is the acceleration due to gravity (in $m\ s^{-2}$), R is the moment arm of the F_{func} (in meters), L is the mean muscle fascicle length (in meters), d is the muscle density (in $kg\ m^{-3}$), cos θ is the cosine of the mean angle of muscle fascicle pennation, σ is the maximum isometric stress (force/area; in $N\ m^{-2}$) of the muscles, c is the fraction of maximum exertion by the muscles, and r is the mean moment arm of the muscles (in meters).

Finally, I substituted some parameters from Eq. 9 with constant values. My quasi-static analysis assumed that static equilibrium must be maintained at mid-stance, when the vertical velocity of the center of mass is zero and the body is accelerating upward, even during running (Blickhan, 1989). Hence, the "relative activity factor" G for mid-stance of fast running was increased relative to quiet one-legged standing. At mid-stance of fast running, the GRF (which is proportional to F_{func}) often reaches or exceeds a magnitude of 2.5 times the body weight supported by one leg (Table 2), in a wide size range of animals (Alexander, 1985; Taylor, 1985; Blickhan and Full, 1993). Therefore, I assumed that G = 2.5 in my analysis. Much higher values of G have been observed in animals that are accelerating quickly (e.g., Clark and Alexander, 1975; Thorpe et al., 1998; Roberts and Scales, 2002), such as during jumping or sprinting starts, and values of G > 2.5 are not uncommon in fast-moving animals (Table 2). Because hopping animals have much higher G values despite having double limb support (e.g., Cavagna et al., 1977; Perry et al., 1988; Farley et al., 1993), I raised the value of G to 3.0 for the *Macropus* model, better matching the experimental data from Alexander and Vernon (1975).

I set the value of $g = 9.81\ m\ s^{-2}$. Vertebrate striated muscle has a relatively constant density, so $d = 1.06 \times 10^3\ kg\ m^{-3}$ (Mendez and Keys, 1960; Hutchinson, unpubl. data from bird muscles). I set $\sigma = 3.0 \times 10^5\ N\ m^{-2}$, the maximum isometric stress commonly measured in vertebrate striated muscle (Calow and Alexander, 1973; Johnston, 1985, 1991; Zajac, 1989; Biewener and Full, 1992; Roberts, 2001), which is independent of size in vertebrates (Medler, 2002). To represent the value of m_i during maximum muscular exertion (100% of all muscle fibers contracting), the value of c = 1. This was a conservative assumption that estimated the *minimum* m_i required to support rapid running with an F_{func} of 2.5 times m_{body} on one leg. Entering these values into Eq. 9 allowed me to formulate the final governing equation for estimating m_i:

$$m_i = (R \cdot L \cdot d)/(\cos\theta \cdot r \cdot 1.767\ m) \quad (10)$$

Thus, in my initial analysis the muscle mass (m_i) required to be acting about any joint *i* in order to support the body on one leg at mid-stance of fast running (or on two legs during hopping in the kangaroo) depended only on three linear (R, L, and r) and one angular (θ) variables (Tables 3, 4). The exact value of body mass did not affect the results, although at least the linear parameters would be tightly correlated with body mass and size.

To minimize computational complexity, I used some simplifying assumptions. As explained above (Eq. 1; Fig. 2), the F_{func} moment arm R was derived from the MatLab model as a component of M_{musc}. The values for L, θ, and r were entered as mean values for all active muscles acting about the joint (Table 3), weighted by the A_{phys} of the individual muscles (as in Biewener, 1989; Thorpe et al., 1998; Roberts, 2001). Appendix C explains which muscles were included in the model as data from my dissections or the literature. As mentioned above, the value of r about each joint depended on the limb orientation entered for the MatLab model, whereas the other parameters were constant for a particular animal. The values of r in Table 3 were measured at roughly the same joint angles as shown in Figure 1. Appendix D outlines the major assumptions of the model. In general, my assumptions were conservative in that they predisposed the calculations to estimate the *minimum* muscle mass needed to sustain fast running. This biases the analysis to rule out fewer activities, which suits the exclusionary goal of the models: to show what activities would be impossible for a musculoskeletal system to attain. I calculated m_i values for the hip (m_h), knee (m_k), ankle (m_a), and toe (m_t) joints. The latter abbreviations thus refer to the muscle masses required to be actively contracting about the respective joints in order to support fast running. The *actual* muscle masses that could act about each joint *i* (m_I) in the extant taxa, which I present in the Results, use capitalized subscripts, not lower case (see Appendix E).

TABLE 3. Muscle dimensions and initial results from the biomechanical analysis of the models from Table 1 (for joint angles, see Table 4)

Non-birds					Birds				
	Homo					*Eudromia*			
	hip	knee	ankle	toe		hip	knee	ankle	toe
L (m)	0.113	0.091	0.049	0.040	L (m)	0.050	0.023	0.020	0.016
θ (°)	0	5	20	20	θ (°)	0	20	20	20
r (m)	0.039	0.040	0.037	0.016	r (m)	0.014	0.0065	0.0034	0.0025
R (m)	0.17	0.012	0.10	n/a	R (m)	0.041	0.022	0.045	(0.023)
m_I (% m_{body})	5.2	3.7	1.7	(0.66)	m_I (% m_{body})	1.4	1.4	1.8	(0.84)
m_i (% m_{body})	3.5	0.20	1.2	n/a	m_i (% m_{body})	1.1	0.10	2.4	(1.4)
m_I/m_i	1.5	19	1.4	n/a	m_I/m_i	1.3	14	0.75*	(0.60*)
	Macropus					*Gallus*			
	hip	knee	ankle	toe		hip	knee	ankle	toe
L (m)	0.060	0.018	0.049	n/aG	L (m)	0.085	0.051	0.031	0.0026
θ (°)	5	20	30	n/a	θ (°)	0	25	20	20
r (m)	0.031	0.018	0.015	n/a	r (m)	0.038	0.026	0.0090	0.0039
R (m)	0.16	0.045	0.13	n/a	R (m)	0.067	0.0049	0.068	(0.031)
m_I (% m_{body})	6.1	3.4	1.7	n/a	m_I (% m_{body})	3.7	3.1	3.5	(1.5)
m_i (% m_{body})	1.0	0.40	0.80	n/a	m_i (% m_{body})	1.1	0.10	2.1	(1.9)
m_I/m_i	6.2	8.5	2.1	n/a	m_I/m_i	3.4	31	1.7	(0.79*)
	Basiliscus					*Meleagris*			
	hip	knee	ankle	toe	*Meleagris*	hip	knee	ankle	toe
L (m)	0.018	0.017	0.0070	0.0040	L (m)	0.045	0.040	0.030	0.029
θ (°)	15	20	25	20	θ (°)	0	20	25	30
r (m)	0.0060	0.0030	0.0040	0.0020	r (m)	0.033	0.010	0.0080	(0.0060)
R (m)	0.039	0.013	0.034	0.0085	R (m)	0.043	0.029	0.061	(0.0080)
m_I (% m_{body})	4.0	1.8	0.98	1.2	m_I (% m_{body})	2.1	1.6	2.4	(1.1)
m_i (% m_{body})	1.0	n/a	0.60	0.20	m_i (% m_{body})	0.50	1.0	2.1	(0.38)
m_I/m_i	4.0	n/a	1.6	6.0	m_I/m_i	4.2	1.6	1.1	(2.9)
	Iguana					*Dromaius*			
	hip	knee	ankle	toe		hip	knee	ankle	toe
L (m)	0.036	0.038	0.030	0.030	L (m)	0.164	0.078	0.057	0.039
θ (°)	10	10	25	25	θ (°)	5	15	25	30
r (m)	0.016	0.0060	0.0080	0.0030	r (m)	0.061	0.046	0.024	0.018
R (m)	0.081	0.036	0.070	0.019	R (m)	0.062	0.14	0.070	(0.037)
m_I (% m_{body})	1.8	0.58	0.71	0.73	m_I (% m_{body})	4.9	4.2	6.4	(2.7)
m_i (% m_{body})	1.5	n/a	2.7	2.2	m_i (% m_{body})	1.1	1.6	1.4	(0.78)
m_I/m_i	1.2	n/a	0.26*	0.33*	m_I/m_i	4.5	2.6	4.6	(3.5)
	Alligator					*Struthio*			
	hip	knee	ankle	toe		hip	knee	ankle	toe
L (m)	0.092	0.039	0.037	0.019	L (m)	0.135	0.097	0.064	0.042
θ (°)	20	15	20	20	θ (°)	10	15	25	25
r (m)	0.019	0.013	0.017	0.0050	r (m)	0.10	0.080	0.036	0.030
R (m)	0.12	0.085	0.084	0.032	R (m)	0.067	0.15	0.075	(0.031)
m_I (% m_{body})	2.6	0.48	0.36	0.24	m_I (% m_{body})	4.6	3.6	4.0	(1.5)
m_i (% m_{body})	4.9	n/a	1.7	1.1	m_i (% m_{body})	0.60	1.3	1.2	(0.41)
m_I/m_i	0.53*	n/a	0.21*	0.22*	m_I/m_i	7.7	2.8	3.3	(3.7)

For each model and each joint (hip/knee/ankle/toe), fascicle length (L), pennation angle (θ; rounded to the nearest 5° because of the vagaries of accurately measuring pennation angles; Zajac, 1989), extensor muscle moment arm (r), moment arm of F_{func} (R), actual extensor mass about each joint (m_I), extensor mass required (m_i), and ratio of m_I/m_i are presented (denoted with an asterisk if <1.0). Knee extensor required masses (m_k) are not applicable (n/a) in the *Basiliscus, Iguana,* and *Alligator* models because knee flexor, not extensor muscles (for which data are still presented), were needed. The muscle masses for the toe joint in the human, kangaroo, and bird models are in parentheses because of the plantigrade foot in the human model (rendering m_t values inconsequential) and the redundancy of ankle extensors/toe flexors in these animals.

TABLE 4. Sensitivity analysis of joint angles (see Fig. 1 for initial model images)

		Angles (in degrees)				
Taxon:	Model	Pelvis	Hip	Knee	Ankle	Toe
Homo	1	65	130	140	105	30
Macropus	1	−5	40	100	100	45
Basiliscus	1	10	70	125	90	25
Basiliscus	2	0	70	160	140	50
Basiliscus	3	0	50	110	140	80
Basiliscus	4	45	110	130	140	75
Iguana	1	10	70	125	90	25
Iguana	2	0	70	160	140	50
Iguana	3	0	50	110	140	80
Iguana	4	45	110	130	140	75
Alligator	1	20	90	160	100	10
Alligator	2	0	70	160	100	10
Alligator	3	20	70	140	140	50
Alligator	4	20	40	90	120	50
Eudromia	1	15	50	90	120	65
Eudromia	2	0	35	90	120	65
Eudromia	3	15	50	110	160	85
Eudromia	4	10	45	105	150	80
Gallus	1	15	50	90	120	65
Gallus	2	0	35	90	120	65
Gallus	3	15	50	110	160	85
Gallus	4	10	45	105	150	80
Meleagris	1	15	50	90	120	65
Dromaius	1	40	45	70	150	85
Struthio	1	40	45	70	150	85
Struthio	2	0	35	90	120	65
Struthio	3	15	50	110	160	85
Struthio	4	10	45	105	150	80
giant *Gallus*	1	15	50	90	120	65
giant *Gallus*	2	0	50	90	120	80

The basis for the alternative poses was a sampling of joint angles from literature on the kinematics of sauropsids (e.g., Snyder, 1949, 1962; Clark and Alexander, 1975; Alexander et al., 1979; Gatesy, 1991, 1999a; Gatesy and Biewener, 1991; Muir et al., 1996; Reilly and Elias, 1998; Irschick and Jayne, 1999, 2000; Reilly, 2000; Blob and Biewener, 2001; Hsieh, 2003) to examine the effects of other possible poses on the m_i values (see Figs. 3, 4).

RESULTS

The validity of the modeling procedure seems to be supported because the models showed that alligators and larger iguanas are poorly suited for running (high m_i values compared to m_I), whereas *Basiliscus*, extant basal birds, kangaroos, and humans are capable runners (relatively low m_i values), as shown in Table 3 and Figures 3–5. Yet these were only initial results; sensitivity analysis was required to understand the general significance of the models. I focus especially on the ratio between m_I, the actual muscle mass present in the dissected animal, vs. m_i, the muscle mass required for fast running from my inverse dynamics analysis (m_I/m_i); in units of percent m_{body} per hindlimb. The ratio of m_I/m_i for all major hindlimb joints must be 1.0 or greater in order for the analysis to show that fast bipedal running (with G = 2.5) could be attained by that taxon in that limb orientation. This analysis addresses a primary question of this study: is there a difference (e.g., m_I/m_i ratios) between the capability of proximal vs. distal limb muscles to support rapid running?

Because limb orientation is uncertain for several key models, I also conducted a sensitivity analysis (Table 4, Figs. 3, 4) to see how much the unknown parameters and simplifying assumptions changed the initial results for some models. The limb orientation for humans and kangaroos is known, so no additional sensitivity analysis was done for those taxa. Recall that all models were posed bipedally, so even typically quadrupedal reptiles were modeled exclusively as bipeds, gaining no support from the limbs or tail. Although *Basiliscus* was supported as a good runner (m_I/m_i ratios for the hip, ankle, and toe joints >1) regardless of the pose assumed, this was not the case for *Iguana* and *Alligator*. *Iguana* had sufficiently large hip extensor muscles for fast running (m_H/m_h = 1.2), unlike *Alligator* (m_H/m_h = 0.53). However, the distal antigravity muscles (ankle and toe) were far too weak for running (m_I/m_i ratios ~0.21–0.33). As with *Basiliscus*, alternative poses did not change my results greatly, except that some required much more moment production by distal joint extensors (Fig. 3). Even with generous assumptions, limb design in *Iguana* and *Alligator* was shown to be very poorly suited for bipedal running.

I obtained quite different results for the bird models. In the tinamou *Eudromia*, the hip and knee had adequate m_I/m_i ratios of 1.3 and 14, whereas the low ankle m_A/m_a (0.75) was particularly interesting. If taken at face value, this would indicate that tinamous cannot run with G = 2.5 because their ankle muscles could not support the joint moments incurred. However, tinamou kinematics (and speeds) are presently unknown, so I tried alternative limb orientations that were within the ranges of values published for small birds. Two poses (Table 4, Fig. 4: models 3 and 4) with more extended knee and ankle joints raised the m_A/m_a to 1.3–1.8 (hip and knee values changed little overall), in greater agreement with fast running potential in tinamous. A similar finding was obtained for the toe joint. In stark contrast to the *Iguana* and *Alligator* models, my analysis showed that chickens are proficient runners because their extensors acting about their major limb joints are "overbuilt" by a factor of at least 1.7 for level running, which compares well with experimental data from running turkeys (Roberts, 2001). The *Gallus* model was more realistic than the *Alligator* model, because galliform birds can run well, and their kinematics and muscle activity patterns during bipedal running are known (e.g., Gatesy 1999a,b), whereas bipedal alligators are fanciful. Two anomalous observations deserve comment. First, the ankle and toe m_i values were very sensitive to the joint angles entered, with m_I/m_i ratios perilously close to 1.0. Similar to the tinamou, only certain poses (*Gallus* models 3, 4) had toe m_t values low enough to consider running in that pose possible. Second, the exceptionally high initial knee extensor m_K/m_k ratios (14–31) in the tinamou and

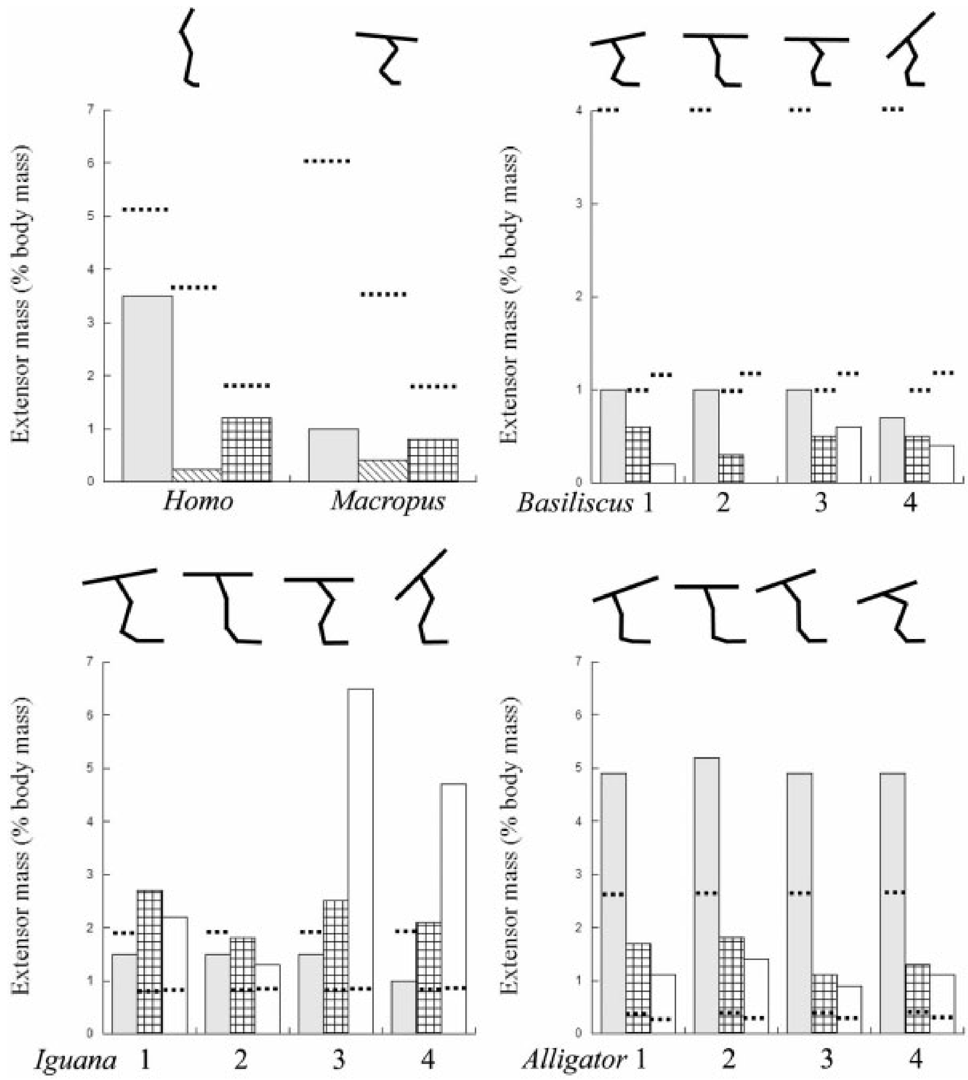

Fig. 3. Results for the models of the non-birds used in this analysis. The bar graphs show the required extensor muscle masses (m_i values) for the joints (solid gray = hip; diagonal hashed = knee; mesh = ankle; solid white = toe) as well as the actual muscle masses (m_I values; dashed horizontal lines). The knee is absent for the lizards and alligator; the toe is absent for the others because of simplifying assumptions (see text). The limb orientations (see Table 4 for joint angle values) are above the corresponding graphs. Figure 1 has the scales. See text for discussion. Note that the ankle tends to have the lowest "safety factor" (m_A/m_a ratio).

chicken are presumably related to the sensitivity of joint moments to the assumed limb orientations.

The latter anomalies were not present in the other bird models (Table 4, Fig. 4). The turkey I dissected was noticeably more slender (like the tinamou) compared to the chicken, explaining the lower total extensor muscle mass (5.5% m_{body}) and suggesting that, as expected, the domestic chicken (presumably bred for large muscles to increase edible meat content) was unusually muscular for galliform birds. Nonetheless, the same conclusions hold for all models: smaller birds are supported as capable of fast running. Contrary to expectation, the emu model had similar results to the smaller birds: generally high m_I/m_i ratios despite the larger size, although in the one pose modeled the ankle m_A/m_a ratio was not as limiting as in other models (Table 4, Fig. 4). The enormous Mm. gastrocnemii and M. fibularis longus (together 4.7% m_{body} per leg, as much muscle as in the entire limb of some smaller birds) explain the high m_A/m_a value, unlike in the other birds. Although the large leg muscles of ratites enable fast running, the ostrich I dissected had relatively smaller extensor muscles than the emu, especially for the ankle (3.2% m_{body} for Mm. gastrocnemii and M. fibularis longus). Limb orientation changed the m_i values slightly (Fig. 4): flexing the ankle joint increased the m_i values, but m_I/m_i remained >1.0 for all joints. Otherwise, although the pose of emus and ostriches at mid-stance during fast running is poorly known, the limb muscles seem to have sufficiently large masses and moment arms to balance many potential poses during fast running (Fig. 4). To my knowledge, these two birds have relatively the largest total hindlimb extensor muscles yet recorded for any tetrapods.

DISCUSSION

Inferences on Running Mechanics

Animals that are known to be fast bipedal runners (or hoppers) are consistently shown to be such in my

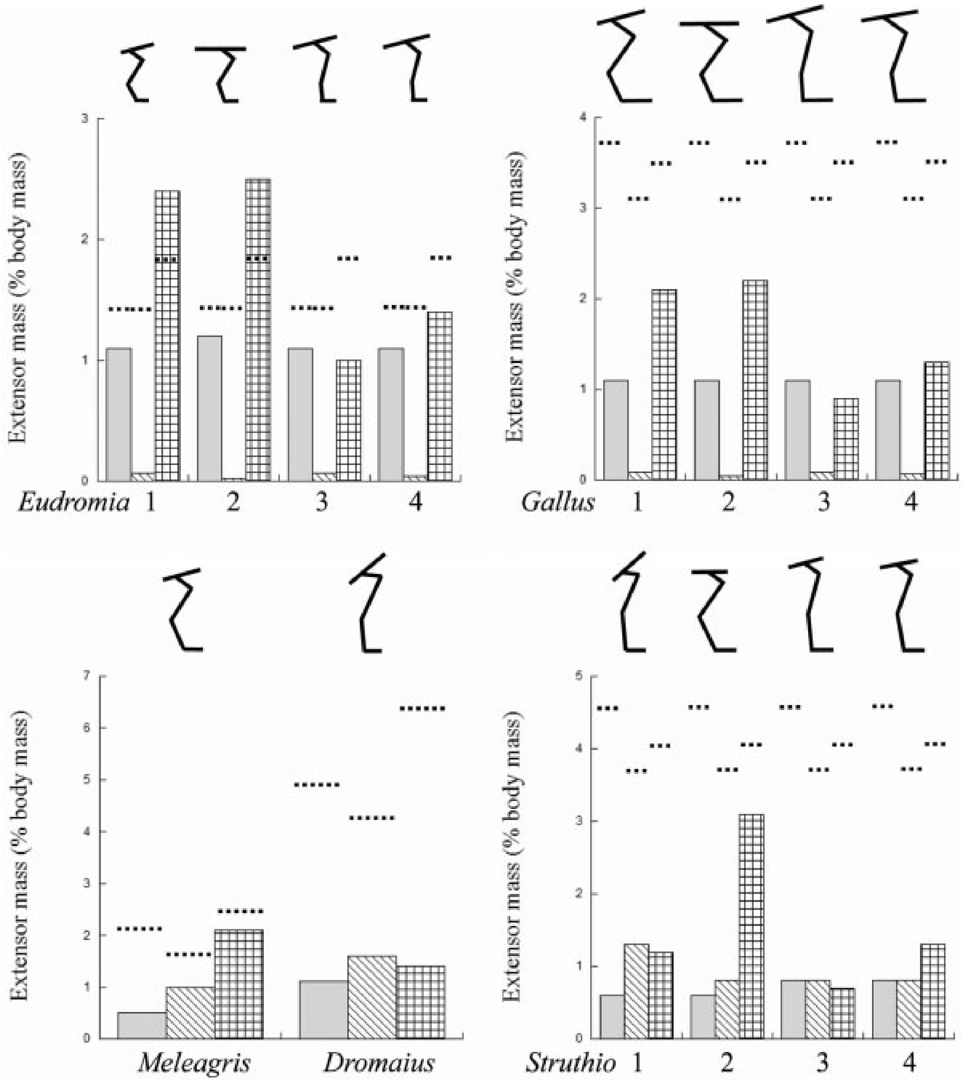

Fig. 4. Results for the models of the birds used in this analysis, as in Figure 3.

models, strengthening the validity of this simple biomechanical approach for estimating bipedal running ability. Thus, the results of Hutchinson and Garcia (2002) continue to be supported by additional data from extant taxa, and this simple approach is promising for examining other possible runners, including extinct forms.

What is "fast running?" The mechanistic definition of running is linked to the Froude number (Fr), a gauge of dynamic similarity, $Fr = v^2 * g^{-1} * l^{-1}$, where v = forward velocity, g = acceleration due to gravity, and l = hip height (e.g., Alexander and Jayes, 1983; Donelan and Kram, 1997, 2000). The Fr is equivalent to the ratio of kinetic to gravitational potential energies—or centripetal (inertial) to gravitational forces—during locomotion. Theoretically, at $Fr > 1.0$ centripetal forces drawing the center of mass of the body off the ground should overcome gravitational forces "pulling" downward. Thus, an aerial phase and a switch from walking to running should be necessary, with some exceptions (e.g., Gatesy and Biewener, 1991; Hutchinson et al., 2003). Most animals switch to a running gait at a lower Fr (~0.5), ostensibly because of energetic or mechanical triggers (Alexander and Jayes, 1983; Farley and Taylor, 1991; Vilensky et al., 1991; Kram et al., 1997; Gatesy, 1999a; Prilutsky and Gregor, 2001; Ahlborn and Blake, 2002).

As in Hutchinson and Garcia (2002), I define "fast running" as roughly equivalent to Fr 17, or about 12 m s^{-1} for a sprinting ostrich (Alexander et al., 1979) or human athlete. This is an arbitrary definition, but by terrestrial animal standards it is certainly a relatively fast running speed. Studies such as Donelan and Kram (1997, 2000), Irschick and Jayne (1999), and Hutchinson et al. (2003) have shown that dimensional similarity is often violated in locomoting animals, so Froude numbers may indicate approximate rather than strict dynamic similarity (see Alexander and Jayes, 1983, for more details). At Fr = 17, the smaller animals in this study would be moving at 4–7 m s^{-1}, whereas the

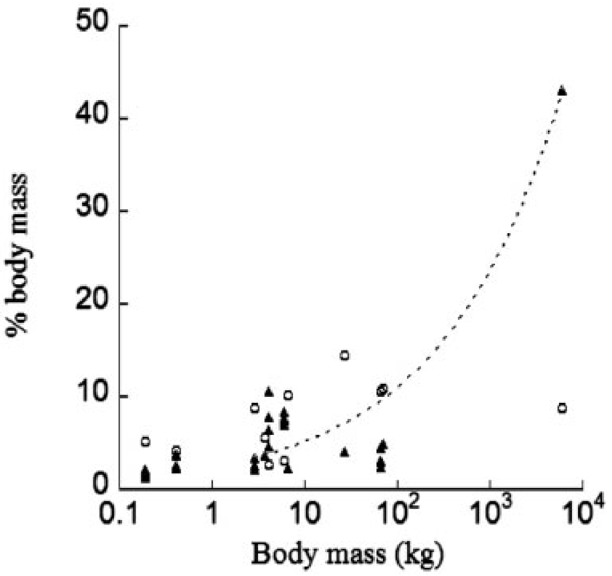

Fig. 5. Relative total extensor muscle mass per leg compared to body mass for all models, including different poses used. The open circles indicate the values of A (actual total extensor muscle mass present), whereas the filled triangles indicate the values of T (total extensor muscle mass required to maintain quasi-static equilibrium of the joints). The dotted line represents isometric scaling of the chicken model to 6,000 kg body mass (see text and Hutchinson and Garcia, 2002).

human, kangaroo, emu, and ostrich would be moving at 10–12 m s^{-1} (and the giant chicken at 22 m s^{-1}). None of these speeds are outside the known speed limits for those animals shown to be proficient runners in this study. Therefore, this rough gauge for comparing bipedal running ability seems reasonable. At G = 2.5, the duty factor for a typical biped should be ~0.31 (Appendix B). Yet for very fast running, this G value may be a conservative assumption, as recorded forces are often higher than expected at slower speeds (Table 2; Farley et al., 1993). Very few experimental data exist for the GRFs incurred by animals, especially bipeds, moving at their fastest speeds. Hence, it is not presently possible to tightly link maximum speeds (or Fr) with G values in my models, but G = 2.5 seems to be a reasonably conservative "relative activity factor" for running at Fr ~17.

What biomechanical and musculoskeletal factors limit fast running? With few exceptions (dependent on limb orientation; Table 4, Figs. 3, 4), my models shared one common pattern: the distal joints, particularly the ankle joint, had the lowest "safety factor" (m_I/m_i ratio). Hence, the distal extensor muscles are a major mechanical limit on supporting joint flexor moments incurred in all fast-running (or hopping) bipeds. This observation is expected to be only partly explained by their distal position, which involves the support of more mass than the hip or knee joints. More crucially, the slenderness of distal limb segments probably excludes distal extensor muscles from having large moment arms or masses compared to more proximal muscles (discussed further below). This conclusion is consistent with other studies, including results for different animals (e.g., rodents in Perry et al., 1988; humans in Novacheck, 1998; Anderson, 1999, and references therein) and for proximal vs. distal skeletal elements (Alexander, 1997). For example, experimental data show that peak muscle moments (especially about the ankle joint) are an important limit on kangaroo speed (Bennett and Taylor, 1995). Roberts (2001) also demonstrated that turkeys use a large fraction of their ankle extensor muscle volume during running, compared with other limb joints. Additional experimental studies of the limits ankle biomechanics place on running ability are needed, as this may be a general pattern in tetrapods. One factor related to this pattern is that distal muscles tend to be specialized for force production and energy-saving elastic energy storage, whereas larger proximal muscles control the amount of work produced by the limb (e.g., Biewener et al., 2004).

More generally, my models show how the ratio of m_I/m_i is crucial for running ability in bipeds. Good bipedal runners typically have a total of 5–14% of m_{body} per leg as extensor muscles (with <7% m_{body} acting about each joint), but only need a total of about 5% m_{body}, resulting in m_I/m_i ratios for most joints near 1–3. Why should animals have excess muscle? As Biewener (1989, 1990) suggested, seemingly excessive supportive tissue mass might seem wasteful, but animals do not only run at a steady state. Higher forces (G values), GRF moment arms (R values), or lower muscle stresses (σ values) would require larger muscle masses than those calculated here. Such values are likely required in extreme nonsteady-state activities, so some of my assumptions may be conservative either with respect to running at maximum speed or running in nonsteady-state conditions.

How do these data from the inverse dynamics model compare to the results of other studies? Few independent comparative data for the biomechanics of the animals I modeled exist, although the inverse dynamics approach I used is comparable to typical approaches (e.g., Alexander et al., 1979; Biewener, 1989; Roberts, 2001). The findings for the human model do not match other data on human locomotion perfectly. For example, my estimated M_{musc} values for the hip, knee, and ankle, respectively, were 240, -20, and 170 N m. Using Anderson's (1999) model with the left (swing phase) limb posed in the appropriate joint angles (Novacheck, 1998) produced somewhat similar results: M_{musc} values for the hip, knee, and ankle of 250, -110, and 60 N m, respectively (m_I/m_i of 1.4, 4.0, and 1.7). Those net moments are different from experimental data from Novacheck (1998) for slower running at 3.9 m s^{-1} (70, -110, and 110 N m, respectively), or from Thorpe et al. (1998) for slower running at 5.0 m s^{-1} (235, -326, and 181 N m, respectively). These studies suggest that the knee joint m_k I calculated may be conservatively low (probably because I ignored co-contraction moments), but even if the m_k was 16× higher (Thorpe et al., 1998) it would not change my conclusions because the m_K/m_k ratio would still be >1. Other experimental data such as Weyand et al. (2000) intimate that human leg muscles may be a major limit of running speed because of their role in generating ground reaction forces.

One result of the models of nonavian reptiles was unusual. A knee flexor, not extensor, M_{musc} was required to maintain static equilibrium in the limb orientations modeled. Relatively short limbs and a cranially positioned CM appear responsible for this result. It remains to be seen whether an assumption of quasi-static equilibrium is realistic for bipedally running lizards. Such lizards tend to move mainly (or exclusively) bipedally at faster speeds (Snyder, 1949, 1962; Irschick and Jayne, 1999, 2000), involving complex 3D dynamics that may obviate requirements of static equilibrium. Regardless, my models are consistent with reality in that *Basiliscus* was shown to be a very competent runner, whereas *Iguana* and *Alligator* were not.

Likewise, in the nonavian reptile models the difference between proximal and distal extensor muscles and between the same joints among various taxa was striking. Gatesy (1990) showed how M. caudofemoralis longus is ancestrally an important hip extensor in saurian reptiles. This muscle would allow a large extensor moment to be generated about the hip in *Alligator* (4.1 N m maximum isometric moment alone), but *Alligator* was less able to generate sufficient hip moment than *Iguana* (5.6 N m maximum isometric moment of M. caudofemoralis longus) despite its slightly larger size. Unlike *Alligator*, the hip extensors of *Iguana* would have been able to support bipedal running if they were all that mattered; distal muscles were the crucial limit. Shorter muscle fascicles were the main reason for this difference in *Iguana*, maximizing muscle force per unit mass (presumably at a cost of limb excursion range). In *Basiliscus*, M. caudofemoralis longus alone (at 1.44% m_{body} per leg) would have been able to support the required hip joint moment during bipedalism, and together the hip extensors could generate 4.0 times the necessary moment.

Similar to the human, kangaroo, and basilisk, the bird models showed good capacities for running. In *Gallus*, the hip extensors were much more capable of exerting the required hip M_{musc} than in *Alligator* despite the diminutive size of the caudofemoral muscles: their maximum M_{musc} is about 3.4 times that needed for fast running. This pattern held for all birds in all poses: the hip extensor m_H/m_h ratio remained well above 1.0, often the highest ratio for all the limb joints. In all birds, the knee extensors were more than capable of exerting the necessary M_{musc} in my initial model (m_K/m_k = 1.6 to 31). This is explainable by the large size of the knee extensors, the large moment arm (r) that the patella and tibial crest provide for knee extension, and the proximity of the knee joint to the whole body CM, which reduced the F_{func} moment arm (R) about the knee particularly in the tinamou and chicken models.

The ankle joint musculature (m_A) of the bird models was more closely matched to the demands of running, usually ~1–3 times the required musculature (m_a); shown in Figure 4. The hypotarsus, tibial cartilage, thick tendons, and expansive distal condyles of bird tarsometatarsi appear to maintain fairly large moment arms (r) of the ankle extensors across a wide range of joint angles. This anatomy facilitates rapid terrestrial locomotion by improving mechanical advantage with respect to the ancestral absence of such structures (Hutchinson, 2002). Nonetheless, my models predict that ankle muscle stresses should be high during running in birds, which is appropriate for muscle-tendon complexes that act like springs (Biewener and Roberts, 2000), and matches experimental data well (e.g., Roberts et al., 1997, 1998; Roberts, 2001).

However, one conspicuous difference between the bird and nonbird models is the distribution of extensor muscle masses from proximal to distal. In all of the non-birds the actual masses (m_I values) tended to decrease from proximal to distal (Table 3; Fig. 3). Unusually, in the birds the ankle muscle masses (m_A) tended to be largest, so the m_I values were distributed more evenly along the limb (Table 3; Fig. 4). A potential explanation for this result may be the apomorphic kinematics of avian runners, with accentuated emphasis on ankle (and toe) joint excursions to power accelerations and generate long strides (Gatesy, 1990, 1999a; Gatesy and Biewener, 1991; Roberts et al., 1998; Reilly, 2000; Roberts, 2001; Roberts and Scales, 2002). Yet for all taxa, because the mean extensor muscle moment arms (r) also decreased proximodistally (necessary for more tapered limbs), there tended to be a proximodistal decrease of the maximum muscle moments (M_{max}) and (less consistently, particularly for the knee joint which was often close to the body CM) the m_I/m_i ratios about each joint (Table 3; Figs. 3, 4).

Influence of Size on Running Ability

My results concur with other studies of lizard locomotion that suggest decreasing relative locomotor performance in larger lizards. Glasheen and McMahon (1996) found that bipedal running ability over water declined with size in an ontogenetic series of *Basiliscus*. This was attributed to hydrodynamic rather than muscular forces, but the same scaling principles of mass and area apply to both problems. Additionally, the relatively longer limbs of juvenile lizards offer one explanation for a similar decline of relative locomotor performance in *Dipsosaurus* (Irschick and Jayne, 2000). Finally, Christian and Garland (1996) showed that relative limb bulk increased with size in monitor lizards, suggesting that muscle mass and body size limit locomotor performance in lizards. My analysis also shows one reason why bipedal running ability may drop precipitously with body mass in lizards, as the 21× heavier *Iguana* has m_I/m_i ratios ~8× lower than *Basiliscus*.

The biomechanical constraints imposed by body size as terrestrial bipeds grow or evolve to extremely large sizes are exemplified by one additional model of a chicken (Fig. 5). Similar to Hutchinson and Garcia (2002), I isometrically scaled the 2.89 kg *Gallus* model up to 6,000 kg (i.e., multiplying all masses by 2,076 and multiplying all linear dimensions by 12.75, the cube root of 2,076) to investigate how well a giant chicken could run, posed in the same limb orientation as a normal chicken during running. The results of this exercise compare well with the previous model (Hutchinson and Garcia, 2002; note the joint angles for that giant chicken model were mistakenly slightly different from the chicken: the pelvic angle was 10°, not 15°; the hip angle was 55°, not 50°; and the toe angle was 75°, not 65°. Thus, the total required muscle mass for that model should have been 62%, as isometric scaling predicts, not 99%). A 6,000 kg chicken would require a total of 43% m_{body} per leg as limb extensors (ignoring the toe joint), which again is absurd. An alternative limb orientation identical to the joint angles used for *Tyrannosaurus* by Hutchinson and Garcia (2002; also Hutchinson, 2004) gave a total required muscle mass of 44% m_{body} (ignoring the knee m_k because of a flexor M_{musc} in this pose). In both models, the ankle joint experienced the largest deficit, requiring over 8× as much ankle extensor mass as extant chickens actually have. The m_i values were 14 for the hip, 0.97 for the knee in the first model, and, respectively 28 or 30, for the ankle (26 or 46 for the toe m_t). Similar results were obtained from scaling other extant birds to the same size. Scaling the chicken up to the dimensions of the ostrich still allowed running ability (high m_I/m_i ratio for all joints), but at larger sizes the viability of isometric scaling inevitably is reduced for fast-running animals (e.g., Biewener, 1989, 1990; Hutchinson, 2004).

Because the m_i values are linearly proportional to R, r, and L (Eq. 10), if the latter parameters scale isometrically during growth or evolution to a larger body size, m_i likewise will increase linearly (Hutchinson and Garcia, 2002). This simply follows from the well-known principle that supportive tissue area scales less quickly with body mass ($\sim m_{body}^{0.67}$) than the stresses that need to be supported ($\sim m_{body}^{1.0}$) (e.g., Biewener, 1989, 1990, and references therein). Thus, the ratio of m_I/m_i drops quickly with size (Figs. 3–5; Hutchinson and Garcia, 2002) unless m_i values are decreased or m_I values are increased. This requirement seems to have a discrete boundary: none of the bipeds modeled have 7% m_{body} of extensor muscle acting about any one joint (indeed, few m_I values exceed 5% m_{body}), so animals with m_i values of 7% or more should not be able to run with G = 2.5. Four parameters can significantly alter m_i (Eqs. 9, 10): the "relative activity factor" (G), the fascicle lengths of extensor muscles (L), the moment arms of the extensor muscles (r) about the joints, and the net moment arm of the internal and external forces (R) about the joints. Certainly, great changes of the model parameters were necessary during the evolution of large animals, because the giant chicken model shows that isometric scaling in a bird to 6,000 kg would leave the animal barely able to stand, let alone run. Yet bipeds of that size did exist, and presumably stood and walked. One solution for such giant bipeds is allometric scaling rather than isometric scaling, considered in more detail by Hutchinson (2004).

Biewener (1989) formulated the ratio of r/R as "effective mechanical advantage," or EMA, revealing that hindlimb EMA in mammalian quadrupeds scales with positive allometry, mainly accomplished by a decrease of R with increased limb extension (Biewener, 1990). It does not seem that G (at a given Fr) can be altered greatly with size unless relative performance is reduced (e.g., increased duty factor; Alexander et al., 1979), so increasing EMA and decreasing the relative magnitude of L should be the main musculoskeletal mechanisms for maintaining running ability at larger sizes. Intermediate running mechanisms such as "Groucho running" can reduce G at a cost of reduced EMA and increased energetic cost of transport (McMahon et al., 1987), but incur limited maximal speed (McMahon and Cheng, 1990). Possible mechanisms for increasing EMA are limited, because a limb can only be so straight (reducing R) and extensor muscle moment arms (r) are constrained by limb orientation and geometry. Furthermore, shortening muscle fascicles (L) and increasing EMA would correspondingly restrict limb excursion, and hence limit stride length. It is unresolved how much L can be decreased and EMA can be increased with size before locomotor performance must be reduced.

How do larger birds cope with these size requirements for running? There is no evidence that larger birds such as ratites have reduced locomotor performance, but basic scaling principles suggest that some factors must change relative to smaller birds in order to maintain or increase relative running performance in larger birds. Emus and ostriches dedicate more body mass to extensor muscles than smaller birds, having 22–29% m_{body} as total extensor muscles (both legs). These masses are roughly 2–3× the amount in *Eudromia* and *Meleagris*. Thus, ratites keep their m_I/m_i ratios high by increasing m_I, which contradicts Leahy's (2002) assertion that ostriches have "no relative increase in leg extensor mass" compared with smaller birds. The poses mod-

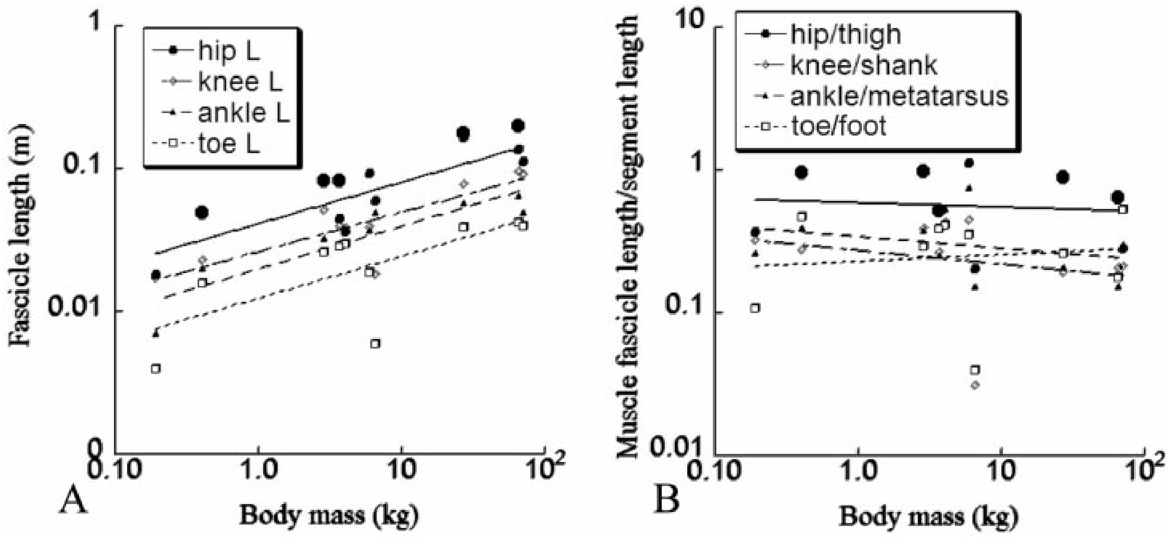

Fig. 6. Scaling of extensor muscle fascicle length (L) in bipeds. Least-squares logarithmic plots, with fascicle lengths expressed as the weighted harmonic mean (weighted by m_I) for a joint. All four joints for all animals modeled are included even though some models excluded some joints. The large filled circles toward the top of the graphs emphasize the hip extensor data for the birds. Scaling equations are: **A:** hip L = 0.0411 $m_{body}^{0.291}$ (R^2 = 0.661); knee L = 0.0261 $m_{body}^{0.277}$ (R^2 = 0.850); ankle L = 0.0197 $m_{body}^{0.300}$ (R^2 = 0.797); and toe L = 0.0123 $m_{body}^{0.294}$ (R^2 = 0.629). **B:** Muscle fascicle length normalized to segment length (thigh/shank/metatarsus/foot for the hip/knee/ankle/toe extensors) = 0.591 $m_{body}^{-0.0306}$ (R^2 = 0.00869); knee L = 0.273 $m_{body}^{-0.0963}$ (R^2 = 0.106); ankle L = 0.341 $m_{body}^{-0.0814}$ (R^2 = 0.0323); and toe L = 0.223 $m_{body}^{0.0467}$ (R^2 = 0.0130).

eled for these larger birds (see Alexander et al., 1979; Gatesy and Biewener, 1991) generally have more straightened limbs than the smaller birds, and hence lower the m_i values by relative reduction of R values (increasing EMA), also violating Leahy's (2002) contention that such birds have "similar limb flexion." These poses (and perhaps allometrically increased extensor muscle moment arms; see Hutchinson, 2004) also explain why the m_i values for the ratite joints are low even in comparison to smaller birds, and thus why ratites seem to have relatively higher "safety factors" about their joints.

Do all muscle fascicle lengths (L) always scale with negative allometry, maintaining lower m_i values? Figure 6 shows L plotted against body mass for the animals in this study. As in other studies (e.g., Maloiy et al., 1979; Alexander et al., 1981; Pollock and Shadwick, 1994; Bennett, 1996; Olmos et al., 1996), there is a proximal-to-distal gradient in the scaling of extensor muscle fascicle lengths, with muscles acting about more distal joints having shorter fascicles, relative to body size, in larger birds. Roberts et al. (1998) and Roberts (2001) noted that, with their longer limbs, birds have relatively longer muscle fascicle lengths than other runners, explaining their higher cost coefficient for the cost of transport because a larger volume of active muscle is used (i.e., parameter c in this study is high). This pattern is shown when mean fascicle length normalized by segment length is plotted against body mass (Fig. 6B). The proximal-to-distal gradient breaks down, suggesting that muscle fascicle lengths and leg segment lengths need not be tightly linked. Additionally, the hip extensor muscle fascicles seem unusually long in birds relative to other animals (Fig. 6B), perhaps related to the long pelvis and short subhorizontal femur of birds, which requires some pelvic muscles to cross a long distance to reach their femoral insertions. Thus, although birds enjoy long stride lengths and ground contact times because of their long limbs (Gatesy and Biewener, 1991), this advantage comes at a cost of higher m_i values than would be obtained by having shorter limbs (and correspondingly reduced L and R values), because the muscle fascicles are still long relative to body size.

Evolutionary Implications

My analysis has broader implications for the evolution of archosaur locomotion. Figure 7 focuses on this clade and its lepidosaur outgroups (the two mammal models are excluded). Without much more data from key extant and fossil taxa, only general inferences are possible. The general musculoskeletal anatomy of *Alligator* is similar to the ancestral archosaurian condition (Hutchinson and Gatesy, 2000; Hutchinson, 2002). Together, the unspecialized anatomy of basal saurians and archosaurs, and the derived musculoskeletal anatomy of *Basiliscus* (Snyder, 1949, 1962), suggest that the poor bipedal running ability shown for *Alligator* and *Iguana* was ancestral for these clades, and *Basiliscus* is derived relative to this condition.

My biomechanical analyses complement other studies (e.g., Gatesy, 1990) by showing why in-

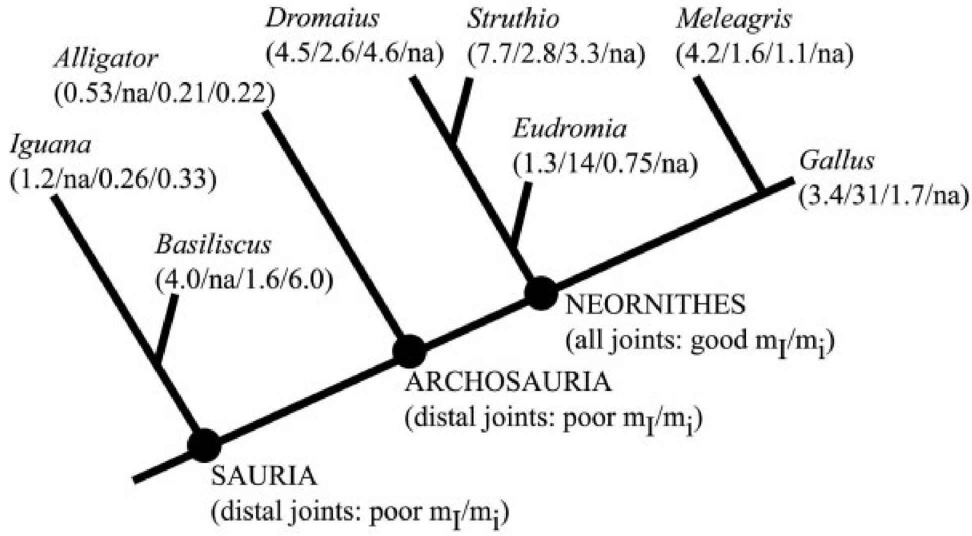

Fig. 7. Evolution of archosaur running ability. Phylogeny based on Gauthier (1986), Cracraft and Clarke (2001), and references therein. The numbers below each taxon are the m_I/m_i ratios from my initial models (Table 3; Figs. 3, 4) for the hip (m_h), knee (m_k), ankle (m_a), and toe (m_t; for the lizard and alligator models); "na" is a reminder that the joint was generally ignored in my analysis.

creases of lower limb extensor muscle masses and moment arms were vital for bipedal running ability in the predecessors to birds, whereas the hip extensors required relatively less expansion with the origin of bipedalism in the dinosaurian forebears to birds. The hindlimb musculoskeletal anatomy of the bird models in this study is representative of basal Neornithes in general (Hutchinson and Gatesy, 2000; Hutchinson, 2002). Thus, the results of these models support the inference that the ancestors of crown clade birds had already achieved good running capacity by having large ankle extensor muscles, and this condition was inherited by extant birds. Ratites are derived in having a rather high running capacity via mechanisms described above, despite their dramatically larger size relative to basal birds. Note that this running potential remains in crown-group birds despite the increase of R about the hip joint caused by the more cranial position of the CM in birds (lacking a massive tail; Gatesy, 1990) and the reduction or complete loss of an ancestrally important hip extensor: M. caudofemoralis pars caudalis (= longus of nonavian saurians). All birds dissected except *Eudromia* had the smaller part of M. caudofemoralis, pars pelvica (= brevis of nonavian saurians), but pars caudalis was present only in the chicken. Pars caudalis was ancestrally present in Neornithes; however (Hutchinson, 2002), it was lost independently in some paleognaths and many neognath birds. Together, the two parts of M. caudofemoralis constitute a tiny percentage ($<0.13\%$ per limb) of body mass in these extant birds, whereas in the nonavian saurians dissected they were 1.1% in *Iguana* and 1.8% in *Alligator* and *Basiliscus*. This illustrates Gatesy's (1990) distinction between the mechanics of limb propulsion in basal reptiles vs. extant birds, showing that birds experienced a decrease in the relative mass of this muscle group of about 1/100 during their evolution from nonavian archosaurs. However, birds still need large hip extensor muscles (1–5% m_{body}) to support their cranially positioned CM (which incurs a large hip flexor moment), and as such may not have reduced their total hip extensor mass during their evolution. Information from fossil taxa will be vital for unraveling how and when such key changes evolved, what the consequences of anatomical changes were for the locomotor performance of particular taxa, and how the size of bipeds larger than ostriches influences their locomotion (Hutchinson, 2004).

ACKNOWLEDGMENTS

Mariano Garcia was enormously helpful in writing Matlab code, discussing our initial analyses, and many other contributions and advice. Thorough and insightful reviews of an early draft of this paper by Steve Gatesy and two anonymous reviewers are greatly appreciated as they helped me to greatly improve it. I thank Kevin Padian and Scott Delp for sage advice during my graduate and postdoctoral education at the University of California and Stanford University. Jens Vindum (California Academy of Sciences) kindly supplied the basilisk specimen, and Tonia Hsieh was very helpful in discussing basilisk kinematics. F. Clay Anderson, Allison Arnold, Andrew Biewener, Matt Carrano, Per Christiansen, Robert Full, Steve Gatesy, Katie Hammond, Tony Keaveny, Rodger Kram, Gregory S. Paul, Tom Roberts, Jonas Rubenson, Alan Wilson, and friends at the Berkeley Friday Biomechanics Seminar and Stanford Neuromuscular Biomechanics Lab meetings have provided stimulating discussions. I thank Manuel Garrido and José Mérida for kind technical comments, ideas, and data-checking. This material is based on work supported by the National Science Foundation under a grant awarded in 2001.

LITERATURE CITED

Ahlborn BK, Blake RW. 2002. Walking and running at resonance. Zoology 105:165–174.

Alexander RMcN. 1977. Allometry of the limbs of antelopes (Bovidae). J Zool 183:125–146.

Alexander RMcN. 1985. The maximum forces exerted by animals. J Exp Biol 115:231–238.

Alexander RMcN. 1997. A theory of mixed chains applied to safety factors in biological systems. J Theor Biol 184:247–252.

Alexander RMcN, Jayes AS. 1983. A dynamic similarity hypothesis for the gaits of quadrupedal mammals. J Zool 201:135–152.

Alexander RMcN, Vernon A. 1975. The mechanics of hopping by kangaroos (Macropodidae). J Zool 177:265–303.

Alexander RMcN, Maloiy GMO, Njau R, Jayes AS. 1979. Mechanics of running of the ostrich (*Struthio camelus*). J Zool 187:169–178.

Alexander RMcN, Jayes AS, Maloiy GMO, Wathuta EM. 1981. Allometry of the leg muscles of mammals. J Zool 194:539–552.

An KN, Takahashi K, Harrigan TP, Chao EY. 1984. Determination of muscle orientations and moment arms. J Biomech Eng 106:280–283.

Anderson FC III. 1999. A dynamic optimization solution for a complete cycle of normal gait. Ph.D. Dissertation, University of Texas.

Arampatzis A, Brüggemann G-P, Metzler V. 1999. The effect of speed on leg stiffness and joint kinetics in human running. J Biomech 32:1349–1353.

Armstrong RB, Taylor CR. 1982. Relationship between muscle force and muscle area showing glycogen loss during locomotion. J Exp Biol 97:411–421.

Armstrong RB, Marum P, Saubert CW IV, Seeherman HJ, Taylor CR. 1977. Muscle fiber activity as a function of speed and gait. J Appl Physiol 43:672–677.

Bennett MB. 1996. Allometry of the leg muscles of birds. J Zool 238:435–443.

Bennett MB, Taylor GC. 1995. Scaling of elastic strain energy in kangaroos and the benefits of being big. Nature 378:56–59.

Biewener AA. 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 AA. 1989. Scaling body support in mammals: limb posture and muscle mechanics. Science 245:45–48.

Biewener AA. 1990. Biomechanics of mammalian terrestrial locomotion. Science 250:1097–1103.

Biewener AA, Full RJ. 1992. Force platform and kinematic analysis. In: Biewener AA, editor. Biomechanics—structures and systems: a practical approach. Oxford, UK: Oxford University Press. p 45–73.

Biewener AA, Roberts TJ. 2000. Muscle and tendon contributions to force, work, and elastic energy savings: a comparative perspective. Exerc Sport Sci Rev 28:99–107.

Biewener AA, McGowan C, Card GM, Baudinette RV. 2004. Dynamics of leg muscle function in tammar wallabies (*M. eugenii*) during level versus incline hopping. J Exp Biol 207:211–223.

Blickhan R. 1989. The spring-mass model for running and hopping. J Biomech 22:1217–1227.

Blickhan R, Full RJ. 1993. Similarity in multilegged locomotion: bouncing like a monopode. J Comp Physiol A 173:509–517.

Blob R, Biewener AA. 2001. Mechanics of limb bone loading during terrestrial locomotion in the green iguana (*Iguana iguana*) and American alligator (*Alligator mississipiensis*). J Exp Biol 204:1099–1122.

Bryant JD, Bennett MB, Burst J, Alexander RMcN. 1987. Forces exerted on the ground by galloping dogs (*Canis familiaris*). J Zool 213:193–203.

Calow LJ, Alexander RM. 1973. A mechanical analysis of a hind leg of a frog (*Rana temporaria*). J Zool 171:293–321.

Carrier DR, Heglund NC, Earls KD. 1994. Variable gearing during locomotion in the human musculoskeletal system. Science 265:651–653.

Cavagna GA, Heglund NC, Taylor CR. 1977. Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. Am J Physiol 233:R243–261.

Chang Y-H, Huang H-WC, Hamerski CM, Kram R. 2000. The independent effects of gravity and inertia on running mechanics. J Exp Biol 203:229–238.

Christian A, Garland T Jr. 1996. Scaling of limb proportions in monitor lizards (Squamata: Varanidae). J Herpetol 30:219–230.

Christiansen P. 1998. Strength indicator values of theropod long bones, with comments on limb proportions and cursorial potential. Gaia 15:241–255.

Christiansen P. 2002. Locomotion in terrestrial mammals: the influence of body mass, limb length and bone proportions on speed. Zool J Linn Soc 136:685–714.

Clark J, Alexander RMcN. 1975. Mechanics of running by quail (*Coturnix*). J Zool 176:87–113.

Coombs WP Jr. 1978. Theoretical aspects of cursorial adaptations in dinosaurs. Q Rev Biol 53:393–418.

Cracraft J, Clarke J. 2001. The basal clades of modern birds. In: Gauthier JA, Gall LF, editors. New perspectives on the origin and early evolution of birds: proceedings of the international symposium in honor of John H. Ostrom. New Haven: Peabody Mus Nat Hist. p 143–156.

Delp SL, Hess WE, Hungerford DS, Jones LC. 1999. Variation of rotation moment arms with hip flexion. J Biomech 32:493–501.

Donelan JM, Kram R. 1997. The effect of reduced gravity on the kinematics of human walking: a test of the dynamic similarity hypothesis for locomotion. J Exp Biol 200:3193–3201.

Donelan JM, Kram R. 2000. Exploring dynamic similarity in human running using simulated reduced gravity. J Exp Biol 203:2405–2415.

Farley CT. 1997. Maximum speed and mechanical power output in lizards. J Exp Biol 200:2189–2195.

Farley CT, Taylor CR. 1991. A mechanical trigger for the trot-gallop transition in horses. Science 253:306–308.

Farley CT, Glasheen J, McMahon TA. 1993. Running springs: speed and animal size. J Exp Biol 185:71–86.

Gans C, De Vree F. 1987. Functional bases of fiber length and angulation in muscle. J Morphol 192:63–85.

Gatesy SM. 1990. Caudofemoral musculature and the evolution of theropod locomotion. Paleobiology 16:170–186.

Gatesy SM. 1991. Hind limb movements of the American alligator (*Alligator mississippiensis*) and postural grades. J Zool 224: 577–588.

Gatesy SM. 1997. An electromyographic analysis of hindlimb function in *Alligator* during terrestrial locomotion. J Morphol 234:197–212.

Gatesy SM. 1999a. Guineafowl hind limb function. I. Cineradiographic analysis and speed effects. J Morphol 240:115–125.

Gatesy SM. 1999b. Guineafowl hind limb function. II. Electromyographic analysis and motor pattern evolution. J Morphol 240:127–142.

Gatesy SM, Biewener AA. 1991. Bipedal locomotion: effects of speed, size and limb posture in birds and humans. J Zool 224: 127–147.

Gauthier JA. 1986. Saurischian monophyly and the origin of birds. In: Padian K, editor. The origin of birds and the evolution of flight. Mem Calif Acad Sci 8:1–55.

Glasheen JW, McMahon TA. 1996. Size-dependence of water-running ability in basilisk lizards (*Basiliscus basiliscus*). J Exp Biol 199:2611–2618.

Heglund NC, Cavagna GA, Taylor CR. 1982. 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 97:41–56.

Herzog W, Leonard TR. 2002. Force enhancement following stretching of skeletal muscle: a new mechanism. J Exp Biol 205:1275–1283.

Hill AV. 1950. The dimensions of animals and their muscular dynamics. Sci Prog 150:209–230.

Hsieh ST. 2003. Three-dimensional hindlimb kinematics of water running in the plumed basilisk lizard (*Basiliscus plumifrons*). J Exp Biol 206:4363–4377.
Hutchinson JR. 2002. The evolution of hindlimb tendons and muscles on the line to crown-group birds. Comp Biochem Physiol A 133:1051–1086.
Hutchinson JR. 2004. Biomechanical modeling and sensitivity analysis of bipedal running ability. II. Extinct taxa. J Morphol 262:441–461.
Hutchinson JR, Garcia M. 2002. *Tyrannosaurus* was not a fast runner. Nature 415:1018–1021.
Hutchinson JR, Gatesy SM. 2000. Adductors, abductors, and the evolution of archosaur locomotion. Paleobiology 26:734–751.
Hutchinson JR, Famini D, Lair R, Kram R. 2003. Are fast-moving elephants really running? Nature 422:493–494.
Ingen Schenau GJ van, de Koning JJ, de Groot G. 1994. Optimization of sprinting performance in running, cycling, and speed skating. Sports Med 17:259–375.
Iriarte-Díaz J. 2002. Differential scaling of locomotor performance in small and large terrestrial animals. J Exp Biol 205: 2897–2908.
Irschick DJ, Jayne BC. 1999. Comparative three-dimensional kinematics of the hindlimb for high-speed bipedal and quadrupedal locomotion of lizards. J Exp Biol 202:1047–1065.
Irschick DJ, Jayne BC. 2000. Size matters: ontogenetic variation in the three-dimensional kinematics of steady-speed locomotion in the lizard *Dipsosaurus dorsalis*. J Exp Biol 203:2133–2148.
Johnston IA. 1985. Sustained force development: specializations and variation among the vertebrates. J Exp Biol 115:219–251.
Johnston IA. 1991. Muscle action during locomotion: a comparative perspective. J Exp Biol 160:167–185.
Jones JH, Lindstedt SL. 1993. Limits to maximal performance. Annu Rev Physiol 55:547–569.
Koechling J, Raibert M. 1988. How fast can a legged robot run? In: Youcef-Toumi K, Kazeroni H, editors. Symposium in robotics, DSC-vol. 1. New York: American Society of Mechanical Engineering. p 49–72.
Kram R, Domingo A, Ferris DP. 1997. Effect of reduced gravity on the preferred walk-run transition speed. J Exp Biol 200:821–826.
Leahy GD. 2002. Speed potential of tyrannosaurs great and small. J Vert Paleont 22(3 Suppl):78A.
Maloiy GMO, Alexander RMcN, Njau R, Jayes AS. 1979. Allometry of the legs of running birds. J Zool 187:161–167.
Marsh RL. 1999. How muscles deal with real-world loads: the influence of length trajectory on muscle performance. J Exp Biol 202:3377–3385.
McGeer T. 1990. Passive bipedal running. Proc R Soc Lond B 240:107–134.
McMahon TA, Cheng GC. 1990. The mechanics of running: how does stiffness couple with speed? J Biomech 23:65–78.
McMahon TA, Valiant G, Frederick EC. 1987. Groucho running. J Appl Physiol 62:2326–2337.
Medler S. 2002. Comparative trends in shortening velocity and force production in skeletal muscle. Am J Physiol Regulat Integr Comp Physiol 283:R368–R378.
Mendez J, Keys A. 1960. Density and composition of mammalian muscle. Metabolism 9:184–188.
Muir GD, Gosline JM, Steeves JD. 1996. Ontogeny of bipedal locomotion: walking and running in the chick. J Physiol 493: 589–601.
Nordin M, Frankel VH. 1989. Basic biomechanics of the musculoskeletal system, 2nd edition. Philadelphia: Lea & Febiger.
Novacheck TF. 1998. The biomechanics of running. Gait Post 7:77–95.
Olmos M, Casinos A, Cubo J. 1996. Limb allometry in birds. Ann Sci Nat, Zool 17:39–49.
Paul GS. 1988. Predatory dinosaurs of the world. New York: Simon & Schuster.
Perry AK, Blickhan R, Biewener AA, Heglund NC, Taylor CR. 1988. Preferred speeds in terrestrial vertebrates: are they equivalent? J Exp Biol 137:207–219.
Pollock CM, Shadwick RE. 1994. Allometry of muscle, tendon, and elastic energy storage capacity in mammals. Am J Physiol 266:R1022–R1031.
Pratt JE. 2000. Exploring inherent robustness and natural dynamics in the control of bipedal walking robots. Ph.D. dissertation, Massachusetts Institute of Technology.
Prilutsky BI, Gregor RJ. 2001. Swing- and support-related muscle actions differentially trigger human walk-run and run-walk transitions. J Exp Biol 204:2277–2287.
Reilly SM. 2000. Locomotion in the quail (*Coturnix japonica*): the kinematics of walking and increasing speed. J Morphol 243: 173–185.
Reilly SM, Elias JA. 1998. Locomotion in *Alligator mississipiensis*: kinematic effects of speed and posture and their relevance to the sprawling-to-erect paradigm. J Exp Biol 201:2559–2574.
Roberts TJ. 2001. Muscle force and stress during running in dogs and wild turkeys. Bull Mus Comp Zool 156:283–295.
Roberts TJ, Scales JA. 2002. Mechanical power output during running accelerations in wild turkeys. J Exp Biol 205:1485–1494.
Roberts TJ, Marsh RL, Weyand PG, Taylor CR. 1997. Muscular force in running turkeys: the economy of minimizing work. Science 275:1113–1115.
Roberts TJ, Chen MS, Taylor CR. 1998. Energetics of bipedal running. II. Limb design and running mechanics. J Exp Biol 201:2753–2762.
Rome LC, Funke RP, Alexander RMcN, Lutz G, Aldridge H, Scott F, Freadman M. 1988. Why animals have different fibre types. Nature 335:824–827.
Shahar R, Banks-Sills L. 2002. Biomechanical analysis of the canine hind limb: calculation of forces during three-legged stance. Vet J 163:240–250.
Snyder RC. 1949. Bipedal locomotion of the lizard *Basiliscus basiliscus*. Copeia 1949:129–137.
Snyder RC. 1962. Adaptations for bipedal locomotion of lizards. Am Zool 2:191–203.
Sullivan TE, Armstrong RB. 1978. Rat locomotory muscle fiber activity during trotting and galloping. J Appl Physiol 44:358–363.
Taylor CR. 1985. Force development during sustained locomotion: a determinant of gait, speed and metabolic power. J Exp Biol 115:253–262.
Thorpe SKS, Li Y, Crompton RH, Alexander RMcN. 1998. Stresses in human leg muscles in running and jumping determined by force plate analysis and from published magnetic resonance images. J Exp Biol 201:63–70.
Vilensky JA, J. Njock-Libii J, Moore AM. 1991. Trot-gallop transitions in quadrupeds. Physiol Behav 50:835–842.
Weyand PG, Lee CS, Martinez-Ruiz R, Bundle M, Bellizi MJ, Wright S. 1999. High-speed running performance is largely unaffected by hypoxic reductions in aerobic power. J Appl Physiol 86:2059–2064.
Weyand PG, Sternlight DB, Bellizi MJ, Wright S. 2000. Faster top running speeds are achieved with greater ground forces not more rapid leg movements. J Appl Physiol 89:1991–1999.
Williams TM, Dobson GP, Mathieu-Costello O, Morsbach D, Worley MB, Phillips JA. 1997. Skeletal muscle histology and biochemistry of an elite sprinter, the African cheetah. J Comp Physiol B 167:527–535.
Zajac FE. 1989. Muscle and tendon: properties, models, scaling, and application to biomechanics and motor control. Crit Rev Biomed Eng 17:359–411.

APPENDIX A
Muscle Physiological Cross-Sectional Area

A more complete explanation of the derivation of the physiological cross-sectional area of muscle (A_{phys}) is warranted here. To solve for A_{phys}, I will first need to express the cross-sectional area of the muscle (A_{cs}) as a function of the muscle length and volume. Second, I will need to express A_{phys} as a function of A_{cs}. Figure 8 shows an explanatory diagram with most of the terms used here.

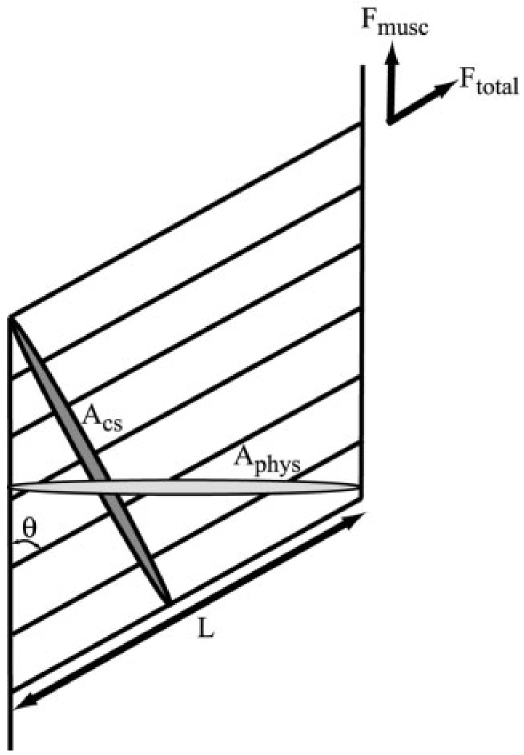

Fig. 8. Graphical explanation of physiological cross-sectional area (see Appendix A). The force output by a muscle along its line of action (F_{musc}) is calculated with its physiological cross-sectional area (A_{phys}), which is the cross-sectional area (A_{cs}) modified by the pennation angle of the fibers (θ), and the total force along its fibers or fascicles (F_{total}). The mass of muscle can be calculated using A_{phys}, fascicle length (L), cos θ, and density (1.06×10^3 kg m^{-3}), as explained in the text.

Also see Calow and Alexander (1973), Alexander and Vernon (1975), Gans and DeVree (1987), and Biewener and Full (1992) for more discussion.

A_{cs} is defined as the cross-sectional area of the muscle that is perpendicular to the line of action of the muscle fibers (F_{total}; Fig. 8). In a parallel-fibered muscle, A_{cs} is the same as A_{phys}, but this is not the case for a pennate muscle.

Let the volume (V) of a muscle equal its fiber (or fascicle) length (L) times A_{cs}:

$$V = A_{cs} \cdot L \quad (A1)$$

In a completely parallel-fibered muscle this equation needs no modification; thus A_{phys} is solved for as:

$$A_{phys} = V/L \quad (A2)$$

A_{phys} must be a function of the muscle force along the line of action of the whole muscle (F_{musc}; equal to F_{total} in a parallel-fibered muscle) and muscle stress (σ):

$$A_{phys} = F_{musc}/\sigma \quad (A3)$$

In a pennate muscle, F_{musc} is related to F_{total} as follows:

$$F_{musc} = F_{total} \cdot \cos\theta \quad (A4)$$

F_{total} is a function of the cross-sectional area of the muscle (A_{cs}) and the muscle stress (σ):

$$F_{total} = A_{cs} \cdot \sigma \quad (A5)$$

Combining Eqs. A1–5 to solve for A_{phys} produces Eq. 5 from the text: $A_{phys} = (V * \cos\theta) / L$.

APPENDIX B
Relative Activity Factor

To phrase the "relative activity factor" (G) in a different perspective, G may be related to the duty factor (β), or the fraction of the stride that the limb is in contact with the ground. Alexander (1977) and Alexander et al. (1979) used an equation to estimate the value of the peak GRF for a biped supporting itself on one leg, based on β:

$$\text{Peak GRF (or } G \cdot W) = (\pi \cdot W)/(4 \cdot \beta) \quad (B1)$$

Therefore, the expected duty factor in a biped that was experiencing a peak GRF equal to 2.5× body weight (G ~2.5, not including internal forces such as segmental weights and joint contact forces) is:

$$\beta = (\pi \cdot W)/(4 \cdot 2.5 \cdot W) \quad (B2)$$

In that case, β = 0.31, which is similar to the low duty factor (0.29) observed for an ostrich running at 12 m s^{-1} (Alexander et al., 1979), or a human running at 6 m s^{-1} (Gatesy and Biewener, 1991). Combining Eqs. 2 and B2, for activities involving single limb support and a particular duty factor, G is calculated as:

$$F_{func}/W = (\pi \cdot W)/(4 \cdot \beta \cdot W) \quad (B3)$$

Or, because G is twice the value of F_{func} / W for bipedal running, simply:

$$G = \pi/(4 \cdot \beta) \quad (B4)$$

Thus at a duty factor (β) of 0.5 (maximum walking speed), G = 1.6. This theoretical relationship between G and β is useful for calculating the "relative activity factor" (G) during activities with different duty factors (β), with the caveat that, as noted in the main text, this relationship of G and β may vary widely in fast-moving animals. Bryant et al. (1987) noted that this theoretical relationship may significantly underestimate peak forces compared to results from experiments on running animals, because mediolateral and/or horizontal forces at mid-stance may require increased peak vertical GRFs. Similar conclusions can be drawn from studies such as Cavagna et al. (1977; minimum duty factors of 0.25 for hopping, 0.35 for running but close to 0.50 for the running birds, and 0.43 for trotting) (also see Table 2). Hence, this approach is a conservative assumption, potentially underestimating G for any given speed, β, or Froude number.

APPENDIX C
Muscle Data

All muscle data for extant taxa were from the same single specimen of each taxon that I dissected, following the procedure outlined by Biewener and Full (1992:68–70). The data on human anatomy, muscle action, and dynamics are from dissection and experimental or modeling data published by Anderson (1999) and Novacheck (1998). The toe joint and muscles were omitted from the human model because of the plantigrade stance; the foot was treated as a single segment including the metatarsus. This is because when the joint was included, nonsensical digital extensor values for M_{musc} were obtained because of the distal location of the joint in the foot. Active muscles from Anderson's (1999) model included the hamstrings and Mm. gluteus medius 3, gluteus minimus 3, gluteus maximus 1–3, rectus femoris, vasti anterior, medialis, et lateralis, gastrocnemii medialis et lateralis, soleus, tibialis posterior, flexor digitorum longus, and flexor hallucis longus. The kangaroo data were scaled isometrically from a dissected specimen to a different experimental individual, following Alexander and Vernon (1975). The latter authors noted that the specimen's anatomy did not scale with perfect isometry in some dimensions, but it was not so deviant from isometry that entering alternative parameter values into my model would have greatly changed my results. All muscles with extensor moment arms were included in the model. The toe joint and muscles were omitted from my results because Alexander and Vernon (1975) did not report their dimensions or moment arms about the toe joint, and much of the muscle mass acting about the ankle joint would have been able to exert moments about the toes anyway.

I incorporated some assumptions about which muscles would actively contract (using published electromyographic data) about each joint. Because data on active muscles in bipedally running *Alligator* are not possible, I adopted the conservative assumption that if bipedal running were possible, all muscles with extensor moment arms would be active. Therefore, I included M. iliotibialis 3, M. iliofibularis, all five heads of the flexor tibialis group, M. adductor femoris 2, M. pubo-ischio-femoralis externus 3, M. ischiotrochantericus, and Mm. caudofemorales brevis et longus as active hip extensors. Most of these muscles (except M. iliofibularis, which acts during swing phase) are active at mid-stance in crocodylians (Gatesy, 1997). I used the same assumption for distal joints. For the knee extensors in *Alligator*, I included M. iliotibialis 1 and 2, M. ambiens 1 and 2, and M. femorotibialis internus. M. ambiens 1 and 2 are normally quiescent during stance in *Alligator* (Gatesy, 1997) but were included nonetheless because otherwise the knee extensor muscles of *Alligator* are very small. As a very conservative assumption, I did not include any hip flexor moments that these knee extensors would have induced. The knee extensor moment arms of other "triceps femoris" muscles were negligible in the pose modeled. All muscles with extensor moment arms about the ankle and toe joints were included. M. iliofibularis, M. flexor tibialis externus, and M. ambiens 2 have thin, complex distal tendons that interlace with muscles acting distal to the knee, but their potential action about distal joints was deemed negligible pending deeper experimental investigation. Comparable muscle activation assumptions were used for *Iguana* and *Basiliscus*, considering similar lizard electromyographic data (Gatesy, 1999b; also see Blob and Biewener, 2001).

For the extant neornithines, the following hip extensor muscles were included, which are all active at mid-stance in birds (Gatesy, 1999b) and have extensor moment arms in the poses I modeled: M. iliotibialis lateralis pars postacetabularis, M. iliofibularis, Mm. flexores cruris medialis et lateralis (pars accessoria and pars pelvica), Mm. puboischiofemorales medialis et lateralis, and Mm. caudofemoralis pars pelvica et pars caudalis. The activity of M. ischiofemoralis is unknown but it has a hip extensor moment arm, so I included it. Knee extensors that I included as active muscles include M. iliotibialis lateralis (both heads), M. ambiens, and Mm. femorotibiales (all three heads). M. iliotibialis cranialis is active during swing phase, not stance phase, and has a large hip flexor moment arm, so it was excluded. The activity of the muscles acting about the ankle and toe joints is less well known (although heads of M. gastrocnemius are clearly active; Roberts et al., 1997; Gatesy, 1999b). I therefore included all muscles that my measurements showed had extensor moment arms about these joints (as in Roberts, 2001). Muscle activity patterns are unknown for many neornithines, especially ratites (*Struthio, Dromaius*, and *Eudromia*), but I assumed the same motor patterns for all muscles. Some extensor muscles (e.g., M. caudofemoralis pars caudalis) were absent in some birds and hence not included in those models.

APPENDIX D
Model Assumptions

I discuss how uncertainty about the values of some dimensions and angles could affect my estimation of m_i in the main text with sensitivity analysis. However, here I must make my simplifying assumptions explicitly clear. The following assumptions apply to all of my models.

First, the models assumed that 100% of the muscle fibers were actively contracting ($c = 1$). Available data suggest that a fairly high (close to 100%) percentage of muscle volume can be isometrically active at mid-stance in fast-moving animals (Taylor, 1985; Perry et al., 1988; Biewener, 1989, 1990; Roberts, 2001), although much of these data are indirect estimates from biomechanical and anatomical data. More direct physiological measurements of muscle recruitment as in Armstrong et al. (1977), Sullivan and Armstrong (1978), and Armstrong and Taylor (1982) generally concur with these studies. The measured percentage of active muscle volume seldom approaches 100% and is often much lower, closer to 30–40%, although in most cases such lower values seem to be from submaximal speeds. In any case, this assumption is valid for estimating the *minimum* amount of muscle recruited. It is a conservative assumption because it probably underestimates the m_i values, as less muscle mass is needed if all muscle fibers are active ($m_i \sim c^{-1}$).

Second, these models assumed that the muscle fibers were experiencing maximum isometric stress ($\sigma = 3.0 \times 10^5$ N m^{-2}), not actively shortening or lengthening. This is generally the case at mid-stance in moving animals, at least for most muscles (Biewener, 1989; Roberts et al., 1997), and indeed stresses are often lower (e.g., Clark and Alexander, 1975; Thorpe et al., 1998; Medler, 2002; Biewener et al., 2004). In active muscles that are being lengthened by an external force, the stress can exceed 3×10^5 N m^{-2} by as much as 180% (Johnston, 1985, 1991; Biewener and Full, 1992; Marsh, 1999; Roberts, 2001). However, active lengthening typically occurs in extensors (particularly those acting about the ankle and toe joints) at early stance, not mid-stance (by which time passive stretch force enhancement has all but vanished; e.g., Biewener and Roberts, 2000; Herzog and Leonard, 2002). At mid-stance in most extant tetrapods, the limb joints are extending rather than flexing (e.g., Novacheck, 1998; Gatesy, 1999a; Irschick and Jayne, 1999), and hence most extensor muscles are either isometrically contracting or actively shortening. Some hamstring-like muscles might be actively lengthening at mid-stance, but these muscles incur a knee flexor moment as well as a hip extensor moment, so leaving this complication out of my analysis was another conservative assumption. Blob and Biewener (2001) estimated that a few strides of fast-moving quadrupedal *Iguana* and *Alligator* had actively stretching knee extensors near mid-stance, but this was neither the typical pattern nor does it match other data from more erect animals, and in my models its effects would be offset by co-contracting knee flexor muscles.

Third, the models assumed that mid-stance of locomotion could be approximated with inverse dynamics as a situation requiring quasi-static equilibrium; i.e., the body segments lacked any inertial effects. This is reasonably accurate at the exact midpoint of stance phase when the vertical position of the CM is at its maximum (in walking) or minimum (in running) and the vertical velocity of the body is zero, while the peak ground reaction forces are high (Blickhan, 1989). At this point, limb muscles and tendons act about joints to push against the ground, accelerating the body upward for late stance. Although at mid-stance the hindlimb joints are typically accelerating, and hence mid-stance does not strictly fit the conditions for static equilibrium, it is a reasonable approximation.

Fourth, I omitted antagonistic flexor muscle co-contraction about the limb joints. Roberts et al. (1998), Thorpe et al. (1998), and Roberts (2001) showed that co-contraction of some knee flexors against extensors increased the necessary extensor muscle moments about the knee by up to 50% in humans, dogs, and turkeys. This is a common pattern for many vertebrate limb joints (e.g., Anderson, 1999; Blob and Biewener, 2001; Shahar and Banks-Sills, 2002) and was presumably present in all taxa modeled here. By omitting flexor co-contraction I was making a conservative assumption that minimized the m_i estimates; including it would only have increased m_i. Yet assuming that many biarticular hip extensors were entirely inactive, rather than including them as active but ignoring the antagonistic co-contraction as I did, would have drastically lowered the amount of muscle mass available to generate the necessary extensor M_{musc}. The same applies to many biarticular or multiarticular knee flexor, ankle extensor, and toe flexor muscles such as heads of M. gastrocnemius and parts of the long digital flexors (Roberts, 2001).

Fifth, a related factor not fully considered in the present analysis is the role of multiarticular muscles. Because the m_i required to act about each of the four limb joints was calculated in isolation from the others, the potential for muscles that cross two or more joints to exert a muscle moment was excluded. In living tetrapods, many hip extensor muscles also cross the knee joint to exert a flexor moment about the knee. This co-contraction would increase the M_{musc} that the knee extensors would need to exert in most limb orientations, as mentioned above. Yet in models where the M_{musc} at the knee was estimated to be a *flexor* (rather than the usual extensor) moment, such two-joint muscles could have maintained equilibrium at the hip and knee. In these cases I ignored m_k (the required knee extensor mass), assuming that any two-joint hip extensors and knee flexors could be fully stabilizing both joints. This was another conservative assumption, although I am unaware of any tetrapods that habitually use this strategy. In addition, because almost all toe flexor musculature also crosses the ankle joint in humans, kangaroos, and birds, here I do not focus on the m_t (required toe flexor mass) for those taxa. The animals in the other bipedal models had toe flexors that did not cross the ankle, although their m_t values were typically low (see discussion in Hutchinson and Garcia, 2002). Additionally, one muscle (M. iliotibialis lateralis pars postacetabularis) in birds is able to extend both the hip and knee joints (Clark and Alexander, 1975; Gatesy, 1999b; Marsh, 1999; Roberts, 2001), but my model was not sufficiently complex to consider such unusual possibilities. However, that muscle was not counted twice in calculation of total actual extensor muscle masses.

Sixth, my models did not consider the exact position of the left leg, which should be in mid-swing phase when the right leg is in mid-stance. Given that many legs I modeled constituted as much as 10–20% of body mass, adding the exact position of the left leg CM into the model could have moved the "trunk" CM further cranially and hence increased R and m_i. This was a conservative simplifying assumption, but I kept the left leg mass as a part of the "trunk" mass.

Seventh, the models were simple 2D sagittal-plane models that did not account for forces and moments in the mediolateral direction, or allow joint positions out of the sagittal plane. This simplifying assumption maintains the focus on peak vertical GRFs, which dwarf mediolateral GRFs in extant animals with highly erect postures (adducted limb joints; e.g., Clark and Alexander, 1975; Biewener, 1989). Adding a third dimension to the models would be interesting, but unlikely to change my general conclusions.

Eighth, I did not vary the moment arms of muscles with the joint angles during my sensitivity analyses (see Results). Moment arms were measured in a reference position at the joint angles entered for the initial models (but see Alexander and Vernon, 1975). Experimental and modeling work has shown that muscle moment arms do change, often greatly, with joint angles (An et al., 1984; Anderson, 1999; Delp et al., 1999), often increasing with limb extension (Biewener, 1989, 1990; Carrier et al., 1994). Future studies need to examine this omission, but I expect that my conclusions will not differ dramatically, as the moment arms entered were very reasonable and probably close to actual values.

Finally, my estimation of the m_i ignored the contribution of passive (noncontractile) structures that could have been producing forces, and hence moments about joints. Most experimental work has shown the contribution of ligaments to be minimal except near the outer limits of joint motion (e.g., Anderson, 1999). Because I was modeling normal limb orientation (standing and mid-stance of running) rather than very extreme limb orientations, it was a fair assumption that the importance of ligaments for maintaining static equilibrium was negligible relative to the importance of the moments exerted by the muscles. Like my other assumptions, this one can be tested with more experimental and modeling analyses. Tendons must normally be experiencing the same forces as the muscles they are attached to, and hence are unable to reduce muscle stresses by sharing loads. However, substantial internal tendons that are present as elastic elements parallel to the contractile units (Zajac, 1989) might lower the forces that muscle fascicles need to bear but only in some muscles and in some animals; this is a poorly understood phenomenon.

APPENDIX E

Glossary of Symbols Used (and Units)

A	actual total limb extensor mass (% m_{body})
A_{cs}	muscle cross-sectional area (m^2)
A_{phys}	physiological cross-sectional area (m^2)
c	recruited fraction of muscle volume
d	muscle density (kg m^{-3})
F_{func}	limb "functional" force (N)
F_{max}	maximum isometric muscle force (N)
Fr	Froude number (= $v^2 g^{-1} l^{-1}$)
G	relative activity factor (multiples of W)
g	acceleration due to gravity (m s^{-2})
l	hip height (m)
L	muscle fascicle (fiber) length (m)
m_{body}	body mass (kg)
m_I	*actual* muscle mass about joint *i* (% m_{body})
m_i	*required* muscle mass about joint *i* (% m_{body})
m_H	*actual* muscle mass about hip (% m_{body})
m_h	*required* muscle mass about hip (% m_{body})
m_K	*actual*muscle mass about knee (% m_{body})
m_k	*required* muscle mass about knee (% m_{body})
m_A	*actual* muscle mass about ankle (% m_{body})
m_a	*required* muscle mass about ankle (% m_{body})
m_T	*actual* muscle mass about toe (% m_{body})
m_t	*required* muscle mass about toe (% m_{body})
m_{musc}	muscle mass (kg)
M_{musc}	muscle moment about joint *i* (N m)
R	moment arm of F_{func} (m)
r	muscle moment arm (m)
T	required total limb extensor mass (% m_{body})
v	forward velocity of locomotion (m s^{-1})
V	volume of muscle (m^3)
W	body weight (N)
β	duty factor (foot contact as % of a stride)
θ	muscle fiber pennation angle (°)
σ	maximum muscle isometric stress (N m^{-2})