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

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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 differ 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. © 2004 Wiley-Liss, Inc.

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-

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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 outgroups (*Ali- ligator, 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 macropod 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 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, 1949; 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
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]) in Table 1. 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
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 similar angles and forces are defined. The foot joint angles were constrained to be fully 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 models were taken from Alexander et al. (1979), at galliform birds. Joint angles for the Eudromia tinamou (Roberts, 2001). No kinematic data are published for the weaver, 1991). Because some uncertainty exists for all limb orientations (Irschick and Jayne, 1999) published joint angles for much smaller bipedal lizards with 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. Alligatator 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 off the ground (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 derived from Eq. 1 as:  

\[ M_{\text{musc}} = F_{\text{func}} \cdot R \]  

(1)

The \( M_{\text{musc}} \) was calculated for all four limb joints of each animal in each pose modeled. The value of the \( F_{\text{func}} \) 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 to the knee, and hence \( M_{\text{musc}} \) 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 \( F_{\text{func}} \) magnitude incurred by the negative leg during quiet standing; \( R \) was equal to body weight (W). Body weight is the body mass (\( m_{\text{body}} \)) times the acceleration due to gravity (g), so the \( M_{\text{musc}} \) in the MatLab model was derived from Eq. 1 as:

\[ M_{\text{musc}} = m_{\text{body}} \cdot g \cdot R \]  

(2)

This \( M_{\text{musc}} \) 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 \( M_{\text{musc}} \) (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. \( M_{\text{musc}} \) 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 \( M_{\text{musc}} \) 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 joint angles were strongly flexed), \( M_{\text{musc}} \) 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 joint angles were strongly extended). In the next section, I explain how the muscle mass required to produce these moments was estimated.
Muscle Masses

The next step in my analysis was calculating how much muscle mass would be required to produce the $M_{\text{musc}}$ calculated in the MatLab model. As a conservative approach to find the minimum muscle mass required to produce $M_{\text{musc}}$, I calculated the maximum moment that extensor muscles could generate and equated that with $M_{\text{musc}}$. The maximum moment that the muscles acting about a given joint can exert during isometric contraction ($M_{\text{max}}$) is equal to the maximum isometric force ($F_{\text{max}}$) 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 $F_{\text{max}}$ 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., 1999; Roberts, 2001):

$$M_{\text{max}} = F_{\text{max}} \cdot r$$  \hspace{1cm} (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 ($F_{\text{max}}$) of the muscles acting about a given joint is the product of the physiological cross-sectional area ($A_{\text{phys}}$; Calow and Alexander, 1973; Alexander and Vernon, 1975; Gans and DeVree, 1987) of the muscles and the force per unit area, or isotonic stress within the muscles ($\sigma$):

$$F_{\text{max}} = A_{\text{phys}} \cdot \sigma$$  \hspace{1cm} (4)

Gans and DeVree (1987; also see Biewener and Full, 1992) explained how $A_{\text{phys}}$ is equal to the volume ($V$) of the muscle times the cosine of the mean pennation angle of the muscle fascicles ($\theta$), 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.

$$A_{\text{phys}} = (V \cdot \cos \theta)/L$$  \hspace{1cm} (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 ($m_{\text{musc}}$) divided by the muscle density ($d$), so the maximum moment that a given mass of muscle could generate about a joint is:

$$M_{\text{max}} = (m_{\text{musc}} \cdot \cos \theta \cdot \sigma \cdot r)/(L \cdot d)$$  \hspace{1cm} (6)

Next, I assumed that the net muscle moment ($M_{\text{musc}}$) 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 ($M_{\text{max}}$). I then solved for $M_{\text{musc}}$:

$$M_{\text{musc}} = (m_{\text{musc}} \cdot c \cdot \cos \theta \cdot \sigma \cdot r)/(L \cdot d)$$  \hspace{1cm} (7)

During any particular activity, the $m_{\text{musc}}$ acting about any one joint is a certain fraction of body mass ($m_{\text{body}}$), which was expressed as a percentage, termed $m$. The factor $m$ is important because it standardizes comparisons of muscle mass among taxa of different body masses. I then solved for $m$, the percentage of body mass that would be required as actively contracting muscles.
to maintain static equilibrium about any joint $i$, in a particular limb orientation:

$$m_i = (100 \cdot M_{\text{max}} \cdot L \cdot d) / (\cos \theta \cdot \alpha \cdot \beta \cdot \gamma \cdot \alpha_i \cdot \beta_i \cdot \gamma_i \cdot m_{\text{body}})$$  

(8)

To estimate the $M_{\text{max}}$ 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 GRF multiplier of body weight commonly cited in dynamic studies of locomotion. It could be varied to represent changes of the $F_{\text{func}}$ (Eq. 1) during different activities as compared with one-legged standing. I reformulated Eq. 8 to express $M_{\text{max}}$ as a function of body mass.

$$m_i = (100 \cdot G \cdot m_{\text{body}} \cdot \alpha \cdot \beta \cdot \gamma \cdot \alpha_i \cdot \beta_i \cdot \gamma_i \cdot (R \cdot L \cdot d) / (\cos \theta \cdot \alpha \cdot \beta \cdot \gamma \cdot r \cdot m_{\text{body}})$$  

(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 $F_{\text{func}}$ (in meters), $L$ is the mean muscle fascicle length (in meters), $d$ is the muscle density (in kg m$^{-3}$), $\cos \theta$ is the cosine of the mean angle of muscle fascicle pennation, $\alpha$ 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 $F_{\text{func}}$) 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., Alexander and Vernon, 1975; 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 $F_{\text{func}}$ of 2.5 times $m_{\text{body}}$ on one leg. Entering these values into Eq. 9 allowed me to formulate the final governing equation for estimating $m_i$:

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

(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 ($\theta$) variable (Table 3). 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 $F_{\text{func}}$ moment arm $R$ was derived from the MatLab model as a component of $M_{\text{max}}$. The values for $L$, $\theta$, and $r$ were entered as mean values for all active muscles acting about the joint (Table 3), weighted by the $A_{\text{myo}}$ 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 $i$ 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)

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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_{ext} (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 \new{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.
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 (mI/mi 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 (mH/mh = 1.2), unlike Alligator (mH/mh = 0.53). However, the distal antigravity muscles (ankle and toe) were far too weak for running (mI/mi 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 mI/mi ratios of 1.3 and 1.4, whereas the low ankle mA/ma (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 mI/mi 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 mI values were very sensitive to the joint angles entered, with mI/mi ratios perilously close to 1.0. Similar to the tinamou, only certain poses (Gallus models 3, 4) had toe mI values low enough to consider running in that pose possible. Second, the exceptionally high initial knee extensor mK/mk ratios (14–31) in the tinamou and
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% mbody) 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_A ratios despite the larger size, although in the one pose modeled the ankle m_I/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% mbody per leg, as much muscle as in the entire limb of some smaller birds) explain the high m_A/m_n 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% mbody for Mm. gastrocnemii and M. fibularis longus). Limb orientation changed the m values slightly (Fig. 4): flexing the ankle joint increased the m values, but 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
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, \( Fr = \frac{v^2}{g} \frac{l^{-1}}{H^{1/3}} \), 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
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 $\frac{m_I}{m_i}$ 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 $\frac{m_I}{m_i}$ 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 (mI/m, 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, -20).
and 181 N m, respectively). These studies suggest that the knee joint mK calculated may be conservatively low (probably because I ignored co-contraction moments), but even if the mK was 16× higher (Thorpe et al., 1998) it would not change my conclusions because the mD/mK 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, Mmusc 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% mbody 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 Mmusc than in Alligator despite the diminutive size of the caudofemoral muscles: their maximum Mmusc is about 3.4 times that needed for fast running. This pattern held for all birds in all poses: the hip extensor mD/mK 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 Mmusc in my initial model (mK/mK = 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 Ffunc moment arm (R) about the knee particularly in the tinamou and chicken models.

The ankle joint musculature (mI) of the bird models was more closely matched to the demands of running, usually ~1–3 times the required musculature (mK); 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 (mI values) tended to decrease from proximal to distal (Table 3; Fig. 3). Unusually, in the birds the ankle muscle masses (mA) tended to be largest, so the mI 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 (Mmax) and (less consistently, particularly for the knee joint which was often close to the body CM) the mI/mI 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, Chris-
tian 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 mI/mi 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% mbody 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% mbody (ignoring the knee because of a flexor Mmusc 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 mI 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 mI). 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 mI/mi 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 mI 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, mI 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 (~mbody^0.67) than the stresses that need to be supported (~mbody^1.0) (e.g., Biewener, 1989, 1990, and references therein). Thus, the ratio of mI/mI drops quickly with size (Figs. 3–5; Hutchinson and Garcia, 2002) unless mI values are decreased or mI values are increased. This requirement seems to have a discontinue boundary: none of the bipeds modeled have 7% mbody of extensor muscle acting about any one joint (indeed, few mI values exceed 5% mbody), so animals with mI values of 7% or more should not be able to run with G = 2.5. Four parameters can significantly alter mI (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% mbody as total extensor muscles (both legs). These masses are roughly 2–3× the amount in Eudromia and Meleagris. Thus, ratites keep their mI/mI ratios high by increasing mI, which contradicts Leahy’s (2002) assertion that ostriches have “no relative increase in leg extensor mass” compared with smaller birds. The poses mod-
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 mi 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 mi 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 mi 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 mi 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 sauroids 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-
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 \( \frac{R}{m} \) 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, which 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% of body mass) 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).

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LITERATURE CITED


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 ($A_m$) as a function of the muscle length and volume.

Second, I will need to express $A_{phys}$ as a function of $A_m$. Figure 8 shows an explanatory diagram with most of the terms used here.
F_{\text{total}} \text{ is a function of the cross-sectional area of the muscle (} A_{\text{cs}} \text{) and the muscle stress (} \sigma \text{):}

\begin{equation}
F_{\text{total}} = A_{\text{cs}} \cdot \sigma \quad (A5)
\end{equation}

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

**APPENDIX B**

**Relative Activity Factor**

To phrase the “relative activity factor” (G) in a different perspective, G may be related to the duty factor (\beta), 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 \beta:

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

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

\begin{equation}
\beta = (\pi \cdot W) / (4 \cdot 2.5 \cdot W) \quad (B2)
\end{equation}

In that case, \beta = 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:

\begin{equation}
F_{\text{func}} / W = (\pi \cdot W) / (4 \cdot \beta \cdot W) \quad (B3)
\end{equation}

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

\begin{equation}
G = \pi / (4 \cdot \beta) \quad (B4)
\end{equation}

Thus at a duty factor (\beta) of 0.5 (maximum walking speed), G = 1.6. This theoretical relationship between G and \beta is useful for calculating the “relative activity factor” (G) during activities with different duty factors (\beta), with the caveat that, as noted in the main text, this relationship of G and \beta 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, \beta, 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 $M_{\text{musc}}$ 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. gastrocnemius 3, gastrocnemius minimus 1–3, rectus femoris, vastus anterior, medialis, et lateralis, gastrocnemius 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. iliobibialis 3, M. iliobibialis, all five heads of the flexor tibialis group, M. adductor femoris 2, M. pubo-ischio-femoris externus 3, M. ischiofemoralis, and Mm. caudofemorales brevis et longus as active hip extensors. Most of these muscles (except M. iliobibialis, which acts during swing phase) are active at mid-stance in crocodilians (Gatesy, 1997). I used the same assumption for distal joints. For the knee extensors in Alligator, I included M. iliobibialis 1 and 2, M. ambiens 1 and 2, and M. femorotibiales 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. iliobibialis, M. flexor tibialis externus, and M. ambiens 2 have thin, complex distal tendons that interface 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. iliobibialis lateralis pars postacetabularis, M. iliobibialis, Mm. flexores cruris medialis et lateralis (pars accessorius and pars pelvica), Mm. puboischiofemorales medialis et lateralis, and Mm. caudofemorales 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. iliobibialis lateralis (both heads), M. ambiens, and Mm. femorotibiales (all three heads). M. iliobibialis 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. caudofemorales 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 moment arms could affect my estimation of muscle moment arms in the main text, using sensitivity analysis. However, here I must make my simplifying assumptions explicit. 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 percentage (up to 100%) of muscle fibers 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 this 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 muscle mass needed if all muscle fibers are active (m, ~ c1).

Second, these models assumed that the muscle fibers were experiencing maximum isometric stress (σ = 5.0 × 105 N/m²), 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; Meijlder, 2002; Biewener et al., 2004). In active muscles that are being lengthened by an external force, the stress can exceed 3 × 10⁵ N/m² by as much as 150% (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; Herzig 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 early stance, but these muscles incur a knee flexion 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 some of the time, 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_i (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_i (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_i values were typically low (see discussion in Hutchinson and Garcia, 2002). Additionally, one muscle (M. iliobrachialis 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 would be interesting, but unlikely to change my general conclusions.

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)**

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>actual total limb extensor mass (% m_body)</td>
</tr>
<tr>
<td>A_cs</td>
<td>muscle cross-sectional area (m²)</td>
</tr>
<tr>
<td>A_phys</td>
<td>physiological cross-sectional area (m²)</td>
</tr>
<tr>
<td>c</td>
<td>recruited fraction of muscle volume</td>
</tr>
<tr>
<td>d</td>
<td>muscle density (kg m⁻³)</td>
</tr>
<tr>
<td>Ffunc</td>
<td>limb &quot;functional&quot; force (N)</td>
</tr>
<tr>
<td>F_max</td>
<td>maximum isometric muscle force (N)</td>
</tr>
<tr>
<td>Fr</td>
<td>Froude number (= v² g⁻¹ 1⁻¹)</td>
</tr>
<tr>
<td>G</td>
<td>relative activity factor (multiples of W)</td>
</tr>
<tr>
<td>g</td>
<td>acceleration due to gravity (m s⁻²)</td>
</tr>
<tr>
<td>h</td>
<td>hip height (m)</td>
</tr>
<tr>
<td>L</td>
<td>muscle fascicle (fiber) length (m)</td>
</tr>
<tr>
<td>m_body</td>
<td>body mass (kg)</td>
</tr>
<tr>
<td>m_i</td>
<td>actual muscle mass about joint i (% m_body)</td>
</tr>
<tr>
<td>m_i ₁</td>
<td>required muscle mass about joint i (% m_body)</td>
</tr>
<tr>
<td>m_H</td>
<td>actual muscle mass about hip (% m_body)</td>
</tr>
<tr>
<td>m_h</td>
<td>required muscle mass about hip (% m_body)</td>
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<td>m_K</td>
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<td>m_k</td>
<td>required muscle mass about knee (% m_body)</td>
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<td>m_A</td>
<td>actual muscle mass about ankle (% m_body)</td>
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<td>m_a</td>
<td>required muscle mass about ankle (% m_body)</td>
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<td>m_T</td>
<td>actual muscle mass about toe (% m_body)</td>
</tr>
<tr>
<td>m_t</td>
<td>required muscle mass about toe (% m_body)</td>
</tr>
<tr>
<td>M_musc</td>
<td>muscle moment about joint i (Nm)</td>
</tr>
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<td>R</td>
<td>moment arm of F_func (m)</td>
</tr>
<tr>
<td>r</td>
<td>muscle moment arm (m)</td>
</tr>
<tr>
<td>T</td>
<td>required total limb extensor mass (% m_body)</td>
</tr>
<tr>
<td>v</td>
<td>forward velocity of locomotion (m s⁻¹)</td>
</tr>
<tr>
<td>V</td>
<td>volume of muscle (m³)</td>
</tr>
<tr>
<td>W</td>
<td>body weight (N)</td>
</tr>
<tr>
<td>β</td>
<td>duty factor (foot contact as % of a stride)</td>
</tr>
<tr>
<td>σ</td>
<td>muscle fiber pennation angle (°)</td>
</tr>
<tr>
<td>( \sigma )</td>
<td>maximum muscle isometric stress (N m⁻²)</td>
</tr>
</tbody>
</table>