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## RESEARCH ARTICLE

# Stride frequency or length? A phylogenetic approach to understand how animals regulate locomotor speed

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## ABSTRACT

Speed regulation in animals involves stride frequency and stride length. While the relationship between these variables has been well documented, it remains unresolved whether animals primarily modify stride frequency or stride length to increase speed. In this study, we explored the interrelationships between these three variables across a sample of 103 tetrapods and assessed whether speed regulation strategy is influenced by mechanical, allometric, phylogenetic or ecological factors. We observed that crouched terrestrial species tend to regulate speed through stride frequency. Such a strategy is energetically costly, but results in greater locomotor maneuverability and greater stability. In contrast, regulating speed through stride length is closely tied to larger arboreal animals with relatively extended limbs. Such movements reduce substrate oscillations on thin arboreal supports and/or helps to reduce swing phase costs. The slope of speed on frequency is lower in small crouched animals than in large-bodied erect species. As a result, substantially more rapid limb movements are matched with only small speed increases in crouched, small-bodied animals. Furthermore, the slope of speed on stride length was inversely proportional to body mass. As such, small changes in stride length can result in relatively rapid speed increases for small-bodied species. These results are somewhat counterintuitive, in that larger species, which have longer limbs and take longer strides, do not appear to gain as much speed increase out of lengthening their stride. Conversely, smaller species that cycle their limbs rapidly do not gain as much speed out of increasing stride frequency as do larger species.

KEY WORDS: Allometry, Locomotion, Arboreal, Posture, Velocity, Tetrapods

## INTRODUCTION

Supported by a repetitive motor program, speed regulation in animals involves two basic parameters: stride frequency and stride length (Schubert et al., 2014; Strang and Steudel, 1990). While the relationship between these variables has been demonstrated in numerous studies (see Table S1), it remains unresolved whether animals primarily modify stride frequency or stride length to increase speed, and what factors contribute to this regulation strategy.

Most discussion for why animals primarily modulate stride length over stride frequency to increase speed originates from an energetic optimization standpoint. The predominant energy-consuming process in locomotion is the generation of muscular force (Kram and Taylor, 1990; Pontzer, 2016); during movement 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), and stride distance is an important determinant of stance phase duration (Pontzer, 2016), selection for reduction in the energetic costs of locomotion is expected to favor species that increase speed through stride length. This strategy has been argued to be especially important for large-bodied animals, and has been posited as one of the mechanisms underlying the negative relationship between locomotor cost and body size (Heglund and Taylor, 1988; Reilly et al., 2007).

An alternative ecological hypothesis originates from the well-documented finding that primates tend to have much larger joint angular excursions, and therefore greater relative stride lengths, compared with non-primate mammals (Larson et al., 2000, 2001; Strang and Steudel, 1990). The adaptive benefits of these extended stride lengths are thought to increase stability by reducing the number of strides needed to travel a given distance and therefore lower potential substrate oscillations on thin arboreal supports (Demes et al., 1990; Granatosky et al., 2019b; Larson et al., 2000, 2001; Strang and Steudel, 1990; Vereecke et al., 2006). While the 'uniqueness' of primate gait characteristics has been noted in a number of studies (Larson et al., 2000, 2001; Schmitt, 1999), it seems that the strategy for increasing speed primarily through stride length should extend to other arboreal species. The results have been equivocal, and studies of arboreal gait mechanics across a number of primate and non-primate species reveal the reliance on stride length to increase speed may not be ubiquitous (Clemente et al., 2013; Granatosky et al., 2019b, 2021; Karantanis et al., 2017).

Primarily altering speed through stride frequency has been argued to be advantageous for small-bodied, crouched species as it allows greater opportunities to adjust heading, thus allowing the animal to be more maneuverable (Reilly et al., 2007). Such performance is likely advantageous for predator avoidance. Furthermore, many small-bodied, crouched species access tight spaces (e.g. tunnels or burrows) where long stride lengths would only impede maneuverability (Horner et al., 2016). However, modulating speed primarily through stride frequency comes at a metabolic cost based on multiple factors. First, each stance phase is associated with some muscular effort to support the body weight and this effort is greater when the limbs are flexed (Horner et al., 2016; Reilly et al., 2007). Second, additional muscle activity is needed to swing limbs faster than the limbs' intrinsic frequency and faster rates of muscle force generation cost more (Heglund and Cavagna, 1987; Kram and Taylor, 1990). Third, at small body size, muscle stiffness does not allow for the limb to benefit from pendular mechanics or elastic

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energy savings (Hooper, 2012; Sutton et al., 2022 preprint). As such, muscular effort is required to both support the body and 'reset' the limb for the next stance phase. Across crouched animals, the smallest species move with the highest stride frequencies and, correspondingly, have the highest metabolic costs of locomotion (Heglund and Taylor, 1988; Reilly et al., 2007). As size increases and stride frequency decreases, locomotor cost drops in crouched animals. Therefore, the greater metabolic cost of locomotion in crouched animals can be primarily explained by the fact that they take more steps with their shorter legs than larger erect animals to cover the same distance (Heglund and Taylor, 1988; Reilly et al., 2007; Strang and Steudel, 1990).

Some evidence suggests that the tendency to primarily increase speed through stride frequency may be attributable to the conserved nature of locomotor motor patterns (Buchwitz et al., 2021; Cuff et al., 2019; Goslow et al., 1989; Lauder and Shaffer, 1988; Peters and Goslow, 1983; Wainwright et al., 1989). Utilizing a salamander model, Ijspeert and colleagues (2006, 2007, 2008) demonstrated that spinal stimulation of increasing intensity results in frequency-related changes in axial and appendicular movements. In their model, low intensity spinal stimulations result in slow walking gaits, while the more intense signaling elicits the rapid oscillatory movements required for swimming. Extrapolating from these data, it seems probable that 'primitive' species (e.g. amphibians and lepidosaurs) may be limited to frequency-dependent speed increases based on a locomotor constraint attributable to 'simpler' spinal circuitry. Pierce et al. (2020) and Granatosky (2020) independently support this reasoning by demonstrating that muscle activity patterns of many walking tetrapods have broad-scale similarities, potentially indicating conservation of some aspects of neuromuscular function. Similar muscle activity patterns indicate that the potential for drastic kinematic adjustments (e.g. modulating stride length) are likely limited. Furthermore, Granatosky et al. (2019a) show that while limb joint kinematics are highly labile across evolutionary history, much of the diversity in limb kinematics is a recent, suggesting mammalian, innovation. Finally, utilizing trackway evidence, Buchwitz et al. (2021), proposed that temnospondyls (extinct primitive amphibians) showed little ability to modulate stride length. Such capabilities do not appear in the ichnofossil record until the emergence of Cotylosauria (Amniota+Didectomorpha). Taken together, there appears to be strong evidence for the presence of a neuromuscular constraint in speed regulation primarily through stride frequency for tetrapods.

Beyond primarily increasing either stride frequency or stride length, Strang and Steudel (1990) and Reilly et al. (2007) documented notable allometric consequences for how animals regulate speed. Across a large range of body sizes, the ability to generate high stride frequencies decreases, but stride length increases (Biewener, 1983; Heglund and Taylor, 1988). Because speed effects are substantial, these stride characteristics are commonly reported as the slope of each parameter regressed against speed. When examining these slopes, no significant differences in the slope of speed on stride length are noted across animals of differing body mass or posture (crouched or extended limbs). In other words, animals of all sizes increase stride length similarly as they move faster. In contrast, the slope of speed on frequency is much lower in small crouched animals compared with that in erect species. As a result, substantially more rapid limb movements are matched with only small speed increases in crouched animals (Reilly et al., 2007; Strang and Steudel, 1990).

With these considerations in mind, we explored the interrelationships between stride length, stride frequency and locomotor speed across a broad phylogenetic sample of tetrapods. We used this sample to assess whether patterns of these three variables are primarily driven by mechanical (Heglund and Taylor, 1988; Reilly et al., 2007; Strang and Steudel, 1990), allometric (Reilly et al., 2007), phylogenetic (Buchwitz et al., 2021; Larson et al., 2001) or ecological factors (Granatosky et al., 2019b; Karantanis et al., 2017; Nyakatura et al., 2008).

## MATERIALS AND METHODS
### Data collection
To draw biologically meaningful comparisons concerning the relationship between speed and stride frequency and length, we searched the literature for studies from a range of tetrapod species that reported how each of these variables correspond to each other (i.e. belong to the same sequences) so as not to distort their interrelatedness (see Table S1). These data were assembled by searching previously published material in academic search engines and supplemented with previously unpublished data from M.C.G. The search engines used included Academic Search, BioOne, Google Scholar, Microsoft Academic, PubMed and Web of Science. All data points reported on figures, rather than in tables, were extracted using DataThief III (Tummers, 2016), which has been shown to be a reliable and repeatable data extraction tool (Flower et al., 2016). Studies or species that did not have at least 10 cycles were excluded from the subsequent statistical analyses.

Data for each species were isolated to a single study so as to mitigate any interobserver effects (see Table S1). All data were collected from adults and data from different sexes and substrates were pooled. All data for galloping were excluded from analyses as most species are unable to modify stride frequency once galloping begins (Herbin et al., 2004; Hudson et al., 2012; Pfau et al., 2011). As such, this results in a curvilinear relationship that impacts the applicability of the models detailed below. Such exclusion was only applied to three species in the sample [i.e. *Mus musculus* (Herbin et al., 2004), *Canis lupus familiaris* (Bryce and Williams, 2017) and *Vicugna pacos* (Pfau et al., 2011)]. There was variability in how different studies measured speed during a trial; for example, some studies used stride averaged speed, while others used average speed across several strides. Mathematically, the average speed for a stride must equal the product of that stride's length and frequency. We took advantage of this mathematical relationship to recompute running speed for each measured stride in our dataset as the product of the reported stride length and stride frequency.

### Statistical analysis
We developed a custom-written MATLAB (MathWorks Inc., Natick, MA, USA) code that calculated [assuming a linear relationship; exclusion of galloping tends to result in a linear relationship between the three variables of interest (Herbin et al., 2004; Pfau et al., 2011)] the slope, coefficient of determination ($R^2$) and statistical significance for the stride length versus speed model and the stride frequency versus speed model for each species. The use of $R^2$ in this study to reflect speed modulation strategy is not a new or unsubstantiated variable (Granatosky et al., 2021; Herbin et al., 2004; Karantanis et al., 2015; Pfau et al., 2011; Zaaf et al., 2001). Namely, when correlating speed changes to either stride length or frequency, a low $R^2$ represents inconsistency, while a high $R^2$ represents consistent modulation. The use of $R^2$ in this manner is ideal because it provides a quantifiable measure of goodness of fit that produces a value between 0 and 1. Further, unlike other measures of variability (e.g. variance), when calculated independently between models (e.g. one $R^2$ for the relationship

between stride length and speed and a second $R^2$ for the relationship between stride frequency and speed) of equal sample size (Table S1), $R^2$ is not influenced by magnitude differences between the samples. We chose to use raw values, as opposed to size-adjusted values, for stride length, stride frequency and speed for these calculations because they were all done within each species.

To quantify an animals' strategy for regulating speed via stride length or stride frequency, we divided the $R^2$-value from the stride frequency versus speed model by the $R^2$-value from the stride length versus speed model. The resulting $R^2$ ratio was then log-transformed such that species with a negative $R^2$ ratio primarily regulated speed via stride length and any species with a positive $R^2$ ratio primarily regulated speed via stride frequency. Increased velocity during locomotion can be achieved by: increasing primarily stride frequency and, at a lesser rate, stride length (a positive $R^2$ ratio; Granatosky et al., 2021; Karantanis et al., 2017; Nyakatura et al., 2008; Pfau et al., 2011); by increasing primarily stride length and, at a lesser rate, stride frequency (a negative $R^2$ ratio; Granatosky et al., 2019b; Strang and Steudel, 1990); or by increasing stride frequency and stride length simultaneously (and $R^2$ ratio equal to 0). It should be noted that, although an animal may consistently modulate either stride frequency (a positive $R^2$ ratio) or stride length (a negative $R^2$ ratio) to influence speed, this does not necessarily imply that consistent modulation results in the greatest effect on speed. The effectiveness of the modulation strategy is better reflected by the slopes of the stride length versus speed model and the stride frequency versus speed model for each species (Reilly et al., 2007). For example, it is possible that a species might primarily modulate speed via changes in stride frequency (a positive $R^2$ ratio). However, a shallow slope between stride frequency and speed means the same species would not gain much speed increase despite rapid limb cycling. Such a possibility was proposed by Reilly and colleagues (2007), but these are the first data to test whether such a discrepancy between consistency versus effectiveness in modulation strategies for speed increases exists in nature.

We first tested for phylogenetic signal in stride length versus speed slopes, stride frequency versus speed slopes, and log-transformed $R^2$ ratio by estimating Blomberg's $K$ and testing it using 10,000 randomizations. To assess the hypothesized causal factors contributing (e.g. mechanical, allometric, phylogenetic or ecological) to whether a species primarily regulates speed via stride length or stride frequency, and to test Reilly and colleagues' (2007) allometric hypotheses about the interrelationship of these variables, we used two approaches, as described below.

First, we calculated phylogenetic general least squares models (Garland et al., 1992; Revell, 2012; Symonds and Blomberg, 2014). These models quantified the relationships between the log-transformed $R^2$ ratio, the slope for stride frequency versus speed model, or the slope for stride length versus speed model, and substrate (arboreal versus terrestrial), limb posture (extended versus crouched), log-transformed body mass, number of individuals within a species and number of cycles within a species as fixed effects. These models also included the interaction between substrate and log-transformed body mass and the interaction between posture and log-transformed body mass as fixed effects to test for slope heterogeneity across these factors and body mass. The sample phylogeny was constructed by pruning a recent supertree (Hedges et al., 2015) to include only the species in our study (Fig. 1). Phylogenetic signal in each model was quantified using Pagel's $\lambda$ (Pagel, 1999), which was estimated using a maximum likelihood approach. Body mass and coding criteria for

substrate use were based on species accounts from the original studies (Table S1) and/or Wilson et al. (2019) and del Hoyo et al. (2010). Limb posture was more difficult to categorize as studies rarely report effective limb length or a quantifiable distinction between crouched or extended limbs. Whenever possible, we used descriptions from the original study to categorize species posture (Table S1). All reptiles and amphibians were considered sprawling and included in the crouched category for statistical analyses. In cases where a species was not classified in the original study, categorization was based on definitions provided by Reilly and colleagues (2007) and/or Wilson et al. (2019) and del Hoyo et al. (2010).

Second, we compared whether specific clades (primate versus non-primate mammals and lizard versus amphibian versus crocodilian versus turtle versus bird versus mammal) primarily regulate speed via stride length or stride frequency. To do this, we ran phylogenetic general least squares models with log-transformed $R^2$ ratio, the slope for stride frequency versus speed model as responses and clade as the main effect. Differences between clades were assessed with Tukey honestly significant difference (HSD) tests. All analyses were performed in the statistical packages phytools (Revell, 2012), ape (Paradis et al., 2004), nlme (https://CRAN.R-project.org/package=nlme) and geiger (Harmon et al., 2007) using R (v. 4.0.2; http://www.R-project.org/).

## RESULTS
In total, we collected data for stride frequency, stride length and speed across 38,408 cycles and 103 species. Stride length was a significant predictor (total sample slope=3.65±4.08; total sample $R^2$=0.61±0.28) of speed in 97 species. There was a significant but relatively weak phylogenetic signal in stride length versus speed slope ($K$=0.312, $P$<0.001), a marginally significant but weak phylogenetic signal in stride frequency versus speed slope ($K$=0.143, $P$=0.057) and no signal in log-transformed $R^2$ ratios ($K$=0.098, $P$=0.358).

The phylogenetic generalized least squares model revealed a significant interaction between body mass and substrate ($P$<0.001), such that smaller arboreal species had steeper stride length versus speed slopes than larger arboreal species or any sized terrestrial species (Fig. 2A). There was also an overall body mass effect ($P$<0.001), such that larger species tended to have smaller stride length versus speed slopes compared with smaller species (Fig. 2B). No other factors significantly affected the stride length versus speed slopes (all $P$>0.353). Phylogeny had little effect on this model (Pagel's $\lambda$=−0.026).

Stride frequency was a significant predictor (total sample slope=0.70±0.90; total sample $R^2$=0.62±0.31) of speed in 89 species. The phylogenetic least squares model revealed a significant interaction between body mass and substrate ($P$=0.009) and body mass and posture ($P$<0.001). There was a positive relationship between the stride frequency versus speed slope and body mass for terrestrial species but a relatively flat relationship with body mass for arboreal species (Fig. 2C). Species with extended limb postures showed a steeper increase in the stride frequency versus speed slope with body mass compared with species with crouched postures (Fig. 2D). No other factors had significant influence (all $P$≥0.169) on the slope of stride frequency versus speed. Phylogeny had little effect on this model (Pagel's $\lambda$=0.024).

Primarily regulating speed through stride frequency (53 species) versus stride length (50 species) was split fairly evenly across the sample species (total sample log-transformed

**Fig. 1. Phylogeny of species used in this study and bar graphs of the variables of interest.** (A) Sample phylogeny constructed by pruning a recent supertree (Hedges et al., 2015) to include only the species in our study ($n$=103 species). (B–C) Bar-plots (outer, positive; inner, negative) imposed on the sample phylogeny illustrating (B) whether a species primarily regulates speed via stride length or stride frequency (log-transformed $R^2$ ratio; a negative $R^2$ ratio indicates a species primarily regulates speed via stride length and a positive $R^2$ ratio indicates a species primarily regulates speed via stride frequency), (C) stride length versus speed slope, and (D) stride frequency versus speed slope.

$R^2$ ratio=−0.08±1.35). The phylogenetic generalized least squares model revealed an interaction between body mass and substrate ($P$=0.018), such that larger arboreal species had negative log-transformed $R^2$ ratios, indicating that they regulate speed primarily via stride length (Fig. 2E). Posture also had a significant effect on the log-transformed $R^2$ ratios ($P$=0.036), such that crouched species tended to regulate via stride frequency (crouched log-transformed $R^2$ ratio=0.15±1.33) while extended species tended to regulate via stride length (extended log-transformed $R^2$ ratio=−0.52±1.27;

Fig. 2F). No other factors had a significant influence (all $P$≥0.104) on log-transformed $R^2$ ratios. Phylogeny had little effect on this model (Pagel's λ=−0.061).

Specific clade comparisons revealed lizards (0.09±0.09) had lower slopes of stride frequency versus speed compared with birds (1.13±0.67) and mammals (0.82±1.08, $P$=0.002; Fig. 3C); phylogeny had a relatively weak effect on this model (Pagel's λ=0.108). Clades did not differ in stride length versus speed ($P$=0.653; Fig. 3A) or whether they regulated speed more by stride
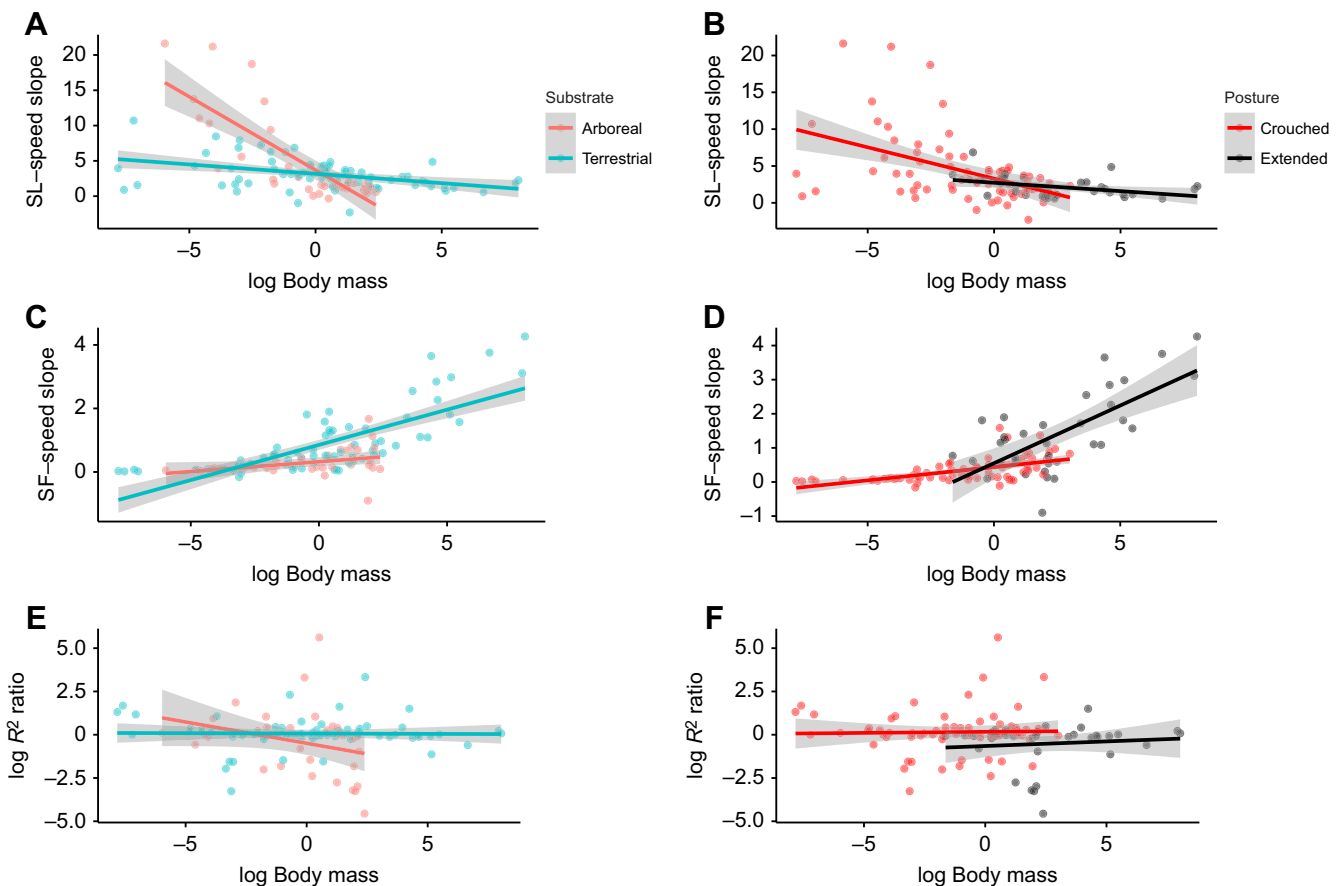
**Fig. 2. Bivariate plots showing the relationships between body mass and stride length/frequency versus speed slope.** (A–D) log Body mass and stride length (SL) versus speed slope (A,B) and stride frequency (SF) versus speed slope (C,D). (E,F) log-transformed $R^2$ ratios. Lines are linear regression of $y$ on log body mass; gray shading around each line is the 95% confidence interval of the fit. A, C and E plot separate regression lines for substrate use and within each panel those lines have significantly different slopes. B, D and F plot separate regression lines for posture.

frequency versus stride length ($P$=0.691; Fig. 3E), with a weak phylogenetic effect on both models (Pagel's λ∼0.001).

Primates had shallower slopes of stride length versus speed (1.41 ±0.65) compared with non-primate mammals (4.53±5.57, $P$=0.015; Fig. 3B); phylogeny had a weak effect on this model (Pagel's λ=0.204). Primates also regulated speed more by stride length than stride frequency (−0.67±1.87) compared with non-primate mammals (0.04±0.67, $P$=0.043; Fig. 3F); phylogeny had a weak effect on this model (Pagel's λ=0.200). Primates (0.58±0.86) did not differ from non-primate mammals (0.98±1.20) in the slopes of stride frequency versus speed ($P$=0.195; Fig. 3D); phylogeny had a weak effect on this model (Pagel's λ=−0.005).

## DISCUSSION
Across the sample, we observed that most species regulate speed through changes in both stride length and frequency, and there is no single strategy for how animals primarily regulate speed. The strategy a species will favor is based on substrate use, limb posture and body mass. Phylogenetic signal in the speed regulation strategy (i.e. log-transformed $R^2$ ratios) was generally weak or not observed and phylogeny had a weak effect on observed relationships between hypothetical causal factors and speed regulation strategy. Such a finding provides no support for the 'neuromuscular constraint' hypothesis. It should be noted that categorization of limb posture is difficult as studies rarely provide data on effective limb length or a quantifiable definition of extended or crouched posture. As such, it

is possible that our choice of posture categorization influenced interpretation of the data. All raw data used in statistical analyses are provided in Table S1. We hope others will reanalyze our findings if they find our categorization inappropriate.

Consistent with the predictions of Strang and Steudel (1990) and Reilly and colleagues (2007), the slope of speed on frequency is lower in small crouched animals compared with that in large-bodied erect species. As a result, substantially more rapid limb movements are matched with only small speed increases in crouched, small-bodied animals. In contrast with their predictions (Strang and Steudel, 1990; Reilly et al., 2007), however, the slope of speed on stride length was inversely proportional to body mass. As such, small changes in stride length can result in relatively rapid speed increases for small-bodied species. These results are somewhat counterintuitive, in that larger species, which have longer limbs and take longer strides, do not appear to gain as much speed increase out of lengthening their stride when compared with smaller species with shorter limbs. Conversely, smaller species that cycle their limbs rapidly do not gain as much speed out of increasing stride frequency as do larger species. This contrasting pattern may have important implications for how natural selection acts on population-level variation in limb functional morphology and locomotor performance. Our results suggest that selection for increased running speed in small species should favor longer strides, which could be achieved by longer limbs and/or altering locomotor kinematics. Conversely, selection for increased running speed in
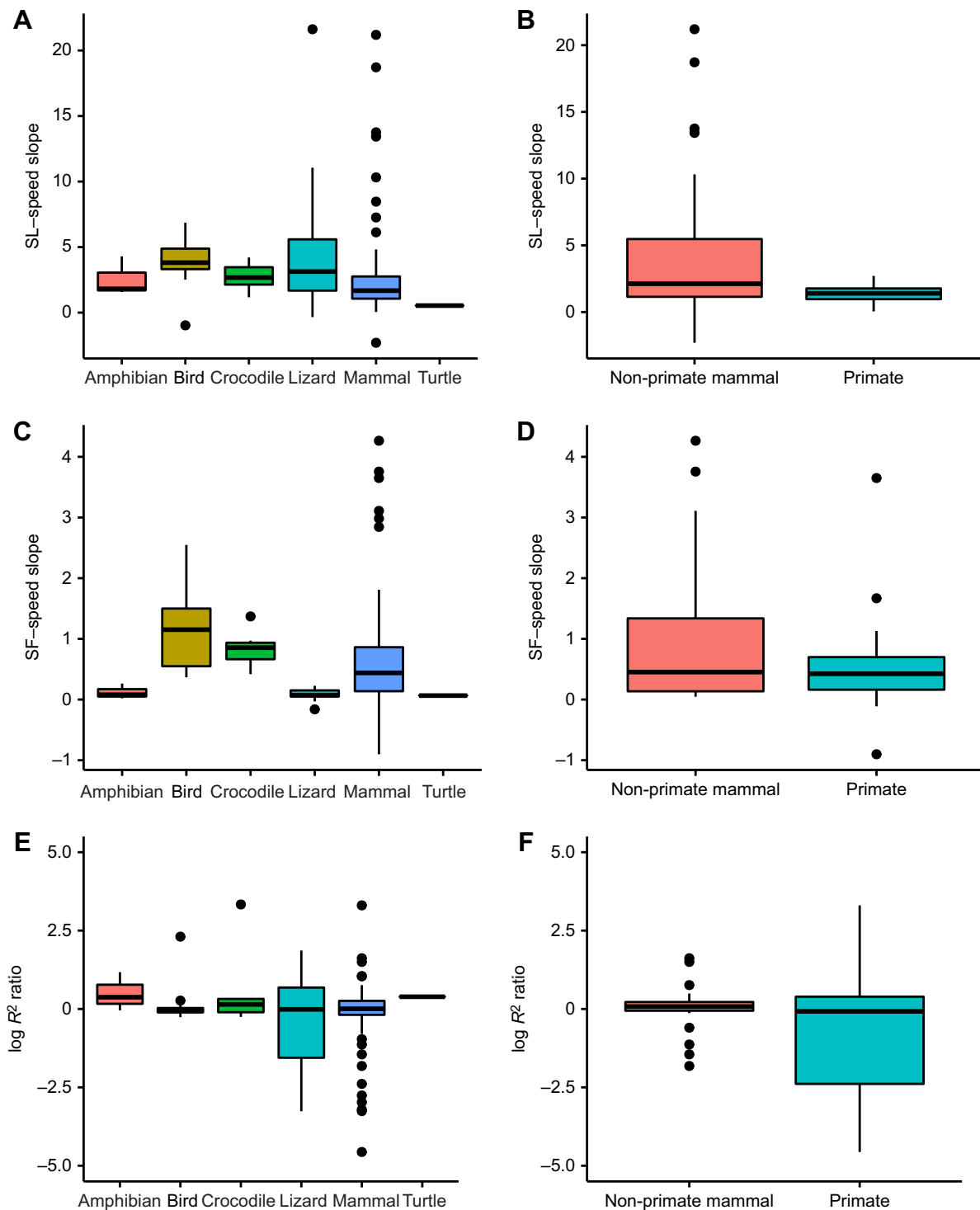
**Fig. 3. Clade differences in stride length/frequency versus speed slope.** (A,B) Stride length versus speed slope and (C,D) stride frequency versus speed slope. (E,F) log-transformed $R^2$ ratio. B, D and F show the same responses as in A, C and E but with the dataset restricted to mammalian species and comparing primate versus non-primate mammals. The box plots are as follows: thick line is the median, top/bottom of box are the 25th and 75th quartiles, whiskers are 1.5 times the interquartile range, and dots are outliers.

larger species should favor greater stride frequency, which could be achieved by altered limb functional anatomy and/or muscle physiology. Testing this hypothesis would not be easy, as one needs to estimate natural selection on locomotor performance and functional morphology across a sample of species that vary in body size.

Although primates rely more on regulating speed primarily through stride length, this strategy is not solely a primate strategy (Larson et al., 2001), but one used by larger arboreal animals. By predominantly using stride length to increase locomotor speed, larger arboreal animals can maintain lower stride frequencies, which might reduce adverse branch oscillations during arboreal travel (Demes

et al., 1990; Granatosky et al., 2019b; Schmidt, 2005; Schmitt, 1999; Vereecke et al., 2006). By keeping stride frequencies low, larger arboreal animals can increase duty factor, thereby ensuring support from at least one limb to prevent toppling (Granatosky et al., 2019b). Furthermore, when arboreal mammals do increase speed through stride frequency, there appears to be only a modest speed increase (mean slope=0.29) compared with that for terrestrial species (mean slope=0.90). Such a finding may indicate that larger-bodied arboreal animals are actively dampening limb cycle frequency to prevent too rapid limb movements (assuming similar limb lengths/effective limb lengths between species; Sutton et al., 2022 preprint). We also note that only larger arboreal species show a bias towards a stride length modulation strategy, which suggests that moving through trees at larger sizes places different demands on locomotion compared with that for small species. These hypotheses are confounded by the limited size range and sample size of the arboreal species. Most arboreal species were mammals (27 mammalian, 7 non-mammalian) and 19 of the 27 arboreal mammalian species were primates. Thus, future research should further test these patterns using a greater diversity of arboreal species from other non-mammalian clades and non-primate mammals.

Beyond considerations of arboreal stability, the energetic cost of swinging the limb may also contribute to the observed speed regulation strategies within the sample. The energetic expenditure of swinging the limbs has only become evident in recent years and accounts for approximately 8–33% of total locomotor costs (Doke et al., 2005; Marsh et al., 2004; Pontzer, 2007). These swing costs are thought to be especially high for relatively large-bodied animals because, assuming isometric scaling, muscle cross-sectional area is proportional to body mass$^{2/3}$, whereas limb mass moment of inertia scales to body mass$^{5/3}$ (Kilbourne and Hoffman, 2013, 2015; Nauwelaerts et al., 2011). That is, with increasing body mass, the limb's inertia (i.e. resistance to acceleration) rises at a greater rate than the force-generating capabilities of the limb musculature. As such, isometric similarity would leave larger bodied mammals with a decreased capability to accelerate and decelerate their limbs, making stride frequency-modulated changes to speed especially costly (Kilbourne and Hoffman, 2013, 2015; Raichlen et al., 2013). Our results are partially in line with this hypothesis. Specifically, considerations of swing phase cost provide a satisfactory explanation concerning the discrepancy between the steeper stride frequency versus speed slopes (i.e. the potential to make relatively large increases in speed with only modest increases in stride frequency; Fig. 2D) and stride length-modulated speed regulation strategies (i.e. negative log-transformed $R^2$ ratios; Fig. 2E,F) in relatively large-bodied animals. However, if swing phase costs were solely responsible for patterns of speed regulation strategies, then our analyses would have revealed a significant negative correlation between log-transformed $R^2$ ratios and body mass regardless of substrate type or posture (Fig. 2E,F). Kilbourne and Hoffman (2015) provide an explanation for this inconsistency by demonstrating that while across mammals limb mass moment of inertia scales to body mass$^{5/3}$, large-bodied cursorial species show a negative allometric relationship, thus providing evidence for a morphological strategy for reducing swing phase cost. Further, as demonstrated experimentally (Myers and Steudel, 1985; Raichlen et al., 2013), it is not the total mass of the limb that solely influences swing phase cost, but where that mass is distributed along the limb. Thus, arboreal animals with their relatively heavy distal limb masses are expected to incur especially high costs associated with swinging the limb (Raichlen et al., 2013). These anatomical considerations associated with swing phase cost provide an alternative, or

complementary, explanation for the finding that relatively larger-bodied arboreal animals tend to regulate speed primarily by modulating stride length (Fig. 2E).

In this study, we demonstrate that crouched/sprawled terrestrial species tend to mainly regulate speed through stride frequency. Based on the number of distantly related species that increase speed primarily through stride frequency, there must be some factor that makes this strategy favorable; however, the reasoning remains elusive. Heglund and Taylor (1988) and Reilly et al. (2007) demonstrate that increased stride frequency is a major contributing factor to the higher locomotor costs of small crouched/sprawled animals. This, paired with the confirmatory finding (Reilly et al., 2007) that substantially more rapid limb movements are matched with only small speed increases in crouched/sprawled animals, suggests that energetic minimization is not the primary optimality criterion for this strategy. Schubert et al. (2014), based on a review of the clinical literature, proposed that increasing speed primarily through stride frequency results in decreased center of mass vertical excursion [a factor known to increase locomotor costs (Gordon et al., 2009)], ground reaction force magnitude, impact shock and attenuation, and energy absorbed at the hip, knee and ankle. While some of these findings are questionable [e.g. increased stride frequency results in decreased duty factors that in turn result in higher ground reaction forces (Biewener, 1983; Schmitt and Hanna, 2004)], assuming their accuracy still does not provide a satisfactory explanation for why crouched/sprawled terrestrial animals primarily increase speed through stride frequency as numerous studies have demonstrated that crouched/sprawled animals tend to have limbs bones 'over-designed' for the normal locomotor forces they experience (Biewener, 1983; Blob et al., 2014). As such, selection does not need neuromuscular mechanisms (i.e. primarily increase speed through stride frequency) to mitigate the risk of catastrophic limb bone failure. While the ability to experimentally modulate stride frequency and length through auditory and visual cues as in humans (Laurent and Pailhous, 1986) is likely impossible for amphibians, lepidosaurs and most other tetrapods, potentially utilizing bio-inspired robotics (Karakasiliotis et al., 2016; Nyakatura et al., 2019) to isolate stride frequency and length from each other could provide a reason why so many species modulate speed through stride frequency despite limited adaptive explanations.

One possibility is that crouched/sprawling species tend to be smaller, and smaller species are generally more capable of higher accelerations and greater maneuverability compared with larger and more erect species (Dial et al., 2008; Domenici, 2001). One way that smaller species can achieve superior maneuverability is by coupling a crouched limb posture with stride frequency modulation strategies. Crouched limbs can be thought of as 'loaded' and ready to be deployed at any moment during locomotion. For example, a crouched species running at moderate speeds is doing so with a limb that is not fully extended and thus has a muscular 'reserve' that could be deployed to achieve a rapid change in direction, jump or acceleration, all of which are the very definition of maneuvering. Additionally, using a stride frequency modulation strategy allows for more limb contacts per unit time and distance, giving crouched species more opportunities to start, stop, change direction, jump, etc. Further, a crouched posture has been associated with greater limb compliance, and the ability to modify limb stiffness according to substrate conditions has been shown to facilitate stability (in certain conditions; Blum et al., 2011). Thus, a crouched posture coupled with stride frequency modulation could provide smaller species with a selective advantage when it comes to evading and out-maneuvering larger species and overall locomotor stability.

## Conclusion

Despite certain limitations in study design (e.g. unequal taxonomic sampling, inconsistent experimental protocols between studies, and resampling data from figures), our analyses support a number of conclusions. First, consistent with Reilly et al. (2007), the slope of speed on frequency is much lower in small crouched animals compared with that in large-bodied erect species. However, these data refute Reilly and colleagues' (2007) prediction that animals of all sizes increase stride length similarly as they move faster. Instead, we demonstrate that for a small-bodied species, small changes in stride length can result in relatively rapid speed increases. Despite this potentially advantageous method for increasing speed, crouched/ sprawled terrestrial animals primarily increase speed through stride frequency. An adaptive reason for this strategy remains elusive, but could be grounded in greater locomotor maneuverability. Future experimental studies potentially utilizing bio-inspired robotics (Karakasiliotis et al., 2016; Nyakatura et al., 2019) could test this hypothesis. Finally, regulating speed through stride length is closely tied to larger animals that move on arboreal substrates with relatively extended limbs. By predominantly using stride length to increase locomotor speed, arboreal animals can maintain lower stride frequencies, which might reduce adverse branch oscillations during travel (Demes et al., 1990; Granatosky et al., 2019b; Schmitt, 1999; Vereecke et al., 2006) or reduce potentially high locomotor costs associated with swinging the limb. Furthermore, when arboreal animals do increase speed through stride frequency, there appears to be only a modest speed increase compared with that for terrestrial species. This finding may indicate that arboreal animals are actively dampening limb cycle frequency to prevent too rapid limb movements, but future work is required to verify such a hypothesis. Finally, the weak influence of phylogenetic relationships we observed across analyses suggests that the observed influences of posture, habitat and body size on speed modulation are molded more by contemporaneous selective forces and less by historical factors.

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**Table S1.**

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