Joint angular excursions during cyclical behaviors differ between tetrapod feeding and locomotor systems

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Abstract

Tetrapod musculoskeletal diversity is usually studied separately in feeding and locomotor systems. However, comparisons between these systems promise important insight into how natural selection deploys the same basic musculoskeletal toolkit—connective tissues, bones, nerves and skeletal muscle—to meet the differing performance criteria of feeding and locomotion. In this study, we compare average joint angular excursions during cyclic behaviors–chewing, walking and running–in a phylogenetic context to explore differences in the optimality criteria of these two systems. Across 111 tetrapod species, average limb-joint angular excursions during cyclic locomotion are greater and more evolutionarily labile than those of the jaw joint during cyclic chewing. We argue that these findings reflect fundamental functional dichotomies between tetrapod locomotor and feeding systems. Tetrapod chewing systems are optimized for precise application of force over a narrower, more controlled and predictable range of displacements, the principal aim being to fracture the substrate, the size and mechanical properties of which are controlled at ingestion and further reduced and homogenized (respectively) by the chewing process. In contrast, tetrapod limbed locomotor systems are optimized for fast and energetically efficient application of force over a wider and less predictable range of displacements, the principal aim being to move the organism at varying speeds relative to a substrate whose geometry and mechanical properties need not become more homogenous as locomotion proceeds. Hence, the evolution of tetrapod locomotor systems has been accompanied by an increasing diversity of limb-joint excursions, as tetrapods have expanded across a range of locomotor substrates and environments.

Introduction

Evolutionary biomechanical studies of vertebrate feeding and locomotor systems have provided important insights into the ways that natural selection deploys a basic toolkit of musculoskeletal components—connective tissues, bones, nerves and skeletal muscle—to meet a variety of performance criteria in different lineages (Hildebrand et al., 1985; Thomason, 1997; Wainwright, 1994). Most of these studies have focused on explaining cross-lineage diversity within feeding and locomotor systems, separately. For example, diversity in feeding-system morphology has been related to variation in feeding behavior and diet in a wide range of vertebrates, including fish, birds, lizards and mammals (Olsen, 2017; Reilly and McBrayer, 2007; Westneat, 2004), and diversity in locomotor morphology has been linked to variation in locomotor mode, ecology, substrate preference, and overall habitat (Fabre et al., 2017; Garland and Losos, 1994; Higham, 2007; Reilly et al., 2007). In contrast with the many studies examining diversity within feeding and locomotor systems, studies that explicitly compare the two systems are much less common, despite the insight they provide into general principles of musculoskeletal design (Ahn et al., 2018; English, 1985; Higham, 2007; Ross et al., 2017). Here we relate variation in joint angular excursions during cyclic behaviors—chewing, walking, running—to variation in the functional optimality criteria and mechanical constraints governing evolution of feeding and locomotor systems. By examining these patterns in a phylogenetic context, we relate this variation to the evolution of disparity in jaw- and limb-joint excursions during tetrapod evolution.

Cyclic Behaviors: Chewing vs. Walking and Running

The function of oral food processing—biting and chewing—is to fracture the food substrate, facilitating digestive efficiency and formation of food boluses with material properties and small size needed to make them safe to swallow (Iriarte-Díaz et al., 2011; Prinz and Lucas, 1997). The size of the food item is also important at the start of chewing because most tetrapod jaws function as 3rd class levers[1] (Turnball, 1970) and the ability of the jaw-closing muscles to produce force depends on their length-tension relationships, a combination that creates trade-offs between bite force and jaw gape that are well documented in lizards and mammals (Dumont and

[1] As 3rd class levers, the jaw-elevator muscle resultant lies between the jaw joint and the bite point. The trade-off also obtains in the case of 2nd class lever arrangements, argued to occur in some mammals (Turnbull, 1970).

Herrel, 2003; Eng et al., 2009; Gidmark et al., 2013; Herrel and O'Reilly, 2005; Hylander, 2013; Meyers et al., 2018; Ross and Iriarte-Diaz, 2014; Ross et al., 2018; Santana, 2016; Taylor and Vinyard, 2009; Taylor and Vinyard, 2009; Williams et al., 2009). Hence, chewing is often preceded by ingestive behaviors[2], such as incisor biting and cropping, which function in part to reduce the food substrate to sizes and shapes that allow tooth-food-tooth and/or tooth-tooth contact, usually at low jaw gape angles (Bramble and Wake, 1985; Hiiemae and Crompton, 1985; Hiiemae and Kay, 1973; Reed and Ross, 2010). Because most chewing occurs on posterior teeth, where proximity to the jaw joint increases both mechanical advantage and bite force, the force-gape trade-off imposes particularly strict limits on the size of the bolus that can be fractured efficiently. Chewing systems, moreover, operate at relatively consistent speeds—there is no fast chewing speed analogous to running or galloping: selection for improved feeding performance does not appear to result in faster chewing (Ross and Iriarte-Diaz, 2014; Ross et al., 2017). In sum, tetrapod chewing involves precise application of force over a narrow, controlled and predictable range of displacements, the principal aim of chewing being to fracture the substrate, the size and mechanical properties of which are controlled at ingestion and further reduced and homogenized (respectively) by the chewing process. Together, these functional demands and mechanical constraints on tetrapod feeding-system design support the prediction that angular excursions of tetrapod jaws during chewing will be narrow and not especially variable, at least compared with angular excursions of tetrapod limbs during locomotion, discussed next.

By comparison, the functions of the locomotor system are to move the organism from place to place to acquire food and mates while avoiding predation and minimizing competition. Locomoting animals confront substrates that vary in regularity, mechanical properties and complexity, requiring limbed tetrapods to modulate overall speed and limb-joint excursion in order to maintain dynamic stability (Daley et al., 2006; Granatosky et al., 2018). Moreover, unlike chewing sequences, the goal of which is to reduce food item size, progression through a locomotor bout is not inevitably associated with progressive reduction in substrate size and complexity: the goal of locomotion is not to make the substrate flatter and/or more homogeneous. In addition, unlike chewing, the energetic costs of locomotion make up a large

[2] Here we refer to ingestion sensu stricto, the introduction of food into the oral cavity (Hiiemae and Crompton, 1985; Ross and Iriarte-Diaz, 2014)

proportion of the overall energy budget, so many tetrapod lineages have evolved morphologies and kinematic strategies—including limb angular excursion—that reduce the overall cost of transport (Kram and Taylor, 1990; Pontzer, 2016; Reilly et al., 2007). The predominant energy-consuming process in locomotion is the generation of muscular force (Kram and Taylor, 1990; Pontzer, 2016); during locomotion on level substrates, forces produced by limb muscles, integrated over the stance phase, must support body weight and propel the animal forward. Because rates of muscle-force production per unit of body mass—and the overall metabolic cost of supporting the body—are reduced by lengthening stance phase (Kram and Taylor, 1990; Pontzer, 2016; Reilly et al., 2007; Roberts et al., 1998), and whole limb angular excursion is an important determinant of stance phase duration (Pontzer, 2007; Pontzer, 2016), selection for reduction in energetic costs of locomotion is expected to increase limb joint excursions.

Hence, we hypothesize that, because of their differing functional goals and mechanical constraints, tetrapod jaw-joint excursions during chewing are smaller and less variable than limb-joint excursions during walking and running, not only within clades, but across tetrapods as a whole. Here we corroborate this hypothesis on a broad phylogenetic sample of living tetrapods, identify important clade-specific patterns in limb- and jaw-joint excursions, and show that the kinematic differences between feeding and locomotor systems are associated with differences in evolutionary (phylogenetic) rates of change in joint-angle excursions across tetrapods.

Materials and Methods

To draw biologically meaningful comparisons between cyclical behaviors performed by the feeding (i.e., chewing) and locomotor (e.g., walking, trotting, running) systems we compared average two-dimensional (2D) joint-angle excursions in degrees (°) during cyclical behavior sequences. During chewing, joint excursion angles were calculated at the jaw joint (i.e., quadrate-articular and dentary-squamosal) following examples by Cleuren and de Vree (1992), Heiss and colleagues (2019) and Schwenk and Throckmorton (1989). During walking and running, data were collected on anteroposterior angular excursions at the wrist, elbow, shoulder, ankle, knee and hip joints following examples by Fischer et al. (2002), Herrel et al. (2013), and Verstappen et al. (2000). In bipeds (i.e., birds and humans), data were only collected from the joints of the hind/lower limb. Data in this study combines *de novo* analyses supplemented by existing data from the literature. All *de novo* data collection protocols were approved by New

York University Committee on Activities Involving Human Subjects (protocol number 11–8561), Hunter College Human Research Protection Program (protocol number 11–08-165–4471), Ohio University Institutional Animal Care and Use Committee (IACUC; protocol number U-99-03), Duke University IACUC (protocol no. A270-11-10), Duke Lemur Center (protocol number MO-10-11-3), and University of Chicago IACUC (protocol numbers 71489, 71565, 71689, 72351, and 72430).

Jaw-joint excursions were measured during chewing on foods ranging in material and geometric properties, which were pooled for analyses. Angular excursions of the jaw joint during cyclical chewing were calculated following two separate methodologies, depending on how the data were initially collected. For some species, lateral-view video recordings (*Moloch horridus*, *Mandrillus sphinx, Pogona henrylawsoni,* and *Uma scoparia*) and videoradiographic recordings (*Salvator merianae*) were available. For these videos, the jaw joint and the anterior-most points of the upper and lower jaws were digitized in each frame of each cycle in DLT Dataviewer (Hedrick, 2008) in MATLAB (Mathworks, Natick, MA). Angular movements about the jaw joint were calculated using MATLAB scripts and joint excursion was measured by calculating the maximum change in joint-angle during jaw closing (i.e., maximum gape to minimum gape within a chew cycle). For *Sapajus apella, Papio anubis, Macaca mulatta* and *Homo sapiens,* kinematic data were collected using 3D motion-capture methods described in detail elsewhere (Iriarte-Díaz et al., 2011; Laird et al., 2016; Reed and Ross, 2010). Briefly, at least three reflective markers were coupled to the mandible and cranium and jaw movements recorded in 3D using a six- or ten-camera Vicon system at either 100 or 250 frames per second. Inter-marker distances were calculated from the subjects and then matched with Vicon recordings to reconstruct angular movements during cyclical chewing. By quantifying jaw-joint excursion relative to the anatomical jaw joint (rather than the true axis of rotation), jaw excursion is slightly overestimated (Ross et al., 2017; Weijs et al., 1989). In those species with streptostyly and/or mesokinesis (at least seven of our lizard species, plus the duck, *Anas*) estimates of jaw joint excursion about the quadrate-articular joint slightly overestimate excursions at that joint.

All locomotion data were collected from videos taken in lateral view at 60-120 frames per second. Only strides in which the animal was traveling in a straight path and not accelerating or decelerating (i.e., steady-state locomotion) were selected for analysis. Steady-state locomotion was determined by calculating the instantaneous velocity between subsequent video frames

throughout the entire stride, and then using regression analysis to determine whether velocity changed throughout the stride (Granatosky, 2016). Angular movements of joints during locomotion were digitized from these lateral-view video recordings by calculating the maximum change in joint angle throughout stance phase. All limb-joint angles were digitized using DLT Dataviewer (Hedrick, 2008) in MATLAB following previously established protocols (Granatosky, 2016).

As our goal was to include excursion data from as many tetrapod taxa as possible, we supplemented our own data with angular excursion data collated from the literature. Some of these studies addressed variation in feeding and locomotor behaviors across different substrates (e.g., different food items or arboreal versus terrestrial), in which case we combined means and standard deviations for each substrate in order to create a pooled mean and standard deviation for a given species. In cases where authors did not report means and standard deviations for angular excursion data, but instead only reported angular movements for "representative cycles", these cycles were digitized using ImageJ and means and standard deviations calculated. In total, joint excursion data were obtained from 111 species (Table S1).

Several studies report that limb-joint excursions covary with body mass and/or locomotor speed (Gatesy, 1994; Reilly and Delancey, 1997; Reilly and Elias, 1998). To test the effect of body mass on jaw and limb joint excursion in our sample, each joint excursion was regressed against $\log_{10}$ body mass. To test the effect of locomotor speed on limb joint excursion in our sample, each limb joint excursion was regressed against $\log_{10}$ speed. Our sample exhibited a negative correlation between angular excursions and $\log_{10}$ body mass at all joints (all regression coefficients $P \leq 0.02$), but there was no significant association with speed (all $P > 0.25$) (Fig. S1). This is likely a result of sampling excursion and speed interspecifically rather than intraspecifically, and therefore the scale of the sample may mask velocity associations. Furthermore, because many studies do not report limb lengths, relative measures of locomotor speed using Froude number could not be calculated. Most of the locomotor data was collected from animals moving freely in naturalistic settings but some of the data are from studies of animals moving on treadmills (Table S1). While there is always concern related to treadmill versus naturalistic locomotor performance, data collected by Fischer (1999) and Fischer et al. (2002) suggest these effects are minimal and within our dataset only a slight treadmill effect is

observed in the knee (Fig. S2). As such, we do not consider a treadmill effect in further statistical tests.

Joint excursions could covary with phylogeny, thus analyses incorporated a phylogenetic component. All phylogenetic analyses were performed in R-Studio (Ver. 1.1.383) and R (Ver. 3.4.2). We generated a sample of 100 phylogenetic trees to account for phylogenetic uncertainty using the template of a recently published study on European tetrapods (Roquet et al., 2014). To do this, we first built the trunk of the phylogenetic tree to include the most recent common ancestor (mrca) of each of the following crown groups: Amphibia, Mammalia, Lepidosauria, Testudines, Crocodylia, and Aves. Tree topology was fixed to widely accepted relationships among these major groups and the depth of each mrca node was fixed to the mean value reported at www.timetree.org (Hedges et al., 2006; Hedges et al., 2015; Kumar and Hedges, 2011; Kumar et al., 2017). Next, we grafted samples of trees for each crown group onto this trunk. To do this, we retrieved 1000 posterior samples of trees from www.vertlife.org/phylosubsets that were generated from phylogenetic analyses of squamates (Tonini et al., 2016), birds (Jetz et al., 2014) and amphibians (Jetz and Pyron, 2018) We used a posterior sample of 100 trees for mammals (Kuhn et al., 2011) which was based on a recent supertree analysis (Hedges et al., 2006; Hedges et al., 2015; Kumar and Hedges, 2011; Kumar et al., 2017). The mammalian trees did not include *Pygathrix cinerea*, for which we have excursion data, so we assigned it the position of its close relative *Pygathrix nigripes*. Our dataset included two turtle and two crocodilian species, the branching times for which were estimated using values from www.timetree.org (Hedges et al., 2006; Hedges et al., 2015; Kumar and Hedges, 2011; Kumar et al., 2017). We then randomly chose one sample of each of these trees, rescaled them to the depth of the associated mrca node on the trunk and then grafted them onto that node. We repeated this procedure 100 times to produce a posterior sample of 100 trees that accounted for uncertainty in branch lengths and topology. These trees were not ultrametric due to the decimal precision of the branch length estimates in the grafted trees; therefore, we forced them to be ultrametric by adding the minimal branch lengths needed (see http://blog.phytools.org/2017/03/forceultrametric-method-for-ultrametric.html for additional explanation). The final sample of 100 ultrametric, dated phylogenetic trees was used in all subsequent analyses. The maximum clade credibility tree from this sample had 100% nodal support for all nodes except for the following: 43%, *Trachypithecus poliocephalus* and *Trachypithecus hatinhensis*, 52% *Aotus nancymaae*:*Sanguinus oedipus*, 37%

Lemur catta:*Eulemur fulvus* and 45% *Varecia variegata*: ancestor of (*Lemur catta*:*Eulemur fulvus*). The results of subsequent comparative analyses are presented as the mean ± standard deviation of the test statistic as computed from the sample of 100 trees. R-packages used to construct the trees included ape (Paradis et al., 2004) and phangorn (Schliep, 2011).

To determine whether phylogenetic relationships among species influence measures of jaw- and limb-joint excursion, phylogenetic signal in each joint was quantified using Blomberg's *K* and tested for significance with 999 randomizations (Blomberg et al., 2003) using the R package phytools (Revell, 2012). Only the jaw, and proximal and middle limb-joint excursions exhibited significant phylogenetic signal (Blomberg's *K* (mean ± s.d. across 100 phylogenies): jaw = 0.69 ± 0.02, $P = 0.001$; hip = 0.39 ± 0.01, $P = 0.001$; knee = 0.28 ± 0.01, $P = 0.001$; shoulder = 0.31 ± 0.04, $P = 0.001$; elbow = 0.56 ± 0.05, $P = 0.001$). Hence, subsequent analyses account for mass and phylogeny, but not speed, when testing for differences in mean joint excursions.

The hypothesis that average jaw-joint excursion during chewing is lower than average limb-joint excursions during walking and running was tested using three methods. First, ANCOVA with $\log_{10}$ body mass as the covariate was used to compare angular excursion data from the jaw and each of the limb joints across all species. This approach could be applied to the entire dataset, but was problematic in that data for each joint were not always statistically independent (i.e., 15 of 111 taxa in the dataset have jaw as well as (some) limb joint excursion data available for analyses). An additional concern was that species are phylogenetically related, also violating the assumption of independence. We addressed the issue of statistical and phylogenetic non-independence by using phylogenetic paired *t*-tests to compare angular excursions between joint pairs (Revell, 2012) using the R package phytools. Resulting *P*-values from each set of tests were separately adjusted to minimize Type 1 error using the Bonferonni method.

The hypothesis that jaw excursion was less variable than limb joint excursions across species was tested using three methods. First, non-phylogenetic Levene's tests were used to compare the variance in jaw excursion to the variance in each limb-joint excursion across species. Second, we incorporated phylogeny into this analysis by fitting a Brownian motion model of evolution (Felsenstein, 1985) to each joint and then comparing the magnitude of the rate parameter across joints. Maximum likelihood ancestral states were reconstructed at each

joint assuming a Brownian motion model and then plotted into traitgrams to visualize trait covariation with phylogeny. These evolutionary analyses were done using the packages phytools and geiger (Harmon et al., 2007; Revell, 2012). Third, we used analysis of disparity through time to visualize how trait disparity (i.e., the range of morphological diversity within a group) accumulates through evolutionary time and to compute a morphological disparity index for each joint to quantitatively assess the accumulation of variation and its overlap among clades; these analyses were performed using geiger (Harmon et al., 2003; Harmon et al., 2007). The morphological disparity index is computed as the difference in relative trait disparity between the observed data and that expected under a null hypothesis of Brownian motion. Positive values indicate that subclades exhibit substantial overlap in trait values, indicating that trait variance accumulates near the tips. Negative values indicate that trait variation accumulates rapidly near the root of the phylogeny such that subclades show little overlap. Values near zero could indicate that trait variance accumulates steadily, as expected by a Brownian motion model of trait evolution.

Results

Joint excursion data for all 111 species are provided in Supplementary Table 1. Joint excursions are significantly lower (ANCOVA, main effect of joint: $P < 0.001$) in the jaw joint (23.33° ± 9.95°) than in every joint of the forelimb (shoulder = 70.26° ± 25.49°; elbow = 39.30° ± 19.79°; wrist = 51.15° ± 20.73°) and hindlimb (hip = 73.75° ± 29.00°; knee = 40.16 ± 21.39°; wrist = 47.24 ± 24.50°) (Figure 1). One-tailed paired *t*-tests on the sub-sampled data are also significant for all jaw- and limb joint comparisons (Supplemental Table 2). When accounting for phylogeny this difference remains significant for all joints (Supplemental Table 2), indicating these differences are not merely attributable to shared evolutionary history.

Jaw excursion was less variable when compared to limb joint excursions at all joints (non-phylogenetic Levene's tests, $P \leq 0.002$ for all comparisons, Fig. 1). The rate parameter from the Brownian motion model fitted to jaw excursions (σ^2 [mean±standard deviation computed across trees]= 0.54±0.01 degrees million-years^{-1}) was an order of magnitude smaller than the rate parameter for all limb joints (hip σ^2: 7.59±0.28, knee σ^2: 7.42±0.19, ankle σ^2: 12.4±0.20, shoulder σ^2: 7.05±1.16, elbow σ^2: 5.95±0.61, wrist σ^2: 9.19±0.06 degrees million-

years^{-1}), indicating that jaw-joint excursion evolved more slowly than limb-joint excursions. The pattern in which variation in joint excursions accumulates during the evolutionary history of tetrapods is different across joints (Figs. 2-4). Most variation in ankle, knee, wrist and elbow angular excursions accumulated near the tips of the tree, a pattern deviating from Brownian motion (Figs. 3 and 4), as reflected in their relatively larger morphological disparity index values (mean±s.d. from fit across sample of 100 trees: ankle = 0.30±0.01, knee = 0.34±0.01, wrist = 0.39±0.01, elbow = 0.25±0.01). Conversely, jaw, hip and shoulder-joint excursions follow a Brownian motion model of trait evolution with variation accumulating steadily during their evolutionary histories (Figs. 2-4); their morphological disparity index values are near zero (jaw = 0.04±0.01, hip = 0.12±0.02, shoulder = 0.05±0.01).

Discussion

The data presented here support the hypothesis that across tetrapods joint excursions during commonly employed cyclical behaviors—chewing, walking and running—are smaller in the feeding system than the locomotor system. The data also reveal that across tetrapods cyclic jaw-joint excursions evolved at slower rates than cyclic limb joint excursions.

In discussing these results, it is important to recognize several constraints on our study that limit the scope of its applicability. First, most tetrapods likely generate larger jaw- and/or limb- joint excursions during discrete, non-cyclic behaviors than during cyclic behaviors (Essner, 2002; Herring and Herring, 1974; Hylander, 2013; Malfait et al., 2014; Rundquist et al., 2009; Vinyard et al., 2011; Williams et al., 2009). That said, we restricted our analysis to data from cyclic (repeated) behaviors because they are important behaviors in all tetrapods, they are available at larger sample sizes across a wider taxonomic breadth than discrete behaviors, and because, unlike maximum jaw joint excursions (Hylander, 2013), reliable estimates of maximum limb joint excursions are difficult to replicate (DeRousseau et al., 1983; Hammond, 2014; Hammond et al., 2017). Discrete and cyclic behaviors are also fundamentally different in their dynamic properties and, therefore, in their motor control, suggesting that combining their joint excursion data in one analysis would be inappropriate (Hogan and Sternad, 2007; Schaal et al., 2004). Future work comparing joint excursions during discrete behaviors with those during cyclic behaviors would certainly be of interest. Second, although the data from the literature were collected under non-identical experimental conditions, and jaw-and limb-joint excursion

data were seldom available from the same species or individual, the consistency of our results across multiple limb joints and clades, and the magnitude of the differences between limb and jaw joints, are compelling, leading us to doubt that a perfectly sampled dataset of jaw and limb excursions from as wide a taxonomic sample of individuals would yield results to appreciably alter our interpretations and conclusions. Third, in this study we estimated jaw-joint angular excursions in non-mammals about the quadrate-articular joint. By estimating jaw-joint excursions about the quadrate-articular joint, we over-estimate excursion at that joint by including excursions associated with streptostyly and mesokinesis in some of our lizards and our *Anas* data. While this is not ideal, subtraction of the effects of streptostyly and mesokinesis would in most cases actually decrease angular excursions at the quadrate–articular joint, thereby further decreasing excursions at the jaw joint in comparison with the limb joints. Finally, our sample only considers two-dimensional (2D) joint rotations. The goal of this study was to look at as broad of a phylogenetic sample of tetrapods as possible to understand evolutionary patterns of joint angular excursions. As such, 2D data are certainly sufficient to provide an initial broad comparative assessment of these evolutionary patterns. We do not explicitly test whether considering 3D data would affect our findings because the reduction in taxonomic breadth (i.e., from 111 species down to 24 species) would so alter our species composition that any differences between the two sets of data could be ascribed to taxonomic sampling. Furthermore, in the feeding system, the open-close jaw excursions analyzed here are by far the largest rotational components of jaw movement (Buschang et al., 2000; Davis, 2014; Iriarte-Díaz et al., 2011; Menegaz et al., 2015). In the limbs, abduction/adduction and long axis rotation can be quite high (Baier and Gatesy, 2013; Fischer et al., 2010; Kambic et al., 2014; Kambic et al., 2015; Nyakatura et al., 2010; Nyakatura et al., 2019; Schmidt and Fischer, 2010), especially in sprawling tetrapods (Baier and Gatesy, 2013; Fischer et al., 2010; Nyakatura et al., 2019). Thus comparisons of jaw and limb excursion patterns in these anatomical planes are unlikely to alter the major findings of this study. Further considerations of 3D joint movements are beyond the scope of this study, but as precise 3D kinematic data becomes increasingly easier to collect, we can anticipate that others will explicitly analyze 3D joint movements between the feeding and locomotor systems.

These limitations notwithstanding, we argue that our results highlight a fundamental functional dichotomy between cyclical behaviors performed by the feeding and locomotor

systems: namely, chewing is more strongly optimized for the generation of precisely controlled force and displacement over narrow ranges of gapes, whereas walking and running are more strongly optimized for speed and energetic efficiency. The energetic costs of locomotion can be quite high [reaching upwards of 34% of an animal's daily energy costs (Hoyt and Kenagy, 1988; Karasov, 1992); in humans they represent ca. 8.5 times the cost of cyclic chewing (20.7 ± 9.86 J/sec during chewing versus ~175 J/sec during locomotion) (Hanna and Wall, 2016)]. It is therefore no surprise that tetrapods seem to have adopted a range of strategies to reduce locomotor costs (Alexander, 1990; Alexander, 1991a; Alexander, 1991b; Biewener, 1998; Hoyt et al., 2000; Kram and Taylor, 1990; Reilly et al., 2007). One of these strategies—increases in total step length and stance duration—can be directly linked to the relatively large limb-joint excursions shown here to characterize a wide range of tetrapods. Lengthening steps through increased joint excursion reduces the frequency of muscle activation over a given distance moved, reducing the metabolic cost of locomotion (Pontzer, 2007; Pontzer, 2016; Reilly et al., 2007; Roberts et al., 1998).

In contrast, the feeding system does not appear to be designed to minimize the overall energy cost of chewing. Preliminary data from humans reveal similar rates of energy consumption for chewing and digestion [chewing, 20.7 ± 9.86 J/sec (Hanna and Wall, 2016); digestion, ~20 J/sec (Secor, 2009)], yet digestion-related costs last for ca. 8-10 hours (Westerterp, 2004), an order of magnitude greater duration than that used for chewing (Hanna and Wall (2016). The relatively high energetic costs of digestion may well impose functional demands on chewing performance, but the low absolute cost of chewing makes it the cheapest energetic investment of the whole feeding system. Avoidance of fatigue might favor energetically efficient chewing, although interspecific scaling analyses of mammal feeding times suggest that many mammals are not time constrained during feeding (Organ et al., 2011; Ross and Iriarte-Diaz, 2014; Ross et al., 2009). Hence, as we argue elsewhere, when chewing is a critical component of feeding, the need to minimize energy expenditure is much less important than the ability of the feeding system to produce highly controlled bite forces, minimizing tooth wear and the probability of tooth breakage (Ross and Iriarte-Diaz, 2014; Ross et al., 2007) this is especially important in mammals, with only one set of adult teeth. We suspect that minimizing tooth damage through precise control of jaw movements might also explain the smaller and less variable jaw excursions during chewing in other tetrapods.

Evolution of joint excursions

Our phylogenetic analysis reconstructs relatively low jaw joint excursions (~25^{o}) and relatively high limb joint excursions (~50-75^{o}) as the basal conditions for tetrapods (Figs. 2-4): if our hypothesis is correct, optimization of precisely controlled bite force and displacement during cyclical chewing and long stride lengths during cyclical locomotion was present in early tetrapods. The shift from water to land early in tetrapod evolution was accompanied by a change from aquatic suction-feeding, involving high jaw-joint excursions and rapid jaw opening and closing velocities (Oufiero et al., 2012), to chewing on terrestrial prey with low excursions and velocities (Markey and Marshall, 2007). Future studies incorporating underwater feeding strategies in fish would be an interesting way to explore this hypothesis further. Our analysis reconstructs further reductions in jaw-joint excursions in the early evolutionary history of mammals (Fig. 2), reflecting an emphasis in mammalian chewing (mastication) on bite force generation near or in occlusion—at smaller gapes—and reduction of food items to small sizes to facilitate efficient digestion (Reilly et al., 2001). However, the relatively slow rate at which jaw excursion has evolved among tetrapods suggests to us that the functional demands on the mammal chewing system are merely an extreme instance of those on tetrapod chewing systems more generally: their principal aim being to fracture the substrate, the size and mechanical properties of which are controlled at ingestion and further reduced and homogenized (respectively) by the chewing process itself. If all tetrapod chewing does indeed function to reduce and homogenize the substrate, it is not surprising that jaw joint excursion during cyclical chewing is not characterized by particularly high variation across tetrapods.

In contrast, limb joint excursions are consistently larger and more evolutionarily labile than jaw joint excursions (Figs 3-4). This may in part be due to greater complexity of the locomotor system (e.g., more joints, bones and muscles) compared with the feeding system. However, we argue that it primarily reflects the fact that, in combination with limb morphology (Adamowicz et al., 2008; Bergmann and McElroy, 2014; Carroll, 2001), tetrapod limbed locomotor systems are more highly optimized for fast and energetically efficient application of force over a wider and less predictable range of displacements, the principal aim being to move the organism at varying speeds relative to substrates whose geometry and mechanical properties need not become flatter and more homogenous as locomotion proceeds. Optimization for these

functions means that, as tetrapod lineages expand their range of locomotor modalities (e.g., cursoriality and arboreality), environments, and substrate geometries, they will also exhibit a wider range of limb excursions. If correct, this means that the contrasting patterns of joint excursion evolution in tetrapod feeding and locomotor systems during cyclical behaviors are explicable with reference to differences in the optimality criteria underlying their functional design.

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Competing interests

The authors report no competing interests or conflict of interest.

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Author contributions

MCG, CFR, and ABT designed the study. MCG collected data from the literature and provided locomotor data from mammals. EJM conducted all phylogenetic analyses. EJM and SMR provided data on reptile locomotion. MFL provided kinematic data from human chewing. JID and CFR provided kinematic data from primate chewing. MCG, EJM, MFL, JID, ABT, SMR and CFR wrote and edited the manuscript.

Data accessibility

All data used for analyses are present in Table S1.

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Figures

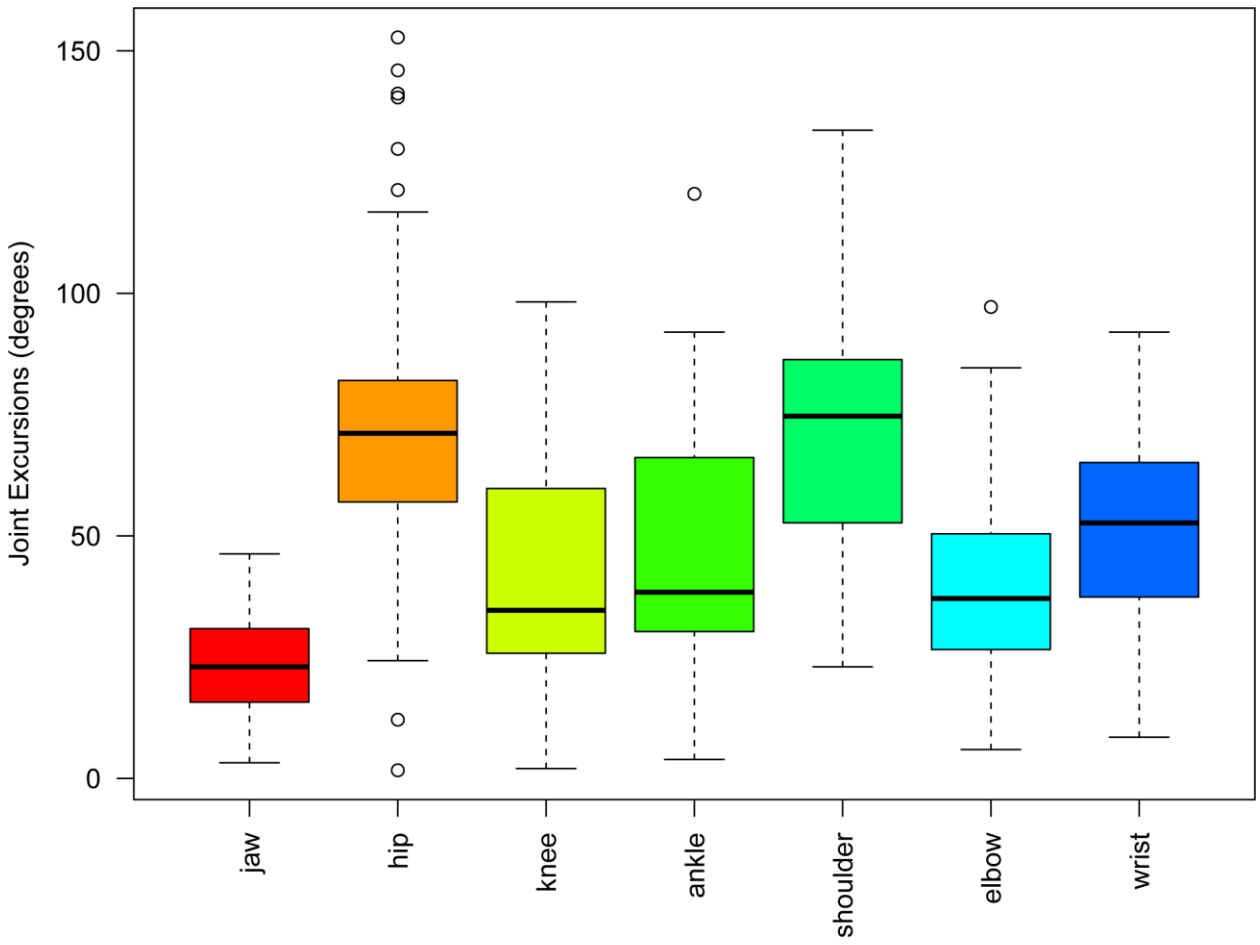

Fig 1: Box plots of joint angular excursions. Heavy black bar is median, boxes are bounded by the 25th and 75th quartiles and whiskers are 1.5x the interquartile range or the maximum & minimum values. Hollow dots are values beyond 1.5x the interquartile range. Mean joint excursion and the variance in joint excursion is lower for the jaw compared to all limb joints.

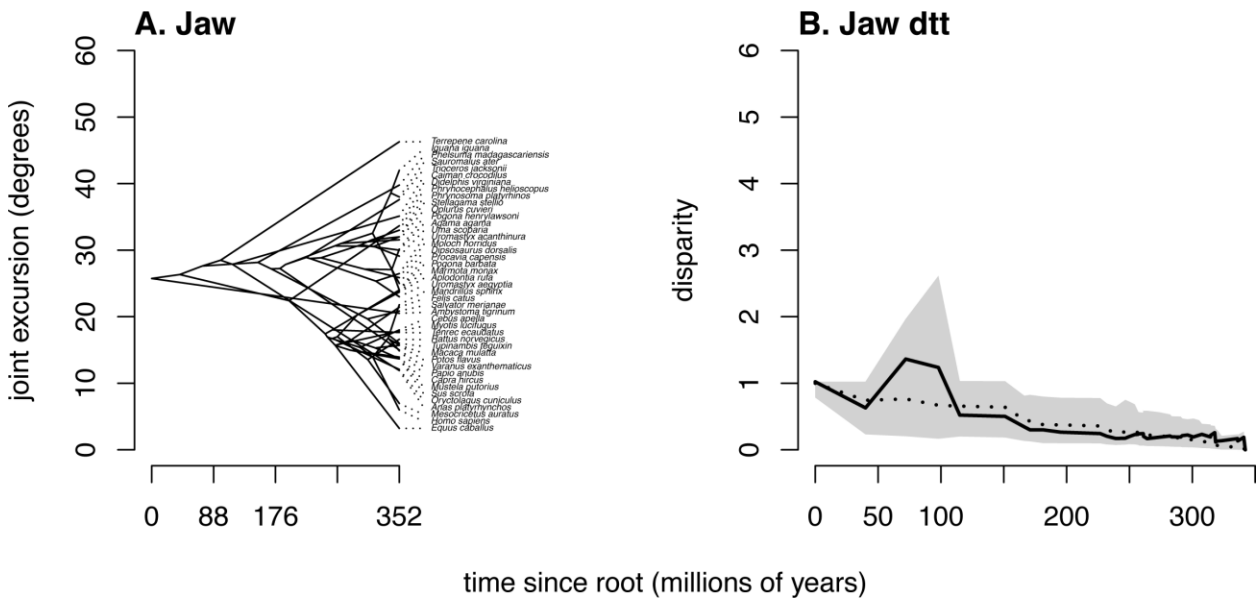

Fig 2: Panel A: Traitgram showing the maximum likelihood ancestral trait reconstructions of jaw joint angular excursions under a Brownian motion model of evolution. Panel B: Plot of disparity through time (dtt) showing how disparity in jaw joint angular excursion changed during the evolutionary history of tetrapods. Solid black line is disparity based on the data, dashed line is the median values expected under a null model of Brownian motion based on 1000 simulations. The grey polygon contains 95% of those simulations. Disparity in jaw joint excursion does not differ from a null model of Brownian motion.

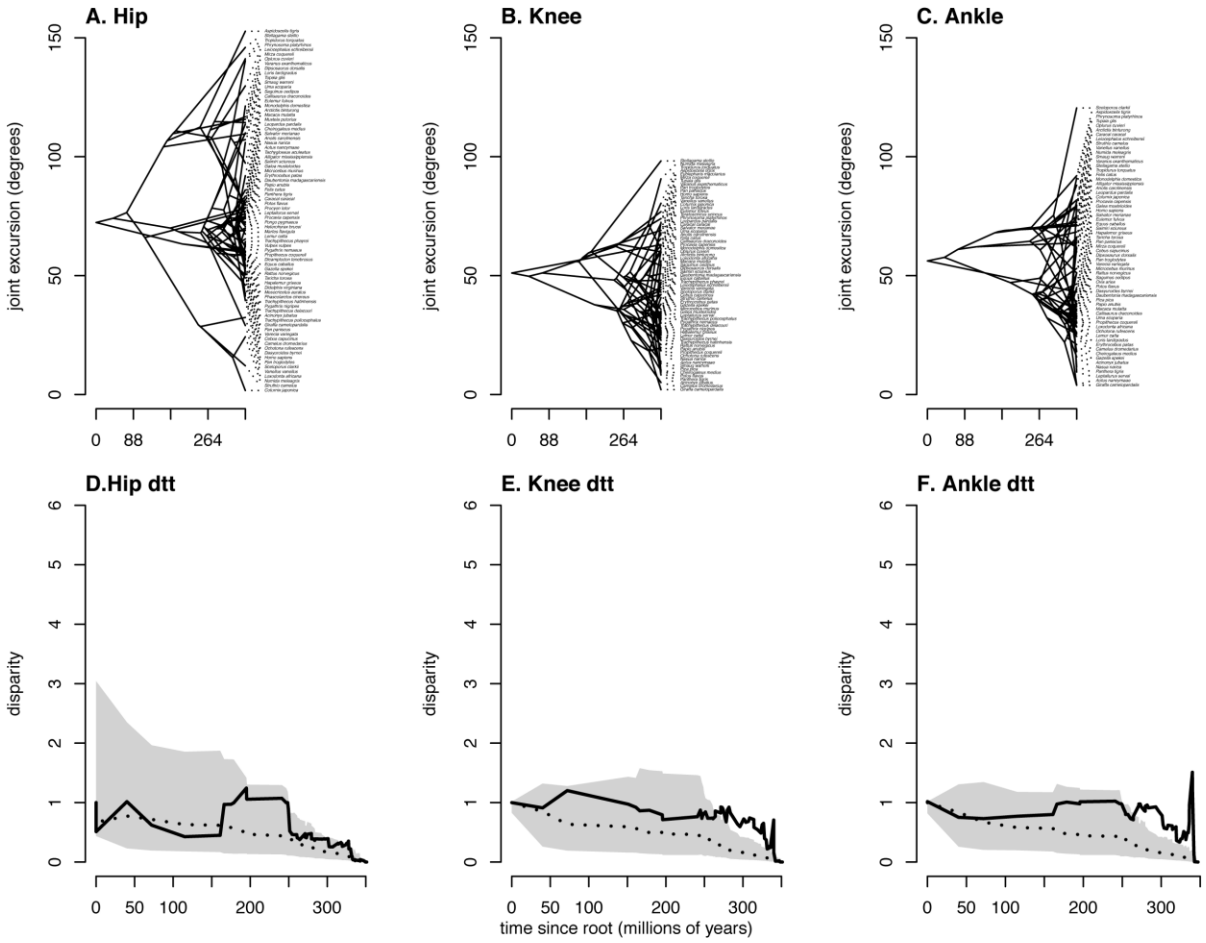

Fig 3: Panels A-C: Traitgrams showing the maximum likelihood ancestral trait reconstructions of hindlimb joint angular excursions under a Brownian motion model of evolution. Panels D-F: Plot of disparity through time (dtt) showing how disparity in hindlimb joint angular excursions changed during the evolutionary history of tetrapods. Solid black lines are disparity based on the data, dashed lines are the median values expected under a null model of Brownian motion based on 1000 simulations. The grey polygons contain 95% of those simulations. Disparity in hip joint excursion does not differ from a null model of Brownian motion. Disparity in knee and ankle joint excursion is significantly greater than expected by Brownian motion over the last ~ 100 million years of their evolutionary history.

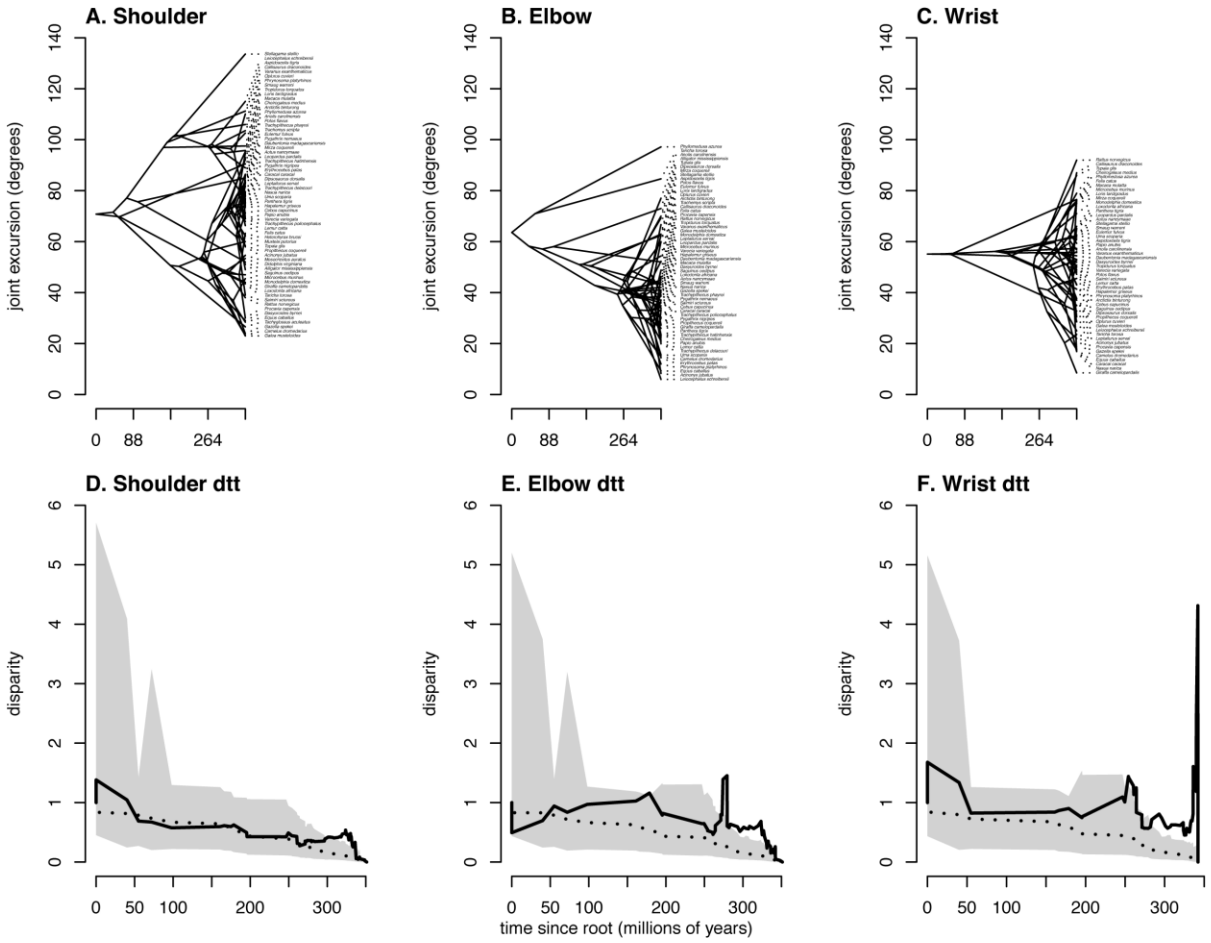

Fig 4: Panels A-C: Traitgrams showing the maximum likelihood ancestral trait reconstructions of forelimb joint angular excursions under a Brownian motion model of evolution. **Panels D-F: Plot of disparity through time (dtt) showing how the disparity in forelimb joint angular excursions changed during the evolutionary history of tetrapods.** Solid black lines are disparity based on the data, dashed lines are the median values expected under a null model of Brownian motion based on 1000 simulations. The grey polygons contain 95% of those simulations. Disparity in shoulder joint excursion does not differ from a null model of Brownian motion for most of its history, except the last ~50 million years. Disparity in elbow and wrist joint excursion is significantly greater than expected by Brownian motion over the last ~ 100 million years of their evolutionary history.

Table S1. Summary statistics, data source, and average joint excursions observed within species.

Group	Species	Body mass	Treadmill	Gait type	Data source	Individuals*	Cycles*	Jaw	Shoulder	Elbow	Wrist	Hip	Knee	Ankle
Urodela	*Ambystoma tigrinum*	0.13	-	-	(Reilly and Lauder, 1990)	4	42	20.51 ± 1.98	-	-	-	-	-	-
	Dicamptodon tenebrosus	0.07	Yes	Walk, Running trot	(Ashley-Ross, 1994)	5	30	-	-	-	-	60.30 ± 17.55	-	-
	Taricha torosa	0.01	Yes	Walk	(Ashley-Ross et al., 2009)	5	25	-	43.46	84.63	32.76	59.72	63.05	43.09
Anura	*Phyllomedusa azurea*	0.00	No	Walk	(Herrel et al., 2013)	R	R	-	90.50	97.18	76.54	-	-	-
Squamata	*Agama agama*	0.31	-	-	(Kraklau, 1991)	4	16	30.00 ± 12.40	-	-	-	-	-	-
	Agama stellio	0.30	-	-	(Herrel et al., 1996)	2	146	32.00 ± 7.00	-	-	-	-	-	-
	Amphibolurus barbatus	0.69	-	-	(Throckmorton and Clarke, 1981)	3	29	23.29 ± 3.69	-	-	-	-	-	-
	Anolis carolinensis	0.00	No	Running trot	(Foster and Higham, 2012)	S, W, H: 4; E, K, A: R	S, W, H: 5; E, K, A: R	-	88.96 ± 7.11	77.02	56.01 ± 8.81	31.23 ± 3.67	48.07	61.92

Callisaurus draconoides	0.01	Yes	Running trot	(Irschick and Jayne, 1999)	R	R	-	110.09	48.82	87.03	97.30	46.44	30.30
Cnemidophorus tigris	0.02	Yes	Running trot	(Irschick and Jayne, 1999)	R	R	-	111.25	62.40	57.32	152.75	76.89	92.01
Cordylus warreni	0.04	No	Running trot	this study	4	9	-	97.54 ± 17.33	34.03 ± 6.01	61.74 ± 22.40	109.60 ± 2.27	13.84 ± 8.08	72.38 ± 10.08
Dipsosaurus dorsalis	0.07	Yes	Running trot	(Irschick and Jayne, 1999; Schwenk and Throckmorton, 1989)	S, E, W, H, K, A: R; J: 2	S, W, H: 4; E, K, A: R; J: 10	25.00 ± 4.00	76.76	69.26	41.34	114.37	35.77	37.84
Eublepharis macularius	0.05	No	Running trot	(Fuller et al., 2011)	R	R	-	-	-	-	-	73.98	-
Iguana iguana	3.18	-	-	(Schwenk and Throckmorton, 1989)	1	4	42.00 ± 10.00	-	-	-	-	-	-
Laudakia stellio	0.05	No	Running trot	this study	2	15	-	133.62 ± 15.45	62.95 ± 10.30	62.38 ± 14.58	145.96 ± 11.59	98.23 ± 9.03	70.93 ± 13.43
Leiocephalus schreibersi	0.04	No	Running trot	this study	2	20	-	115.05 ± 26.72	5.94 ± 1.93	34.91 ± 12.80	129.77 ± 14.3	33.89 ± 14.30	79.35 ± 6.89
Moloch horridus	0.05	-	-	this study	1	9	25.87 ± 2.70	-	-	-	-	-	-

Oplurus cuvieri	0.05	No	Running trot	(Delheusy and Bels, 1992)	S, E, W, H, K, A: 3; J: 4	S, E, W, H, K, A: 25; J: 60	31.56 ± 6.24	103.55 ± 36.90	54.37 ± 11.21	37.08 ± 3.52	116.77 ± 11.34	43.01 ± 14.73	81.81 ± 15.29
Phelsuma madagascariensis	0.06	-	-	(Delheusy and Bels, 1999)	4	28	39.78 ± 5.06	-	-	-	-	-	-
Phrynocephalus helioscopus	0.06	-	-	(Schwenk and Throckmorton, 1989)	2	8	33.00 ± 8.00	-	-	-	-	-	-
Phrynosoma platyrhinos	0.05	Yes	Running trot	(Irschick and Jayne, 1999; Schwenk and Throckmorton, 1989)	S, E, W, H, K, A: R; J: 1	S, E, W, H, K, A: 1; J: 5	32.00 ± 1.00	102.61	11.94	47.19	140.37	59.77	90.96
Pogona barbata	0.59	-	-	(Schwenk and Throckmorton, 1989)	1	6	28.00 ± 4.00	-	-	-	-	-	-
Pogona henrylawsoni	0.68	-	-	this study	1	10	30.16 ± 3.47	-	-	-	-	-	-
Sauromalus obesus	0.90	-	-	(Schwenk and Throckmorton, 1989)	3	10	38.00 ± 7.00	-	-	-	-	-	-

Sceloporus clarkii	0.03	Yes	Walk	(Reilly and Delancey, 1997)	2	10	-	-	-	-	39.50 ± 12.65	33.00 ± 12.65	120.50 ± 11.07
Teratoscincus scincus	0.01	No	Running trot	(Fuller et al., 2011)	R	R	-	-	-	-	-	60.00	-
Triceros jacksonii	1.00	-	-	(So et al., 1992)	3	11	37.60 ± 1.57	-	-	-	-	-	-
Tropidurus torquatus	0.03	No	Running trot	this study	3	8	-	95.77 ± 13.21	43.13 ± 8.12	52.67 ± 15.68	141.17 ± 8.92	80.41 ± 3.41	68.37 ± 13.62
Tupinambis merianae	6.80	Yes	Walk	(Sheffield et al., 2011)	H, K, A: 3; J: 1	H, K, A: 49; J: 30	20.86 ± 3.55	-	-	-	80.00	54.16	51.08
Tupinambis teguixin	6.80	-	-	this study	4	42	16.00 ± 1.00	-	-	-	-	-	-
Uma scoparia	0.75	Yes	Running trot	(Irschick and Jayne, 1999)	S, E, W, H, K, A: R; J: 1	S, E, W, H, K, A: R; J: 7	29.11 ± 4.81	74.36	15.52	59.33	107.19	50.77	30.24
Uromastix acanthinurus	1.50	-	-	(Herrel and Vree, 1999)	4	31	26.48 ± 5.47	-	-	-	-	-	-
Uromastyx aegyptius	1.50	-	-	(Schwenk and Throckmorton, 1989)	4	8	23.00 ± 2.00	-	-	-	-	-	-
Varanus	5.00	No	Running trot	(Elias et al., 2000)	S, E, W, H,	S, E, W, H, K, A:	15.00 ± 2.00	105.96 ± 21.95	43.12 ± 16.29	55.73 ± 14.99	115.73 ± 15.99	69.00 ± 12.84	71.40 ± 17.17

	exanthematicus					K, A: 2; J: 4	13; J: 29							
Testudines	*Terrepene carolina*	0.36	-	-	(Bels et al., 1997)	3	61	46.29 ± 1.37	-	-	-	-	-	-
	Trachemys scripta	0.24	Yes	Walk	(Rivera and Blob, 2010)	7	123	-	85.00 ± 2.30	52.00 ± 1.10	-	-	-	-
Crocodilia	*Alligator mississippiensis*	181.44	Yes	Walk	(Baier and Gatesy, 2013; Reilly and Elias, 1998)	3	S, E: 20; H, A: 60	-	52.00 ± 12.00	73.00 ± 23.00	-	77.00 ± 15.49	-	63.75 ± 13.56
	Caiman crocodilus	30.00	-	-	(Cleuren and de Vree, 1992)	3	29	35.12 ± 8.46	-	-	-	-	-	-
Aves	*Anas platyrhynchos*	1.36	-	-	(Dawson et al., 2011)	3	242	11.91 ± 1.88	-	-	-	-	-	-
	Coturnix japonica	0.09	Yes	Walk, Bipedal run	(Reilly, 2000)	5	60	-	-	-	-	1.67 ± 15.49	61.33 ± 18.07	61.33 ± 18.07
	Numida meleagris	1.32	Yes	Walk	(Kambic et al., 2015)	1	15	-	-	-	-	24.27 ± 5.38	90.69 ± 6.69	74.38 ± 6.84
	Pica pica	0.23	No	Walk, Bipedal run	(Verstappen et al., 2000)	3	K: 20; A: 28	-	-	-	-	-	13.00 ± 14.50	33.00 ± 10.00

	Struthio camelus	100.00	No	Bipedal run	(Smith et al., 2010)	R	3	-	-	-	-	12.09 ± 4.44	32.39 ± 6.45	78.95 ± 8.04
	Vanellus vanellus	0.25	Yes	Walk, Bipedal run	(Nyakatura et al., 2012)	4	6	-	-	-	-	32.40 ± 8.24	62.59 ± 10.84	75.06 ± 12.52
Mammalia	*Acinonyx jubatus*	53.50	No	Walk	this study	2	12	-	57.93 ± 18.61	8.28 ± 5.21	28.51 ± 9.32	54.25 ± 7.81	8.20 ± 4.78	18.06 ± 12.34
	Aotus nancymae	0.77	No	Walk	this study	3	35	-	82.96 ± 17.96	34.83 ± 11.06	62.66 ± 5.12	78.64 ± 7.38	18.39 ± 2.62	4.01 ± 1.22
	Aplodontia rufa	1.13	-	-	(Druzinsky, 1995)	6	100	23.70 ± 4.17	-	-	-	-	-	-
	Arctictis binturong	11.50	No	Walk	this study	5	21	-	92.26 ± 13.22	52.29 ± 6.22	45.55 ± 12.12	83.38 ± 4.32	42.08 ± 6.32	81.10 ± 11.23
	Camelus dromedarius	408.23	No	Walk	this study	2	14	-	23.14 ± 14.34	14.87 ± 4.32	21.98 ± 12.35	50.32 ± 7.78	5.04 ± 3.68	25.45 ± 17.21
	Capra aegagrus hircus	45.36	-	-	(Musinsky, 2012)	R	9	13.93 ± 1.56	-	-	-	-	-	-
	Caracal caracal	16.00	No	Walk, Running trot	this study	2	24	-	77.71 ± 16.78	27.49 ± 2.48	17.20 ± 9.45	72.59 ± 3.69	54.79 ± 9.21	79.65 ± 17.21
	Cebus capucinus	3.08	No	Walk	this study	3	9	-	71.32 ± 21.35	29.88 ± 5.66	43.15 ± 9.67	50.71 ± 4.71	32.92 ± 6.67	38.31 ± 8.23
	Cheirogaleus medius	0.28	No	Walk, Running trot	this study	2	27	-	92.97 ± 19.02	23.33 ± 9.27	79.00 ± 6.76	80.77 ± 8.67	10.25 ± 6.51	24.44 ± 10.63
	Dasyuroides byrnei	0.10	No	Walk, Running trot	(Fischer et al., 2002)	2	19	-	29.00 ± 7.00	37.00 ± 8.50	53.00 ± 8.16	46.00 ± 10.33	25.00 ± 6.66	34.00 ± 9.00

Daubentonia madagascariensis	2.94	No	Walk	this study	3	30	-	83.26 ± 15.70	38.60 ± 8.59	54.44 ± 9.90	74.35 ± 6.25	34.66 ± 8.15	33.22 ± 8.42
Didelphis virginiana	2.31	No	Walk	(Hiiemae and Crompton, 1971; Jenkins, 1971)	S, H: 3; J: R	H, S: R; J: 12	33.67 ± 5.77	53.37	-	-	58.59	-	-
Equus ferus caballus	816.47	No	Walk	(Bonin et al., 2007; Hodson et al., 2000; Hodson et al., 2001)	S, E, W, H, K, A: R; J: 4	S, E, W, H, K, A: R; J: 24	3.22 ± 0.32	28.39	9.32	17.66	60.28	34.57	46.50
Erythrocebus patas	9.45	No	Walk	this study	1	8	-	77.89 ± 15.43	14.42 ± 5.32	48.80 ± 11.32	74.94 ± 9.12	32.01 ± 4.89	26.05 ± 13.80
Eulemur fulvus	2.21	Yes	Walk	(Schmidt, 2005a)	2	S: 60; E: 35; W: 30; H: 31; K: 28; A: 20	-	84.00 ± 9.00	60.00 ± 7.00	61.00 ± 8.00	92.00 ± 6.00	60.00 ± 6.00	51.00 ± 9.00
Felis catus	3.50	No	Walk	(Thexton et al., 1980); this study	S, E, W, H, K, A: 3; J: 5	S, E, W, H, K, A: 15; J: 31	21.43 ± 7.85	66.29 ± 6.23	46.28 ± 5.44	76.32 ± 12.78	74.20 ± 9.76	47.30 ± 6.32	66.27 ± 14.32
Galea mustelo ides	0.50	Yes	Walk, Running trot	(Fischer et al., 2002)	2	S: 27; E, W: 26; H: 47; K:	-	23.00 ± 3.67	42.00 ± 3.00	37.00 ± 3.83	75.00 ± 4.83	28.00 ± 6.83	53.00 ± 6.66

						74; A: 72							
Gazella spekei	20.00	No	Walk	this study	5	20	-	23.87 ± 17.90	33.23 ± 5.21	23.58 ± 8.68	60.13 ± 9.23	31.58 ± 5.34	20.99 ± 11.21
Giraffa reticulata	1192.00	No	Walk	this study	3	16	-	45.47 ± 19.43	25.95 ± 12.23	8.50 ± 13.21	53.40 ± 7.35	2.04 ± 4.42	3.89 ± 2.67
Hapalemur griseus	0.94	No	Walk	this study	2	17	-	73.38 ± 24.54	39.05 ± 9.72	48.04 ± 5.27	58.84 ± 6.35	25.78 ± 6.61	43.95 ± 1.44
Heterohyrax brucei	1.20	No	Walk	(Jenkins, 1971)	3	U	-	63.25	-	-	69.02	-	-
Homo sapiens	80.70	No	Walk	this study	H, K, A: 6; J: 5	H, K, A: 269; J: 351	6.01 ± 1.68	-	-	-	42.34 ± 4.98	65.45 ± 3.78	51.23 ± 7.73
Lemur catta	2.21	No	Walk	this study	3	30	-	67.91 ± 6.08	19.94 ± 4.38	49.96 ± 8.73	65.40 ± 8.07	25.19 ± 6.10	28.43 ± 9.87
Leopardus pardalis	13.61	No	Walk, Running trot	this study	1	12	-	81.79 ± 12.43	40.12 ± 6.32	65.01 ± 16.32	82.00 ± 10.43	56.22 ± 9.54	61.46 ± 15.32
Leptailurus serval	11.79	No	Walk, Running pace	this study	2	15	-	76.72 ± 19.21	40.79 ± 8.32	30.45 ± 12.32	70.67 ± 11.30	26.77 ± 3.28	9.44 ± 6.23
Loris tardigradus	2.21	No	Walk	this study	2	31	-	95.32 ± 12.10	59.71 ± 8.98	75.94 ± 13.64	113.67 ± 14.27	60.82 ± 2.72	28.42 ± 10.29
Loxodonta africana and Elephas maximus	5443.11	No	Walk	(Ren et al., 2008)	15	S, E: 8; W: 14; H, K: 21; A: 18	-	44.00 ± 5.66	36.00 ± 2.83	66.00 ± 3.74	29.00 ± 4.58	42.00 ± 4.58	30.00 ± 4.24
Macaca mulatta	9.90	No	Walk, Running trot	this study	S, E, W, H, K, A: 2; J: 4	S, E, W, H, K, A:	15.74 ± 4.83	94.71 ± 14.63	37.09 ± 2.98	76.02 ± 5.57	82.11 ± 5.50	40.76 ± 4.50	31.97 ± 12.60

						16; J: 5,769							
Mandrillus sphinx	22.25	-	-	this study	2	41	21.80 ± 3.62	-	-	-	-	-	-
Marmota monax	3.90	-	-	(Druzinsky, 1995)	4	50	23.80 ± 5.83	-	-	-	-	-	-
Martes flavigula	2.50	No	Walk	(Larson et al., 2001)	U	2	-	-	-	-	67.46	-	-
Mesocricetus auratus	0.10	No	Walk	(Jenkins, 1971)	3	U	6.97 ± 1.76	54.64	-	-	58.54	-	-
Microcebus murinus	0.12	No	Walk	(Schmidt, 2005a)	2	S, H, K: 75; E: 74; W: 63; A: 67	-	49.00 ± 8.00	40.00 ± 8.00	76.00 ± 9.00	75.00 ± 7.00	30.00 ± 7.00	36.00 ± 9.00
Mirza coquereli	0.31	No	Walk, Running trot	this study	2	16	-	83.21 ± 21.88	66.69 ± 5.40	75.08 ± 1.21	121.29 ± 14.70	72.40 ± 10.46	38.39 ± 8.84
Monodelphis domestica	0.11	No	Walk, Running trot	(Fischer et al., 2002)	2	S, E, W, H, K: 16; A: 13		47.00 ± 5.33	41.00 ± 5.00	71.00 ± 15.00	86.00 ± 5.50	44.00 ± 5.00	66.00 ± 11.66
Mustela putorius	0.90	No	Walk	(Davis, 2014; Jenkins, 1971)	S, H: 3; J: 4	S, H: U; J: 64	13.70 ± 3.56	62.24	-	-	82.03	-	-
Myotis lucifugus	0.01	-	-	(Kallen and Gans, 1972)	25	6	17.82 ± 4.01	-	-	-	-	-	-
Nasua narica	4.00	No	Walk	this study	2	45	-	74.97 ± 15.33	33.75 ± 17.20	16.85 ± 5.56	78.64 ± 14.59	19.68 ± 3.82	15.81 ± 6.35
Ochotona	0.25	Yes	Walk, Running trot	(Fischer et al., 2002)	2	29	-	-	-	-	49.00 ± 5.17	21.00 ± 3.83	30.00 ± 3.66

rufescens													
Oryctolagus cuniculus	0.25	-	-	(Morimoto et al., 1985)	4	400	12.08 ± 3.64	-	-	-	-	-	-
Ovis aries	23.80	Yes	Walk	(Safayi et al., 2015)	17	150	-	-	-	-	-	-	36.00 ± 5.30
Pan paniscus	38.20	No	Walk	(D'Août et al., 2002)	9	33	-	-	-	-	53.10 ± 15.00	67.30 ± 11.70	39.20 ± 9.20
Pan troglodytes	53.00	Yes	Walk, Running trot	(Pontzer et al., 2014)	4	4	-	26.26 ± 11.39	12.67 ± 8.75	10.81 ± 3.27	17.77 ± 8.17	31.53 ± 10.95	23.89 ± 7.11
Panthera tigris	103.00	No	Walk	this study	4	32	-	73.91 ± 13.32	23.47 ± 2.12	65.22 ± 9.53	73.93 ± 4.32	9.37 ± 4.23	11.72 ± 7.32
Papio anubis	19.20	No	Walk	this study	2	S, E, W, H, K, A: 8; J: 5,764	14.87 ± 5.17	69.05 ± 20.67	20.98 ± 2.79	56.76 ± 7.34	74.28 ± 5.21	22.78 ± 2.15	32.52 ± 6.89
Phascolarctos cinereus	9.30	No	Walk	(Larson et al., 2001)	U	9	-	-	-	-	58.40	-	-
Pongo pygmaeus	57.00	No	Walk	(Larson et al., 2001)	U	9	-	-	-	-	69.97	-	
Potos flavus	3.75	No	Walk, Running trot	(Davis, 2014); this study	2	S, E, W, H, K, A: 72; J: 50	15.70 ± 4.54	86.42 ± 17.36	62.38 ± 2.53	50.79 ± 13.16	72.37 ± 5.17	19.06 ± 6.35	35.14 ± 8.42
Procavia capensis	4.00	Yes	Walk, Running trot	(Fischer et al., 2002; Janis, 1979)	S, E, W, H, K, A: 2; J: U	S, E: 44; W: 39; H, K, A: 21; J: 4	24.01 ± 4.02	30.00 ± 7.00	45.00 ± 9.50	25.00 ± 6.83	70.00 ± 8.33	45.00 ± 5.50	60.00 ± 12.33

Procyon lotor	6.50	Yes	Walk	(Jenkins and Camazine, 1977)	3	7	-	-	-	-	71.60 ± 6.30	-	-
Propithecus coquereli	4.38	No	Walk	this study	3	30	-	58.37 ± 9.66	25.97 ± 11.47	37.66 ± 6.86	62.18 ± 8.31	22.76 ± 6.75	30.20 ± 6.93
Pygathrix cinerea	9.23	No	Walk	this study	2	15	-	78.12 ± 17.49	27.18 ± 8.41	-	56.98 ± 17.26	25.89 ± 8.04	-
Pygathrix nemaeus	9.23	No	Walk	this study	2	7	-	83.50 ± 10.73	30.31 ± 14.34	-	62.81 ± 22.14	26.07 ± 8.24	-
Rattus norvegicus	0.50	Yes	Walk, Running trot	(Fischer et al., 2002; Weijs and Dantuma, 1975)	S, E, W, H, K, A: 3; J: 5	S, E, W: 27; H, K, A: 23; J: 16	16.60	38.00 ± 4.50	44.00 ± 4.83	92.00 ± 12.00	60.00 ± 5.50	24.00 ± 3.50	36.00 ± 4.33
Saguinius oedipus	0.49	No	Walk	(Schmidt, 2005a)	2	S: 27; E: 35; W: 25; H: 21; K: 25; A: 22	-	51.00 ± 8.00	36.00 ± 6.00	43.00 ± 9.00	106.00 ± 8.00	38.00 ± 8.00	36.00 ± 9.00
Saimiri sciureus	0.72	No	Walk	(Schmidt, 2005b)	2	S: 73; E: 65; W: 45; H: 47; K: 72; A: 68	-	39.00 ± 9.00	30.00 ± 6.00	50.00 ± 10.00	76.00 ± 9.00	35.00 ± 7.00	45.00 ± 9.00
Sapajus apella	3.08	-	-	this study	3	6492	18.01 ± 6.40	-	-	-	-	-	-

Sus scrofa	68.04	-	-	(Menegaz et al., 2015)	3	32	13.67 ± 1.93	-	-	-	-	-	-
Tachyglossus aculeatus	5.00	No	Walk	(Jenkins, 1971)	R	U	-	26.57	-	-	78.30	-	-
Tenrec ecuadatus	0.10	-	-	(Oron and Crompton, 1985)	2	44	17.64 ± 2.27	-	-	-	-	-	-
Trachypithecus crepusculus	10.00	No	Walk	this study	2	11	-	86.27 ± 17.85	33.12 ± 8.04	-	64.32 ± 13.59	34.14 ± 7.97	-
Trachypithecus delacouri	10.00	No	Walk	this study	2	6	-	75.33 ± 12.86	19.89 ± 10.45	-	56.58 ± 3.24	25.92 ± 8.02	-
Trachypithecus hatinhensis	10.00	No	Walk	this study	2	12	-	79.61 ± 7.89	23.34 ± 10.68	-	57.00 ± 10.51	24.89 ± 9.76	-
Trachypithecus poliocephalus	10.00	No	Walk	this study	2	10	-	68.88 ± 7.09	27.45 ± 6.29	-	54.06 ± 9.30	26.19 ± 4.41	-
Tupaia glis	0.17	Yes	Walk, Running trot	(Fischer et al., 2002)	2	S, E, W: 28; H, K: 30; A: 29	-	60.00 ± 8.17	70.00 ± 10.50	86.00 ± 16.50	110.00 ± 5.17	72.00 ± 9.33	88.00 ± 7.83

Vareica variegata	3.49	No	Walk	this study	3	30	-	68.93 ± 16.72	39.07 ± 10.56	51.91 ± 15.07	51.81 ± 5.76	33.26 ± 8.98	36.95 ± 9.09
Vulpes vulpes	5.50	Yes	Walk	(Jenkins and Camazine, 1977)	1	6	-	-	-	-	63.20 ± 2.90	-	-

*Data availability often was based on differing sample sizes for each joint (J= Jaw, S = shoulder, E = Elbow, W = Wrist, H = Hip, K = Knee, A = Ankle, R = data collected from representative cycle, U = unknown).

-Data not available or not applicable

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Table S2. Results of paired t-tests and phylogenetic paired T-tests comparing jaw joint excursion with limb joint excursions. *P*-values are adjusted using the false discovery rate. d = mean paired difference, d_{phylo} = mean paired phylogenetic difference. * indicates all p-values were less than the reported value. Note: s.d. of 0.01 include values $\leq$ 0.01. ** p values are significant (all $p < 0.005$) after Bonferroni correction.

Joints	d	t	df	p**	d_{phylo}	Pagel's λ	σ^2	t_{phylo}	df_{phylo}	p_{phylo}**	K
Jaw-Hip	66.5	11.1	17	<0.001	69.1±0.26	0.84±0.01	1.77±0.02	5.70±0.07	15	<0.001*	0.89±0.02
Jaw-Knee	26.5	5.06	14	<0.001	26.5±0.01	0.00±0.01	1.23±0.01	5.24±0.01	12	<0.001*	0.41±0.01
Jaw-Ankle	32.7	7.25	14	<0.001	32.7±0.01	0.00±0.01	0.91±0.01	7.51±0.01	12	<0.001*	0.24±0.01
Jaw-Shoulder	53.1	7.93	15	<0.001	57.4±0.21	0.71±0.01	2.81±0.04	3.90±0.07	13	0.002±0.01	0.56±0.01
Jaw-Elbow	18.9	3.45	12	0.005	18.9±0.01	0.00±0.01	1.15±0.01	3.60±0.01	10	0.004±0.01	0.49±0.02
Jaw-Wrist	32.4	5.27	12	0.002	32.2±0.01	0.07±0.01	1.45±0.01	4.91±0.03	10	<0.001*	0.47±0.01

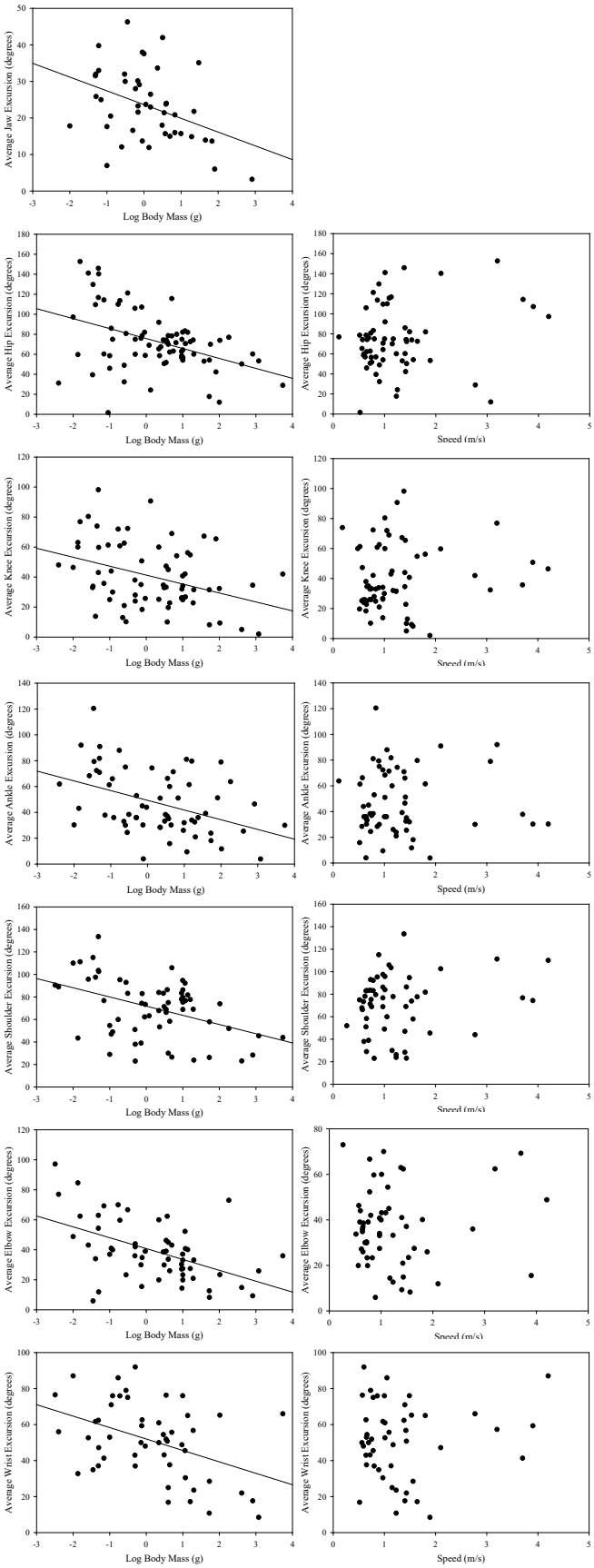

Fig. S1. Scatterplots average joint angular excursion as a function of log-transformed body mass (g) (left panels) and speed (m/s) (right panels). Our sample exhibited a negative correlation between angular excursions and $\log_{10}$ body mass at all joints (all $P \leq 0.02$), but there was no significant association with locomotor speed (all $P > 0.25$).

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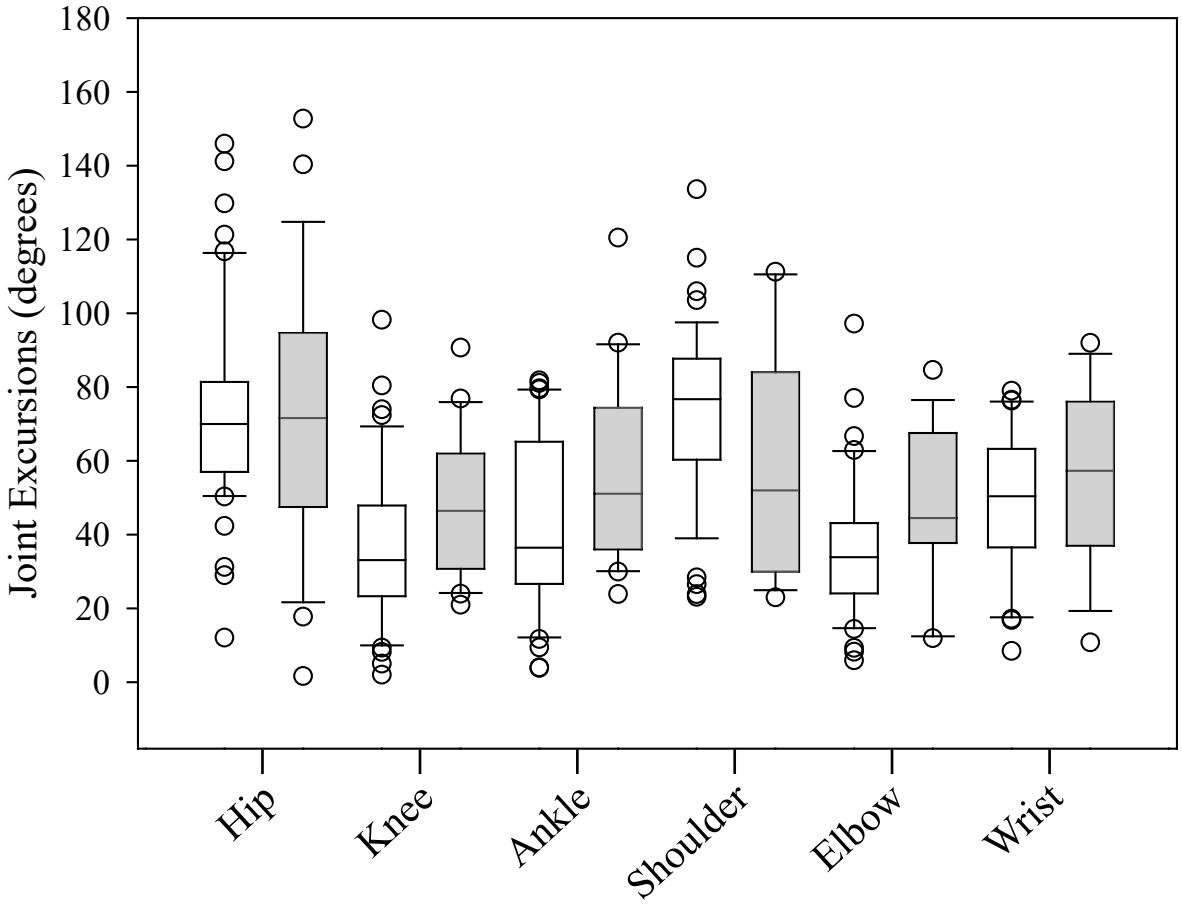

Fig. S2. Box plots of joint angular excursions during freely moving locomotion (white) compared to locomotion on treadmills (gray). Data plotted as median, 10th, 25th, 75th, and 90th percentiles. Open circles represent outliers in the data. Average knee angular excursion is significantly greater for animals moving on treadmills ($P = 0.035$), but no other significant differences (all $P \leq 0.051$) are observed.