A QUANTITATIVE METHOD FOR INFERRING LOCOMOTORY SHIFTS IN AMNIOTES DURING ONTOGENY, ITS APPLICATION TO DINOSAURS AND ITS BEARING ON THE EVOLUTION OF POSTURE

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Abstract: Evolutionary transitions between quadrupedal and bipedal postures are pivotal to the diversification of amniotes on land, including in our own lineage (Hominini). Heterochrony is suggested as a macroevolutionary mechanism for postural transitions but understanding postural evolution in deep time is hindered by a lack of methods for inferring posture in extinct species. Dinosaurs are an excellent natural laboratory for understanding postural evolution because they demonstrate at least four instances of quadrupedality evolving from bipedality, and heterochronic processes have been put forward as an explanatory model for these transitions. We extend a quantitative method for reliably inferring posture in tetrapods to the study of ontogenetic postural transitions using measurements of proportional limb robusticity. We apply this to ontogenetic series of living and extinct amniotes, focusing on dinosaurs. Our method correctly predicts the general pattern of ontogenetic conservation of quadrupedal and bipedal postures in many living amniote species and infers the same pattern in some dinosaurs. Furthermore, it correctly predicts the ontogenetic postural shift from quadrupedal crawling to bipedal walking in humans. We also infer a transition from early ontogenetic quadrupedality to late-ontogenetic bipedality in the transitional sauropodomorph dinosaur Masiakasaurus intermedius and possibly in the early branching ceratopsian Psittacosaurus intermedius but not in the sauropodomorph Massospondylus carinatus. The phylogenetic positions of these ontogenetic shifts suggest that heterochrony may play a role in the macroevolution of posture, at least in dinosaurs. Our method has substantial potential for testing evolutionary transitions between locomotor modes, especially in elucidating the role of evolutionary mechanisms like heterochrony.

Key words: ontogeny, locomotion, amniote, dinosaur, posture.

Changes in posture, from quadrupedal to bipedal or vice-versa, have occurred rarely in tetrapod evolution. However, these changes characterize several successful living and extinct amniote lineages. Despite a wealth of studies on the anatomical changes associated with these shifts, and some studies exploring their pattern, little is known about how these changes in locomotion came to evolve several times independently, or whether they share an underlying mechanism such as heterochrony.

Most living amniotes are habitual quadrupeds (Maidment et al. 2014) but several extant groups represent independent locomotory transitions to bipedalism from quadrupedal ancestors. For example, in mammals these include several different groups of small rodents that use ricochetal locomotion such as dipodines (Eilam & Shefer 1997), Neomys (Stein 1990) and Pedetes (Peinke & Bernard 2005), as well as bipedally hopping Macropodiformes (including both small-bodied taxa, e.g. Potorous, and larger species of the genus Macropus) (Buchmann & Guiler 1974) and humans. The latter are the most intensively studied example but despite 100 years of research on the origins of bipedality in Hominoida, it remains controversial how, when and why our
Similar to modern mammals, dinosaurs also underwent multiple independent postural transitions, albeit with reversed polarity. The ancestral condition for Dinosauria is bipedal posture, but quadrupedality evolved as a derived condition multiple times across two major lineages (at least once in Sauropodomorpha and at least three times in Ornithischia) (Sereno 1997; Maidment & Barrett 2012; Maidment et al. 2014; Barrett & Maidment 2017; McPhee et al. 2018). The origins of locomotory shifts in dinosaurs appear to coincide with lineage diversification; for example, in Sauropodomorpha the evolution of quadrupedality is considered to be a key adaptation that facilitated the enormous body sizes of later-branching members (Sander et al. 2011; Sander 2013). Because of their time-extensive record, well-understood phylogeny, and history of in-depth anatomical research, dinosaurs represent an excellent study system in which to understand macroevolutionary locomotory shifts.

Patterns of postural evolution in dinosaurs have been characterized (Sereno 1997; Sander et al. 2011; Maidment et al. 2014; McPhee et al. 2018) but process-based hypotheses explaining these patterns have been lacking. In dinosaurs at least, paedomorphosis has been proposed as a mechanism by which postural shifts might occur (Bona-partre & Vince 1979), allowing an hypothesized juvenile phase of quadrupedality in ancestor species (with bipedal adults) to be retained in adults of descendant species (with quadrupedal adults). However, observed ontogenetic postural shifts are rare among extant amniotes. This makes it difficult to test a heterochronic model for postural evolution using data from extant species only. Indeed, we know of only one extant species that has protracted quadrupedal and bipedal phases during its ontogeny: Homo sapiens.

In contrast, postural ontogenetic shifts have been hypothesized in several dinosaur species and may have been widespread. These include shifts from bipedalism to quadrupedalism (such as in the ornithopods Maiasaura peeblesorum (Dilkes 2001) and Iguanodon bernissartensis (Norman 1980)) and from quadrupedalism to bipedalism in the basal ceratopsian Psittacosaurus lujainuminesis (Zhao et al. 2013), the ornithopod Dryosaurus lehaviworbecki (Heinrich et al. 1993), as well as the sauropodomorphs Massospondylus carinatus (Reisz et al. 2005) and Mus- saurus patagonicus (Otero et al. 2019). Dinosaur species with ontogenetic changes in posture might therefore be instructive in understanding how shifts occur in other lineages and represent an opportunity for testing process-based models.

The relationship between phylogeny and ontogeny has been highly debated since the publication of the Biogenetic Law in 1866 (Haeckel 1866; Gould 1977; Nelson 1978). Nevertheless, studying ontogenetic series has been shown to be a useful way of exploring transitions between distinctive phenotypic states in lineages (Heers et al. 2014). However, the study of posture in the ontogenetic series of dinosaurs presents a threefold problem that must be overcome if they are to be used to test this question. First, determining the posture (bipedal, quadrupedal) of extinct species is difficult and few methods have been demonstrated to be reliable (Carrano 1985; Alexander 1985; Carrano 1998; Carrano & Biewener 1999; Bonnar & Senter 2007; Mallison 2010a, b; Grossi et al. 2014; Maidment et al. 2014; Barrett & Maidment 2017; Otero et al. 2017). These studies generally agree where a phenotypic signal is clear (e.g. bipedal theropods with reduced arms or gigantic sauropods with columnar, quadrupedal postures) but give varying answers about taxa with less decisive characteristics. Because these studies are often not validated on extant taxa with known postures (but see Sereno & Shichin 1988; Carrano & Biewener 1999), it has been difficult to resolve the uncertainties about extinct taxa.

Among the disparate techniques used so far to infer postural shifts, only limb bone length allometry is broadly applicable and non-invasive (Norman 1980; Heinrich et al. 1993; Dilkes 2001; Reisz et al. 2005; Zhao et al. 2013). However, a recent method for assessing amniote posture showed that such measurements had essentially zero predictive power for determining posture in amniotes (McPhee et al. 2018). That study described a single, consistent quantitative method for assessing posture in adult individuals, using measurements of forelimb and hindlimb robusticity (we use ‘robustness’ and ‘robusticity’ to refer to the ratio of the minimum circumference around the humeral and femoral shafts) (McPhee et al. 2018). Based on validation in extant species, this method can be used to confidently infer posture in extinct species. Furthermore, it is non-destructive, and can be used on poorly preserved or incomplete specimens that minimally preserve just the humeral and femoral shafts.

Here we modify McPhee et al’s (2018) method for postural determination for use on ontogenetic series. We validate this approach using growth series of extant amniotes and use it to assess postural changes during ontogeny in extinct dinosaurs. Our results have bearing on the role of heterochrony during the evolution of dinaosaurian posture, and by extension, the macroevolutionary processes behind postural shifts in amniotes.
METHOD

We compiled a database of limb measurements (minimum circumferences of the humeral and femoral diaphyses and total bone lengths) across ontogenetic series of living and extinct amniote species from published literature (Campione & Evans 2012; Kilbourne & Makovicky 2012; McPhee et al. 2018) and by measuring specimens using digital calipers and a tailor’s tape (see Chapelle et al. 2019, S1). For fossils embedded in matrix, we either estimated circumferences using diameters, or took measurements from reconstructed CT scans (Chapelle et al. 2019, S1).

We included non-volant, terrestrial amniote taxa with a range of locomotory habits (e.g., bipeds, quadrupeds, fossorial species and taxa with both known and hypothesized ontogenetic postural transitions). Powered flight and aquatic locomotion impart special demands on limb bone cortices (Habib & Ruff 2008) and taxa with these behaviours were therefore omitted. The final dataset (hereinafter ‘ontogenetic dataset’) included ontogenetic series of 29 mammal species, 1 squamate, 2 crocodylians, 4 birds, and 6 non-avian dinosaurs (Chapelle et al. 2019, S2). For extant taxa, we assessed each species’ posture (i.e., bipedal|quadrupedal) by focusing on the predominant mode of locomotion during travel, rather than the use of other postures during slow-speed and sporadic behaviours. For example, large-bodied macropodiforms use their tails to execute ‘pentapedal hopping’ while grazing but are obligate bipeds during travel (Dawson & Taylor 1973). Furthermore, c. 50 species of lizards have at least some bipedal capabilities, predominantly for escape behaviours (Aerts et al. 2003). However, escape behaviours are generally sporadic, forming a small part of the animal’s repertoire. In the context of the definition of posture (bipedality/quadrupedality during travel) used here, our statistical analyses can be seen as tests of the hypothesis that posture during travel plays an important role in structuring the relative robustness of the humerus compared to that of the femur.

To predict the posture of each specimen in the ontogenetic dataset, we calibrated a discriminant function analysis (DFA; Manly 2016) using a training dataset comprising 303 adult amniote taxa with known posture. Of these, 31 are bipeds and 272 are quadrupeds. The training dataset was compiled by combining the data of McPhee et al. (2018) (in turn extended from Campione & Evans 2012) and the largest available specimens (and thus probably ontogenetically mature individuals) of living taxa from our ontogenetic dataset. We used the ratio of log_{10}(humeral shaft circumference) (HC) to log_{10}(femoral shaft circumference) (FC) as predictor variables of posture. The analysis was conducted using R Studio v. 1.1.453 (RStudio Team 2016) and its package MASS (Ripley et al. 2002) with visualizations developed in its package ggplot2 (Wickham et al. 2013). Because of unequal sample sizes between bipeds and quadrupeds, we randomly subsampled our training dataset to 20 bipedal and 20 quadrupedal taxa, then generated postural class predictions (i.e., bipedal or quadrupedal) for each specimen in the ontogenetic series. We repeated this process 10 000 times to generate mean posterior probabilities of being bipedal (pp_{bipedal}) for each specimen in the ontogenetic dataset. In assigning posture to specimens, we chose arbitrary cutoffs in order to predict posture only where a reasonable level of confidence is present: specimens with pp_{bipedal} ≤ 0.333 were predicted as being quadrupeds; specimens with 0.333 < pp_{bipedal} ≤ 0.666 were predicted as being equivocal; and specimens with pp_{bipedal} ≥ 0.666 were predicted as being bipeds (Chapelle et al. 2019, S3). We report simple descriptive log_{10}HC/log_{10}FC ratios for selected taxa, and distributions of posterior postural predictions for all dinosaurian taxa included (Chapelle et al. 2019, S4).

The same analyses were conducted using humeral and femoral lengths (HL and FL), which have been widely used to infer posture in previous works (Norman 1980; Heinrich et al. 1993; Dilkes 2001; Reisz et al. 2005).

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; BP, Bernard Price Institute, University of the Witwatersrand, Johannesburg, South Africa (now ESI); DMNH, Delaware Museum of Natural History, Wilmington, USA; ESI, Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa; FMNH, Field Museum of Natural History, Chicago, USA; IVPP, Institute of Vertebrate Paleontology & Paleoanthropology, Beijing, China; MPM, Museo ‘Padre Molina’, Rio Gallegos, Argentina; MLP, Museo de La Plata, La Plata, Argentina; NHMUK: National History Museum, London, UK; OUMNH, Oxford University Museum of Natural History, Oxford, UK; PVL, Instituto ‘Miguel Lillo’, Tucumán, Argentina; QB, Zimbabwe Natural History Museum, Bulawayo, Zimbabwe; RDC, Raymond Dart Collection, Department of Anatomical Sciences, University of the Witwatersrand, Johannesburg, South Africa; ROM, Royal Ontario Museum, Ontario, Canada; SAM, South African Museum (Iziko Museums of Cape Town), Cape Town; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA (formerly United States National Museum); WLSM, Wits Life Sciences Museum, Johannesburg, South Africa; YPM, Yale Peabody Museum, New Haven, USA.

RESULTS

Comparisons of humeral and femoral shaft circumference are effective in assessing posture in individual amniotes. A split between bipeds and quadrupeds is clearly observed when log_{10}HC is plotted against log_{10}FC (Fig. 1A). This pattern is mostly validated by our discriminant function analysis (Fig. 2; Chapelle et al. 2019, S3). Data from ontogenetic series of obligate quadrupeds plot within the region of quadrupedal adults (Fig. 1A), and this is also true for...
most bipeds (except for some specimens in three of the ontogenetic series: *Macropus giganteus*, *Macropus rufus* and *Smutsia temminckii*) (Fig. 1A). Our DFA predicts that humans make a transition from early quadrupedality, to a mix between quadrupedal and equivocal, to a late-ontogenetic mix between bipedal and equivocal during ontogeny (Fig. 1A) \(0.084 \leq p_{bipedal} \leq 0.296\) for specimens with \(FC \leq 37\) mm except for one equivocal specimen with \(p_{bipedal} = 0.414\); \(0.307 \leq p_{bipedal} \leq 0.523\) for specimens with \(38 \leq FC \leq 59\) mm; and \(0.445 \leq p_{bipedal} \leq 0.773\) for specimens with \(FC > 59\) mm except for one adult with \(p_{bipedal} = 0.277\) and therefore predicted as being quadrupedal). Even for equivocal specimens, all adult *Homo sapiens* specimens with \(FC > 59\) mm have a \(\log_{10} HC/\log_{10} FC \leq 0.949\) (except for the one outlier specimen with \(FC = 77\) mm and \(\log_{10} HC/\log_{10} FC = 0.968\)). Other closely related adult hominids are quadrupeds and have proportionally more robust humeri with \(\log_{10} HC/\log_{10} FC = 1\) for

**FIG. 1.** Humeral to femoral circumference ratios during ontogeny. Line and point colours reflect observed posture during habitual locomotion (travel) and/or qualifiers such as hypothesized shifts and unobservable conditions. *Homo sapiens* in grey. Point shapes reflect posture predicted by the DFA. Silhouettes for small, medium and large size class bipeds/quadrupeds and dinosaurs. A, extant amniotes. B, ontogenetic series of sauropodomorph dinosaurs in red overlying extant amniotes. C, ontogenetic series of ornithischian dinosaurs in red overlying extant amniotes. D, ontogenetic series of theropod dinosaur *Limusaurus* in red overlying extant amniotes. Silhouettes courtesy of Phylopic (S. Hartman, J.J.W. Sertich, M.A. Loewen, P. Buchholz, M. Wedel, V.-V. Sinkkonen, M. Martyniuk, G. Shaw, J.A. Venter, H.H.T. Prins, D.A. Balfour, R. Slotow, M. Karala, S. Werning).
Gorilla gorilla, log_{10}HC/log_{10}FC = 0.987 for Pan troglodytes and log_{10}HC/log_{10}FC = 1.02 for Pongo pygmaeus (see McPhee et al. 2018, suppl.)

The ontogenetic series of some taxa are predicted to be either partially equivocal and partially correctly identified (1 of 36 species or 2.8% of taxa studied), or partially
equivocal and partially misclassified (4 of 36 species or 11% of taxa studied). The nine-banded armadillo (*Dasypus novemcinctus*) and the tree-kangaroo (*Dendrolagus lumholtzi*) fall in a region of graph space intermediate between known quadrupeds and bipeds, but natural history observations show that they are predominantly quadrupedal (Taber 1945; Heise-Pavlov 2017). As also found by McPhee et al. (2018), the posture of the tree kangaroo *Dendrolagus lumholtzi* is inferred as being a mix between bipedal and equivocal by the DFA (0.350 ≤ p_{bipedal} ≤ 0.834), and the same is true of *Dasypus novemcinctus* which is inferred as being a mix between bipedal, quadrupedal and equivocal by the DFA (0.235 ≤ p_{bipedal} ≤ 0.811) (Fig. 2). Most individuals of *Macropus giganteus* and *Macropus rufus* are correctly inferred to be bipeds by our DFA (Fig. 2; Chapelle et al. 2019, S3) and natural history observations show they are bipedal throughout development (Worland & Dagg 1971; McGowan et al. 2008). However, the largest individuals are inferred to be quadrupeds or equivocal. Although observed as being habitual bipeds (Steyn et al. 2018) all four ground pangolin specimens (*Smutsia temminckii*) are predicted by the DFA to be quadrupedal or equivocal (0.167 ≤ p_{bipedal} ≤ 0.561) (Fig. 2).

Dinosaurs show a variety of patterns. In sauropodomorphs, *Rapetosaurus* is predicted to be quadrupedal or marginally equivocal throughout its ontogeny (0.218 ≤ p_{bipedal} ≤ 0.393); *Massospondylus carinatus* is predicted to be bipedal throughout ontogeny (0.734 ≤ p_{bipedal} ≤ 0.946) except for the embryonic data point, which is equivocally classified (p_{bipedal} = 0.415); and *Maiasaura* shifts from quadrupedal to bipedal during its ontogeny (0.014 ≤ p_{bipedal} ≤ 0.969) (Figs 1B, 2). Within ornithischians, *Maiasaura* is predicted to be bipedal throughout ontogeny (0.896 ≤ p_{bipedal} ≤ 0.985), whereas the 22 individuals of *Psittacosaurus lufengensis* are alternately classified as bipedal, equivocal or quadrupedal with no discernible ontogenetic pattern (0.033 ≤ p_{bipedal} ≤ 0.863) (Figs 1C, 2). The hatching specimen of *Psittacosaurus lufengensis* is predicted to be quadrupedal (p_{bipedal} = 0.033). The theropod *Limusaurus* is bipedal throughout ontogeny (0.989 ≤ p_{bipedal} ≤ 0.999) (Figs 1D, 2).

The use of log-transformed humeral and femoral lengths as predictor variables does not distinguish bipedal amniotes from quadrupedal amniotes (Chapelle et al. 2019, S5, S6). In the DFA results using humeral and femoral lengths, 39% of the amniote’s ontogenetic trajectories are misidentified. Of the 22 strictly quadrupedal taxa, 9 are misclassified as being almost strictly bipedal throughout ontogeny, or as shifting from quadrupedalism to bipedalism (Fig. 3; Chapelle et al. 2019, S7). These include: *Antilocapra americana* (the 4 smallest specimens are equivocal with 0.447 ≤ p_{bipedal} ≤ 0.647 and the rest of the series is bipedal with 0.688 ≤ p_{bipedal} ≤ 0.807); *Bison bison* (2 equivocal specimens with 0.653 ≤ p_{bipedal} ≤ 0.656 and the rest of the series bipedal with 0.665 ≤ p_{bipedal} ≤ 0.884); *Connochaetes taurinus* (5 specimens are equivocal with 0.574 ≤ p_{bipedal} ≤ 0.593 and the rest of the series is bipedal with 0.749 ≤ p_{bipedal} ≤ 0.835); *Dendrolagus lumholtzi* (all bipedal with 0.668 ≤ p_{bipedal} ≤ 0.731); *Hippopotamus amphibius* (2 smallest specimens are equivocal with 0.430 ≤ p_{bipedal} ≤ 0.647 and the rest of the series is bipedal with 0.842 ≤ p_{bipedal} ≤ 0.915); *Myrmecophaga tridactyla* (5 of the smallest specimens are equivocal with 0.349 ≤ p_{bipedal} ≤ 0.597 and the rest of the series is bipedal with 0.728 ≤ p_{bipedal} ≤ 0.827); *Odocolleus virginianus* (13 smallest specimens are quadrupedal or equivocal with 0.184 ≤ p_{bipedal} ≤ 0.630 and the rest of the series is bipedal with 0.733 ≤ p_{bipedal} ≤ 0.850); *Okapia johnstoni* (9 smallest specimens are quadrupedal or equivocal with 0.086 ≤ p_{bipedal} ≤ 0.632 and the rest of the series is bipedal with 0.717 ≤ p_{bipedal} ≤ 0.804); and *Ursus americanus* (7 smallest specimens are quadrupedal or equivocal with 0.037 ≤ p_{bipedal} ≤ 0.635 and the rest of the series is bipedal with 0.699 ≤ p_{bipedal} ≤ 0.836). Natural observations of these taxa show that they are strictly quadrupedal or ambiguous in the case of the tree kangaroos (Geist et al. 2004; Kingdon 2015). The ontogenetic shift from quadrupedal crawling to bipedal walking in *Homo sapiens* is correctly identified (smallest 8 specimens are quadrupedal with 0.223 ≤ p_{bipedal} ≤ 0.326; middle 18 specimens are equivocal with 0.358 ≤ p_{bipedal} ≤ 0.658; and 34 largest specimens are bipedal with 0.687 ≤ p_{bipedal} ≤ 0.938). In bipedal mammals, *Macropus rufus* is predicted as undergoing a shift from quadrupedal to bipedal although in reality it is observed as being strictly bipedal throughout ontogeny (0.042 ≤ p_{bipedal} ≤ 0.910). In ratites, *Rhea americana* and *Struthio camelus* are predicted as being strictly quadrupedal or equivocal although they are known bipeds (0.087 ≤ p_{bipedal} ≤ 0.384 and 0.383 ≤ p_{bipedal} ≤ 0.434 respectively). Among dinosaurs, *Massospondylus carinatus* is predicted as being strictly bipedal (0.907 ≤ p_{bipedal} ≤ 0.969), *Massaaurus* and *Rapetosaurus* appear to undergo a shift from quadrupedal to bipedal (0.045 ≤ p_{bipedal} ≤ 0.976 and 0.066 ≤ p_{bipedal} ≤ 0.718 respectively) and *Psittacosaurus lufengensis* appears to be mostly equivocal and quadrupedal with a few bipedal specimens (15 specimens with 0.012 ≤ p_{bipedal} ≤ 0.553 and 5 specimens with 0.662 ≤ p_{bipedal} ≤ 0.760).

**DISCUSSION**

Postural predictions in extant ontogenetic series using limb robusticity

Humeral and femoral minimum circumference have been shown to reliably predict posture in living amniotes
Here, we show that they are also useful in predicting posture across developmental series (in 86% of cases, mainly mammals). Quadrupedal amniotes have proportionally robust humeri compared to bipedal taxa due to hypothesized differences in limb loading (McPhee et al. 2018). We show that this is true

FIG. 3. Mean posterior probabilities obtained from the DFA analysis using humeral and femoral maximum lengths. Log_{10}(Femoral Length) used as proxy for body mass. Silhouettes indicate different size class examples. Silhouettes courtesy of Phylopic (S. Hartman, J.J.W. Sertich, M.A. Loewen, P. Buchholz, M. Wedel, M. Martyniuk, G. Shaw, J.A. Venter, H.H.T. Prins, D.A. Balfour, R. Slotow, M. Karala, S. Werning).

| Bipedal birds | Rhea americana | Struthio camelus |
| Bipedal mammals | Macropus agilis | Macropus giganteus | Macropus rufogriseus | Macropus rufus | Pedetes capensis | Smutsia temminckii |
| Shifting mammals | Homo sapiens |
| Quadrupedal mammals & reptiles | Antilocapra americana | Bison bison | Bradypus insensatus | Caiman crocodilus | Choloepus hoffmannii | Connochaetes taurinus | Crocodylus niloticus | Dasypus novemcinctus | Dendrolagus dorianus | Dendrolagus lumholtzi | Felis silvestris | Hippopotamus amphibius | Iguana iguana | Myrmecophaga tridactyla | Odocoileus virginianus | Okapia johnstoni | Phascolarctos cinereus | Phataginus tetradactyla | Phataginus tricuspis | Procyon lotor | Smutsia gigantea | Ursus americanus |
| Dinosaurs | Massospondylus carinatus | Malasaurus peeblesorum | Mussaurus patagonicus | Rapetosaurus krausei | Psittacosaurus luluiatensis |

Log_{10}(Femoral Length) used as proxy for body mass. Silhouettes indicate different size class examples. Silhouettes courtesy of Phylopic (S. Hartman, J.J.W. Sertich, M.A. Loewen, P. Buchholz, M. Wedel, M. Martyniuk, G. Shaw, J.A. Venter, H.H.T. Prins, D.A. Balfour, R. Slotow, M. Karala, S. Werning).
throughout ontogeny for 21 animals that are known to be quadrupedal at early ontogenetic stages and remain so throughout their development (e.g. Procyon lotor, Ursus americanus and Hippopotamus amphibius) (Figs 1, 2; Chapelle et al. 2019, S3). The ratio of humeral shaft circumference to femoral shaft circumference is also conserved through ontogeny in 10 bipedal taxa with proportionally gracile humeri (such as Jaculus jaculus, Macropus agilis and Struthio camelus) (Figs 1, 2; Chapelle et al. 2019, S3). In our sole example where ontogenetic postural shifts are known to occur (humans), this transition is correctly identified by application of our method.

Some bipedal animals have robust humeri, including the ground pangolin Smutsia temminckii, which is a burrower (Steyn et al. 2018), and large kangaroos (Macropus giganteus and Macropus rufus). Smutsia temminckii was classified as a biped in our dataset, and indeed makes relatively little use of the forelimb during locomotion. However, we also observed that the forelimb contacts the ground every 3–5 steps of the hindlimbs. Its posture during travel is therefore arguably best classified as being equivocal. Large kangaroos have strong sexual dimorphism with stereotypical male behaviours and concomitant sexual selection involving the forelimb (Jarman 1983; Warburton et al. 2013). The largest specimens of Macropus rufus and Macropus giganteus in our sample are males, and are predicted to be equivocal or quadrupedal, whereas smaller specimens are predicted to be bipedal. Male kangaroos are known to reach twice the body mass of females (making it difficult to look at ontogeny in a mixed-sex sample) and to use their forearms in combat with other males (Jarman 1983; Warburton et al. 2013). If only female kangaroos were used, we hypothesize that the humerus to femoral robustness ratio would be conserved during ontogeny and would plot with other bipedal taxa. Positive allometry of forelimb robustness is also present in ratites (Rhea Americana and Struthio camelus) (Chapelle et al. 2019, S2), which use forelimb feather arrays during sexual display, although large individuals of our ratite sample are nevertheless correctly inferred as bipeds. These results indicate that the proportional robusticity can be overprinted by certain lineage-specific behaviours, but this only rarely leads to misclassifications with our method. Proportionally robust humeri were found in all quadrupeds regardless of whether their habitual forelimb posture was erect (e.g. in mammals) or sprawling (e.g. in non-dinosaurian reptiles).

Some extant taxa are predicted as having a mix of locomotory postures during ontogeny and have circumference ratios intermediate between those of most bipeds and most quadrupeds. These include the armadillo Dasypus novemcinctus (a quadrupedal species in which the majority of the specimens were classified as being equivocal) and the tree-kangaroo Dendrolagus lumholtzi (a quadrupedal species that our method predicts variably to be bipedal, equivocal or quadrupedal). The predominant locomotory habits of armadillos are not observed to vary during development (Taber 1945; Geist et al. 2004), however tree-kangaroos appear to have an ambiguous predominant locomotory posture, alternating between quadrupedalism and bipedalism both arboreally and terrestrially (Heise-Pavlov 2017).

Detailed behavioural studies of these living, equivocal or misclassified taxa have great potential to enlighten the reasons for these seemingly erroneous inferences. For example, Dasypus engages in some bipedal alert behaviours (McDonough & Loughry 2013) and uses the hindlimbs and tail for support when initiating digging with its forelimbs (Clerici et al. 2018) but is exclusively quadrupedal during locomotion (Costa et al. 2019). However, some species of armadillo employ plantigrade hindlimb postures and unguligrade forelimb postures during locomotion, suggesting a greater role for the hindlimbs in weight-bearing in at least some cingulates (Vizcaíno & Milne 2002). The closely related, extinct glyptodonts have also been interpreted as having posteriorly positioned centres of mass and possibly bipedal behaviours when using their armoured tails for defence (Vizcaíno et al. 2011). The apparent tendency for armoured terrestrial mammals to possess posteriorly positioned centres of mass (including the bipedal ground pangolin) may indicate a role for elongate and/or armoured tails and axial rigidity in transmitting the majority of the animal’s mass through the hindlimbs, and may explain the prevalence of forelimb-assisted fossorial behaviours in these animals.

Tree kangaroos spend the majority of their time as arboreal quadrupeds. However, observations of various Dendrolagus species in the wild show that they do frequently engage in bipedal saltation when locomoting terrestrially, exhibit bipedal alert postures when feeding perched on tree limbs, and primarily use the hindlimbs for power when climbing vertically (Procter-Gray & Ganslosser 1986). Dendrolagus lumholtzi and D. imustus are early-diverging species of tree kangaroo among extant taxa (Eldridge et al. 2018) and engage in some bipedal locomotor behaviours not reported in other Dendrolagus species (Procter-Gray & Ganslosser 1986). Dendrolagus dorianus, phylogenetically nested among more arboreally adapted tree kangaroos, uses a quadrupedal walk during terrestrial locomotion, and was accurately predicted to be a quadruped in this study.

**Postural predictions in extant ontogenetic series using limb length measurements**

Long bone length ratios are very poor indicators of posture in amniotes. Although the use of relative lengths
correctly identifies the postural shift seen in humans, it also results in the erroneous identification of an ontogenetic locomotor transition in many species where it is in fact absent (39% false positive rate for locomotory shifts). For example, Felis silvestris, Connochaetes taurinus and Crocodylus niloticus all have a negative allometric relationship between$log_{10}HL$ and$log_{10}FL$ during growth ($slope \leq 1$; Chapelle et al. 2019, S6), but these animals are quadrupedal throughout their ontogeny. This falsifies previous hypotheses that a negative allometric relationship between humerus length and femoral length during ontogeny is a reliable indicator of a shift toward bipedalism (Reisz et al. 2005). This extremely high false positive rate causes us to reject this approach.

Postural predictions in ontogenetic series of extinct dinosaurs using limb robusticity

Dinosaurs exhibited a variety of ontogenetic patterns, even within major groups. Taxa deeply nested within presumed bipedal groups are predicted to remain bipedal throughout their ontogeny by our method. These include the only non-avian theropod in the study, Limusaurus inextricabilis, the early branching sauropodomorph Massospondylus carinatus, and the hadrosaurid Maiasaura peeblesorum. The derived sauropod Rapetosaurus krausei, which is deeply nested in a quadrupedal group, was predicted to be quadrupedal throughout ontogeny by our method. This result corroborates previous studies that suggested that members of Sauropoda are obligate quadrupeds throughout their development based on near isometry of limb proportions during ontogeny (Rogers et al. 2016).

Previous inferences of ontogenetic shifts from quadrupedalism to bipedalism in non-avian dinosaur taxa were used to hypothesize a more widespread pattern of ontogenetic postural change in Dinosauria (Reisz et al. 2005; Zhao et al. 2013), however our results contradict some of the conclusions on which this hypothesis was based.

In particular, we reject the hypothesis that Massospondylus carinatus had an early quadrupedal phase in its ontogeny (Reisz et al. 2005), which was previously supported by observations of allometric scaling of the relative limb lengths (shown here to have high error rates). Instead, Massospondylus carinatus has limb bone shaft circumference ratios that remain consistent throughout ontogeny (Chapelle et al. 2019, S3) and is predicted to be bipedal from hatching to adult stage, suggesting that it was strictly bipedal throughout its development. This is consistent with previous observations of functional morphology (Bonnan & Senter 2007) and with observations of the endosseous labyrinth (Neenan et al. 2018). We also reject the hypothesis that Maiasaura was bipedal as a juvenile and became quadrupedal as an adult, which was previously suggested based on biomechanical and morphometric analyses (Dilkes 2001). More ontogenetic series of non-avian dinosaur taxa that can be confidently inferred to contain postural shifts are necessary to construct general hypotheses about the prevalence of this phenomenon within Dinosauria.

Two taxa are inferred to have undergone ontogenetic postural shifts: Massosaurus patagonicus within transitional Sauropodomorpha; and the early ceratopsian Psittacosaurus lujiatunensis within Ornithischia (Bonnan & Yates 2007; Otero & Pol 2013; Barrett & Maidment 2017). An ontogenetic postural transition from early-ontogenetic quadrupedalism to late-ontogenetic bipedalism is confidently inferred in Massosaurus (Fig. 2). Massosaurus had been hypothesized as being erect and at least facultatively bipedal as an adult (Otero et al. 2017), and a recent study has hypothesized a shift from quadrupedalism to bipedalism during ontogeny based on change in the body plan and its centre of mass (Otero et al. 2019).

Psittacosaurus lujiatunensis has a mix of quadrupedal, equivocal and bipedal posture predictions throughout its ontogeny. However, the hatching is confidently inferred as being quadrupedal and the largest two specimens as bipedal, supporting the hypothesis of a lengthy ontogenetic transition from quadrupedality to bipedality. This is consistent with previous research that hypothesized an ontogenetic postural shift from quadrupedalism to bipedalism based on limb length allometry as well as osteohistology (vascularization showing that the hindlimb grew rapidly during the during the middle part of development) (Zhao et al. 2013).

Postural predictions in embryos

Caution should be taken when including fossil embryos in locomotory studies if the developmental stage is not identifiable. The sole dinosaur embryo in our study, an in-ovo individual of Massospondylus carinatus, is predicted to be equivocal ($PP_{bip} = 0.415$). All larger individuals of Massospondylus carinatus, including the smallest juvenile (which has an appropriate size to be a recent hatching), are predicted to be bipedal. Previous inferences on the ontogenetic locomotory shifts of this taxon were based on samples that included this embryo (Reisz et al. 2005), under the assumption that it was near hatching. However, the equivocal prediction of the embryo could be due to it being earlier in development than previously hypothesized and could therefore be explained by one of two hypotheses: (1) in the absence of limb loading, embryonic limbs might respond to simple growth promotion signals during development, thus having more equivalent limb robusticities; (2) In the absence of loading, embryos could develop towards what their
functional demands as young individuals are likely to be (i.e. as hatchlings, the embryos would be quadrupedal and then shift to bipedalism later in development). To confirm which of these two explanations is correct, it would be necessary to include embryonic specimens in the ontogenetic sample of each extant amniote used in this study.

The implications of ontogenetic locomotory shifts

Although studying ontogenetic series has been shown to be useful for looking at macroevolutionary patterns in lineages (Heers et al. 2014), there is little consensus on the relationship of these hypothesized ontogenetic patterns with dinosaur macroevolution. The ontogenetic shift from quadrupedality to bipedality in the early ceratopsian *Psittacosaurus lujiatunensis* was suggested to reflect pleisiomorphic retention of the ancestral condition of quadrupedal basal archosaurs at early ontogenetic stages (Zhao et al. 2013). A hypothesized shift from quadrupedalism to bipedalism during the ontogeny of the early branching sauropodomorph *Massospondylus carinatus* prompted the hypothesis that quadrupedalism in later-branching sauropods could have evolved through paedomorphism (Reisz et al. 2005). This would imply a pattern whereby the early ontogenetic stages of progressively more derived sauropodomorphs have a quadrupedal posture which is retained at progressively later ontogenetic stages in more crownward taxa. Although not formally tested, it has been shown that the pattern of evolution of quadrupedality in sauropodomorphs is complex, with at least two, and possibly three, independent origins (at least among ontogenetically mature individuals) (Mcphee et al. 2018). We found the *Massospondylus carinatus* embryo to be equivocal and the next specimen after the embryo in the *Massospondylus carinatus* growth series is approximately hatchling size and predicted to be bipedal. This counters previous hypotheses that basal members of the three major dinosaur clades had quadrupedal hatchlings and therefore that the quadrupedal to bipedal ontogenetic shifts correspond to a recapitulation of the postural shift seen from basal quadrupedal archosaurs to bipedal avemetatarsalians (Zhao et al. 2013).

The two taxa with probable locomotory ontogenetic shifts occupy parts of the dinosaur tree where evolutionary transitions of posture are likely to have occurred based on optimizations of adult stances (Fig. 4). *Mussaurus* is more closely related to the obligately quadrupedal sauropods, and is nested within a clade that shows high incidence of quadrupedal adults (McPhee et al. 2018). We have the highest confidence in inferring a postural shift in *Mussaurus* among the dinosaurs in our study, and the macroevolutionary significance of this is different depending on phylogenetic hypotheses. If *Mussaurus* is phylogenetically placed among quadrupedal sauropodomorphs, then it represents a recent evolutionary origin of bipedalism from quadrupedal ancestors. If so, then its ontogenetic trajectory is potentially recapitulatory, because the hypothesized ancestral state for posture in sauropodomorphs is bipedalism throughout ontogeny, as supported by our observations in the earlier-branching *Massospondylus* and from other recent studies (Otero et al. 2017; McPhee et al. 2018). If *Mussaurus* is instead optimized as ancestrally bipedal, then it implies that the quadrupedality that characterizes all sauropods might have appeared first among juveniles of ancestral species with bipedal adults. *Psittacosaurus lujiatunensis*, being an intermediate ceratopsian, represents one of three independent transitions from bipedality to quadrupedality in Ornithischia (Maidment et al. 2014). While earlier-branching ceratopsians are probably bipeds (e.g. *Yinglong downsi*; Han et al. 2018), derived members such as ceratopsids are certain obligate quadrupeds.

Most extinct and extant amniote species conserve their posture throughout their ontogeny. Even though our sample is limited, the scarcity of ‘transitional’ locomotory values may be a result of macroevolutionary transitions in posture being fleeting events that involve rapid changes in the ontogenetic sequence and thus are unlikely to have been preserved in the fossil record. This rapidity of change in posture was also suggested by McPhee et al. (2018) based on optimization of a smaller sample of adult postures of sauropodomorph dinosaurs, but our analysis supports a more general application of this hypothesis.

CONCLUSION

Proportional humeral and femoral robusticity is more reliable than the ratio of humeral to femoral length for predicting habitual amniote posture across ontogenetic trajectories. Most living and extinct amniote species examined conserve their posture across ontogeny, and where a shift does occur in *Homo sapiens*, our method correctly identifies it. We falsify previous hypotheses that such shifts were widespread in dinosaurs, at least among the dinosaurs we measured. Instead we hypothesize only two such shifts occurred: in the sauropodomorph *Mussaurus patagonicus* and potentially in the ornithischian *Psittacosaurus lujiatunensis*. These two hypothesized shifts occur in lineages that are temporally and phylogenetically proximate to hypothesized macroevolutionary postural changes. The lack of widespread ‘transitional’ postural values more distal to these inferred changes suggests that postural shifts are evolutionarily rapid and leave only ephemeral signals in the fossil record and in ontogenetic sequences. Complex locomotor repertoires, forelimb assisted digging and
adaptations for axial stiffness may confound inferences of habitual locomotor posture using limb robusticity.

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Data for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.j4869rd

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