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Inter-stride variability triggers gait transitions in mammals and birds

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Speed-related gait transitions occur in many animals, but it remains unclear what factors trigger gait changes. While the most widely accepted function of gait transitions is that they reduce locomotor costs, there is no obvious metabolic trigger signalling animals when to switch gaits. An alternative approach suggests that gait transitions serve to reduce locomotor instability. While there is evidence supporting this in humans, similar research has not been conducted in other species. This study explores energetics and stride variability during the walk–run transition in mammals and birds. Across nine species, energy savings do not predict the occurrence of a gait transition. Instead, our findings suggest that animals trigger gait transitions to maintain high locomotor rhythmicity and reduce unstable states. Metabolic efficiency is an important benefit of gait transitions, but the reduction in dynamic instability may be the proximate trigger determining when those transitions occur.

1. Background

A general feature of terrestrial locomotion by mammals and birds is that, as they increase speed, they switch between gaits (e.g. walk, run, trot and gallop)—they perform gait transitions [1–7]. For many species, the speeds at which gait transitions occur are highly constrained to what are referred to as preferred transition speeds (PTS) [1,5,8–12]. While numerous studies have characterized gait transitions from kinematic, kinetic and metabolic perspectives, the mechanism triggering gait transitions remains unclear [13].

The most commonly cited function of gait transitions is to minimize energetic expenditure [1,4,5,8,9,13]. In an idealized situation (electronic supplementary material, figure S1a), plots of the energetic cost of transport (COT) per unit distance ($\text{J kg}^{-1} \text{m}^{-1}$) against locomotor speed reveal intersecting curvilinear relationships for different gaits (e.g. walking, trotting and galloping) [1,5,14]. The peaks of the lines are locomotor speeds with a high COT and the valleys are speeds with lower energetic costs. For the most part, when animals are allowed to move at self-selected paces, they select the most economical speeds within a given gait type and avoid speeds that are more energetically costly [5,15]. However, as animals adopt speeds near the peaks of their gait-specific COT curves, energy costs increase rapidly. This makes it energetically costly to maintain those gaits, and gait transitions become critical for energy conservation [1,4,5,8,9,14]. The speed at which the COT curve for one gait (e.g. walking) intersects the COT curve for another (e.g. trotting) is the energetically optimal transition speed (EOTS) [8,9,16]. In many species the EOTS and the PTS are very similar, suggesting that increasing energetic costs might play a role in triggering gait transitions [1,5,14,17].

This energy minimization hypothesis for gait transitions is not without its critics [2,9,13,18,19]. It is unclear what sensorimotor feedback mechanism

would indicate to an animal that they could save energy by changing gaits [8,20]. In the words of Farley & Taylor [2], 'It is difficult to imagine how energetic cost could trigger a gait transition as an animal rapidly changes speed.' Hreljac [8] demonstrated that when human participants rated their perceived exertion at and around their PTS (i.e. when subjects changed gaits from a walk to a run) their sense of effort decreased by 26.2%, but their actual energy costs *increased* by around 16%. Monteiro *et al.* [20] later showed that perceived effort is highly variable, but for most participants the highest level of perceived effort occurs after they have already made the transition from a walk to a run. Moreover, although some studies suggest that the PTS and EOTS can be concurrent, other research with humans demonstrates that the PTS can occur either before or after the EOTS [2,8,9,16,21]. Finally, gait transitions do not always result in a reduction of energetic expenditure. In particular, small-bodied species show a more monotonic decrease (reversed J-shape) in COT when they walk, such that there is no reciprocal increase in COT after the minimum value for walking is reached, and the COT of trotting is near the minimum COT of walking [14,22,23]. Together these findings suggest that, although gait transitions do have energetic benefits, energetic increases are not the primary trigger for gait transitions.

An alternative approach to understanding gait transitions emerges from a dynamical systems perspective of animal movement [3,9,19,24–29]. When animals adopt speeds close to the optimal stride length and frequency for a particular gait type (e.g. walking or trotting), the muscular input force required to sustain oscillation of the system is minimal [3,15,26,30]. This represents an attractor state wherein locomotion is stable, highly rhythmic, and energetically efficient [3,9,15,26,27,29,31,32]. In physics, stability relates to the way a system behaves following a perturbation. If the system is stable, a perturbation will not lead to a change in state variables. In locomotion, such a state change usually refers to either interlimb interference or falling [3,9,19,26,31,32]. While moving at an optimal stride length and frequency for a particular gait type is usually stable for an animal, speeding up or slowing down drives them away from this attractor state and they enter more variable, potentially unstable locomotor conditions (electronic supplementary material, figure S1b) [3,9,19,26,31,32]. This suggests that unstable, highly variable locomotor states, like those preceding a gait transition [3,28,29,33–35], are noisier and less predictable than steady-state movement [7,9,15,28]. Sensorimotor feedback about these unstable conditions could help guide the animal to a new stable locomotor state [24,26,35–37]. In this dynamical systems context, it has been suggested that gait transitions serve to reduce locomotor variability and avoid unstable states that might lead to injury or unnecessary energy expenditure trying to avoid tripping and falling [3,9,19,25–27,30,33].

Empirical support for this dynamic stability hypothesis has been demonstrated during human locomotion [3,9,31,32] (but see [38]), with robotic models [26,36,37] and in simulations [24]. As demonstrated by Diedrich & Warren [3], speeds nearing a gait transition are characterized by greater inter-stride variability in some kinematic variables compared to preferred locomotor speeds. Brisswalter & Mottet [9] explicitly compared the impacts of locomotor variability and energetics on gait transitions in humans. Inter-stride variability increased as their subjects approached the PTS, and subsequently

decreased after the walk–run transition. Energy expenditure also decreased after the walk–run transition, but the PTS preceded the EOTS. Similar results have been confirmed by more recent work [26,31,32,39].

While the dynamic stability hypothesis has been addressed in humans, it has yet to be tested in other animals. We hypothesized that gait transitions represent predictive, anticipatory switching of movement types to minimize high variability and avoid unstable dynamic states. To test this hypothesis, we collected spatio-temporal variability metrics and energetic expenditure data during walking and trotting in three mammalian tetrapods (Virginia opossums, *Didelphis virginiana*; tufted capuchins, *Sapajus apella*; domestic dogs, *Canis lupus familiaris*) and collated previously published data on an additional six species (brush-tailed bettong, *Bettongia penicillata* [40]; Australian water rat, *Hydromys chrysogaster* [17]; American mink, *Neovison vison* [41]; North American river otter, *Lontra canadensis* [10,42]; Svalbard rock ptarmigan, *Lagopus muta hyperborea* [14]; common ostrich, *Struthio camelus* [11,12]). We also tested the predictions of the energy minimization hypothesis in the same sample to determine which mechanism best explains the patterns of gait transitions in our dataset. We tested two competing hypotheses:

Hypothesis 1: Gait transitions minimize inter-stride variability.

Prediction 1: Inter-stride variation is highest near the preferred transition speed.

Prediction 2: Inter-stride variation is reduced after a gait transition.

Hypothesis 2: Gait transitions minimize energetic expenditure.

Prediction 1: The preferred transition speed and energetically optimum transition speed are concurrent.

Prediction 2: A reduction in energetic expenditure always occurs after a gait transition.

2. Methods

(a) Subjects and permissions

Virginia opossums (*Didelphis virginiana*), tufted capuchins (*Sapajus apella*) and domestic dogs (*Canis lupus familiaris*) were used in this study (electronic supplementary material, table S1). Data for the domestic dogs were collected in a previous study [43] and consist of three breed categories: northern breeds, hounds and retrievers. All animals were adults and determined by veterinarians to be free of any gait pathologies. All experimental protocols were approved by the Institutional Animal Care and Use Committees of the University of Chicago and the University of California, Santa Cruz.

(b) Preferred transition speed and inter-stride variation

Each animal was trained to exercise within a clear Plexiglas metabolic chamber (electronic supplementary material, table S2) that rested on top of a moving treadmill belt. The design of the metabolic chamber followed those published previously [44,45]. A small ribbon of weather stripping was attached to the bottom of the chamber so that the belt surface on the treadmill effectively slid across the bottom edge of the chamber. The chamber for the Virginia opossums and tufted capuchins was

only open to the room through a 0.15 m diameter circular intake hole cut into its back wall. The training regime consisted of mixed periods of exercise and rest over approximately six weeks. Animals were trained to move at a range of speeds (electronic supplementary material, table S2). Training familiarized the animals with the treadmill (i.e. reduced experimentally induced stress) and improved their fitness levels so that at the end of the training period all animals could sustain the 6–10 min of steady-state locomotion at any particular speed required for metabolic measurements.

After the training period was complete, the preferred transition speed (PTS) from a walk to a trot was determined by placing the animal onto the enclosed treadmill and incrementally increasing the speed of the moving belt every 15 s by specific speed increments (electronic supplementary material, table S2). During all trials, animals were recorded from a lateral view with the camera placed between 1.65 and 2.00 m away from the subject. This protocol was repeated four times for each individual to capture the range in the PTS for each species. Although the walk–trot transition could be observed visually, video recordings were used to calculate duty factor to determine the PTS for each trial.

While there are many metrics that can be used to represent inter-stride variability, we elected to use variability in stride cycle duration as our proxy as it is simple to replicate and has been shown to have important biomechanical consequences for gait stability [32,33]. At each speed interval (electronic supplementary material, table S2) for each individual Virginia opossum and tufted capuchin, we chose 30 strides at random and calculated the stride duration mean and standard deviation. At each speed interval (electronic supplementary material, table S2) for each breed of domestic dog, we calculated the stride duration mean and standard deviation based on 2–16 strides. Coefficients of variation (CV*) of stride cycle durations were calculated within individuals for Virginia opossums and tufted capuchins and within breeds for domestic dogs at each speed interval using $CV^* = (1 + 1/4n)CV$, where n is equal to the number of strides. The speed interval at which CV* was highest was also recorded for each individual or breed.

(c) Metabolic measurements and energetic costs

For each animal, metabolic data were collected in temperature-controlled rooms at a temperature range of 22–24°C at specific speed intervals (electronic supplementary material, table S2). Open flow respirometry following well-established protocols [43–45] was used to measure CO₂ production, O₂ consumption, water vapour pressure, barometric pressure, room temperature and air flow rates using a Field Metabolic System (Sable Systems International, Las Vegas, NV). Water vapour was scrubbed from the air column with Drierite (WA Hammond Drierite Co., Xenia, OH) after the recording of water vapour pressure and before the recording of CO₂ and O₂. The main pump (FlowKit Mass Flow Generator, Sable Systems International, Las Vegas, NV, USA) pulled air through the chamber to collect expired air. An internal circulation fan and the high flow rates (electronic supplementary material, table S2) of the system ensured that all of the expired gas from the animals was collected and hypoxic conditions were not reached. Instrument readings were recorded at 2 Hz. Readings were digitally converted by the UI-2 software in the Field Metabolic System. The digital data were then relayed to a computer using EXPEDATA software (Sable Systems, Inc., Las Vegas, NV).

During data collection, the order of the speeds was randomized, and no more than five trials for Virginia opossums and tufted capuchins and two trials for domestic dogs were collected from any one animal on a single day. This ensured that the animals were sufficiently well rested and post-absorptive for each locomotor trial. For each individual, we attempted to collect at

least three trials for each speed interval. Baseline measures of all respirometry variables were made before and after each recording session. A pre-exercise resting metabolic rate measurement was collected each individual for 10 min before each locomotor session. All locomotor trials lasted 6–10 min. The rate of oxygen consumption was determined for the last 3–5 min of the trial after oxygen consumption had reached a steady-state plateau [43,45]. The gait type used at each speed was determined by visual inspection at slow speeds and high speeds, but video recordings were used to verify gait type near the walk–trot transition. Near the PTS animals usually wavered between gait types at the beginning of the trial but quickly settled on either walking or trotting within the first few strides. Only trials where the animal predominately (approx. 90%) used one locomotor gait were used for analysis.

Calculations of the dry-corrected main flow rate (L min⁻¹), CO₂ production (VCO_2 , L min⁻¹) and O₂ consumption (VO_2 , L min⁻¹) were generated using established formulae [5,43,46–48] in EXPEDATA and a custom-designed EXCEL (Microsoft, Seattle, WA) spreadsheet. The energetic cost was converted to watts (J s⁻¹) using the formula $[(VO_2 \times 1000 \times 20.1)/60]$ assuming a negligible contribution from anaerobic glycolysis [43,45]. Speed-specific energetic cost per kilogram per unit distance (COT; J kg⁻¹ m⁻¹) was calculated for each trial measurement by dividing mass-specific metabolic cost by the trial speed. In order to make COT comparable with previously published datasets [10–12,14,17,40,41,43], the total mass-specific COT, which includes locomotor, postural and maintenance costs associated with each animal's resting rate, was used for all analyses.

(d) Data processing

All analyses were performed in MATLAB (v. 2017b; MathWorks, Natick, MA, USA) unless otherwise stated. Once COT was calculated for each trial, the relationship between COT and speed was determined for walking and trotting gaits for each individual using the Curve Fitting Toolbox in MATLAB. As previously reported COT/speed curves tend to be either linear or quadratic (e.g. [5,9,14,40]), we constrained curve fitting between these two options. The coefficient of determination (i.e. R^2 -value) was used to assess whether a quadratic function provided an equal or better fit than a linear relationship between COT and speed for each locomotor type for each individual. For the domestic dog data, no single individual from any of the breeds completed a trial at a broad enough range of speed intervals for reliable curve fitting reconstructions. Therefore, we analysed each breed together as if they were a single individual. We are aware that this treatment of the data might result in unaccounted variance due to differences in limb length or other morphological differences between the breeds. However, a Kruskal–Wallis test between the three breeds revealed no significant difference (d.f. = 2, $F = 3.49$, $p = 0.052$) in limb length. Therefore, we believe treating the data in this manner is appropriate.

We calculated the energetically optimal transition speed (EOTS) by determining the speed at which the COT/speed curve for walking intersected the COT/speed curve for trotting for each individual for opossums and capuchins, and for each breed for the domestic dogs. During the EOTS calculations for the domestic dogs it was often the case that the two COT/speed curves for each locomotor type did not intersect. In these instances, we determined the EOTS as the speed where the two COT/speed curves were closest to each other.

(e) Independent datasets

To further supplement the phylogenetic breadth of our sample, we searched the literature for studies that followed similar protocols to those described above and reported: (i) some metric of energy consumption per unit distance plotted against locomotor

speed for walking and the next fastest gait type (e.g. trotting, grounded running or bounding); (ii) the PTS; and (iii) stride cycle duration mean and standard deviation for a given speed. Based on these criteria, we included data from eight previous studies on an additional six species: the brush-tailed bettong (*Bettongia penicillata*) [40], Australian water rat (*Hydromys chryso-gaster*) [17], American mink (*Neovison vison*) [41], North American river otter (*Lontra canadensis*) [10,42], Svalbard rock ptarmigan (*Lagopus muta hyperborea*) [14] and common ostrich (*Struthio camelus*) [11,12]. For most studies, stride frequency was reported instead of stride cycle duration, so the data were inverted for inclusion in our study. Gait transitions in birds function differently than in mammals, as no trotting or bounding gait is observed. Instead, birds transition from a walk to an aerial run at high speeds and use a third gait type at medium speeds referred to as a grounded running [11,12,14]. During grounded running, the centre of mass movements switch to those consistent with an aerial running gait, but there is an absence of an aerial phase and other marked kinematic transitions. Interestingly, grounded running has been argued to result in a reduction in energy expenditure similar to that which has been observed during the walk–trot transition in mammals [11,12,14]. Therefore, we focused our analyses on the transition between walking and grounded running in birds rather than between walking and aerial running.

As raw data are rarely available in published work, we developed a protocol for simulating the data assuming normality based on the available information provided by the authors. All data points reported on figures, rather than tables or in text, were extracted using DATATHIEF III [49], which has been shown to be a reliable and repeatable data extraction tool [50]. For the PTS, it was common for a range of transition speeds to be reported rather than a mean and standard deviation. Therefore, statistical analyses were based on the range. For some species, the range for the PTS was not reported, so the fastest walking speed and the slowest trot, bound or grounded run speed were used to represent the range of the PTS.

To determine the EOTS for each species, we first converted all metabolic measures into total mass-specific COT in order to generate a COT/speed curve for each locomotor mode. In most studies, data points were reported such that only a single EOTS could be determined for each species. To assess intraspecific variation, we used a jack-knifing method in which a single data point was removed at random from one of COT/speed curves. From the remaining points, the Curve Fitting Toolbox in MATLAB was used to determine the best-fit lines from the COT/speed curves for each locomotor type. As described above, we constrained curve fitting between either a linear or a quadratic function for each iteration. The coefficient of determination was used to assess whether a quadratic function provided an equal or better fit compared with a linear relationship between COT and speed for locomotor type for each iteration. The EOTS was determined based on the intersection of the best-fit COT/speed curves for each locomotor type for each iteration. This resampling was repeated until all unique combinations had been sampled. For data on the Svalbard rock ptarmigan, the authors report only a mean and standard deviation for COT for each speed interval rather than individual data points. To generate data points for the analysis described above on this species, we used the normal random number generator function in MATLAB based on the reported mean and standard deviation. As the authors report four to six trials in their analysis, we elected to generate five data points for each speed interval. During the EOTS calculations for the American mink, it was often the case that the two COT/speed curves for each locomotor type did not intersect. In these instances, we determined the EOTS as the speed where the two COT/speed curves were closest to each other.

To assess intraspecific variance of CV* across speeds for each species, we used the normal random number generator function in MATLAB based on the reported mean and standard deviation of stride cycle duration for each speed interval. This procedure was necessary to compare CV* statistically across speed intervals. The number of points we generated were based on the number of trials reported by the authors at each specific speed interval. For some datasets, stride cycle duration was reported as a single point at a specific speed rather than a mean and standard deviation at a specific speed interval. For these datasets, the range of locomotor speeds was broken up into equally distributed speed interval bins using the histogram and discretize function in MATLAB. The mean speed of each bin was used for subsequent analyses (electronic supplementary material, table S3). Once each speed interval bin was populated with data points of stride cycle duration, we used a jack-knifing method in which a data point was removed at random from each bin and CV* was calculated based on the resampled mean and standard deviation of the new speed interval bin. The speed interval at which CV* was highest was also recorded for each resampling. This resampling protocol was repeated until all unique combinations had been sampled.

(f) Statistical analyses

We used the Mann–Whitney *U*-test to determine whether: (1) a gait transition results in a decrease in COT; (2) a gait transition results in a decrease in CV*; (3) the EOTS and PTS were concurrent events in domestic dogs, tufted capuchins and Virginia opossums; and (4) CV* was highest at a speed near the PTS in domestic dogs, tufted capuchins and Virginia opossums. Because PTS was often reported as a range in previously published studies, we tested whether: (1) the EOTS would fall within the range of the PTS; and (2) CV* would be highest at speeds within the range of the PTS using the χ^2 -test. All statistical tests were conducted within species (i.e. no interspecific comparisons) with $p \leq 0.05$.

3. Results

There was a great deal of interspecific variation in the relationship between energy consumption per unit distance and locomotor speed (electronic supplementary material, table S4; figure 1). In most species, the relationship between COT and speed is parabolic during walking. By contrast, during trotting, bounding or grounded running, a linear relationship was commonly observed. In the Virginia opossums, tufted capuchins, brush-tailed bettongs and Australian water rats, switching from a walking gait to a trot or bound resulted in a significant (all p -values ≤ 0.006) reduction in the COT. However, for the domestic dogs, Svalbard rock ptarmigan, common ostrich and North American river otter, no significant (all p -values ≥ 0.098) difference was observed in the COT after switching from a walk to a trot, bound or grounded run (figure 1; electronic supplementary material, figure S2).

In the tufted capuchins, Virginia opossums and domestic dogs, the EOTS was significantly lower (all p -values ≤ 0.004) than the PTS. Similarly, the likelihood that the EOTS occurred within the range of the PTS was significantly lower than expected for the American mink (d.f. = 1, $\chi^2 = 13.33$, $p = 0.002$), Svalbard rock ptarmigan (d.f. = 1, $\chi^2 = 13.33$, $p = 0.002$) and common ostrich (d.f. = 1, $\chi^2 = 4.65$, $p = 0.031$). For both the American mink and common ostrich, the EOTS occurred before the PTS, but for the Svalbard rock ptarmigan the opposite pattern was observed. For the North

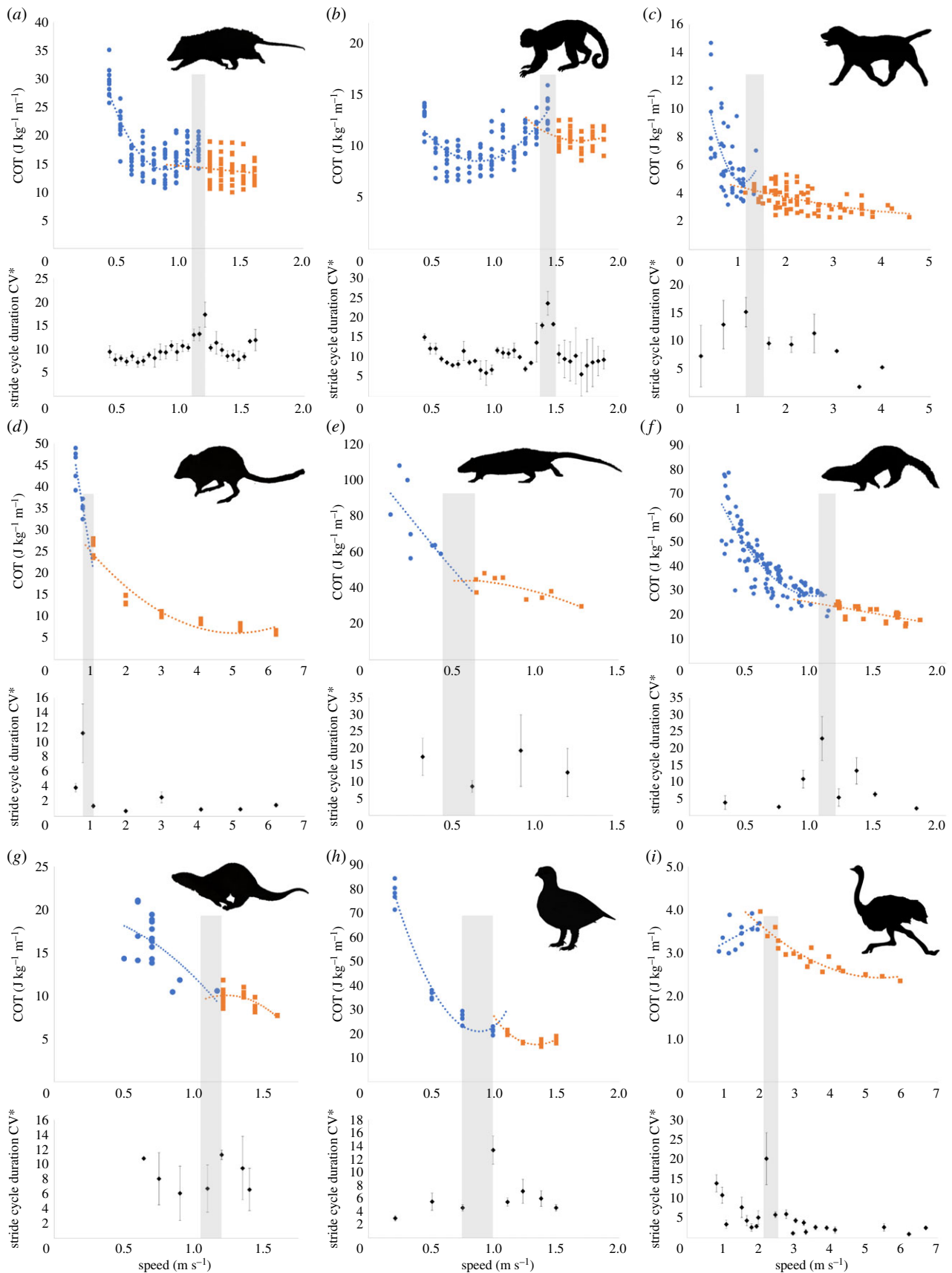


Figure 1. COT ($\text{J kg}^{-1} \text{m}^{-1}$) and coefficients of variation (CV*) of stride cycle durations (mean \pm s.d.) plotted against locomotor speed (m s^{-1}) for (a) Virginia opossum (*Didelphis virginiana*), (b) tufted capuchin (*Sapajus apella*), (c) domestic dog (*Canis lupus familiaris*), (d) brush-tailed bettong (*Bettongia penicillata*), (e) Australian water rat (*Hydromys chrysogaster*), (f) American mink (*Neovison vison*), (g) North American river otter (*Lontra canadensis*), (h) Svalbard rock ptarmigan (*Lagopus muta hyperborean*) and (i) common ostrich (*Struthio camelus*). Circles (blue in online version) represent COT for walking gaits, and squares (orange in online version) represent trotting (a–c,e), bounding (d,f–g) or grounded running (h–i). The energetically optimal transition speed is determined as the speed at which the best-fit line for walking intersects with the best-fit line for trotting, bounding or grounded running. The box represents the observed speeds where gait transitions occur. Calculations of CV* for each speed were based on 2–30 stride cycle durations depending on the species (electronic supplementary material, table S3). (Online version in colour.)

American river otter (d.f. = 1, $\chi^2 = 75$, $p < 0.001$), brush-tailed bettong (d.f. = 1, $\chi^2 = 155.56$, $p < 0.001$) and Australian water rat (d.f. = 1, $\chi^2 = 120$, $p < 0.001$), the likelihood that the EOTS occurred within the range of the PTS was significantly greater than expected by chance (table 1).

In all species, coefficients of variation of stride cycle durations varied across the range of speeds tested and, in almost all species, were highest at speeds near the PTS. In all species except the Australian water rat, a gait transition from walking to trotting, bounding or grounded running resulted in a significant (all p -values ≤ 0.047) reduction of CV*. In the Australian water rat, there was no significant ($p = 0.257$) difference between CV* at speeds after the walk-trot transition compared with CV* during the PTS (figure 1 and electronic supplementary material, figure S2).

In the tufted capuchins, Virginia opossums and domestic dogs, no significant (all p -values ≥ 0.235) difference was observed between the PTS and the speed at which CV* was highest. Furthermore, the likelihood that the speed with the highest CV* fell within the PTS range was significantly higher than expected for the American mink (d.f. = 1, $\chi^2 = 105.19$, $p \leq 0.001$), Svalbard rock ptarmigan (d.f. = 1, $\chi^2 = 152.27$, $p \leq 0.001$), common ostrich (d.f. = 1, $\chi^2 = 105.36$, $p \leq 0.001$), North American river otter (d.f. = 1, $\chi^2 = 65.74$, $p < 0.001$) and brush-tailed bettong (d.f. = 1, $\chi^2 = 151.651$, $p < 0.001$). In contrast to the other species, the likelihood that the speed with the highest CV* fell within the range of the PTS was significantly lower than expected for the Australian water rat (d.f. = 1, $\chi^2 = 17.79$, $p < 0.001$; table 1).

4. Discussion

In this study, we tested whether the energy minimization or dynamic stability hypothesis best explains the triggering of gait transitions in a broad phylogenetic sample of mammals and birds. Our findings indicate that energy minimization does not reliably predict gait transitions in our dataset. By contrast, in all species except the Australian water rat, the need to reduce inter-stride variation and leave dynamically unstable states appears to be an important factor in determining when a gait transition will occur. Our data agree with other works (e.g. [3,9,29]) suggesting that gait transitions in birds and mammals represent predictive, anticipatory switching of movement types to minimize high kinematic variability and unstable dynamic states.

At its most basic level, the energy minimization hypothesis assumes that gait transitions will always result in a reduction in the COT after the gait transition occurs, and that the PTS will be concurrent with the EOTS [1,4,5,8,9,14]. In our dataset, the energetic profiles of some of the species did follow these predictions, but out of all nine species, only the brush-tailed bettong and Australian water rat satisfied both of these assumptions. Interestingly, gait transitions did not always result in a reduction of the COT. This was mostly the case for species that show a more monotonic decrease (reversed J-shaped) in COT when they walk, such that there is no reciprocal increase in COT after the minimum value for walking is reached, and the COT of trotting, bounding or grounded running is near the minimum COT of walking. Similar findings have been reported for small mammals [14,22,23,51,52], but even larger species in our dataset (dogs and ostriches) demonstrated this pattern. Is it the

case that the species that do not demonstrate a reduction in the COT after a gait transition are the same species that demonstrate discordance between the PTS and EOTS? Our data do not support this suggestion, as some of the species that demonstrate a reduction in the COT after a gait transition also show discordance between the EOTS and PTS. In these species, the PTS usually occurred at higher speeds than the EOTS. This means that these animals maintained a walking gait despite the fact that switching to a trot, bound or grounded run would have likely been more energetically efficient. Only the Svalbard rock ptarmigan had a lower PTS than the EOTS, indicating that this species switched to a grounded run despite the fact that maintaining a walking gait would be energetically more efficient. The fact that different species show differing patterns of discordance between the PTS and the EOTS raises questions about the validity of the energy minimization hypothesis.

Patterns of kinematic CV* varied as animals moved from a walk to a trot, bound or grounded run. In all species except the Australian water rat, CV* was always highest at speeds near the PTS and decreased in the next time interval after a gait transition. This pattern was observed in species with differing phylogenetic histories (e.g. birds versus mammals), body sizes (0.67–114 kg) and gait transition types (walk-trot versus walk-bound). Patterns of inter-stride variation during human locomotion show the same pattern [25,31,32]. These findings are in accordance with the view that gaits are stable states in complex dynamic systems and that gait transitions occur when the stability of a gait decreases so much that switching to a new gait improves stability [3,9,19,24–26]. Our results suggest that mammals and birds monitor aspects of inter-stride variability during locomotion and make gait transitions at a critical level of variation, entering or maintaining a more rhythmic, less unstable locomotor state.

Maintaining rhythmicity during cyclic behaviours has a number of performance benefits, principal among them being greater predictability of kinematic events [33]. For example, predictability of limb movements allows animals to coordinate oscillating musculoskeletal and nervous components during locomotion, and reduces the probability of interlimb interference or falling [33,53]. Currently, information on the frequency of interlimb interference in wild animals is unavailable, but the equine veterinary literature is well acquainted with the lacerations, and potentially associated osteomyelitis, that may occur from forging, brushing, cross-firing and other forms of interlimb interference [54,55]. While many things may precipitate interlimb interference injuries, chief among them are neuromuscular disorders that limit the ability of the animal to coordinate the movement of the limbs relative to each other [54]. Low inter-stride variation has also been linked with an overall lower likelihood of falling in general [53]. Normal variation in behavioral contexts requires animals to increase locomotor speeds, and our data, in combination with previously conducted studies (e.g. [3,9,32,35]), suggest this inevitably results in increases in inter-stride variation. By making gait transitions, mammals and birds can minimize high inter-stride variation and unstable dynamic states, reducing the risk of interlimb interference, tripping or falling.

Synthesizing the energy minimization and dynamic stability hypotheses, high inter-stride variability might also

Table 1. Summary statistics and frequency data for speed (m s^{-1}) related variables.

species	gait transition	preferred transition speed (m s^{-1} ; mean \pm s.d.)	range of preferred transition speed (m s^{-1})	energetically optimal transition speed (m s^{-1} ; mean \pm s.d.)	frequency at which EOTS occurs within the range of preferred transition speeds (%)	speed at which stride cycle duration is highest (m s^{-1} ; mean \pm s.d.)	frequency at which maximum $\text{Cl}^{\#}$ occurs within the range of preferred transition speeds (%)
Virginia opossum	walk–trot	1.19 \pm 0.05	1.10–1.21	1.07 \pm 0.04	—	1.18 \pm 0.04	—
tufted capuchin	walk–trot	1.43 \pm 0.05	1.36–1.48	1.29 \pm 0.09	—	1.40 \pm 0.05	—
domestic dog	walk–trot	1.37 \pm 0.11	1.16–1.39	1.11 \pm 0.04	—	1.25 \pm 0.27	—
brush-tailed bettong	quadrupedal bound–bipedal hop	—	0.80–1.10	1.00 \pm 0.03	100	—	99
Australian water rat	walk–trot	—	0.43–0.64	0.52 \pm 0.04	100	—	45
American mink	walk–quadrupedal bound	—	1.03–1.16	0.93 \pm 0.01	0	—	85
North American river otter	walk–quadrupedal bound	—	1.05–1.20	1.13 \pm 0.05	94	—	70
Svalbard rock ptarmigan	walk–grounded run	—	0.75–1.00	1.04 \pm 0.01	0	—	98
common ostrich	walk–grounded run	—	2.20–2.49	1.82 \pm 0.04	0	—	75

be associated with increased energy expenditure during locomotion [9,15,26,30]. As deviations from preferred locomotor state result in greater variability of the centre of mass movements and limb inertial changes, avoiding falling and interlimb interference might necessitate more muscle recruitment, and therefore more work by limbs and limb muscles. Furthermore, beyond active correction, highly variable gaits might be more energetically costly solely because more strides include step lengths and durations that do not coincide with minimum energy expenditure [15,26]. Hence, the high inter-stride variation might not only be dynamically unstable, but it might result in additional energy expenditure in attempts to minimize instability, or simply as a consequence of those strides deviating from the energetically optimal preferred gait state [9,15,30].

A study of this nature has a number of limitations. First, the statistical treatment of published data makes a number of assumptions about normality and homoscedasticity that are difficult to evaluate. We suggest that our approach is preferable to subjective, qualitative interpretation of previously published data and provide detailed methods for reconstructing our analyses. Another potential limitation is that all of these interpretations are based on studies of animals moving on treadmills, rather than in naturalistic settings. Currently, it is unclear whether the same energetic or variability patterns are present in animals in the wild. Using available data from ostriches running in the wild [56], we calculated CV* for each individual across the differing locomotor speeds. Consistent with our results, there is a large spike in CV* just prior to the onset of grounded running (electronic supplementary material, figure S3), indicating that the same patterns observed in this study are likely to be present during locomotion in more natural settings. Finally, our study only explored energetic and inter-stride variability measures around the transition from walk to trot, bound or grounded run: we did not explore energetics and inter-stride variability around the trot–gallop transition or the trot–walk transition. We expect that the same energetic and inter-stride variability patterns should emerge in future work to refute or corroborate the hypothesis presented here by expanding our analyses to other gait transitions.

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5. Conclusion

Across nine diverse species of mammals and birds, energy savings do not predict gait transition patterns. Instead, our findings suggest that gait transitions function to maintain dynamic stability across a range of speeds. More rhythmic, less variable locomotor states improve the predictability of kinematic events and reduce energetic costs associated with locomotor instability. Our data, in concert with other previously published works (e.g. [3,9,29]), suggest that gait transitions represent predictive, anticipatory switching of movement types to minimize high variability and avoid unstable dynamic states. Furthermore, it is likely that energy savings associated with switching gaits, when they are present, are ancillary and secondary to the reduction of inter-stride instability accompanying gait transitions. Birds and mammals have probably convergently evolved sensorimotor mechanisms for monitoring inter-stride stability during locomotion and for triggering gait transitions at critical levels of variation. Investigation of those mechanisms would be of great interest.

Ethics. The authors report no breach in ethics. All experimental protocols were approved by the Institutional Animal Care and Use Committees of the University of Chicago and the University of California, Santa Cruz.

Data accessibility. All data necessary for future analysis are provided in text and as electronic supplementary material files.

Authors' contributions. M.C.G. and C.F.R. designed the study. M.C.G., M.F.L. and K.S. collected data from tufted capuchins and Virginia opossums. C.M.B. collected data from domestic dogs. J.H. and C.E.W. provided expertise on experimental design and analysis. M.C.G. and A.F. conducted all statistical analysis. M.C.G., C.M.B., J.H., M.F.L., A.F., C.E.W. and C.F.R. prepared and edited the manuscript.

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