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.

KEY WORDS: biomechanics; biped; scaling; dinosaur; locomotion; running; size; *Tyrannosaurus*

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 theropods (bipedal, predatory) dinosaurs could run (Thulborn, 1990; Irby, 1996), as their avian descendants do today. There is also tantalizing evidence from trackway data 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 (Alex- ander, 1976; Thulborn, 1990; but see Alexander, 1991) using the Froude number (Fr), a gauge of dynamic similarity. Fr = v² * 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)?

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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.
MODELS OF RUNNING IN EXTINCT BIPEDS

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 segments 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 re-measured 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_{muscles}) 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:

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

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_{muscles} 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 \times 10^3 kg m\(^{-3}\)), cos \theta is the cosine of the mean angle of muscle fascicle pennation, \sigma is the maximum isometric stress (force/area; 3.0 \times 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 \theta 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 (\theta = 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:

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

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...
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 mi 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 mi values will then be compared to actual extensor muscle masses (mI 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 mi as a percentage of mbody (see Hutchinson, 2004). Thus, entering any different mbody value for any of my models has negligible effects on the mi estimated for the model; mbody is not a term in Eqs. 1, 2. This is a crucial point for the models of extinct taxa: the exact value of mbody, 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
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 ($M_{\text{musc}}$), 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, prescribing 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 (Gatey, 1990; Carrano, 1998; Hutchinson and Gatey, 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 ($\theta$) 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

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

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:

<table>
<thead>
<tr>
<th>Extant taxa</th>
<th>Fascicle length/segment length:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>hip/thigh</td>
</tr>
<tr>
<td>Basiliscus</td>
<td>0.367</td>
</tr>
<tr>
<td>Iguana</td>
<td>0.411</td>
</tr>
<tr>
<td>Alligator</td>
<td>1.13</td>
</tr>
<tr>
<td>Euadromia</td>
<td>0.990</td>
</tr>
<tr>
<td>Gallus</td>
<td>1.00</td>
</tr>
<tr>
<td>Meleagris</td>
<td>0.536</td>
</tr>
<tr>
<td>Dromaius</td>
<td>0.911</td>
</tr>
<tr>
<td>Struthio</td>
<td>0.659</td>
</tr>
<tr>
<td>Homo</td>
<td>0.282</td>
</tr>
<tr>
<td>Macronus</td>
<td>0.202</td>
</tr>
<tr>
<td>Average</td>
<td>0.649</td>
</tr>
<tr>
<td>Reptilia</td>
<td>0.751</td>
</tr>
<tr>
<td>Archosaurus</td>
<td>0.976</td>
</tr>
<tr>
<td>Birds</td>
<td>0.819</td>
</tr>
</tbody>
</table>

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 “Archosaurus” shows the ratio of L to segment length calculated for the average of (Alligator + Birds), used for model “T. rex-scalearch.”

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) because 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 re-examine my conclusions.
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 *Tyranosaurus* (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-

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For each model and each joint (hip/knee/ankle/toe), extensor muscle moment arm (r), moment arm of $F_{\text{ext}}$ (R), extensor mass needed acting about each joint (mi; as % m_body), and maximum ratio of actual vs. required extensor muscle masses (“mI/mi (max)”), based on an upper limit of 7% m_body (Hutchinson, 2004), are presented. Additionally, total extensor 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 mi was excluded from calculating T, as in Hutchinson (2004), and hence those values are in parentheses. Values for maximum mI/mi ratios that are less than 1, and mi values that are greater than observed mI values in extant bipeds (7% m_body or more), are denoted with an asterisk.
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 ($\theta$; 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 cranially (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 $F_{fume}$ application (Fig. 2), and hence R,
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 (“$T. \text{rex}_\text{cmatzero}$” 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 $m_k$, 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 “$T. \text{rex}_1$” model while leaving other parameters unchanged (Fig. 4). In the models “$T. \text{rex}_\text{alltrunkmass}$” (6,000 kg trunk mass and massless limbs), “$T. \text{rex}_\text{doublelegmass}$” (leg masses doubled, keeping total body mass at 6,000 kg), “$T. \text{rex}_\text{nolegmass}$” (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 $m_k/m_i$ 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
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\textsubscript{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\textsubscript{func} and hence the m\textsubscript{i} required for rapid running. A more columnar limb orientation reduced the magnitude of R and m\textsubscript{i}, whereas a more crouched limb orientation increased R. Some joint m\textsubscript{i} values were very sensitive to the assumed mid-stance joint angles (Table 5, Figs. 3, 4). In particular, the knee joint m\textsubscript{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\textsubscript{a} (and toe m\textsubscript{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\textsubscript{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\textsubscript{func}. This lowered the m\textsubscript{i} values close to 0, except for the hip m\textsubscript{h}, which was unchanged because the pelvic pitch was not varied (see below). As such more columnar limb orientations could lower m\textsubscript{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\textsubscript{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\textsubscript{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\textsubscript{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\textsubscript{h} increased over 50%, from 6.9% to over 10% m\textsubscript{body} with this more realistic assumption, which would prohibit fast running (m\textsubscript{h} > 7% m\textsubscript{body}; the knee m\textsubscript{k} decreased to 0.99% but the ankle m\textsubscript{a} increased to 6.6% m\textsubscript{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\textsubscript{i}; although the R values for more distal joints can be reduced by adopting more straightened limbs, it is not possible to change the m\textsubscript{h} by reorienting the limbs. This is because the hip extensor m\textsubscript{h} depends only on pelvic pitch and CM position, which have little potential for behavioral alteration in theropods.
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” and “T. rex_chickenpose” models) would have been extremely high: 5–11% m\textsubscript{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; Leath, 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\text{t} values (Fig. 3; Table 5) by up to 100%, bringing the total muscle masses down to ~3–5% of body mass and individual m\text{t} values near 0.0, except for m\text{a}, 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\text{t}/m\text{a} 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\text{t} values appreciably because of the more flexed ankle (and hence a large ankle extensor m\text{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\text{a} 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\text{a} (or T) to plausible values (~7% or less) for fast running in smaller theropods, but not in Tyrannosaurus.

Muscle fascicle lengths (L). The m\text{a} 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\text{a} values by 1.15× 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\text{a} 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_scalearch” shows (Fig. 4), I conservatively underestimated the m\text{a} 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\text{a} 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\textsubscript{L} 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\textsubscript{A} to the required mass m\textsubscript{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\textsubscript{L} values. My observation that the hip m\textsubscript{L} 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\textsubscript{L}, reducing locomotor activity may be the only option remaining for very large animals, even if the limits imposed by the ankle extensor m\textsubscript{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-
Extinguished 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 (Table 6). See text for discussion.

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<td>0.09</td>
<td>0.13</td>
<td>0.060</td>
</tr>
<tr>
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<td>0.070</td>
<td>0.090</td>
<td>0.030</td>
</tr>
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<td>0.13</td>
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<tr>
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<td>0.16</td>
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<tr>
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<td>0.37</td>
<td>0.28</td>
<td>0.14</td>
<td>0.11</td>
</tr>
</tbody>
</table>

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

**Exterior moments should be much larger than isometry predicts** ($m_{\text{body}}^{0.4}$) 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% $m_{\text{body}}$ 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% $m_{\text{body}}$ 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 all autopomorphies 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 (~$m_{\text{body}}^{0.4}$; 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 $M_{\text{musc}}$ during unipodal standing by 2.5 to simulate running. My assumed value of $G$ is probably conservatively low for $Fr = 17$ (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_A 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_h (5.3) to feasibly low values (<7% m_body). Alternatively, with G = 1.6 for model “T. rex_columnar,” the distal m_l values would decrease to lie easily within reasonable biomechanical bounds (m_l/m_h > 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 > 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; Leary, 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$_{m}/$m$_{e}$ values noted. My results support the inference that running ability increased in the bipedal predecessors to theropod dinosaurs, which reached m$_{m}/$m$_{e}$ 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 increased 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$_{m}/$m$_{e}$ 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 *Gigantosaurus* (Blanco and Mazzetta, 2001) is unlikely given the weight of biomechanical evidence showing the decrease of m$_{m}/$m$_{e}$ ratios with body size.

This proposed pattern of reduced running ability was secondarily reversed, however, in maniraptoriform theropods, which gained higher m$_{m}/$m$_{e}$ 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$_{e}$ values calculated for smaller coelurosaur 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$_{m}/$m$_{e}$ 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
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...
that, 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 \textit{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 \textit{Tyrannosaurus} and other large theropods (Alexander, 1985a, 1989; Farlow et al., 1995; Christiansen 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.

\section*{ACKNOWLEDGMENTS}

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\section*{LITERATURE CITED}

Carrano MT. 1999. What, if anything, is a cursor? Categories


Lauder GV. 1995. On the inference of function from structure. In: Thomason JI, editor. Functional morphology in vertebrate pa-


APPENDIX A

Glossary of Symbols Used (and Units)

A actual total limb extensor mass (% mbody)
c recruited fraction of muscle volume
d muscle density (kg m⁻³)
Ffunc limp “functional” force (N)
Fr Froude number (= v² g⁻¹ l⁻¹)
G relative activity factor (x body weight)
g acceleration due to gravity (m s⁻²)
l hip height (m)
L muscle fascicle (fiber) length (m)
mbody body mass (kg)
m_{li} actual muscle mass about joint i (% mbody)
m_{ri} required muscle mass about joint i (% mbody)
m_{H} actual muscle mass about hip (% mbody)
m_{K} actual muscle mass about knee (% mbody)
m_{k} required muscle mass about knee (% mbody)
m_{A} actual muscle mass about ankle (% mbody)
m_{a} required muscle mass about ankle (% mbody)
m_{T} actual muscle mass about toe (% mbody)
m_{t} required muscle mass about toe (% mbody)
M_{musc} muscle moment about joint i (N m)
R moment arm of Ffunc (m)
r muscle moment arm (m)
T required total limb extensor mass (% mbody)
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 172530; east 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 wetherillii* (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.