

**A peer-reviewed version of this preprint was published in PeerJ on 11 June 2015.**

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Hutchinson JR, Rankin JW, Rubenson J, Rosenbluth KH, Siston RA, Delp SL. 2015. Musculoskeletal modelling of an ostrich (*Struthio camelus*) pelvic limb: influence of limb orientation on muscular capacity during locomotion. PeerJ 3:e1001 <https://doi.org/10.7717/peerj.1001>

## **Musculoskeletal modeling of an ostrich (*Struthio camelus*) pelvic limb : Influence of limb orientation on muscular capacity during locomotion**

We developed a three-dimensional, biomechanical computer model of the 36 major pelvic limb muscle groups in an ostrich (*Struthio camelus*) to investigate muscle function in this, the largest of extant birds and model organism for many studies of locomotor mechanics, body size, anatomy and evolution. Combined with experimental data, we use this model to test two main hypotheses. We first query whether ostriches use limb orientations (joint angles) that optimize the moment-generating capacities of their muscles during walking or running. Next, we test whether ostriches use limb orientations at mid-stance that keep their extensor muscles near maximal, and flexor muscles near minimal, moment arms. Our two hypotheses relate to the control priorities that a large bipedal animal might evolve under biomechanical constraints to achieve more effective static weight support. We find that ostriches do not use limb orientations to optimize the moment-generating capacities or moment arms of their muscles. We infer that dynamic properties of muscles or tendons might be better candidates for locomotor optimization. Regardless, general principles explaining why species choose particular joint orientations during locomotion are lacking, raising the question of whether such general principles exist or if clades evolve different patterns (e.g. weighting of muscle force-length or force-velocity properties in selecting postures). This leaves theoretical studies of muscle moment arms estimated for extinct animals at an impasse until studies of extant taxa answer these questions. Finally, we compare our model's results against those of two prior studies of ostrich limb muscle moment arms, finding general agreement for many muscles. Some flexor and extensor muscles exhibit self-stabilization patterns (posture-dependent switches between flexor/extensor action) that ostriches may use to coordinate their locomotion. However, some conspicuous areas of disagreement in our results illustrate some cautionary principles. Importantly, tendon travel empirical measurements of muscle moment arms

must be carefully designed to preserve 3D muscle geometry lest their accuracy suffer relative to that of anatomically realistic models. The dearth of accurate experimental measurements of 3D moment arms of muscles in birds leaves uncertainty regarding the relative accuracy of different modelling or experimental datasets such as in ostriches. Our model, however, provides a comprehensive set of 3D estimates of muscle actions in ostriches for the first time, emphasizing that avian limb mechanics are highly three-dimensional and complex, and how no muscles act purely in the sagittal plane. A comparative synthesis of experiments and models such as ours could provide powerful synthesis into how anatomy, mechanics and control interact during locomotion and how these interactions evolve. Such a framework could remove obstacles impeding the analysis of muscle function in extinct taxa.

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5 **Musculoskeletal modeling of an ostrich (*Struthio camelus*) pelvic limb: Influence of limb**  
6 **orientation on muscular capacity during locomotion**  
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22 Short title: Ostrich pelvic limb muscle model  
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24 Keywords: Paleognathae, ratite, biomechanics, gait, muscle, moment arm, posture, bird.  
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29 For submission to PeerJ [www.peerj.org](http://www.peerj.org)  
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## 32 Introduction

33  
34 As the largest living avian bipeds, ostriches (*Struthio camelus* Linnaeus 1758) are  
35 important for understanding how body mass influences locomotor mechanics in birds. In  
36 addition, ostriches are among the fastest of living terrestrial animals, and are the fastest living  
37 (perhaps even the fastest ever) bipedal runners. These birds can reach maximum speeds  $>15$   
38  $\text{ms}^{-1}$  (Alexander et al., 1979); similar to another biped that is coincidentally of similar size:  
39 red kangaroos (*Macropus rufus*) (Bennett & Taylor, 1995). Examination of their locomotor  
40 dynamics may reveal some of the complex factors that determine maximum running speed in  
41 land animals and guide the development of fast running machines. Ostriches are also of  
42 similar body size to humans, which other than birds are the only obligate striding bipeds  
43 today, making comparisons of bipedal locomotor function in these two species possible (e.g.,  
44 Gatesy and Biewener, 1991; Rubenson et al., 2011). Additionally, as the largest extant birds,  
45 ostriches are important “endpoints” for studies of body size effects on locomotion (e.g.,  
46 Maloiy et al., 1979; Gatesy et al., 2009; Brassey et al., 2013a,b; Kilbourne, 2013).  
47 Furthermore, ostriches are members of the ratite bird clade, whose evolution from basal  
48 flying birds into large cursorial flightless animals has been of longstanding scientific interest.  
49 However, the evolutionary patterns and processes that produced the diversity of living ratites  
50 and their unusual locomotor mechanisms remain uncertain (Baker et al., 2014 and references  
51 therein). In turn, ratite birds including ostriches occupy relatively basal positions in extant  
52 avian phylogeny (e.g., Clarke and Cracraft, 2001; Baker et al., 2014). Despite their  
53 remarkable cursorial specializations and evolutionarily increased body size, ostriches can  
54 offer clues to the structure and function of earliest crown clade birds, and thereby about the  
55 evolution of avian locomotion from their theropod dinosaur forebears (e.g., Gatesy, 1990).  
56 Ostriches have also often been employed as analogues for dinosaur locomotion (e.g., Russell,  
57 1972; Paul, 1998) despite some major anatomical differences (Gatesy, 1990,1995;  
58 Hutchinson and Gatesy, 2000; Hutchinson, 2002; Gatesy et al., 2009; Hutchinson & Allen,  
59 2009), so ostriches and extinct dinosaurs may be reciprocally informative.

60 A general problem facing those interested in examining the above questions in detail  
61 is that ostrich locomotion, including pelvic limb structure-function relationships during  
62 movement, remains incompletely understood. Numerous studies have empirically  
63 investigated the locomotor kinematics and kinetics of ostriches (e.g., Alexander et al., 1979;  
64 Gatesy and Biewener, 1991; Abourachid, 2001; Abourachid and Renous, 2000; Rubenson et  
65 al., 2004,2007,2011, Smith et al., 2006,2007,2010,2013; Jindrich et al., 2007; Schaller et al.,  
66 2009,2011) and much focus has been given to the whole-body mechanics and energetics of  
67 ostriches (e.g., Fedak and Seeherman, 1979, Fedak et al., 1982; Rubenson et al., 2004,  
68 Watson et al., 2011). However, detailed understanding of the interactions between the various  
69 components of the musculoskeletal system and the environment during these movements  
70 remain poorly understood. Due to the complex, non-linear dynamics of the musculoskeletal  
71 system, correlating whole-body level measures of locomotion to specific muscle function-  
72 structure relationships cannot yet be adequately performed.

73 Furthermore, ostrich myology was not carefully described until recently  
74 (Weissengruber et al., 2003; Gangl et al., 2004; Zinoviev, 2006; also knee joint functional  
75 morphology by Fuss, 1996; foot/ankle function by Schaller et al., 2009,2011). Previous  
76 myological studies were marred by errors in interpreting ostrich anatomy and by confusing  
77 application of mammalian anatomy to ostriches (e.g., Haughton, 1864; Macalister, 1864) or  
78 provided only a superficial treatment of proximal pelvic limb anatomy (e.g., Mellett, 1994).  
79 Even Gadow (1880), a classic comparative reference, contains antiquated concepts of  
80 homology (Rowe, 1986). These prior studies of ostrich myology augment comparative work  
81 on the pelvic limb myology of other ratites (e.g., Haughton, 1867a,b; Gadow, 1880;

82 McGowan, 1979; Vanden Berge, 1982; Patak and Baldwin, 1998; Picasso 2010,2012; Lamas  
83 et al., 2014; Regnault et al., 2014). Additionally, data are available on muscle physiology in  
84 ostriches (Velotto and Crasto, 2004) and other ratites (e.g., McGowan, 1979; Patak and  
85 Baldwin, 1993), although biomechanical data characterizing muscle force-velocity and force-  
86 length relationships for avian pelvic limb muscles are scant (e.g., Nelson et al., 2004).

87 This body of prior research provides the strong foundation necessary for detailed  
88 examination of ostrich limb muscle function using anatomically-realistic biomechanical  
89 modelling in order to advance understanding of how the largest living bird supports its body  
90 weight and moves itself with its pelvic limb muscles. Here, to provide new insight into  
91 ostrich locomotor structure-function relationships, we investigate how pelvic limb muscle  
92 functions relate to limb orientation (i.e., posture/pose or joint angles; Gatesy, 1995; Gatesy  
93 et al., 2009) in ostriches. To do this, we integrate data from experimentally measured joint  
94 kinematics and ground reaction forces with a biomechanical computer model that was  
95 constructed by digitizing the bones, muscles, and tendons of an adult ostrich. By replicating  
96 ostrich structure and behavior, the musculoskeletal model provides estimates of individual  
97 muscle moment arms (Pandy, 1999) and maximum capacity for moment generation during  
98 those behaviors: quantities that are otherwise difficult or impossible to accurately measure  
99 non-invasively, especially for all thirty-six major pelvic limb muscles simultaneously. Here  
100 we use this model to address some fundamental mysteries about locomotion in ostriches as  
101 well as birds, non-avian dinosaurs and bipeds.

102 Larger mammalian species tend to have straighter limbs than smaller species to  
103 improve their effective mechanical advantage during movement (Biewener, 1989, 1990). Yet  
104 it remains unclear how much of this improvement is achieved by reducing the moment arms  
105 of ground reaction forces about the limb joints using less flexed limb joint orientations or by  
106 increasing muscle moment arms via increased anatomical leverage (e.g., relatively larger  
107 trochanters) or straightened limb orientation (i.e., which shifts muscles further away from  
108 joint centres; Hutchinson et al., 2005). Our ostrich musculoskeletal model will facilitate  
109 discerning this relationship in birds, for whom it seems a similar pattern to mammals of  
110 having improved mechanical advantage in larger species holds (Gatesy and Biewener, 1991;  
111 Hutchinson, 2004; Günther et al., 2004; Brassey et al., 2013; Kilbourne et al., 2013).

112 Previous studies (e.g., Hutchinson et al., 2005; and references therein) suggested that  
113 limb antigravity muscle moment arms (or moment-generating capacity; Full and Ahn, 1995)  
114 may peak in very upright limb orientations, which intimates that smaller animals with more  
115 crouched poses (e.g., birds) employ sub-optimal joint angles for supporting their body weight  
116 (Biewener, 1989; Günther et al., 2004), presumably as a tradeoff to provide other benefits  
117 such as increased maneuverability (e.g., Daley and Usherwood, 2010). As the largest living  
118 birds, ostriches stand and move with straighter limbs than smaller birds (Gatesy and  
119 Biewener, 1991). However ostriches are bipeds that still habitually support themselves with  
120 markedly flexed hip and knee joints, which make them a useful case study of this mechanical  
121 relationship between posture and antigravity muscle capacity. Understanding this relationship  
122 impacts the broader question of why animals choose certain postures—do they select postures  
123 that favour larger moment arms for economical force production (e.g., Fujiwara, 2009;  
124 Fujiwara et al., 2011; Fujiwara and Hutchinson, 2012) or other factors such as muscle force-  
125 length properties (e.g., McClearn, 1985; Lieber & Boakes, 1988a,b; Lieber & Brown, 1992;  
126 Lieber & Shoemaker, 1992; Lieber, 1997)?

127 The moment arms of ostrich pelvic limb muscles have been studied before with two  
128 different methodologies: two-dimensional (2D) experimental (“tendon travel”) measurements  
129 of defleshed limbs (Smith et al., 2007) and 3D musculoskeletal computer models constructed  
130 from literature data, dissections and scanned skeletons (Bates and Schachner, 2012). The  
131 question remains open, how accurate are these experimental measurements and models, and

132 how consistently can different researchers construct such models given the inherent  
133 subjectivity involved? This methodological question impacts many of the questions above; a  
134 weak model impairs the ability to test hypotheses. Here, we use our 3D musculoskeletal  
135 model and previously collected experimental data to address three main questions related to  
136 the issues described above: (1) Do ostriches adopt limb orientations during walking or  
137 running that optimize their capacity to generate maximal moments about the pelvic limb  
138 joints? (2) Are the moment arms of limb muscles maximized (for antigravity/extensor  
139 muscles; or minimized in the case of antagonistic flexor muscles) at mid-stance of  
140 locomotion (optimizing weight support), or at highly extended limb orientations, as prior  
141 studies of dinosaurs inferred (e.g., Hutchinson et al., 2005)? Finally, (3) how accurate or  
142 repeatable are estimates of limb muscle moment arms in ostriches using different methods?

143 We also integrate our results with previous studies of ostriches and other large birds  
144 (cited above) to infer how the pelvic limb muscles function in locomotion. This provides a  
145 three-dimensional perspective on avian musculoskeletal function, a necessary shift away  
146 from past planar (2D) simplifications of this system (e.g., Alexander et al., 1979; Abourachid,  
147 2001; Hutchinson, 2004; Gatesy et al., 2009) because recent studies have shown complex 3D  
148 limb dynamics during avian movement (Gatesy, 1994, Hutchinson and Gatesy, 2000;  
149 Rubenson et al., 2007,2011; Goetz et al., 2008; Abourachid et al., 2011; Andraka et al., 2013;  
150 Kambic et al., 2014). Finally, we synthesize our results with similar data from other bipeds,  
151 including humans and *Tyrannosaurus rex*, to infer how limb muscle moment-generating  
152 capacity more generally relates to limb orientation and body size.

153

154

## 155 **Materials and Methods**

156

### 157 *Animals*

158 Experimental biomechanics data were collected from three female adult ostriches  
159 (70.0, 78.7, 75.9 kg body mass), from which a single representative animal's data was used as  
160 model input (78.7 kg). Birds were housed in a large outdoor paddock (5000 m<sup>2</sup>) and provided  
161 with unlimited access to food and water. All experiments were performed in accordance with  
162 the Animal Ethics Committee of the University of Western Australia. Architectural and  
163 geometric data for the muscle-tendon units, and skeletal dimensions used in the computer  
164 model, were measured in a third female ostrich (65.3 kg), which had no musculoskeletal  
165 pathologies and was culled from a commercial ostrich herd (The Ostrich Meat Company,  
166 Merced, California). We subsequently verified these anatomical data by qualitative  
167 comparisons with three other adult specimens of qualitatively similar size, as well as  
168 literature descriptions (Gangl et al., 2004; Zinoviev, 2006).

169

### 170 *Kinematic measurements*

171 The experiments and 3D kinematic analyses are described in detail elsewhere  
172 (Rubenson et al., 2004,2007,2011). Briefly, the birds were trained to walk and run across a  
173 50m long fenced runway surfaced with high-density rubber matting (10 mm thickness). An  
174 eleven-parameter direct linear transformation (DLT) was used to construct a 3D image  
175 volume from two high-speed cameras (200 Hz) positioned at 45° angles to the runway (Peak  
176 Motus; Peak Performance, Centennial, CO). The DLT was calculated using a custom-built 48-  
177 point moveable calibration frame. The video footage from the two cameras were gen-locked  
178 and synchronized manually using a hand held switch that caused a barcode in each video  
179 field to turn white. All data collection was performed after sunset under artificial lighting. A  
180 wide range of speeds was recorded in prior studies (Rubenson et al., 2004,2007,2011), but we  
181 only used representative kinematic data for a single walking at 1.22 ms<sup>-1</sup> and slow running

182 (at  $3.46 \text{ ms}^{-1}$ ). These two trials were within 1 S.D. of the mean kinematic data for trials from  
183 Rubenson et al. (2007).

184 The 3D position and orientation of the ostrich limb segments were determined by  
185 videotaping clusters of non-linear, retro-reflective markers placed on the pelvis, femur,  
186 tibiotarsus, and tarsometatarsus and a single marker placed on the end of the third phalanx.  
187 These markers were used to define segment rigid-body Technical Coordinate Systems (TCS;  
188 Cappozzo et al., 1995). Prior to walking and running trials, static calibration trials were  
189 performed in order to identify several key anatomical landmarks necessary to construct  
190 segment Anatomical Coordinate Systems (ACS; see Rubenson et al. (2007,2011) for  
191 details). Anatomical landmarks were identified using a 6-marker pointer device and expressed  
192 in the segment TCSs. The static calibration trials thus allowed for the reconstruction of each  
193 segment ACS across walking/running strides using the motion data of the segment marker  
194 clusters alone.

195 Three-dimensional marker trajectory data were filtered using a fourth order zero-lag  
196 Butterworth low-pass filter (4-12 Hz) and compiled in c3d format (Motion Lab Systems,  
197 USA). Kinematics were computed using BodyBuilder modelling software (Oxford Metrics;  
198 Oxford, UK). Joint angles were calculated by determining the Euler angles associated with  
199 the transformation between the ACSs of the proximal and distal segments of a joint (Grood  
200 and Suntay, 1983). Segment ACSs in both the model (below) and in the experimental animals  
201 were constructed using the same landmarks (anatomical landmarks and numerically derived  
202 axes) and same ordered set of rotations between proximal and distal ACSs. Thus, 3D joint  
203 motion was defined equivalently in the musculoskeletal model and in the experimental  
204 animals and we were able to use experimentally derived joint angles as input into our  
205 musculoskeletal model to estimate muscular mechanics *in vivo* during walking and running.  
206  
207

### 208 *3D coordinate systems for anatomical dissection*

209 We used a Polaris optical tracking system (Northern Digital Inc., Waterloo, Ontario)  
210 to record the positions of anatomic landmarks and relevant joint kinematics during dissection  
211 sessions. This tracking system is accurate to within 1.5 mm with the  $1.5 \text{ m}^3$  measurement  
212 volume used in this study (Traxtal Inc., Toronto, Ontario), and in order to ensure this  
213 accuracy we performed appropriate calibrations before collecting our data.

214 We first skinned the right pelvic limb of the ostrich specimen. Before dissection of  
215 the muscles, we attached LED-emitting reference frames (AdapTrax trackers, Traxtal Inc.,  
216 Toronto, Ontario) to each bone segment using orthopaedic bone screws. Each reference frame  
217 contained a cluster of LEDs that allowed the tracking system to record the 3D position and  
218 orientation of each segment (establishing the segment TCSs for the dissections, comparable  
219 to that for the experiments). Figure 1 shows the apparatus we used. We used a digitizing  
220 probe (Northern Digital Inc., Waterloo, Ontario) to digitize the 3D coordinates of the  
221 musculoskeletal geometry in each session relative to these trackers. Unlike the LED-emitting  
222 reference frames, the digitizing probe had a cluster of highly reflective spheres, making it an  
223 untethered and mobile tool. When these spheres were visible to the tracking system, the 3D  
224 position of the tip of the probe (calibrated in advance) could be recorded with respect to the  
225 TCS. Three rigid permanent points (marked with a drill as points on the bones) were  
226 measured on each segment to provide a local bone coordinate system for all  
227 digitizing/dissection sessions. This step allowed the TCS to be removed from the bone and  
228 reattached in a different area to facilitate the dissection process while still preserving the  
229 overall relationship of digitized points on a given bone between sessions.



230 Building a musculoskeletal model required points to be expressed in the segment  
231 ACSs (Figure 2 and Rubenson et al., 2007,2011). The pelvis reference frame was defined as  
232 follows: the origin at the midline of the pelvis halfway between the left and right side hip  
233 joint centres; the unit vector IL SUL (x-axis; positive being anterior); the cross-product of the  
234 x-axis and the unit vector SUL SYN (y-axis; positive being cranial), and cross-product of the  
235 x-axis and y-axis (z-axis). To locate the hip joint centres, we digitized 10-20 points in and  
236 around the acetabulum and femoral head, and then used least-squares optimization to fit a  
237 sphere to each of the two resulting point clouds. The centre of this best-fit sphere was the hip  
238 joint centre. To establish the reference frames for the other segments, we first estimated the  
239 medial-lateral joint rotational axis for the remaining joints by flexing and extending each  
240 joint and recording the 3D position and orientation of the distal bone with respect to the  
241 proximal one as a series of homogeneous transformation matrices. With these transformation  
242 matrices, we were able to calculate the average kinematic screw (helical) axes (Bottema and  
243 Roth, 1990) that best approximated the flexion-extension axis between those segments.

244 The femur coordinate system was defined as: the origin at the proximal joint centre;  
245 the segment z-axis along the medial-lateral joint rotational axis (positive being lateral); the y-  
246 axis as the cross-product of the z-axis and the unit vector between the proximal and distal  
247 joint centers; and the x-axis as the cross-product of the y- and x-axes. The tibiotarsus and  
248 tarsometatarsus coordinate systems were defined as: the origin at the proximal joint centre;  
249 the y-axis as unit vector between the proximal and distal joint centers; the segment z-axis as  
250 the cross product of the medial-lateral joint rotational axis and the y-axis; and the x-axis as  
251 the cross-product of the y- and z-axes. The pes coordinate system was defined as: the origin  
252 at the proximal joint centre; the segment x-axis as the unit vector between the proximal joint  
253 center and the end of the segment; the z-axis as the cross product of the medial-lateral joint  
254 rotational axis and the x-axis; and the y-axis as the cross-product of the x- and z-axes. Putting  
255 any digitized points into these ACSs required two linear transformations: from the TCS into  
256 the local bone coordinate system and subsequently into the ACS. Table 1 provides data on  
257 axis positions used in the final model.

258

### 259 *Anatomical digitization and musculoskeletal model construction*

260 We began by dissecting the specimen proceeding from superficial to deep structures.  
261 The positions of muscles and bone geometry or other relevant anatomical features on each  
262 limb segment were measured using the digitizing probe. In particular, before removing  
263 muscles we digitized the circumferences of muscle origins and insertions as well as the 3D  
264 paths of the muscles from origin to insertion, using from 1-30 (depending on extent of the  
265 structure) x,y,z coordinate points to characterize each structure of interest. In addition, we  
266 measured other musculoskeletal features used as references, such as bone surfaces (for later  
267 alignment of complete 3D bone images from CT data), condylar contours, and those  
268 ligaments that influence muscle-tendon unit paths. All 3D points for use in the model were  
269 converted into the ACS.

270 After dissection the bones were defleshed and macerated, but with articular cartilages  
271 and menisci remaining as intact as possible. The bones were then CT scanned (1.5-3 mm  
272 slices, 120-130 kPa, 109-150 mA, on a Picker PQ5000 CT scanner) and the resulting slices  
273 digitized in Mimics software (Materialise, Inc; Leuven, Belgium) to produce rendered 3D  
274 polygonal meshes. Ultimately ASCII (ASC) format images were used (decimated to <50,000  
275 polygons each) as bone images in the model. Importantly, the bones were only visual aids  
276 and not inherent obstacles to joint or muscle motion, but they are crucial for visualizing  
277 musculoskeletal function.

278 We used these anatomical data and bone images to construct a 3D musculoskeletal  
279 computer model of the right pelvic limb using SIMM software (Musculographics, Inc.;

280 Chicago, IL; Delp et al., 1990,1992; Delp and Loan, 1995,2000). The right limb was mirrored  
 281 as a left limb. The digitized muscle paths were used as a template for developing the muscle  
 282 paths in the final model (Figures 3, 4). Paths were represented using a combination of “via  
 283 points” (i.e., static points fixed relative to a segment) and “wrapping surfaces” that prevented  
 284 translation of points outside of a predefined area (see Delp and Loan, 1995, 2000 for details;  
 285 also Hutchinson et al., 2005, for a similar procedure we used for *Tyrannosaurus rex*). Table 2  
 286 presents the muscles modelled, with abbreviations used throughout the paper. Table 3  
 287 describes all the muscle wrapping surfaces assumed in the model and Figure 5 displays  
 288 examples.

289 Inevitably, because the 3D musculoskeletal geometry was complex, we had to  
 290 cautiously judge where to position wrapping surfaces and what size and shape they should be.  
 291 Additional ostrich cadaveric material was used along with the literature (Gangl et al., 2004;  
 292 Zinoviev, 2006) to qualitatively refine the model as we iteratively progressed, checking that  
 293 paths and attachments were represented reasonably and consistently. We took care to  
 294 visualize the model in many different 3D joint positions to ensure that muscles did not pass  
 295 through areas occupied by other soft tissues or especially bones and to eliminate other  
 296 numerical errors generated by interactions of the muscle-tendon unit paths with wrapping  
 297 surfaces (e.g., “loops” in muscles caused by contradictory constraints in the model).  
 298 Importantly, because we intended to compare our model’s results with data from Smith et al.  
 299 (2007) and Bates and Schachner (2012), we kept our model construction blind to the results  
 300 of these studies, avoiding any comparisons and indeed finishing the major steps in  
 301 completing our model before these studies were published.

### 302 *Muscle-tendon unit architecture and physiology*

303 After we dissected, digitized, and removed the muscles, we separated them from their  
 304 proximal/distal tendons and other connective tissue. We then used digital calipers ( $\pm 0.1$  mm),  
 305 an electronic balance ( $\pm 0.001$  g), and a protractor ( $\pm 1^\circ$ ) to measure muscle fascicle lengths  
 306 ( $L$ ), masses ( $m_{musc}$ ), and resting pennation angles ( $\theta$ ) for calculating physiological cross-  
 307 sectional area ( $A_{phys}$ ), taking an average of five randomized measurements for  $L$  and  $\theta$  in  
 308 larger muscles.

309 Using water displacement (immersing sectioned muscles in graduated cylinders) to  
 310 calculate muscle belly (sans tendon) density ( $d$ ) from (volume  $m_{musc}^{-1}$ ), we obtained a mean  
 311 value of  $1.0645 \times 10^3$  (n=10; S.D.=0.0347)  $\text{kg m}^{-3}$ , matching measurements of mammalian  
 312 muscle (Mendez and Keys, 1960; Brown et al., 2003a). Hence we assumed a conventional  
 313 value of  $d$  as  $1.06 \times 10^3 \text{ kg m}^{-3}$ . As commonly practiced, we assumed  $L$  to be equivalent to  
 314 optimal fiber length ( $l_o^m$ ; Zajac, 1989). We could thus calculate  $A_{phys}$  as (e.g., Alexander et al.,  
 315 1979; Lieber & Boakes, 1988a; Brown et al., 2003b; Hutchinson, 2004):

$$316 \quad A_{phys} = m_{musc} \cos \theta (L d)^{-1} \quad (\text{Equation 1})$$

317  
 318 Equation 2 then estimates  $F_{max}$ , maximum isometric force capacity:

$$319 \quad F_{max} = 3.0 \times 10^5 \text{ m}^{-2} A_{phys} \quad (\text{Equation 2})$$

320  
 321 In which the constant is isometric stress under maximal activation (Medler, 2002;  
 322 Nelson et al., 2004). Note that the musculoskeletal model varies  $\theta$  with  $L$  to maintain constant  
 323 muscle thickness (Zajac, 1989). Muscle maximal contraction velocity was not calculated in  
 324 the present model, but could be added (see Smith et al., 2006 for example) for more complex  
 325 simulations, using published fibre type data for ostriches (Velotto and Crasto, 2004) and  
 326 ostrich or other avian muscle force-velocity data (e.g., Nelson et al., 2004). We also did not

330 include measurements of tendon force-length data here, but either dimensionless estimates  
331 (Zajac, 1989) or specific measurements can be added to future simulations. For simplicity, we  
332 chose to focus in this initial study on near-isometric muscle action and progress to more  
333 complex, dynamic parameters in later work.

334 Muscles were identified as in Table 2 following Gangl et al. (2004) and Zinoviev  
335 (2006) (see Appendix 1 for additional details). For simplicity, we combined some muscle  
336 heads into single functional muscles in the model (cf. Gangl et al., 2004:table 1) and omitted  
337 some tendinous/minute muscles which were grouped with other similar muscles nearby or  
338 omitted in the case of *M. popliteus* (rotates fibula around tibia; Fuss, 1996); these  
339 simplifications are outlined in the Supplementary Text. However, some muscles (e.g., *M.*  
340 *iliofibularis*, *M. ilirotrochantericus caudalis*) were large enough that separation into two heads  
341 was deemed important, as some heads might have very different flexor/extensor moment  
342 arms than more cranial/caudally-positioned ones.

343

#### 344 *Limb muscle biomechanics: Calculations and hypothesis testing*

345 The musculoskeletal model was then imported into OpenSim ([opensim.stanford.edu](http://opensim.stanford.edu))  
346 software in order to take advantage of the programme's established analysis capabilities.  
347 OpenSim uses the 'virtual work' method (change of muscle-tendon unit length per unit joint  
348 rotation) explained by Delp and Loan (1995, 2000) and Pandy (1999) to compute muscular  
349 moment arms over a range of motion. Maximal muscular moments then can be estimated  
350 using muscle  $F_{max}$  and potentially  $l_o^m$  (see above and Zajac, 1989).

351 To test whether ostrich muscle moment-generating capacity is optimized to match  
352 peak loads during walking and running (our Question 1), we compared the results from  
353 estimated maximal muscle moments to experimentally-calculated internal and external  
354 moments (Rubenson et al., 2011), addressed in the Discussion. First, each muscle's maximal  
355 isometric muscle force ( $F_{max}$ ) was multiplied by the flexor/extensor moment arm calculated  
356 by OpenSim, for each pose adopted throughout the representative walking and running gait  
357 cycle trials (every 1% of gait cycle) to obtain the relationship between locomotor kinematics  
358 and isometric muscle moments. Second, OpenSim was used to calculate individual muscle  
359 moments directly, taking into account muscle force-length relationships (set as dimensionless  
360 in a Hill model as per Zajac, 1989), in order to provide a more realistic estimate of the  
361 variation of maximal moment-generating capacity throughout the same gait cycles. Both  
362 approaches were static, ignoring time/history-dependent influences on muscles. The second  
363 approach allowed non-isometric muscle action to be represented, but did not incorporate  
364 force-velocity effects, which would require a more dynamic simulation to resolve. Total  
365 extensor and flexor maximal moments were calculated in OpenSim as well as the net  
366 (extensor + flexor) maximal moment.

367 To determine if ostrich limb muscle moment arms peak at extended limb orientations  
368 or at mid-stance of locomotion (our Question 2), we used the model to calculate the mean  
369 moment arm of all extensor or flexor muscles across the full range of motion of each joint in  
370 flexion/extension (set at constant values for midstance of running in other degrees of  
371 freedom), summed these mean moment arms, and divided that sum by the summed maximal  
372 moment arms for each muscle across the same range of motion (as in Hutchinson et al.,  
373 2005). We then inspected whether our representative mid-stance poses in walking or running  
374 matched maximal or minimal averaged moment arms corresponding to those poses.

375 To compare the degree of matching between muscle moment arms in our model and  
376 the experimental data of Smith et al. (2007) and Bates and Schachner (2012) (our Question  
377 3), we obtained the published experimental and modelling data (K.T. Bates, provided by  
378 request), transformed their joint angle definitions to be consistent with our model definitions,  
379 and plotted the muscle moment arms vs. each joint angle with our moment arm data,

380 restricting the other studies' ranges of motion to those presented in the original studies. For  
381 the knee and joints distal to it, in this study we focus only on flexor/extensor moment arms  
382 for simplicity and because the importance of long-axis and ab/adduction muscle (vs. passive  
383 tissue) moments at these distal joints is unclear, although our model could be adjusted to  
384 calculate those non-sagittal moment arms and moments.

385  
386

## 387 **Results**

388 Here we present our data for addressing our main questions, proceeding in order with  
389 maximal muscular moments, maximal/minimal moment arms, and then general moment arm  
390 patterns compared with other studies'. The model is downloadable from the repository at  
391 <https://simtk.org/home/opensim> and can be manipulated in open source software OpenSim.  
392 Supplementary Movie S1 shows the model animated through the representative running  
393 stride.

394

### 395 *Maximal muscular moments*

396 Our 3D ostrich limb model predicted how the maximal capacity to generate muscle  
397 moments should vary with limb orientation during walking and running (Figures 6, 7).  
398 Maximal flexor moments increase if force-length properties are ignored (treating all muscles  
399 as isometric). This indicates that most muscles in the model are at disadvantageously short  
400 fibre lengths during locomotion, with walking having a generally greater capacity for flexor  
401 moment generation (especially about the hip) than running. These curves do not change much  
402 across the gait cycle. The pattern for extensor moments is more complex. Peak capacity tends  
403 to be in late swing phase (reasonably consistent across all joints). Force-length properties  
404 here provide an advantage, presumably because the muscles are lengthened. Data during the  
405 stance phase do not support the hypothesis, regardless of assumptions about muscle-force  
406 length states, that postures used around mid-stance of walking or running optimize the  
407 moment-generating capacity of pelvic limb muscles in ostriches: the maximal moments early  
408 or late in stance phase, and late in swing phase, are of similar or greater magnitudes. The  
409 relatively flattened shapes of most moment curves without force-length properties enforced  
410 ("Fmax"; dotted lines in Figures 6,7) indicate that muscle moment arm variation across  
411 postures used *in vivo* during locomotion is a smaller contributor to moment generation than  
412 force-length properties ("F-L"; solid lines) in *Struthio*.

413

### 414 *Maximal/minimal muscle moment arms and limb orientation*

415 Do ostriches' limb muscle moment arms peak at very extended limb orientations or at  
416 midstance of walking/running (Figure 8)? We find that the mean hip extensor moment arms  
417 decrease from a peak at full extension as hip joint flexion increases, and the hip flexors  
418 behave similarly. However, knee and ankle moment arms each exhibit different patterns. The  
419 knee extensor and flexor moment arms tend to peak at moderate knee flexion angles (~60-  
420 90°), as do the ankle extensors (plantarflexors), but the ankle flexors have a near-plateau for  
421 most angles, quickly decreasing with extreme dorsiflexion (>100° ankle angle).

422 When the poses that ostriches use during periods of peak limb loading (near  
423 midstance of walking and running; Rubenson et al., 2007) are compared against these  
424 patterns (Figure 8), it becomes evident that there is no clear optimization of muscle moment  
425 arms for supportive (large extensor or small flexor values) roles during these periods of  
426 potential biomechanical constraints. This is in agreement with the maximal moment data  
427 from Figures 6 and 7. Hip extensors and flexors as well as ankle extensors are relatively far  
428 (~60-85% of maximal mean moment arms) from optimal values at midstance of walking and  
429 running. Knee extensor/flexor moment arms are closer to maximal values, especially for

430 walking. However, the co-contraction of multiarticular hip extensor/knee flexors (e.g. ILFB,  
431 FCLP) against knee extensors would eliminate associated benefits—i.e., the ratio of peak  
432 knee extensor to peak knee flexor moment arms would have not have minimized the net knee  
433 extensor moments required at midstance of either walking or running. At moderate knee  
434 flexion values, both the capacity of muscles to extend and to flex the knee are near-maximal  
435 (Figure 8).

436

#### 437 *Moment arms: general trends and comparisons with prior studies*

438 Figures 9-11 show our results for hip flexion/extension moment arms of ostrich  
439 muscles, with comparable data from Smith et al. (2007) and Bates and Schachner (2012) also  
440 plotted if available (abbreviated in this section as S.E.A. and B.A.S. respectively). Here we  
441 focus on the major findings. The two AMB muscles (Figure 9) compare reasonably well  
442 among all three studies, showing a decrease of hip flexion moment arms at strongly flexed  
443 limb poses and in some cases (our AMB<sub>1,2</sub> and the AMB of B.A.S.) a switch from flexor to  
444 extensor action with flexion (~30-90°). The IC muscles likewise have reasonably comparable  
445 results, but only our IC muscle switches action at extreme flexion. Our model agrees well  
446 with the data of S.E.A. and especially B.A.S. for the IL muscle, including its decreasing hip  
447 extensor moment arm with increasing hip flexion and a switch from hip extensor to flexor  
448 action at typical *in vivo* positions (~40-70°). We have similar findings for the ILFB muscle,  
449 although no switch to hip flexor moment arms is observed in either of the two parts of this  
450 muscle in our model (S.E.A. and B.A.S. represented it as one part) (Figure 9).

451 Uniarticular muscles acting about the hip joint consistently display flexor action for  
452 the IFE, IFI, ISF and OM muscles (Figure 10). We find fair agreement among studies for the  
453 IFE (note confusion caused by misidentification of muscles in prior studies-- see Appendix 1;  
454 the “IFE - Smith” in Fig. 10 is equivalent to our IFE and ITC), ITC, IFI, ITM and ITCR  
455 muscles’ general changes of moment arms. Our IFE moment arm values are smaller than for  
456 S.E.A. and B.A.S. apparently because of the aforementioned identification issue (the top left  
457 panel in Fig. 10 shows our IFE plotted against S.E.A.’s IFE+ITC combined). Notably, the  
458 curves for the two parts of ITC in our data and those of B.A.S. are remarkably similar (and  
459 consistent with S.E.A.’s experimental data for their “IFE – Smith” as well as “ITC - Smith”)  
460 despite the subjectivity inherent in partitioning this large muscle into two paths. These  
461 moment arms grade from flexor to extensor action with strong flexion (~40-70°). A similar  
462 trend is evident for the ITM and ITCR muscles (but note the identification issues outlined in  
463 Appendix 1; S.E.A.’s “ITC” is actually the ITM, which their data otherwise lacks, so the top  
464 right panel in Fig 10 compares their actual ITM [“ITC – Smith”] vs. our ITM). The  
465 antagonistic OM and ISF muscles concur less closely between the latter two studies,  
466 however, displaying more convex curves tending to indicate hip flexor action in our data,  
467 with more concave, flattened arcs favouring hip extensor action in B.A.S. (Figure 10).

468 The “hamstring”, caudofemoral and adductor hip muscles uniformly display extensor  
469 action, befitting their more caudal paths relative to the hip, but agree less well among studies  
470 than the prior muscles (Figure 11). Our data for the FCM, FCLP, CFP and PIFML muscles  
471 portray peak moment arms at low hip extension angles (~0-30°), decreasing with flexion  
472 away from these ranges. These trends qualitatively agree with the S.E.A. and B.A.S. data, but  
473 moment arm values tend to be substantially smaller in those data, especially for the FCLP and  
474 FCM muscles. Our PIFML data show less variation with joint angle than the S.E.A. and  
475 B.A.S. data because we had to constrain this muscle’s path in 3D to avoid it cutting through  
476 bones or other obstacles in some poses. Note also how the S.E.A. results in general show  
477 strong changes with joint angles, whereas the more constrained muscle geometry of our  
478 model and B.A.S.’s results in more modest changes (Figure 11).

479 Long-axis rotation (LAR; in Figures 12,13) moment arms for hip muscles only allow  
480 comparisons between our data and those of B.A.S. Furthermore, as B.A.S. plotted these  
481 moment arms against hip flexion/extension joint angle, we show them that way here but also  
482 plot them against hip LAR joint angle in the Supporting Information (Supplementary Figures  
483 S1,S2); however we do not discuss the latter results here. For the AMB1,2 muscles we find  
484 consistently weak, near-zero LAR action (lateral/external rotation), whereas B.A.S. showed a  
485 steeply increasing hip medial/internal LAR moment arm as the hip is extended (Figure 12). In  
486 contrast, our IC muscle data agree well with B.A.S.'s in having a shallow increase of the  
487 medial/internal LAR moment arm with hip flexion. The two heads of the IL muscle show  
488 opposite trends in our results vs. B.A.S.'s (in our data, becoming less effective at  
489 lateral/external rotation as the hip is flexed). Our results for the two parts of the ILFB muscle  
490 are very different from B.A.S.'s in trending toward stronger medial/internal rotation function,  
491 whereas B.A.S.'s favour lateral/external rotation. The results for the OM muscle have a more  
492 intermediate quality of matching between studies but still indicate a lateral/external rotation  
493 action for this large muscle. Contrastingly, our ISF data and those of B.A.S. match fairly  
494 closely, with consistent lateral/external rotator action. The FCM and FCLP muscles have  
495 among the largest LAR moment arms for all muscles (~0.08m; also observed for our ILp  
496 muscle) in our data, but both muscles reduce their lateral rotator action with increasing hip  
497 extension. In B.A.S.'s data a weaker, opposite (medial/internal rotator) trend was found for  
498 these muscles (Figure 12).

499 The uniarticular hip muscles' LAR moment arms tend to switch more often from  
500 medial to lateral rotation or vice versa (Figure 13). The IFI, however, remains mainly as a  
501 weak medial rotator except at extreme hip flexion ( $>60^\circ$ ). B.A.S.'s data favoured a stronger  
502 medial/internal rotation moment arms for the IFI. Our IFE muscle's data indicate a switch  
503 from lateral rotation into medial rotation near a  $30^\circ$  hip flexion angle, whereas again B.A.S.'s  
504 data had a consistent lateral rotator action. Our results for the two-part ITC muscle concur  
505 qualitatively with B.A.S.', consistently having a strong medial rotator action but smaller at  
506 more extended joint angles. Finally, as in B.A.S.'s data, but featuring smaller moment arms,  
507 our data show that the CFP and PIFML muscles have consistent lateral rotation action in  
508 ostriches; decreasing with increased hip flexion. The ITM and ITCR's medial rotator moment  
509 arms peak at hip angles of  $30\text{-}60^\circ$ , then decrease; a pattern qualitatively matched by B.A.S.'s  
510 data. (Figure 13).

511 Abduction and adduction moment arms for the hip muscles show strong postural  
512 dependency like the LAR moment arms do (Figures 14-15). Again, as for the LAR data  
513 above, we supply these data plotted against abduction/adduction hip joint angle in the  
514 Supporting Information (Supplementary Figures S3, S4), but we do not discuss those results  
515 here. The PIFML muscle has a discontinuity in its hip abductor moment arm (Fig. S4) in our  
516 model at extreme hip abduction angles ( $>40^\circ$ ) but this is well outside normal *in vivo*  
517 abduction angles used ( $<25^\circ$ ; Rubenson et al., 2007). The two AMB muscles in our model  
518 have peak adductor moment arms at different flexion angles ( $\sim 30^\circ$  and  $80^\circ$ ), then decrease.  
519 B.A.S.'s data, in contrast, showed their AMB muscle to act as an abductor. Our IC muscle  
520 has a similar adductor moment arm curve as our AMB2, and a similar divergence from  
521 B.A.S.'s results. Our IL muscle parts agree reasonably well with B.A.S.'s, showing them to  
522 act as adductors. Both our ILFB muscle parts have little variation in their hip abductor  
523 actions; B.A.S.'s representation changed steeply and became an adductor with extreme hip  
524 flexion. The OM muscle, which runs very close to the plane of the acetabulum, is an adductor  
525 at extended joint angles and an abductor at flexed angles in our model, whereas it remained  
526 an adductor in B.A.S.'s data. While the ISF muscle is mainly an abductor in our model, it was  
527 exclusively an adductor in the B.A.S. model. The FCL and FCM muscles compare only  
528 qualitatively between our data and B.A.S.'s, remaining as hip abductors. It is noteworthy that

529 throughout the full ranges of hip motion we examined, most muscles would act as hip  
530 abductors; the dorsal AMB2 and IC muscles are the only consistently strong hip adductors  
531 (Figure 14).

532 Uniarticular “deep dorsal” and antagonistic muscles show similar trends as the above  
533 muscles for adduction/abduction capacities (Figure 15). The IFI has weak adductor action, vs.  
534 abductor in B.A.S.’s data, whereas our data and B.A.S.’s agree well on the hip abductor  
535 moment arm of the IFE. Our representations of the ITCa/p muscle parts switch from  
536 abduction to adduction function as hip flexion surpasses 45-60°; B.A.S.’s did not.  
537 Postacetabular muscles such as the CFP and PIFML in our model are almost exclusively hip  
538 abductors, but the caudofemoral muscles of B.A.S. are weak adductors and the PIFML  
539 equivalents in that study switched to that same action with flexion. Again, our results are  
540 generally opposite B.A.S.’s in the case of the ITM and ITCR muscles, which convert from  
541 abductor to adductor action at 10-40° hip angles in our model and did not change much in  
542 B.A.S.’s (Figure 15).

543 We only focused on flexion/extension moment arms for more distal joints, starting  
544 with the knee (Figures 16,17). Good agreement between knee extensor moment arms for the  
545 AMB2 (dorsal) muscle is evident with the two other studies. The AMB1 (ventral) component  
546 only has data from our model (mainly a weak knee flexor), as does the IC (very weak knee  
547 flexor/extensor at flexed/extended angles). We estimate a larger knee extensor moment arm  
548 for the FMTL muscle but this is because of misidentification of part of that muscle in the  
549 S.E.A. and B.A.S. data (only a distal head was included in this muscle; see Appendix 1).  
550 Similar differences of anatomical representation are likely explanations for the deviation  
551 between our result (weak knee flexor) and S.E.A.’s (strong knee extensor) for the FMTM  
552 (see Discussion). Our model presents slightly different moment arms for its two IL muscle  
553 heads, peaking in extensor values at 30-90° flexion, whereas B.A.S. had identical moment  
554 arms increasing throughout extension.

555 We estimate the knee flexor moment arms as identical (peaking at 90-120° flexion)  
556 for the two parts of the ILFB muscle in our model, which match S.E.A.’s data well, whereas  
557 B.A.S. had moment arms switching from extensor to flexor at 70° of knee flexion, peaking at  
558 quite extended knee poses (Figure 16) (see Discussion). Other “hamstring” muscles (no  
559 comparable data for S.E.A. or B.A.S.) include the FCM and FCLP, which shift steeply from  
560 knee extensor to flexor moment arms at high flexion angles and then peak near 90° in its  
561 flexor moment arm value (Figure 16). The FL muscle shows an almost mirror image pattern,  
562 acting as a knee extensor. Muscles running past the ankle joint (Figure 17), such as the FPD3  
563 and FPD4 groups, have a similar pattern to the FCM and FCLP at the knee, but the TCf  
564 muscle has almost no knee moment arm; consistently acting as a very weak extensor. Finally,  
565 parts of the gastrocnemius muscle group (e.g. GIM) reach peak knee flexor moment arms of  
566 about 0.07m at intermediate knee flexion angles (60-90°). The data for S.E.A. and B.A.S. and  
567 for our GL muscle remain(ed) near smaller knee flexor values, with less postural variation  
568 (Figure 17).

569 Ankle musculature displays fairly congruent patterns in our model and S.E.A. and  
570 B.A.S.’s data (Figures 18,19). The TCf and TCt heads generally have an ankle extensor  
571 action, like the EDL muscle group does, albeit with some switches to extensor action with  
572 extreme (dorsi)flexion in the B.A.S. dataset (and our TCf). Surprisingly, ankle extensors  
573 reveal more variation: our FDL’s ankle extensor moment arm is almost twice as large of that  
574 in the S.E.A. and B.A.S. data, showing little change with ankle posture, whereas the B.A.S.  
575 dataset exhibited a decreased moment arm with flexion. Our other digital flexor muscles  
576 (FPD3, FPD4) and those of S.E.A. display roughly similar values but opposite trends,  
577 increasing with ankle flexion in our model. Our FL muscle’s extensor moment arm is smaller  
578 than those of S.E.A. and B.A.S. The model of B.A.S. had a M. fibularis brevis (FB) muscle

579 (Figure 18), which is reduced to a ligament in *Struthio* and thus not included in our model; no  
580 studies have data for the ligamentous M. plantaris (Zinoviev, 2006). The extensor moment  
581 arms for our gastrocnemius muscles are all identical and fairly constant with ankle flexion,  
582 whereas the curves for the data of S.E.A. and B.A.S. increased steadily and tended to be  
583 larger (Figure 19).

584 Digital flexor muscle moment arms all stay fairly constant (slight increase with  
585 extension of the MTP joint) in our model whereas they showed a stronger decrease in  
586 S.E.A.'s experiment (Figure 20). Our EDL muscle has stronger moment arms than in  
587 S.E.A.'s data but a similarly shallow curve. Finally, our FL muscle exhibits digital flexor  
588 moment arms similar to those of the other digital flexors.

589

590

## 591 Discussion

592

593 The results of our combined experimental and theoretical approach show first that,  
594 while ostrich limb muscles are capable of generating large flexor and extensor moments  
595 about their limb joints during locomotion (Figures 6,7), they do not seem to match maximal  
596 muscle moment-generating capacity with instants of peak loading in walking or slow  
597 running. Second, the moment arms of ostrich flexor/extensor muscles often change greatly  
598 with limb orientation, but they are not consistently matched to minimize the former and  
599 maximize the latter during key periods of weight support in locomotion (Figure 8). Third,  
600 there is mostly reasonable consistency in three different studies of ostrich muscle moment  
601 arms (Figures 9-20), indicating at least fair repeatability with distinct methods, but still some  
602 striking disagreements, especially in the little-explored area of non-flexor/extensor muscle  
603 mechanics. We explore these topics in more detail below and then consider broader issues  
604 related to our findings.

605

### 606 *Maximal muscle moments and kinematics*

607 Our Question 1 asked, "Do ostriches adopt limb orientations during walking or  
608 running that optimize their capacity to generate maximal moments about the pelvic limb  
609 joints?". We find no convincing evidence of such optimization -- maximal capacities to  
610 produce joint moments often peak either early in stance phase or during swing phase (Figures  
611 6,7). In both cases, net joint moments obtained from inverse dynamics analysis are low  
612 (Rubenson et al., 2011). Peak flexor moments (requiring extensor/antigravity muscle activity)  
613 occur at or near midstance in running ostriches (Rubenson et al., 2011:Figure 7), reaching  
614 magnitudes  $>2 \text{ Nm kg}^{-1}$  (i.e.  $>150 \text{ Nm}$  for our subject). Note that these magnitudes are far  
615 below the capacities of hip, knee and ankle muscles ( $>400 \text{ Nm}$ ; Figures 6, 7) but approach  
616 those of the digital flexors ( $\sim 150\text{-}200 \text{ Nm}$ ; Figure 7). On this basis, we infer that either  
617 passive tissues (including muscle passive force-length properties) play an important role in  
618 balancing moments about the tarsometatarsophalangeal joint in running ostriches (cf.  
619 Haughton, 1864; Schaller et al., 2009,2011), especially at faster speeds, or that muscle  
620 moment-generating capacity is near its limits for this joint in particular, even at slower  
621 speeds. Nevertheless, more proximal limb muscles seem further from their moment-  
622 generating limits.

623 In his classic biomechanical analysis of ostrich anatomy, Haughton (1864) assumed  
624 that "the greatest possible amount of muscular force shall be expended in straightening or  
625 unbending the legs", and thus that early and late stance respectively placed the greatest  
626 demands on these forces. Available data no longer support this notion, but there is no  
627 question that ostriches have muscle masses able to produce greater moments (and work) in



628 extension than in flexion, as Haughton explained, but by a factor of about three times for the  
629 hip and knee rather than ten (*vide* Smith et al., 2006,2007).

630 There are several potential explanations for our observations that lead us to a negative  
631 answer to our study's first question. First, we have only examined walking and slow running.  
632 Near maximal speed, moment capacity and requirements around midstance might be more  
633 closely matched (e.g. Hutchinson, 2004), as forces surely increase. At a duty factor of 0.42,  
634 Rubenson et al. (2011) obtained peak vertical ground reaction forces of 1500-2000 N or  
635 about 2.17-2.89 times body weight (BW), whereas Alexander et al. (1979) estimated 2.7 BW  
636 peak forces for an ostrich at near top speed (duty factor 0.29). The latter study used an  
637 equation that probably underestimates peak forces for ostriches, as Rubenson et al.'s (2011)  
638 data show (peak forces are 16-55% greater than predicted from duty factor). Second, our  
639 present model is still static, not considering force-velocity or other dynamic interactions that  
640 would alter moment-generating capacities. It is possible that these parameters, or highly  
641 complex interactions (e.g., muscle moment arms and "power amplification"), could be more  
642 influential than the isometric and force-length properties that our model considers. Third,  
643 entirely different factors could determine locomotor and postural optimization, such as  
644 energetic costs or stability/manoeuvrability (e.g., Daley and Usherwood, 2010).

645 Comparison of our results with other studies of the relationship between limb  
646 orientation and muscle mechanics reveal a fourth potential explanation, that the optimization  
647 of anatomy, posture, physiology and other factors in locomotor dynamics could be highly  
648 species-, task-, limb-, joint- or muscle-specific. Lieber and colleagues (Lieber & Boakes,  
649 1988a,b; Mai & Lieber, 1990; Lieber & Brown, 1992; Lieber & Shoemaker, 1992) conducted  
650 an elegant series of studies that constitute a model system for addressing this issue. They  
651 elucidated that maximal moment production by the semitendinosus muscle in frog hindlimbs  
652 showed a strong dependence on muscle isometric force capacity and moment arms. Some of  
653 these studies found less dependence of moment production on joint angle-dependent moment  
654 arm values (e.g., Lieber & Boakes, 1988a,b), but this dependency varied for the hip and knee  
655 joints (Mai & Lieber, 1990; Lieber and Shoemaker, 1992)—and might be expected to vary  
656 for other muscles, too. Indeed, the moment arm did not vary much with knee joint angle for  
657 the semitendinosus (e.g., 0.37-0.44 cm about knee, across 10-160° range of flexion/extension;  
658 Lieber & Boakes, 1988a:Figure6A) so this muscle could not contribute much variation to  
659 muscle moment production. One might predict more dependency of maximal muscle moment  
660 production on moment arms for muscles that have more variable moment arms, but this has  
661 not been conclusively determined. Lieber & Brown (1992) found that there was no simple  
662 relationship between muscle fibre length and moment arm in seven frog hindlimb muscles,  
663 with differences evident between muscles acting about the hip and knee, suggesting diverse  
664 adaptations to moment production demands.

665 The aforementioned studies' reviews of numerous others in humans, cats and other  
666 species likewise note some variability and uncertainty in what factors determine maximal  
667 moment capacity in limbs, so consensus has been elusive. Furthermore, Brown et al.'s  
668 (2003b) modelling/experimental study of horse forelimbs found that while the moment-  
669 producing capacities of flexor muscles were determined mostly by muscle properties (e.g.,  
670  $F_{max}$  or muscle force-length), muscle moment arms could have greater effects on moments  
671 than those properties for some extensor muscles. Young et al. (1993) also found variability  
672 from 50-100% of resting fascicle length in the amount of length change that cat ankle  
673 muscles used throughout their range of motion. Thus strict "sarcomere equivalency"  
674 (constant usage of maximal muscle range of motion; e.g. discussions in McClearn, 1985;  
675 Lieber, 1997; Bates & Schachner, 2012) is not expected, but an approximate "tuning" of  
676 moment arms to muscle fiber lengths (and joint ranges of motion) is expected at least in some  
677 cases. Lieber and Shoemaker (1992) explained how a greater muscle fibre length to moment

678 arm ratio would cause muscle force-length properties to become less influential on muscle  
679 moment production. Therefore, in the long-fibred proximal muscles of ostriches and other  
680 birds that run closer to the hip and knee joints and thus have smaller moment arms (e.g.,  
681 Smith et al., 2006,2007), individual muscles' moment arms might be quite influential. This  
682 speculation has yet to be conclusively tested, let alone integrated into studies of whole limbs  
683 and locomotor dynamics.

684 Regardless, recent studies of the hindlimbs of mice (Lieber, 1997), rats (Johnson et  
685 al., 2008), and chimpanzees (O'Neill et al., 2013), as well as horse forelimbs (Brown et al.,  
686 2003a,b) favour some optimization of locomotor tasks and muscle moment arms, as do broad  
687 comparative studies of elbow muscles by Fujiwara and colleagues (Fujiwara, 2009; Fujiwara  
688 et al., 2011; Fujiwara and Hutchinson, 2012) and a comparative study of mammalian  
689 carnivores (McClern, 1985). So far, however, general principles that extend across lineages,  
690 behaviours or anatomies remain elusive. We consider this ambiguity's effect on inferences  
691 about extinct taxa further below.

692

### 693 *Muscle moment arm-joint angle dependencies*

694 Our Question 2 asked, Are the moment arms of limb muscles maximized (for  
695 antigravity/extensor muscles; or minimized in the case of antagonistic flexor muscles) at mid-  
696 stance of locomotion (optimizing weight support), or at highly extended limb orientations, as  
697 prior studies of dinosaurs inferred (e.g., Hutchinson et al., 2005)?

698 The peak extensor muscle moment arms that ostrich pelvic limb antigravity muscles  
699 have about the hip joint lie close to a completely columnar (i.e., vertical or  $0^\circ$ ) hip angle,  
700 approximately  $5^\circ$  (Figure 8), similar to prior results for *Tyrannosaurus rex* (Hutchinson et al.,  
701 2005). Ostriches, however, do not stand or normally move with such extended hip joints  
702 (Rubenson et al., 2007). We suspect this difference is because of their two orders of  
703 magnitude smaller body size (65+ kg vs. ~6000+ kg) and hence the lack of necessity for  
704 extreme postural changes to maintain lower muscle stresses in order to maintain locomotor  
705 performance (Biewener, 1989, 1990). However, ostriches may also have a greater importance  
706 for non-isometric muscle force-length properties in determining the limb orientation used  
707 (Figures 6,7), as per the section above. Such speculations can be tested better once such  
708 physiological data exist for ostrich muscles. Our data also do not strongly support Smith et  
709 al.'s (2007) suggestion that hip extensor (or other muscle) moment arms are at peak values  
710 toward the end of stance phase (Figures 6-8). Overall, unfortunately the factors that  
711 determine limb orientation in locomoting ostriches, as the largest extant striding biped (and  
712 theropod dinosaur) available for study, remain inconclusive, leaving the application of such  
713 principles to reconstructing limb orientations and locomotion in extinct theropods (e.g.,  
714 Hutchinson et al., 2005; Gatesy et al., 2009) on shakier empirical and theoretical ground.

715

### 716 *How accurate and repeatable are estimates of ostrich limb muscle moment arms?*

717 Our Question 3 dealt with a methodological comparison among the three main studies  
718 of ostrich pelvic limb muscle moment arms. Agreement seems fair overall, especially for  
719 flexion/extension actions, but several main messages emerge from our comparisons, some of  
720 which were also voiced by the other two studies of ostrich pelvic limb moment arms.

721 Circumstantial support for all three methods' accuracy also comes from tendon travel  
722 measurements of cranial and caudal parts of the IL muscle in guineafowl by Carr et al.  
723 (2011). General patterns (their Figure 7) for the IL moment arms about the knee (concave arc,  
724 peaking  $\sim 100^\circ$  knee angle in flexion) and the hip (increasing with extension) agree  
725 reasonably well with these three ostrich studies (Figures 12, 16). However, all moment arms  
726 for the ostrich IL muscle infer a switch to hip flexor action in strongly flexed poses, and little  
727 or no levelling off of the moment arm curve at strong hip flexion angles.

728 Key areas of disagreement between our results and those of B.A.S. and/or S.E.A.  
729 include occasionally major differences in if, or how, muscles switch between flexion and  
730 extension (e.g., the AMB1 and AMB2, IC, ILFB about the hip; Figures 9-11), whether certain  
731 muscles are flexors or extensors (e.g., the OM; see “Implications for ostrich limb muscle  
732 function” below), or the absolute magnitudes or relative trends in the data (e.g., our near-  
733 constant moment arms about the ankle for the FDL and gastrocnemius muscles; Figures  
734 18,19; and for the digital muscles, Figure 20). We also found some differences in LAR and  
735 ab/adduction moment arms about the hip for B.A.S.’s data, but these are likely explained by  
736 differing muscle paths (e.g. via points and wrapping); see Figures 12-15. Bates and  
737 Schachner (2012) acknowledge that their model could not use both via points and wrapping  
738 surfaces for the same muscle, which explained the switch of their ILFB knee moment arm  
739 from flexor to extensor with knee flexion (unlike Smith et al.’s (2007) data); our model only  
740 exhibits this switch at extreme knee flexion ( $\sim 150^\circ$  vs.  $90^\circ$ ; Figure 16).

741 Contrastingly, the “M. femorotibialis medialis” (see Appendix 1; equivalent to part of  
742 our FMTL; Figure 16, “FTE-Bates”) muscle’s moment arm changed with knee extension  
743 similar to other knee extensors in B.A.S.’s model, but S.E.A. found a progressive decline  
744 with knee extension. By comparing homologous muscles, it is evident that the experimental  
745 data (“FMTM-Smith” in Figure 16) match our model somewhat (FMTL; Figure 16), whereas  
746 the two distal parts of FMTL (“FTE” in Figure 16; B.A.S. and S.E.A. data) match each other  
747 somewhat, but only our model represents the anatomy and function of the actual medial head  
748 of M. femorotibialis (FMTM; Figure 16). Thus, a combination of incorrect classification of  
749 muscles (Appendix 1) and methodological differences explains divergence between some  
750 results. We noted similar problems with misidentifications (IFE, ITC, ITM muscles;  
751 Appendix 1) above in describing the results shown in Figure 10.

752 We raise the point here of the mistaken notion that tendon travel estimates of moment  
753 arms are free of errors in joint centre estimation, which is often repeated (e.g., Smith et al.,  
754 2007; Channon et al., 2010). This is only partly correct-- by using the virtual work principle  
755 that moment arms are equal to the change in musculotendinous length (“tendon travel”) per  
756 unit of joint rotation, tendon travel experiments do minimize errors in estimating moment  
757 arms, but still require joint centre estimates to calculate joint rotations, forming the traditional  
758 x-axis of moment arm vs. joint angle plots. However, admittedly all studies carry this burden  
759 of error; our model is different in using empirically measured 3D joint axes. Yet by  
760 attempting to restrict limb joints to flexion-extension axes, typical tendon travel experiments  
761 still introduce another error, by introducing inevitable kinematic cross-talk between  
762 flexion/extension movements and motions about other planes (i.e. limb joints that are  
763 manually flexed/extended through a range of motion will also involve some motion in LAR  
764 and ab/adduction-- see Rubenson et al., 2007). Only the most rigorously constrained studies,  
765 which measure joint axes and constrain motions to strictly flexion-extension planes, avoid  
766 this problem. Models like ours and B.A.S.’s can explicitly avoid it. Our model’s data show  
767 that, because moment arms of muscles covary with all joint angles (flex/extension,  
768 ab/adduction, long-axis rotation) (Figures 12-16, S1-S4), changes in multiple joint angles at  
769 once (i.e., kinematic cross-talk) will tend to produce different moment arms than changes in  
770 one angle at a time.

771 Bates and Schachner (2012:p.1342) inferred that, because their model’s outputs  
772 matched experimental data, “predicted abduction/adduction and long-axis rotation moments  
773 are good estimates”. We find some important differences between our results and those of  
774 either or both studies that somewhat weaken this inference. However, we reiterate and  
775 celebrate that all three studies discussed here obtain broadly similar results for most muscles,  
776 in particular emphasizing that moment arms are not constant for most muscles. Furthermore,

777 both Smith et al. (2007) and Bates and Schachner (2012) noted limitations similar to those  
778 mentioned above.

779 Some comparative data exist from studies of other ratites or more restricted datasets  
780 for ostriches. Hutchinson (2004a) provided estimates weighted by physiological cross-  
781 sectional area ( $A_{\text{phys}}$ ) of “antigravity” (extensor) muscle moment arms for a 2D model of an  
782 ostrich, using the same specimen and hence congruent with our results. Alexander et al.  
783 (1979) created a simple 2D geometric model of an ostrich whose limb dimensions were  
784 similar to ours (cf. their Table I and our Table 1), obtaining comparable muscle moment arm  
785 measurements: femorotibialis 5.1cm about the knee (ours ~5 cm), gastrocnemius 3.8 cm  
786 about the ankle (ours ~4 cm), and digital flexors 3.2 cm about the MTP joint (ours ~2 cm).  
787 This ostrich was 64% of the body mass of ours but had muscle masses about 85% of ours,  
788 helping to explain its ~30% greater  $A_{\text{phys}}$  and  $F_{\text{max}}$  values (in addition, surely, to shorter  
789 muscle fascicles; Equations 1, 2), and attributable to its wild-caught status as opposed to our  
790 specimen’s farm provenance.

791 Goetz et al. (2008) created a musculoskeletal model of an emu using a procedure  
792 grossly similar to ours, and obtained similar results—e.g. ILFB muscle having the largest hip  
793 extensor moment arm (but see Appendix 1). Troy et al. (2009) assumed that only the IFE,  
794 ITM, ITCR and PIFML muscles (homologous to ours) would resist hip adduction in their  
795 simplified emu model, but our analysis reveals that several more hip abductors exist, namely  
796 the IL, ILFB, FCM/L and CFP muscle groups (Table 4; Figures 14,15). See Lamas et al.  
797 (2014) for more consideration of emu muscle function.

798 There are anatomical and methodological reasons to suggest that musculoskeletal  
799 modelling approaches (this study and Bates & Schachner (2012)) can sometimes be more  
800 reliable than tendon-travel-based empirical data (e.g. Smith et al., 2007; also possibly Carr et  
801 al., 2011). First, the typical experimental method, as applied to date with birds, removes  
802 surrounding muscles and replaces whole 3D muscle bellies with quasi-2D strings (often  
803 lacking key “via points” or wrapping surfaces) that must alter the lines of action and thus  
804 moment arms of the *in situ* muscles. The potential for such alteration is experimentally  
805 testable, but existing studies of moment arms in various species (especially humans) already  
806 give strong precedent for this inference: analogous comparisons of “straight-line” 2D  
807 measurements (e.g., Jensen & Davy, 1975) vs. 3D medical imaging or *in situ* measurements  
808 (e.g., Young et al., 1993; Arnold et al., 2001) vs. anatomically-realistic 3D musculoskeletal  
809 models (Delp et al., 1999; Arnold et al., 2000; Kargo & Rome, 2002; Brown et al., 2003b;  
810 Burkholder & Nichols, 2004; Blemker et al., 2006; O’Neill et al., 2013) show better  
811 agreement between the latter two methods, and areas where simple 2D measurements are  
812 imprecise or misleading. To be fair, poorly designed musculoskeletal models can have the  
813 same problems—faithful representations of anatomical geometry are vital for both methods.

814 Bates and Schachner (2012, their electronic supplementary material) note that their  
815 model obtained an “extremely close match to the experimental data, particularly given the  
816 level of intra-specific variation present in muscle moment arms for ostriches”. Smith et al.  
817 (2007) did attribute some of their experimental variation to individual differences in  
818 morphology that might alter moment arms, but as they noted some of the variation may have  
819 instead been due to experimental error. Young et al. (1993), using a rigorous, validated *in situ*  
820 experimental apparatus for muscles crossing cat ankle joints, still found some individual  
821 variability that they attributed to muscles tethered by soft tissues as opposed to those  
822 restricted by bony wrapping surfaces or travelling in simple straight lines without any  
823 obstacles. We caution that these different sources of error need to be weighed separately;  
824 individual variability is an interesting biological reality, but experimental error needs  
825 minimizing. We suspect that some of the issues raised above about unrealistic representation  
826 of musculoskeletal anatomy in tendon travel experiments might be due to experimental error.

827 Bates and Schachner (2012) also raised the latter issue, finding that trends evident in Smith et  
828 al.'s (2007) moment arm data would leave the hip extensors too weak to balance the hip joint  
829 moments during stance phase, with a premature shift to hip flexor action. Our results (Figs. 9-  
830 20) indicate that tendon travel measurements of moment arms often exhibit steeper changes  
831 with joint angle in some cases, or constant moment arms where models show good reason to  
832 suspect variable moment arms with joint angle.

833 O'Neill et al.'s (2013; also Howlowka & O'Neill, 2013) musculoskeletal modelling  
834 and experimental analysis of chimpanzee pelvic limb moment arms came to similar  
835 conclusions as we have here, concerning model vs. tendon travel estimates of moment arms  
836 (see also Brown et al., 2003a,b for horses). Importantly, they noted that non-linear trends in  
837 moment arm vs. joint angle data are to be expected, so tendon travel studies that enforce the  
838 fitting of largely linear (or simple polynomial) curves to their data may introduce errors.  
839 O'Neill et al. (2013) also cautioned that (p.3721) "the 3D orientation of the pelvis and thigh  
840 segments during tendon-excursion experiments can have a significant effect on moment arm  
841 metrics." Channon (2010) used cubic spline functions to characterize gibbon hindlimb muscle  
842 moment arms, presenting an improvement over the method used for ostriches by Smith et al.  
843 (2007) and considering some of the potential errors in tendon travel methods. Tightly  
844 controlled experiments with cats (Young et al., 1993) have shown good agreement with  
845 model-based moment arm data (Burkholder and Nichols, 2004).

846 Nonetheless, there is room for improvement in all methodologies. In particular,  
847 human experiments have shown that moment arms may depend on muscle activation levels  
848 (Maganaris, 2004; Tsaopoulos et al., 2007), a phenomenon that few moment arm studies have  
849 assimilated. Numerous studies have also shown that sarcomere or fibre length changes in real  
850 3D muscles, as opposed to line segments, may be highly heterogeneous and complex (e.g.,  
851 Blemker et al., 2005; Carr et al., 2011).

852 The accuracy of avian musculoskeletal models remains unresolved. Studies of  
853 moment arms for ostriches and other avian species badly need stronger validation tests —  
854 ideally 3D, *in vivo* and across a range of behaviours – to test where different methods succeed  
855 or fail. O'Neill et al. (2013) noted that model-based estimates of moment arms should be less  
856 sensitive to the origins of muscles than to the insertions, and given that those insertions tend  
857 to be more easily circumscribed in ostriches (as in chimpanzees), a focus on improving the  
858 placement of muscle insertions could be powerful. At present, there is no published gold  
859 standard measurement that the aforementioned studies can be compared against, and thus it is  
860 unclear which estimates of moment arms are truly better than others. Our judgements above  
861 might prove to be incorrect. We assume here, except where noted, that our moment arm  
862 estimates are generally an improvement over previous studies' because they are 3D, based on  
863 precise, subject-specific anatomical measurements of a single cadaver *in situ*, and incorporate  
864 modern data on the 3D complexity of avian limb joint axes. However, our assumption of  
865 improved accuracy demands a test against a gold standard, with clear criteria for what a  
866 "good" agreement between moment arm curves is; a question that no studies (including ours)  
867 have answered.

868

### 869 *Model assumptions and potential refinements*

870 Some simplifications of joint systems were necessary in our model but could be  
871 improved with later iterations. The tibio-fibular articulation is slightly mobile in ostriches  
872 (Fuss, 1996) and other birds, but we maintained it as an immobile joint. Likewise, the  
873 (proximal; see Regnault et al., 2014) patella surely translates during knee flexion/extension in  
874 birds as in humans (e.g. Walker et al., 1988) but we maintained it in the same resting position  
875 (with respect to the femur), represented simply by a wrapping surface. Adding such  
876 translation would influence the moment arm curves for knee extensor muscles. The intertarsal

877 (ankle) joint's motions during swing phase (extreme dorsiflexion) seemed unrealistic,  
878 laterally rotating the tarsometatarsus to a seemingly disarticulated position, but we kept this  
879 as-is in the model rather than invent a subjective solution, as it would have minimal influence  
880 on our results here and maintained strict fidelity to our anatomical and kinematic data. Future  
881 implementations of the model emphasizing ankle joint mechanics may need to adjust these  
882 kinematics. The proximal interphalangeal joint of digit III was kept immobile in the model as  
883 our kinematic data lacked its joint motion, but the model has the capacity to allow the joint to  
884 flex and extend if desired (Table 1), and could involve internal mechanisms such as those  
885 described by Schaller et al. (2011) if necessary for research questions addressed with it.

886 Our model's muscles were simplified, as the Methods and Supplementary Text  
887 explain. Our digitizing procedure, performed in 2002, was simplistic (similar to that of  
888 Burkholder and Nichols, 2004), whereas more recent techniques have fused CT and MRI  
889 imaging modalities to produce quite accurate and complex 3D musculoskeletal models (e.g.,  
890 Zarucco et al., 2005, Harrison et al., 2014). Real muscles have complex 3D structure but we  
891 have simplified them into basic Hill model muscles of 2D structure. Internal tendons were  
892 observed in some muscles (e.g., M. iliopsoas, M. ilioband, M. gastrocnemii, many  
893 digital flexors; Gangl et al., 2004). The Hill model does not discretely represent these  
894 features, which can affect muscle forces and gearing. Ligaments and other passive tissues  
895 were not represented in our model, and these would be particularly important features to  
896 consider in a complete dynamic model, as Haughton (1864) suggested and Schaller et al.  
897 (2009) demonstrated experimentally. Finally, a test of the validity of our moment arm  
898 estimates against a "gold standard" empirical measurement (see above) with explicit criteria  
899 for an acceptable level of precision would be immensely valuable.

900 Yet like any model, simple or complex, our model is a useful starting point for a  
901 continually iterative process of improvement that progressively approximates reality. It has  
902 the advantage of being able to estimate muscle forces, moments, and length changes that are  
903 unlikely or even impossible to be measurable *in vivo*, especially simultaneously across a full  
904 stride.

#### 905 906 *Implications for ostrich limb muscle function*

907 Table 4 shows our classification of the major actions of ostrich pelvic limb muscles  
908 (also see Lamas et al., 2014 for emu muscles). This approach, as opposed to the classical  
909 perspective in comparative anatomy and biomechanics, emphasizes the three-dimensional  
910 nature of avian limbs and the capacity of muscles to generate moments about many joints and  
911 degrees of freedom (see also the categorization for cat ankle muscles provided by Young et  
912 al. (1993); also model-based assessments using isometric force-fields by Kargo & Rome  
913 (2002) and endpoint forces by Burkholder & Nichols (2004)). Standard functional anatomy  
914 papers tend to emphasize flexion/extension and only present other actions (or any actions  
915 about other joints than those deemed to be the main joints of action) in a seemingly arbitrary  
916 fashion (e.g., Smith et al., 2007: Table 2; cf. our Table 4), with at least the implicit  
917 assumption that non-parasagittal actions are less important. Our approach also reveals how  
918 the functions of some muscles have been misclassified before (or remain uncertain), for  
919 ostriches and perhaps for other avian species--to the degree that ostriches are representative  
920 of ancestral muscle functions, which remains to be determined. The degree of uncertainty  
921 about avian pelvic limb muscle function particularly applies to 3D actions about the hip joint;  
922 many muscles have actions (e.g., flexion/extension) that switch depending on the joint angles  
923 adopted.

924 Examples of somewhat surprising 3D actions of hip muscles include the M.  
925 obturatorius medialis (OM), which we find to mainly fulfill a lateral rotator and flexor action  
926 at the hip, whereas Smith et al. (2006,2007), Bates and Schachner (2012), Bates et al.

927 (2012a,b) favour an extensor action of this muscle (in addition to lateral rotation) in ostriches  
928 and other archosaurs. In the model of B.A.S., this seems to be at least partly due to a distal  
929 insertion of the OM muscle on the femur, rather than very proximally onto the trochanteric  
930 crest (Gangl et al., 2004; Zinoviev, 2005). Furthermore, some “antigravity muscles” act in  
931 one direction synergistically with other muscles, resisting gravity, but in other directions they  
932 act antagonistically to gravity. Clear examples include the PIFML and CFP muscles, which  
933 are presumably active in hip extension but incur lateral rotator and abductor moments about  
934 the hip (Table 4). These muscles probably oppose other antigravity muscles such as the ITC  
935 in medial rotation and potential adductors such as AMB1 (cf. moment data in Rubenson et  
936 al., 2011).

937 The analysis of Rubenson et al. (2011:Figure 7) indicates that hip adduction, not  
938 abduction, must be resisted during stance phase in locomoting ostriches, and thus abductor  
939 muscle activity is predicted, a moment that many hip extensors create anyway. However, hip  
940 adduction capacity is far more limited-- only the IC, AMB1, 2 and IFI muscles have clear  
941 actions in hip adduction. Smith et al. (2006:Table 2) assigned adductor actions to other  
942 muscles such as the flexor cruris (FC) heads, PIFML and OM whereas we find these to be  
943 abductors. Indeed, the actions of the two heads of AMB may oppose each other (Table 4), so  
944 it would be interesting to know how they are coordinated. The ITC muscle’s parts have clear  
945 roles in medial rotation, but their actions in flexion/extension vary with limb posture (see also  
946 Gatesy, 1994), rendering it less clear whether (or when) they play a predominant hip extensor  
947 (e.g. Rubenson et al., 2006) or hip flexor (e.g. Smith et al., 2006,2007) role in ostriches or  
948 other birds. How any birds balance this complex interaction of long-axis and ab/adductor  
949 moments at the hip or other joints remains almost unexplored (but see Gatesy 1994), yet  
950 modelling (and simulation) approaches such as ours offer one way to tease apart the  
951 complexity. Bates and Schachner (2012) found that *Alligator* and *Struthio* had similar hip  
952 extensor moment arms but there were large abduction and small adduction moment arms in  
953 their ostrich, along with large long-axis rotation moment arms. The functional and  
954 evolutionary implications of these differences remain unclear, and dependent on  
955 understanding force balance about the hip joint in extant archosaurs such as *Struthio*.

956 Complex function is not restricted to proximal muscles, however. Complex anatomy  
957 of distal limb muscles is a pernicious problem in avian locomotor biomechanics, and difficult  
958 to render realistically in biomechanical models such as ours. As the Supplementary Text  
959 describes, we could not model all origins (or subdivided tendons; e.g., digital flexors) of all  
960 muscle parts. Indeed, in some cases the origins are diffuse—e.g. M. gastrocnemius medialis  
961 originates mainly from the medial side of the proximal tibiotarsus, but the surrounding fascia  
962 it is attached to continue proximally past the knee joint, via the proximal patella and other  
963 structures. It is not clear if some of these distal muscles exert important moments about the  
964 knee joint (some forces may be going directly to their distal origins from the tibiotarsus), and  
965 the dynamics of the patella (not represented in our model except as a static wrapping surface)  
966 further complicates matters. Thus it is unclear how forces are balanced across ostrich (or  
967 other avian) knees, complicating comparisons with other species (e.g. Higham et al., 2008;  
968 Andrada et al., 2013).

969 Young et al. (1993) and Johnson et al. (2012) noted that some muscles in cat and rat  
970 hindlimbs seemed to have intrinsically stabilizing properties, shifting from flexor to extensor  
971 moment arms in a linear fashion with increasing joint flexion. Eight modelled ostrich limb  
972 muscles also show this pattern: the AMB1, AMB2, IC, ITCa, ITCp, ITM, ITCR and ISF  
973 exhibit stabilization function in flexion-extension (Figures 9,10). Weaker evidence for self-  
974 stabilization is present for the OM muscle in hip ab/adduction (Figure 14) and the four ankle  
975 flexors in flexion/extension (TCf, TCt, EDL, and FL; Figure 18), so any self-stabilization  
976 properties must be interpreted as being largely restricted to the hip’s flexion-extension

977 function (see also Table 4). Judging from these hip muscles' paths, their long lines of action  
978 (due to the elongate pelvis and limb) running close to the hip seem to predispose them to  
979 these intrinsic stabilization properties. These patterns deserve more examination in a  
980 comparative context with other species in the future -- for example, similar hip muscles show  
981 similar moment arm patterns that hint at intrinsic stabilization in various extinct dinosaurs  
982 and other archosaurian reptiles (Hutchinson et al., 2005,2008; Bates and Schachner, 2012;  
983 Bates et al, 2012a,b; Maidment et al., 2013).

#### 984 *Musculoskeletal models of limb function: past, present and future*

985 A wide variety of studies have used musculoskeletal models to reconstruct limb  
986 function in extant and extinct animals, but there remains little agreement for standards of  
987 model design, analysis and validation. The same software (SIMM) or other packages  
988 (GaitSym, Anybody, varieties of Adams, etc.) has been used to estimate limb muscle moment  
989 arms in other extant species including chimpanzees and other hominins (O'Neill et al., 2013;  
990 Holowka & O'Neill, 2013; and references therein), horses (Brown et al., 2003a,b; Zarucco et  
991 al., 2006; Harrison et al., 2010), domestic cats (Burkholder & Nichols, 2004), rats (Johnson et  
992 al., 2008), emus (Goetz et al., 2008), *Alligator* and ostriches (Bates and Schachner, 2012),  
993 frogs (Kargo and Rome, 2002; Kargo et al., 2002), cockroaches (Full & Ahn, 1995), and  
994 others, in addition to simpler past approaches (e.g. for small mammals, McClearn, 1985). It is  
995 not clear which software packages most accurately estimate muscle moment arms, but our  
996 comparisons with the data from Bates and Schachner (2012) suggest some advantages of our  
997 approach. Regardless, comparative biologists seeking to harness the power of  
998 musculoskeletal modelling techniques have much to learn from the considerable progress  
999 made in analyzing and validating similar models of human limb muscles (e.g., Delp et al.,  
1000 1990,1992,1999; Arnold et al., 2000,2001; Holzbauer et al., 2005; Nikooyan et al., 2011).

1002 There has been a recent flourishing of musculoskeletal models of extinct taxa,  
1003 especially hominins (e.g., *Australopithecus* in Nagano et al., 2005) and dinosaurs or other  
1004 archosaurs. Theropod dinosaurs have featured prominently, including *Allosaurus*,  
1005 *Struthiomimus* (Bates and Schachner, 2012; Bates et al. 2012a), *Tyrannosaurus* (Hutchinson  
1006 et al., 2005), and *Velociraptor* (Hutchinson et al., 2008), among other taxa (Allen, 2010), and  
1007 more recently sauropodomorph (Mallison, 2010a,b) as well as ornithischian dinosaurs have  
1008 enjoyed a new focus (Mallison, 2010c; Bates et al., 2012b; Fujiwara and Hutchinson, 2012;  
1009 Maidment et al., 2013). Other extinct taxa studied have included the stem crocodile  
1010 *Poposaurus* (Bates and Schachner, 2012) and related taxa (Molnar, 2014), a pterosaur (Costa  
1011 et al., 2013), and the early tetrapod *Ichthyostega* (Pierce et al., 2012). Whether the focus is on  
1012 limb joint ranges of motion, muscle moment arms, or dynamic simulation, there is a need for  
1013 more scrutiny of models of extant taxa to establish how accurate and reliable these modelling  
1014 approaches truly are, and ultimately a renewed examination and synthesis of those findings  
1015 with past studies of extinct taxa. Studies using models to estimate muscle moment arms need  
1016 to consider not only this, but also how or whether those parameters actually matter for  
1017 particular muscles, joints, behaviors or species (see also Bates and Schachner, 2012; Bates et  
1018 al., 2012b; Maidment et al., 2013). To the degree that general principles of moment arm  
1019 usage exist, they should clarify under what circumstances a moment arm is optimized to  
1020 perform a certain function. An understanding of this link between muscle mechanics,  
1021 kinematics and moment arms could link the disparate palaeobiological/comparative studies  
1022 on limb joint ranges of motion and orientations (e.g., Mallison, 2010a,b,c; Pierce et al., 2012;  
1023 Molnar, 2014) with those of limb muscle moment arms (Hutchinson et al., 2005,2008; Allen,  
1024 2010; Bates and Schachner, 2012; Bates et al., 2012b; Fujiwara and Hutchinson, 2012;  
1025 Maidment et al., 2013). Such a synthesis could lead to a robust, sustainable future for



1026 comparative musculoskeletal modeling and simulation, and new insights into the evolution of  
1027 musculoskeletal function and locomotor dynamics.

1028  
1029

### 1030 **Acknowledgments**

1031

1032 We thank Peter Loan for kind and patient technical support. Thanks to Aaron Daub  
1033 for his proficient assistance in the ostrich digitization and dissection. This paper benefited  
1034 from discussions with F. Clay Anderson, Allison Arnold, Silvia Blemker, Steve Gatesy, and  
1035 Karl Bates, as well as with members of the Stanford Neuromuscular Biomechanics  
1036 Laboratory and the Structure & Motion Laboratory at The Royal Veterinary College.

1037

1038

### 1039 **APPENDIX 1:**

1040 A few observations from our dissections revealed differences in muscle identifications  
1041 from previous studies, which themselves have had much disagreement (reviewed in Gangl et  
1042 al., 2004; Zinoviev, 2006). However, generally our findings agree well with the excellent  
1043 study by Gangl et al. (2004). Zinoviev (2006) made some amendments to the latter study that  
1044 our dissections independently have confirmed.

1045 First, rather than treat “*M. pectineus*” as a novel muscle unrelated to *M. ambiens* (e.g.,  
1046 Mellett, 1994; Gangl et al., 2004) or as a part of *M. femorotibialis medialis* (= FMTM or  
1047 “internus”; Zinoviev, 2006), we refer to the muscle here as *M. ambiens 1* (AMB1; for its  
1048 pubic origin as in most other Reptilia; Hutchinson, 2002) and refer to the muscle with the  
1049 derived iliac origin as *M. ambiens 2* (AMB2; i.e., the dorsal head) (Table 2). We do not  
1050 intend for this to be a formal nomenclatural change but it is used for convenience within this  
1051 paper and to suggest that the homologies (and thus formal nomenclature) of these two muscle  
1052 heads deserve reconsideration. Our nomenclature avoids confusion with the mammalian *M.*  
1053 *pectineus* which has no homology with these muscles, and maintains the same nomenclature  
1054 for the homologous *M. ambiens* (whether one or two parts) in extant Sauropsida. We deem  
1055 these homologies and nomenclature marginally more parsimonious than other interpretations  
1056 (reviewed by Zinoviev, 2006), the latest of which (favored by Zinoviev, 2006) requires loss  
1057 of the origin of *M. ambiens* from the pectineal (preacetabular) process that is  
1058 plesiomorphically present in birds (Hutchinson, 2002) and gain of a new head of the FMTM  
1059 muscle (the “*pars pectineus*”). In our scenario, mainly a new head of *M. ambiens* (AMB2) is  
1060 required; a phenomenon that is not unknown in other birds and is pervasive in Crocodylia  
1061 (Hutchinson, 2002).

1062 Second, we agree with Zinoviev (2006) that Gangl et al. (2004) confused the two  
1063 crura of “*M. iliofemoralis externus*” with *M. iliotrochantericus caudalis*, which engendered  
1064 further errors in identifying other muscles. We have confirmed this from dissections of three  
1065 additional ostrich cadavers, and hence the position of our *M. iliotrochantericus caudalis*  
1066 (ITCa,ITCp in Table 2) differs from theirs (also data in Smith et al., 2006,2007). We consider  
1067 *M. iliofemoralis externus* (IFE) to be weakly differentiated from the latter muscle, also  
1068 intimated by Gangl et al. (2004:p.113; and Gadow, 1880), but we represent it in our model as  
1069 a separate head (IFE), again agreeing with Zinoviev (2006). This is corroborated by the main  
1070 muscle in question (ITC) having a large internal tendon, preacetabular position (between the  
1071 heads of *Mm. iliotibiales*; IC and IL), and overlaying *Mm. iliotrochanterici medius et*  
1072 *cranialis* (ITM, ITCR), which are traits diagnostic of *M. iliotrochantericus caudalis*, not “*M.*  
1073 *iliofemoralis externus*” as in Gangl et al. (2004). This then explains why the latter study did  
1074 not find *M. iliotrochantericus medius* – it identified it as *M. iliotrochantericus caudalis*,  
1075 noting some fusion and distolateral insertion with *M. iliotrochantericus cranialis*, which are

1076 diagnostic of *M. iliotrochantericus medius* instead. Hence our *M. iliotrochantericus medius*  
1077 (ITM) corresponds to their “*M. iliotrochantericus caudalis*”; but our *M. iliotrochantericus*  
1078 *cranialis* (ITCR) corresponds to theirs. Smith et al. (2006,2006) perpetuated the errors caused  
1079 by Gangl et al.’s misidentifications, which complicates comparisons with our data (see our  
1080 Results section, Fig. 10). Bates and Schachner (2012) appear to have avoided these errors.

1081 A third point of discordance between this study and Gangl et al.’s (2004) is that we  
1082 consider the latter study’s “*Mm. femorotibiales externus et medius*” to be two parts  
1083 (superficial and deep) of *M. femorotibialis lateralis* (FMTL; *vide* Zinoviev, 2006), because  
1084 this avian muscle typically originates on the lateral surface of the femur, deep to *M.*  
1085 *iliotibialis lateralis* (IL), as the former two parts do. Gangl et al.’s (2004) “*Mm.*  
1086 *femorotibiales internus et accessorius*” then correspond to our *Mm. femorotibiales medialis et*  
1087 *intermedius* (FMTM, FMTIM), because their topological connections more closely match  
1088 these muscles in birds. Zinoviev (2006) again gave a detailed correction that we concur with,  
1089 whereas Smith et al. (2006,2007) and possibly Bates and Schachner (2012) used Gangl et  
1090 al.’s (2004) misidentifications.

1091 Accepting these identifications renders ostrich anatomy more similar to other birds:  
1092 *M. iliotrochantericus caudalis* remains large and originating dorsal to *M. iliotrochantericus*  
1093 *medius*, which originates cranial to *M. iliotrochantericus cranialis*, and the insertions of these  
1094 muscles retain similar proximodistal positions (the first on the lateral surface of the proximal  
1095 femur, the second two sequentially distal on the craniolateral edge of the trochanteric crest;  
1096 Rowe, 1986; Hutchinson, 2002). Furthermore, *Mm. femorotibiales* in our view then match  
1097 avian anatomical positions more reasonably.

1098 However, ostrich pelvic muscle anatomy is still derived in the large relative size of *M.*  
1099 *iliofemoralis internus* (IFI; “*cuppediticus*” of Rowe, 1986; Table 2) and the two distinct heads  
1100 of *M. ambiens* (i.e., the novel dorsal head, AMB2). Additionally, *M. iliotrochantericus*  
1101 *medius* (ITM) is slightly derived in having a markedly more dorsal position (required by the  
1102 dorsally shifted *M. ambiens* and *M. iliofemoralis internus* (IFI)) than in typical neornithines,  
1103 and *Mm. femorotibiales* have strong division of the lateral head (FMTL) into two parts, but  
1104 not a novel “*accessorius*” head. Furthermore, *M. obturatorius medialis* (OM) in ostriches is  
1105 extraordinary in its mostly lateral origin, whereas normally in birds it is confined to the inside  
1106 of the pelvis.

1107 Similar problems with muscle identifications vex other studies of ratite limb form and  
1108 function. Patak & Baldwin’s (1998) anatomical description of emu pelvic limb muscles was  
1109 used to formulate Goetz et al.’s (2008) musculoskeletal model of an emu, incorporating  
1110 analogous errors that deserve correction in future studies (see Lamas et al., 2014). The issues  
1111 outlined in this appendix drive home the point that a firm grasp of avian myology, ideally  
1112 based upon understanding of fundamental groups of muscles likely present in the ancestral  
1113 neornithine bird and hence homologous among its living descendants, is critical for any  
1114 biomechanical and comparative analyses of muscle form, function and evolution (see also  
1115 Zinoviev, 2006).

1116 **References**

1117

1118 Abourachid, A. 2001. Kinematic parameters of terrestrial locomotion in cursorial (ratites),  
1119 swimming (ducks), and striding birds (quail and guinea fowl). *Comparative Biochemistry and*  
1120 *Physiology A* 131:113-119.

1121

1122 Abourachid, A., & Renous, S. 2000. Bipedal locomotion in ratites (Paleognatiform) [*sic*]:  
1123 examples of cursorial birds. *Ibis* 142:538-549.

1124

1125 Abourachid, A, Hackert, R., Herbin, M., Libourel, P. A., Lambert, F., Gioanni, H., Provini,  
1126 P., Blazevic, P., & Hugel, V. 2011. Bird terrestrial locomotion as revealed by 3D kinematics.  
1127 *Zoology* 114: 360-368.

1128

1129 Alexander R. McN, Maloiy, G.M.O., Njau, R., & Jayes, A.S. 1979. Mechanics of running of  
1130 the ostrich (*Struthio camelus*). *Journal of Zoology* 187:169-178.

1131

1132 Allen, V. 2010. The evolution of avian hindlimb conformation and locomotor function.  
1133 Unpublished PhD dissertation, The Royal Veterinary College, University of London, United  
1134 Kingdom.

1135

1136 Andrada, E., Nyakatura, J. A., Bergmann, F., & Blickhan, R. 2013. Adjustments of global  
1137 and local hindlimb properties during terrestrial locomotion of the common quail (*Coturnix*  
1138 *coturnix*). *Journal of Experimental Biology* 216: 3906-3916.

1139

1140 Arnold, A. S., & Delp, S. L. 2001. Rotational moment arms of the medial hamstrings and  
1141 adductors vary with femoral geometry and limb position: implications for the treatment of  
1142 internally rotated gait. *Journal of Biomechanics* 34:437-447.

1143

1144 Arnold, A. S., Salinas, S., Asakawa, D. J., & Delp, S. L. 2000. Accuracy of muscle moment  
1145 arms estimated from MRI-based musculoskeletal models of the lower extremity. *Computer*  
1146 *Aided Surgery* 5:108-119.

1147

1148 Baker, A.J., Haddrath, O., McPherson, J. R., & Cloutier, A. 2014. Genomic support for a  
1149 moa-tinamou clade and adaptive morphological convergence in flightless ratites. *Molecular*  
1150 *Biology and Evolution*, in press.

1151

1152 Bates, K. T., & Schachner, E. R. 2012. Disparity and convergence in bipedal archosaur  
1153 locomotion. *Journal of the Royal Society Interface* 9: 1339-1353.

1154

1155 Bates, K. T., Benson, R. B., & Falkingham, P. L. 2012a. A computational analysis of  
1156 locomotor anatomy and body mass evolution in Allosauroida (Dinosauria: Theropoda).  
1157 *Paleobiology* 38: 486-507.

1158

1159 Bates, K. T., Maidment, S. C., Allen, V., & Barrett, P. M. 2012b. Computational modelling  
1160 of locomotor muscle moment arms in the basal dinosaur *Lesothosaurus diagnosticus*:  
1161 assessing convergence between birds and basal ornithischians. *Journal of Anatomy* 220: 212-  
1162 232.

1163

1164 Bennett, M. B., & Taylor, G. C. 1995. Scaling of elastic strain energy in kangaroos and the  
1165 benefits of being big. *Nature* 378: 56-59.

1166  
1167 Biewener, A. A. 1989. Scaling body support in mammals: limb posture and muscle  
1168 mechanics. *Science* 245:45-48.  
1169  
1170 Biewener, A. A. 1990. Biomechanics of mammalian terrestrial locomotion. *Science*  
1171 250:1097-1103.  
1172  
1173 Blemker, S. S., Pinsky, P. M., & Delp, S. L. 2005. A 3D model of muscle reveals the causes  
1174 of nonuniform strains in the biceps brachii. *Journal of Biomechanics* 38: 657-665.  
1175  
1176 Bottema, O., & Roth, B. 1990. *Theoretical Kinematics*. Vol. 1. Dover Publications.  
1177  
1178 Brassey, C. A., Kitchener, A. C., Withers, P. J., Manning, P. L., & Sellers, W. I. 2013. The  
1179 role of cross-sectional geometry, curvature, and limb posture in maintaining equal safety  
1180 factors: A computed tomography study. *Anatomical Record* 296: 395-413.  
1181  
1182 Brassey, C. A., Holdaway, R. N., Packham, A. G., Anné, J., Manning, P. L., & Sellers, W. I.  
1183 2013. More than one way of being a moa: Differences in leg bone robustness map divergent  
1184 evolutionary trajectories in Dinornithidae and Emeidae (Dinornithiformes). *PLoS one*, 8(12):  
1185 e82668.  
1186  
1187 Brown, N. A. T., Pandy, M. G., Buford, W. L., Kawcak, C. E., & McIlwraith, C. W. 2003a.  
1188 Moment arms about the carpal and metacarpophalangeal joints for flexor and extensor  
1189 muscles in equine forelimbs. *American Journal of Veterinary Research* 64:351-357.  
1190  
1191 Brown, N. A. T., Pandy, M. G., Kawcak, C. E., & McIlwraith, C. W. 2003b. Force- and  
1192 moment-generating capacities of muscles in the distal forelimb of the horse. *Journal of*  
1193 *Anatomy* 203:101-113.  
1194  
1195 Burkholder, T. J., & Nichols, T. R. 2004. Three-dimensional model of the feline hindlimb.  
1196 *Journal of Morphology* 261: 118-129.  
1197  
1198 Cappozzo, A., Catani, F., Della Croce, F., & Leardini, A. 1995. Position and orientation in  
1199 space of bones during movement: anatomical frame definition and determination. *Clin.*  
1200 *Biomech.* 10, 171-178.  
1201  
1202 Carr, J. A., Ellerby, D. J., Rubenson, J., & Marsh, R. L. 2011. Mechanisms producing  
1203 coordinated function across the breadth of a large biarticular thigh muscle. *Journal of*  
1204 *Experimental Biology* 214: 3396-3404.  
1205  
1206 Channon, A. J., Crompton, R. H., Günther, M. M., & Vereecke, E. E. 2010. Muscle moment  
1207 arms of the gibbon hind limb: implications for hylobatid locomotion. *Journal of Anatomy*  
1208 216: 446-462.  
1209  
1210 Costa, F. R., Rocha-Barbosa, O., & Kellner, A. W. A. 2013. A biomechanical approach on  
1211 the optimal stance of *Anhanguera piscator* (Pterodactyloidea) and its implications for  
1212 pterosaur gait on land. *Historical Biology*, (ahead-of-print), 1-9.  
1213  
1214 Cracraft, J., & Clarke, J. 2001. The basal clades of modern birds. In: Gauthier JA, Gall LF,  
1215 editors. *New perspectives on the origin and early evolution of birds: proceedings of the*

- 1216 international symposium in honor of John H. Ostrom. New Haven, CT: Peabody Mus Nat  
1217 Hist. p 143-156.
- 1218
- 1219 Daley, M. A., & Usherwood, J. R. 2010. Two explanations for the compliant running  
1220 paradox: reduced work of bouncing viscera and increased stability in uneven terrain. *Biology*  
1221 *Letters* 6: 418-421.
- 1222
- 1223 Delp, S. L., & Zajac, F. E. 1992. Force- and moment-generating capacity of lower-extremity  
1224 muscles before and after tendon lengthening. *Clinical Orthopaedics* 284:247-259.
- 1225
- 1226 Delp, S. L., & Loan, J. P. 1995. A graphics-based software system to develop and analyze  
1227 models of musculoskeletal structures. *Computers in Biology and Medicine* 25:21-34.
- 1228
- 1229 Delp, S. L., & Loan, J. P. 2000. A computational framework for simulating and analyzing  
1230 human and animal movement. *IEEE Computing in Science and Engineering* 2:46-55.
- 1231
- 1232 Delp, S. L., Loan, J. P., Hoy, M. G., Zajac, F. E., Topp, E. L., & Rosen, J. M. 1990. An  
1233 interactive graphics-based model of the lower extremity to study orthopaedic surgical  
1234 procedures. *IEEE Transactions in Biomedical Engineering* 37:757-767.
- 1235
- 1236 Delp, S. L., Hess, W. E., Hungerford, D. S., & Jones, L. C. 1999. Variation of rotation  
1237 moment arms with hip flexion. *Journal of Biomechanics* 32:493-501.
- 1238
- 1239 Fedak, M. A. & Seeherman, H. J.. 1979. Reappraisal of energetics of locomotion shows  
1240 identical cost in bipeds and quadrupeds including ostrich and horse. *Nature* 282:713-716.
- 1241
- 1242 Fedak, M. A., Heglund, N. C., & C. R. Taylor. 1982. Energetics and mechanics of terrestrial  
1243 locomotion. II. Kinetic energy changes of the limbs and body as a function of speed and body  
1244 size in birds and mammals. *Journal of Experimental Biology* 79:23-40.
- 1245
- 1246 Fujiwara, S. I. 2009. Olecranon orientation as an indicator of elbow joint angle in the stance  
1247 phase, and estimation of forelimb posture in extinct quadruped animals. *Journal of*  
1248 *Morphology* 270: 1107-1121.
- 1249
- 1250 Fujiwara, S. I., & Hutchinson, J. R. 2012. Elbow joint adductor moment arm as an indicator  
1251 of forelimb posture in extinct quadrupedal tetrapods. *Proceedings of the Royal Society B:*  
1252 *Biological Sciences* 279: 2561-2570.
- 1253
- 1254 Fujiwara, S. I., Endo, H., & Hutchinson, J. R. 2011. Topsy-turvy locomotion: biomechanical  
1255 specializations of the elbow in suspended quadrupeds reflect inverted gravitational  
1256 constraints. *Journal of Anatomy* 219: 176-191.
- 1257
- 1258 Full, R., & Ahn, A. 1995. Static forces and moments generated in the insect leg: comparison  
1259 of a three-dimensional musculo-skeletal computer model with experimental measurements.  
1260 *Journal of Experimental Biology* 198: 1285-1298.
- 1261
- 1262 Fuss, F. K. 1996. Tibiofibular junction of the South African ostrich (*Struthio camelus*  
1263 *australis*). *Journal of Morphology* 227:213-226.
- 1264

- 1265 Gadow, H. 1880. Zur vergleichenden Anatomie der Muskulatur des Beckens und der hinteren  
1266 Gliedmasse der Ratiten. Jena, G. Fischer.  
1267
- 1268 Gangl D., Weissengruber, G.E., Egerbacher, M., & Forstenpointer, G. 2004. Anatomical  
1269 description of the muscles of the pelvic limb in the ostrich (*Struthio camelus*). Anatomia  
1270 Histologia Embryologia 33:100-114.  
1271
- 1272 Gatesy S. M. 1990. Caudofemoral musculature and the evolution of theropod locomotion.  
1273 Paleobiology 16:170-186.  
1274
- 1275 Gatesy, S. M. 1994. Neuromuscular diversity in archosaur deep dorsal thigh muscles. Brain  
1276 Behavior and Evolution, 43: 1-14.  
1277
- 1278 Gatesy, S.M. 1995. Functional evolution of the hindlimb and tail from basal theropods to  
1279 birds. Pp. 219-234 in Thomason, J.J. (ed.), Functional Morphology in Vertebrate  
1280 Paleontology. Cambridge University Press, UK.  
1281
- 1282 Gatesy, S.M., & Biewener, A.A. 1991. Bipedal locomotion - effects of speed, size and limb  
1283 posture in birds and humans. Journal of Zoology 224:127-147.  
1284
- 1285 Gatesy, S. M., Bäker, M., & Hutchinson, J. R. 2009. Constraint-based exclusion of limb  
1286 poses for reconstructing theropod dinosaur locomotion. Journal of Vertebrate Paleontology  
1287 29: 535-544.  
1288
- 1289 Goetz, J. E., Derrick, T. R., Pedersen, D. R., Robinson, D. A., Conzemius, M. G., Baer, T. E.,  
1290 & Brown, T. D. 2008. Hip joint contact force in the emu (*Dromaius novaehollandiae*) during  
1291 normal level walking. Journal of Biomechanics 41: 770-778.  
1292
- 1293 Grood, E. S., & Suntay, W. J. 1983. A joint coordinate system for the clinical description of  
1294 three-dimensional motions: application to the knee. Journal of Biomechanical Engineering  
1295 105, 136-44.  
1296
- 1297 Günther, M., Keppler, V., Seyfarth, A., & R. Blickhan. 2004. Human leg design: optimal  
1298 axial alignment under constraints. Journal of Mathematical Biology 48:623-646.  
1299
- 1300 Houghton, R. 1864. On the muscular mechanism of the leg of the ostrich. Annals &  
1301 Magazine of Natural History 3<sup>rd</sup> Series 15:262-272.  
1302
- 1303 Houghton, R. 1867a. Notes on animal mechanics. No. X. Muscular anatomy of the emu  
1304 (*Dromaeus novae hollandiae*). Proceedings of the Irish Academy of Science 9:487-497.  
1305
- 1306 Houghton, R. 1867b. Notes on animal mechanics. No. XI. Muscular anatomy of the rhea  
1307 (*Struthio rhea*). Proceedings of the Irish Academy of Science 9:497-504.  
1308
- 1309 Higham, T. E., Biewener, A. A., & Wakeling, J. M. 2008. Functional diversification within  
1310 and between muscle synergists during locomotion. Biology Letters 4: 41-44.  
1311
- 1312 Holowka, N. B., & O'Neill, M. C. 2013. Three-dimensional moment arms and architecture of  
1313 chimpanzee (*Pan troglodytes*) leg musculature. Journal of Anatomy 223: 610-628.  
1314

- 1315 Holzbaur, K.R., Murray, W.M. & Delp, S.L. 2005. A model of the upper extremity for  
1316 simulating musculoskeletal surgery and analyzing neuromuscular control. *Annals of*  
1317 *Biomedical Engineering* 33:829-840.  
1318
- 1319 Hutchinson, J.R. 2002. The evolution of hindlimb tendons and muscles on the line to crown-  
1320 group birds. *Comparative Biochemistry and Physiology A* 133:1051-1086.  
1321
- 1322 Hutchinson, J. R. 2004. Biomechanical modeling and sensitivity analysis of bipedal running  
1323 ability. I. Extant taxa. *Journal of Morphology* 262:421-440.  
1324
- 1325 Hutchinson, J. R., & Allen, V. 2009. The evolutionary continuum of limb function from early  
1326 theropods to birds. *Naturwissenschaften* 96: 423-448.  
1327
- 1328 Hutchinson, J. R., & Gatesy, S. M. 2000. Adductors, abductors, and the evolution of  
1329 archosaur locomotion. *Paleobiology* 26: 734-751.  
1330
- 1331 Hutchinson, J.R., Anderson, F.C., Blemker, S.S., & Delp, S.L. 2005. Analysis of hindlimb  
1332 muscle moment arms in *Tyrannosaurus rex* using a three-dimensional musculoskeletal  
1333 computer model. *Paleobiology* 31:676-701.  
1334
- 1335 Hutchinson, J. R., Miller, C., Fritsch, G., & Hildebrandt, T. 2008. The anatomical foundation  
1336 for multidisciplinary studies of animal limb function: examples from dinosaur and elephant  
1337 limb imaging studies. *In: Anatomical Imaging* (eds. Fritsch, G. and Frey, R.), pp. 23-38.  
1338 Springer, Japan.  
1339
- 1340 Jensen, R. H., & Davy, D. T. 1975. An investigation of muscle lines of action about the hip:  
1341 A centroid line approach vs the straight line approach. *Journal of Biomechanics* 8: 103-110.  
1342
- 1343 Jindrich, D. L., Smith, N. C., Jespers, K., & Wilson, A. M. 2007. Mechanics of cutting  
1344 maneuvers by ostriches (*Struthio camelus*). *Journal of Experimental Biology*, 210: 1378-  
1345 1390.  
1346
- 1347 Johnson, W. L., Jindrich, D. L., Roy, R. R., & Edgerton, V. R. 2008. A three-dimensional  
1348 model of the rat hindlimb: musculoskeletal geometry and muscle moment arms. *Journal of*  
1349 *Biomechanics* 41: 610-619.  
1350
- 1351 Kambic, R. E., Roberts, T. J., & Gatesy, S. M. 2014. Long-axis rotation: a missing degree of  
1352 freedom in avian bipedal locomotion. *Journal of Experimental Biology*, jeb-101428;  
1353 published online.  
1354
- 1355 Kargo, W. J., & Rome, L. C. 2002. Functional morphology of proximal hindlimb muscles in  
1356 the frog *Rana pipiens*. *Journal of Experimental Biology* 205:1987-2004.  
1357
- 1358 Kargo, W. J., Nelson, F. & Rome, L. C. 2002. Jumping in frogs: assessing the design of the  
1359 skeletal system by anatomically realistic modeling and forward dynamic simulation. *Journal*  
1360 *of Experimental Biology* 205:1683-1702.  
1361
- 1362 Kilbourne, B. M. 2013. On birds: scale effects in the neognath hindlimb and differences in  
1363 the gross morphology of wings and hindlimbs. *Biological Journal of the Linnean Society*,  
1364 110: 14-31.

1365  
1366  
1367  
1368  
1369  
1370  
1371  
1372  
1373  
1374  
1375  
1376  
1377  
1378  
1379  
1380  
1381  
1382  
1383  
1384  
1385  
1386  
1387  
1388  
1389  
1390  
1391  
1392  
1393  
1394  
1395  
1396  
1397  
1398  
1399  
1400  
1401  
1402  
1403  
1404  
1405  
1406  
1407  
1408  
1409  
1410  
1411  
1412  
1413  
1414

Lamas, L., Main, R.P., & Hutchinson, J.R. 2014. Ontogenetic scaling patterns and functional anatomy of the pelvic limb musculature in emus (*Dromaius novaehollandiae*). PeerJ PrePrints 2:e508v1 <https://peerj.com/preprints/508v1/> (paper in review)

Lieber, R. L., & Boakes, J. L. 1988a. Sarcomere length and joint kinematics during torque production in frog hindlimb. *American Journal of Physiology* 254: C759-C768.

Lieber, R. L., & Boakes, J. L. 1988b. Muscle force and moment arm contributions to torque production in frog hindlimb. *American Journal of Physiology* 254: C769-72.

Lieber, R. L., & Brown, C. G. 1992. Sarcomere length-joint angle relationships of seven frog hindlimb muscles. *Cells Tissues Organs* 145: 289-295.

Lieber, R. L., & Shoemaker, S. D. 1992. Muscle, joint, and tendon contributions to the torque profile of frog hip joint. *American Journal of Physiology* 263: R586-R586.

Lieber, R. L. 1997. Muscle fiber length and moment arm coordination during dorsi- and plantarflexion in the mouse hindlimb. *Acta Anatomica* 159:84-89.

Macalister, A. 1864. On the anatomy of the ostrich (*Struthio camelus*). *Proceedings of the Royal Irish Academy* 9: 1-24.

Mai, M. T., & Lieber, R. L. 1990. A model of semitendinosus muscle sarcomere length, knee and hip joint interaction in the frog hindlimb. *Journal of Biomechanics* 23: 271-279.

Maganaris, C. N. 2004. Imaging-based estimates of moment arm length in intact human muscle-tendons. *European Journal of Applied Physiology* 91:130-139.

Maidment, S. C., Bates, K. T., Falkingham, P. L., VanBuren, C., Arbour, V., & Barrett, P. M. 2013. Locomotion in ornithischian dinosaurs: an assessment using three-dimensional computational modelling. *Biological Reviews*, published online. DOI: 10.1111/brv.12071

Mallison, H. 2010a. The digital *Plateosaurus* I: body mass, mass distribution, and posture assessed using CAD and CAE on a digitally mounted complete skeleton. *Palaeontologia Electronica* 13(13.2).

Mallison, H. 2010b. The digital *Plateosaurus* II: An assessment of the range of motion of the limbs and vertebral column and of previous reconstructions using a digital skeletal mount. *Acta Palaeontologica Polonica*, 55: 433-458.

Mallison, H. 2010c. CAD assessment of the posture and range of motion of *Kentrosaurus aethiopicus* Hennig 1915. *Swiss Journal of Geosciences*, 103: 211-233.

Maloiy, G. M. O., R. Mc N. Alexander, R. Njau, and A. S. Jayes. 1979. Allometry of the legs of running birds. *Journal of Zoology* 187:161-167.

McClearn, D. 1985. Anatomy of raccoon (*Procyon lotor*) and coati (*Nasua narica* and *N. nasua*) forearm and leg muscles: Relations between fiber length, moment-arm length, and joint-angle excursion. *Journal of Morphology* 183: 87-115.



- 1415  
1416 McGowan, C. 1979. The hind limb musculature of the Brown Kiwi, *Apteryx australis*  
1417 *mantelli*. Journal of Morphology 160:33-74.  
1418  
1419 Medler, S. 2002. Comparative trends in shortening velocity and force production in skeletal  
1420 muscle. Am J Physiol Regulat Integr Comp Physiol 283:R368-R378.  
1421  
1422 Mendez, J., Keys, A. 1960. Density and composition of mammalian muscle. Metabolism-  
1423 Clinical and Experimental 9:184-188.  
1424  
1425 Molnar, J. 2014. The biomechanics of vertebrae across evolutionary transitions between  
1426 water and land: examples from early Tetrapod and Crocodylomorpha. Unpublished PhD  
1427 dissertation, The Royal Veterinary College, University of London, United Kingdom.  
1428  
1429 Nagano, A., Umberger, B. R., Marzke, M. W. & Gerritsen, K. G. M. 2005.  
1430 Neuromusculoskeletal computer modeling and simulation of upright, straight-legged, bipedal  
1431 locomotion of *Australopithecus afarensis*. American Journal of Physical Anthropology 126:  
1432 2-13.  
1433  
1434 Nelson, F. E., Gabaldón, A. M., & Roberts, T. J. 2004. Force-velocity properties of two avian  
1435 hindlimb muscles. Comparative Biochemistry and Physiology A 137:711-721.  
1436  
1437 Nikooyan, A. A., Veeger, H. E. J., Chadwick, E. K. J., Praagman, M. & van der Helm, F. C.  
1438 T. 2011. Development of a comprehensive musculoskeletal model of the shoulder and elbow.  
1439 Medical & Biological Engineering & Computing 49:1425-1435.  
1440  
1441 Pandy, M. G. 1999. Moment arm of a muscle force. Exercise and Sport Science Reviews  
1442 27:79-118.  
1443  
1444 Patak, A., & Baldwin, J. 1993. Structural and metabolic characterization of the muscles used  
1445 to power running in the emu (*Dromaius novaehollandiae*), a giant flightless bird. Journal of  
1446 Experimental Biology 175:233-249.  
1447  
1448 Patak, A., & Baldwin, J. 1998. Pelvic limb musculature in the emu *Dromaius*  
1449 *novaehollandiae* (Aves: Struthioniformes: Dromaiidae): Adaptations to high-speed running.  
1450 Journal of Morphology 238:23-37.  
1451  
1452 Paul, G.S. 1998. Limb design, function and running performance in ostrich-mimics and  
1453 tyrannosaurs. Gaia 15:257-270.  
1454  
1455 Picasso, M. B. J. 2010. The hindlimb muscles of *Rhea americana* (Aves, Palaeognathae,  
1456 Rheidae). Anatomia Histologia Embryologia 39: 462-472.  
1457  
1458 Picasso, M. B. J. 2012. Postnatal ontogeny of the locomotor skeleton of a cursorial bird:  
1459 greater rhea. Journal of Zoology 286: 303-311.  
1460  
1461 Pierce, S. E., Clack, J. A., & Hutchinson, J. R. 2012. Three-dimensional limb joint mobility  
1462 in the early tetrapod *Ichthyostega*. Nature 486: 523-526.  
1463

- 1464 Regnault, S., Pitsillides, A.A., & Hutchinson, J.R. 2014. Structure, ontogeny and evolution of  
1465 the patellar tendon in emus (*Dromaius novaehollandiae*) and other palaeognath birds. PeerJ  
1466 PrePrints 2:e404v1 <https://peerj.com/preprints/404/> (paper in review)  
1467
- 1468 Rowe, T. 1986. Homology and evolution of the deep dorsal thigh musculature in birds and  
1469 other Reptilia. *Journal of Morphology* 189: 327-346.  
1470
- 1471 Rubenson, J., Heliam, D.B., Lloyd, D.G., & Fournier, P.A. 2004. Gait selection in the  
1472 ostrich: mechanical and metabolic characteristics of walking and running with and without an  
1473 aerial phase. *Proceedings of the Royal Society B: Biological Sciences* 271:1091-1099.  
1474
- 1475 Rubenson, J., Henry, H. T., Dimoulas, P. M., & Marsh, R. L. 2006. The cost of running  
1476 uphill: linking organismal and muscle energy use in guinea fowl (*Numida meleagris*). *Journal*  
1477 *of Experimental Biology* 209: 2395-2408.  
1478
- 1479 Rubenson, J., Lloyd, D. G., Besier, T. F., Heliam, D. B., & Fournier, P. A. 2007. Running in  
1480 ostriches (*Struthio camelus*): three-dimensional joint axes alignment and joint kinematics.  
1481 *Journal of Experimental Biology* 210: 2548-2562.  
1482
- 1483 Rubenson, J., Lloyd, D. G., Heliam, D. B., Besier, T. F., & Fournier, P. A. 2011.  
1484 Adaptations for economical bipedal running: the effect of limb structure on three-dimensional  
1485 joint mechanics. *Journal of the Royal Society Interface* 8: 740-755.  
1486
- 1487 Russell, D. A. 1972. Ostrich dinosaurs from the Late Cretaceous of Western Canada.  
1488 *Canadian Journal of Earth Sciences* 9:375-402.  
1489
- 1490 Schaller, N. U., Herkner, B., Villa, R., & Aerts, P. 2009. The intertarsal joint of the ostrich  
1491 (*Struthio camelus*): anatomical examination and function of passive structures in locomotion.  
1492 *Journal of Anatomy* 214: 830-847.  
1493
- 1494 Schaller, N. U., D'Août, K., Villa, R., Herkner, B., & Aerts, P. 2011. Toe function and  
1495 dynamic pressure distribution in ostrich locomotion. *Journal of Experimental Biology* 214:  
1496 1123-1130.  
1497
- 1498 Smith, N. C., Wilson, A. M., Jespers, K. J., & Payne, R. C. 2006. Muscle architecture and  
1499 functional anatomy of the pelvic limb of the ostrich (*Struthio camelus*). *Journal of Anatomy*,  
1500 209: 765-779.  
1501
- 1502 Smith, N. C., Payne, R. C., Jespers, K. J., & Wilson, A. M. 2007. Muscle moment arms of  
1503 pelvic limb muscles of the ostrich (*Struthio camelus*). *Journal of Anatomy* 211: 313-324.  
1504
- 1505 Smith, N. C., Jespers, K. J., & Wilson, A. M. 2010. Ontogenetic scaling of locomotor kinetics  
1506 and kinematics of the ostrich (*Struthio camelus*). *Journal of Experimental Biology* 213: 1347-  
1507 1355.  
1508
- 1509 Smith, N. C., & Wilson, A. M. 2013. Mechanical and energetic scaling relationships of  
1510 running gait through ontogeny in the ostrich (*Struthio camelus*). *Journal of Experimental*  
1511 *Biology* 216: 841-849.  
1512

- 1513 Troy, K. L., Brown, T. D., & Conzemius, M. G. 2009. Contact stress distributions on the  
1514 femoral head of the emu (*Dromaius novaehollandiae*). Journal of Biomechanics 42: 2495-  
1515 2500.
- 1516
- 1517 Tsaopoulos, D. E., Baltzopoulos, V., Richards, P. J., & Maganaris, C. N. 2007. In vivo  
1518 changes in the human patellar tendon moment arm length with different modes and intensities  
1519 of muscle contraction. Journal of Biomechanics 40: 3325-3332.
- 1520
- 1521 Vanden Berge, J.C. 1982. Notes on the myology of the pelvic limb in kiwi (*Apteryx*) and in  
1522 other birds. The Auk 99:309-315.
- 1523
- 1524 Velotto, S., & Crasto, A. 2004. Histochemical and morphometrical characterization and  
1525 distribution of fibre types in four muscles of ostrich (*Struthio camelus*). Anatomia Histologia  
1526 Embryologia 33:251-256.
- 1527
- 1528 Walker, P. S., Rovick, J. S., & Robertson, D. D. 1988. The effects of knee brace  
1529 hinge design and placement on joint mechanics. Journal of Biomechanics 21:965-974.
- 1530
- 1531 Watson, R. R., Rubenson, J., Coder, L., Hoyt, D. F., Propert, M. W., & Marsh, R. L. 2011.  
1532 Gait-specific energetics contributes to economical walking and running in emus and  
1533 ostriches. Proceedings of the Royal Society B: Biological Sciences 278: 2040-2046.
- 1534
- 1535 Weissengruber, G.E., Forstenpointner, G., & Gangl, D. 2003. Gut zu Fuß – funktionell-  
1536 anatomische Aspekte des bipeden Laufens beim Afrikanischen Strauß (*Struthio camelus*  
1537 Linné, 1758). Veterinary Medicine Austria Wiener Tierärztliche Monatsschrift 90:67-78.
- 1538
- 1539 Young, R. P., Scott, S. H., & Loeb, G. E. 1993. The distal hindlimb musculature of the cat:  
1540 multiaxis moment arms at the ankle joint. Experimental Brain Research 96: 141-151.
- 1541
- 1542 Zajac, F. E. 1989. Muscle and tendon: properties, models, scaling, and application to  
1543 biomechanics and motor control. Critical Reviews in Biomedical Engineering 17:359-411.
- 1544
- 1545 Zarucco, L., Wisner, E. R., Swanstrom, M. D., & Stover, S. M. 2006. Image fusion of  
1546 computed tomographic and magnetic resonance images for the development of a three-  
1547 dimensional musculoskeletal model of the equine forelimb. Veterinary Radiology &  
1548 Ultrasound 47: 553-562.
- 1549
- 1550 Zinoviev, A. V. 2006. Notes on the hind limb myology of the Ostrich (*Struthio camelus*).  
1551 Ornithologia 33: 53-62.

1552 **Figure Captions**

1553

1554 Figure 1. Digitizing apparatus used during anatomical dissection of ostrich. “LED Ref”  
1555 indicates the proximal (in trochanteric crest of the femur) and distal (in tibiotarsus by the  
1556 ankle) reference frames, “Dig. Probe” indicates the digitizing probe used to collect  
1557 landmarks.

1558

1559 Figure 2. Ostrich model joint axes (x, y, z) shown in right lateral (A) and oblique right  
1560 dorsolateral (B) views. The x-axis corresponded to ab/adduction, the y-axis to long-axis  
1561 rotation, and the z-axis to flexion/extension.

1562

1563 Figure 3. Ostrich musculoskeletal model in right lateral view, with muscle-tendon units  
1564 labeled (red lines). See Table 2 for muscle abbreviations.

1565

1566 Figure 4. Ostrich musculoskeletal model in right caudolateral view, with muscle-tendon units  
1567 labeled (red lines). See Table 2 for muscle abbreviations.

1568

1569 Figure 5. Ostrich musculoskeletal model: wrapping surface examples. See Table 2 for muscle  
1570 abbreviations. Lateral (A), caudolateral (B), and craniolateral (C) views of eight muscle  
1571 wrapping objects (in blue), as half and whole cylinders, ellipses and a torus. The PIFML and  
1572 ILFB wrapping surfaces are shown as meshes, for added clarity.

1573

1574 Figure 6. Maximal muscle moments about proximal limb joints (hip and knee), for  
1575 representative walking and running trials (see Methods). “F-L” curves incorporate effects of  
1576 muscle force-length properties into moment calculations; “Fmax” curves only assume  
1577 maximal isometric muscle stress and thus ignore F-L effects.

1578

1579 Figure 7. Maximal muscle moments about distal limb joints (ankle and metatarsophalangeal  
1580 [MTP]), for representative walking and running trials (see Methods). See caption for Figure  
1581 6.

1582

1583 Figure 8. Sum of extensor moment arms (left column) or flexor moment arms (right column)  
1584 normalized by sum of maximal extensor or flexor moment arms, plotted against extension or  
1585 flexion joint angle for the hip, knee and ankle joints (MTP joint data follow Figure 20), with  
1586 representative mid-stance limb poses for walking and running indicated.

1587

1588 Figure 9. Hip flexor/extensor moment arms plotted against joint angle for key proximal thigh  
1589 muscles in our model, with corresponding data from Smith et al. (2005) labelled as “Smith”  
1590 and from Bates and Schachner (2012) labelled as “Bates”. Extreme extended/flexed right hip  
1591 joint poses shown along the x-axis. Muscle abbreviations are in Table 2.

1592

1593 Figure 10. Hip flexor/extensor moment arms plotted against joint angle for key proximal  
1594 thigh muscles. See caption for Figure 9.

1595

1596 Figure 11. Hip flexor/extensor moment arms plotted against joint angle for key proximal  
1597 thigh muscles. See caption for Figure 9.

1598

1599 Figure 12. Hip long-axis rotation (LAR) moment arms plotted against hip flexion/extension  
1600 joint angle for key proximal thigh muscles. See caption for Figure 9.

1601

1602 Figure 13. Hip long-axis rotation (LAR) moment arms plotted against hip flexion/extension  
1603 joint angle for key proximal thigh muscles. See caption for Figure 9.

1604  
1605 Figure 14. Hip abduction/adduction moment arms plotted against hip flexion/extension joint  
1606 angle for key proximal thigh muscles. See caption for Figure 9.

1607  
1608 Figure 15. Hip abduction/adduction moment arms plotted against hip flexion/extension joint  
1609 angle for key proximal thigh muscles. See caption for Figure 9.

1610  
1611 Figure 16. Knee flexor/extensor moment arms plotted against knee flexion/extension joint  
1612 angle for key thigh muscles. See caption for Figure 9.

1613  
1614 Figure 17. Knee flexor/extensor moment arms plotted against knee flexion/extension joint  
1615 angle for key thigh and distal knee muscles. See caption for Figure 9.

1616  
1617 Figure 18. Ankle flexor/extensor moment arms plotted against ankle flexion/extension joint  
1618 angle for key muscles crossing the ankle. See caption for Figure 9.

1619  
1620 Figure 19. Ankle flexor/extensor moment arms plotted against ankle flexion/extension joint  
1621 angle for the M. gastrocnemius muscle group. See caption for Figure 9.

1622  
1623 Figure 20. Metatarsophalangeal (MTP) joint flexor/extensor moment arms plotted against  
1624 MTP flexion/extension joint angle for digital flexors (left) and extensors, plus tendinous  
1625 connection of M. fibularis longus (right). See caption for Figure 9.

1626  
1627

1628 **Supplementary files:**

1629 Supplementary Text

1630

1631 Supplementary Figures S1-S4: Hip muscle moment arms in long-axis rotation (LAR) or  
1632 ab/adduction plotted against hip LAR or ab/adduction angles (cf. Figures 12-15 plotted  
1633 against hip flexion/extension angles), for key proximal thigh muscles. See caption for Figure  
1634 9.

1635

1636

1637 **Supplementary movie:**

1638

1639 Movie S1: Musculoskeletal model of the right and left pelvic limbs of an ostrich, visualized  
1640 statically to show 3D anatomy represented in the model; posed at mid-stance of running  
1641 (right limb) and corresponding swing phase (left limb).

1642

**Figure 1**(on next page)

Figures 1-20

Captions in main text file (end)

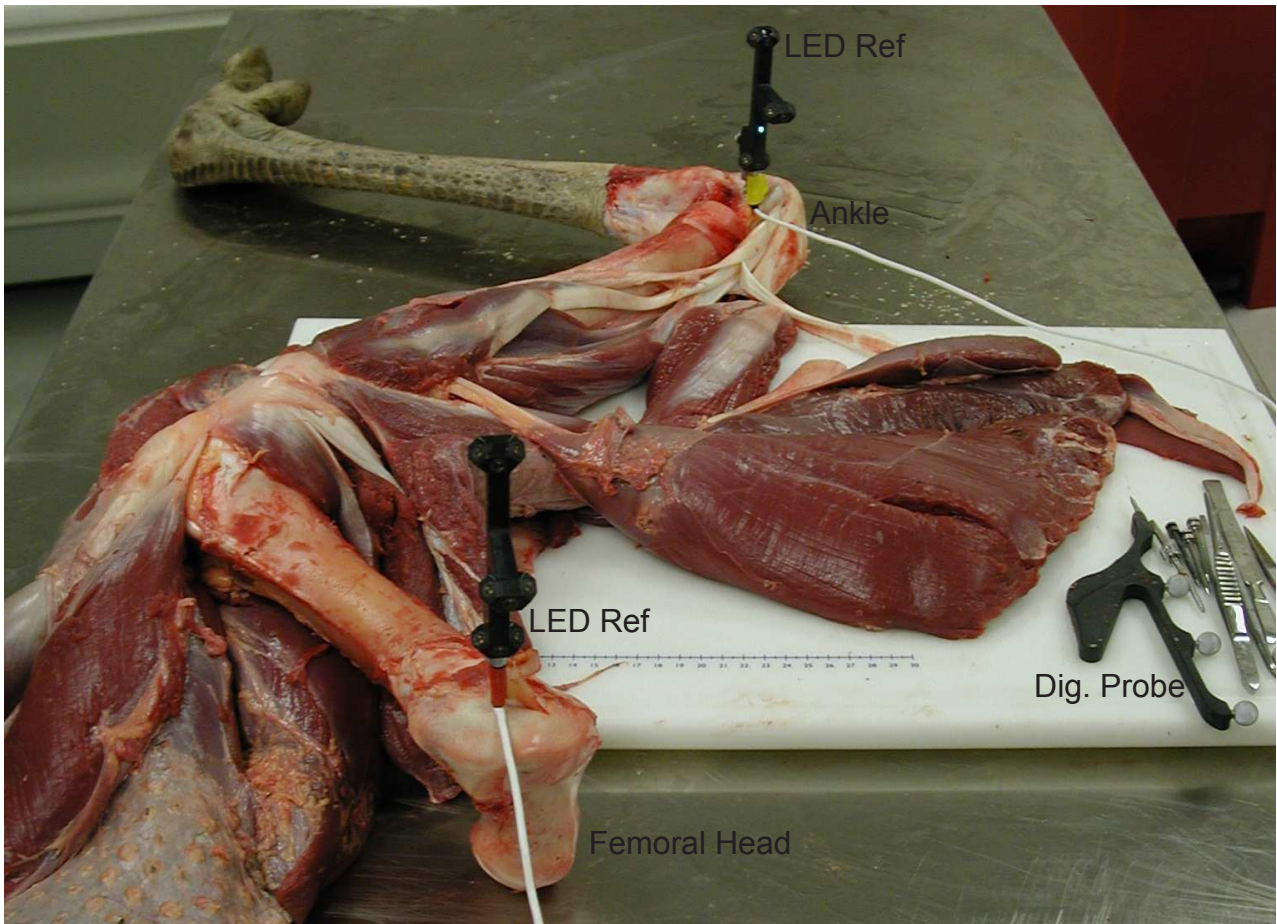


Figure 1

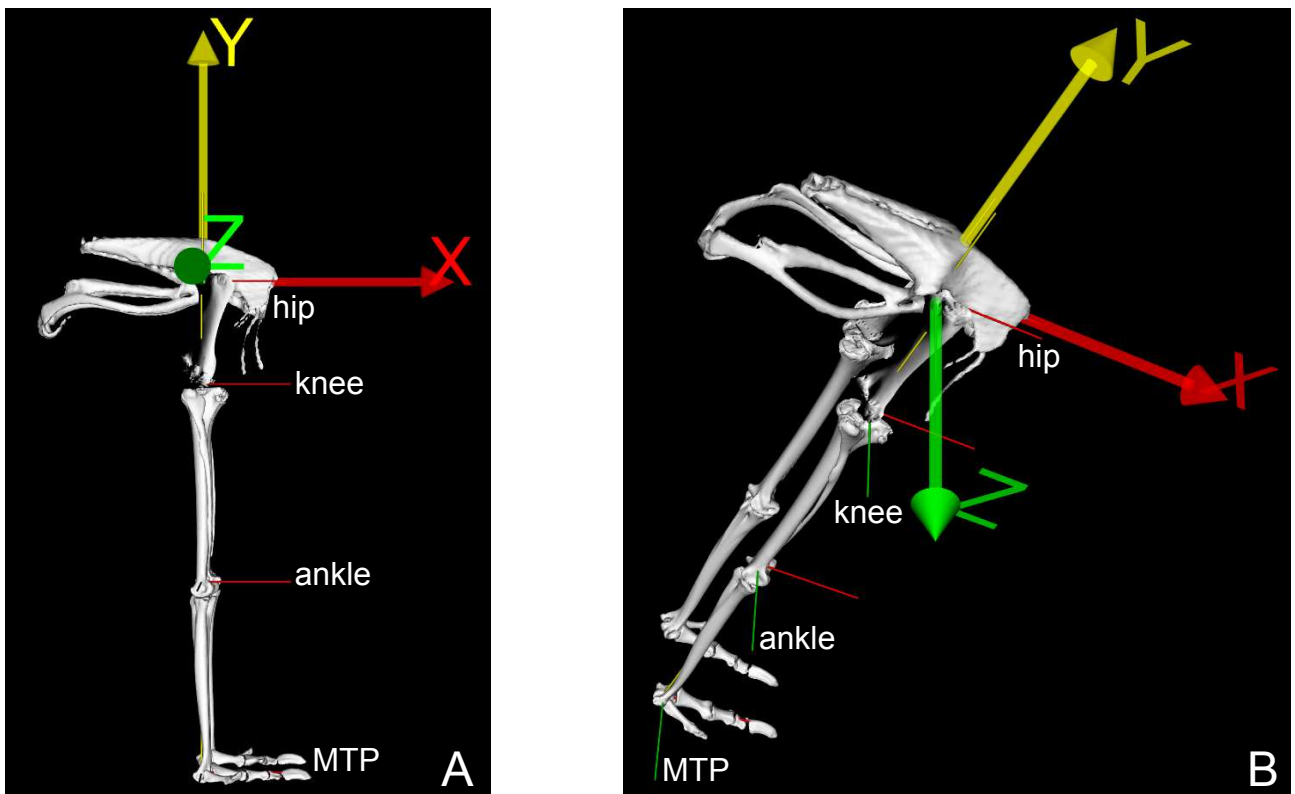


Figure 2



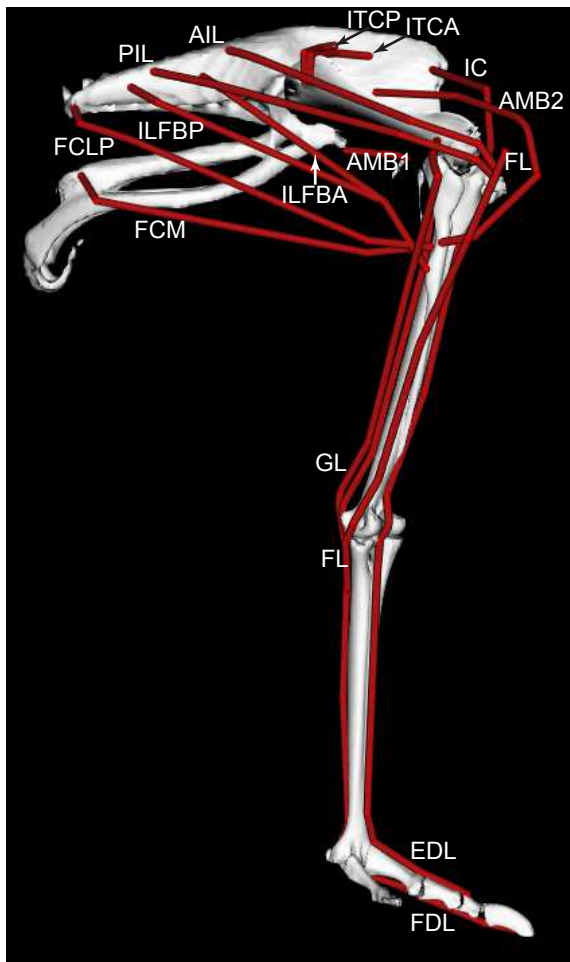


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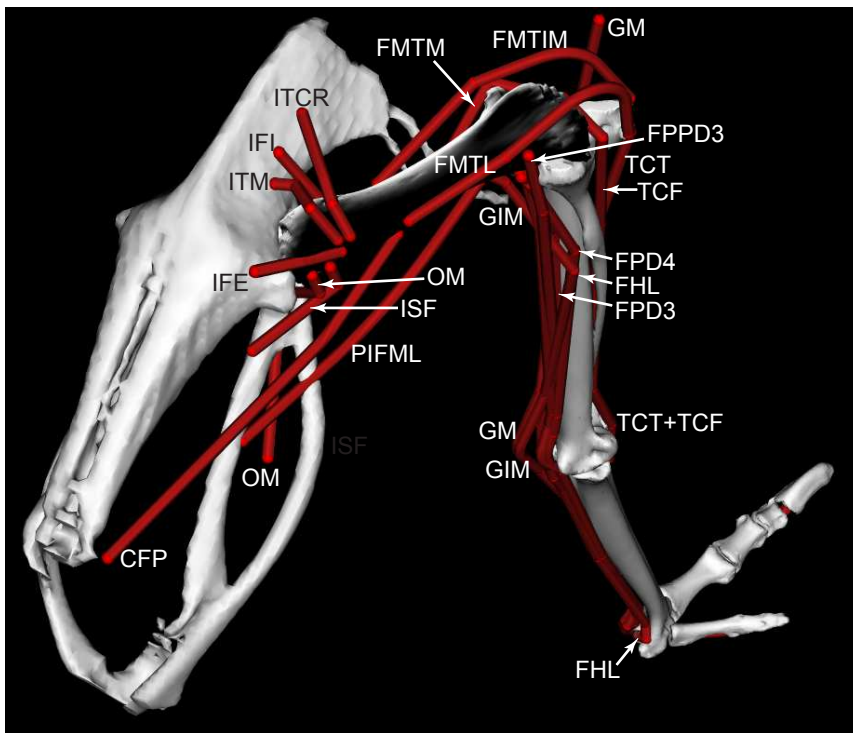


Figure 4

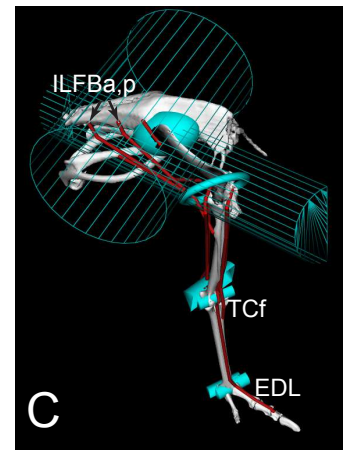
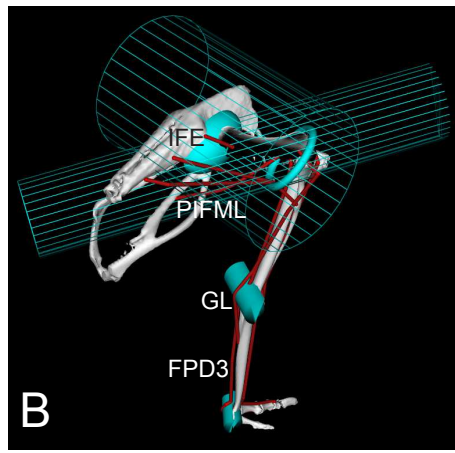
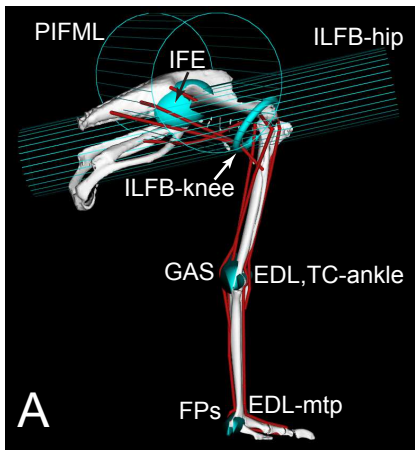


Figure 5

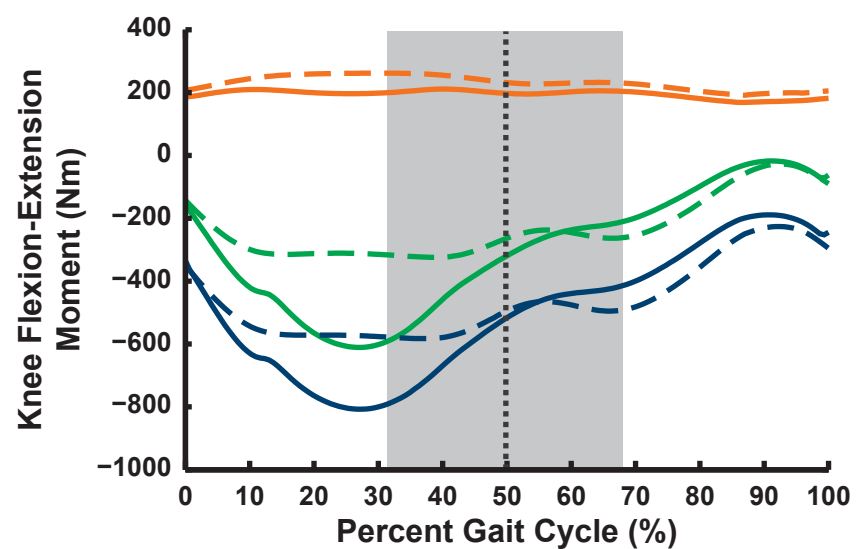
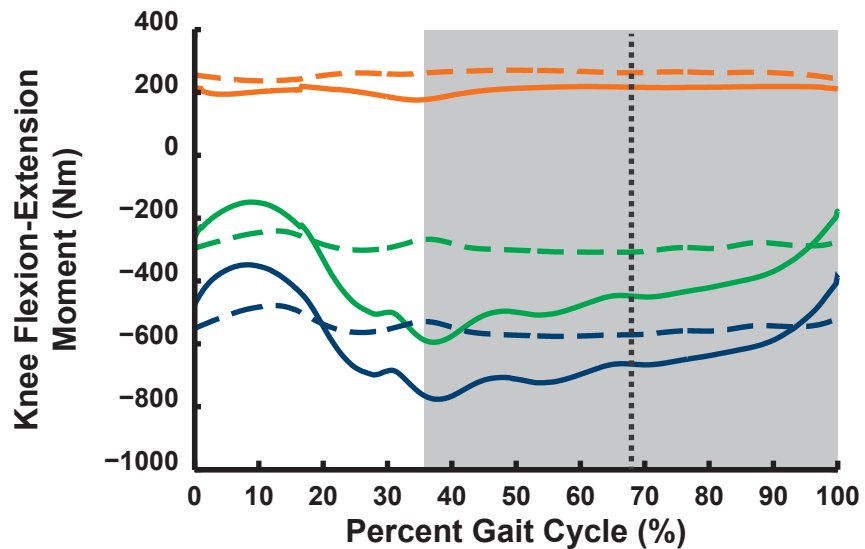
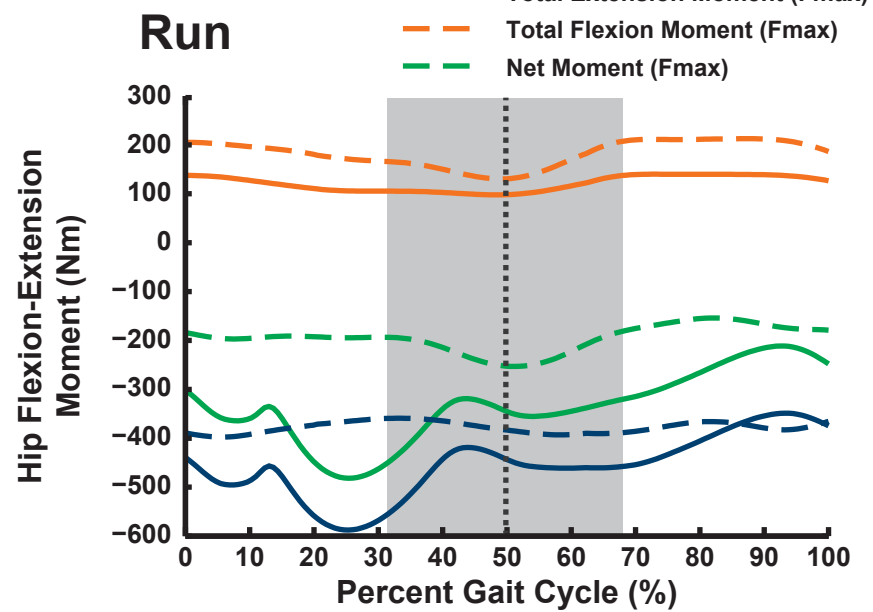
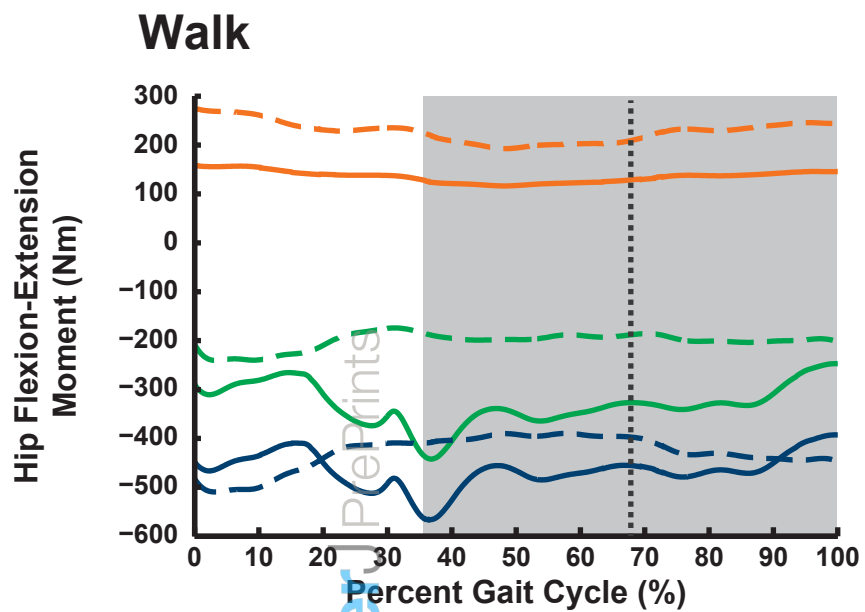


Figure 6

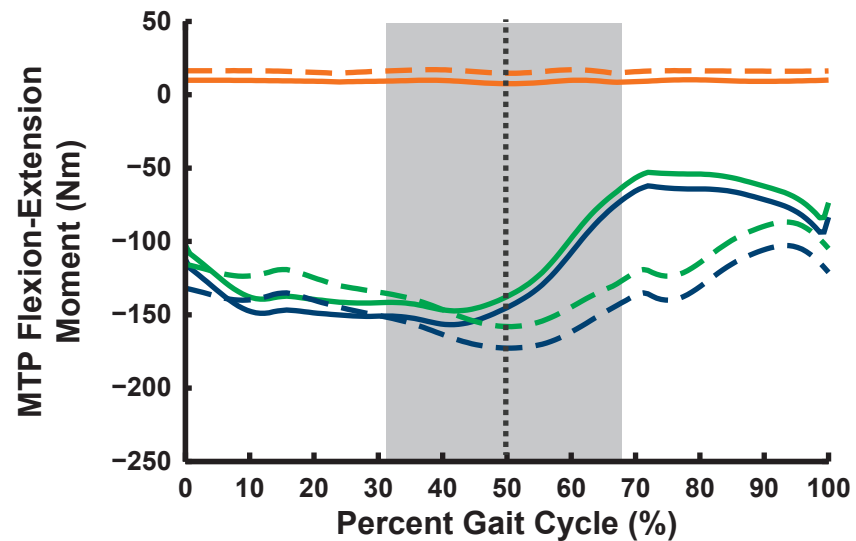
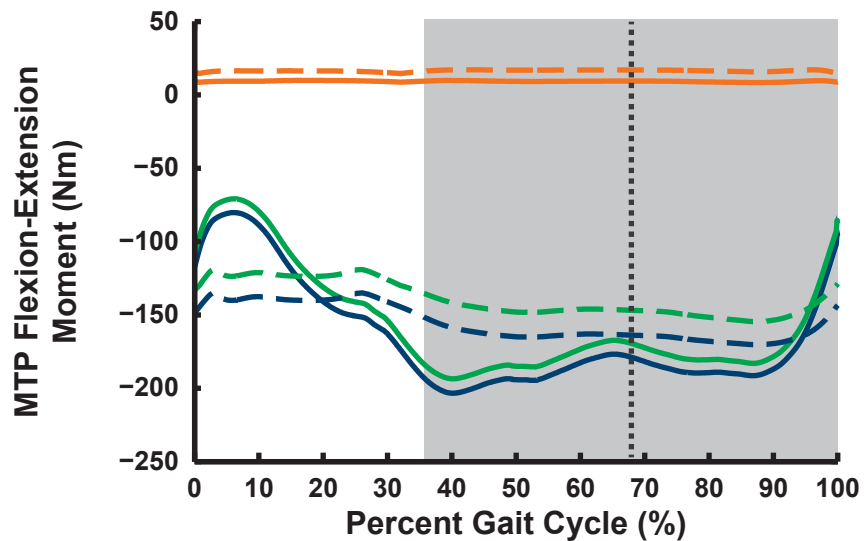
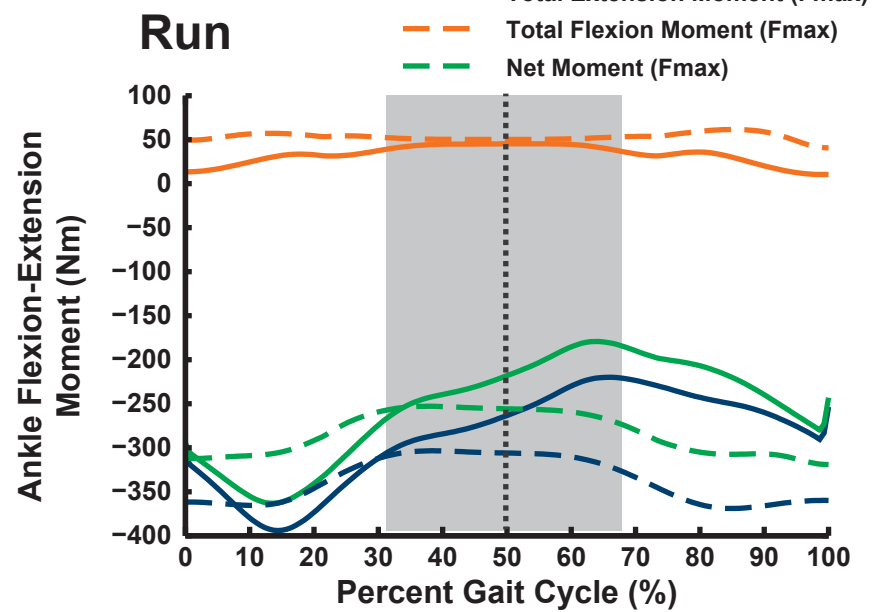
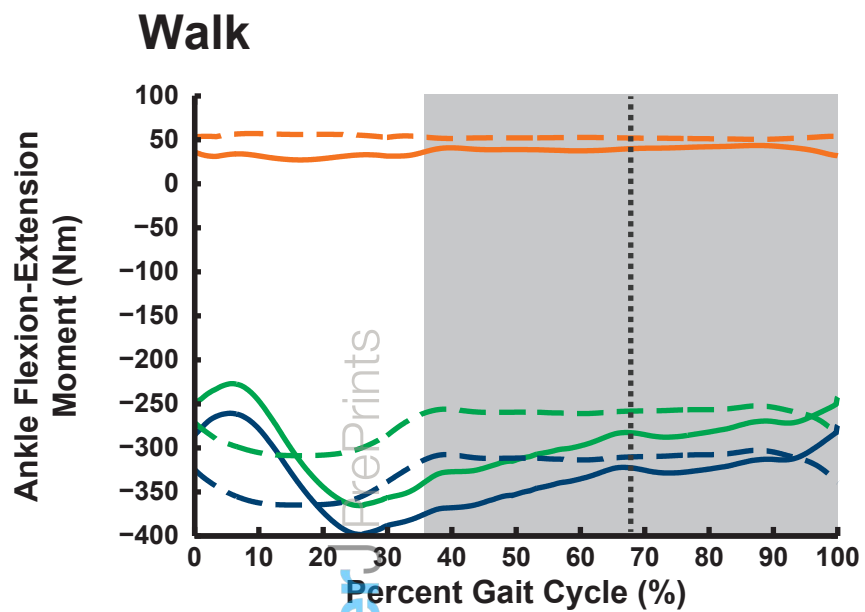


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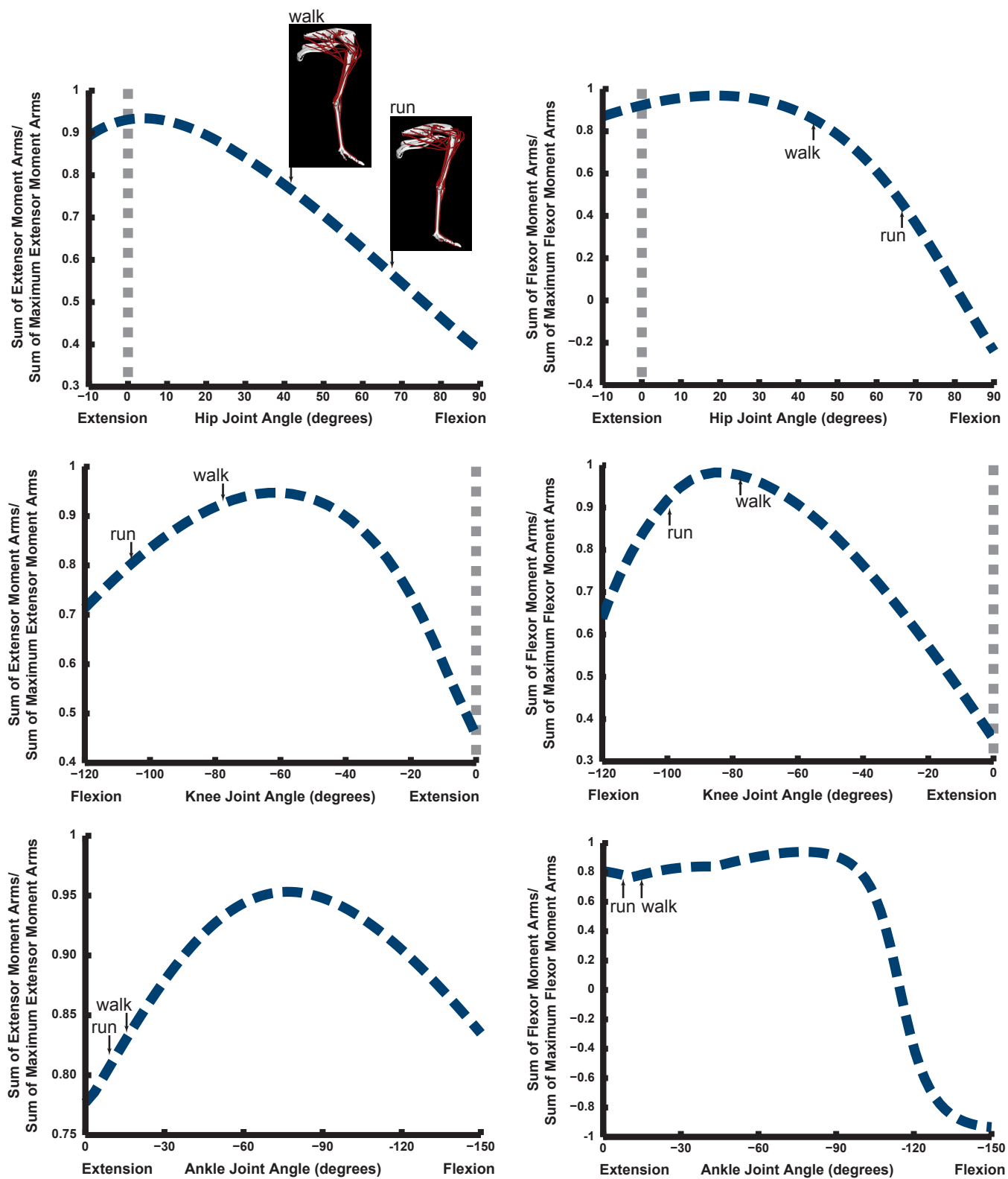


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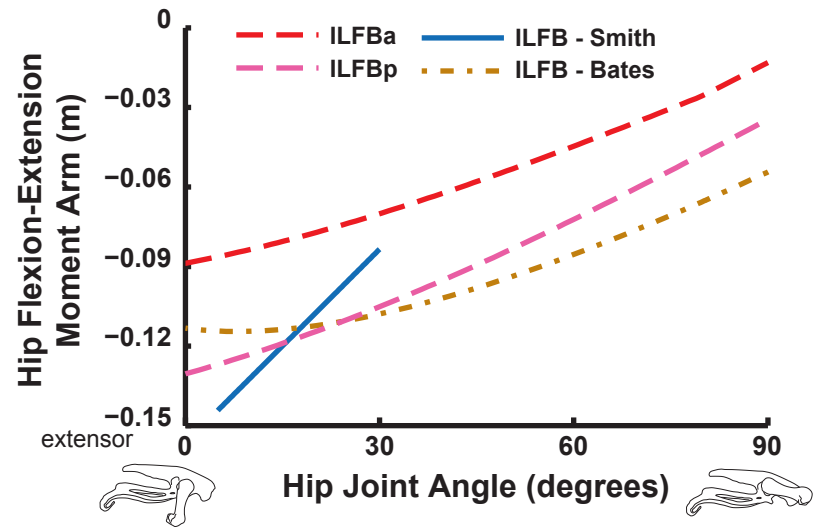
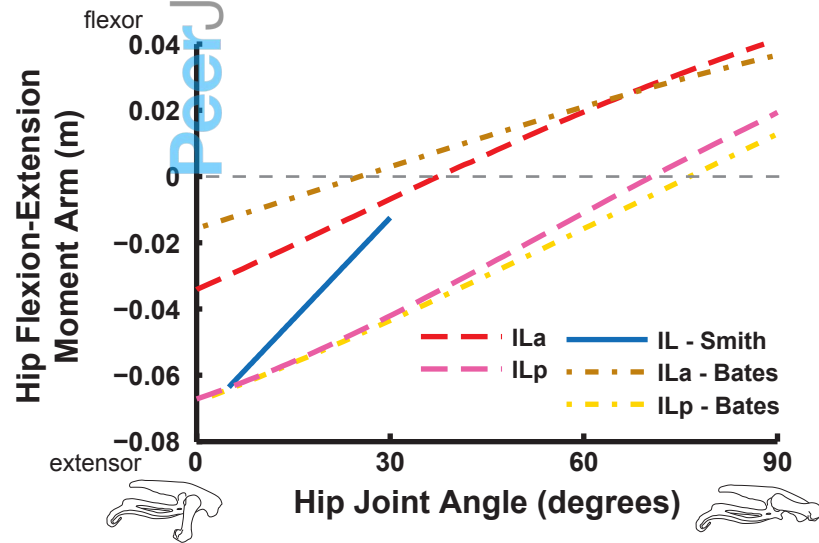
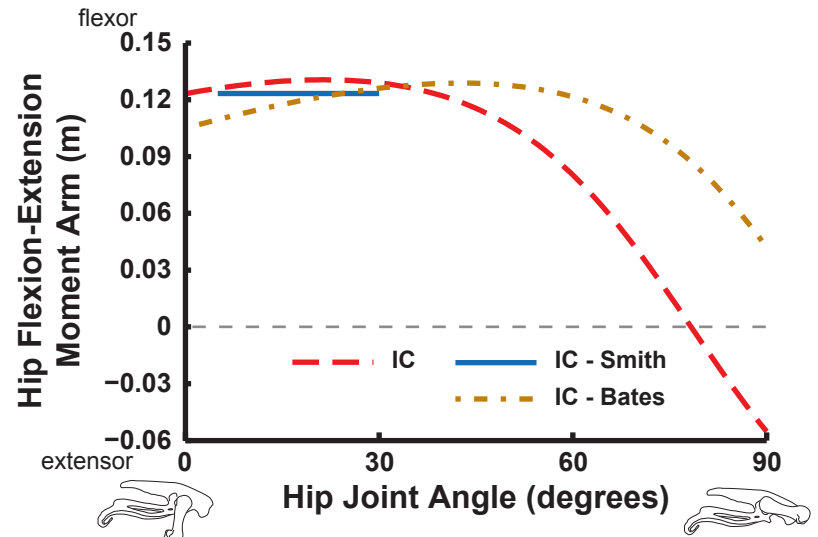
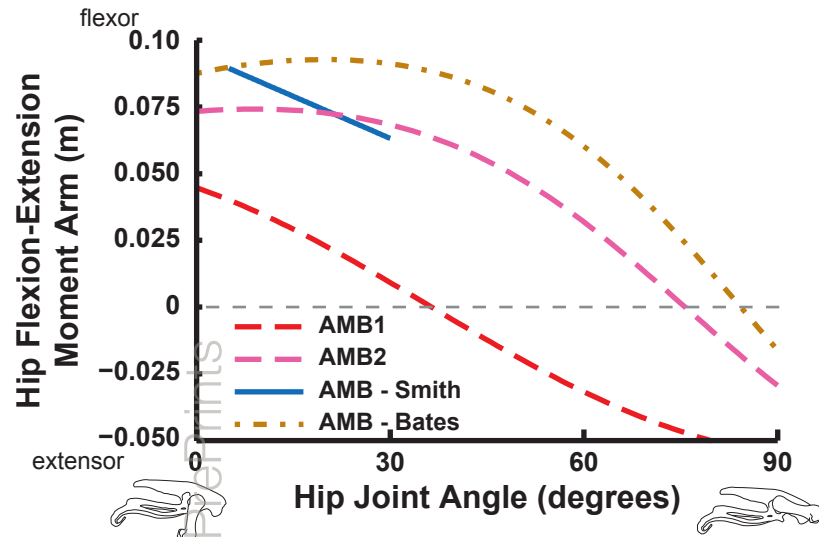


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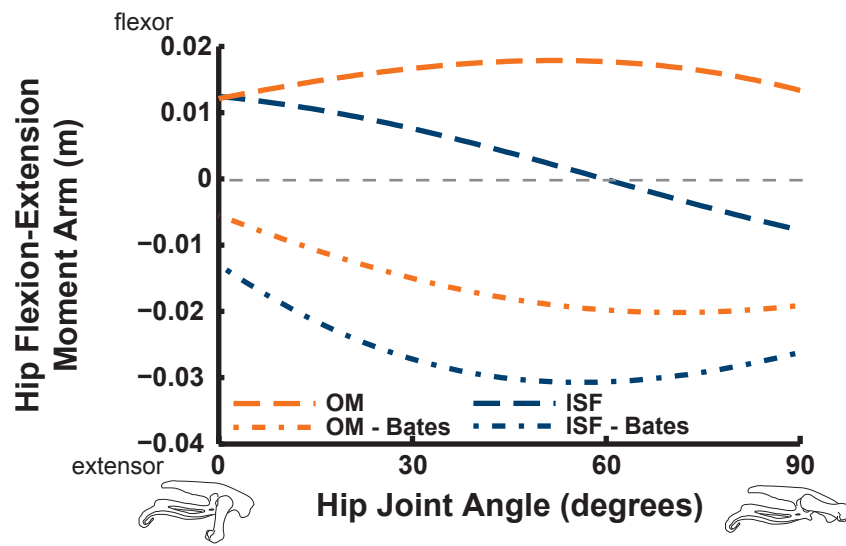
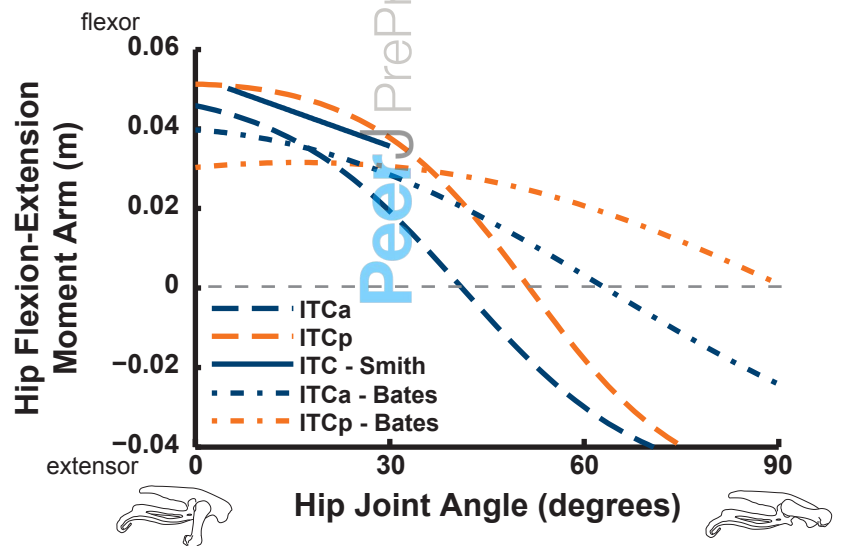
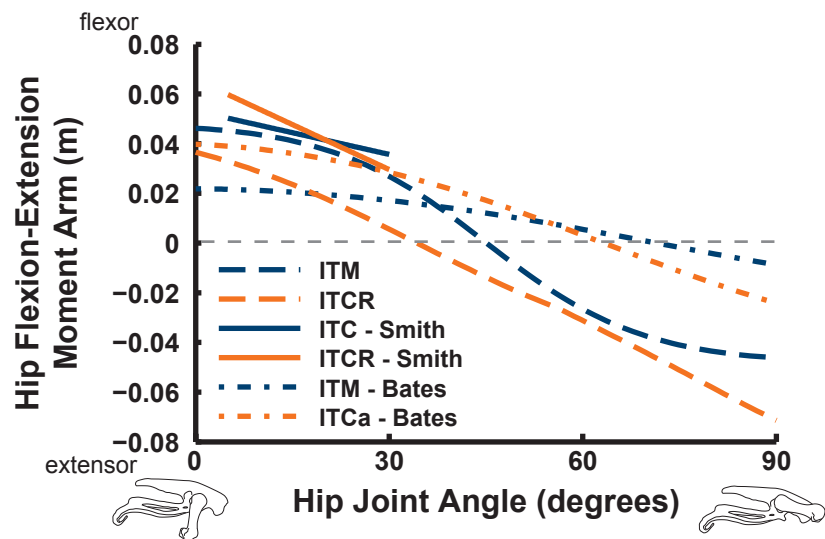
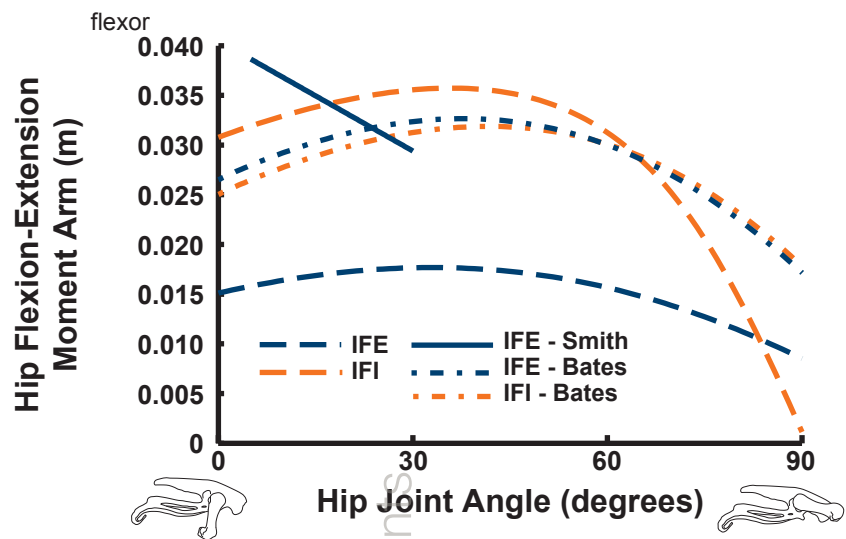


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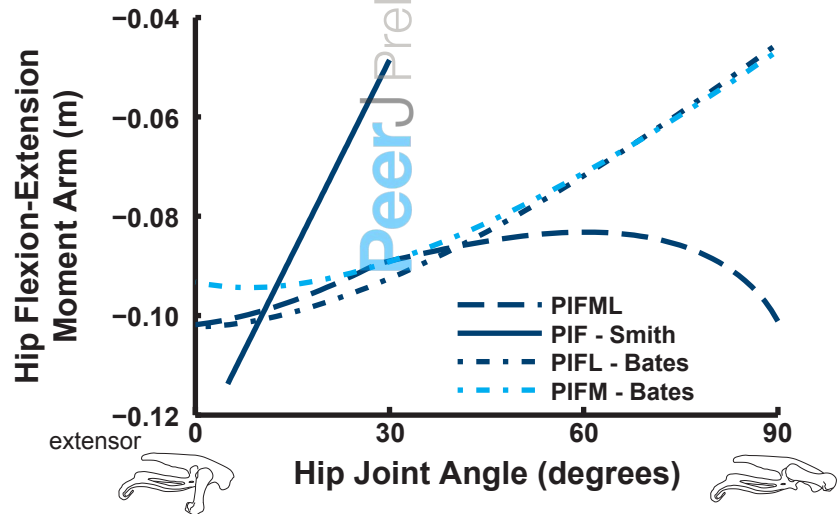
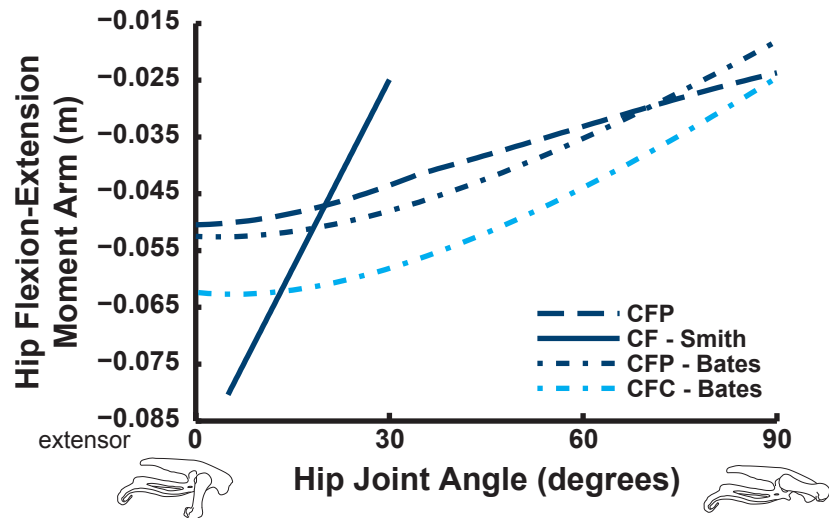
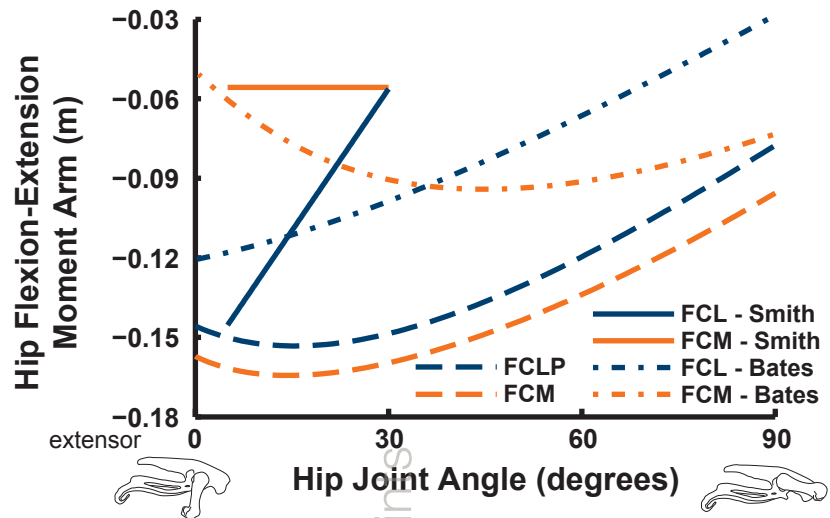


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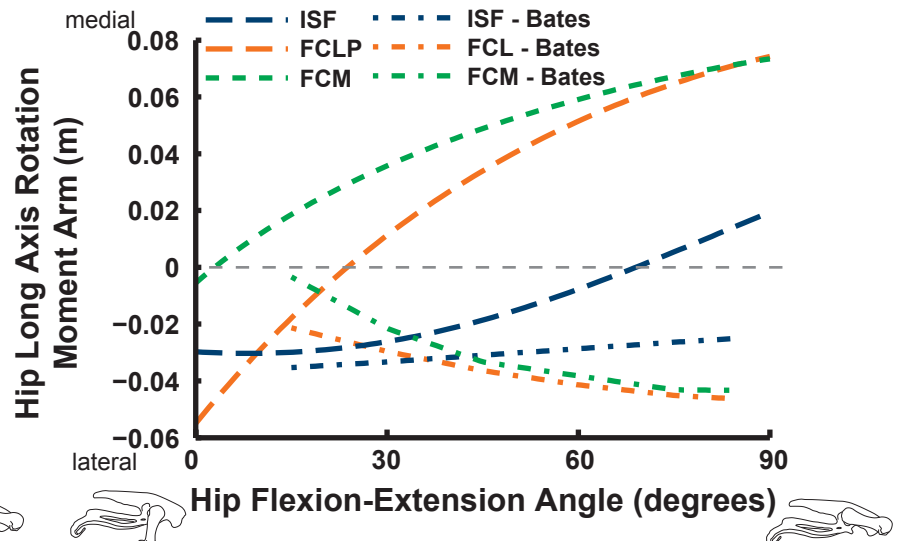
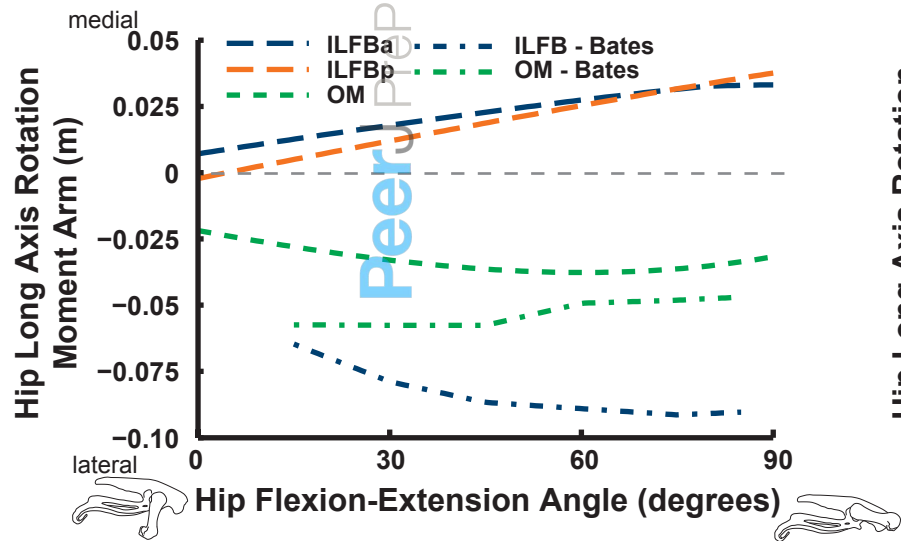
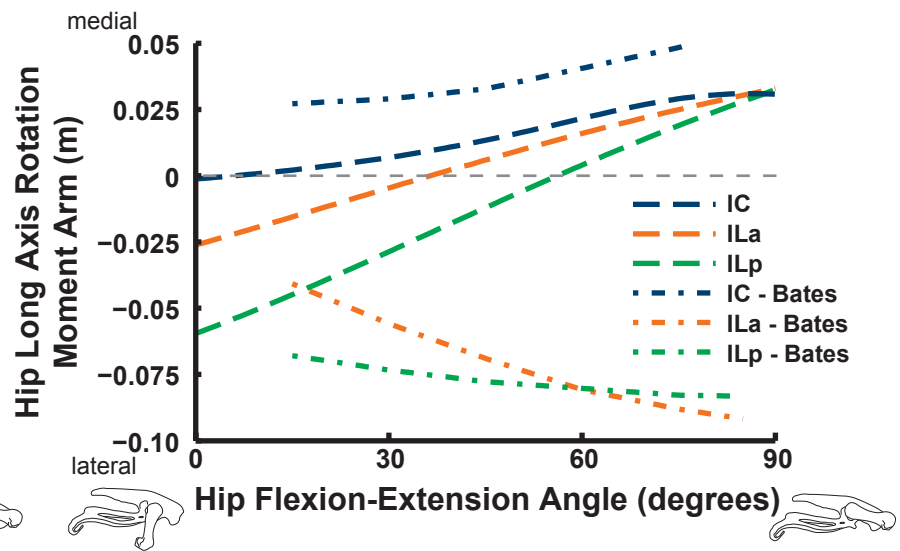
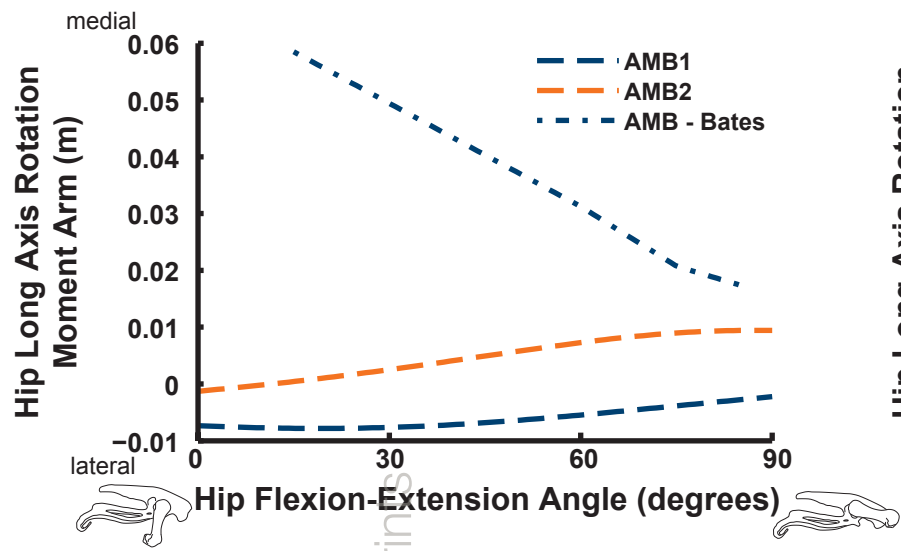


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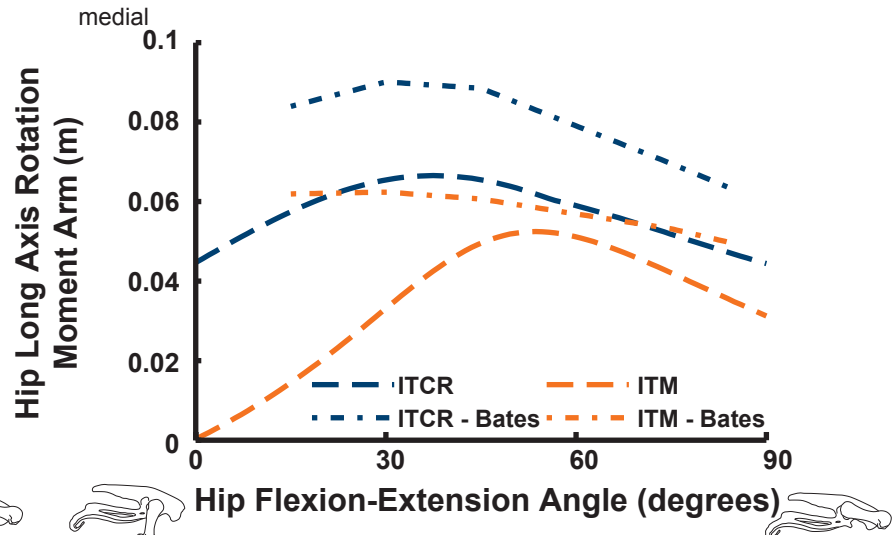
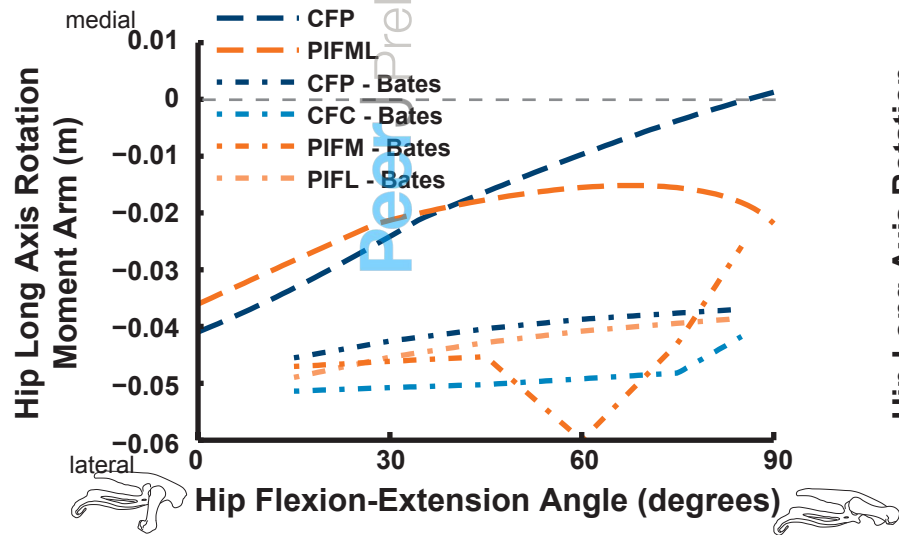
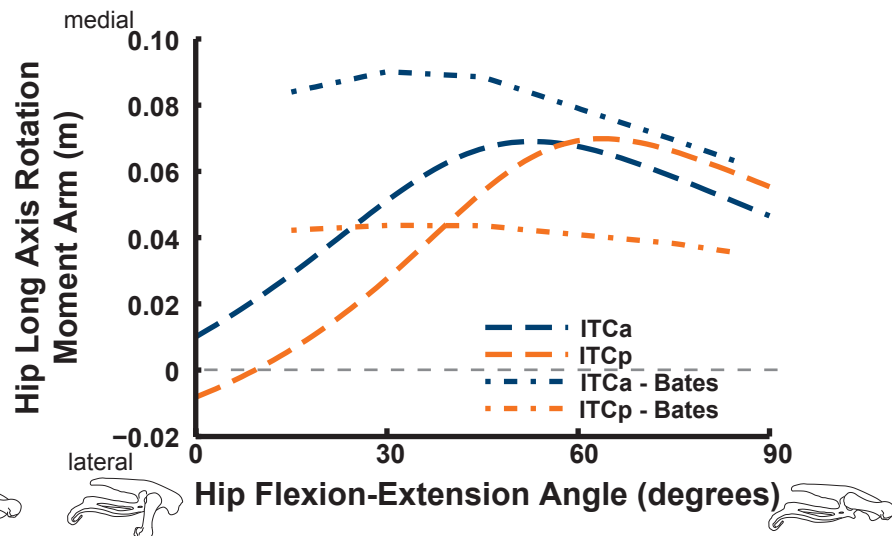
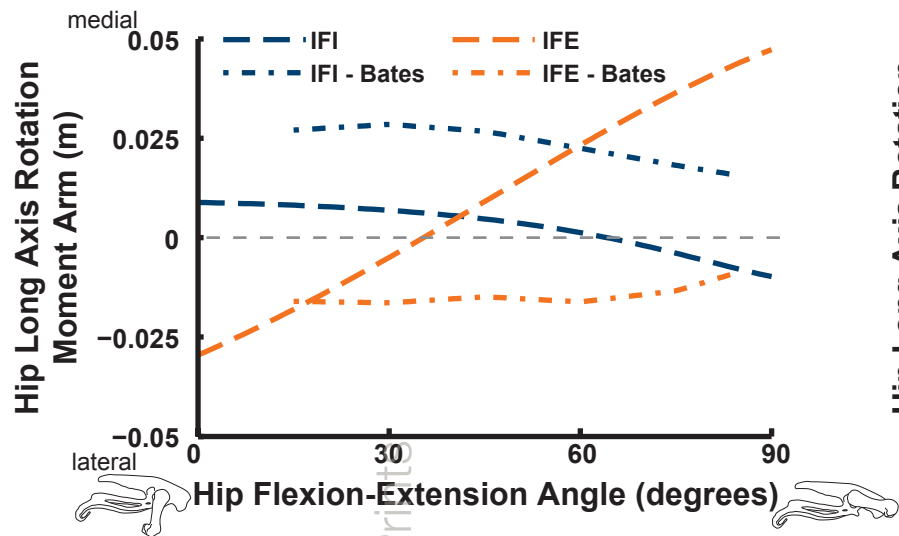


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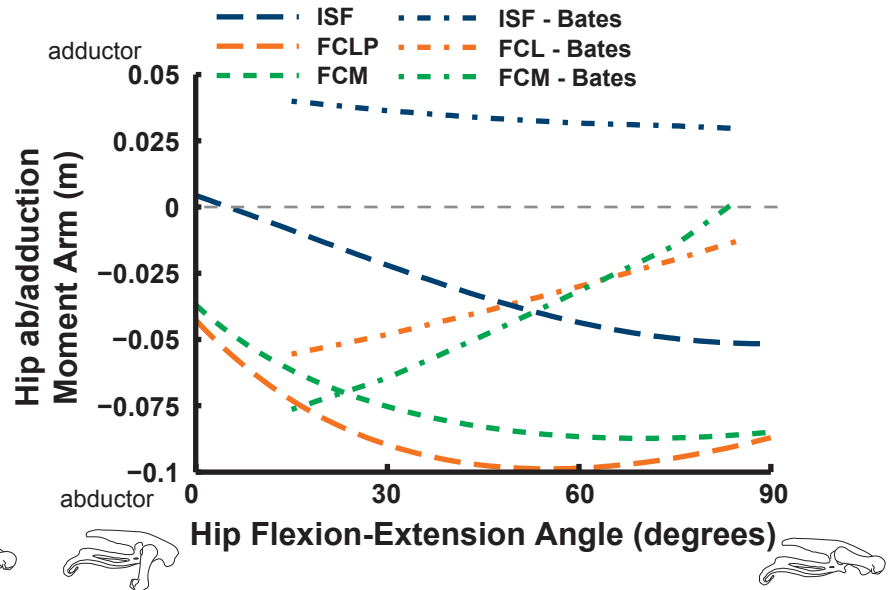
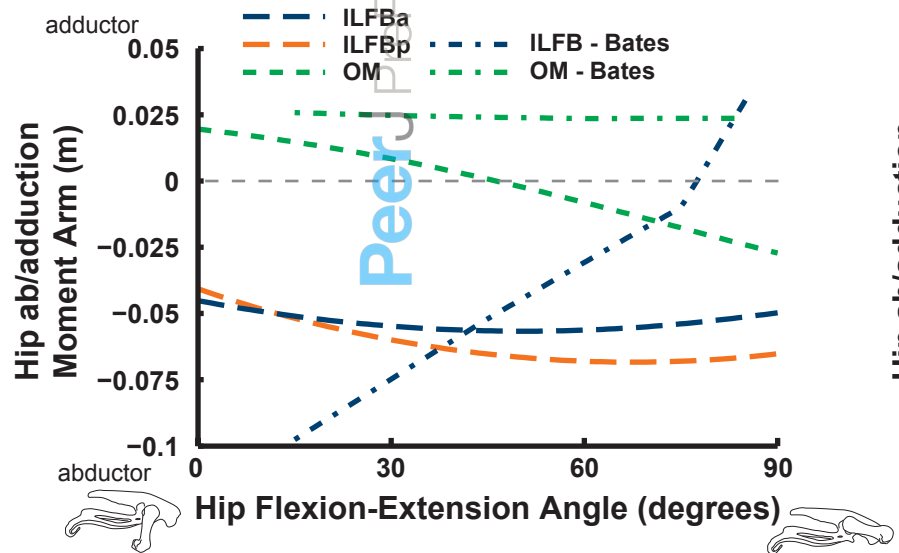
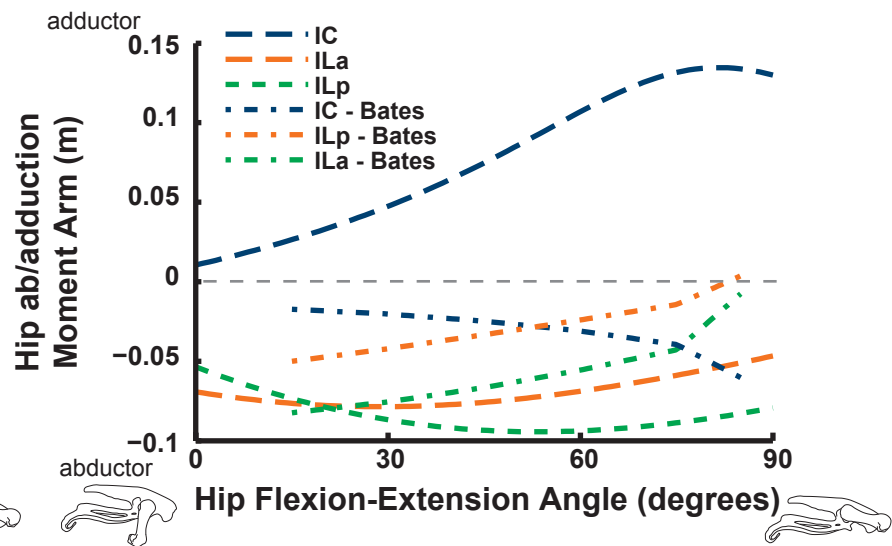
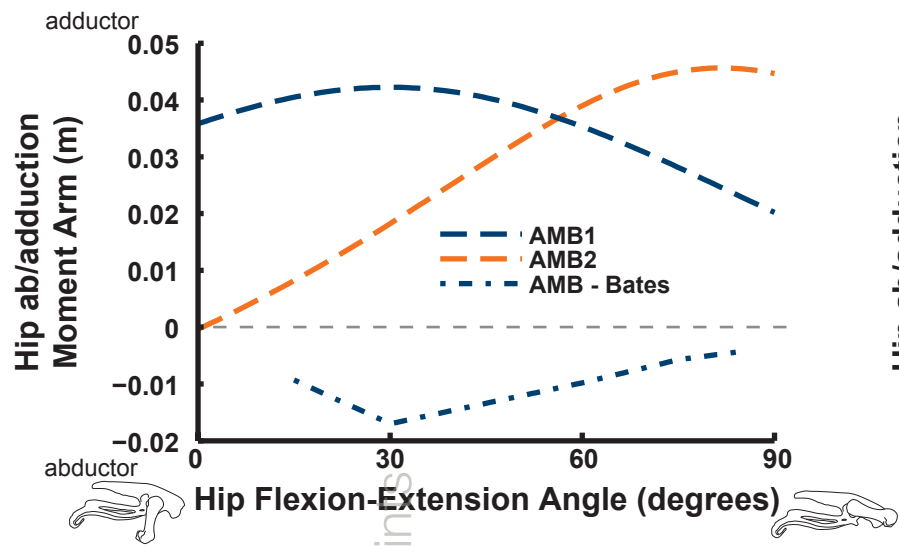


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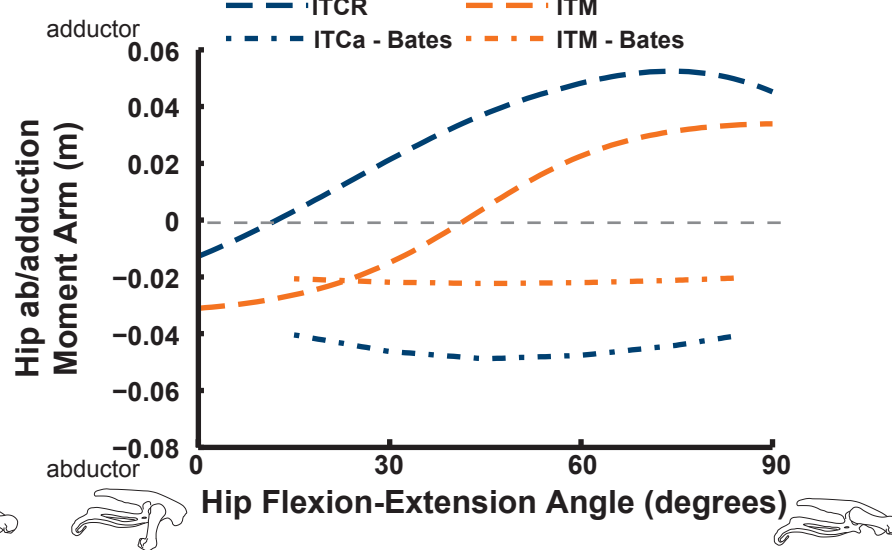
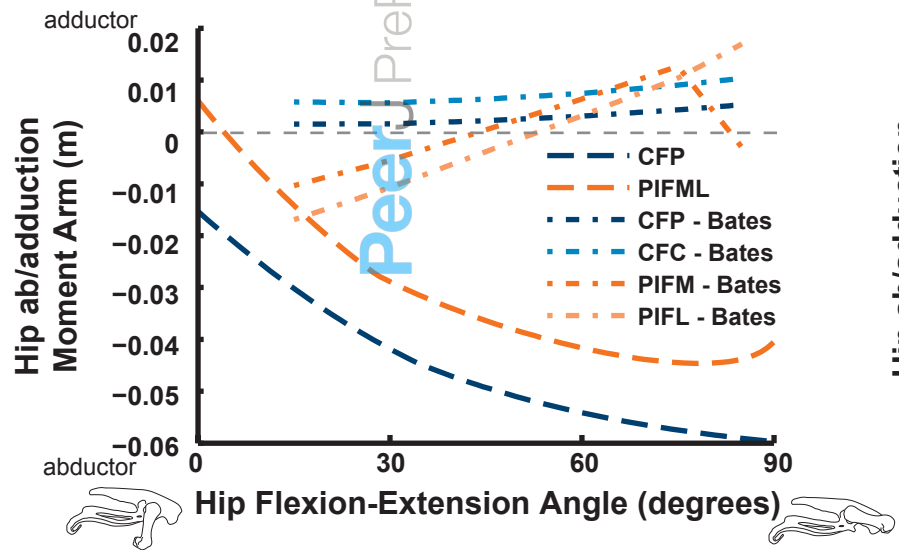
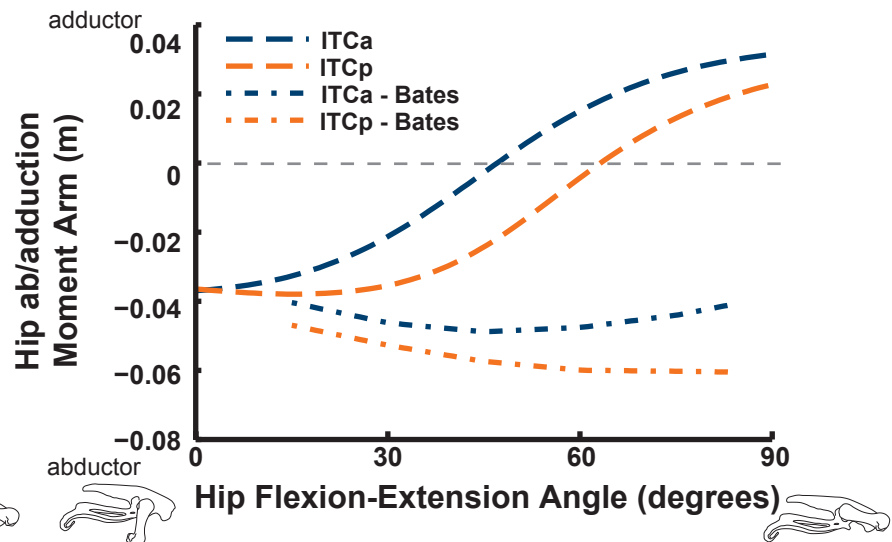
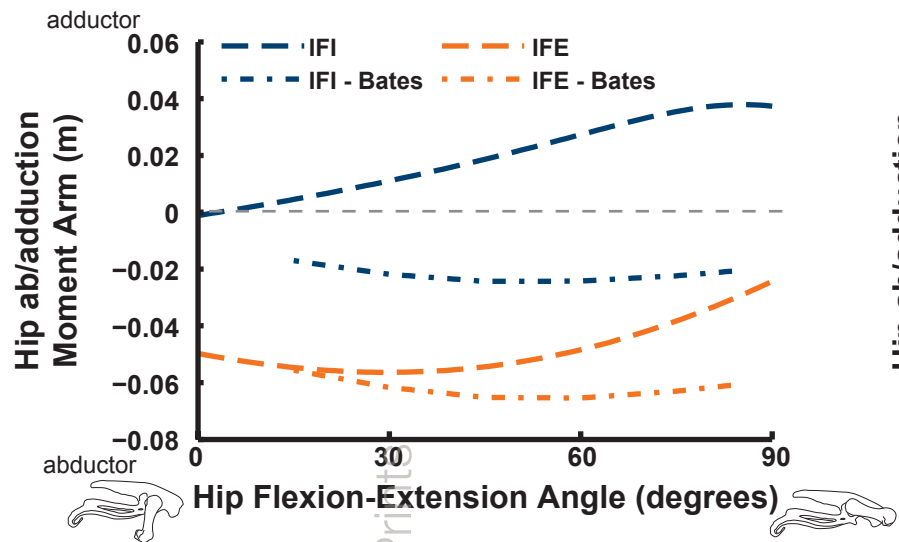


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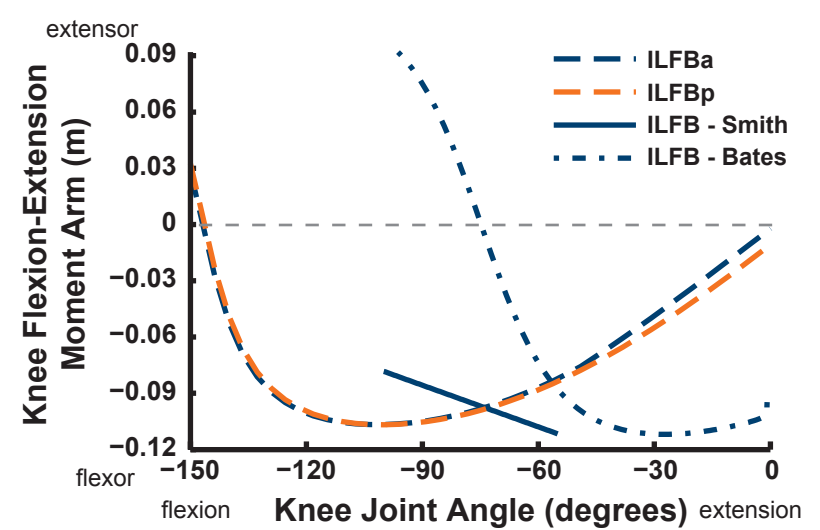
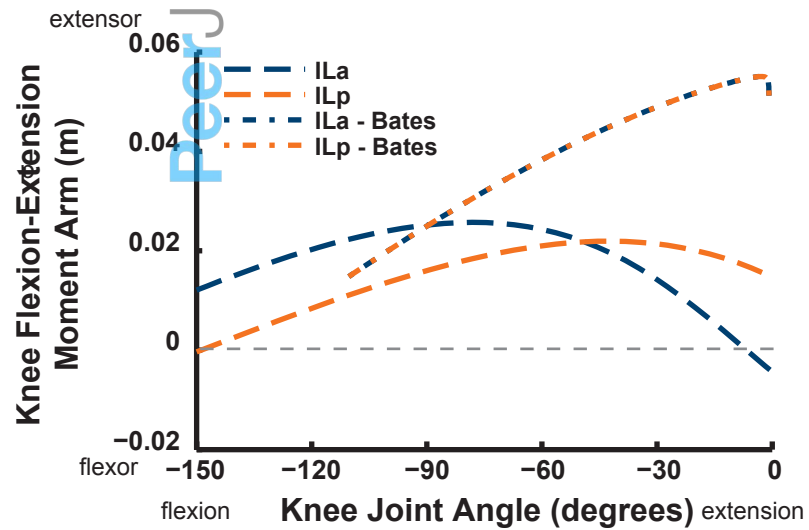
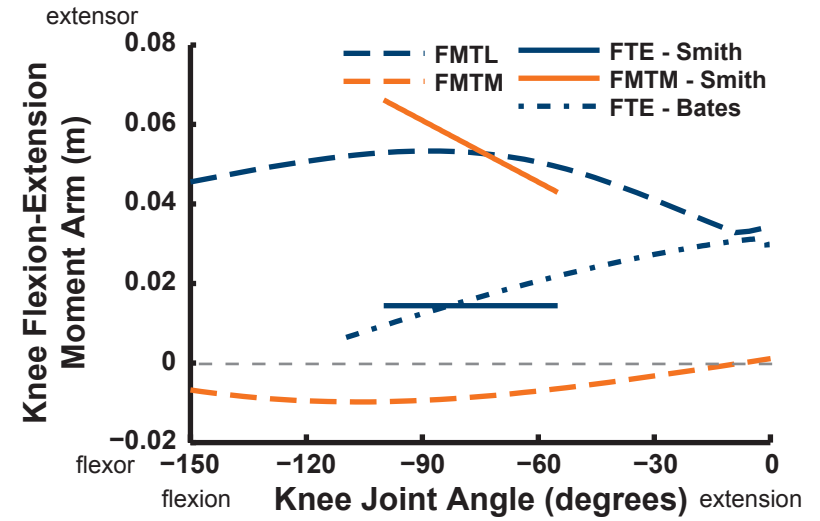
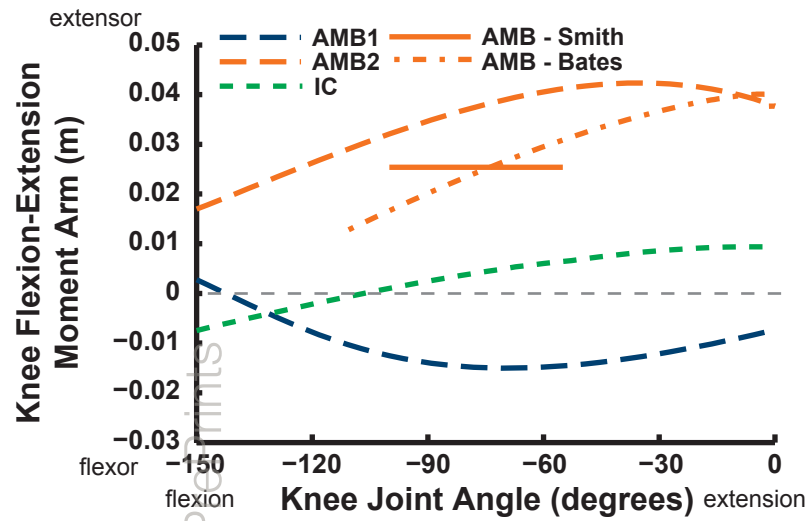


Figure 16

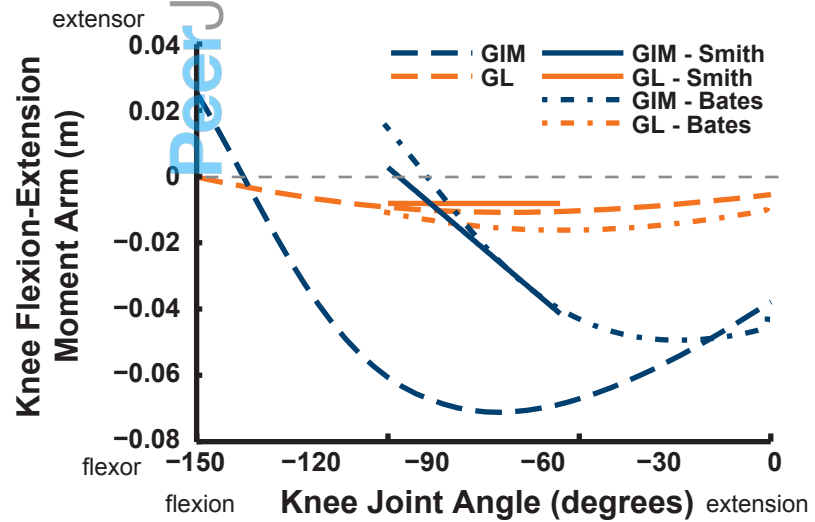
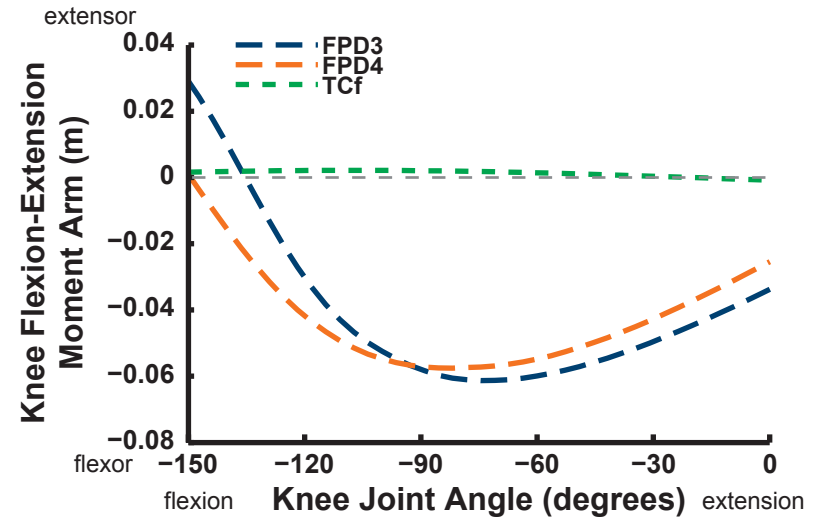
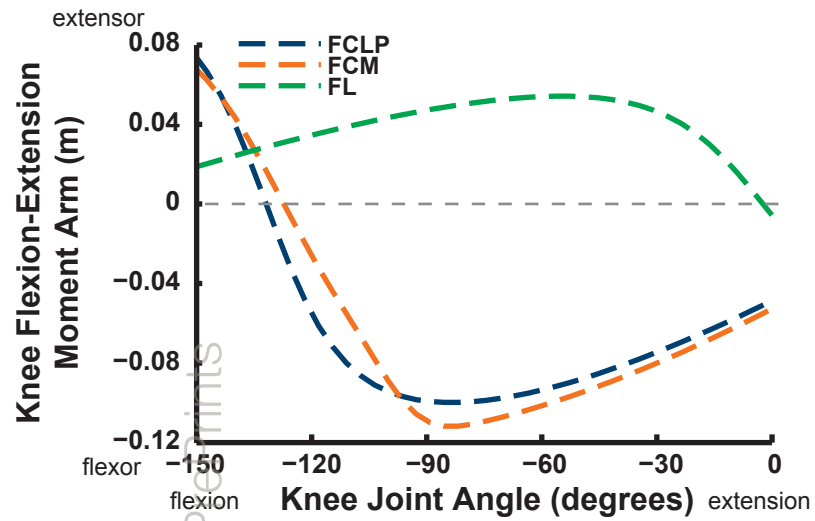


Figure 17

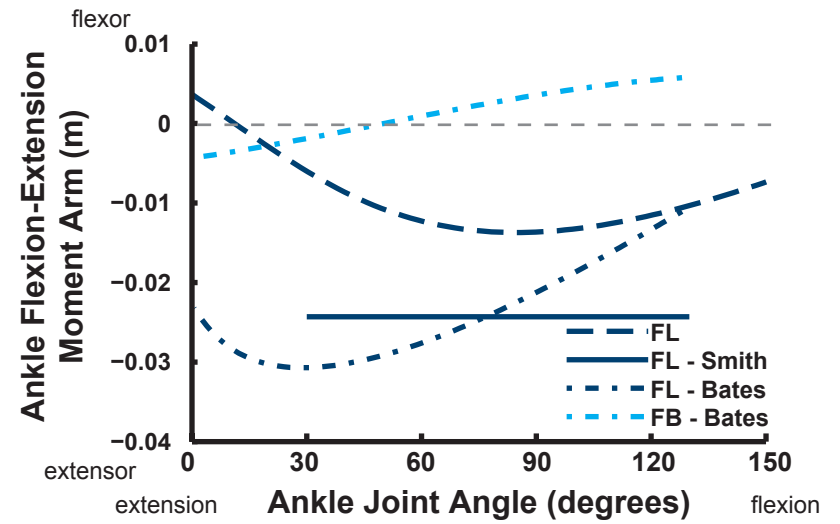
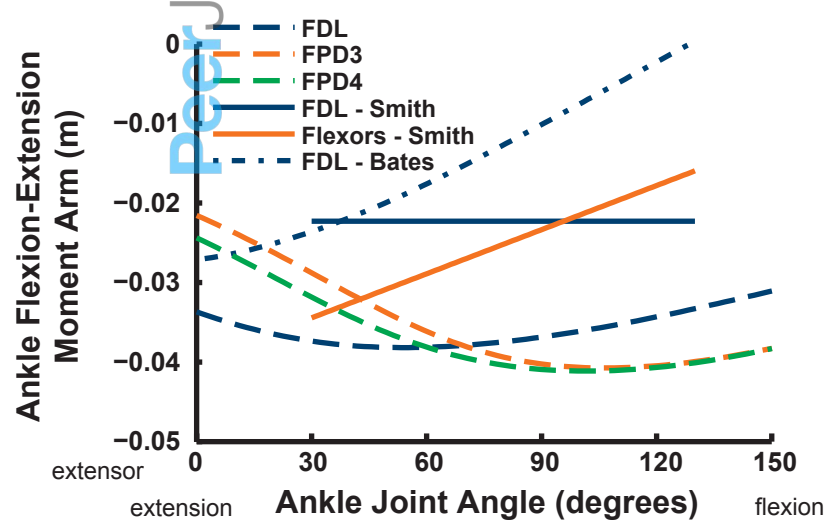
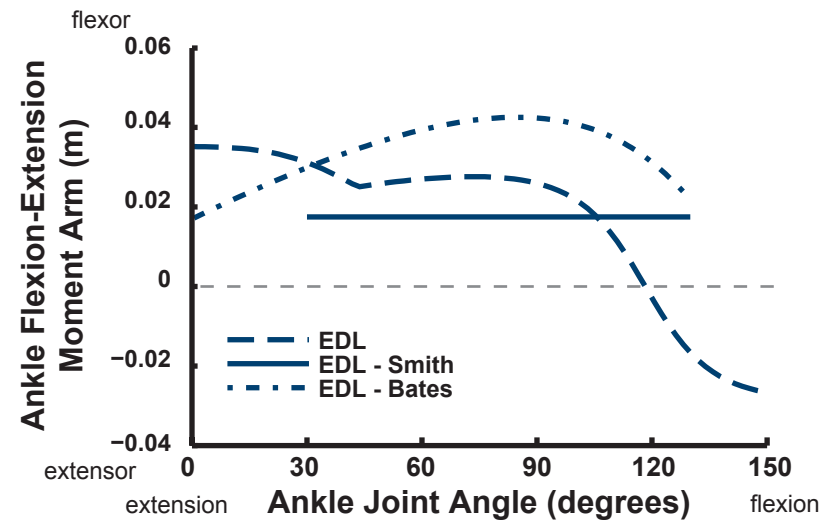
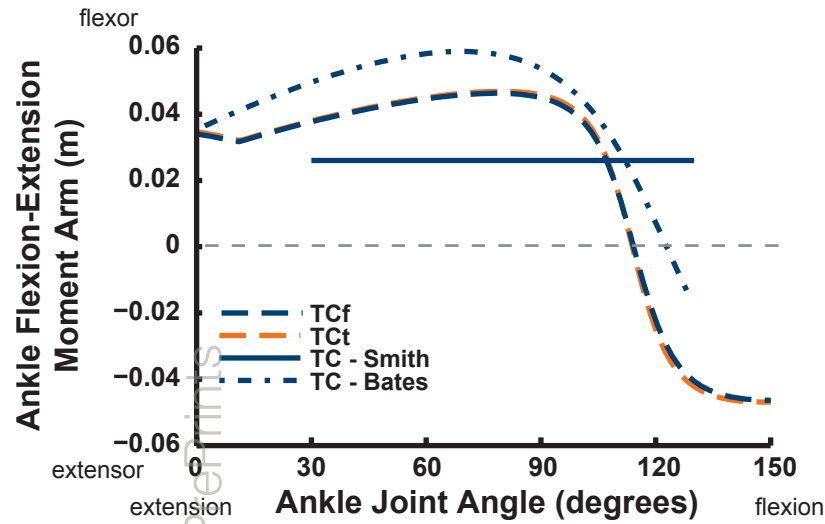


Figure 18



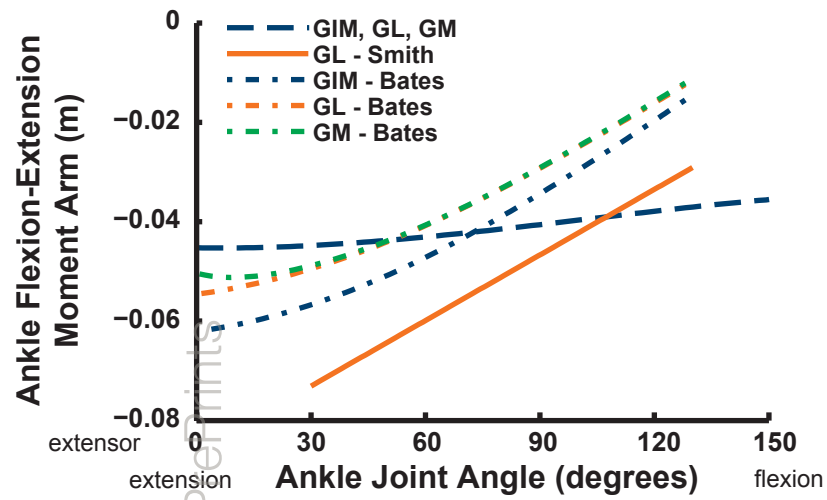


Figure 19

PeerJ PrePrints

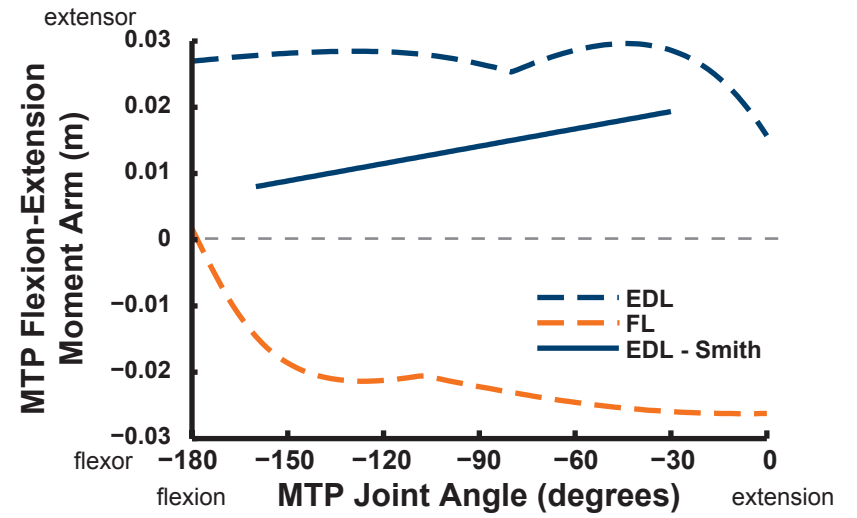
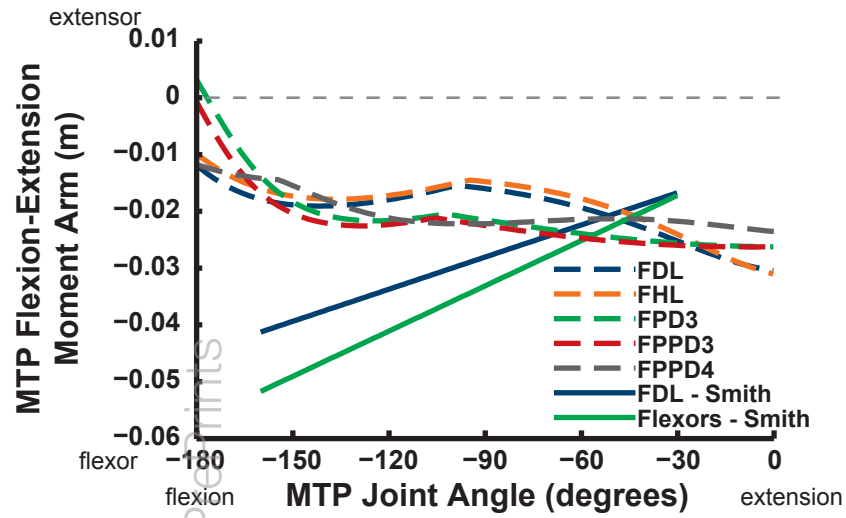


Figure 20

PeerJ PrePrints

## **Table 1** (on next page)

Tables (all)

All tables with captions

## Tables

Joint or segment	centre x (m)	centre y (m)	centre z (m)	Motion axes	Ranges of motion (°)
Pelvis	0	0	0	x,y,z	[-180/180; -180/180; -180/180]
Hip (acetabular/antitrochanteric)	0	0	0.0355	x,y,z	[-45/45; -45/45; -65/10]
Knee (femorotibial)	0	-0.2338	0.0543	x,y,z	[-45/45; -45/45; -180/10]
Ankle (intertarsal)	0	-0.442	0	x,z	[-45/45; -10; -10/180]
Metatarsophalangeal (MTP III)	0	-0.426	0	z	[5; 24; -180/90]
[Proximal interphalangeal (D III)]	[0	-0.089	0]	[z]	[not estimated]

Table 1. Joint axes for the ostrich musculoskeletal model. Each joint centre is listed in (x,y,z)-coordinate space as a distance from the segment origin. The pes was 0.141m long and an interphalangeal joint's location is noted here in the final row, but was not included in the model. Each joint was defined relative to the one proximal to it, with the pelvis segment placed at the origin of the world coordinate system.

Muscle abbreviation	Muscle full name	Muscle mass; $m_{\text{musc}}$ (kg)	Fascicle length; L (m)	Pennation angle; $\theta$ (°)	Maximal isometric force; $F_{\text{max}}$ (N)
IC	M. iliotibialis cranialis	0.3788	0.174	0	615
ILa	M. iliotibialis lateralis (cranial part)	1.074	0.174	0	875
ILp	M. iliotibialis lateralis (caudal part)		0.174	0	875
AMB1	M. ambiens, ventral (pubic) head	0.093	0.039	10	672
AMB2	M. ambiens, dorsal (iliac) head	0.1994	0.044	15	1240
FMTL	M. femorotibialis lateralis	0.3181	0.088	15	992
FMTIM	M. femorotibialis intermedius	0.387	0.084	25	1180
FMTM	M. femorotibialis medialis	0.272	0.089	30	753
ILFBa	M. iliofibularis (cranial part)	1.0623	0.176	0	867
ILFBp	M. iliofibularis (caudal part)		0.176	0	867
ITCa	M. iliotrochantericus caudalis (cranial part)	0.3114	0.064	25	622
ITCp	M. iliotrochantericus caudalis (caudal part)		0.064	25	622
IFE	M. iliofemoralis externus	0.03264	0.025	25	331
ITM	M. iliotrochantericus medius	0.0256	0.058	0	125
ITCR	M. iliotrochantericus cranialis	0.0432	0.053	10	228
IFI	M. iliofemoralis internus	0.0407	0.041	0	284
FCM	M. flexor cruris medialis	0.1192	0.036	35	767
FCLP	M. flexor cruris lateralis pars pelvica	0.3182	0.24	0	376
FCLA	M. flexor cruris lateralis pars accessoria	0.0211	0.125	0	47.8
ISF	M. ischiofemoralis	0.0348	0.033	15	290
PIFML	Mm. puboischiofemorales medialis + lateralis	0.1273	0.089	15	389
OM	M. obturatorius medialis	0.457	0.055	25	2160
CFP	M. caudofemoralis pars pelvica (et caudalis)	0.3069	0.108	15	778
GL	M. gastrocnemius pars lateralis	0.5706	0.12	20	1269
GIM	M. gastrocnemius pars intermedia	0.2526	0.125	15	552
GM	M. gastrocnemius pars medialis	0.762	0.094	20	2160
FL	M. fibularis longus	0.4791	0.081	20	1570
FDL	M. flexor digitorum longus	0.1424	0.048	20	782
FPPD3	M. flexor perforans et perforatus digitorum 3	0.0822	0.025	30	798
FPD3	M. flexor perforans digitorum 3	0.1605	0.017	35	2220
FPD4	M. flexor perforans digitorum 4	0.0955	0.026	20	992
FHL	M. flexor hallucis longus	0.0505	0.04	25	324
EDL	M. extensor digitorum longus	0.115	0.049	30	576
TCf	M. tibialis cranialis (femoral head)	0.165	0.045	25	474
TCt	M. tibialis cranialis (tibial head)		0.045	25	474

Table 2. Muscles included in the ostrich musculoskeletal model, with their associated abbreviations and physiological/architectural parameters. Data were obtained via dissection. Blank cells for muscle masses (ILp, ILFBp, ITCp, TCt) indicate that the second part of the muscle shares the mass value, which was divided equally to calculate  $A_{\text{phys}}$  and hence  $F_{\text{max}}$ .

Muscle(s)	Location	Shape	r (x)	r (y)	r (z)	t (x)	t (y)	t (z)	Radius	Length
ILFB	pelvis	cylinder	17.11	57.87	-34.76	0.0309	-0.0609	0.0622	0.095	1.000
PIFML	pelvis	cylinder	0.92	-5.72	-29.06	0.0020	0.0820	0.1000	0.170	0.500
CFP	pelvis	cylinder	-8.51	0.41	35.68	-0.0211	0.0722	0.1396	0.090	0.500
ITC,ITM	femur	cylinder	-16.00	19.60	0.00	0.0086	-0.0017	-0.0067	0.020	0.500
ITCR	femur	cylinder	-16.00	-2.17	-0.19	0.0395	-0.0379	-0.0034	0.020	0.500
ITCR	femur	cylinder	74.00	0.00	-19.60	0.0086	-0.0882	0.0181	0.055	0.500
GL,GIM,FHL,FPD3	femur	cylinder	37.16	40.49	-20.39	-0.0197	-0.2006	0.0799	0.015	0.200
ILFBp	femur	torus	51.43	-21.08	-22.24	-0.0202	-0.1827	0.0609	0.01*	0.08*
FMTIM,FMTL	tibiotarsus	cylinder	0.00	0.00	44.69	-0.0014	0.0103	0.0093	0.038	0.500
GL,GIM,GM	tibiotarsus	cylinder	0.00	0.00	0.00	-0.0058	-0.4435	-0.0090	0.040	0.150
FP&PD3,FPD3,FPD4	tibiotarsus	cylinder	6.47	-7.64	40.43	0.0031	-0.4537	0.0090	0.030	0.200
FDL,FHL	tibiotarsus	cylinder	0.00	0.00	40.00	-0.0014	-0.4501	0.0001	0.030	0.500
AMB2	tibiotarsus	cylinder	0.00	0.00	0.00	0.0250	0.0126	-0.0012	0.038	0.100
IC	tibiotarsus	cylinder	0.00	5.00	0.00	-0.0143	0.0098	-0.0054	0.030	0.500
EDL,TCf,TCt	tibiotarsus	cylinder	3.37	-15.47	0.32	0.0111	-0.4530	0.0009	0.020	0.100
FP&PD3,FPD3,FL	tarsometatarsus	cylinder	0.64	-6.17	-1.51	-0.0020	-0.4296	0.0002	0.023	0.100
FDL,FHL	tarsometatarsus	cylinder	-3.48	-13.61	-0.29	0.0025	-0.4319	-0.0024	0.022	0.100
FPD4	tarsometatarsus	cylinder	0.00	-35.00	0.00	0.0002	-0.4326	0.0025	0.017	0.100
EDL	tarsometatarsus	cylinder	-1.19	-2.69	0.68	0.0029	-0.4312	-0.0152	0.023	0.100

<u>Muscle</u>	<u>Location</u>	<u>Shape</u>	<u>r (x)</u>	<u>r (y)</u>	<u>r (z)</u>	<u>t (x)</u>	<u>t (y)</u>	<u>t (z)</u>	<u>Radius (x)</u>	<u>Radius (y)</u>	<u>Radius (z)</u>
IL	pelvis	ellipsoid	-2.79	-1.44	-100.93	-0.0020	-0.0020	0.0649	0.100	0.200	0.050
IFE	pelvis	ellipsoid	0.00	0.00	0.00	-0.0010	0.0110	0.0302	0.090	0.060	0.060
FCLP	pelvis	ellipsoid	-17.65	8.20	-84.13	-0.2258	-0.0290	0.0532	0.075	0.500	0.050

Table 3. Muscle wrapping surfaces assumed in the ostrich musculoskeletal model, with dimensions. Examples are in Figure 5.

Muscle	Action					
	Hip F/E	Hip LAR	Hip Ab/Ad	Knee F/E	Ankle F/E	MTP F/E
IC	F+*	M	AD+	F/E		
ILa	F/E	M/L	AB+	E+		
ILp	E+	M/L	AB+	E+		
AMB1	E*	L	AD	F		
AMB2	F*	M/L	AD	E		
FMTL				E+		
FMTIM				E		
FMTM				F		
ILFBa	E	M	AB	F+		
ILFBp	E+	M	AB	F+		
ITCa	F/E*	M+	AB/AD			
ITCp	F/E*	M+	AB/AD			
IFE	F	M/L	AB			
ITM	F/E*	M	AB/AD			
ITCR	F/E*	M+	AB/AD			
IFI	F	M/L	AD			
FCM	E	M	AB	F		
FCLP	E+	M+	AB+	F		
FCLA	E	M	AB			
ISF	F/E*	L	AB			
PIFML	E	L	AB			
OM	F+	L+	AB/AD*			
CFP	E	L	AB			
GL				F	E+	
GIM				F	E	
GM				(F/E)	E+	
FL				E	F*	F
FDL					E+	F+
FPPD3				(F/E)	E+	F+
FPD3				(F/E)	E+	F+
FPD4				(F)	E+	F+
FHL				(F)	E	F
EDL					F+*	E+
TCf				0	F+*	E+
TCt					F+*	E+

Table 4. Muscle actions, following results from Figures 9-20, to describe the major 3D potential functions of each ostrich pelvic limb muscle. Classifications: E=extensor, F=flexor, M=medial (internal) rotator, L=lateral (external) rotator, AB=abductor, D=adductor, 0=no moment arm *per se* despite crossing the joint. Blank cells indicate the muscle does not cross or act about the joint. “+” signs added to classifications indicate a major potential role in these functions based upon moment arm and muscle relative size (i.e., moment generation capacity), subjectively assessed. “/” combinations (F/E; M/L; AB/AD) indicate a strong sensitivity of muscle moment arm, and hence action, to joint angle. Annotation with an asterisk indicates a potential role for intrinsic stabilization about that axis of motion (see Discussion). “( )” indicates that our model’s single origin for each muscle (or part thereof) did

not allow such an action, but sub-parts of those muscles might have such actions if modelled in more detail.