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

2   **in archosaurs**

3

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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.

44

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

eight exemplar ornithischian taxa we were able to quantify similarities and differences among

individual taxa, between quadrupedal and bipedal taxa, and among taxa representing the

three major ornithischian lineages (Thyreophora, Ornithopoda, Marginocephalia).

Recently, Hutchinson et al. (2014) compared moment arm predictions from our ostrich

musculoskeletal model (Bates & Schachner, 2012; Bates et al., 2012) to their own model,

which was developed using a more exhaustive experimental protocol. This study found a

strong match between the flexion-extension moment arms of the two models, but noted

systematic differences between the abduction-adduction and long axis rotation moment arms

of some hip muscles (Hutchinson et al., 2014). Re-inspection of our models has revealed that

these differences are due to a coding error, one that is present in all of our published models

(Bates & Schachner, 2012; Bates et al., 2012; Maidment et al., 2014; Maidment, Bates &

Barrett, 2014). The error relates to the specification of joint axes in the models: as the posture

of the models were modified to output moment arms across a range of hip joint angles, the

axes of the hip joint remained in its initial orientation rather than rotating with the femoral

segment and knee joint of the models. Thus the abduction-adduction and long axis rotation

data presented in our previous study represents muscle moment arms calculated about

anatomically and functionally inappropriate axes. Hutchinson et al. (in press) subsequently

compared their data to our corrected abduction-adduction and long axis rotation and found a

much stronger agreement between the models.

The purpose of this paper is to present corrected abduction-adduction and long axis

rotation moment arms for all our models, and to evaluate the impact of this new data on the

conclusions of our previous studies (Bates & Schachner, 2012; Bates et al., 2012; Maidment et

al., 2014; Maidment, Bates & Barrett, 2014).

MATERIALS AND METHODS

Our protocol follows our previous studies exactly, apart from the necessary correction made

to the hip joint axes. We recommend Bates et al. (2012) and Maidment et al. (2014) for

detailed descriptions of our prior methodology.

RESULTS AND DISCUSSION

All corrected moment arm data for hip abduction-adduction and long axis rotation are

tabulated in the supplementary material. In general our new corrected data differ only

slightly from our original data, and there were very few qualitative changes in muscle

moments (e.g. muscles originally identified as abductors remained abductors). Rather than

describe every quantitative change in moment arm values we focus on the muscles relevant to

the hypotheses and conclusions in each of our previous studies. For clarity we address each

study individually in the following sections.

Bates & Schachner (2012)

The majority of the functional and evolutionary conclusions drawn by Bates & Schachner

(2012) are upheld because the corrected moment arm magnitudes differ only slightly from

our published values, and because the correction tends to affect all taxa equally and,

therefore, the relative differences and similarities between the models have been preserved

(Figure 1).

Bates & Schacher (2012) concluded that muscle moment arm polarities and joint angle

relationships in key hip muscle groups (Hutchinson & Gatesy, 2000) are generally

conservative despite the shifts in skeletal architecture, posture, body size and locomotor

behaviour covered by our sampled taxa. This suggests that muscle origins and insertions

remained relatively stable with respect to the hip joint across Archosauria. This conclusion is

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).

145

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 ischotrochantericus 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

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.

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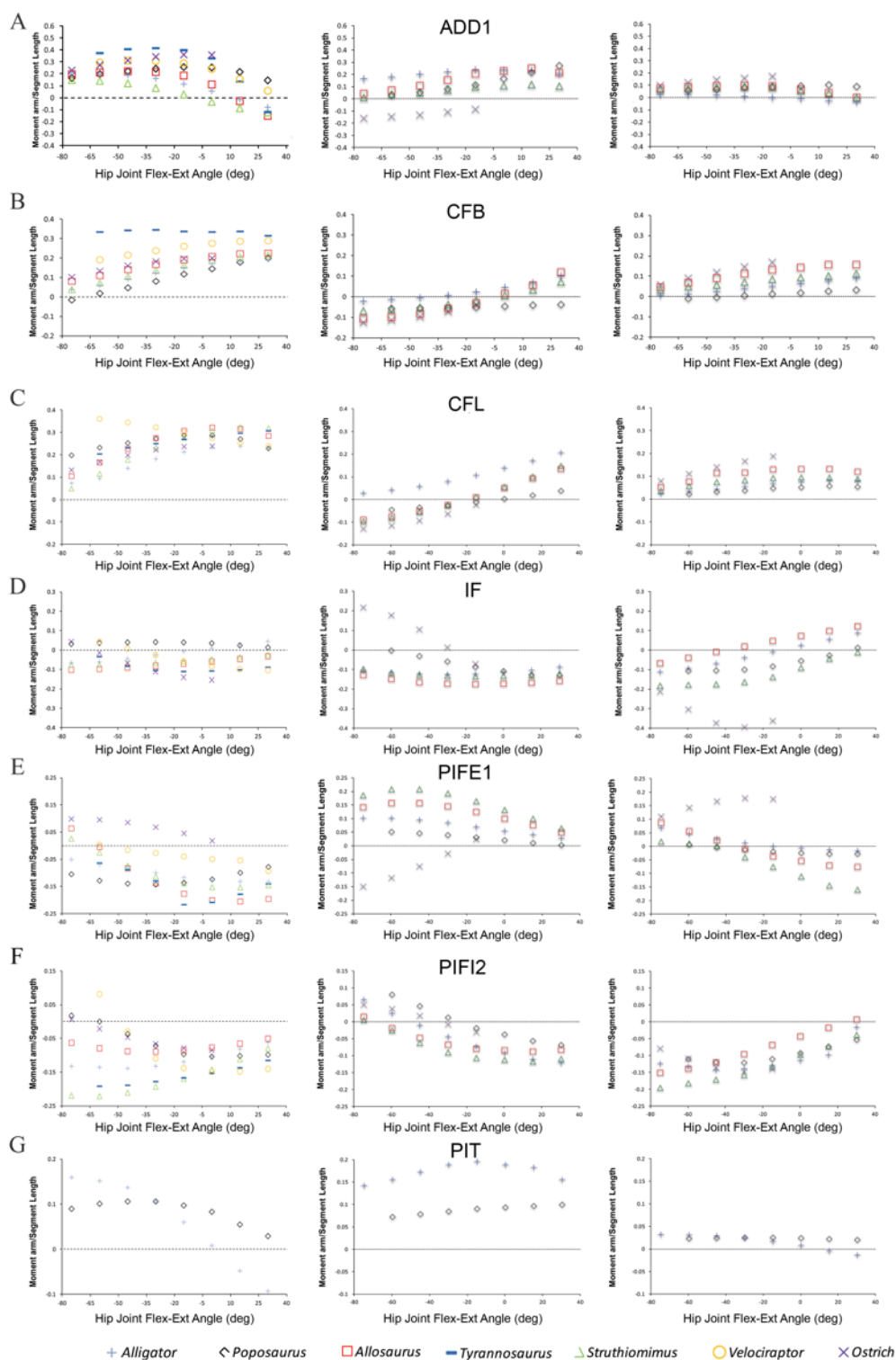
Figure 1. Predicted pelvic muscle moment arms for hip flexion–extension (left), and

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.

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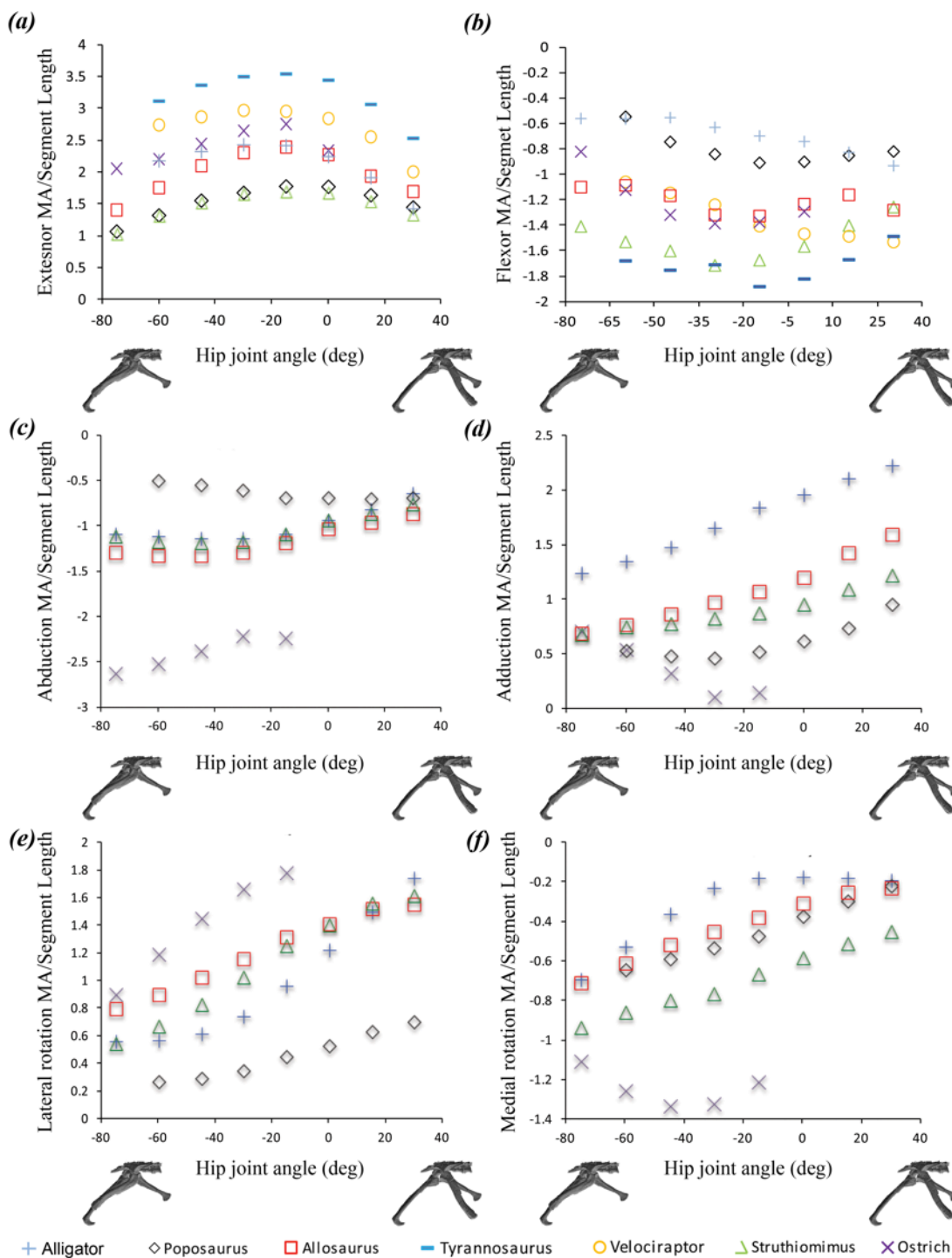
Figure 2. Sum of (a) hip extensor, (b) hip flexor, (c) hip abduction, (d) adduction, (e) lateral

femoral rotation and (f) medial femoral rotation muscle moment arms normalized by

segment length for *Poposaurus*, *Alligator* and ornithodiran bipeds. All data normalized by

femoral length. Only flexion–extension data are available for *Tyrannosaurus* and *Velociraptor*

from previous studies (Hutchinson et al., 2005; Hutchinson et al., 2008).
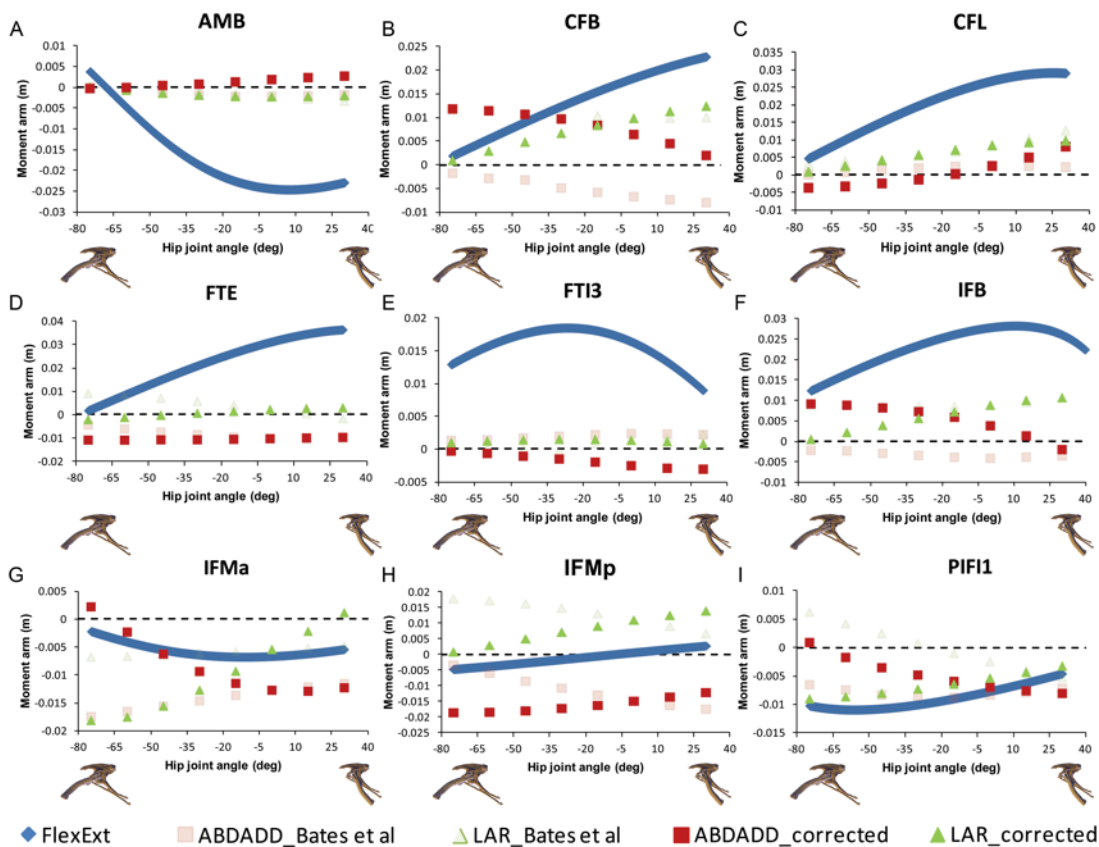
Figure 3. Corrected hip muscle moment arm predictions for (a) AMB, (b) CFB, (c) CFL, (d) FTE, (e) FTI3, (f) IFB, (g) IFMa, (h) IFMp and (i) PIFI1 for a range of hip flexion/extension angles in *Lesothosaurus*. A positive hip joint angle (x-axis) indicates hip extension (femoral retraction), while a negative 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.

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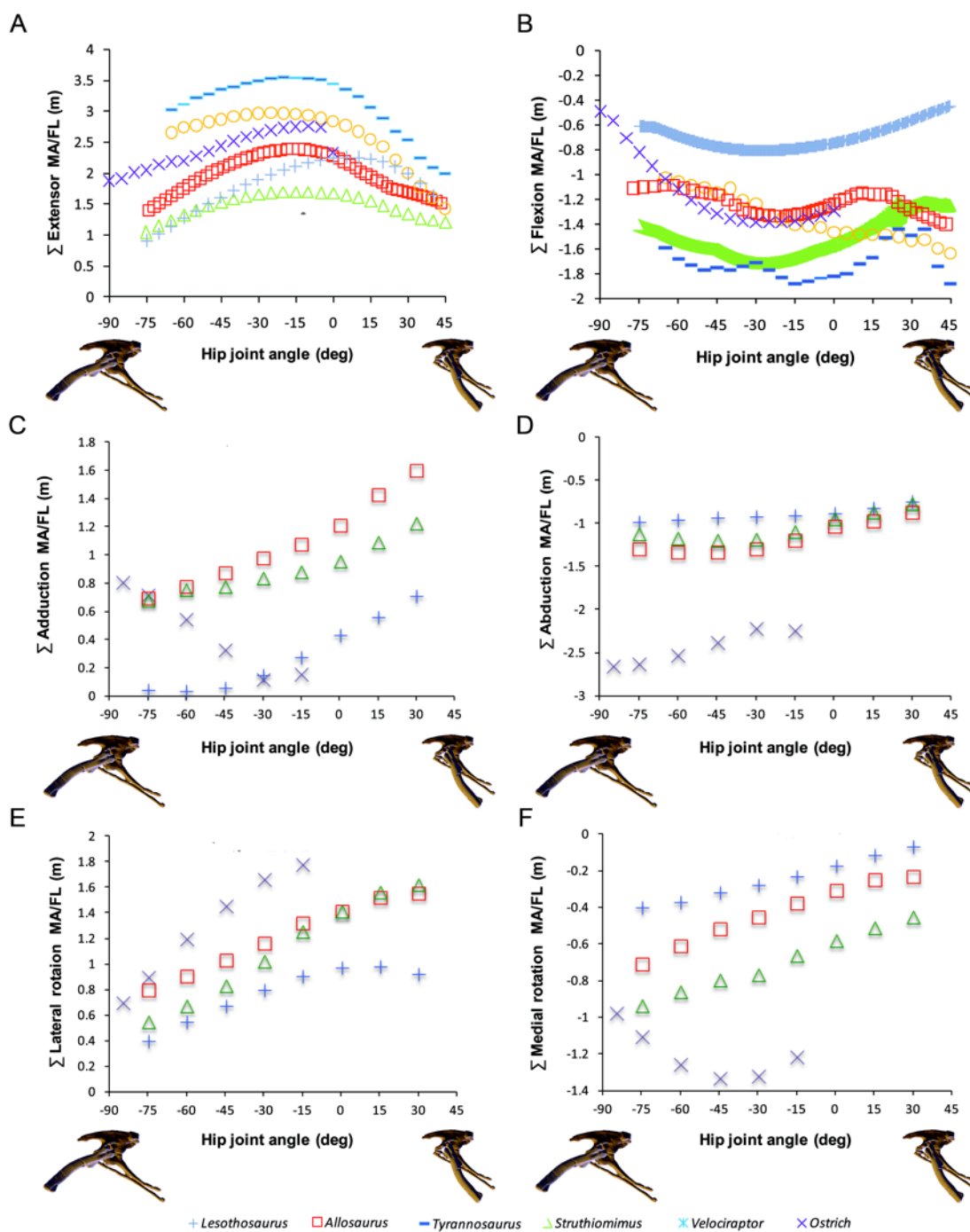
Figure 5. Corrected data for sum of (a) hip extensor, (b) hip flexor, (c) adduction, (d)

abduction, (e) lateral femoral rotation and (f) medial femoral rotation muscle moment arms

normalized by segment length for *Lesothosaurus* and other dinosaurian bipeds.

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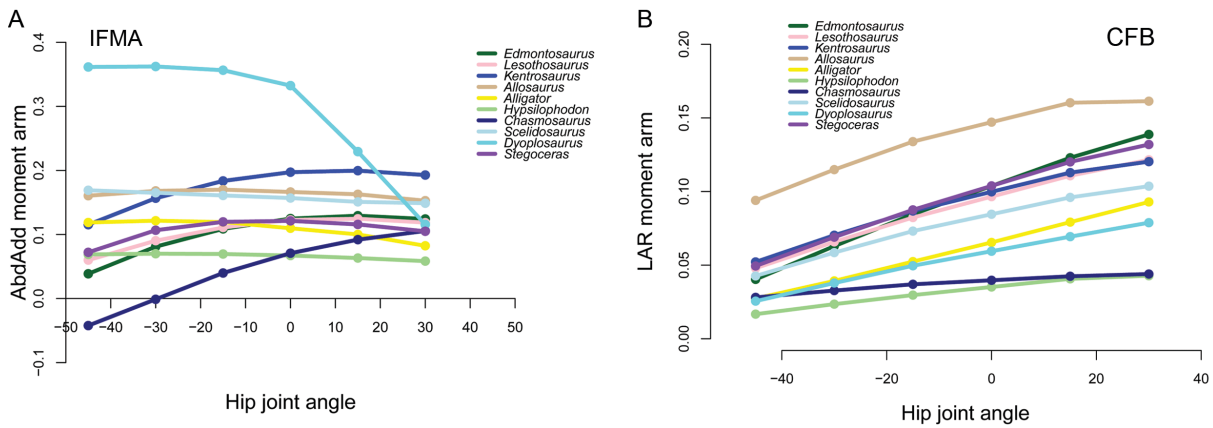
Figure 6. Examples of generally lower moment arms in *Chasmosaurus* and *Hypsilophodon* in our corrected data. Negative values are adduction, medial rotation and flexion, while positive values correspond with abduction, lateral rotation and extension. **A**, Abduction-adduction moment arms for IFMA across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

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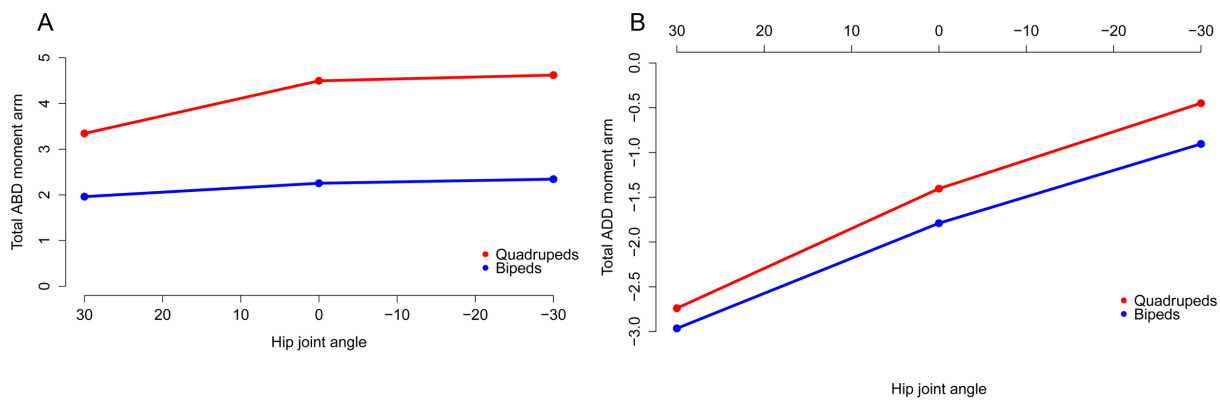
Figure 7. Summed abduction (**A**) and adduction (**B**) moment arms for quadrupeds
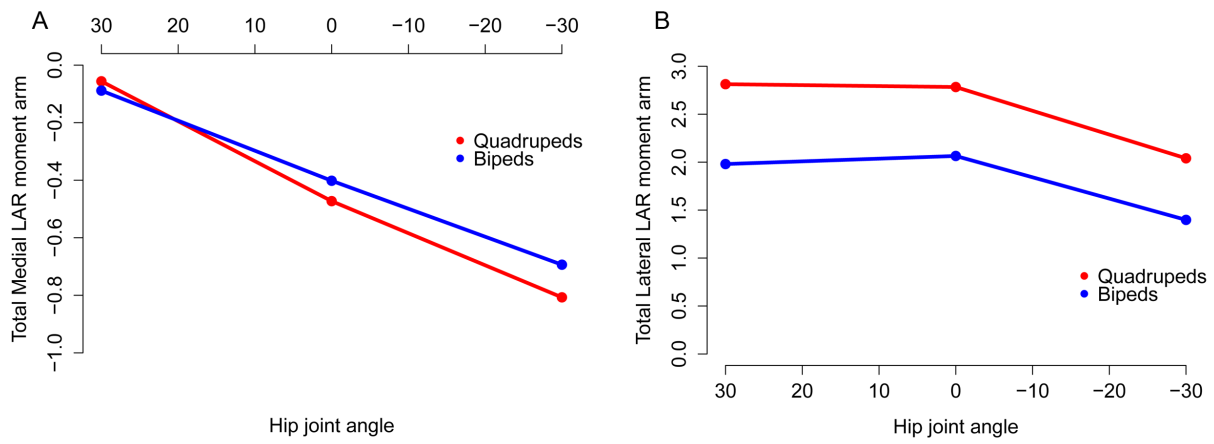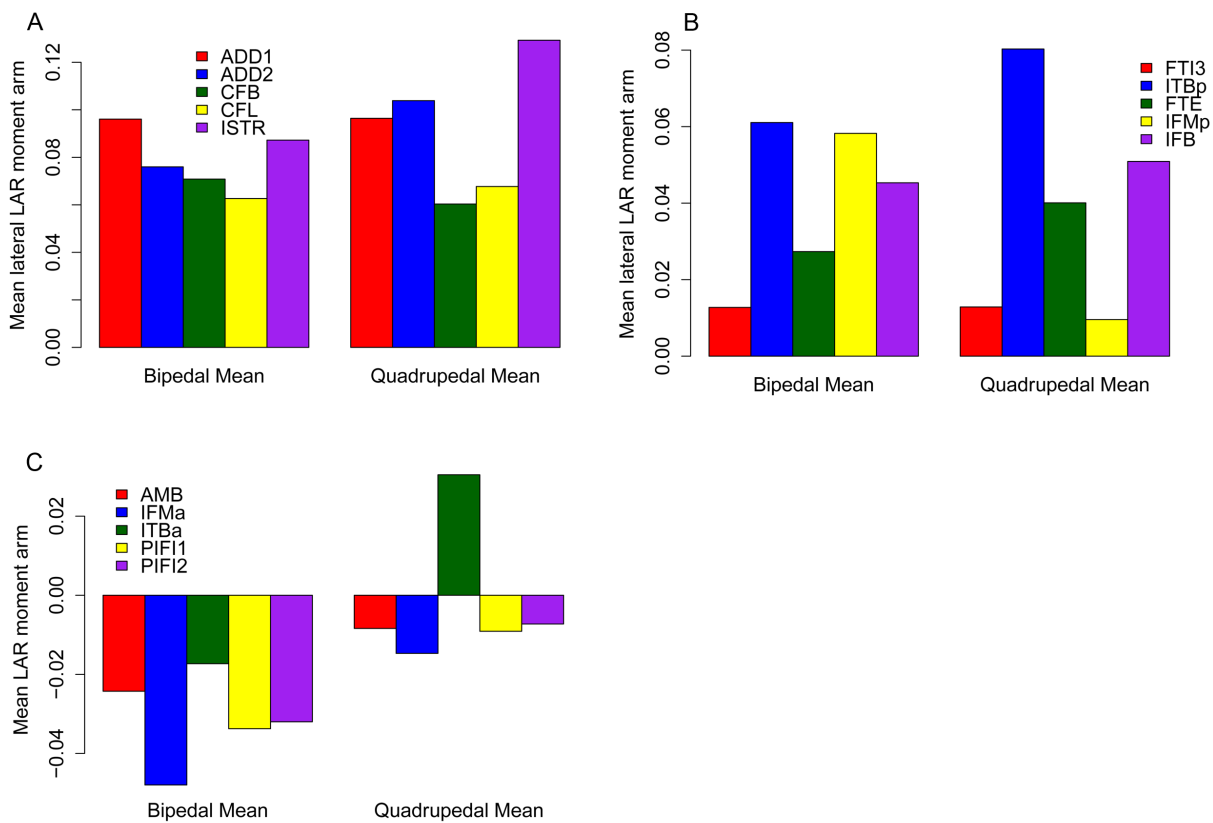
357 (*Kentrosaurus, Dyoplosaurus, Chasmosaurus*) and bipeds (*Lesothosaurus, Hypsilophodon,*

358 *Stegoceras*) across a range of hip flexion-extension angles. All moment arms are normalized

359 by femoral length. Negative values are adduction and flexion, while positive values

360 correspond with abduction and extension.

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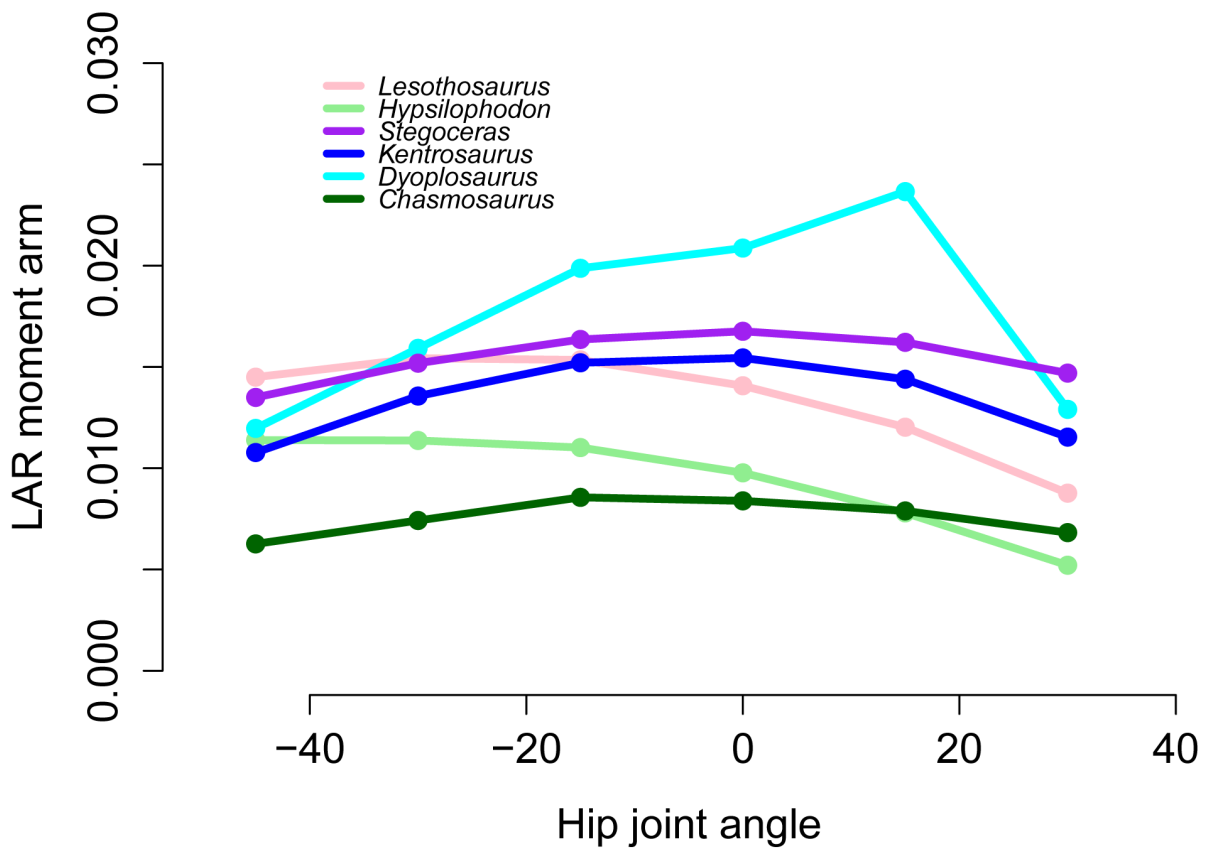
Figure 9. Mean long axis rotation moment arms for quadrupeds (*Kentrosaurus, Dyoplosaurus, Chasmosaurus*) and bipeds (*Lesothosaurus, Hypsilophodon, Stegoceras*). All moment arms are normalized by femoral length. Negative values are medial rotation, while positive values correspond with lateral rotation.

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

FTI3.