

A peer-reviewed version of this preprint was published in PeerJ on 8 October 2015.

[View the peer-reviewed version](https://doi.org/10.7717/peerj.1272) (peerj.com/articles/1272), which is the preferred citable publication unless you specifically need to cite this preprint.

Bates K, Maidment SCR, Schachner ER, Barrett PM. 2015. Comments and corrections on 3D modeling studies of locomotor muscle moment arms in archosaurs. PeerJ 3:e1272 <https://doi.org/10.7717/peerj.1272>

**Comments and corrections on 3D modeling studies of locomotor muscle moment arms
in archosaurs**

Karl T. Bates^{1*}, Susannah C.R. Maidment², Emma R. Schachner³ & Paul M. Barrett⁴

¹Department of Musculoskeletal Biology, Institute of Aging and Chronic Disease, University of
Liverpool, Duncan Building, Daulby Street, Liverpool L69 3GE, UK;

²Department of Earth Science and Engineering, Imperial College, South Kensington Campus,
London, SW7 2AZ, UK;

³Laboratory for Equine and Comparative Orthopedic Research, Department of Veterinary
Clinical Sciences, School of Veterinary Medicine, Louisiana State University, Baton Rouge, LA
70803;

⁴Department of Earth Sciences, The Natural History Museum, Cromwell Road, London SW7
5BD, UK.

*Correspondence to: k.t.bates@liverpool.ac.uk

Short title: archosaur muscle moment arms

Key words: moment arms, computational modeling, archosaurs, bipedalism, locomotion,
quadrupedalism.

For submission to PeerJ (www.peerj.org)

27 **ABSTRACT**

28 In a number of recent studies we used computer modeling to investigate the evolution of
29 muscle leverage (moment arms) and function in extant and extinct archosaur lineages
30 (crocodilians, dinosaurs including birds and pterosaurs). These studies sought to quantify the
31 level of disparity and convergence in muscle moment arms during the evolution of bipedal
32 and quadrupedal posture in various independent archosaur lineages, and in doing so further
33 our understanding of changes in anatomy, locomotion and ecology during the group's >250
34 million year evolutionary history. Subsequent work by others has led us to re-evaluate our
35 models, which revealed a methodological error that impacted on the results obtained from
36 the abduction-adduction and long-axis rotation moment arms in our published studies. In this
37 paper we present corrected abduction-adduction and long axis rotation moment arms for all
38 our models, and evaluate the impact of this new data on the conclusions of our previous
39 studies. We find that, in general, our newly corrected data differed only slightly from that
40 previously published, with very few qualitative changes in muscle moments (e.g. muscles
41 originally identified as abductors remained abductors). As a result the majority of our
42 previous conclusions regarding the functional evolution of key muscles in these archosaur
43 groups are upheld.

45 **INTRODUCTION**

46 In recent years mathematical-computational approaches have become an increasingly
47 popular tool for studying the functional anatomy and locomotor biomechanics of extinct
48 animals (e.g. reviews in Hutchinson & Allen, 2009; Hutchinson, 2011; Bates, 2013; Maidment
49 et al., 2014). Modeling methods are particularly important because they allow the function of
50 unique morphological structures seen in extinct animals to be investigated directly, without
51 need for reference to analogous living taxa (Bates et al., 2010). This is particularly appealing
52 in the case of animals such as non-avian dinosaurs that lack direct morpho-functional

53 analogues among living animals (Hutchinson & Allen, 2009; Hutchinson, 2011). For this
54 reason, such computational approaches have been applied extensively to non-avian
55 dinosaurs, which possessed body shapes, sizes and skeletal morphologies dissimilar to those
56 of extant terrestrial vertebrates (Hutchinson & Allen, 2009; Maidment et al., 2014). Dinosaurs
57 radiated into a diverse array of body shapes and sizes during their long (>150 million year)
58 evolutionary history, and, for example, underwent several evolutionary transitions between
59 obligate bipedalism and quadrupedalism (e.g. Maidment & Barrett, 2012, 2014). Living birds
60 are the direct descendants of theropod dinosaurs and thus the fossil record of this group
61 provides direct evidence of the morphological and potential functional changes that occurred
62 during the evolution of their terrestrial, aerial and aquatic styles of locomotion (e.g.
63 Hutchinson & Allen, 2009; Allen et al., 2013).

64 In several recent studies (Bates & Schachner, 2012; Bates et al., 2012; Maidment et al.,
65 2014; Maidment, Bates & Barrett, 2014) we used computer modeling to investigate the
66 evolution of muscle leverage (moment arms) and function in various archosaur lineages.
67 Specifically, we sought to quantify the level of disparity and convergence in muscle moment
68 arms among bipedal archosaurs, namely poposaurids (bipedal crurotarsans) and various
69 ornithischians and non-avian theropods, and to draw inferences on how muscle leverage and
70 recruitment during gait may have changed during the evolution of the flexed femoral postures
71 and rotation-based mode of lateral limb support characteristic of extant birds (Bates &
72 Schachner, 2012; Bates et al., 2012). In further work we employed the same modeling
73 approach to examine changes in muscle moment arms during ornithischian evolution, with a
74 particular focus on the evolution of quadrupedality within the group (Maidment et al., 2014;
75 Maidment, Bates & Barrett, 2014). Ornithischian dinosaurs were primitively bipedal with
76 forelimbs modified for grasping, but quadrupedalism evolved in the clade on at least three
77 independent occasions (Maidment & Barrett, 2012). By building and analyzing models of

78 eight exemplar ornithischian taxa we were able to quantify similarities and differences among
79 individual taxa, between quadrupedal and bipedal taxa, and among taxa representing the
80 three major ornithischian lineages (Thyreophora, Ornithopoda, Marginocephalia).

81 Recently, Hutchinson et al. (2014) compared moment arm predictions from our ostrich
82 musculoskeletal model (Bates & Schachner, 2012; Bates et al., 2012) to their own model,
83 which was developed using a more exhaustive experimental protocol. This study found a
84 strong match between the flexion-extension moment arms of the two models, but noted
85 systematic differences between the abduction-adduction and long axis rotation moment arms
86 of some hip muscles (Hutchinson et al., 2014). Re-inspection of our models has revealed that
87 these differences are due to a coding error, one that is present in all of our published models
88 (Bates & Schachner, 2012; Bates et al., 2012; Maidment et al., 2014; Maidment, Bates &
89 Barrett, 2014). The error relates to the specification of joint axes in the models: as the posture
90 of the models were modified to output moment arms across a range of hip joint angles, the
91 axes of the hip joint remained in its initial orientation rather than rotating with the femoral
92 segment and knee joint of the models. Thus the abduction-adduction and long axis rotation
93 data presented in our previous study represents muscle moment arms calculated about
94 anatomically and functionally inappropriate axes. Hutchinson et al. (in press) subsequently
95 compared their data to our corrected abduction-adduction and long axis rotation and found a
96 much stronger agreement between the models.

97 The purpose of this paper is to present corrected abduction-adduction and long axis
98 rotation moment arms for all our models, and to evaluate the impact of this new data on the
99 conclusions of our previous studies (Bates & Schachner, 2012; Bates et al., 2012; Maidment et
100 al., 2014; Maidment, Bates & Barrett, 2014).

101

102

103 MATERIALS AND METHODS

104 Our protocol follows our previous studies exactly, apart from the necessary correction made
105 to the hip joint axes. We recommend Bates et al. (2012) and Maidment et al. (2014) for
106 detailed descriptions of our prior methodology.

108 RESULTS AND DISCUSSION

109 All corrected moment arm data for hip abduction-adduction and long axis rotation are
110 tabulated in the supplementary material. In general our new corrected data differ only
111 slightly from our original data, and there were very few qualitative changes in muscle
112 moments (e.g. muscles originally identified as abductors remained abductors). Rather than
113 describe every quantitative change in moment arm values we focus on the muscles relevant to
114 the hypotheses and conclusions in each of our previous studies. For clarity we address each
115 study individually in the following sections.

117 Bates & Schachner (2012)

118 The majority of the functional and evolutionary conclusions drawn by Bates & Schachner
119 (2012) are upheld because the corrected moment arm magnitudes differ only slightly from
120 our published values, and because the correction tends to affect all taxa equally and,
121 therefore, the relative differences and similarities between the models have been preserved
122 (Figure 1).

123 Bates & Schacher (2012) concluded that muscle moment arm polarities and joint angle
124 relationships in key hip muscle groups (Hutchinson & Gatesy, 2000) are generally
125 conservative despite the shifts in skeletal architecture, posture, body size and locomotor
126 behaviour covered by our sampled taxa. This suggests that muscle origins and insertions
127 remained relatively stable with respect to the hip joint across Archosauria. This conclusion is
128 supported by our corrected data (Figure 1). Functional interpretations regarding specific key

129 muscles, notably the iliofemoralis (IF) and puboischiofemoralis externus (PIFE), also retain
130 their support. Specifically, the cranial portion of the IF group has a much larger medial
131 rotation moment arm in the ostrich (Figure 1d), while PIFE1 and 2 extend the hip and rotate
132 the femur laterally in the ostrich, but are hip flexors and medial rotators in all other taxa
133 (Figure 1e). Our summary observations that abduction-adduction and long-axis rotation
134 moment arms are consistently low in *Poposaurus*, whereas adduction moment arms are
135 generally low in the ostrich but high in *Alligator* (Figures 1-2) are still supported. However,
136 two changes are notable, although neither impacts the main conclusions of our previous
137 study. Previously, the caudofemoralis brevis (CFB) muscle was considered a femoral abductor
138 in *Poposaurus*, but an adductor in all other taxa (Figure 3b in Bates & Schachner, 2012). Our
139 corrected data shows that while CFB remains an obligatory abductor in *Poposaurus*, its
140 function changes with joint angle in all other models, such that this muscle exerts an abductor
141 moment at flexed postures and an adductor moment at extended postures (Figure 1b). The
142 other notable change is the overall reduction in medial long axis rotation moment arms in the
143 *Alligator* model, which have dropped below the magnitudes predicted for *Poposaurus* (Figure
144 2).

146 **Bates et al. (2012)**

147 In this study we first presented detailed analyses of muscle moment arms in the basal, bipedal
148 ornithischian dinosaur *Lesothosaurus*, and subsequently compared these data to a range of
149 other dinosaurs (models from Bates & Schachner, [2012]). We follow the same protocol here,
150 first highlighting changes to our *Lesothosaurus* model, and then discussing changes to our
151 comparative analysis.

152 Corrections to our original analyses indicate that several muscles in *Lesothosaurus*
153 incur minor changes in abduction-adduction moment arms. The caudofemoralis longus (CFL)
154 and ischiochantericus muscles (ISTR) and PIFE group were previously found to maintain

155 adduction moment arms across the range of postures tested (Figures 4&5 in Bates et al.
156 [2012]). Our corrected data suggest that these muscles exerted an adduction moment at
157 extended postures, but switched to an abduction moment at flexed postures (Figure 3-4; but
158 see Bates et al. [2012] for discussion of uncertainty in predictions for PIFE and ISTR muscles).
159 Previously, the puboischiofemoralis internus 2 (PIFI2) muscle was found to be an abductor
160 (Figure 5 in Bates et al., [2012]), but now it switches from an abduction moment at extended
161 postures to exert a very weak adduction moment at flexed femoral postures (Figure 4). The
162 angular dependency of cranial portion of the IF group is also reversed in our corrected data:
163 the muscle is now predicted to be a weak adductor at flexed postures and a weak abductor at
164 extended postures (Figure 3).

165 Modest changes to femoral long axis rotation moment arms in the *Lesothosaurus* model
166 were also found. The long axis rotation moment arms of the adductor femoris (ADD1 and
167 ADD2) muscles now show only very modest postural dependency (Figure 4), as does the
168 PIFI1 muscle (Figure 3) and cranial portion of the iliotibialis group (ITBa, or IT1 in other
169 studies), which are now found to be medial rotators at all hip joint angles tested (Figure 4).
170 Three muscles incurred reversals in the angular or postural dependency of their long axis
171 rotation moment arms. The femorotibialis externus (FTE) and caudal portion of iliotibialis
172 group (ITBp) muscles are now found to be weak medial rotators at flexed postures and weak
173 lateral rotators at extended postures (Figures 3-4). The caudal portion of the IF group is now
174 found to be a weak lateral rotator at flexed postures, with an increasingly larger lateral
175 rotation moment arm as the hip is extended (Figure 4).

176 In our comparative analysis we made a number of statements regarding comparative
177 trends in our moment arm data. We stated that summed adductor moment arms decreased
178 slightly with hip flexion (Figure 6c in Bates et al., [2012]) in all non-avian dinosaurs, while
179 summed abductor moment arms increased slightly with hip extension (based on Figure 6d in
180 Bates et al., [2012]). Adduction moment arms remained relatively unaffected by our corrected

181 joint axes, although abduction moment arms now tend to decrease with increasing hip
182 extension (Figure 5). Our conclusion that *Lesothosaurus* and the ostrich had low summed
183 moment arms for adduction, while those of *Struthiomimus* and *Allosaurus* were higher (Figure
184 6c in Bates et al., [2012]) remains valid, as does our inference that *Lesothosaurus* had the
185 lowest summed abductor moment arms, with non-avian theropods exhibiting intermediate
186 summed abductor moment arms, and the ostrich showing the highest values (Figure 6c-d in
187 Bates et al. [2012]; Figure 5). We previously stated that summed moment arms for both
188 adduction and abduction decreased slightly with hip flexion in the ostrich model (based on
189 Figure 6b in Bates et al. [2012]). This statement represents a typographic error, as our
190 previous analyses (and with our corrected data; Figure 5) showed that adduction moment
191 arms increased with increasing hip flexion. In our corrected data abduction moment arms
192 also increase with increasing hip flexion (Figure 5).

193 We previously concluded that summed long axis rotator moment arms displayed a
194 taxonomic signal with hip flexion and extension (Figure 6e-f in Bates et al., [2012]).
195 *Lesothosaurus* had an extremely weak summed medial rotator moment arm (Figure 6f in
196 Bates et al., [2012]) compared with those of theropods, while its summed moment arm for
197 lateral rotation (Figure 6e in Bates et al., [2012]) was similar to that of non-avian theropods in
198 magnitude. The ostrich had significantly higher summed medial and lateral rotator moment
199 arms than any other dinosaur modeled (Figure 6e-f in Bates et al., [2012]). All of these
200 conclusions are still supported by our corrected data (Figure 5).

201 There are few changes of note in our comparative analysis of individual muscles. As in
202 Bates & Schachner (2012), our inferences regarding CFB require adjustment. We previously
203 concluded that CFB has an adduction moment arm in the theropods examined, while it has an
204 abduction moment in *Lesothosaurus* (Figure 7b in Bates et al., [2012]), but this distinction is
205 no longer supported in our corrected data. We also previously stated that PIFE has a lateral

206 rotator moment in the ostrich and *Lesothosaurus*, while it has a medial rotator moment arm in
207 the non-avian theropods (Figure 9c-f in Bates et al. [2012]). This statement largely holds
208 following analysis of the corrected data (Figures 1,3), although the non-avian theropod
209 models do have weak lateral rotation moment arms at postures >45 degrees hip flexion.
210 However, the conclusion that *Lesothosaurus* and the ostrich have similar moment arms for
211 this muscle, and that both of these are different from those of non-avian theropods, is still
212 supported (Figures 1,4).

213 214 **Moment arms and muscle function evolution in ornithischian dinosaurs**

215 Maidment, Bates & Barrett (2014) presented a preliminary analysis of muscle moment arm
216 evolution in ornithischian dinosaurs, which was subsequently expanded upon in Maidment et
217 al. (2014) by the addition of five further models. We therefore discuss the implications of our
218 corrected data for both studies synchronously.

219 The majority of our original conclusions regarding muscle moment arm and functional
220 evolution within Ornithischia are still supported by analysis of our corrected data.
221 *Chasmosaurus* and *Hypsilophodon* are still distinguished by low moment arms for many
222 muscles and functions (e.g. Fig. 6). Quadrupedal taxa (*Kentrosaurus*, *Dyoplosaurus*,
223 *Chasmosaurus*) are also found to maintain higher abductor (Fig. 7A) but lower adductor (Fig.
224 7B) moment arms than bipedal taxa (*Lesothosaurus*, *Hypsilophodon*, *Stegoceras*), as found
225 previously. In our original data, differences between long axis rotation moment arms in
226 quadrupeds and bipeds were not clear. There was little difference when summed medial
227 rotation moment arms were examined, and this observation remains the case (Fig. 8A). A
228 much greater difference between quadrupeds and bipeds is observed, however, when lateral
229 rotation moment arms are examined (Fig. 8B). In our original data, there was some suggestion
230 that lateral rotator moment arms were greater among quadrupedals, and this is more

231 strongly supported by our corrected data. Our corrected data also supports our original
232 assertion that bipeds appear to have higher mean medial rotation moment arms than
233 quadrupeds (Fig. 9). The one other change of note occurs in the long axis rotation moment
234 arm of the flexor tibialis internus 3 (FTI3) muscle. We previously concluded that FTI3 was a
235 lateral rotator at high flexion angles but became a medial rotator at high extension angles in
236 quadrupeds and the reverse in bipeds (Maidment et al., 2014). In our corrected data (Fig. 10)
237 there is no difference in the action of FTI3 between quadrupeds and bipeds, and it is a lateral
238 rotator at all hip angles in all taxa.

239

240 CONCLUSION

241 Our reanalysis of corrected data from four previously published studies on archosaur
242 locomotion shows few substantive differences from our previously published results,
243 although several reinterpretations of specific muscle functions have resulted. Nevertheless,
244 these minor amendments do not undermine our earlier conclusions regarding the function
245 and evolution of these locomotor systems and in some cases provide additional support for
246 our previous interpretations. Our corrected data is available in the supplementary material
247 for use in future studies on these interesting taxa.

248

249 ACKNOWLEDGEMENTS

250 We thank John Hutchinson for discussions, and our previous co-authors (Viv Allen, Peter
251 Falkingham, Collin VanBuren and Victoria Arbour) for their contributions to earlier studies.

252

253 REFERENCES

254 **Allen V, Bates KT, Li ZH, Hutchinson JR. 2013.** The evolution of body shape and locomotion
255 in bird-line archosaurs. *Nature* **497**:104-107.

256 **Bates KT. 2013.** Dinosaur Locomotion. *Encyclopedia of Life Sciences*. Macmillan, London.

257 **Bates, KT, Manning PL, Margetts L, Sellers WI. 2010.** Sensitivity analysis in evolutionary
 258 robotic simulations of bipedal dinosaur running. *Journal of Vertebrate Paleontology* **30**:458-
 259 466.

260 **Bates KT, Schachner ER. 2012.** Disparity and convergence in bipedal archosaur locomotion.
 261 *Journal of the Royal Society Interface* **70**:1339-1353.

262 **Bates KT, Maidment SCR, Allen V, Barrett PM. 2012.** Computational modelling of
 263 locomotor muscle moment arms in the basal dinosaur *Lesothosaurus diagnosticus*: assessing
 264 convergence between birds and basal ornithischians. *Journal of Anatomy* **220**:212-232.

265 **Hutchinson JR. 2011.** On the inference of function from structure using biomechanical
 266 modelling and simulation of extinct organisms. *Biology Letters* **8**:115-118.

267 **Hutchinson JR, Gatesy SM. 2000.** Adductors, abductors, and the evolution of archosaur
 268 locomotion. *Paleobiology* **26**:734-751.

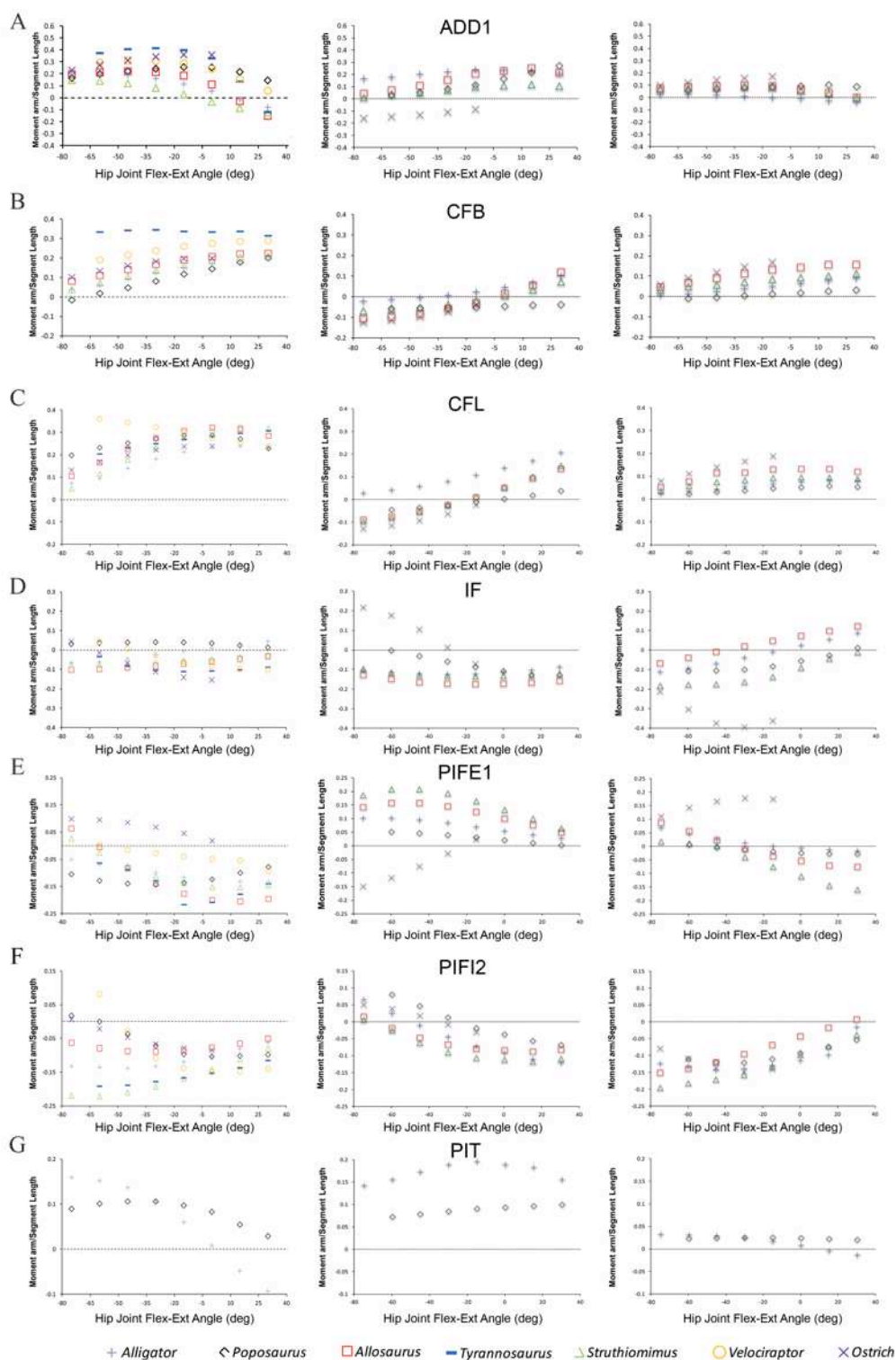
269 **Hutchinson JR, Allen V. 2009.** The evolutionary continuum of limb function from early
 270 theropods to birds. *Naturwissenschaften* **96**:423-448.

271 **Hutchinson, J.R., Anderson, F.C., Blemker, S., Delp, S.L. 2005.** Analysis of hindlimb muscle
 272 moment arms in *Tyrannosaurus rex* using a three-dimensional musculoskeletal computer
 273 model. *Paleobiology* **31**:676-701.

274 **Hutchinson, J.R., Miller, C.E., Fritsch, G., Hildebrandt, T. 2008** The anatomical foundation
 275 for multidisciplinary studies of animal limb function: examples from dinosaur and elephant
 276 limb imaging studies. In: Frey R., Endo, H. (eds.), *Anatomical Imaging: Towards a New*
 277 *Morphology*. Berlin: Springer-Verlag, pp. 23-38.

278 **Hutchinson JR, Rankin JW, Rubenson J, Rosenbluth KH, Siston RA, Delp SL. 2014.**
 279 Musculoskeletal modelling of an ostrich (*Struthio camelus*) pelvic limb: Influence of limb
 280 orientation on muscular capacity during locomotion. *PeerJ PrePrints* 2:e513v1
 281 <http://dx.doi.org/10.7287/peerj.preprints.513v1>.

282 **Hutchinson JR, Rankin JW, Rubenson J, Rosenbluth KH, Siston RA, Delp SL. IN PRESS.**
 283 Musculoskeletal modelling of an ostrich (*Struthio camelus*) pelvic limb: Influence of limb
 284 orientation on muscular capacity during locomotion. *PeerJ*.
 285 **Maidment SCR, Barrett PM. 2012.** Does morphological convergence imply functional
 286 similarity? A test using the evolution of quadrupedalism in ornithischian dinosaurs.
 287 *Proceedings of the Royal Society of London B: Biological Sciences* **279**:3765–3771.
 288 **Maidment SCR, Barrett PM. 2014.** Osteological correlates for quadrupedality in
 289 ornithischian dinosaurs. *Acta Palaeontologica Polonica* **59**:53-70.
 290 **Maidment SCR, Bates KT, Falkingham PL, VanBuren C, Arbour V, Barrett PM. 2014.**
 291 Locomotion in Ornithischian Dinosaurs: An Assessment Using Three-Dimensional
 292 Computational Modelling. *Biological Reviews* **89**:588-617.
 293 **Maidment SCR, Bates KT, Barrett PM. 2014.** Three-dimensional computational modelling of
 294 pelvic locomotor muscle moment arms in *Edmontosaurus* (Dinosauria: Hadrosauridae) and
 295 comparisons with other archosaurs. In: *Hadrosaurs* (ed. DA Eberth, DC Evans). Indiana
 296 University Press: Bloomington, Indiana.
 297
 298
 299



300

301

302

303

304

305

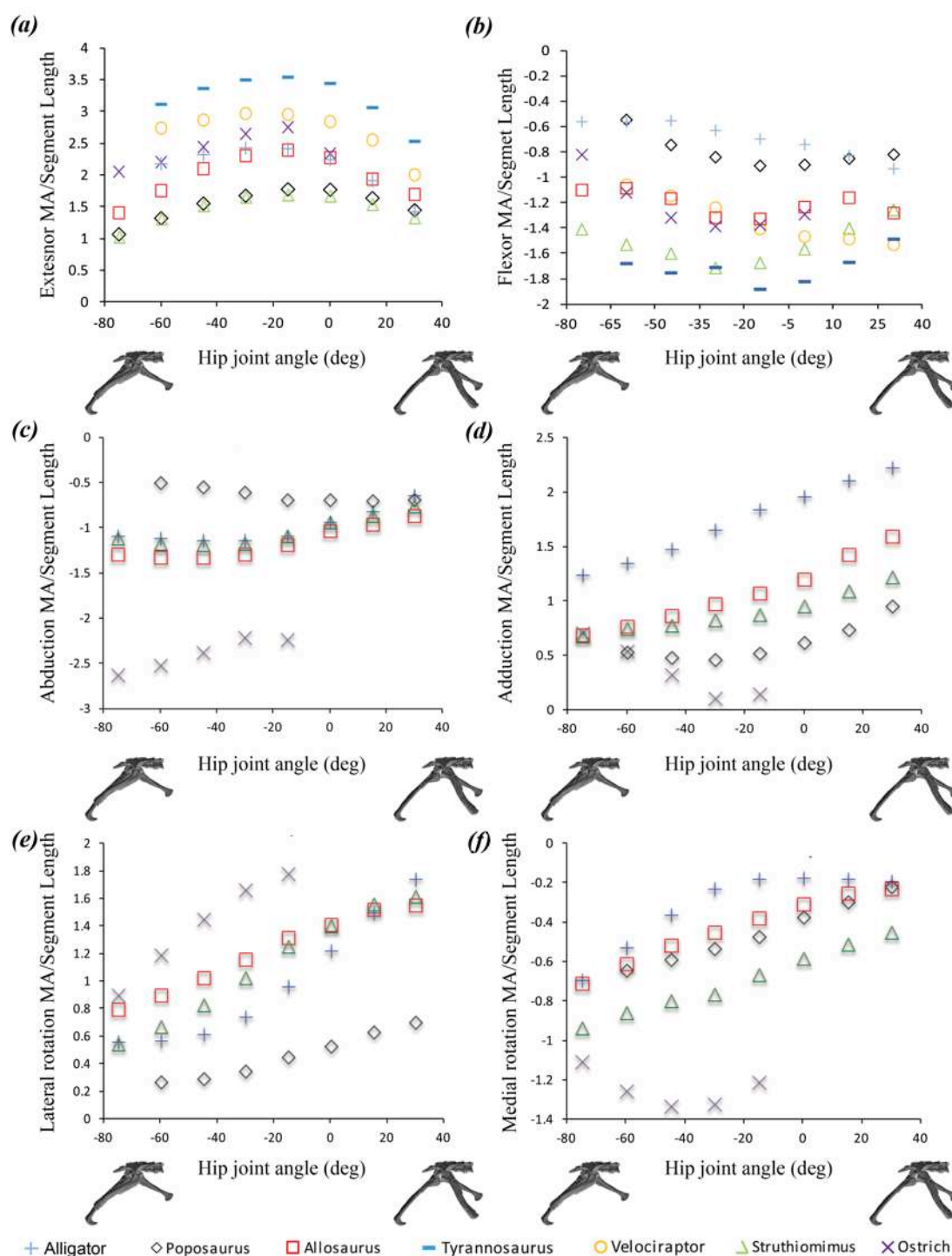
Figure 1. Predicted pelvic muscle moment arms for hip flexion–extension (left), and corrected data for abduction–adduction (centre) and long-axis rotation (right) in key muscle groups (a) ADD1, (b) CFB, (c) CFL, (d) IF, (e) PIFE1, (f) PIFI2 and (g) PIT over a range of hip joint flexion–extension angles. See table 1 for abbreviations. All data normalized by femoral length. Only flexion– extension data are available for *Tyrannosaurus* and *Velociraptor* from

306 previous studies (Hutchinson et al., 2005; Hutchinson et al., 2008), while PIT is present only
307 in *Poposaurus* and *Alligator*, having been lost in ornithodirans.

308

309

310



311

312 **Figure 2.** Sum of (a) hip extensor, (b) hip flexor, (c) hip abduction, (d) adduction, (e) lateral
 313 femoral rotation and (f) medial femoral rotation muscle moment arms normalized by
 314 segment length for *Poposaurus*, *Alligator* and ornithodiran bipeds. All data normalized by
 315 femoral length. Only flexion–extension data are available for *Tyrannosaurus* and *Velociraptor*
 316 from previous studies (Hutchinson et al., 2005; Hutchinson et al., 2008).

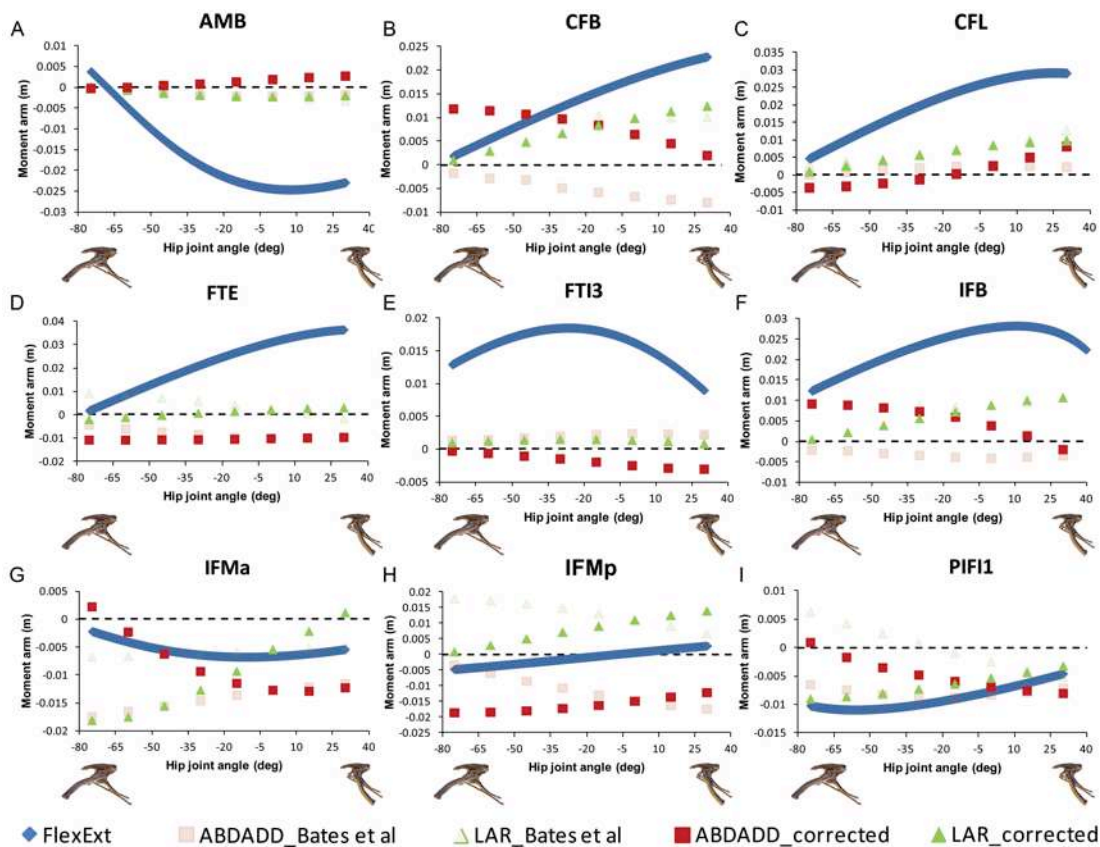


Figure 3. Corrected hip muscle moment arm predictions for (a) AMB, (b) CFB, (c) CFL, (d) FTE, (e) FTI3, (f) IFB, (g) IFMa, (h) IFMp and (i) PIFI1 for a range of hip flexion/extension angles in *Lesothosaurus*. A positive hip joint angle (x-axis) indicates hip extension (femoral retraction), while a negative hip joint angle indicates hip flexion (femoral protraction), as shown by the small images of the pelvis of *Lesothosaurus* in the left lateral view along the x-axis of each graph. A negative moment arm (y-axis) for flexion/extension is a moment arm for flexion; a negative moment arm for abduction/adduction is a moment arm for abduction; a negative moment arm for long axis rotation is a moment arm for medial rotation. FlexExt, flexion/extension; ABDADD, abduction/adduction; LAR, long axis rotation.

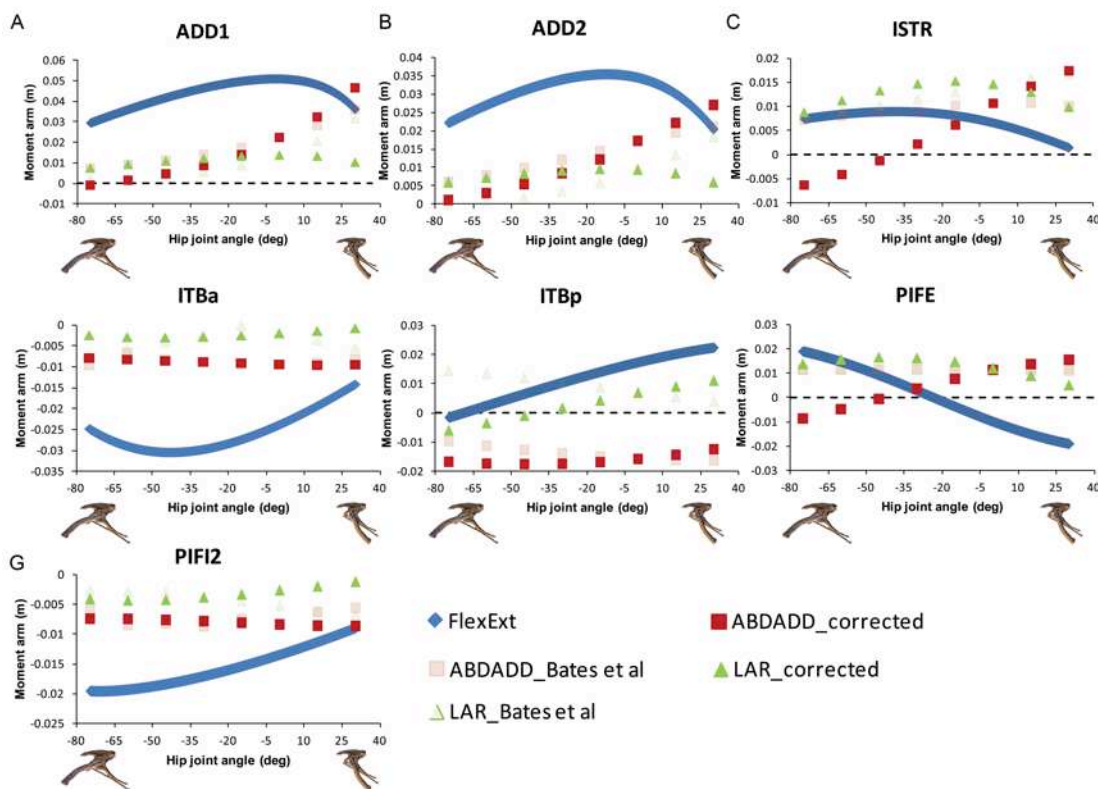
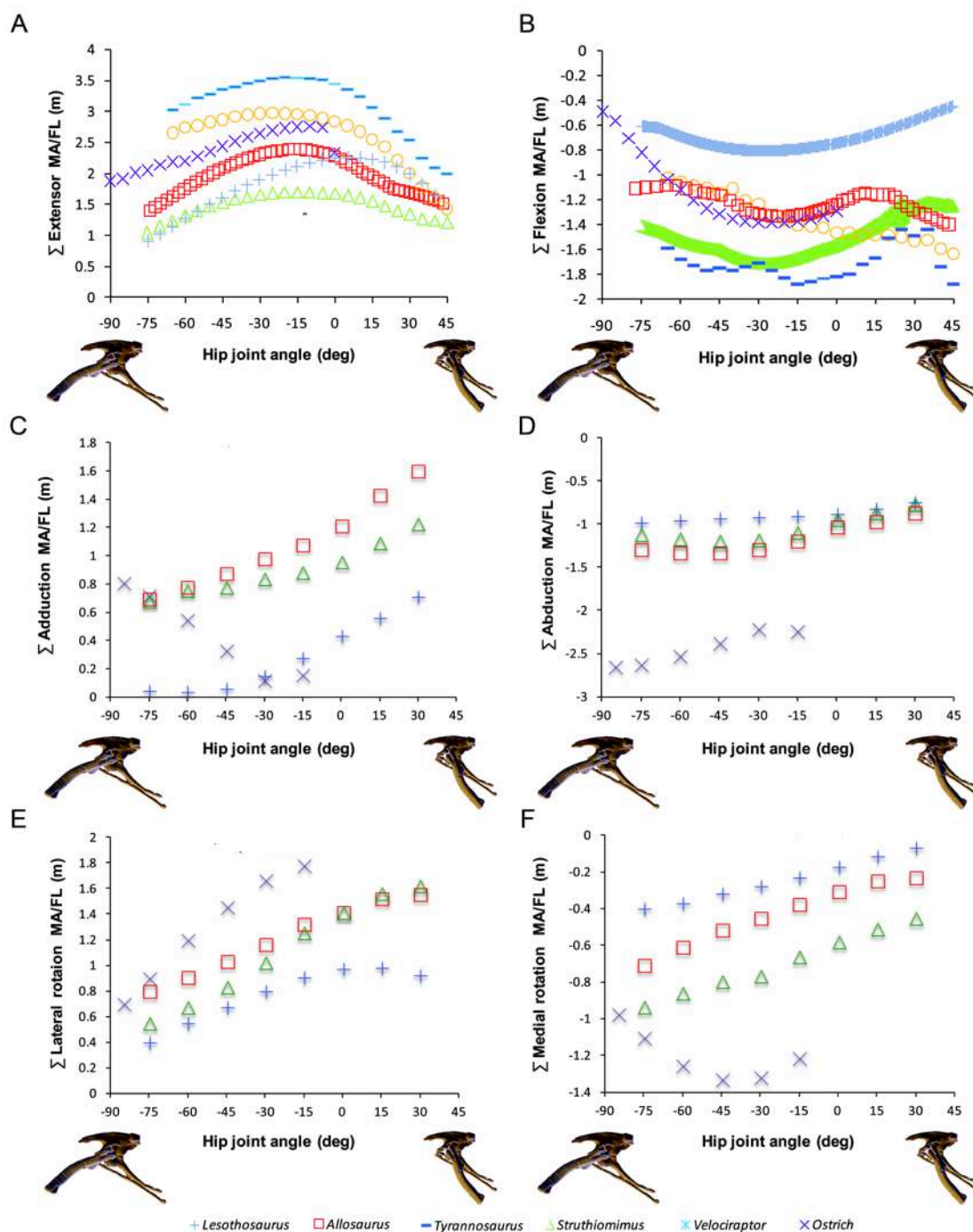


Figure 4. Corrected hip muscle moment arm predictions for (a) ADD1, (b) ADD2, (c) ISTR, (d) ITBa, (e) ITBp, (f) PIFE, (g) PIFI2, the muscles for which the sensitivity analysis was performed, for a range of hip flexion/extension angles in *Lesothosaurus*. A positive hip joint angle (x-axis) indicates hip extension (femoral retraction), while a negative hip joint angle indicates hip flexion (femoral protraction), as shown by the small images of the pelvis of *Lesothosaurus* in the left lateral view along the x-axis of each graph. A negative moment arm (y-axis) for flexion/extension is a moment arm for flexion; a negative moment arm for abduction/adduction is a moment arm for abduction; a negative moment arm for long axis rotation is a moment arm for medial rotation. FlexExt, flexion/extension; ABDADD, abduction/adduction; LAR, long axis rotation.



343

344

345

346

347

Figure 5. Corrected data for sum of (a) hip extensor, (b) hip flexor, (c) adduction, (d) abduction, (e) lateral femoral rotation and (f) medial femoral rotation muscle moment arms normalized by segment length for *Lesothosaurus* and other dinosaurian bipeds.

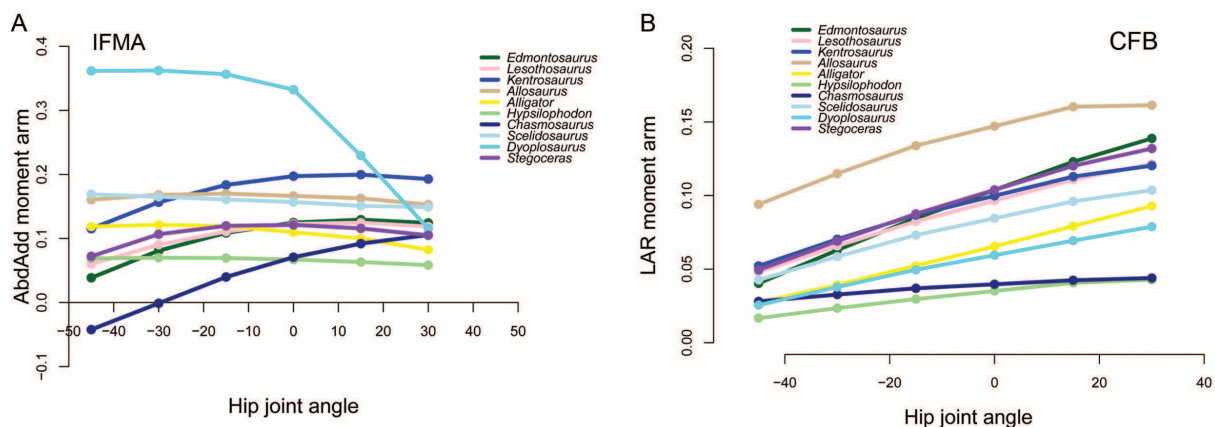
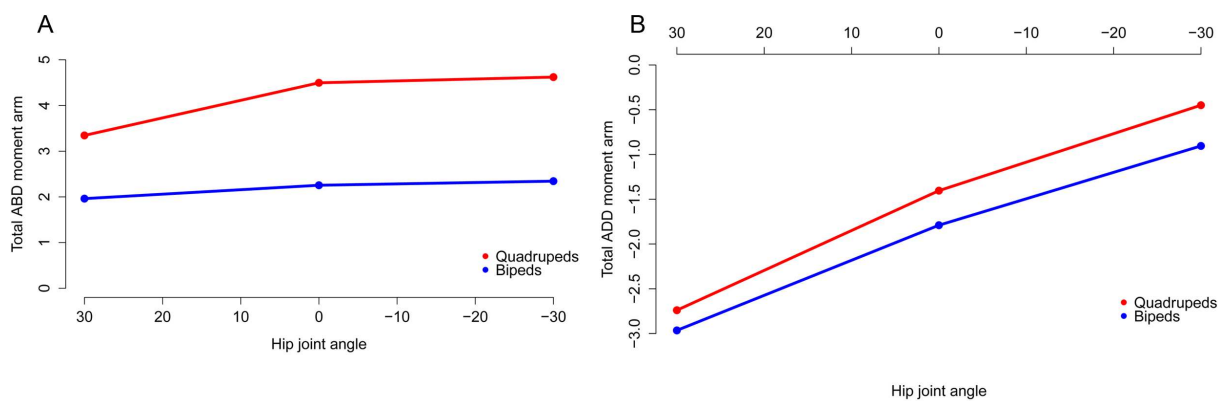


Figure 6. Examples of generally lower moment arms in *Chasmosaurus* and *Hypsilophodon* in our corrected data. Negative values are adduction, medial rotation and flexion, while positive values correspond with abduction, lateral rotation and extension. **A**, Abduction-adduction moment arms for IFMA across a range of hip flexion-extension angles; **B**, Long axis rotation moment arms for CFB across a range of hip flexion-extension angles.



355

356

357

358

359

360

361

Figure 7. Summed abduction (A) and adduction (B) moment arms for quadrupeds (*Kentrosaurus*, *Dyoplosaurus*, *Chasmosaurus*) and bipeds (*Lesothosaurus*, *Hypsilophodon*, *Stegoceras*) across a range of hip flexion-extension angles. All moment arms are normalized by femoral length. Negative values are adduction and flexion, while positive values correspond with abduction and extension.

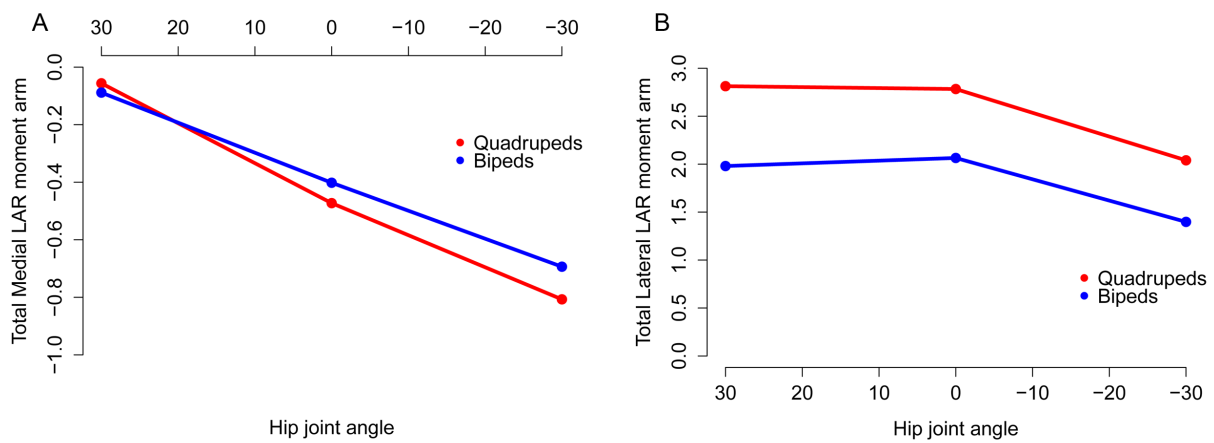


Figure 8. Summed medial (A) and lateral (B) long axis rotation moment arms for quadrupeds (*Kentrosaurus*, *Dyoplosaurus*, *Chasmosaurus*) and bipeds (*Lesothosaurus*, *Hypsilophodon*, *Stegoceras*) across a range of hip flexion-extension angles. All moment arms are normalized by femoral length. Negative values are medial rotation and flexion, while positive values correspond with lateral rotation and extension.

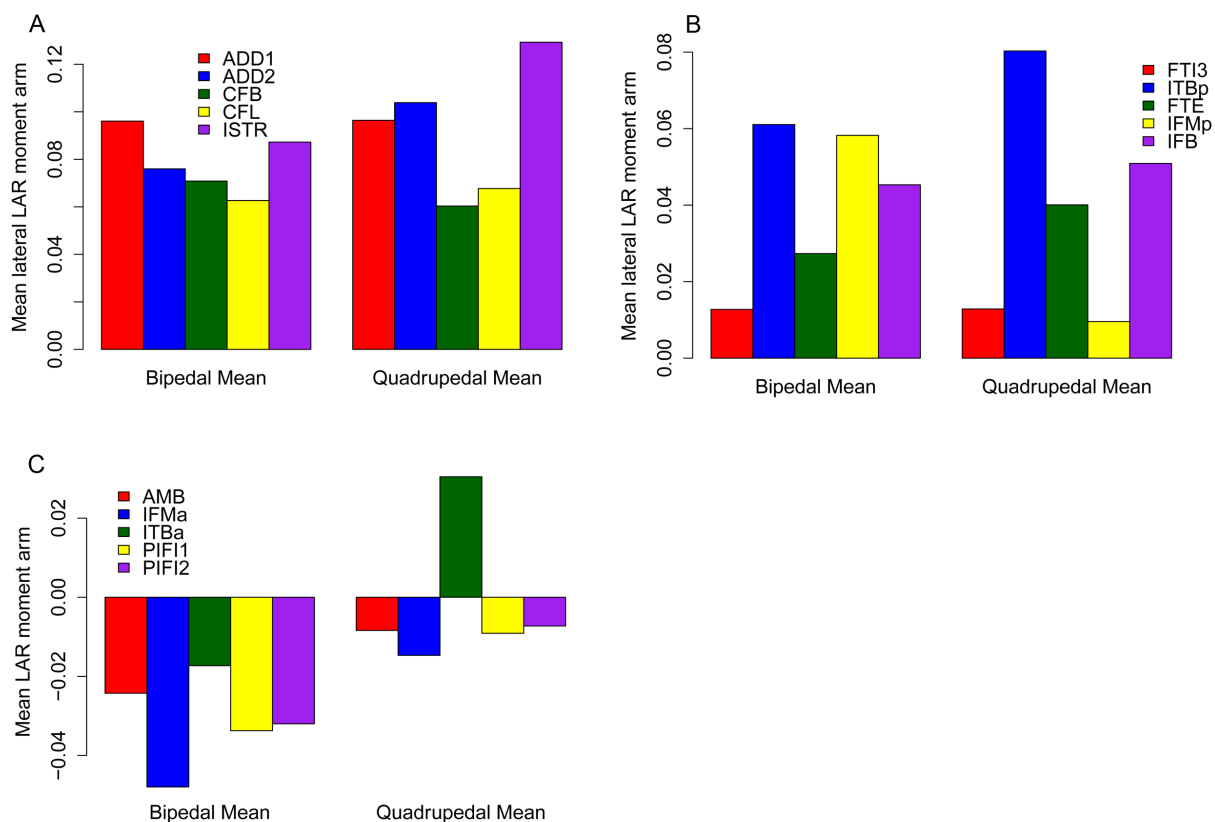


Figure 9. Mean long axis rotation moment arms for quadrupeds (*Kentrosaurus*, *Dyoplosaurus*, *Chasmosaurus*) and bipeds (*Lesothosaurus*, *Hypsilophodon*, *Stegoceras*). All moment arms are normalized by femoral length. Negative values are medial rotation, while positive values correspond with lateral rotation.

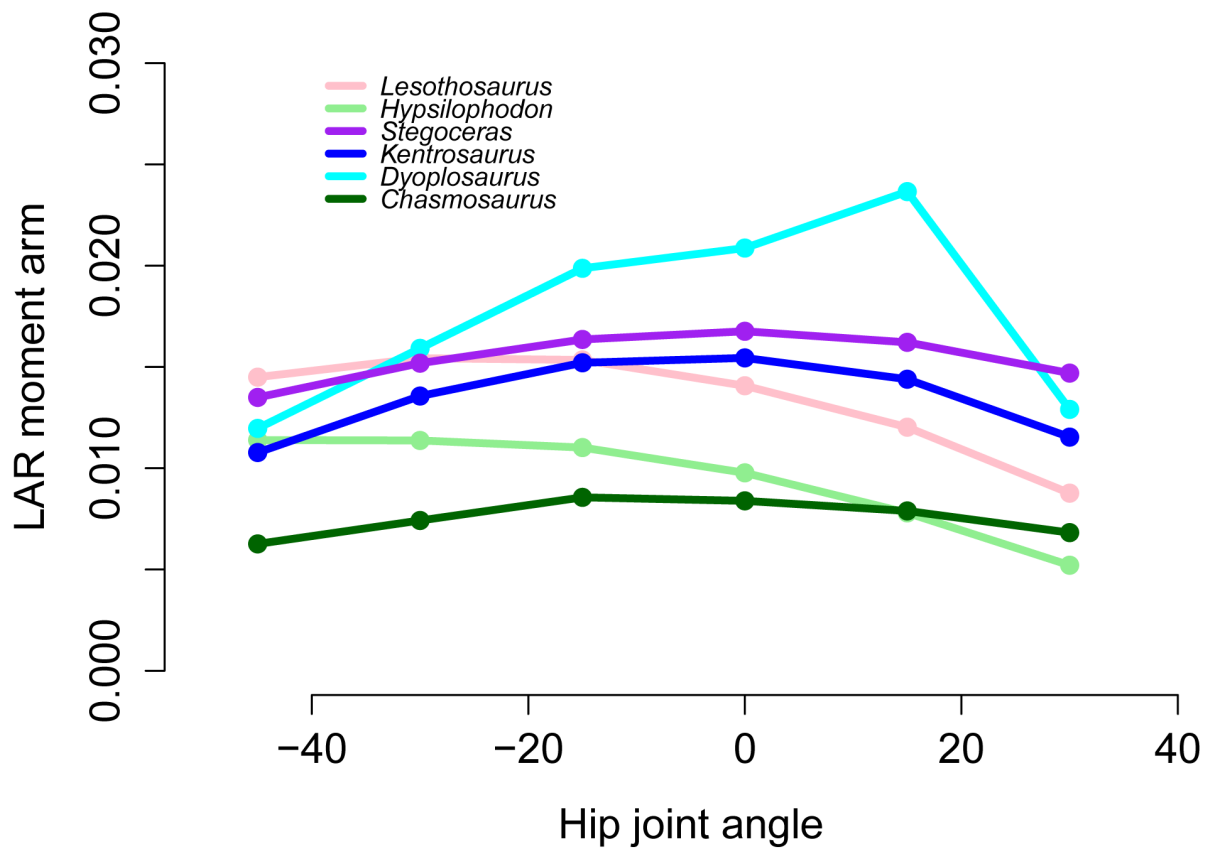


Figure 10. Lateral rotator moment arms across a range of hip flexion-extension angles for FTI3.