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Using step width to compare locomotor biomechanics between extinct, non-avian theropod dinosaurs and modern obligate bipeds.

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Running head

Step width and theropod locomotion

Abstract

How extinct, non-avian theropod dinosaurs locomoted is a subject of considerable interest, as is the manner in which it evolved on the line leading to birds. Fossil footprints provide the most direct evidence for answering these questions. In this study, step width – the mediolateral (transverse) distance between successive footfalls – was investigated with respect to speed (stride length) in non-avian theropod trackways of Late Triassic age. Comparable kinematic data was also collected for humans and 11 species of ground-dwelling birds. Permutation tests of the slope on a plot of step width against stride length showed that step width decreased continuously with increasing speed in the extinct theropods ($P < 0.001$), as well as the five tallest bird species studied ($P < 0.01$). Humans, in contrast, showed an abrupt decrease in step width at the walk-run transition. In the modern bipeds, these patterns reflect the use of either a discontinuous locomotor repertoire, characterized by distinct gaits (humans), or a continuous locomotor repertoire, where walking smoothly transitions into running (birds). The non-avian theropods are consequently inferred to have had a continuous locomotor repertoire, possibly including grounded running. Thus, features that characterize avian terrestrial locomotion had begun to evolve early in theropod history.

Keywords

Step width, locomotion, theropods, birds, fossil footprints.

Introduction

How extinct dinosaurs stood and moved has always been a question of great interest for palaeontologists. Locomotion in non-avian theropods is a controversial topic, owing to interest surrounding their carnivorous lifestyle and often gigantic size. Additionally, the recognition that Theropoda includes birds [1-5] provides a further rationale for understanding locomotion in extinct theropods: charting the evolution of locomotion on the line to birds [6-8].

Terrestrial locomotion in modern birds is distinct from that of humans, the only other extant obligate, striding biped [9, 10]. It is characterized by a crouched, digitigrade, parasagittal posture, with a subhorizontally oriented femur during much of the stride [11-27]. A further curious aspect is that birds employ ‘grounded running’ at certain speeds [14, 16, 21, 24, 28-32]. Here, the whole-body centre-of-mass (COM) exhibits little exchange of kinetic and potential energies, characteristic of running, despite there being double-support phases in the stride (i.e., duty factors are greater than 0.5; characteristic of walking). Therefore, birds run without an aerial phase; only at greater speeds do duty factors decrease below 0.5, resulting in an aerial run. Birds hence show more ‘continuous’ gaits compared to humans. Reflecting this, many kinematic parameters that have been previously measured in birds often show a continuous change with increasing speed, whereas in humans they typically change discontinuously at the walk-run transition [14, 16, 17, 21, 26, 29-31, 33-37].

The distinct locomotor repertoire of modern birds raises the question as to whether their non-avian ancestors exhibited a similar repertoire, and if not, when did this distinct suite of behaviours first evolve? In answering this question, the most direct evidence of locomotion in extinct, non-avian theropods is fossil footprints and trackways, because they record the actual placement and motions of the feet during locomotion [38-40]. All known non-avian theropod footprints and trackways show that they were digitigrade, obligatorily striding, parasagittal bipeds that did not drag their tails along the ground, much like modern birds [39, 40].

Fossil theropod trackways have also facilitated estimates of trackmaker speeds, using stride length as a proxy [39, 41-44], but how locomotor kinematics changed with speed remains less investigated. The patterns exhibited by birds and humans lead to the prediction that whether a given non-avian theropod trackmaker exhibited continuous or discontinuous locomotor behaviour, this should be detectable in measurements of its tracks. One such measurement is

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2 step width, the mediolateral (transverse) distance between successive footfalls, which can be
3 measured for both fossil trackways and modern animals. Step width is linked to the
4 maintenance of stability and energetic efficiency during locomotion in humans [45-50].
5 Indeed, stability may be paramount for large bipeds, such as giant non-avian theropods,
6 because the consequences of falling could be dire [51]. Consequently, analyses of step width
7 have the potential to offer insight into non-avian theropod locomotor biomechanics.
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13 There are only three known non-avian theropod trackway sites where the trackmakers made
14 an appreciable change in speed. These sites provide the opportunity to examine how
15 locomotion changed with speed in non-avian theropods, enabling comparison to locomotion
16 in birds and humans. One site, in England, suggests that step width decreased with increasing
17 speed [52, 53], but it is unclear whether this occurred gradually or abruptly. A second site in
18 South Korea [54] is also too small for thorough analysis. The third site, the Culpeper Crushed
19 Stone Quarry trackways, from the Late Triassic (approximately 211 Ma) of Virginia, USA,
20 comprises 20 individual trackways [55-57], some of which are quite extensive. Based on
21 measured stride lengths, it is clear that in some trackways, the trackmaker progressed from a
22 slow walk to a fast run [57], so a large part of their speed spectrum was captured in these
23 trackways.
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33 This study investigated the pattern of step width change versus speed in non-avian theropods,
34 using the dataset of the Culpeper Quarry trackways. The results obtained from analysis of the
35 trackways were compared to three-dimensional (3-D) kinematic measurements collected for
36 humans and a range of extant, ground-dwelling birds. It is hypothesized that birds show a
37 more continuous change in step width with increasing speed, whereas humans show a
38 discontinuous change. Comparison of the patterns observed in the trackways to those
39 observed in modern bipeds will hence provide insight into non-avian theropod locomotion.
40 Additionally, the importance of mediolateral limb movements in bipedal animals (living and
41 extinct) can be better clarified.
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52 **Methods**

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55 A summary of the methodology is given below, with a detailed outline provided in the
56 Supplementary Material. All protocols used were approved by institutional research ethics
57 committees (approvals AHS/01/14/AEC, SBS/102/14/ARC). Collection of the three wild bird
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1 species was approved by the Queensland Department of Environment and Heritage Protection
2 (permit WISP14699514). Written informed consent was obtained from the human subjects
3 prior to the study.
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8 *Theropod trackways*

9 Data collection

10 Morphological similarity in all of the footprints examined suggests that a single genus, if not
11 species, was recorded in the trackways [56, 57]. Moreover, the size of the footprints indicates
12 that the trackmakers were similar in size [57]. Hence, by focusing only on the Culpeper
13 Quarry trackways, this study effectively controlled for the potentially confounding factors of
14 differing species, body sizes or shapes, patterns of leg movements and substrate conditions.
15 The only factor likely responsible for any systematic change of step width with speed is
16 therefore speed itself.
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28 Two measurements were made along each trackway (figure 1a–c): pace length (distance from
29 one footprint to the next) and pace bearing (compass bearing from one footprint to the next).
30 The reference point for each footprint was at the posterior end of the digit III impression
31 (figure 1b). None of the trackways studied showed any indication of pathology, such as
32 limping [58].
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38 Data analysis

39 From measured pace bearings and pace lengths, the pace angulation at each footprint (θ_N)
40 was determined (figure 1c). The stride length (S_N) and step width (w_N) at each footprint was
41 then calculated trigonometrically (figure 1d). Step width was defined as the perpendicular
42 distance from a footprint to the line of its corresponding stride length. If the feet crossed over
43 the body midline, pace angulation becomes reflex ($\theta_N > 180^\circ$) and step width becomes
44 negative. Calculated stride lengths and step widths were then normalized to the estimated hip
45 height of the trackmakers, to minimize potential size effects on comparisons; hip height was
46 estimated via equation 1 of Thulborn [43]. Normalization of S and w to hip height (producing
47 S^* and w^* , respectively) facilitated fair comparison across the trackways. Additionally,
48 relative stride length is a common proxy for speed of locomotion when speed itself cannot be
49 measured, since animals tend to take longer strides at faster speeds [16, 21, 29–31, 41, 42, 59].
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Humans

Data collection

Three healthy, recreationally active adults (two male, one female) were studied (height 179.3 ± 3.2 cm, mass 79.7 ± 16.8 kg, means \pm s.d.). A sample size of three was deemed sufficient, since this study aimed to elucidate major patterns, for broad comparative purposes [16, 41, 59-61]. Reflective markers were placed on the end of the left and right hallux, and their 3-D trajectories during locomotion were recorded at 200 Hz using a 10-camera VICON MX T40-S motion capture system (Vicon Oxford Metrics, Oxford, UK). The subjects walked and ran barefoot on a split-belt instrumented treadmill (Bertec Limited, Columbus, Ohio, USA) integrated with the motion capture system.

Each subject undertook a number of steady-state walking and running trials at increments of 0.25 m s^{-1} , ranging from slow walking through fast running speeds. Subjects were also tested twice at their (predetermined) walk-run transition speed, in one trial using walking, in the other using running. To elucidate if there was any difference in how step width changes with increasing speed between accelerating and steady-state locomotion, two subjects also undertook accelerating trials. Using the programmable treadmill, each subject undertook a slow and fast acceleration of 1.0 m s^{-2} and 2.5 m s^{-2} , respectively, up to a peak tread speed of 3.25 m s^{-1} .

Data analysis

Step width was measured from the 3-D trajectory data for the hallux markers, and normalized to the hip height of the subjects; this was estimated using standard anthropometry [62] based on the subject's total standing height.

Birds

Animals studied

Eleven species of ground-dwelling bird were studied (table 1). Given logistical limitations and the study's objectives, preference was given to maximizing the diversity of species

1 investigated, rather than achieving more replicates for fewer species. All birds investigated in
2 the present study were considered to be adults based on skeletal maturity, with the possible
3 exception of the domestic turkeys, which had sizeable chondroepiphyses (revealed in
4 postmortem dissection) but were still of adult size. Following the conclusion of experiments,
5 birds were euthanized and immediately weighed. Data collected in the present study was
6 combined with data collected previously for ostriches [18] and emus [63].
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12 Data collection

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17 Two experimental setups were used in the present study, one small indoor racetrack for the
18 quail species, and a larger outdoor one for the remaining species (figure S1). Both racetracks
19 were walled around their entire perimeter, but the middle of one side was replaced with clear
20 acrylic or fine wire mesh, through which filming took place. Birds were filmed at 50–250
21 frames second⁻¹ with two high-speed light video cameras (IL3-100 and HiSpec1, Fastec
22 Imaging, San Diego, USA), synchronized using a manual trigger pulse. For both racetracks, a
23 calibration volume for each day's trials was established using an 11-coefficient direct linear
24 transform [64].
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32 Prior to data collection, feathers from the back and wings were clipped, to allow the
33 placement of small (2–5 mm) markers that were unobstructed from the cameras' views during
34 locomotion. Up to three markers were placed on the midline of the back, as part of another
35 study. A single marker was placed over the trochanteric crest of each hip, which in all species
36 was easily palpable. Non-toxic, white paint was used to mark the base of the claw of digit III
37 of both feet.
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44 Birds moved down the racetrack at a self-selected speed, although sometimes additional
45 motivation was used, such as making loud noises. The speeds used varied from slow walking
46 speeds through fast running speeds. Birds were also filmed during quiet standing, allowing the
47 capture and measurement of the height of the hip marker (taken as standing hip height).
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51 Data analysis – present study and ostrich data

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55 Toe markers were digitized and their 3-D coordinates calculated using DLTdv5 [64], a
56 program written for MATLAB 8.0 (MathWorks, Natick, USA). Markers were digitized when
57 the feet were planted on the ground and fully stationary. Additionally, the hip marker in
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1 standing trials was digitized and its coordinates calculated, either using DLTdv5 or using a
2 reference object of known dimensions within the cameras' fields of view. The coordinates of
3 the toe markers were then used to determine stride lengths and step widths trigonometrically
4 (figure S2). Stride lengths and step widths were normalized to the standing hip height of the
5 birds as for the theropod footprints. The calculations followed the same convention as used
6 for the theropod footprints; if the feet crossed over the midline, step width was negative. A
7 similar process was used to extract and analyse the 3-D kinematic data collected for the
8 ostriches [18].
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10 Data analysis – emu data

11 In the emus [63], a marker was placed only on the right digit III, in addition to two markers on
12 the back midline. Whilst true step width and stride length could not be calculated, they could
13 be estimated, using the trajectory of the back markers as a proxy for the body midline axis
14 (figure S3). Step width and stride length were then normalized to standing hip height.
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16 *Statistics*

17 Two statistical analyses were performed. The first tested whether w^* varied significantly with
18 S^* for a given species, using major axis (MA) regression [65]. As assumptions of normality or
19 homoscedasticity were frequently not met by the data, as determined in PAST 3.09 [66], a
20 permutation test of the slope was performed [67], with significance levels conservatively set
21 to $P = 0.01$. The second statistical analysis examined whether a given dataset showed
22 continuous or discontinuous change in w^* with respect to S^* . Curve fitting was performed in
23 R 3.2.2 (R Foundation, Vienna, Austria), using two continuous curves (linear, power) and one
24 discontinuous curve (logistic). The Akaike Information Criterion (AIC) was then used to
25 determine which curve provided the best fit.
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27 Results

28 *Theropod trackways*

29 Step width decreased with increasing speed (figure 2a), although the correlation is not strong
30 ($r^2 = 0.0587$, $P < 0.001$). After binning w^* into narrow intervals of S^* and taking the mean for
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2 each interval, this pattern is more clearly illustrated (figure 2b): as the theropods moved
3 faster, they placed their feet closer to the midline. At slow speeds, step width was
4 approximately 5–10 % of hip height; at fast speeds ($S^* > 3.0$), the feet typically crossed the
5 midline, as indicated by negative values for w^* . Importantly, the decrease in w^* versus S^* was
6 best modelled by a power function (table S1), indicating no discontinuity.
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10 11 12 **Humans**

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15 Step width decreased with increasing stride length ($P < 0.001$), particularly at the transition
16 from walking to running, with a distinct difference in w^* between the gaits (figure 3a,b). This
17 was well modelled by a logistic function (table S1, figure 3a), indicating a pronounced
18 discontinuity. Abrupt, discontinuous change in w^* was also observed in accelerating-
19 decelerating trials (figure 3c); at the transition from walking to running (or vice versa),
20 w^* changed suddenly over one step. This indicates no difference in how w^* varies with S^* ,
21 whether through acceleration within a trial, or across steady-state trials at different speeds.
22 This supports the validity of comparing steady-state locomotion in humans and birds with
23 largely non-steady-state locomotion in the Culpeper theropod trackways.
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31 32 **Birds**

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35 Four species studied (*Colinus virginianus*, *Coturnix japonica*, *Numida meleagris* and *Gallus*
36 *gallus*) did not show a statistically significant pattern of w^* versus S^* ; values for w^* largely
37 varied between 0–0.2 (figure 4a–d). Two species (*Coturnix chinensis* and *Alectura lathamii*)
38 showed a significant pattern, but the slope of the MA regression was positive (figure 4e,f; w^*
39 increased slightly with S^*). The remaining five species (*Threskiornis moluccus*, *Meleagris*
40 *gallopavo*, *Porphyrio porphyrio*, *Dromaius novaehollandiae* and *Struthio camelus*) all
41 showed a significant pattern with negative MA regression slopes, that is, w^* decreased with
42 increasing S^* (figure 4g–k). In each of these five species, the data was best modelled by a
43 linear or power function (table S1), indicating no discontinuity.
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52 Following these mixed results, further analysis revealed that a measure of bipedal stability
53 could discriminate between species that showed a decrease in w^* with increasing S^* and those
54 that did not (figure 5a). This measure, $h/\sqrt[3]{m}$, expresses hip height (h) relative to body mass
55 (m), assuming isometry. Birds that are relatively tall for their mass have a higher $h/\sqrt[3]{m}$, and
56 are inherently more unstable, since stability decreases as the height of the COM above the
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2 ground increases [68] (figure 5b). All species for which the mean value of $h/\sqrt[3]{m} > 0.24$
3 demonstrated a pattern of decreasing w^* with increasing S^* . This ‘threshold’ may be specific
4 to birds, however, since for the humans studied, $h/\sqrt[3]{m}$ was 0.222 ± 0.012 , yet w^* still
5 decreased with increasing S^* .
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10 11 **Discussion**

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16 This study investigated how step width varies with stride length in one extinct and two extant
17 groups of obligate biped. The non-avian theropods showed a pattern of continuous decrease in
18 w^* with increasing S^* , a pattern that was also observed in about half of the bird species. These
19 species were those that are relatively tall (long-legged) for their mass; in the other bird
20 species, no strong patterns were apparent. In contrast to the non-avian theropods and birds,
21 humans showed a marked and abrupt decrease in w^* at the walk-run transition.
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27 ***Step width in bipedal locomotion***

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31 For all three kinds of biped investigated, it was shown in general that if step width changed
32 with speed, it decreased with increasing speed: at quicker speeds, the feet were placed closer
33 to the body midline, and in fast running cross-over could occur. The observed pattern of step
34 width versus speed in the Triassic-age Culpeper trackways parallels the observation of Day et
35 al. [52, 53], of a large theropod trackway of Middle Jurassic age. Step width has therefore
36 been shown to decrease with increasing speed in two non-avian theropod trackways, more
37 than 40 Ma apart in age. Given that step width also decreased with increasing speed in several
38 of the bird species investigated here, it is phylogenetically conceivable that such a pattern was
39 present in many, if not most, extinct non-avian theropods.
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48 The findings for humans also accord with those of previous studies that have measured step
49 width, for both treadmill and overground locomotion [46, 48, 50, 69]; step width was
50 approximately 10–20% of hip height in walking and was close to zero in running. However,
51 this study is the first to show how step width changes with speed in humans, across the walk-
52 run transition. Almost no previous data exist for how step width changes with speed in
53 modern bird species. One exception is a recent study of walking in broiler chickens [70],
54 which showed that step width decreased with increasing speed in a continuous fashion. That
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1 no such pattern was observed for chickens in the present study is possibly due to different
2 breeds studied.
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5 6 *Step width and bipedal stability* 7

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10 Step width is closely tied to mediolateral stability during bipedal locomotion [45-50], yet why
11 step width decreases with speed remains undetermined. It is suggested here that this
12 phenomenon may represent, at least partly, a trade-off between mediolateral stability and
13 energy economy.
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18 At slow speeds, the body has limited linear momentum directed forwards, so it is relatively
19 easy for lateral forces to displace the trajectory of the COM laterally, leading to postural
20 instability. To counteract this, the feet assume a sizeable non-zero lateral placement relative to
21 the midline. However, this incurs an energetic cost, as energy is expended in mediolateral
22 movement of the COM (successively towards each footfall) instead of forward movement of
23 the COM [69]. This cost, derived from the kinetic energy of lateral movement, would be
24 comparatively greater in larger bipeds, as kinetic energy is proportional to the square of
25 velocity, and hence linear dimensions (e.g., hip height). With increasing speed, dynamic
26 stability increases as linear momentum in the forward direction increases, decreasing the
27 effect of lateral forces on the trajectory of the COM. Consequently, the feet are not required to
28 have such large lateral placements, so step width can be reduced. By reducing step width, and
29 therefore lateral oscillations of the COM [69, 71], less energy is expended in mediolateral
30 movement of the COM and more is expended in forward movement of the COM, improving
31 economy.
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43 The above scenario of a stability-economy trade-off may explain why five of the 11 bird
44 species studied showed a pattern of decreasing w^* with increasing S^* , yet the others did not.
45 Given the expectation that the energetic cost of unnecessarily large lateral displacements is
46 disproportionately greater in taller bipeds, and given that taller bipeds are less stable (figure 5),
47 this makes it more likely that a stability-economy trade-off will exist in relatively taller birds.
48 In turn, step width would be more tightly modulated with respect to speed. An example
49 illustrating this is the comparison between swamphen and guineafowl. The swamphen were
50 only about half the mass of the guineafowl, and yet they were almost 20% taller at the hips;
51 the swamphen showed a significant decrease of step width with increasing speed, while the
52 guineafowl did not.
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3 An additional reason for why step width decreases with speed may be simple anatomical
4 constraints. As speed increases, stride length also increases, providing more room between
5 each step for the legs to be placed closer toward the midline, something that may not be as
6 easily achieved at lower speeds (and stride lengths) without considerable yawing or rolling of
7 the body.
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10 11 12 13 *The gait patterns of non-avian theropods* 14

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17 In the modern bipeds studied, step width displayed the same speed-related pattern as many
18 other previously investigated kinematic parameters: a continuous change with speed reflects a
19 continuous locomotor repertoire, whilst an abrupt change with speed reflects a discontinuous
20 locomotor repertoire, with discrete and distinct gaits defined by those abrupt changes [72]. In
21 the non-avian theropod trackways, step width decreased with increasing speed in a continuous
22 fashion. In light of the patterns exhibited by (long-legged) modern obligate bipeds, this
23 suggests that the theropod trackmakers may not have had discrete gaits, instead having a
24 continuous locomotor repertoire, as in modern birds. That is, grounded running was possibly a
25 component of their locomotor repertoire (figure 6). This realization should not be as
26 surprising as it may first appear, for there are a wide variety of extant animals that habitually
27 employ a continuous locomotor repertoire (to one degree or another), in addition to birds.
28 These animals use a variety of limb postures, and include opossums [73, 74], other marsupials
29 [74], frogs [75], elephants [76], primates [77, 78], sheep [79] and even arthropods [80-82].
30 That grounded running was possibly present in an early, basal theropod suggests that it may
31 have been present in the majority of extinct theropods, both non-avian and avian. Indeed,
32 grounded running may have even been primitive for theropods.
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45 The possibility of grounded running in extinct, non-avian theropods has implications for
46 understanding their palaeobiology. Grounded running could confer several advantages to a
47 bipedal predator, despite potentially higher energy expenditure [83]. Periods of double limb
48 support makes grounded running more stable than aerial running at the same speed, including
49 over uneven terrain [16, 84]. Double limb support also reduces the peak ground reaction
50 forces experienced compared to aerial running [32, 77, 83], which would subsequently reduce
51 bone and muscle stresses. Therefore, the predator can move faster whilst still maintaining
52 stability and lowered musculoskeletal stresses. This would be particularly advantageous for
53 the large to giant species (e.g., *Allosaurus*, *Tyrannosaurus* and *Giganotosaurus*), whose
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1 athletic capabilities have previously been questioned [85-88]. Grounded running may also
2 improve visual acuity by increasing head stability, particularly in the vertical direction [30,
3 83], which would be beneficial when pursuing prey. Given these advantages to a predatory
4 biped, it is tempting to speculate that these advantages may have facilitated the evolution of
5 grounded running in theropods in the first instance.
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10 *Limitations of the study*

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15 This study has some potential limitations arising from logistical constraints on data collection.
16 Firstly, the study compared steady-state locomotion data for humans and birds with largely
17 non-steady-state locomotion data from theropod trackways, although the accelerating trials for
18 humans suggest this had little effect. Secondly, locomotion in the non-avian theropods and
19 birds was overground, whereas locomotion in the human subjects was treadmill-based. Whilst
20 some kinematic differences have previously been found between treadmill and overground
21 locomotion [89], more recent, detailed studies tend to suggest that the kinematics of the two
22 are quantitatively and qualitatively similar [90-93]. Thirdly, human kinematics were recorded
23 with barefoot subjects, possibly influencing their gait since they may have been accustomed
24 to wearing shoes. Although wearing shoes may alter some kinematics compared to barefoot
25 locomotion [94, 95], it is unknown if it affects many variables in the coronal plane, including
26 step width. Moreover, any influence of wearing shoes may also vary with shoe design; hence,
27 for consistency, the subjects walked and ran barefoot in the experiments. Despite these
28 potential limitations, they are considered unlikely to alter the main findings of the present
29 study, which is concerned with major patterns of similarity and difference across species.
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44 **Conclusion**

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47 By integrating ichnological and comparative biomechanical datasets, this study has revealed
48 new insight into the biomechanics of terrestrial locomotion of theropods, and bipeds in
49 general. Across the groups studied, step width tended to decrease with increasing speed, but
50 the manner in which step width changed with speed was decidedly different between humans
51 and theropods. Humans exhibited an abrupt decrease at the walk-run transition, whereas in
52 both non-avian and avian theropods step width decreased gradually with speed, with
53 considerable variability among avian taxa. These differences reflect a discontinuous
54 locomotor repertoire in humans, and a continuous locomotor repertoire in theropods.
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3 The non-avian theropods that made the trackways investigated seemed to have used a more
4 continuous locomotor behaviour, much like modern birds, possibly including grounded
5 running as part of their repertoire. The age and likely basal phylogenetic position of the
6 trackmakers would therefore suggest that the distinct locomotor behaviour of modern birds
7 had begun to appear very early in theropod evolution. The results of this study also indicate
8 that future analyses of locomotion in non-avian theropods cannot simply pigeonhole it into
9 discrete 'walking' or 'running' gaits. Moreover, given that mediolateral limb movements were
10 apparently important in terrestrial locomotion in these animals, future analyses also need to be
11 3-D in order to fully capture the range of limb postures used.
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39 **Author Contributions**

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42 P.J.B., C.J.C., S.A.H., R.S.B. and D.G.L. conceived the study design. P.J.B., C.J.C., R.E.W.,
43 D.F.G., L.P.L., J.R.H., J.R. and D.G.L. contributed or collected data. All authors contributed
44 to data analysis, interpretation and drafting of the manuscript. All authors approved the final
45 draft.
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52 **Competing Interests**

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55 The authors declare no competing interests.
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Data accessibility

All data and scripts used are held in the Geosciences Collection of the Queensland Museum, and will be made available upon request to the Collections Manager.

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Figure captions

Figure 1. The quantitative analysis of trackways to determine step width and stride length. (a) Life reconstruction of the trackmaker, likely to be some form of basal neotheropod. (b) The footprints in plan view; white dots mark the common reference point from which measurements were made. (c) Two principal measurements were made: pace length D , and bearing from one footprint to the next A . This allowed the calculation of pace angulation θ . (d) Step width w and stride length S were then calculated trigonometrically from pace lengths and angulations.

Figure 2. Comparison of how step width changes with stride length in the non-avian theropods. (a) The raw data, with MA regression plotted. (b) Mean values of w^* for each bin of S^* , with MA regression derived from raw data again plotted. In (b), hollow circles are single data points; they are not means of multiple points for a given bin. Hence their apparent outlier nature can be accounted for as simply the only points that fell into those particular bins.

Figure 3. Comparison of how step width changes with stride length in humans. (a) The raw data, with logistic curve plotted (cf. table S1); data for running at walk-run transition speeds were excluded to be more reflective of naturally preferred gaits. S^* is the mean across the trial for each speed tested. (b) Mean values of w^* plotted against mean S^* across each trial; data for running at walk-run transition speeds were included, to emphasize how w^* remains distinctly different between the two gaits, even at the transition. (c) Plot of w^* through 60 consecutive steps for subject 2, across an acceleration of 1.0 m s^{-2} , followed by a slow deceleration. Acceleration and deceleration phases are signified by arrows; subject begins moving at step 1. Note that the change from walking-like to running-like values for w^* takes place over a single step during both acceleration and deceleration.

Figure 4. Comparison of how step width changes with stride length in birds. For visualization, the raw data was binned to intervals of S^* , and the mean w^* determined for each bin. A MA regression derived from the raw data is also plotted for those species in which $P < 0.01$. (a) *C. virginianus* ($n = 221$, n.s.). (b) *C. japonica* ($n = 419$, n.s.). (c) *N. meleagris* ($n = 442$, n.s.). (d) *G. gallus* ($n = 233$, n.s.). (e) *C. chinensis* ($n = 840$, slope = 0.0138 , $r^2 = 0.007$). (f) *A. lathamii* ($n = 154$, slope = 0.0159 , $r^2 = 0.024$). (g) *T. moluccus* ($n =$

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2 124, slope = -0.1067, $r^2 = 0.162$). (h) *M. gallopavo* ($n = 185$, slope = -0.0081, $r^2 = 0.003$). (i)
3 *D. novaehollandiae* ($n = 1,140$, slope = -0.0268, $r^2 = 0.027$). (j) *S. camelus* ($n = 34$, slope = -
4 0.0411, $r^2 = 0.107$). (k) *P. porphyrio* ($n = 78$, slope = -0.0209, $r^2 = 0.019$). Hollow circles are
5 single or double data points; they are not means of many points for a given bin. Hence in
6 some instances, their apparent outlier nature may be accounted for as simply very few points
7 that fell into those particular bins. Note differences in horizontal and vertical scales.
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13 **Figure 5.** Bipedal stability in birds. (a) Comparison of mean (\pm s.d.) value of $h/\sqrt[3]{m}$ for each
14 species studied. Species with a mean value of $h/\sqrt[3]{m}$ greater than 0.24 (white bars)
15 ubiquitously demonstrated a pattern of decreasing w^* with increasing S^* . (b) Bipedal stability
16 is influenced by the length of the legs (or equivalently, hip height) relative to body mass. For
17 a point mass m on a massless leg of length l_1 or l_2 (where $l_2 > l_1$), the mass with leg length l_2
18 exerts a greater moment (by virtue of weight) about the base of support than the mass with leg
19 length l_1 , for the same leg orientation α . Therefore, it is easier for the mass to be shifted away
20 from a stable state and tipped over (i.e., relatively longer legs decrease stability).
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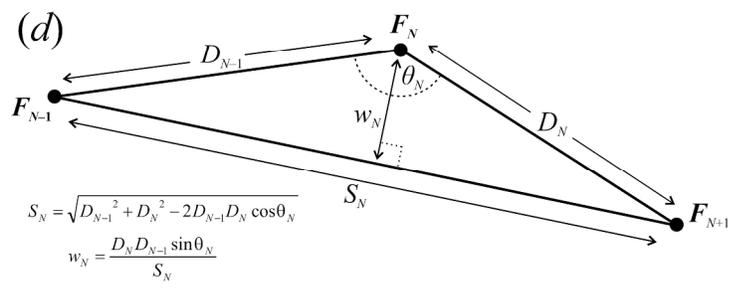
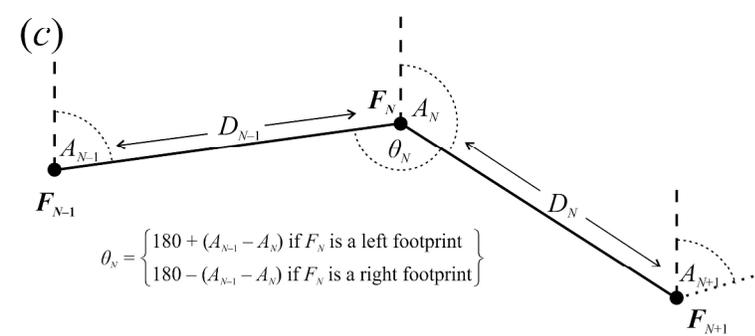
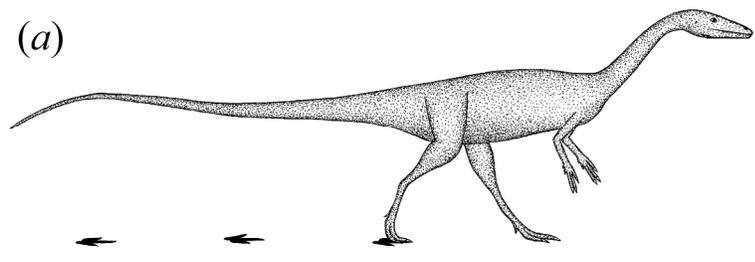
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30 **Figure 6.** The Culpeper theropod trackmakers are inferred to have had a continuous gait
31 pattern, probably including grounded running in their locomotor repertoire. (a) At slow
32 speeds of locomotion, the theropods would have walked in a fashion comparable to slow
33 walking in both modern birds and humans. The centre-of-mass (COM, black and white disc)
34 would have been lowest during double-support phases and highest at single-support phases,
35 and kinetic (KE) and potential energies (PE) of the COM would have oscillated more or less
36 out of phase. (b) At faster speeds, the theropods would have employed grounded running, still
37 having periods of double-support, yet where the COM is highest at double-support and lowest
38 at single-support. Kinetic and potential energies would oscillate more or less in phase. (c) At
39 faster speeds still, the theropods would have become airborne (i.e., aerial running) as the
40 vertical oscillations in the COM increase. Kinetic and potential energies continue to oscillate
41 in phase.
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Tables

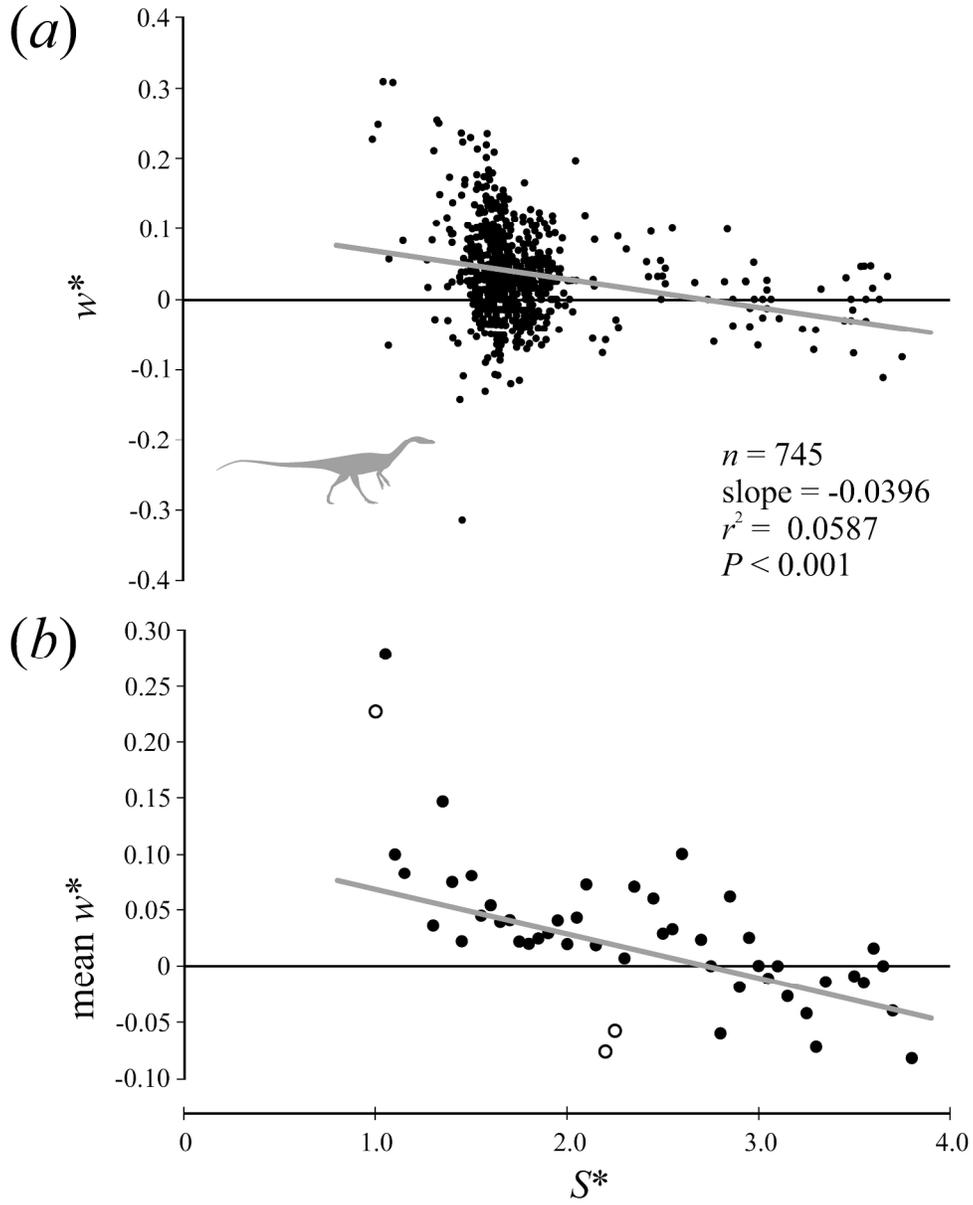
Table 1. The species of bird studied, along with sample sizes and mean (\pm s.d.) masses and hip heights.

Scientific name	Species		<i>n</i>	Mass (kg)	Hip height (mm)	Data collected
	Common name					
<i>Coturnix chinensis</i>	Chinese painted quail		3♂, 2♀ -	0.047 \pm 0.002	58.6 \pm 4.0	this study
<i>Colinus virginianus</i>	Northern bobwhite quail		3♂, 2♀ -	0.170 \pm 0.014	77.8 \pm 10.4	this study
<i>Coturnix japonica</i>	Japanese quail		1♂, 3♀ -	0.301 \pm 0.077	106.25 \pm 7.5	this study
<i>Porphyrio porphyrio</i>	Purple swamphen		3♀ -	0.623 \pm 0.058	239.0 \pm 14.1	this study
<i>Numida meleagris</i>	Helmeted guineafowl		2♂, 1♀ -	1.257 \pm 0.114	201.7 \pm 15.5	this study
<i>Alectura lathami</i>	Australian brush turkey		2♀ -	1.490 \pm 0.057	267.0 \pm 15.6	this study
<i>Threskiornis moluccus</i>	Australian white ibis		2♂ -	1.54 \pm 0.057	282.5 \pm 30.4	this study
<i>Gallus gallus</i>	Domestic chicken (white leghorn breed)		1♂, 2♀ -	1.710 \pm 0.521	254.3 \pm 47.8	this study
<i>Meleagris gallopavo</i>	Domestic turkey (various mixed breeds)		2♂, 3♀ -	3.228 \pm 0.90	365.2 \pm 47.4	this study
<i>Dromaius novaehollandiae</i>	Emu		6♀	38.58 \pm 2.69	903.3 \pm 35.0	[63]
<i>Struthio camelus</i>	Ostrich		3♂ -	74.87 \pm 4.44	1129.3 \pm 10.3	[18]

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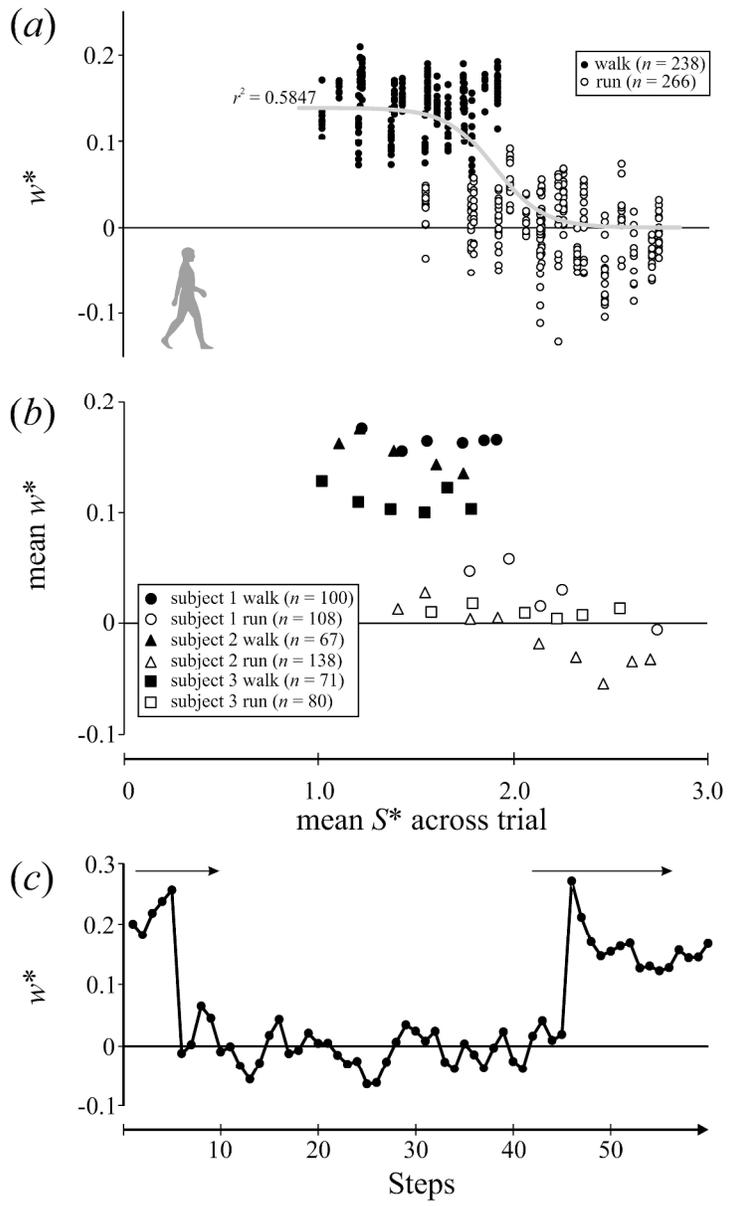
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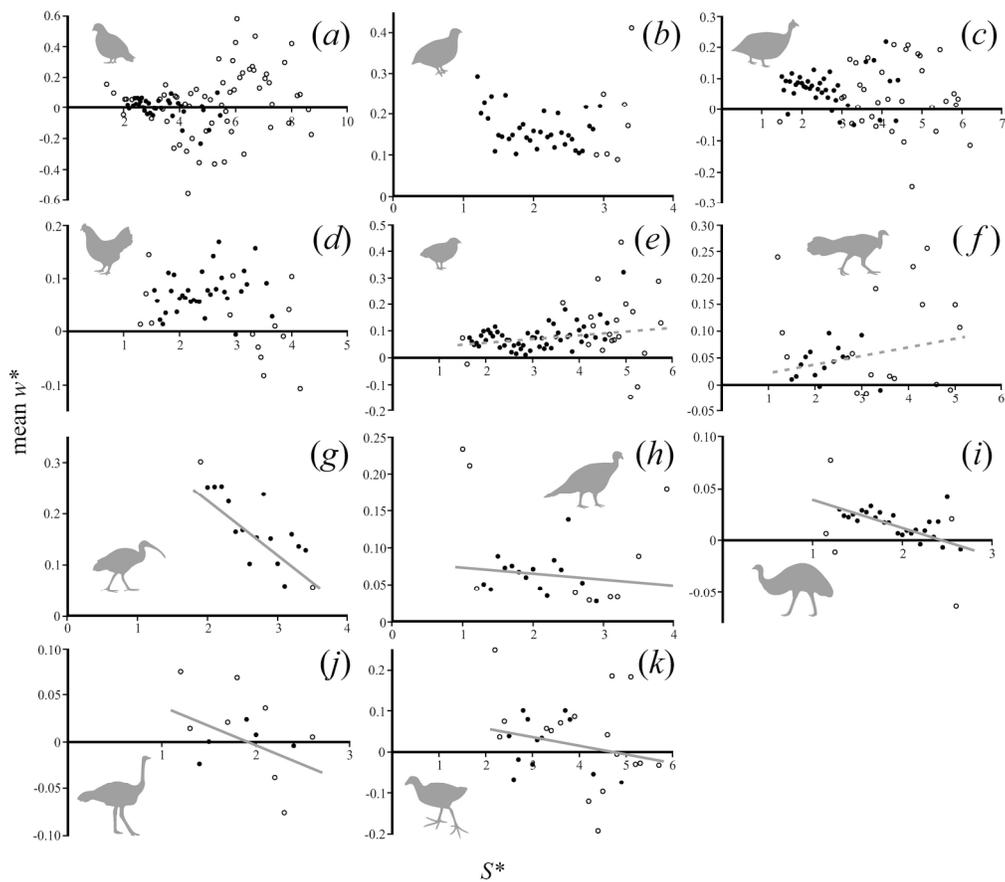
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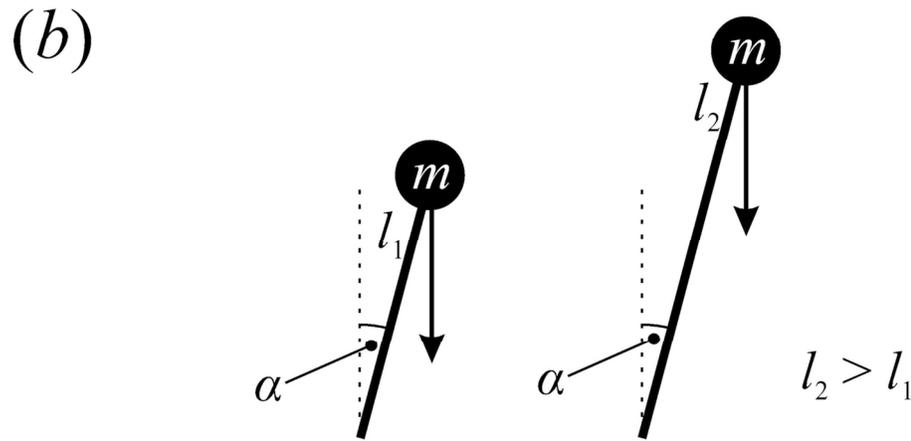
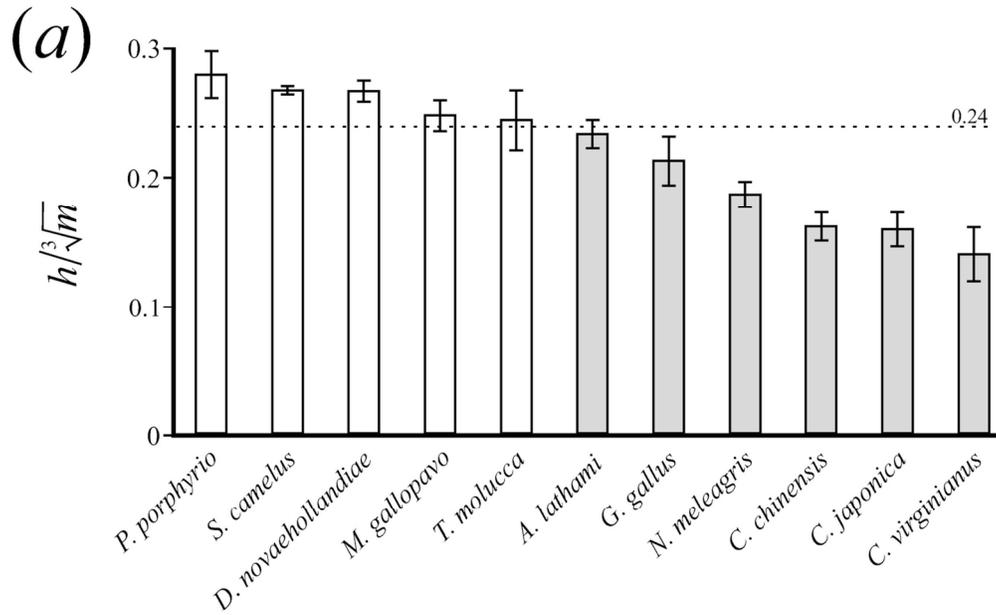
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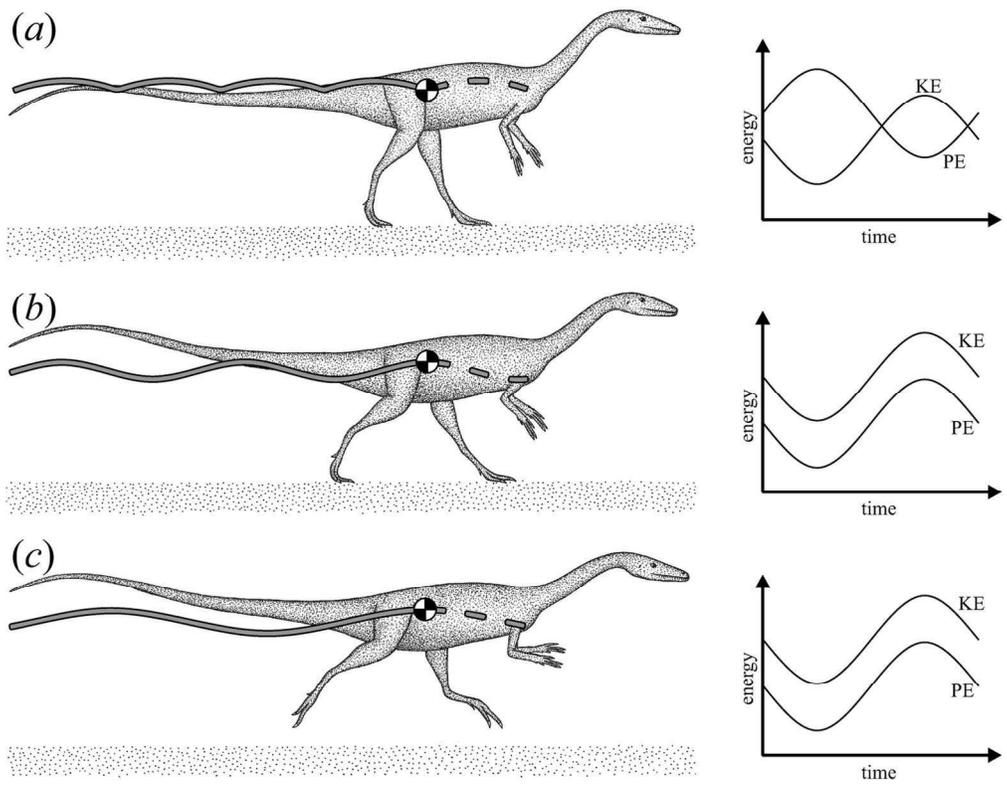
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