Biomechanical Modeling and Sensitivity Analysis of Bipedal Running Ability. II. Extinct Taxa

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ABSTRACT   Using an inverse dynamics biomechanical analysis that was previously validated for extant bipeds, I calculated the minimum amount of actively contracting hindlimb extensor muscle that would have been needed for rapid bipedal running in several extinct dinosaur taxa. I analyzed models of nine theropod dinosaurs (including birds) covering over five orders of magnitude in size. My results uphold previous findings that large theropods such as *Tyrannosaurus* could not run very quickly, whereas smaller theropods (including some extinct birds) were adept runners. Furthermore, my results strengthen the contention that many nonavian theropods, especially larger individuals, used fairly upright limb orientations, which would have reduced required muscular force, and hence muscle mass. Additional sensitivity analysis of muscle fascicle lengths, moment arms, and limb orientation supports these conclusions and points out directions for future research on the musculoskeletal limits on running ability. Although ankle extensor muscle support is shown to have been important for all taxa, the ability of hip extensor muscles to support the body appears to be a crucial limit for running capacity in larger taxa. I discuss what speeds were possible for different theropod dinosaurs, and how running ability evolved in an inverse relationship to body size in archosaurs. J. Morphol. 262: 441–461, 2004.   © 2004 Wiley-Liss, Inc.

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What gaits did extinct dinosaurs use? The consensus is that the huge sauropod dinosaurs were restricted to walking (Bakker, 1986; Alexander, 1985a, 1989; Thulborn, 1989; Christiansen, 1997). Trackway evidence confirms that smaller nonavian theropod (bipedal, predatory) dinosaurs could run (Thulborn, 1990; Irby, 1996), as their avian descendants do today. There is also tantalizing evidence from trackways suggesting that some extinct theropods of medium size (~100–2,000 kg body mass) could move relatively quickly, even run (Farlow, 1981; Kuban, 1989; Day et al., 2002).

Assessments of the running ability of the largest theropods such as an adult *Tyrannosaurus* vary. Certainly *Tyrannosaurus* could stand and walk, and like other extinct dinosaurs it presumably did not use a hopping gait (Thulborn, 1990). Some studies suggest that it could not run at all (Lambe, 1917; Thulborn, 1982, 1989, 1990), whereas others infer that *Tyrannosaurus* and similar massive theropods had limited (if any) running ability (Newman, 1970; Hotton, 1980; Alexander, 1985a, 1989, 1991, 1996; Horner and Lessem, 1993; Farlow et al., 1995; Christiansen, 1998, 1999; Hutchinson and Garcia, 2002), and yet others are certain that large theropods had extreme running proficiency (Osborn, 1916; Coombs, 1978; Bakker, 1986; Paul, 1988, 1998; Holtz, 1995; Blanco and Mazzetta, 2001). Consequently, running speed estimates range from a "conservative" 11 m s^{-1} or less (25 mph; Horner and Lessem, 1993; Farlow et al., 1995; Christiansen, 1998) up to a "heterodox" 20 m s^{-1} (45 mph; Coombs, 1978; Bakker, 1986; Paul, 1988, 1998), although a few studies such as Thulborn (1982, 1989, 1990), Alexander (1989, 1996), and Hutchinson and Garcia (2002) assert even slower speeds, around 5–11 m s^{-1}.

Dinosaur speeds can be estimated roughly from fossil tracks (Alexander, 1976; Thulborn, 1990; but see Alexander, 1991) using 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, 1976, 1989, 1991). Only one purported footprint exists for *Tyrannosaurus* (Lockley and Hunt, 1994). Thus, so far maximum speeds for *Tyrannosaurus* cannot be estimated from trackways, although the minimum step length estimated from this track was 2.8 m (= minimum stride length 5.6 m, similar to stride lengths from medium-sized theropods moving at moderate speeds; Farlow, 1981; Kuban, 1989; Day et al., 2002). The absence of running trackways despite the abundance of walking trackways from very large theropods (Farlow et al., 2000) prompts the question: How fast could the largest theropods run, if they could run at all (Molnar and Farlow, 1990; Biewener, 2002)?

Biomechanical theory holds that larger terrestrial vertebrates are more limited in their athletic prowess because of the near-isometric scaling of the cross-sectional areas of soft tissues and bones with increasing body mass. This scaling results in positive allometry of supportive tissue loads, and eventually lower maximum locomotor performance (Alexander et al., 1979a; Maloiy et al., 1979; Biewener, 1983, 1989, 1990, 2000; Garland, 1983; Calder, 1996; Iriarte-Díaz, 2002; Blanco et al., 2003). Considering long bone scaling and mechanics, this pattern apparently held for dinosaurs as well (Alexander, 1985a, 1989; Gatesy, 1991; Carrano, 1998, 1999; Christiansen, 1998, 1999). As generating supportive force is an important limit on running speed (Weyand et al., 2000), and the relatively smaller cross-sectional area of muscles in larger animals leaves them less capable of generating force, larger dinosaurs should have been relatively slower than smaller dinosaurs, perhaps even absolutely slower. Yet if, as some paleontologists have argued, *Tyrannosaurus* was indeed a remarkably adept runner, unlike a living elephant, or even faster than a living rhinoceros, then our understanding of the limits on terrestrial locomotor performance must be inaccurate. Extinct vertebrates such as large theropod dinosaurs might be thought to offer a provocative challenge to general biomechanical principles based on living animals (Paul, 1998).

Using a simple quasi-static biomechanical analysis of the forces and moments at mid-stance of running, Hutchinson and Garcia (2002) showed that an adult *Tyrannosaurus* would have needed roughly 26–86% (mainly depending on limb orientation) of its body mass as limb extensors in order to run at Fr ~16, roughly 20 m s^{-1}. Our sensitivity analysis of the unknown parameters in the model was brief, but still did not support the "heterodox" hypothesis that *Tyrannosaurus* could run 20 m s^{-1}, and even cast doubt on slower "conservative" speeds around 11 m s^{-1}. This is because it did not seem reasonable that an animal could have had such a high proportion of its mass as extensor muscles, especially if posed in a crouched limb orientation, as in most studies that have advocated high-speed tyrannosaurs.

Hutchinson and Garcia (2002) recognized that in order for an animal to run quickly, first and foremost the limb muscle-tendon units must be able to generate the necessary forces and moments in order to maintain fast running. If that requirement is not met in a running animal, its limbs will collapse underneath it or it will be unable to attain such speeds at all. A second advantage of our study was that we explicitly examined the unknown parameters in our model with sensitivity analysis to check which parameters were most important (Biewener, 2002). Our conclusions were supported within a reasonable range of feasible input parameters, despite the many unknown values in our model. The approach has since been validated for extant bipeds, from basilisk lizards to ostriches and humans (Hutchinson, 2004), by obtaining results that reflect actual locomotor ability.

This study follows up on the analysis begun by Hutchinson and Garcia (2002), investigating how much hindlimb extensor muscle mass theropod dinosaurs would have needed to run quickly. As in that study and Hutchinson (2004), I define "fast running" as Fr ~17; or about 20 m s^{-1} for an animal the size of *Tyrannosaurus*. This relative speed matches the more extreme portrayals of tyrannosaur running (Bakker, 1986, 2002; Paul, 1988, 1998). I recognize, however, that the controversy about tyrannosaur speeds is more than a simple fast vs. slow dichotomy. Indeed, more recent portrayals of large theropod speeds are markedly lower than past "heterodox" assessments, ~11–14 m s^{-1} (Christiansen, 1998; Blanco and Mazzetta, 2001); few still seem to favor speeds of 20 m s^{-1} or more. Thus, I examine how narrowly possible speeds can be bounded for extinct theropod dinosaurs.

Like Hutchinson and Garcia (2002), here I focus much attention on the largest well-known theropod, *Tyrannosaurus*, but this study has a broader phylogenetic, functional, and anatomical scope. Nine theropod taxa are modeled as opposed to three in the previous study. The modeling approach is also explained more thoroughly, identifying the key parameters and assumptions in the method (also see Hutchinson, 2004). Many data are revised and reanalyzed as well. In particular, I conducted a detailed sensitivity analysis to examine how rigorous my conclusions (and those of Hutchinson and Garcia, 2002) are. I also identified some problematic aspects of the model that future studies should inspect. I investigated how narrowly unknown model parameters might be bounded, given what we understand of locomotor biomechanics and archosaur functional anatomy. My perspective here differs from the previous study, in that rather than focus on muscle masses added together for a whole limb, I emphasize how musculoskeletal mechanics might have differed from proximal to distal joints and muscles in theropods of different sizes. This is because (based on Hutchinson, 2004) I expected distal joints such as the ankle to be the crucial limits on running ability. I ask, should this pattern hold for even the largest taxa? Additionally, I discuss how my models reveal the influence of body size on locomotor performance, and reconstruct how bipedal running capacity may have evolved in archosaurs.

MATERIALS AND METHODS

I used inverse dynamic analysis of biomechanical models with various theropods (Fig. 1) to gauge whether at mid-stance of a running step they could have had sufficient muscle mass to support the body. I examined nine extinct taxa: *Archaeopteryx, Compsognathus, Coelophysis, Velociraptor*, a small tyrannosaur, the moa *Dinornis, Dilophosaurus, Allosaurus*, and an adult *Tyrannosaurus*, covering a size range of five orders of magnitude.
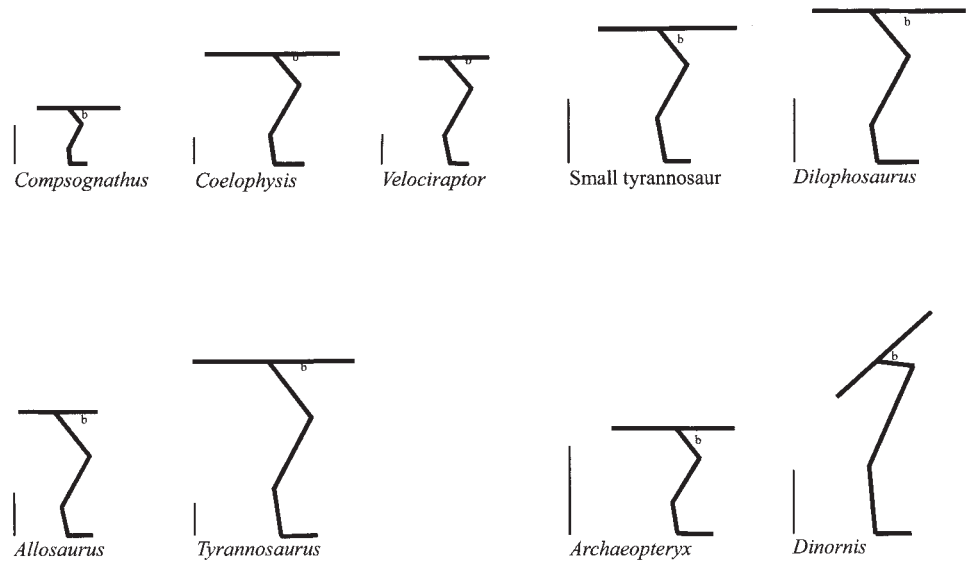
Fig. 1. Images of initial Mat-Lab models showing the poses used in the biomechanical analysis. All are images from the right side of the body in lateral view, showing single-limb support. Depicted trunk lengths had no influence on the analysis. "b" indicates the location of the entire body CM. The vertical scale bars are 0.1 m for the smallest bipeds (*Archaeopteryx, Compsognathus, Coelophysis, Velociraptor*) and 0.5 m for the others. See Table 5 for the exact joint angles used.

Information on the specimen numbers used for the models is in Appendix B.

The oldest known bird, *Archaeopteryx*, is a pigeon-sized basal bird; considering its small size it would be expected to be a decent runner. *Coelophysis* is a basal theropod dinosaur from the Triassic Period that is similar in size and morphology to the presumptive trackmakers of some fossilized running trackways (Irby, 1996; Gatesy et al., 1999; Farlow et al., 2000). *Compsognathus, Velociraptor,* and *Archaeopteryx* are successively closer outgroups to Neornithes (*Tyrannosaurus* is considered basal to all of them except perhaps *Compsognathus*; Sereno, 1999; Holtz, 2001) and are relatively small in size as well. Because it is generally accepted that smaller theropods were proficient runners, modeling these taxa was important to test the validity of the model for extinct taxa, and their phylogenetic positions helped to gauge the polarity of running evolution. I expected that modeling fast running in these taxa would show that these animals all were capable of generating the muscle moments (i.e., torques or rotational forces) needed for fast running.

If body size were an important biomechanical constraint on running ability in extinct nonavian theropods, then smaller theropods, including juveniles, would have had less limited running ability compared to their larger relatives (Currie, 1998). I included a model of a small, presumably immature tyrannosaur for this purpose. *Dilophosaurus* is a larger relative of *Coelophysis*, so I modeled it for comparison with *Tyrannosaurus* as well as smaller and more or less basal taxa. I also modeled the medium-sized *Allosaurus* to estimate running capacity for theropods around 1–2 tons of mass, expecting that such animals would be mediocre runners at best. The extinct flightless ratite bird *Dinornis* (a large moa) was included for comparison to smaller running birds (e.g., Hutchinson, 2004) as well as the similarly sized small tyrannosaur. Models of these larger animals should show more limited running ability compared to much smaller dinosaurs.

Finally, I modeled running in *Tyrannosaurus* to see how limited the running ability of a 6,000-kg biped might have been. Could its muscles have been large enough to generate the moments required for fast running, or at that enormous size would the muscle mass and moments needed to support the body have been too extreme for any "cursorial" specializations to overcome?

Inverse Dynamic Analysis

Data were collected to build a 2D model of a biped standing on its right leg in order to estimate how large the leg muscles needed to be to support that pose during fast running. I entered these data into a computer model to construct a free-body diagram (e.g., see Nordin and Frankel, 1989), explained in Figure 2 and in more detail by Hutchinson (2004; also see Roberts et al., 1998; Hutchinson and Garcia, 2002). Briefly, I estimated joint centers (based on comparison with extant taxa) and measured skeletal limb segment lengths to build 2D models of single-legged support, and posed them in initial limb orientations to analyze the dynamics of each model (explained further below). All data entered were remeasured and recalculated with some different assumptions from Hutchinson and Garcia (2002), so some parameter values differed (see Tables 2–5). I used MatLab software (MathWorks, Natick, MA; v. 6.5, 2002) to calculate the net moments of internal and external forces (M_{musc}) acting about the hindlimb joints during standing on the right leg. Finally, using inverse dynamics the minimum amount of actively contracting extensor muscle required to be acting about a joint (m_i) to balance the moments (from the free-body diagram) was calculated as:

$$m_i = (100 \cdot G \cdot g \cdot R \cdot L \cdot d)/(\cos \theta \cdot \sigma \cdot c \cdot r) \qquad (1)$$

In Eq. 1, G is the "relative activity factor" from the model (= 2.5 to represent the higher forces during fast running relative to standing with G = 0.5), g is the acceleration due to gravity (9.81 m s^{-2}), R is the total moment arm of the forces (F_{func}, in meters) acting about the joint that oppose body support (e.g., the ground reaction force; GRF), L is the mean extensor muscle fascicle length (in meters), d is the muscle density (1.06×10^3 kg m^{-3}), cos θ is the cosine of the mean angle of muscle fascicle pennation, σ is the maximum isometric stress (force/area; 3.0×10^5 N m^{-2}) of the muscles, c is the fraction of maximum exertion by the muscles (set at 1.0 for all models to estimate minimum muscle mass with 100% exertion), and r is the mean moment arm of the extensor muscles (in meters). The term cos θ is close to 1.0 in living animals, difficult to measure accurately (Zajac, 1989), and would lead to a higher estimate of m_i in these models, so it was left out (θ = 0°) as a simplifying conservative assumption. More explanation of these parameters, their input values, and the mathematics and assumptions used in this analysis were presented in Hutchinson (2004). By entering the constant values mentioned above, Eq. 1 collapses to:

$$m_i = R \cdot L \cdot r^{-1} \cdot 1.767 \text{ meters}^{-1} \qquad (2)$$

The values of R, L, and r varied for different taxa and limb orientations (Tables 2–4). The m_i values from all four limb joints
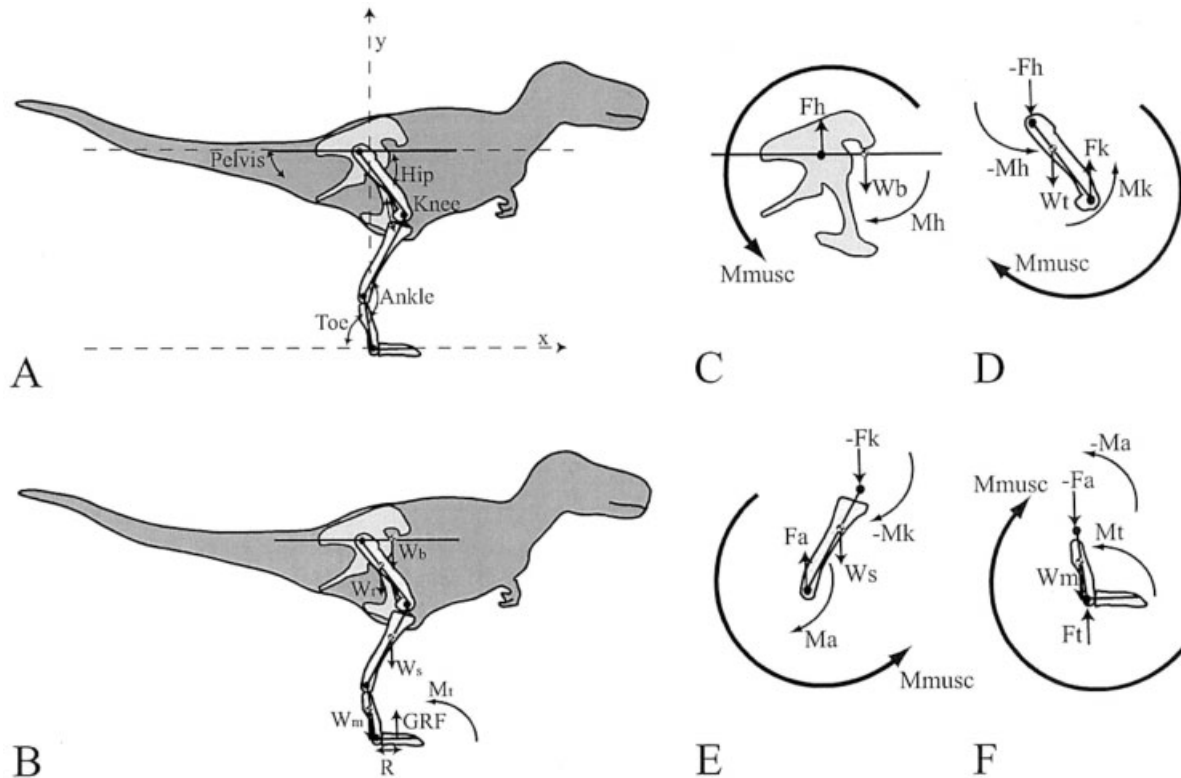
Fig. 2. Schematic explanation of the MatLab model procedure to obtain the value of M_{musc} for this analysis (also see Hutchinson and Garcia, 2002; Hutchinson, 2004). The skeletal illustration of a tyrannosaur was modified from Paul (1988), showing the model in right lateral view as in Figure 1. **A:** 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).

indicated the active muscle masses required to maintain static equilibrium about those joints at mid-stance of running, presented in the Results. Like Hutchinson (2004), but unlike Hutchinson and Garcia (2002), here I focus more on the m_i values for the joints than on the total muscle mass for all joints (T), to examine how muscle masses within a limb needed to be apportioned for body support among various taxa. The m_i values will then be compared to actual extensor muscle masses (m_I values) in extant taxa (from Hutchinson, 2004). The symbols used in this study are summarized in Appendix A.

Modeling Extinct Taxa

The obvious challenge for my modeling procedure with extinct taxa is that most required data from soft tissues are not directly observable in fossils (Bryant and Seymour, 1990), even though much information can be gleaned from muscle scarring and other details (Witmer, 1995; Hutchinson, 2001a,b, 2002; Carrano and Hutchinson, 2002). Only the skeletal segment lengths that are needed for building each model can be directly measured from fossil bones (Tables 1, 2).

Body masses used are listed and explained in Table 2. To remove the confounding effects of unknown body mass from my calculations, I expressed m_i as a percentage of m_{body} (see Hutchinson, 2004). Thus, entering any different m_{body} value for any of my models has negligible effects on the m_i estimated for the model; m_{body} is not a term in Eqs. 1, 2. This is a crucial point for the models of extinct taxa: the exact value of m_{body}, whether it was 4,000–8,000 kg for *Tyrannosaurus*, did not matter for my analysis. Body mass was estimated simply to facilitate comparisons among taxa (Table 2). However, the linear dimensions in the model are tightly correlated with body size, so although my analysis was independent of exact body mass, it was not size-independent.

The position of the center of mass (CM) of the trunk segment is crucial, but also notoriously difficult to estimate (Henderson, 1999). In extant taxa, the body CM position (along the longitudinal axis of the body) is highly variable, even when standardized as a fraction of thigh segment length. Henderson's (1999) models of dinosaur body CM positions place the CM x-coordinate position at a distance of about 50% of thigh segment length in meters cranial to the hip joint. I used this distance as an initial CM value for the extinct taxa because it is the most rigorous published

TABLE 1. Dimensions of biomechanical models used by Hutchinson (2004) for extant taxa, used to calculate dimensions for the extinct taxa in this analysis (see Table 2)

	Homo	*Macropus*	*Basiliscus*	*Iguana*	*Alligator*	*Eudromia*	*Gallus*	*Meleagris*	*Dromaius*	*Struthio*
Mass (% m_{body}):										
thigh	0.1240	0.1230	0.0785	0.0527	0.0220	0.0451	0.0772	0.0511	0.1300	0.0995
shank	0.0494	0.0450	0.0288	0.0157	0.0112	0.0347	0.0626	0.0365	0.1170	0.0674
metatarsus	0.0169	0.0110	0.0126	0.0046	0.0065	0.0086	0.0147	0.0068	0.0173	0.0132
foot	0.0029	-	0.0110	0.0030	0.0088	0.0042	0.0077	0.0047	0.0082	0.0074
m_{body} (kg)	71.0	6.6	0.191	4.04	5.91	0.406	2.89	3.70	27.2	65.3
CM position (% total length from distal end):										
thigh	57	76	61	40	61	55	53	57	78	46
shank	57	62	51	47	48	54	58	68	76	61
metatarsus	61	3.8	67	40	48	32	52	53	31	50
trunk	100	53	79	94	150	83	82	52	44	42

	Average	Reptilia	Birds		Average	Reptilia	Birds
Mass (% m_{body}):				CM position (% total length from distal end):			
thigh	8.03	6.95	8.06	thigh	58	56	58
shank	4.69	4.68	6.37	shank	58	58	63
metatarsus	1.12	1.05	1.21	metatarsus	44	47	43
foot	0.640	0.690	0.640	trunk	78	78	61

Measured masses and relative center of mass (CM) positions (expressed along the long axis of the bone, from the distal end in the limb segments, as percentages of thigh, shank, metatarsus, or foot segment length; or cranially from the hip joint in the trunk segment, as a percentage of thigh segment length) are noted for each segment. The "Average" column represents the average proportions for all 10 taxa from Hutchinson (2004) for comparison. The "Reptilia" column was the average proportions, excluding the two mammals, that were applied to all extinct animal models except *Dinornis*. The latter model used the "Birds" column instead, which contains the average proportions only for the five bird taxa from Hutchinson (2004). *Archaeopteryx* is nominally a bird, but like many other basal maniraptoran dinosaurs its hindlimb anatomy was intermediate between basal theropods and extant birds (Hutchinson, 2002), so the default "Reptilia" scaling was used, not the "Birds" column. This had negligible effects on calculating m_i.

estimate. Using the larger relative values of the CM x-coordinates from extant taxa (about 0.78* thigh segment length in the x-coordinate; Table 1) would have proportionately increased my calculations of the R and m_i values (Table 4; see Discussion). The y-coordinate CM position was placed level with the hip joint. This did not matter for estimating m_i values unless the pelvis was pitched upward and the CM was more ventrally displaced (as in life), in which case it would have tended to increase the m_i values by increasing R. Hence, these CM assumptions were conservative, tending toward low m_i estimates and more generous assessments of running ability.

Limb segment masses and CM locations were fairly consistent among the extant taxa (Table 1), so I used them to enter single values for the extinct taxa in Table 2. This value was based on an average of the relative segment CM positions (see Table 1, "average" column). Limb segment masses appear to scale roughly isometrically in erect tetrapods (e.g., data from Maloiy et al., 1979; Alexander et al., 1981; Hutchinson, 2004), so the use of proportional values for extinct taxa is justifiable. Any inaccuracies in these data are presumably minimal relative to the body mass, which is very large compared with the limb segments in tetrapods. However, omitting these data altogether would have introduced more errors than including a reasonable estimate, because the limb masses shift the whole body CM caudoventrally and thus have an effect on R. The limb masses would tend to overestimate m_i if excluded from the analysis (see Discussion).

Finally, the models of the extinct taxa were posed in a "crouched" limb orientation (as reconstructed by Paul, 1988, 1998, and others) for the initial models. I entered different joint angles in later approaches, which will be discussed in the Sensitivity Analysis section (below). The initial joint angles were the same for most extinct taxa: pelvic angle 0°, hip angle 50°, knee angle 110°, ankle angle 140°, metatarsus angle 80°. One exception is the moa (*Dinornis*) model, which was posed in the same joint angles (40°, 45°, 70°, 150°, and 85°) as the ostrich (*Struthio*) in Hutchinson (2004). These angles are shown in Figure 1 and Table 5.

Muscle Moments

The unknown data on muscular anatomy are at least as vexing as the unknown body dimension data. Equation 2 shows that only three parameters are crucial for the model: R, L, and r. The value of R was output by the MatLab model as a function of the net muscle moment required to maintain static equilibrium (M_{musc}), and was dependent on the limb orientation adopted (Hutchinson, 2004). The remaining values L and r vary widely in extant animals and were estimated separately for each extinct taxon using a phylogenetic approach (Hutchinson, 2001a,b, 2002; Carrano and Hutchinson, 2002).

I entered preliminary values of L at all joints (Table 3) based on the average value of L as a fraction of segment length, presuming that non-neornithine theropod limb muscles had myology, including relative fascicle lengths, that was intermediate between basal reptiles and neornithines (Carrano and Hutchinson, 2002; Hutchinson, 2002). This intermediate anatomy is related to inferred differences from extant archosaurs in kinematics and limb orientation (Gatesy, 1990; Carrano, 1998; Hutchinson and Gatesy, 2000). I will examine this critical assumption in detail with sensitivity analysis. Tables 3 and 4 show the mean values that I entered for each joint. Muscle pennation (θ) was omitted (see Discussion and Hutchinson, 2004).

The value of r about the hip (Table 4) was taken as the distance from the distal end of the fourth trochanter (where major hip extensors would have inserted; Hutchinson, 2001b, 2002) to my estimate of the hip joint center (the middle of the femoral head, as in extant animals). Note that this is a conservative assumption, because in most postures the actual value of r would be less than this distance, as the muscle line of action is at an acute angle to the insertion. The knee extensor r was estimated as the distance from the midpoint of the tibial plateau to the cranial tip of the cnemial crest (pers. obs. of the extant archosaurs dissected and modeled; again a generous estimate).

I estimated r about the 1) ankle and 2) toe joints by measuring the distance respectively from their joint centers (assumed to be

TABLE 2. Dimensions of biomechanical models of extinct taxa used in this analysis, based on the dimensions from Table 1

	Compsognathus	Coelophysis	Velociraptor	Small tyrannosaur	Dilophosaurus	Allosaurus	Tyrannosaurus	Archaeopteryx	Dinornis
Length (m):									
thigh	0.061	0.16	0.16	0.37	0.47	0.69	1.13	0.046	0.30
shank	0.083	0.233	0.221	0.46	0.60	0.71	1.26	0.066	0.86
metatarsus	0.035	0.116	0.108	0.325	0.28	0.35	0.699	0.038	0.51
foot	0.047	0.115	0.076	0.191	0.33	0.30	0.584	0.040	0.30
trunk	0.80	2.9	2.9	3.0	6.0	8.0	12	0.40	2.0
Mass (kg):									
thigh	0.21	1.4	1.4	15	30	110	417	0.017	23
shank	0.14	0.94	0.94	9.8	20	66	281	0.012	18
metatarsus	0.032	0.21	0.21	2.2	4.5	16	63.0	0.0026	3.4
foot	0.021	0.14	0.14	1.4	2.9	9.0	41.0	0.0017	1.8
trunk	2.6	17.3	17.3	182	373	1199	5198	0.20	234
m_{body}	3.0	20	20	210	430	1400	6000	0.25	280
CM position (m):									
thigh	0.034	0.090	0.090	0.21	0.26	0.39	0.63	0.026	0.17
shank	0.048	0.14	0.13	0.27	0.35	0.41	0.73	0.038	0.54
metatarsus	0.017	0.054	0.051	0.15	0.13	0.17	0.33	0.018	0.22
trunk: extant	0.048	0.12	0.12	0.29	0.37	0.54	0.88	0.036	0.18
trunk: thigh/2	0.031	0.080	0.080	0.19	0.24	0.35	0.565	0.023	0.15

Body masses were: for *Compsognathus* and *Archaeopteryx* from Seebacher (2001); for *Coelophysis* from Paul (1988); for *Tyrannosaurus* from Farlow et al. (1995); for *Velociraptor* assumed equal to the similarly sized *Coelophysis*; for the small tyrannosaur, *Dilophosaurus*, and *Allosaurus* isometrically scaled down by femur length from *Tyrannosaurus*; and for *Dinornis* scaled with femur circumference from Campbell and Marcus (1993). The rows "trunk: extant" and "trunk: thigh/2" are, respectively, for scaling the CM distance from the hip joint along the x-coordinate of the trunk segment using the "Average" data for extant Reptilia, or for using the thigh segment length divided by two (as in Hutchinson and Garcia, 2002; following Henderson, 1999), which usually produced lower CM distances.

TABLE 3. *Ratios of extensor muscle fascicle lengths (L) to segment lengths ("meta" = metatarsus) among extant taxa, used to calculate L for the extinct taxa below*

Extant taxa	Fascicle length/segment length:			
	hip/thigh	knee/shank	ankle/meta	toe/foot
Basiliscus	0.367	0.321	0.259	0.108
Iguana	0.411	0.429	0.536	0.417
Alligator	1.13	0.451	0.747	0.358
Eudromia	0.990	0.279	0.392	0.471
Gallus	1.00	0.392	0.376	0.292
Meleagris	0.536	0.267	0.250	0.392
Dromaius	0.911	0.191	0.207	0.262
Struthio	0.659	0.209	0.154	0.177
Homo	0.282	0.212	0.301	0.533
Macropus	0.202	0.0310	0.152	0.0400
Average	0.649	0.278	0.337	0.305
Reptilia	0.751	0.317	0.365	0.310
Archosauria	0.976	0.359	0.512	0.339
Birds	0.819	0.268	0.276	0.319

Extinct taxa	Fascicle length (L) (m):			
	hip	knee	ankle	toe
Compsognathus	0.046	0.026	0.013	0.015
Coelophysis	0.12	0.074	0.042	0.037
Velociraptor	0.12	0.070	0.039	0.024
Small tyrannosaur	0.28	0.15	0.12	0.059
Dilophosaurus	0.35	0.19	0.10	0.10
Allosaurus	0.52	0.23	0.13	0.093
T. rex	0.85	0.40	0.26	0.18
*T. rex*_scaleall	0.73	0.35	0.24	0.18
*T. rex*_scalearcho	1.0	0.40	0.28	0.19
*T. rex*_scalebirds	0.93	0.34	0.19	0.19
Archaeopteryx	0.035	0.021	0.014	0.012
Dinornis	0.25	0.23	0.14	0.096

The row "Average" has the average ratio of L to segment length for all 10 extant taxa from Hutchinson (2004), used only to calculate L for the model "*T. rex*_scaleall." The row "Reptilia" contains the same ratio but averaged only for members of the clade Reptilia (i.e., excluding the two extant mammals), used to calculate L for all other extinct models except the "*T. rex*_scalebirds" and "*Dinornis* models, which used data from the row "Birds." Row "Archosauria" shows the ratio of L to segment length calculated for the average of (*Alligator* + Birds), used for model "*T. rex*_scalearcho."

in similar relative positions as in extant taxa) to: i) the caudal edge of the lateral condyle of the tibiotarsus (astragalus in most extinct theropods), times 1.5 to accommodate for articular cartilage and extensor tendon thickness (again, generous estimates based on dissections from Hutchinson, 2004); and ii) the caudal (plantar) surface of the distal end of the third metatarsal, times only 1.1, as the cartilages and tendons are relatively thinner here in extant taxa (pers. obs.). These values (Table 4) will be checked in future analyses of changes in individual muscle moment arms with joint angles, but are presumably reasonable, even generous, approximations.

RESULTS

Table 4 details the initial results for the nine taxa modeled. I focus here on the m_i values for three of the four major limb joints: the hip (m_h), knee (m_k), and ankle (m_a). I mostly ignore the toe extensor masses (m_t) as in Hutchinson (2004) be-cause the ankle extensors (and plantar ligaments) could have been producing most or all of the required toe joint moments in most cases. The proximity of the knee joint to the body CM kept the m_k values lower in most models. Yet in *Tyrannosaurus* the m_i values for the hip and ankle joints surpass observed maximum masses for extant taxa ($<7\%$ m_{body}, including data from well-muscled ratite and galliform birds; Hutchinson, 2004). In contrast, the smaller theropods are below this threshold, with m_i values generally increasing with size, as expected.

Assuming that these data provide a rough limit for how much muscle mass can be available to support fast running (at Fr ~17), any extinct animal modeled that has one or more m_i values above 7% m_{body} for its limb joints should not have been a good runner. This is unless one makes the more speculative assumption that an animal had relatively more muscle mass than observed in living bipeds. The limb mass in my models (Table 2) was only about 13% m_{body} per leg (16% for *Dinornis*), so for the three main joints (hip, knee, and ankle; ignoring the toe) the maximum total muscle mass allowable for fast running (T) should be much lower than 21% m_{body} (3 joints * 7%/joint)—probably closer to 10% m_{body}. The latter value is comparable to actual total muscle masses (A) in the largest and most adept extant bipedal runners (11–14%; Fig. 5). Additionally, my models of extant taxa (Hutchinson, 2004) support the inference that good runners have "safety factors" of ~1–3 for their major hindlimb joints, presumably because they can run faster than with G = 2.5; their maximum speeds would entail higher forces, perhaps bringing their "safety factors" close to 1. Additionally, unexpected nonsteady-state forces and moments can be much higher than those experienced in regular rapid locomotion (Alexander et al., 1979a,b; Alexander, 1989; Biewener, 1989, 1990). Whatever the limit on total extensor muscle mass is, proceeding with a limit of 7% m_{body} per joint seems extremely generous (e.g., hip and knee extensor masses do not exceed 5% m_{body} even in ratites; Hutchinson, 2004), biasing my analysis to accept extinct animals as good runners.

Considering the data from Table 4 (and Figs. 3, 4), only *Tyrannosaurus* should not have been a fast runner, because its hip and ankle extensors were not large enough to exert the necessary moments. Smaller theropods should have been good runners, as anticipated. Yet, perhaps surprisingly, even medium-sized theropods such as *Dilophosaurus* and *Allosaurus* could have been fairly good runners, although much closer to muscular limits than smaller taxa. Next, in the Discussion I use sensitivity analysis to identify which parameters were the most uncertain and critical for the results of my analysis, and how so, in order that future work may refine these parameters and reexamine my conclusions.

TABLE 4. Initial results from the biomechanical analysis of the models from Tables 2, 3
(for joint angles, see Table 5 and Figs. 1, 3, 4)

	Compsognathus					*Dilophosaurus*			
	hip	knee	ankle	toe		hip	knee	ankle	toe
L (m)	0.046	0.020	0.015	0.013	L (m)	0.35	0.19	0.10	0.10
r (m)	0.021§	0.0090	0.0060	0.0030	r (m)	0.19	0.086	0.041	0.022
R (m)	0.031	0.0091	0.032	(0.026)	R (m)	0.24	0.070	0.23	(0.18)
m_i (% m_{body})	0.52	0.21	0.59	(1.1)	m_i (% m_{body})	3.3	1.3	4.8	(7.1*)
m_I/m_i (max)	14	35	12	(6.4)	m_I/m_i (max)	2.1	5.4	1.5	(0.99*)
T (% m_{body})	1.3		A(max)/T	12	T (% m_{body})	9.4		A(max)/T	1.6

	Coelophysis					*Allosaurus*			
	hip	knee	ankle	toe		hip	knee	ankle	toe
L (m)	0.12	0.74	0.42	0.36	L (m)	0.52	0.23	0.13	0.093
r (m)	0.080	0.028	0.021	0.0070	r (m)	0.30	0.071	0.051	0.017
R (m)	0.080	0.026	0.089	0.070	R (m)	0.34	0.11	0.25	(0.18)
m_i (% m_{body})	0.90	0.56	1.5	(3.2)	m_i (% m_{body})	4.4	2.8	5.3	(8.6*)
m_I/m_i (max)	7.8	12	4.7	(2.2)	m_I/m_i (max)	1.6	2.5	1.3	(0.81*)
T (% m_{body})	3.0		A(max)/T	5.0	T (% m_{body})	13		A(max)/T	1.2

	Velociraptor					*Tyrannosaurus*			
	hip	knee	ankle	toe		hip	knee	ankle	toe
L (m)	0.12	0.70	0.39	0.24	L (m)	0.85	0.40	0.26	0.18
r (m)	0.051§	0.021	0.022	0.011	r (m)	0.37	0.22	0.12	0.070
R (m)	0.080	0.026	0.083	(0.064)	R (m)	0.57	0.18	0.45	(0.32)
m_i (% m_{body})	1.4	0.71	1.3	(1.2)	m_i (% m_{body})	9.7*	2.7	8.3*	(7.1*)
m_I/m_i (max)	5.0	10	5.4	(5.8)	m_I/m_i (max)	0.72*	2.6	0.84*	(0.99*)
T (% m_{body})	3.4		A(max)/T	4.4	T (% m_{body})	21		A(max)/T	0.72

	Small tyrannosaur					*Archaeopteryx*			
	hip	knee	ankle	toe		hip	knee	ankle	toe
L (m)	0.28	0.15	0.12	0.059	L (m)	0.035	0.021	0.014	0.012
r (m)	0.14	0.086	0.056	0.024	r (m)	0.012§	0.0030	0.0020	0.0010
R (m)	0.19	0.054	0.17	(0.12)	R (m)	0.022	0.0073	0.025	(0.018)
m_i (% m_{body})	2.9	0.76	3.2	(2.4)	m_i (% m_{body})	0.45	0.39	1.4	(1.7)
m_I/m_i (max)	2.4	8.8	2.2	(2.9)	m_I/m_i (max)	15	18	5.0	(4.1)
T (% m_{body})	6.9		A(max)/T	2.2	T (% m_{body})	2.2		A(max)/T	6.7

	Dinornis			
	hip	knee	ankle	toe
L (m)	0.25	0.23	0.21	0.14
r (m)	0.17§	0.15	0.075	0.039
R (m)	0.12	0.19	0.18	(0.14)
m_i (% m_{body})	1.2	2.3	2.8	(2.9)
m_I/m_i (max)	5.8	3.0	2.5	(2.4)
T (% m_{body})	6.3		A(max)/T	2.4

For each model and each joint (hip/knee/ankle/toe), extensor muscle moment arm (r), moment arm of F_{func} (R), extensor mass needed acting about each joint (m_i; as % m_{body}), and maximum ratio of actual vs. required extensor muscle masses ("m_I/m_i (max)"), based on an upper limit of 7% m_{body} (Hutchinson, 2004), are presented. Additionally, total extensor muscle mass needed per leg (T; as % m_{body}) and the maximum ratio of total extensor muscle mass actually present per leg assuming 15% of body mass apportioned to the right hindlimb extensors (A; as % m_{body}) vs. T, the required mass, ("A(max)/T") are appended. "§" indicates that a fourth trochanter (sensu stricto) was not apparent, so the hip extensor moment arm was estimated from muscle scarring and by comparison with similar taxa; potential errors would not greatly affect my results. The toe joint m_i was excluded from calculating T, as in Hutchinson (2004), and hence those values are in parentheses. Values for maximum m_I/m_i ratios that are less than 1, and m_i values that are greater than observed m_I values in extant bipeds (7% m_{body} or more), are denoted with an asterisk.

DISCUSSION
Sensitivity Analysis

The extinct taxa included similar unknown assumptions and are generally similar in limb anatomy and body proportions; hence, my sensitivity analysis of *Tyrannosaurus* (to check the conclusions of Hutchinson and Garcia, 2002) should apply well to the others. I consider five key parameters here: center of mass (CM) position (and limb segment masses), joint angles (limb orientation), muscle fascicle lengths (L), muscle moment arms (r), and rel-

Fig. 3.   Results for the models of all taxa except *Tyrannosaurus* (in Fig. 4). The bar graphs show the required extensor muscle masses (m_i values) for the joints (solid gray = hip; diagonal hashed = knee; mesh = ankle; only applicable joints are shown) and what are deemed to be the maximum reasonable muscle masses (m_I values; dashed horizontal lines at 7% m_{body}; after data from extant taxa from Hutchinson, 2004). The limb orientations (see Table 5 for joint angle values) are above the corresponding graphs. Data are for *Compsognathus* (*Comps*), *Coelophysis* (*Coelo*; 1 = initial model; 2 = columnar pose model), *Velociraptor* (*Veloc*), small tyrannosaur (Smrex; 1 = initial model; 2 = columnar pose model), *Dilophosaurus* (*Diloph*), *Allosaurus* (*Allos*), *Archaeopteryx* (*Archaeo*), and *Dinornis* (*Dinorn*; 1 = initial model; 2 = different pose corresponding to "*Struthio*_2" model in Hutchinson, 2004). The toe is absent because of simplifying assumptions (see text), and for taxa in which a knee flexor M_{musc} was required, the knee m_i was zero. Figure 1 has the scales. See text for discussion. Note that, as for extant taxa (Hutchinson, 2004), the ankle should have had the lowest "safety factor" (m_A/m_a ratio assuming that the actual ankle extensor mass m_A was no higher than 7% m_{body}).
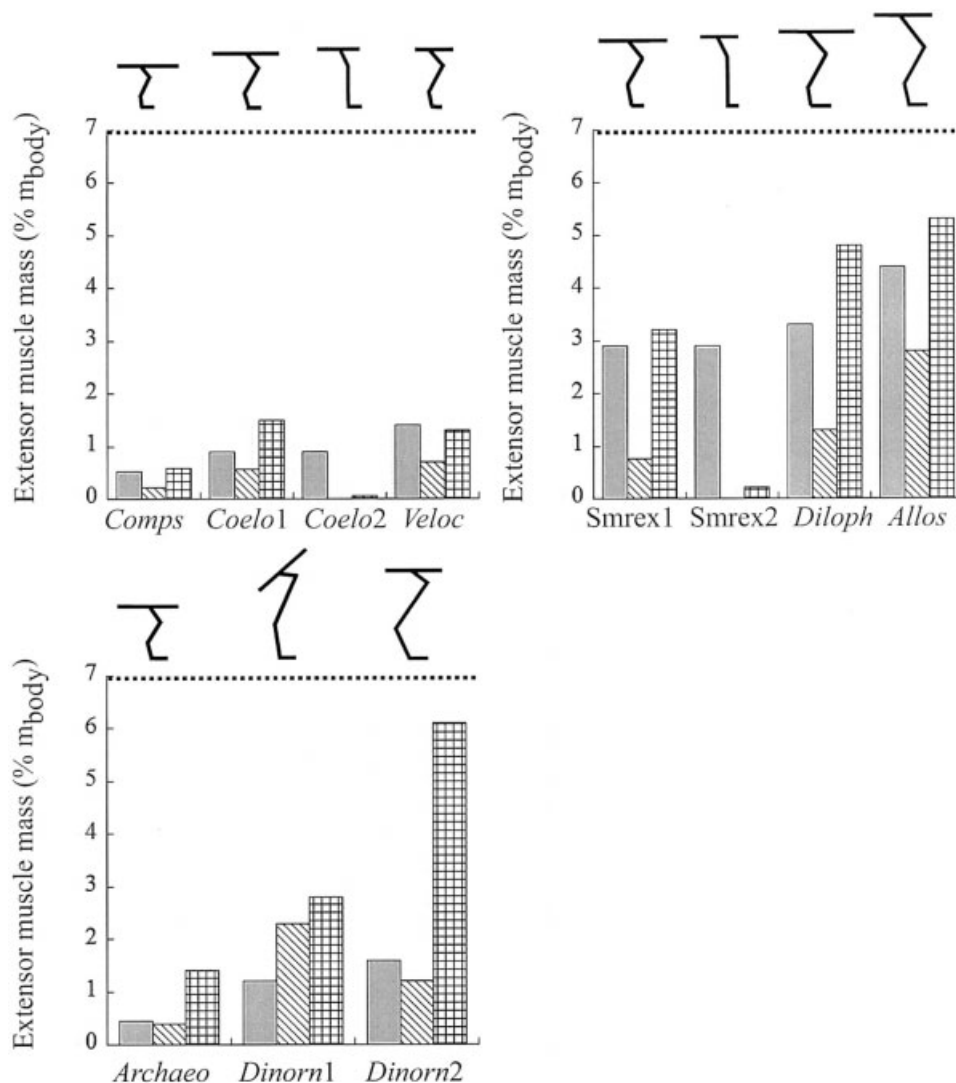
ative activity factor (G). For reasons explained elsewhere in this study and in Hutchinson (2004), I did not conduct detailed sensitivity analysis on other relevant parameters (see Eqs. 1, 2) such as body mass, gravity (g; highly unlikely to have been much different in the Mesozoic), muscle density (d), pennation angle (θ; see fascicle length discussion below), muscle stress (s), or muscle activation (c; a value of 1 being most conservative for estimating required muscle masses).

Center of mass (CM) position. In general, a CM closer to the hip in theropods should reduce m_i values, whereas a more cranial ("avian") CM position should increase m_i values. Most nonavian theropods had a CM relatively closer to the hip than in extant birds, because the tail shortened and the pectoral appendage expanded along the line to birds (Gatesy, 1990). It is difficult to estimate how close the CM was to the hip in any extinct theropod, but sensitivity analysis allows multiple possible CM positions to be investigated.

The x-coordinate positions of the CM that I used as starting assumptions for the extinct theropods (Table 2) are not very far from the hip joint (0.5 * thigh segment length cranial to the hip), but still incurred large moments about many of the hindlimb joints. As the "trunk: extant" row in Table 2 shows, entering values scaled from extant taxa would have shifted the CM further craniad (increasing m_i values by roughly 1.6× and requiring more flexed joint angles). Hence, this is another conservative assumption that kept R and m_i low. In the limb orientations initially examined for the smaller taxa, the knee extensor m_k was somewhat low (below 1.0; Fig. 3). This was because that limb orientation placed the x-coordinate position of the knee joint near the whole body CM, much like my other models (Hutchinson, 2004) and experimental data for many animals (e.g., Roberts, 2001). In larger animals and at some other joints, the m_i values tended to be fairly high, either because of scaling effects or because the center of F_{func} application (Fig. 2), and hence R,
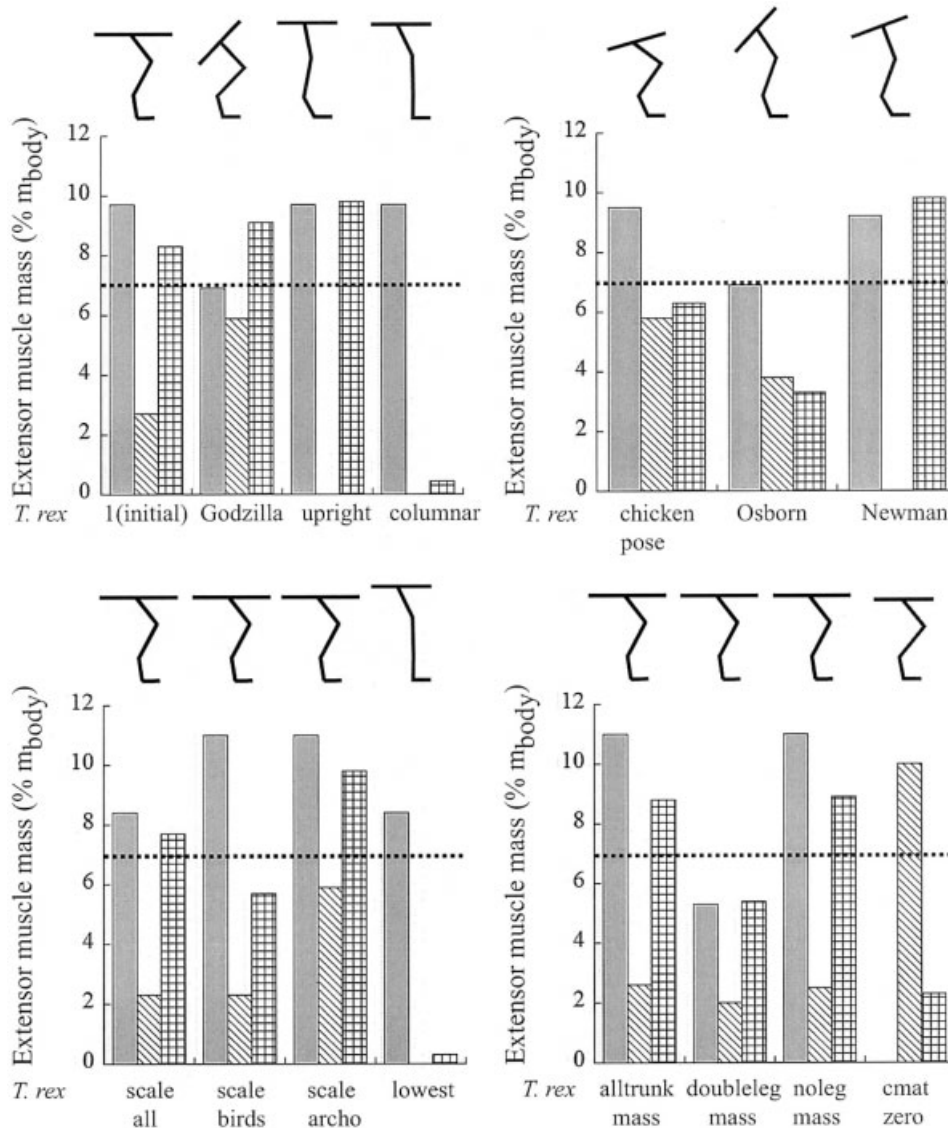
Fig. 4. Results for the models of *Tyrannosaurus rex*; as in Figure 3. Data depicted are (in order from left to right, top to bottom) for: the initial model ("*T. rex_1*"), a Godzilla-like pose, an upright pose with a flexed ankle, a very columnar pose; a pose identical to the chicken in Hutchinson (2004) and two poses favored by Osborn (1916) and Newman (1970); three models with poses identical to the initial model but with extensor fascicles scaled using (Table 3): all extant taxa from Hutchinson (2004), using only bird data, and using only archosaur data, and a model using a columnar pose and the lowest of the fascicle length values from the former scaling approaches ("*T. rex_lowest*"); and, finally, four models with varying segment dimensions: all mass in the trunk, allocation of body mass to the legs doubled, massless legs, and the trunk CM located at the hip joint.

tended to be far from the joints in "crouched" poses (Fig. 1).

Changing the CM position had the expected effects (Fig. 4): moving the CM x-coordinate of the trunk caudally reduced most m_i values. If the CM was moved to lie exactly at the hip joint center ("*T. rex_cmatzero*" model; this required the knee and ankle joint ankles to be flexed to 100° and 130° to maintain equilibrium), the hip extensor m_h was reduced to 0. However, this required an enormous knee extensor m_k of 10% m_{body}, whose presence in the actual animal is extremely dubious, considering actual knee extensor mass (m_K) data from extant taxa, which are ubiquitously below 5% even for ratite birds (Hutchinson, 2004). Future sensitivity analyses, such as 3D simulations of body segment volumes and CMs, will be able to test this CM assumption with more rigor.

I also checked the effects of limb segment masses on m_i values by modifying the initial "*T. rex_1*" model while leaving other parameters unchanged (Fig. 4). In the models "*T. rex_alltrunkmass*" (6,000 kg trunk mass and massless limbs), "*T. rex_doublelegmass*" (leg masses doubled, keeping total body mass at 6,000 kg), "*T. rex_nolegmass*" (massless limbs; 4396 kg trunk mass), the m_i values changed little overall. The second model shows how increased limb segment masses can reduce the hip extensor m_h (from 9.7 to 5.3, with smaller decreases in the other m_i values) by moving the whole body CM caudally, reducing the magnitudes of R about the limb joints. Although this could reduce the potential m_I/mi ratios below 1.0 (Fig. 4), this is a fanciful case simply meant to show how adding more mass to the legs could decrease the m_i values only slightly. It is fanciful because a tyrannosaur with legs twice as
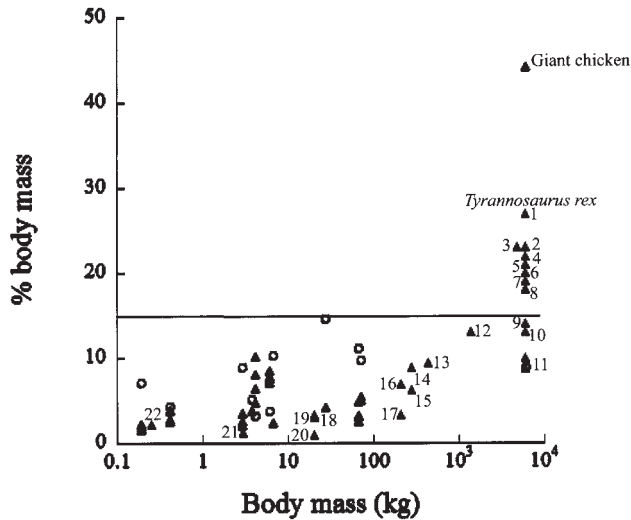
Fig. 5. Relative extensor muscle mass needed per leg, compared to body mass for the models considered in this study (larger symbols) and data for extant taxa from Hutchinson (2004; smaller symbols). The open circles indicate the values of A (actual extensor muscle mass present, for extant taxa), whereas the filled triangles indicate the values of T (extensor muscle mass needed per leg to maintain quasi-static equilibrium of the joints). The horizontal line represents the extreme 15% m_{body} per leg limit for total limb extensor masses, considering data from extant bipeds (Hutchinson, 2004). Numbers identifying the extinct models are: *Tyrannosaurus* (1–11), *Allosaurus* (12), *Dilophosaurus* (13), *Dinornis* (14, 15), small tyrannosaur (16, 17), *Velociraptor* (18), *Coelophysis* (19, 20), *Compsognathus* (21), and *Archaeopteryx* (22). Data for the individual joint m_i values added together to calculate T are in Figures 3 and 4.

large as the initial model would have about 26% of its body mass in each limb, as much as or even more than in extant ratites (19% in an ostrich, 27% in an emu; Hutchinson, 2004) while lacking compelling evidence for such specialization, whereas the initial model had a very reasonable limb mass of 13% m_{body}. Conversely, if the legs were more lightly built and that mass was instead allocated to the trunk ("*T. rex*_alltrunkmass") or eliminated altogether ("*T. rex*_nolegmass") the muscle masses required would have been higher (Fig. 4). Extinct theropods certainly did not have massless limbs, but the exact limb masses used in the models, within a reasonable range of values, do not have a huge impact on the results.

Limb orientation (joint angles). Different limb orientations changed the moment arms (R) of the F_{func} and hence the m_i required for rapid running. A more columnar limb orientation reduced the magnitude of R and m_i, whereas a more crouched limb orientation increased R. Some joint m_i values were very sensitive to the assumed mid-stance joint angles (Table 5, Figs. 3, 4). In particular, the knee joint m_k varied from a flexor muscle mass (when the hindlimb joints were strongly extended) to a large extensor mass (in a crouched limb orientation). The ankle extensor m_a (and toe m_t) also changed in magnitude (but not orientation, unlike the knee, as long as the CM was over the foot as required), depending on the limb orientation.

Many limb orientations that I modeled did not change the estimates of m_i much (e.g., Fig. 4: "*T. rex*_chickenpose"; "*T. rex*_upright"). I found that one limb orientation ("*T. rex*_columnar" and "*T. rex*_lowest"), which is quite straight-legged or columnar, aligned the knee, ankle, and toe joints closely with the F_{func}. This lowered the m_i values close to 0, except for the hip m_h, which was unchanged because the pelvic pitch was not varied (see below). As such more columnar limb orientations could lower m_i drastically for *Tyrannosaurus*, my conclusions on the running ability of *Tyrannosaurus* (and smaller theropods) must carefully consider the assumed limb orientation at mid-stance of fast running.

Controversy over the limb orientation of *Tyrannosaurus* and other theropods has focused on two issues (Fig. 4). First, the orientation of the trunk segment with respect to the horizontal (i.e., pelvic pitch) has been reconstructed ranging from subvertical (~50°; Osborn, 1916; Lambe, 1917; Carrier et al., 2001) to horizontal (~0°; Newman, 1970; Bakker, 1986; Paul, 1988). Poses that were similar to those favored by Osborn (1916; "*T. rex*_Osborn") and Newman (1970; "*T. rex*_Newman") produced generally low m_i values because the pelvis was pitched upward (moving the trunk CM caudally relative to the hip joint) and the pose was more columnar. However, this was not always the case, as exemplified by model "*T. rex*_Godzilla," which had similar m_i values to the initial model (Fig. 4). This finding does not lend support to the notion that theropods stood and moved with "jack-knifed" poses (e.g., Carrier et al., 2001). If the trunk CM were more realistically ventrally displaced (along the y axis) it would have raised the m_i values for models with increased pelvic pitch. To demonstrate this, I changed the y position of the "*T. rex*_Osborn" trunk CM to lie 0.29 m (1/4 thigh length) below the x-axis, in agreement with CM estimations for theropods (Henderson, 1999). The hip extensor m_h increased over 50%, from 6.9% to over 10% m_{body} with this more realistic assumption, which would prohibit fast running ($m_h > 7\%$ m_{body}; the knee m_k decreased to 0.99% but the ankle m_a increased to 6.6% m_{body}). Additionally, anatomical evidence is in favor of a more horizontal vertebral column in most theropods (e.g., Newman, 1970; Paul, 1988; Molnar and Farlow, 1990). In any case, the position of the CM relative to the hip joint provides a crucial limit on the minimum value of m_h: although the R values for more distal joints can be reduced by adopting more straightened limbs, it is not possible to change the m_h by reorienting the limbs. This is because the hip extensor m_h depends only on pelvic pitch and CM position, which have little potential for behavioral alteration in theropods.

TABLEL 5. Sensitivity analysis of joint angles (see Fig. 1 for initial model images, and Table 4 plus Figs. 3, 4 for results)

Taxon	Model	Angles (in degrees)				
		Pelvis	Hip	Knee	Ankle	Toe
T. rex	1 (initial)	0	50	110	140	80
T. rex	Godzilla	45	90	90	120	75
T. rex	upright	0	80	160	140	60
T. rex	columnar	0	63.5	154	180	89.5
T. rex	chickenpose	15	50	90	120	65
T. rex	Osborn	45	100	125	140	70
T. rex	Newman	20	90	140	130	60
T. rex	scaleall	0	50	110	140	80
T. rex	scalearcho	0	50	110	140	80
T. rex	scalebirds	0	50	110	140	80
T. rex	alltrunkmass	0	50	110	140	80
T. rex	doublelegmass	0	50	110	140	80
T. rex	nolegmass	0	50	110	140	80
T. rex	cmatzero	0	50	100	130	80
T. rex	lowest	0	63.5	154	180	89.5
Allosaurus	1	0	50	110	140	80
Dilophosaurus	1	0	50	110	140	80
Small tyrannosaur	1	0	50	110	140	80
Small tyrannosaur	2 (columnar)	0	63.5	154	180	89.5
Coelophysis	1	0	50	110	140	80
Coelophysis	2 (columnar)	0	63.5	154	180	89.5
Velociraptor	1	0	50	110	140	80
Compsognathus	1	0	50	110	140	80
Archaeopteryx	1	0	50	110	140	80
Dinornis	1	40	45	70	150	85
Dinornis	2	0	35	90	120	65

The joint angles were selected to match angles assumed in the literature (e.g., Osborn, 1916; Newman, 1970; Paul, 1988) or to fit mechanical criteria such as minimizing joint moments (e.g., columnar poses), but all had the fundamental requirement of maintaining the whole body CM over the foot, preferrably halfway along the foot, as appropriate for mid-stance.

A second controversy over tyrannosaur poses is the degree of flexion of the hindlimb joints, which has been reconstructed ranging from columnar (i.e., highly extended; Osborn, 1916; Lambe, 1917) to crouched (i.e., strongly flexed; Bakker, 1986, 2002; Paul, 1988, 1998). A more upright pelvic orientation and relatively columnar limb orientation for *Tyrannosaurus* was assumed in many less athletic reconstructions of its locomotion, whereas many studies that inferred a more crouched limb orientation and horizontal vertebral column also favored fast-running tyrannosaurs. My analysis shows that the muscle masses required to stabilize more crouched limb orientations in large theropods (e.g., "*T. rex*_1" and "*T. rex*_chickenpose" models) would have been extremely high: 5–11% m_{body} for most joints (Fig. 4). This poses a problem for advocates of a crouched-limbed, high speed, "roadrunner-like" *Tyrannosaurus* (e.g., Bakker, 1986, 2002; Leahy, 2002; Paul, 1988, 1998). Also, the limb orientation entered for the most columnar *Tyrannosaurus* models (*T. rex*_columnar, *T. rex*_lowest) more closely matches the limb orientation predicted from mammalian scaling of effective mechanical advantage (average whole limb EMA of 2.9; Biewener, 1989, 1990) than the models in crouched poses (Hutchinson and Garcia, 2002).

Paul (1988, 1998) argued vehemently that the configuration of theropod limb joints, especially the knee, requires their pose to be "permanently flexed" (Paul, 1988:117). This anatomical argument deserves more detailed consideration elsewhere, but evidence for this conclusion is not entirely convincing. Soft tissues such as menisci, ligaments, and cartilage have not been well considered by any studies reconstructing theropod poses, and could drastically change reconstructions of limb articulation. Moreover, little is known about how the individual structures interacting about avian joints influence limb orientation, what functions such structures actually perform, or how much bone articular surfaces actually reflect limb orientations normally used (e.g., Christiansen, 1999). Finally, some salient osteological differences separate neornithine and more basal theropod limb joints (e.g., Farlow et al., 2000; Hutchinson and Gatesy, 2000). These differences have not been considered by Paul (1998, 1998) or other studies. Newman (1970) proposed an alternative hypothesis for the theropod knee joint: that the knee joint articulations seen by Paul (1988, 1998) as evidence for constant joint flexion were instead crucial only for preventing mediolateral dislocation of the knee during sitting down and standing up (or simply during any activities involving extreme knee flexion), rather than engaged at all times to prevent dislocation. This and other potential hypotheses have not been explored in much depth or ruled out. A wealth of other anatomical, trackway, and biome-

chanical evidence favors more upright limb orientations in theropods (e.g., Gatesy, 1991; Carrano, 1998, 2001; Christiansen, 1998, 1999; Gatesy et al., 1999; Farlow et al., 2000). Eventually, anatomical, biomechanical, and other lines of evidence should converge on a satisfying answer regarding limb orientation in various nonavian theropods, and it probably will lie somewhere in between the false dichotomy of "flexed" vs. "columnar" poses. Regardless, limb orientation is important for overall limb mechanics, so an understanding of limb orientation is vital for inferring other behaviors in extinct dinosaurs.

The importance of adopting a more upright limb orientation with increased size has been shown for mammals (Alexander et al., 1981; Biewener, 1983, 1989, 1990) and discussed for birds (Gatesy and Biewener, 1991; Hutchinson, 2004) as well as other theropods (Gatesy, 1991; Carrano, 1998; Christiansen, 1999). This is presumably a general principle for terrestrial tetrapods, although perhaps more applicable interspecifically than intraspecifically (Muir et al., 1996; Irschick and Jayne, 2000). The sensitivity analyses of limb orientation shown here (and in Hutchinson, 2004) for various bipeds support this theory.

As Hutchinson and Garcia (2002) argued, a highly columnar-limbed tyrannosaur would have been a terrible strategy for generating the large stride lengths necessary for high velocities. Mid-stance of running is typically when the limb is most flexed (e.g., Biewener, 1989, 1990), so a columnar limb orientation at mid-stance leaves little opportunity for joint excursion earlier or later in stance, limiting stride lengths. Studies of limb stiffness provide an interesting connection between limb orientation and the mechanical limits on running speed, as maximum running speed depends on maximum limb stiffness (e.g., McMahon and Cheng, 1990; also see references in Hutchinson, 2004), which increases with a more columnar limb (McMahon et al., 1987; Farley et al., 1993; Biewener, 2000). Such tradeoffs demand careful consideration of the effects of changing any one model parameter in future studies, because changing single parameters can have cascading nonlinear functional outcomes.

Entering more columnar poses for the smaller theropods such as *Coelophysis* and the small tyrannosaur (using the same pose as for "*T. rex*_columnar") reduced the m_i values (Fig. 3; Table 5) by up to 100%, bringing the total muscle masses down to ~3–5% of body mass and individual m_i values near 0.0, except for m_h, which was unchanged because pelvic pitch was kept constant. This is important validation for my modeling approach, as fossil tracks show that smaller theropods were good runners (Irby, 1996), and so should be reconstructed as such by my models. Regardless of the pose assumed for *Coelophysis* or the small tyrannosaur, the possible m_I/m_i ratios were high enough for fast running to be

an acceptable inference. A pose for the "*Dinornis*_2" model that was identical to the "*Struthio*_2" model from Hutchinson (2004) raised the m_i values appreciably because of the more flexed ankle (and hence a large ankle extensor m_a of 6.1). Leahy (2002) criticized high total muscle mass (T) values for the small theropod biomechanical models in Hutchinson and Garcia (2002) as overestimated "by a factor of over two." This misses the point that the m_i values for the smaller theropods were (as they are here) 2–4 times lower than for *Tyrannosaurus*, and more columnar poses would have reduced m_i (or T) to plausible values (~7% or less) for fast running in smaller theropods, but not in *Tyrannosaurus*.

Muscle fascicle lengths (L). The m_i values estimated by my analyses were linearly proportional to the entered values of L, so this factor was a critical unknown that required careful consideration. I entered reasonably low values of L into the initial models of extinct theropods (Tables 3, 4). My approach is conservative because it calculated the value of L based on the average ratio of L to segment length observed in extant taxa, which appears nearly independent of body mass (although variable; Maloiy et al., 1979; Alexander and Ker, 1990; Roberts et al., 1998; Hutchinson, 2004). Additionally, this approach is conservative because pennation angles were excluded. If the pennation angles were 30° (as in some extant animals, especially for distal muscles; Pollock and Shadwick, 1994; Hutchinson, 2004), this would only have increased the m_i values by $1.15\times$ if included, having little effect on the conclusions considering that θ should covary with L (Pollock and Shadwick, 1994).

My models "*T. rex*_scaleall" and "*T. rex*_scalebirds" show that my assumptions about muscle fascicle lengths, based on available scaled data from extant taxa, do not make an enormous difference, as they produced similar results. Even using the lowest scaled L value for each limb joint in model "*T. rex*_lowest" did not change the m_i values much (Fig. 4) from the otherwise identical model "*T. rex*_columnar." Using L values only from archosaurs (Table 3: row "Archosauria") would have led to slightly higher L estimates, particularly for the hip joint, so my initial approach was fairly conservative. Thus, as model "*T. rex*_scalearcho" shows (Fig. 4), I conservatively underestimated the m_i values if relative L values among extant archosaurs are more indicative (as phylogeny implies) of L values in extinct theropods.

Keeping L values low is an important potential strategy for maintaining relatively low m_i values with increasing size. Alexander et al. (1981; also Alexander and Ker, 1990; Pollock and Shadwick, 1994) showed for mammals that proximal extensor muscle fascicles scaled near isometry, whereas distal fascicles scaled with negative allometry. Part of this negative allometry may be because of the highly specialized limbs of ungulates (Pollock and Shad-

wick, 1994), so available scaling data from mammals must be interpreted with caution, given the potential for phylogenetic effects to skew scaling patterns (e.g., Christiansen, 2002). If the latter pattern held for *Tyrannosaurus* and other extinct theropods, relatively lower values of L would likewise have reduced the m_i values for the distal muscles.

However, a different scaling pattern from mammals was found for running birds (Maloiy et al., 1979; also see Bennett, 1996; Olmos et al., 1996). The observed isometric scaling of ankle extensor L is particularly interesting, as the ratio of actual ankle extensor mass m_A to the required mass m_a seems to be a crucial limit for running ability (Hutchinson, 2004), intimating that very large bipeds might need oversized ankle extensor muscles (although extant ratites seem to remain small enough to avoid this problem; Hutchinson, 2004). Clearly, more needs to be understood about limb muscle allometry (especially for the hip joint) and function in extant birds. Regardless, I accommodated some of these potential allometric patterns by estimating L as a function of segment length (Tables 2–4).

Although the ankle joint seems to be crucial for adept runners in living animals (Hutchinson, 2004), this analysis suggests that in larger animals the near-isometric scaling of hip extensors may unexpectedly provide an additional limit for running ability. Therefore, the scaling of hip extensor maximum strength vs. required strength may decrease the capacity of larger animals to generate the ground reaction forces needed for more extreme activities. Indeed, available data (e.g., Christiansen, 1999) show that relative thigh segment lengths, and thus perhaps hip extensor fascicle lengths, scaled with positive allometry in nonavian theropods, including tyrannosaurids (Currie, 2003). Hence, even if straightened limb orientations reduced the muscular exertion about more distal joints in larger theropods, relatively larger hip extensor L values may have prohibited reduction of hip extensor m_h values. My observation that the hip m_h changed little with limb orientation supports this idea (Figs. 3, 4; Table 5). Considering the limited potential effects of hip extensor L and limb orientation on m_h, reducing locomotor activity may be the only option remaining for very large animals, even if the limits imposed by the ankle extensor m_a have not been reached.

Shorter muscle fibers (and fascicles) reduce muscle volume and mass, and can contribute to spring-like muscle-tendon behavior (Pollock and Shadwick, 1994). Yet again, potential tradeoffs must be considered. Shorter muscle fascicles come at the cost of linearly reduced joint excursion arcs (Alexander et al., 1981; Pollock and Shadwick, 1994) that are detrimental for the generation of long strides essential for fast running, and can reduce joint accelerations (e.g., Gans and de Vree, 1987) crucial for rapid strides. Long muscle fascicles have been correlated with sprinting performance (Kumagai et al., 2000;

Kearns et al., 2002), presenting a potential paradox for studies that advocate short extensor muscle fascicles in order to bolster a hypothesis favoring fast-running tyrannosaurs. A tyrannosaur with short muscle fascicles also might not have been functional for vital behaviors that require wide ranges of joint excursion and consistently high muscle forces, such as standing up, sitting down, or mating.

Muscle moment arms (r). As An et al. (1984), Delp et al. (1999), and others have demonstrated, the moment arms of muscles about joints are a function of the joint angle. I did not vary the value of r with the joint angles beyond the initial input values, although I entered conservatively high values (including consideration of tendon and cartilage thickness). A more comprehensive study, perhaps using 3D models to visualize the complex muscles of the hindlimb (especially around the hip joint) and their variation with joint angles, is needed to conduct more sensitivity analysis of muscle moment arms.

The magnitude of r generally increases with a more columnar limb, because a straightened limb typically draws muscle lines of action further from their joint centers, increasing the mean extensor muscle moment arm, and because larger animals tend to have muscle attachments that are relatively further from their joint centers (Biewener, 1989, 1990, 2000). Indeed, Maloiy et al. (1979), Alexander et al. (1981), and Biewener (1989, 1990) found that hindlimb extensor muscle moment arms tended to scale with positive allometry in running birds and mammals. Considering the underlying principles and anatomical structures, it is likely that this general pattern holds for most tetrapods. Furthermore, an increase of extensor muscle moment arms is beneficial in my simple models, but in a broader functional sense is complicated by an attendant decrease in the maximum joint excursion that the muscles can create (Maloiy et al., 1979; Biewener, 1983, 1990; Gans and de Vree, 1987). How this tradeoff has influenced anatomy and behavior in living runners, let alone extinct taxa, remains poorly understood.

Nonetheless, examination of hindlimb extensor moment arms can reveal much about limb mechanics and relative running ability. Bakker (1986, 2002), Paul (1988, 1998), and other analyses have rhapsodized how even large dinosaurs have a "massive" cnemial crest on the tibia for the insertion of knee extensors (and origin of some ankle extensors and flexors; Carrano and Hutchinson, 2002). The former studies have assumed that such features are indicative of fast running ability, rather than merely useful for less extreme activities. Anatomical features that seem massive to human eyes should be measured and compared to relevant extant models to see if they are actually large in relative terms, and if their size actually compensates for body size in a biomechanical context. This is because an intuitive approach to the influence of morphology on locomo-

TABLE 6. Comparison of extensor muscle moment arms (in meters) about the major limb joints

Extant taxa	Extensor muscle moment arms (r):				Extinct taxa	hip	knee	ankle	toe
	hip	knee	ankle	toe					
Homo	0.17	0.18	**0.16**	**0.070**	*Compsognathus*	0.26	0.11	0.080	0.040
Macropus	0.30	0.17	**0.14**	n/a	*Coelophysis*	**0.53**	0.19	**0.14**	0.050
Basiliscus	0.19	0.09	**0.13**	0.060	*Velociraptor*	**0.34**	0.15	**0.15**	**0.070**
Iguana	0.18	0.070	0.090	0.030	*Sm tyrannosaur*	**0.43**	**0.26**	**0.17**	**0.070**
Alligator	0.19	0.13	**0.17**	0.050	*Dilophosaurus*	**0.46**	0.21	0.10	0.050
Eudromia	0.34	0.16	0.080	0.060	*Allosaurus*	**0.48**	0.12	0.080	0.030
Gallus	**0.48**	**0.33**	0.11	0.050	*Archaeopteryx*	0.34	0.09	0.060	0.030
Meleagris	**0.39**	0.12	0.090	**0.070**	*Dinornis*	**0.47**	**0.42**	**0.21**	**0.11**
Dromaius	0.37	0.28	**0.14**	0.11					
Struthio	**0.45**	**0.36**	**0.16**	**0.14**	*Tyrannosaurus*	0.37	0.22	0.12	0.070

Extant taxa from Hutchinson (2004). All animals have been scaled up isometrically by their body mass to 6,000 kg (multiplying the initial moment arms by a linear scaling factor, equal to the mass scaling factor to the 0.333 exponent) in order to examine how their moment arms would compare to those estimated for *Tyrannosaurus* in this study. Moment arms entered in bold are equal to or greater than those computed for *Tyrannosaurus*. See text for discussion.

tor performance can be very misleading (Lauder, 1995; Koehl, 1996).

Extensor moment arms should be much larger than isometry predicts ($m_{body}^{0.4}$) if locomotor performance was being maintained at a similar relative level (Biewener, 1990), but there is no evidence of such allometry in tyrannosaur muscle leverages. My study accommodates a quantitative biomechanical analysis of the effect of the prominent cnemial crest on the knee extensor moment arm. Although the knee extensor m_k values are generally well below 7% m_{body} for most taxa (including *Tyrannosaurus*; Figs. 3, 4; Table 4), the extensor masses acting about the hip (m_h) and ankle (m_a) are more crucial for running ability, approaching or exceeding 7% m_{body} in larger taxa. Additionally, as Table 6 reveals, the knee extensor moment arm (r = 0.22 m) for *Tyrannosaurus* is greater than some of the expected values for the knee extensor moment arms in animals isometrically scaled to 6,000 kg body mass, but is still below the values expected for a scaled-up small tyrannosaur, and well below the values expected for adept runners such as ratite birds. Likewise, the ankle extensor moment arm for *Tyrannosaurus* (r = 0.12 m) is not much larger than expected when compared with other isometrically scaled theropods (Table 6). A true ossified hypotarsus for the insertion of the ankle extensors Mm. gastrocnemii (as in birds) is absent in *Tyrannosaurus* and other nonavian theropods (Hutchinson, 2002), which might explain part of this pattern. This pattern is even more pronounced for the hip extensor moment arms (Table 6). Additionally, the knee and ankle extensor moment arm values in *Tyrannosaurus* are similar to or lower than those expected from scaling data of mammalian (r = 0.26 m for the ankle; Alexander et al., 1981) or avian (r = 0.32 m for the knee, 0.22 m for the ankle; Maloiy et al., 1979) data. Thus, the hindlimbs of *Tyrannosaurus* lack biomechanical specializations that conclusively indicate fast running. The relative magnitudes of the extensor moment arms are probably plesiomorphies that arose

earlier in bipedal dinosauromorphs (e.g., Hutchinson, 2002), and may have assisted those ancestors in exerting the knee and ankle extensor moments needed for fast running. Extreme positive allometry of either feature (as autapomorphies for large tyrannosaurs) would fit a rigorous biomechanical definition of specialization for generating high forces (including, but not restricted to, those required in fast running). Such allometry ($\sim m_{body}^{0.4}$; e.g., Maloiy et al., 1979; Alexander et al., 1981; Biewener, 1990) does not seem prevalent in tyrannosaur limbs, but judging from Maloiy et al. (1979) and my models, might be present in ratites and perhaps other birds (Table 6).

Relative activity factor (G). By introducing the "relative activity factor" G, I multiplied the M_{musc} during unipodal standing by 2.5 to simulate running. My assumed value of G is probably conservatively low for Fr $\sim$17 (see Hutchinson, 2004: Appendix B). The magnitude of G could have been reduced by using less extreme behaviors. For example, at a duty factor of 0.39 (similar to the mean minimum duty factor of 0.37 for small, fast elephants; Hutchinson et al., 2003; or a rhinoceros at duty factor 0.40; Alexander and Pond, 1992) the value of G would be 2.0 (Alexander et al., 1979a,b). Biewener (1983, 1989, 1990), Alexander (1985b), and Taylor (1985) noted that larger animals tend to use higher duty factors (the fraction of a stride that a given foot is in the stance phase) at physiologically equivalent speeds such as gait transitions, reducing the magnitude of G relative to smaller animals. Ultimately, this increase of the duty factor entails a reduction of the range of locomotor performance at extremely large sizes (Biewener, 1989, 1990).

"Groucho running" (McMahon et al., 1987) is running with a crouched limb orientation, higher duty factors, and no aerial phase. Among other tetrapods, it is used in birds running at intermediate speeds (Gatesy and Biewener, 1991), and perhaps an analogous mechanism exists in elephants (Hutchinson et al., 2003). This running mechanism lowers the peak

forces on the limb, reducing the m_i values isometrically with G, although it also tends to increase the total cost of transport because it raises muscular exertion (McMahon et al., 1987) unless compensatory mechanisms are in place (Roberts et al., 1998). It may be tempting to speculate that large theropods could have "Groucho ran" (also see Christiansen, 1998; Farlow et al., 2000), but there is no convincing evidence for or against this possibility. As noted previously (also see McMahon et al., 1987), a decrease of limb stiffness would reduce running ability, and this may follow directly from a decrease of G, so this tradeoff deserves attention in future studies.

A fast-walking tyrannosaur would have had a minimum duty factor of 0.50, which gives a value of G = 1.6 (see Alexander et al., 1979a,b; Hutchinson, 2004), reducing the estimates of m_i and total extensor mass T to 64% of their values at G = 2.5. In the case of model "*T. rex*_1," this would barely bring the hip extensor m_h (6.2) and ankle extensor m_a (5.3) to feasibly low values (<7% m_{body}). Alternatively, with G = 1.6 for model "*T. rex*_columnar," the distal m_i values would decrease to lie easily within reasonable biomechanical bounds ($m_I/m_i \geqslant 1.0$) but the hip extensor m_h still would be large (6.2). Hence, a *Tyrannosaurus* presumably needed some combination of a trunk CM closer to the hip (lower R; possible but lacking supportive data; e.g., Henderson, 1999), shorter hip extensor fascicles (L < 0.85 m; not supported by available data from extant animals; Table 3) or a larger mean hip extensor moment arm (r > 0.37 m; possible in more columnar poses) to be able to walk quickly (G ~1.6; m_h < 5.0 considering that extant taxa have m_H values of 5.0 or less; Hutchinson, 2004), let alone run. Yet regardless of the pose adopted, a *Tyrannosaurus* seems to have had a rather high value of c (fraction of active hip extensor muscle mass) even at slower speeds (Hutchinson and Garcia, 2002).

Dinosaur Speeds

How fast could extinct dinosaurs run? In a fast-walking *Tyrannosaurus*, at Fr = 1.0 (the theoretically required walk-run transition), speed would have been ~5.0 m s^{-1} (faster in more columnar poses because increased hip height corresponds to a higher velocity for a given Fr). As Hutchinson and Garcia (2002) considered, speeds up to 11 m s^{-1} could be viewed as not beyond the realm of possibility. This is because at 11 m s^{-1} (Fr 4.6; comparable to a rhinoceros at 7 m s^{-1}; Alexander and Pond, 1992) a combination of parameter values (more upright pose, G ~2.0, other factors given generous assumptions, especially to reduce the hip m_h) could reduce the m_i values to below 7.0 for all joints, but I do not see this as reasonably possible for higher G values (~2.5) and speeds (e.g., Fr $\geqslant$ 5). Further studies should narrow down this 5–11 m s^{-1} range further. I

do not advocate a particular pose or maximum speed for *T. rex* here because I feel that no rigorous conclusion is yet possible, except that speeds ~20 m s^{-1} are outrageous on biomechanical grounds, and speeds >11 m s^{-1} remain dubious. This is because conclusions about the maximum speed of the largest tyrannosaurs ultimately depends on how much leg muscle mass is assumed to have been present in these animals, especially for the hip and ankle joints. Data from extant archosaurs (Hutchinson, 2004) show hip extensor muscle masses of 1–5% body mass, and ankle extensors of 0.3–6% body mass. Lacking other unequivocal evidence, presumably tyrannosaurs had muscle masses within or close to this range. If, for example, the hip extensors were as large as 5% of body mass, the maximum G value sustainable by those muscles might have been 1.25 (implying slow walking at best); half those G values if the hip extensors were only 2.5% of body mass (which would leave tyrannosaurs barely able to stand; improbable). Likewise, if the ankle extensors were 6% of body mass, a G value of 1.8 might be maximum performance (slow running); again, half those values (i.e., slow walking) if the ankle extensors were half as large. These maximal G values are highly dependent, however, on the assumptions made about trunk CM position, hip moment arms, etc., but clearly the actual muscle mass is a crucial unknown.

Day et al.'s (2002) trackway does not complicate the results of this or Hutchinson and Garcia's (2002) study, as the size of the trackmaker (similar to the *Allosaurus* model; total limb extensor mass T = 13) and the speed of the trackway (Fr ~3.5, slower than Fr 17; G closer to 1.6 than to 2.5, so perhaps T = 8.3) could have fallen within the bounds suggested here as feasible (if actual limb extensor mass A > 8.3, an A/T ratio > 1.0; much higher if the pose were more columnar). However, sensitivity analysis of unknown parameters in trackway speed estimate formulae should always be cautiously applied (Coombs, 1978; Thulborn, 1990), because such estimates are often off by a factor of two or more, even when applied to living animals whose speed and anatomy are known (Alexander, 1991).

The smaller theropods modeled at Fr ~3–17 would have reached relatively faster speeds. For example, at Fr = 17, a *Coelophysis* would be moving at perhaps 8–9 m s^{-1}, whereas a small tyrannosaur might have reached speeds of 11–14 m s^{-1} at most. These are speeds within the bounds of (even if potential error is small) speed estimates from fossil trackways of fast-moving smaller theropods (8–11 m s^{-1}; Farlow, 1981; Irby, 1996). Thus, my results are consistent with Currie's (1998) speculation that smaller tyrannosaurs may have been more adept runners than large adults. Furthermore, the m_i values (<7.0) estimated for *Dinornis* suggests that this taxon was not a slow runner, unlike other moa, in

agreement with other studies (Cracraft, 1976; Alexander, 1983, 1989).

Some studies of locomotor function in tyrannosaurs use comparisons with elephants and rhinoceroses. Elephants can move moderately quickly, up to 6.8 m s^{-1} for *Elephas* (Hutchinson et al., 2003), and rhinoceroses even faster: at least 7.5 m s^{-1} for *Ceratotherium* (Alexander and Pond, 1992). For both animals, higher speeds (11–12.5 m s^{-1}) have been speculated based on anecdotal accounts or even used as data (e.g., Howell, 1944; Garland, 1983; Garland and Janis, 1993; Christiansen, 2002; Iriarte-Díaz, 2002; Blanco et al., 2003). There are presently no strong scientific data to discern whether large tyrannosaurs moved as fast as or faster than elephants (e.g., Thulborn, 1982, 1989, 1990; Alexander, 1989) or rhinoceroses (e.g., Bakker, 1986, 2002; Paul, 1988, 1998; Christiansen, 1998; Leahy, 2002); both animals seem to fall within the speed range here thought to include the maximum for *Tyrannosaurus*. To resolve this controversy, not only does tyrannosaur running speed need to be more narrowly bounded, but also the fastest speeds of large extant mammals need to be accurately gauged. Given the interest in maximal speeds to paleobiologists (e.g., Christiansen, 2002; Blanco et al., 2003) and biomechanists, it is disconcerting how little effort has been put into accurately measuring it in living larger animals. However, it is more important to resolve what biological factors are the primary limits on running in large animals rather than to continually revisit an artificial dichotomy of speeds using two extant functional analogs, neither of which has great anatomical similarities with tyrannosaurs.

Evolutionary Implications

Figure 6 shows the relationships of the extinct taxa in this study, and the extant taxa from Hutchinson (2004), with the m_I/m_i values noted. My results support the inference that running ability increased in the bipedal predecessors to theropod dinosaurs, which reached m_I/m_i ratios over 1.0. This conclusion is consistent with fossil evidence for increased extensor muscle moment arms and masses in these animals (e.g., Hutchinson, 2002) and fossilized running tracks (Irby, 1996). Evidence suggesting more upright limb orientations in basal theropods (Gatesy, 1990, 1991; Carrano, 1998, 2001; Christiansen, 1999; Gatesy et al., 1999; Farlow et al., 2000; Hutchinson and Gatesy, 2000) supports this inference, because my models show how such poses would facilitate rapid running, albeit with some limits imposed by tradeoffs. However, it is interesting that the calcaneal tuber, which would have maintained larger ankle extensor moment arms, was reduced and then lost in basal dinosaurs, implying increased ankle extensor force (Hutchinson, 2002). One can speculate that this change in-

creased the stiffness or spring-like nature of the ankles of bipedal basal dinosaurs (as higher extensor muscle forces might do), but ultimately it could also have limited their locomotor performance, particularly at larger sizes.

Despite the aforementioned bipedal specializations, it seems that at some point dinosaurs could not have maintained high running performance as they evolved huge sizes. Basal tetanuran theropods evolved larger adult body sizes (Sereno, 1999; Holtz, 2001). The models of theropods of medium size (small tyrannosaur, *Dilophosaurus, Allosaurus*) support the inference that this size change may have corresponded to a decrease of the m_I/m_i ratios and a reduction of running ability in the tetanuran lineage (also see Carrano, 1999). As the data in Figure 5 show (points marked with numbers 12, 13, 16, 17), this reduction may have occurred gradually as body mass increased from 100 to >1,000 kg during evolution and ontogeny. Enormous body size evolved at least five times in theropods (Sereno, 1999; Farlow et al., 2000). If my models of *Tyrannosaurus* apply equally well to other huge tetanurans, then these multiple origins of large body size involved independent reductions of running ability. Rapid running in other large dinosaurs such as *Giganotosaurus* (Blanco and Mazzetta, 2001) is unlikely given the weight of biomechanical evidence showing the decrease of m_I/m_i ratios with body size.

This proposed pattern of reduced running ability was secondarily reversed, however, in maniraptoriform theropods, which gained higher m_I/m_i ratios that seem to have been inherited by birds. Small size, altered limb proportions, and increased muscle moment arms may all have contributed to this evolutionary pattern despite the reduction of some key hip extensors (Gatesy, 1990; Carrano, 1998; Hutchinson and Gatesy, 2000; Hutchinson, 2002, 2004). Birds, however, not only had improved running ability with their small size, but a new mode of locomotion was opened to them: flight. The low m_i values calculated for smaller coelurosaurs such as *Compsognathus* and *Archaeopteryx* corroborate that there was not a biomechanical barrier to fast running in these taxa, so an origin of flight involving running cannot be excluded on such a basis.

CONCLUSIONS

I have shown how running ability probably declined with large body size in theropod dinosaurs. My results demonstrate how larger bipedal animals must reduce their range of locomotor performance as their m_I/m_i ratios drop below 1.0 with increasing size. At the largest sizes they may even reduce their absolute maximum performance. This general principle of biomechanics has been formulated based on data from extant taxa (Biewener, 1983, 1989, 1990, 2000; Calder, 1996; Gatesy and Biewener, 1991; Iriarte-Díaz, 2002; Hutchinson, 2004), including
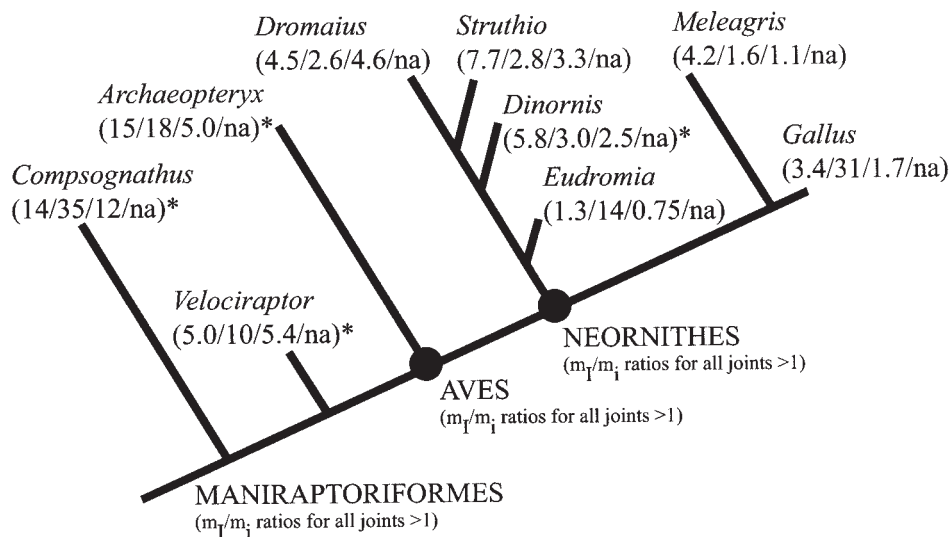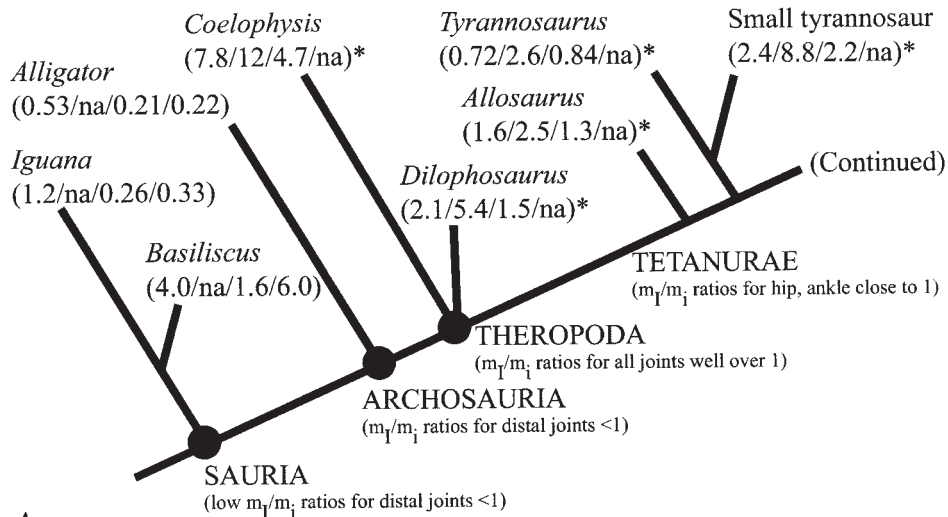
Fig. 6. Evolution of running ability in theropod dinosaurs. Phylogeny based on Gauthier (1986), Sereno (1999), Holtz (2001), and Cracraft and Clarke (2001). The numbers below each taxon are the m_I/m_i ratios from my initial models (Figs. 3, 4) for the hip (m_h), knee (m_k), ankle (m_a), and toe (m_t; for the lizard and alligator models); "na" is a reminder that the joint was generally ignored in my analysis. Extinct taxa have been marked with an asterisk to note that the m_I/m_i ratios are extreme maxima (see Table 4) as these used 7% m_{body} as a limit for the m_I values of any joint, considering data from extant taxa (Hutchinson, 2004).

quadrupeds, and extinct taxa support this principle (Alexander, 1985a, 1989; Christiansen, 1998, 1999; Carrano, 2001). My results are also in firm agreement with Hutchinson and Garcia (2002), strengthening support for our conclusions with a more detailed analysis of joint mechanics and a total of 19 taxa modeled across over five orders of size magnitude, including validation of the modeling procedure using 10 models of extant taxa (Hutchinson, 2004). However, other approaches, such as a superior biomechanical model, could contradict my biomechanical analysis by showing that crucial, realistic new assumptions change the estimates of m_i enough to support the hypothesis that the largest theropods could run much faster than 11 m s^{-1}.

The controversy over tyrannosaur speeds exemplifies a broader controversy over how functional analysis of locomotion should be conducted, especially for extinct animals such as dinosaurs. The methods and evidence used to create reconstructions of the running ability of *Tyrannosaurus* are seldom explicit or even indirectly testable—*Tyrannosaurus* is intuitively concluded to "look fast." From the initial descriptions of tyrannosaurs, scientific and popular accounts of these animals have had a certain fervor, evoking hyperbolic functional inferences such as "*Tyrannosaurus* is the most superb carnivorous mechanism among the terrestrial Vertebrata, in which raptorial destructive power and speed are combined" (Osborn, 1916:762). More recently, similarly bold claims have been issued such as "At full speed, a bull *Tyrannosaurus* could easily have overhauled a galloping white rhino—at speeds above forty miles per hour, for sure" (Bakker, 1986:218), or "it is by no means impossible that *T. rex* could reach 45 mph…. Certainly 30 mph, the speed rhinos run

at, was the very minimum" (Paul, 1988:146). Many authors have based ecological inferences on their assumptions about the running ability of theropods. For example, Horner and Lessem (1993) suggested that *Tyrannosaurus* was a scavenger partly because they inferred that it was a poor runner, whereas Bakker (1986) and Paul (1988, 1998) arrived at opposite conclusions partly because they thought it was an adept runner. Paul (1988, 1998) and Holtz (1995) even used these assumptions to formulate broad-scale generalizations about coevolutionary interactions ("arms-races") among running predatory tyrannosaurs and their herbivorous prey. Considering our poor understanding of the running ability of any extinct dinosaurs, such higher-level inferences (Witmer, 1995) seem particularly tenuous.

Most studies of large theropod locomotion adopt poorly tested assumptions about the correlation of "graviportal" or "cursorial" (Coombs, 1978; Garland and Janis, 1993; Carrano, 1999; Christiansen, 1999, 2002) anatomy with running mechanics, or about the correlation of form and function (e.g., analogies with mammalian or avian functional anatomy). Such intuitive methods for functional analysis are a useful foundation but often are tenuous, assuming more than they demonstrate (Lauder, 1995; Koehl, 1996). Biomechanics is a powerful test of any reconstruction of musculoskeletal function when it is applied properly. Using a biomechanical approach like the one outlined here, specific predictions about anatomy and body dimensions can be made for any particular behavior, with the assumptions remaining explicit. Some studies have attempted to do this for *Tyrannosaurus* and other large theropods (Alexander, 1985a, 1989; Farlow et al., 1995; Christiansen, 1998; Blanco and Mazzetta, 2001; Hutchinson and Garcia, 2002). I contend that biomechanical analysis holds the most promise for resolving this controversy and "raising the bar" for reconstructing locomotor function in paleobiology. Such an emphasis moves beyond the pioneering biomechanical work of authors such as Alexander (1976, 1985a, 1989) in new directions for studying locomotor function in extinct animals, as I have attempted to do here.

ACKNOWLEDGMENTS

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APPENDIX A
Glossary of Symbols Used (and Units)

A	actual total limb extensor mass (% m_{body})
c	recruited fraction of muscle volume
d	muscle density (kg m^{-3})
F_{func}	limb "functional" force (N)
Fr	Froude number (= $v^2 g^{-1} l^{-1}$)
G	relative activity factor ($\times$ body weight)
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 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})
θ	muscle fascicle (or fiber) pennation angle (°)
σ	maximum muscle isometric stress (N m^{-2})

APPENDIX B
Model Specimens and Mass Details

I used nine specimens for my models of extinct theropod dinosaurs: *Archaeopteryx lithographica* (University of California Museum of Paleontology specimen UCMP 173730; cast of the Berlin specimen), *Compsognathus longipes* (UCMP 124884; cast of the holotype), *Coelophysis bauri* (UCMP 77200; cast of American Museum of Natural History specimen AMNH 7224), *Velociraptor mongoliensis* (Mongolian Geological Institute specimen IGM 100/986), a small undescribed juvenile tyrannosaur (Chicago Field Museum of Natural History specimen FMNH PR 2211), *Dinornis maximus* (UCMP 77209), *Dilophosaurus wetherilli* (UCMP 37302), *Allosaurus fragilis* (Museum of the Rockies specimen MOR 693), and *Tyrannosaurus rex* (UCMP cast of MOR 555). For some of these specimens (especially the first three), some parts of bones were missing and their dimensions had to be estimated judiciously from preserved impressions of bones, but these estimations should not be so far off that they would affect my results. Lengths were measured from approximate joint centers as in Hutchinson (2004) and references therein. Measurements from casts were later checked with reference to the originals and found to be reasonable.