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RESEARCH ARTICLE

Asymmetrical gait kinematics of free-ranging callitrichine primates in response to changes in substrate diameter and orientation

Noah T. Dunham[1,2,*], Allison McNamara[3], Liza J. Shapiro[3], Taylor Phelps[4] and Jesse W. Young[4]

ABSTRACT

Arboreal environments present considerable biomechanical challenges for animals moving and foraging among substrates varying in diameter, orientation and compliance. Most studies of quadrupedal gait kinematics in primates and other arboreal mammals have focused on symmetrical walking gaits and the significance of diagonal sequence gaits. Considerably less research has examined asymmetrical gaits, despite their prevalence in small-bodied arboreal taxa. Here, we examined whether and how free-ranging callitrichine primates adjust asymmetrical gait kinematics to changes in substrate diameter and orientation, as well as how variation in gait kinematics affects substrate displacement. We used high-speed video to film free-ranging *Saguinus tripartitus* and *Cebuella pygmaea* inhabiting the Tiputini Biodiversity Station, Ecuador. We found that *S. tripartitus* used bounding and half-bounding gaits on larger substrates versus gallops and symmetrical gaits on smaller substrates, and also shifted several kinematic parameters consistent with attenuating forces transferred from the animal to the substrate. Similarly, *C. pygmaea* shifted from high-impact bounding gaits on larger substrates to using more half-bounding gaits on smaller substrates; however, kinematic adjustments to substrate diameter were not as profound as in *S. tripartitus*. Both species adjusted gait kinematics to changes in substrate orientation; however, gait kinematics did not significantly affect empirical measures of substrate displacement in either species. Because of their small body size, claw-like nails and reduced grasping capabilities, callitrichines arguably represent extant biomechanical analogs for an early stage in primate evolution. As such, greater attention should be placed on understanding asymmetrical gait dynamics for insight into hypotheses concerning early primate locomotor evolution.

KEY WORDS: Locomotion, Arboreal, Stability

INTRODUCTION

Arboreal environments present considerable biomechanical challenges for animals moving over substrates varying in diameter, orientation and compliance. Primates are among the most arboreal of mammalian orders, and the biomechanical challenges associated with arboreality are believed to be important selective pressures leading to the emergence and diversification of primates (Cartmill et al., 2002). As such, a substantial body of research has addressed how primates and other arboreal mammals adjust aspects of their locomotor kinematics to maintain stability when moving through complex arboreal environments. Research on primate locomotion has shown that several features of primate quadrupedal gaits are unique among most other quadrupedal animals, including hindlimb dominance in body weight support, compliant gait kinematics (i.e. large limb excursions, joint yield at mid-support, increased duty factors and a flat center of mass trajectory), and the regular use of diagonal sequence walking and running gaits (Cartmill et al., 2007a; Demes et al., 1994; Larson, 1998; Larson et al., 2000; Lemelin and Schmitt, 2007; Schmitt, 1999; Schmitt and Hanna, 2004; Schmitt and Lemelin, 2002). Most studies of primate quadrupedal gait kinematics have focused on symmetrical gaits (i.e. gaits in which the footfalls of forelimb pairs and footfalls of hindlimb pairs are evenly spaced in time and a forelimb is temporally paired with a hindlimb). Within symmetrical gaits, considerable attention has been placed on diagonal sequence gaits, in particular [i.e. right (R) or left (L) hindlimb (H) touchdown is followed by a contralateral forelimb (F) touchdown; e.g. LH, RF, RH, LF] and their potential adaptive significance in primates (Cartmill et al., 2007a,b; Dunham et al., 2019a; Granatosky et al., 2019; Hildebrand, 1967; Shapiro and Raichlen, 2005, 2007; Stevens, 2008; Usherwood and Smith, 2018; Wallace and Demes, 2008).

Considerably less research has examined asymmetrical gaits, i.e. gaits in which footfalls of forelimb and hindlimb pairs are unevenly spaced in time combined with the temporal pairing of the left and right limbs within the pectoral or pelvic girdle (Hildebrand, 1977). Asymmetrical gaits, including gallops, half-bounds and bounds, are commonly used by mammals at high speeds and frequently include a whole-body aerial phase (Hildebrand, 1977). Asymmetrical gaits are especially prevalent in small-bodied primates and other small-bodied arboreal mammals, and often represent a substantial portion of their locomotor repertoire (Arms et al., 2002; Chadwell and Young, 2015; Clemente et al., 2019; Dunham et al., 2019b; Hesse et al., 2015; Karantanis et al., 2017a,b; Lammers and Zurcher, 2011; Nyakatura and Heymann, 2010; Nyakatura et al., 2008; Schmidt, 2011; Shapiro and Young, 2010; Shapiro et al., 2014, 2016). Asymmetrical gaits are also used by primates at intermediate speeds, i.e. between those of symmetrical walking gaits and true running gaits, and may not include a whole-body aerial phase (Hanna et al., 2006; Schmitt et al., 2006; Shapiro et al., 2016). Only a handful of studies, nearly all laboratory based, have explicitly studied asymmetrical gaits in arboreal mammals and quantified how animals adjust asymmetrical gait kinematics in response to changes in substrate characteristics (Dunham et al., 2019b; Schmidt, 2011; Schmidt and Fischer, 2011; Schmitt et al., 2006; Shapiro et al., 2016; Young, 2009; Young et al., 2016).

Given that early primates were also small-bodied – with estimates ranging from <100 g (Gebo, 2004) to ∼1 kg (Soligo and Martin,

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[1] Division of Conservation and Science, Cleveland Metroparks Zoo, 4200 Wildlife Way, Cleveland, OH 44109, USA. [2] Department of Biology, Case Western Reserve University, 2080 Adelbert Road, Cleveland, OH 44106, USA. [3] Department of Anthropology, University of Texas at Austin, 2201 Speedway Stop C3200, Austin, TX 78712, USA. [4] Department of Anatomy and Neurobiology, Northeast Ohio Medical University, 4209 St. Rt. 44, Rootstown, OH 44272, USA.

*Author for correspondence (ntd@clevelandmetroparks.com)

N.T.D., 0000-0003-0299-7281

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2006) – and likely had diverse positional repertoires incorporating a combination of vertical clinging, claw-climbing and bounding gaits (Bloch and Boyer, 2007), understanding asymmetrical gait kinematic adjustments to changes in substrate characteristics should provide an important context for primate locomotor adaptation and evolution. Members of Callitrichinae range in body mass from ∼120 g in *Cebuella* up to ∼700 g in *Leontopithecus* (Smith and Jungers, 1997), have claw-like nails (tegulae) on all digits other than their hallux, and reduced grasping capabilities compared with other primates (Hamrick, 1998), and incorporate a mixture of claw-climbing, vertical clinging and leaping, and quadrupedal locomotion on both large substrates and small terminal branches (Garber and Leigh, 2001; Porter, 2004; Youlatos, 1999a,b, 2009). Together, these features make the Callitrichinae valid biomechanical and ecological models for an early stage in primate evolution and are among the best extant analogs for the stem primate morphotype, in particular (Nyakatura, 2019; Nyakatura and Heymann, 2010).

Of course, there are important ecological, morphological and locomotor distinctions among members of the Callitrichinae, which include the marmoset and Goeldi's monkey group (*Callithrix*, *Cebuella*, *Mico* and *Callimico*) and the tamarin group (*Saguinus* and *Leontopithecus*). Compared with other callitrichines, marmosets are more dedicated exudate feeders equipped with specialized dentognathic gouging anatomy and also have sharper claws and smaller apical pads consistent with reduced grasping ability (Cartmill, 1974; Hamrick, 1998; Taylor et al., 2009; Vinyard et al., 2009; Youlatos, 1999b, 2009). Pygmy marmosets (*Cebuella pygmaea*), in particular, differ from other callitrichines because of their elongated trunk length and shorter hindlimbs relative to body mass (Davis, 2002). Tamarins are more diverse with regard to substrate use and diet, and feed less frequently on exudates from vertical trunks (though they do not tree gouge *sensu stricto*), while also foraging on fruits and insects among small terminal branches (Garber, 1980, 1984, 1991; Porter, 2004). These disparities in grasping capabilities and substrate use between marmosets and tamarins have been used to explain differences in symmetrical gait use within callitrichines, i.e. regular use of diagonal sequence gaits in tamarins and a propensity for lateral sequence gaits in marmosets (Hesse et al., 2015; Nyakatura and Heymann, 2010; Nyakatura et al., 2008; Schmitt, 2003). Despite the ubiquity of asymmetrical gaits in the Callitrichinae, only three studies, all laboratory based, have explicitly examined how callitrichine individuals adjust asymmetrical gait kinematics to changes in substrate characteristics (Young, 2009; Chadwell and Young, 2015; Young et al., 2016), but these studies were limited by the reduced substrate variability of the laboratory setting.

As part of our previous research on the gait kinematics of 11 species of free-ranging platyrrhines, we observed that golden-mantled tamarins (*Saguinus tripartitus*) used primarily asymmetrical gaits and pygmy marmosets (*Cebuella pygmaea*) used exclusively asymmetrical gaits (Dunham et al., 2019a). These species were excluded from our initial statistical analyses because the study focused on symmetrical gait kinematics. Here, we incorporated additional locomotor strides and examined the gait kinematics of free-ranging *S. tripartitus* and *C. pygmaea* – specifically focusing on asymmetrical gaits. In this study, we sought to identify whether and how free-ranging callitrichines adjust gait type to changes in substrate diameter and orientation. In doing so, we quantified several spatiotemporal kinematic variables and predicted that callitrichines will adjust gait kinematics to promote stability on narrow and non-horizontal substrates. That is, we predicted that both species will use more symmetrical gaits, gallops and/or half-bounds in lieu of higher-impact bounds when moving on narrow and non-horizontal substrates. We also predicted that both species will increase duty factor, mean number of supporting limbs and relative limb lead durations, and decrease percent aerial phase when traveling on narrow and non-horizontal substrates (O'Neill and Schmitt, 2012; Schmitt et al., 2006; Shapiro and Young, 2012; Shapiro et al., 2014; Schmidt, 2011; Young, 2009; Young et al., 2016). Finally, we assessed how gait kinematics affect substrate displacement during locomotor strides and predicted that callitrichines will employ kinematic adjustments to mitigate substrate displacement, thereby promoting stability. We specifically predicted that substrate displacement will have a positive relationship with speed and percent aerial phase and a negative relationship with duty factor, mean number of supporting limbs and relative limb lead durations.

MATERIALS AND METHODS

Study site and study species

Data were collected on free-ranging individuals at Tiputini Biodiversity Station in Ecuador from August to October 2017. Tiputini comprises ∼650 ha of primary forest located within Yasuní Biosphere Reserve – a 1.7 million ha park in northeast Ecuador (Marsh, 2004). We filmed multiple groups of *Saguinus tripartitus* (Milne Edwards 1878) but most of the data come from one semi-habituated group estimated to be composed of ∼20 individuals. We filmed one habituated group of *Cebuella pygmaea* Spix 1823 composed of four individuals (Fig. 1). Average adult body mass for the two species (*S. tripartitus*: 410 g, *C. pygmaea*: 120 g) was from

Fig. 1. Callitrichines inhabiting the Tiputini Biodiversity Station, Ecuador. Left: *Saguinus tripartitus*; right: *Cebuella pygmaea*.

Smith and Jungers (1997) (note, because of the absence of data for *S. tripartitus*, we used body mass values from the closely related *Saguinus fuscicollis*). All procedures for this study were approved by NEOMED IACUC (Protocol 15-021), University of Texas at Austin IACUC (Protocol AUP-2016-00014) and Ecuador Ministerio del Ambiente (permit no. 014-2017-IC-DPAO/AVS).

Data collection

Video recordings

We collected data opportunistically and attempted to film individuals moving quadrupedally at different forest strata and on substrates varying in diameter, orientation angle and type (i.e. tree branch, palm frond and liana). We used a modified GoPro Hero 5 camera (GoPro, Inc., San Mateo, CA, USA) equipped with a Back-Bone Ribcage H5Pro (Back-Bone, Ottawa, ON, Canada) and C mount Fujinon HD 8–80 mm Vari-Focal CCTV lenses (Fujifilm, Tokyo, Japan) (Dunham et al., 2018). We filmed at 1080p resolution and 120 frames s^{-1} which provided sufficient footage for recording limb touchdown and liftoff events. We attempted to film perpendicular to the line of travel when possible; however, parallax is not an issue for timing and digitizing limb touchdown and liftoff events. Our spatial points (i.e. stride length, primate trunk diameter and substrate diameter) were all digitized in the same video frame for a given video clip, which should eliminate distortion due to parallax issues (i.e. all in-plane linear distance metrics would suffer a similar degree of distortion, allowing ratios of these distances to be unbiased).

Substrate diameter

For each video, we digitized substrate diameter in pixels and divided this value by the animal's trunk diameter in pixels to generate a measure of relative substrate diameter. Both substrate diameter and primate trunk diameter were digitized in the same video frame at roughly the midpoint of each stride (n=209 strides).

Substrate orientation

We used a forestry-grade range finder (TruPulse 360R 'missing 3D line setting', Laser Technology Incorporated, Centennial, CO, USA) to quantify substrate orientation angle. We previously found this instrument to be highly accurate (mean error of 2.5 deg; Dunham et al., 2018). We were unable to record substrate orientation for all locomotor strides. We included only those strides with quantified substrate orientation angles (i.e. 151/209 strides) in statistical analyses because of the potential error associated with estimating substrate orientation from camera footage *post hoc* (Bezanson et al., 2012).

Substrate displacement

We quantified substrate displacement throughout an individual stride by digitizing two points within each frame of the video clip: one easily identifiable point roughly centered on the locomotor substrate (e.g. a fork in the branch or discoloration) and a stationary point independent of the locomotor substrate (e.g. tree trunk or branch of adjacent tree). The maximum amplitude of locomotor substrate displacement (in pixels) was quantified relative to the stationary point and scaled to the animal's trunk length (in pixels). Videos lacking easily identifiable points as a result of visibility or camera panning were excluded from this analysis (i.e. 173/209 strides included in analysis).

Digitizing methods

We used GaitKeeper, an open-source MATLAB package, to digitize limb liftoff and touchdown events, stride length, primate body length (i.e. tip of nose to base of tail), primate trunk diameter and substrate displacement (Dunham et al., 2018; program free to download at http://www.younglaboratory.org/GaitKeeper).

Kinematic variables

Gait type

Temporal data on limb phase support events were used for categorical gait coding. To control for differences in forelimb and hindlimb contact intervals, gait coding was based upon the timing of mid-support events, where mid-support is defined as the temporal midpoint between touchdown and liftoff (Hildebrand, 1976). Strides in which the temporal lag between the left and right limbs in each girdle amounted to 50±10% of stride duration were categorized as symmetrical gaits and values outside that range were classified as asymmetrical gaits. Divisions between named symmetrical gaits represent slight modification to the divisions of Hildebrand (1966) and follow those of Cartmill et al. (2002). Limb phase (i.e. the proportion of stride duration separating hindlimb touchdown from ipsilateral forelimb touchdown) values between 0.00 and 0.25 are designated as lateral sequence, lateral couplet (LSLC) gaits, those between 0.25 and 0.50 are lateral sequence, diagonal couplet (LSDC) gaits, those between 0.50 and 0.75 are diagonal sequence, diagonal couplet (DSDC) gaits, and those between 0.75 and 1.00 are diagonal sequence, lateral couplet (DSLC) gaits. Asymmetrical strides in which forelimb and hindlimb stance periods were nearly simultaneous (i.e. the interval between the trailing and leading limb mid-support was ≤10% of total limb pair contact duration) were classified as bounds. Asymmetrical strides in which hindlimb stance periods were nearly simultaneous, but forelimb stance periods were temporally staggered (i.e. the interval between the trailing and leading limb mid-support was ≥10% of total limb pair contact duration) were classified as half-bounds. Finally, remaining asymmetrical strides where both forelimb and hindlimb touchdowns were temporally staggered were classified as gallops (Hildebrand, 1977). We predicted that both callitrichines would utilize more symmetrical gaits, half-bounds and/or gallops versus bounds on narrow and non-horizontal substrates as the former gait types reduce vertical force and center of mass fluctuations (Schmidt, 2011; Young, 2009; Young et al., 2016).

Relative speed

Relative speed is reported in body lengths per second. Body length (i.e. nose tip to base of tail) was digitized in a given video frame within a locomotor sequence. In the same video frame, stride length was recorded by digitizing (a) the point of initial touchdown of a reference limb (e.g. left forelimb) along the length of the arboreal substrate and (b) the point of the subsequent touchdown of the reference limb. Relative stride length was calculated by dividing stride length in pixels by body length in pixels. We then calculated relative speed by dividing relative stride length by stride duration in seconds, resulting in values with units of body lengths per second. Because greater speed has been shown to decrease agility (Hyams et al., 2012; Wheatley et al., 2015; Wynn et al., 2015), we predicted both callitrichine species would decrease speed on narrower and non-horizontal substrates and that speed would have a direct relationship with substrate displacement.

Mean duty factor

Duty factor (DF) was calculated as the quotient of support phase duration and total stride duration. Values were calculated separately for each limb and then averaged across all limbs to generate mean

DF. Controlling for speed, we predicted that callitrichines would increase mean DF to promote stability on narrower and non-horizontal substrates (Shapiro and Young, 2012; Shapiro et al., 2014). We also predicted that, when controlling for speed, mean DF would have an inverse relationship with substrate displacement.

Mean number of supporting limbs

The mean number of supporting limbs (NSL) can theoretically vary between zero (i.e. flying animal) and four (i.e. stationary animal) throughout different portions of a stride. We quantified the portion of stride duration in which individuals were supported by zero, one, two, three or four limbs, to generate mean NSL throughout the stride (Dunham et al., 2019b; Shapiro and Young, 2012; Shapiro et al., 2014). For example, in an exemplar bounding stride from our dataset, 27.0% of stride duration was aerial phase (i.e. zero supporting limbs), 2.2% of stride duration had only one supporting limb, 70.8% of stride duration had two supporting limbs, 0% of stride duration had three supporting limbs, and 0% of stride duration had four supporting limbs. For this stride, mean NSL is therefore equal to $(0.270\times0)+(0.022\times1)+(0.708\times2)+(0\times3)+(0\times4)$, or 1.438 supporting limbs. Controlling for speed, we predicted that callitrichines would have greater mean NSL on narrower and non-horizontal substrates, theoretically conferring greater stability (Shapiro and Young, 2012; Shapiro et al., 2014). We also predicted that, when controlling for speed, mean NSL would have an inverse relationship with substrate displacement.

Relative lead durations

Relative lead durations refer to the interval between touchdowns within a limb girdle divided by the total contact duration of the limb girdle (Hildebrand, 1977; Young, 2009). This method is used to classify asymmetrical gaits based on the simultaneity of limb contact (see bound versus half-bound versus gallop above). That is, a relative lead duration of zero indicates that limbs within a girdle contact at the same time, whereas greater relative lead durations indicate more temporally staggered contact times. Controlling for speed, we predicted that callitrichines would increase relative forelimb lead durations (FLLD) and relative hindlimb lead durations (HLLD) on narrower and non-horizontal substrates, thereby distributing limb contacts more evenly across the stride (Shapiro et al., 2016; Young, 2009). We also predicted that relative lead durations would have an inverse relationship with substrate displacement. More distributed limb contacts attenuate animal–substrate collisions, effectively reducing impact forces, center of mass fluctuations and substrate displacement (O'Neill and Schmitt, 2012; Schmidt, 2011; Young, 2009; Young et al., 2016).

Percent aerial phase

Percent aerial phase refers to the proportion of stride duration in which no limbs are in contact with the substrate. This metric is used, in part, to calculate mean NSL (i.e. percent aerial phase equals the proportion of stride duration in which mean NSL equals zero). We report this metric because we have specific predictions for how aerial phases – which are typical of asymmetrical running gaits and trots – affect arboreal stability. We predicted that callitrichines would decrease percent aerial phase on narrower and non-horizontal substrates in order to reduce whole-body peak forces and substrate oscillations (Schmitt et al., 2006). We also predicted that percent aerial phase would have a direct relationship with substrate displacement.

Statistical analyses

We used χ^2 tests to examine frequencies of different gait types in relation to substrate diameter and orientation. For these analyses, we categorized relative substrate diameter into three categories: small – less than half of an individual's trunk diameter, medium – between half and equal to an individual's trunk diameter, and large – greater than an individual's trunk diameter (Table 1). Similarly, we categorized substrate orientation into three categories: horizontal – between −30 and 30 deg, decline – less than −30 deg, and incline – greater than 30 deg (Table 1). *Post hoc* pairwise comparisons of gait-type profiles (e.g. small versus medium diameter or horizontal versus declined) were also conducted using χ^2 tests, with *P*-values adjusted by the false discovery rate method to mitigate experiment-wise alpha inflation (Benjamini and Hochberg, 1995). We used Cochran–Mantel–Haenszel χ^2 tests to compare *S. tripartitus* gait-type profiles with those of *C. pygmaea* across different substrate diameters and orientations (Agresti, 2002).

We used linear mixed models to examine the effects of substrate diameter and substrate orientation on continuous kinematic variables, including relative speed, mean DF, mean NSL, relative FLLD, relative HLLD and percent aerial phase. Relative speed was entered as a covariate in statistical models for mean DF, mean NSL, relative FLLD, relative HLLD and percent aerial phase in order to control for speed-related effects on these kinematic variables. Individual primate was nested within video clip as a random factor (intercept) in each model (i.e. some video clips contained multiple individuals). We used square root transformations of relative speed and Box–Cox transformations of substrate diameter and substrate displacement to better approximate data normality. We transformed substrate orientation in two ways: (1) sine of substrate orientation angle (i.e. values ranging from −1 to 1) to test for substrate angles ranging from −90 to 90 deg, thus differentiating declines versus inclines, and (2) cosine of substrate orientation angle (i.e. values ranging from 0 to 1 and back to 0) for substrate angles ranging from −90 deg to 0 deg to 90 deg, thus differentiating oblique supports from horizontal supports, but ignoring the distinction between declines and inclines (Dunham et al., 2019a). Though the resulting transformations of substrate angles were not normally distributed themselves, residual error was normally distributed (in all but two of our models), a condition necessary to satisfy the assumptions of linear mixed-effects regression (Harrison et al., 2018). We used binary logistic mixed-effects models for the two models that did not satisfy assumptions of linear mixed-effects regression (i.e. *C. pygmaea* relative FLLD and *C. pygmaea* relative HLLD). Because both relative FLLD and relative HLLD for *C. pygmaea* were dominated by zero values (indicating simultaneous contact of limbs within a girdle), we coded all non-zero values as 1 to test whether relative speed, substrate diameter and substrate orientation influenced the staggering of limb contact within a girdle. Satterthwaite approximations were used to adjust degrees of freedom in cases of heteroscedasticity for all models relating substrate characteristics to gait kinematics.

Table 1. Number of strides for different substrate diameter and orientation categories in free-ranging *Saguinus tripartitus* and *Cebuella pygmaea*

	Substrate diameter			Substrate orientation		
Species	Large	Medium	Small	Horizontal	Incline	Decline
Saguinus tripartitus	13	31	64	32	18	7
Cebuella pygmaea	83	13	5	7	73	21

We then used linear mixed models to examine the effects of gait kinematic variables on substrate displacement – again with individual primate nested within video clip as a random factor and using Satterthwaite approximations to adjust degrees of freedom in cases of heteroscedasticity. None of the statistical tests indicated significant interactive effects among fixed effects; therefore, we tested the effects of these variables independently. Analyses were conducted in R statistical software (http://www.R-project.org/) including add-on packages: lme4 (http://CRAN.Rproject.org/package=lme4) and lmerTest (Kuznetsova et al., 2017).

RESULTS

Effect of substrate diameter on gait selection

Saguinus tripartitus used primarily asymmetrical gaits, including bounds, half-bounds and gallops (97/108 strides; 89.8%), and *C. pygmaea* used almost exclusively asymmetrical half-bounds and bounding gaits (99/101 strides; 98.0%). *Saguinus tripartitus* adjusted gait selection in response to substrate diameter (χ^2=28.4, P<0.0001). *Post hoc* pairwise comparisons indicated that *S. tripartitus* gait-type profile on small-diameter substrates significantly differed from those used on large- and medium-diameter substrates (P=0.0009 and P=0.0007, respectively), with individuals using more symmetrical gaits and gallops on small-diameter substrates and more half-bounds and bounding gaits on large- and medium-diameter substrates (Fig. 2). For *C. pygmaea*, small-diameter substrates were excluded from analysis because of the limited sample size (i.e. n=3 strides on small-diameter substrates). *Cebuella pygmaea* gait selection differed significantly between large- and medium-diameter substrates (χ^2=9.7; P=0.0018), with individuals using more bounding gaits on large-diameter substrates and more half-bounds on medium-diameter substrates (Fig. 2).

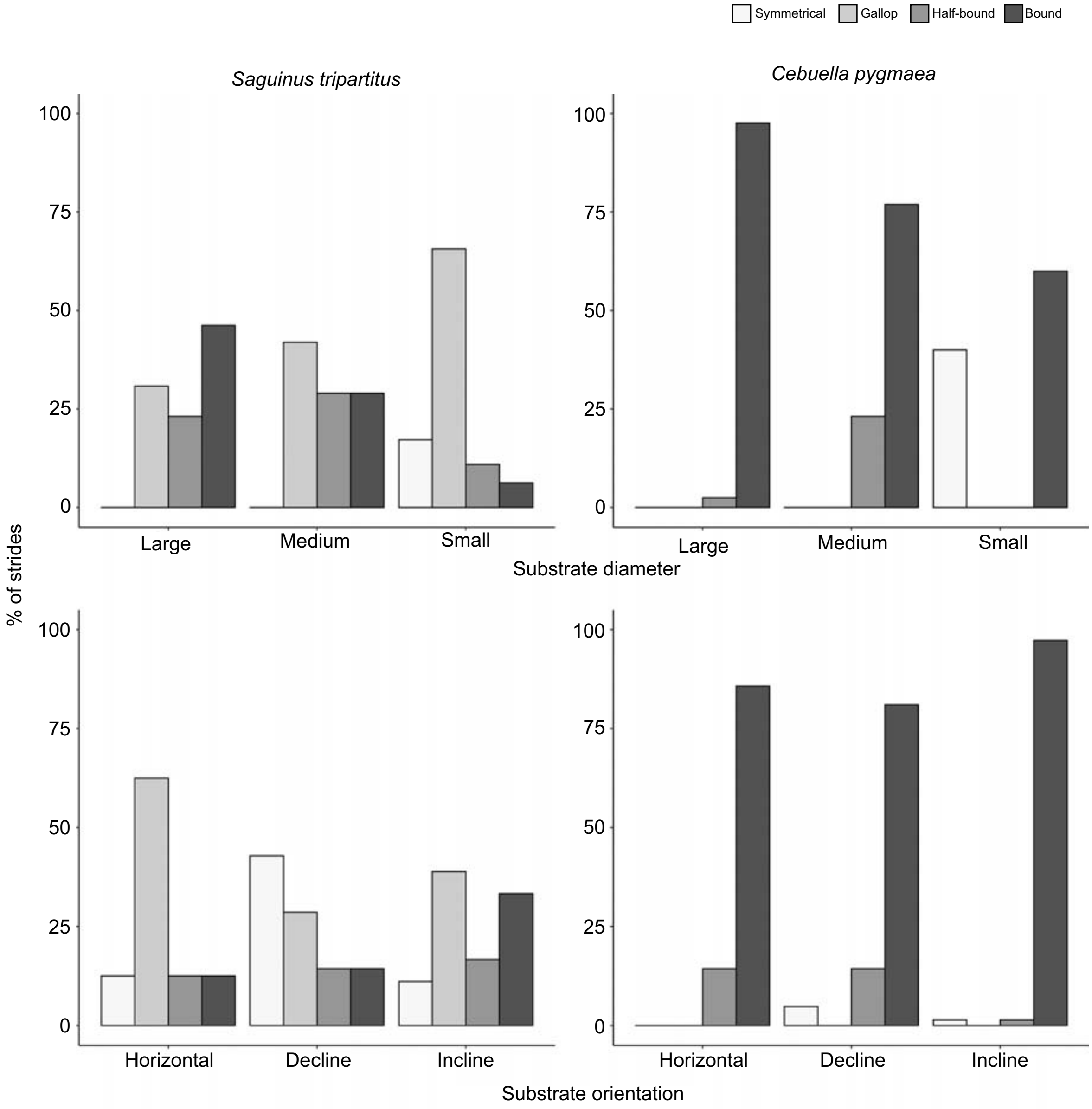

Fig. 2. Gait selection (*n*=209 strides) in free-ranging callitrichines grouped by substrate diameter category and by substrate orientation category. Left: *Saguinus tripartitus*; right: *Cebuella pygmaea*.

Effect of substrate orientation on gait selection

Substrate orientation did not have a significant effect on gait selection in *S. tripartitus* (χ^2=8.6; *P*=0.1925) but did have a significant effect on *C. pygmaea* gait selection (χ^2=7.4; *P*=0.0249). *Post hoc* pairwise comparisons revealed that in *C. pygmaea*, gait selection on inclined substrates differed significantly from that on horizontal and declined substrates (*P*=0.0381 and *P*=0.0083, respectively), with a greater proportion of bounds on inclines and a greater proportion of half-bounds on horizontal and declined substrates (Fig. 2).

Effect of relative speed on asymmetrical gait kinematics

Relative speed had significant effects on gait kinematics in *S. tripartitus* and *C. pygmaea*. For *S. tripartitus*, relative speed had an inverse relationship with mean DF, mean NSL, relative FLLD and relative HLLD (Table 2, Fig. 3). For *C. pygmaea*, relative speed had an inverse relationship with mean DF and mean NSL and a direct relationship with percent aerial phase (Table 2, Fig. 3).

Effect of substrate diameter on asymmetrical gait kinematics

Substrate diameter significantly affected all kinematic variables in *S. tripartitus* (Table 2, Fig. 4). Relative speed and percent aerial phase increased with increasing relative substrate diameter, whereas, controlling for speed, mean DF, mean NSL, relative FLLD and relative HLLD increased as substrate diameter decreased. *Cebuella pygmaea* did not significantly adjust gait kinematics in response to relative substrate diameter (Table 2, Fig. 4).

Effect of substrate orientation on asymmetrical gait kinematics

The sine of substrate orientation angle had significant effects on asymmetrical gait kinematics in *C. pygmaea* but not in *S. tripartitus*. Specifically, *C. pygmaea* increased mean DF and percent aerial phase when moving on more inclined substrates (Table 2, Fig. 5). The cosine of substrate orientation significantly affected asymmetrical gait kinematics in *S. tripartitus*, with increased mean DF and mean NSL and decreased relative speed and relative HLLD on more oblique substrates (Table 2, Fig. 6). The cosine of substrate orientation also significantly affected relative speed in *C. pygmaea*, resulting in slower speeds on more oblique substrates versus higher speeds on more horizontal substrates (Table 2, Fig. 6).

Effect of asymmetrical gait kinematics on substrate displacement

For both callitrichines, gait kinematics did not significantly impact substrate displacement (Table 3, Fig. 7).

Symmetrical gaits

Although both callitrichine species analyzed used predominantly asymmetrical gaits, both also occasionally used symmetrical gaits. Because symmetrical gaits were few in number (*S. tripartitus*: *n*=11 strides; *C. pygmaea*: *n*=2 strides), we did not statistically examine relationships among substrate characteristics and symmetrical gait kinematics. For both species, symmetrical gaits were used exclusively at walking speeds (i.e. DF >50%) (Fig. S1). *Saguinus tripartitus* used primarily diagonal sequence symmetrical gaits (10/11 strides; 90.9%) whereas the two symmetrical strides in *C. pygmaea* were both lateral sequence gaits.

DISCUSSION

We examined the locomotor kinematics of free-ranging callitrichines – small-bodied primates that represent reasonable biomechanical and ecological analogs for a potential early stage in primate evolution (Nyakatura, 2019). We found that both *S. tripartitus* and *C. pygmaea* used primarily asymmetrical gaits across substrates varying in diameter and orientation, and even after controlling for speed, both species adjusted aspects of their asymmetrical gait kinematics in response to changes in substrate diameter and/or orientation. Contrary to predictions, there were no clear relationships among kinematic parameters and empirical measures of substrate displacement.

Adjustments to substrate characteristics

Substrate diameter had profound effects on *S. tripartitus* locomotor kinematics. As predicted, *S. tripartitus* shifted from using more bounding and half-bounding gaits on large- and medium-diameter substrates to using more gallops and symmetrical gaits on small-diameter substrates. *Saguinus tripartitus* also decreased relative speed, and after controlling for speed, increased mean DF, mean NSL and relative FLLD and HLLD, and decreased percent aerial phase when traveling on narrower substrates. Taken together, this suite of kinematic adjustments increases substrate contact time and mitigates the forces transferred from the animal to the substrate, thereby reducing substrate oscillations and presumably improving

Table 2. Effects of relative speed, substrate diameter and substrate orientation on asymmetrical gait kinematics in free-ranging *Saguinus tripartitus* and *Cebuella pygmaea*

	Relative speed			Substrate diameter			Sine of substrate orientation			Cosine of substrate orientation		
Parameter	*F*-value	d.f.	*P*-value	*F*-value	d.f.	*P*-value	*F*-value	d.f.	*P*-value	*F*-value	d.f.	*P*-value
Saguinus tripartitus												
Relative speed	–	–	–	6.72	1, 44.0	0.0128	0.82	1, 35.7	0.3702	4.74	1, 35.9	0.0361
Mean DF	15.70	1, 42.2	0.0003	6.44	1, 39.6	0.0152	0.80	1, 37.5	0.3770	4.80	1, 36.6	0.0350
Mean NSL	6.53	1, 42.0	0.0143	9.24	1, 38.8	0.0042	0.31	1, 36.3	0.5832	4.81	1, 35.2	0.0350
Relative FLLD	4.84	1, 42.2	0.0333	12.59	1, 39.2	0.0010	1.39	1, 37.3	0.2451	0.04	1, 36.2	0.8412
Relative HLLD	9.65	1, 42.4	0.0034	4.17	1, 37.6	0.0481	0.01	1, 38.0	0.9278	4.84	1, 36.1	0.0343
% Aerial phase	3.11	1, 41.9	0.0852	13.42	1, 38.6	0.0007	1.96	1, 33.9	0.1705	0.69	1, 33.2	0.4116
Cebuella pygmaea												
Relative speed	–	–	–	3.35	1, 83.4	0.0706	3.10	1, 55.7	0.0839	18.24	1, 61.5	<0.0001
Mean DF	53.4	1, 88.2	<0.0001	2.42	1, 83.8	0.1235	6.74	1, 51.1	0.0123	0.46	1, 69.9	0.4988
Mean NSL	38.4	1, 85.8	<0.0001	0.99	1, 85.5	0.3221	3.55	1, 49.7	0.0653	0.20	1, 72.2	0.6564
Relative FLLD[1]	–1.84	1	0.0645	–1.05	1	0.2917	–1.51	1	0.1316	0.80	1	0.4259
Relative HLLD[1]	–0.12	1	0.9040	0.01	1	0.9950	–0.13	1	0.8990	0.23	1	0.8150
% Aerial phase	27.11	1, 88.7	<0.0001	0.64	1, 86.7	0.4261	8.94	1, 56.9	0.0041	0.39	1, 75.6	0.5330

DF, duty factor; NSL, number of supporting limbs; FLLD, forelimb lead duration; HLLD, hindlimb lead duration.

[1] Binary logistic mixed-effects models report *Z*-values rather than *F*-values.

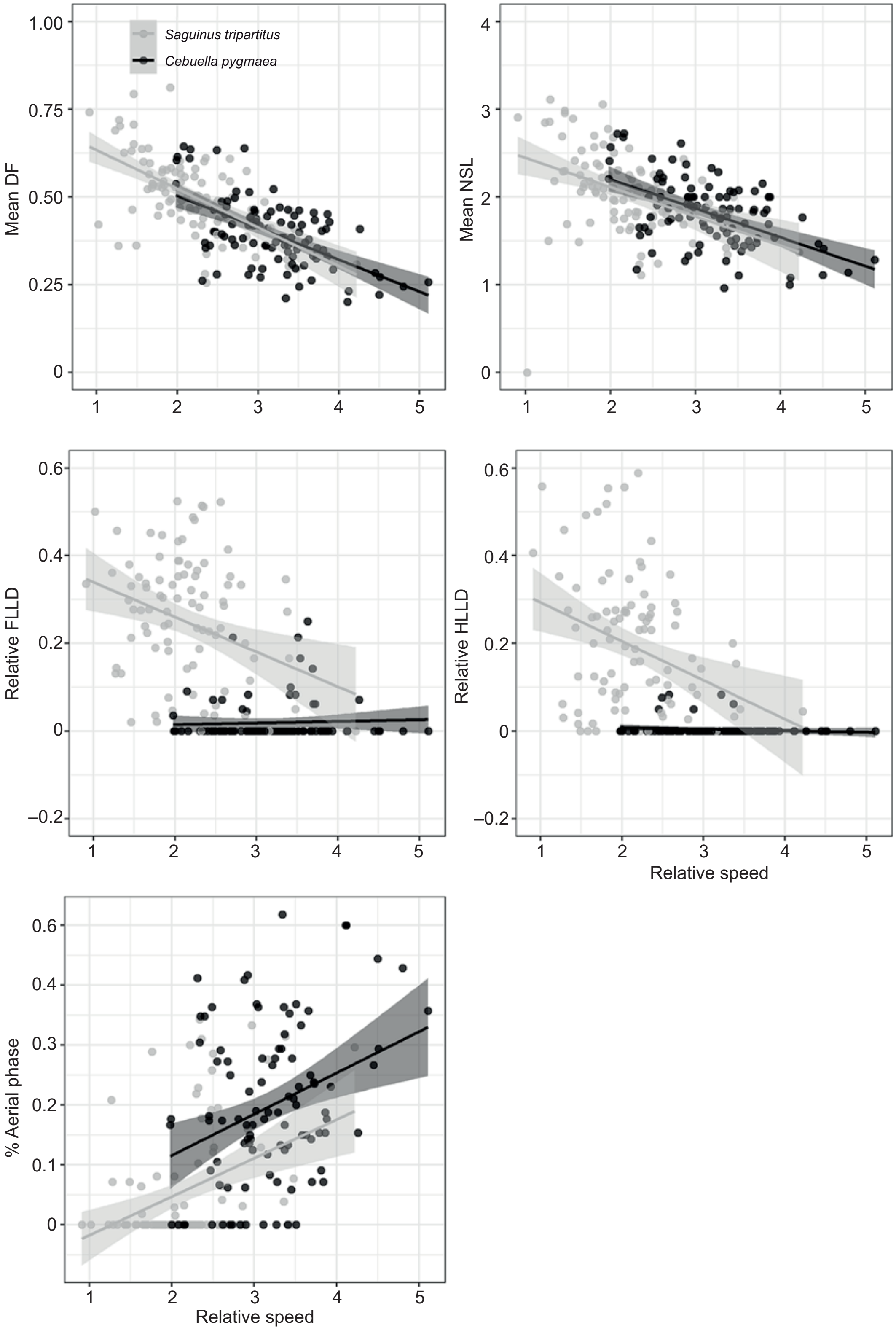

Fig. 3. Variation in callitrichine asymmetrical gait kinematics (*n*=209 strides) in relation to relative speed. DF, duty factor; NSL, number of supporting limbs; FLLD, forelimb lead duration; HLLD, hindlimb lead duration. Circles indicate individual strides. Trend lines indicate reduced maximum likelihood fits from mixed-effects ANCOVA models. Shaded regions indicate 95% confidence intervals.

arboreal stability (Young et al., 2016). Similar asymmetrical kinematic adjustments in response to narrowing substrates have been documented in laboratory and field studies of other small arboreal mammals including acacia rats (Karantanis et al., 2017a), common marmosets (Young et al., 2016), mouse lemurs (Shapiro et al., 2016) and tree squirrels (Schmidt, 2011; Schmidt and Fischer, 2011; Dunham et al., 2019b). Substrate diameter had less-pronounced effects on *C. pygmaea* gait kinematics, although

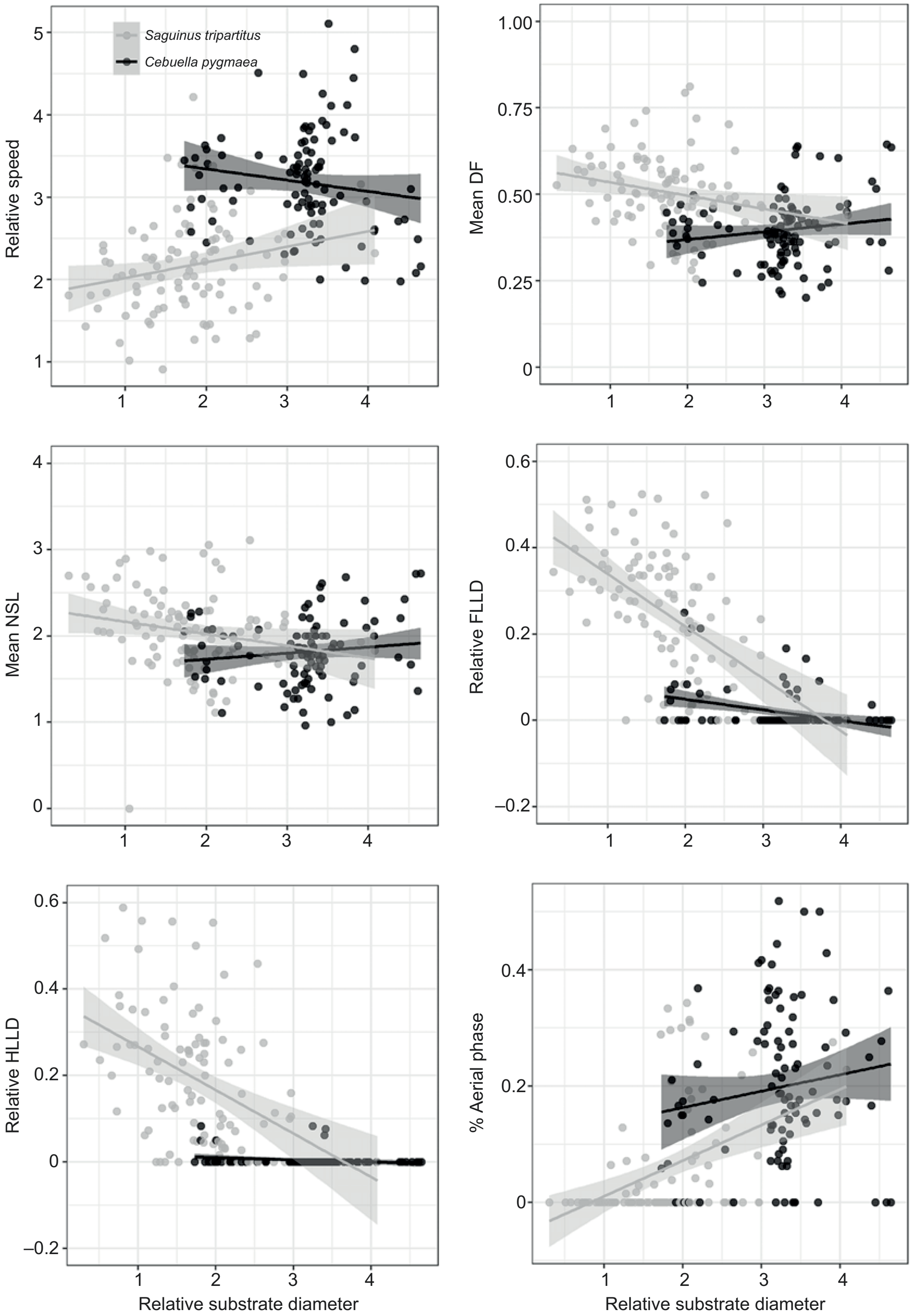

Fig. 4. Variation in callitrichine asymmetrical gait kinematics (*n*=209 strides) in relation to relative substrate diameter. Relative substrate diameter values were Box–Cox transformed to enhance distributional normality.

C. pygmaea shifted from using more bounding gaits on large-diameter substrates to using more half-bounding gaits on medium-diameter substrates. The paucity of strides on small-diameter substrates prevented us from statistically analyzing this substrate category.

Substrate orientation did not significantly affect gait selection in *S. tripartitus*, but it did affect aspects of asymmetrical gait kinematics. Specifically, *S. tripartitus* decreased relative speed, and controlling for speed, increased mean DF and mean NSL, and decreased relative HLLD on more oblique substrates. For *C. pygmaea*, substrate orientation significantly affected gait selection, with more bounding gaits on inclined substrates and more half-bounds on declined and horizontal substrates. *Cebuella*

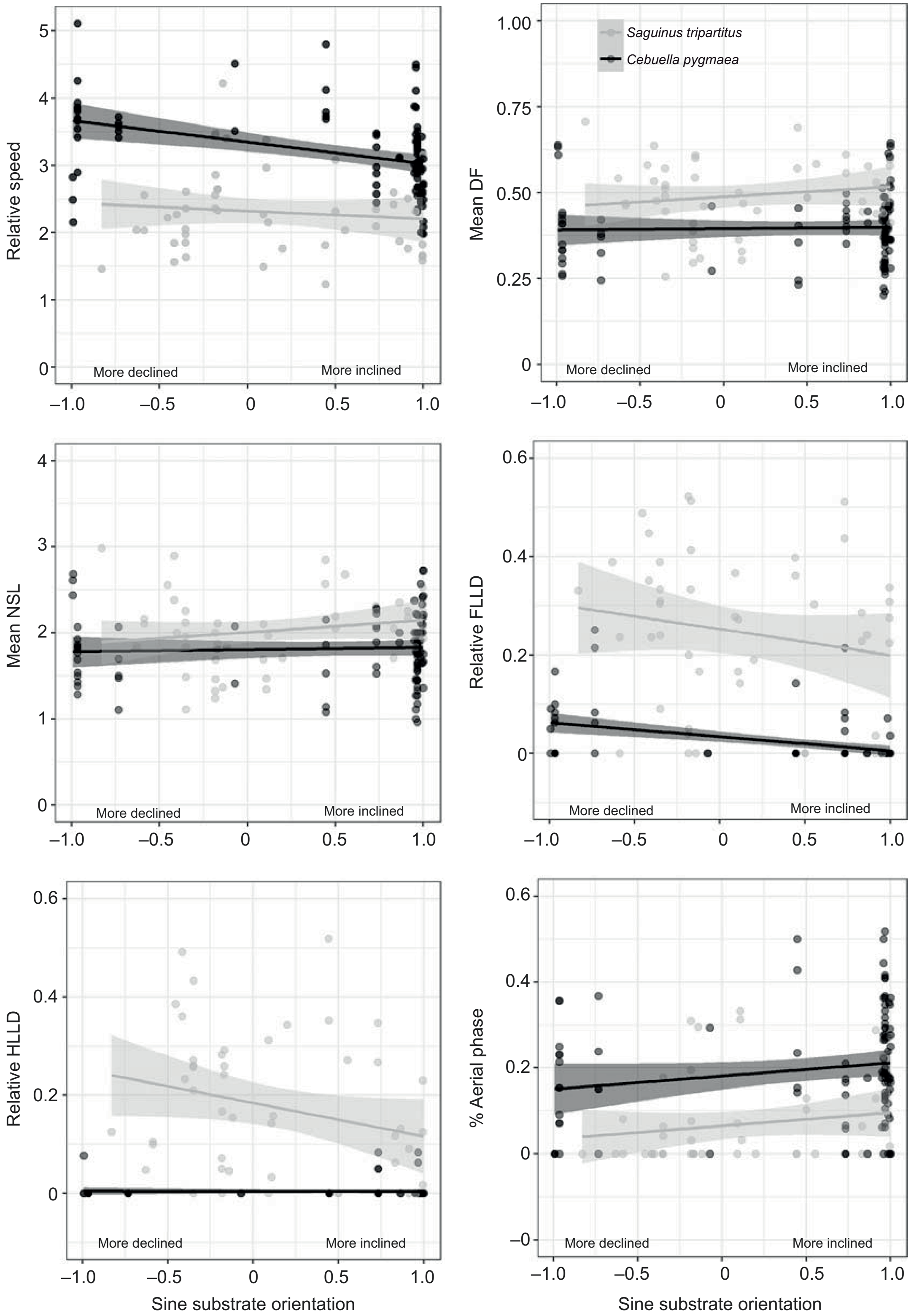

Fig. 5. Variation in callitrichine asymmetrical gait kinematics (*n*=151 strides) in relation to the sine of substrate orientation (i.e. contrasting declined versus inclined substrates).

pygmaea also decreased relative speed when moving on more oblique substrates versus more horizontal substrates. Substrate orientation also influenced *C. pygmaea* asymmetrical gait kinematics, with increased mean DF and percent aerial phase on more inclined substrates, after controlling for speed variation. Decreasing speed and increasing DF on inclined substrates is a common trend among many vertebrate and invertebrate taxa (Birn-Jeffrey and Higham, 2014) as individuals must perform more work to counteract gravity when moving on inclines. The use of bounding gaits in *C. pygmaea*, alongside increased DF, may have

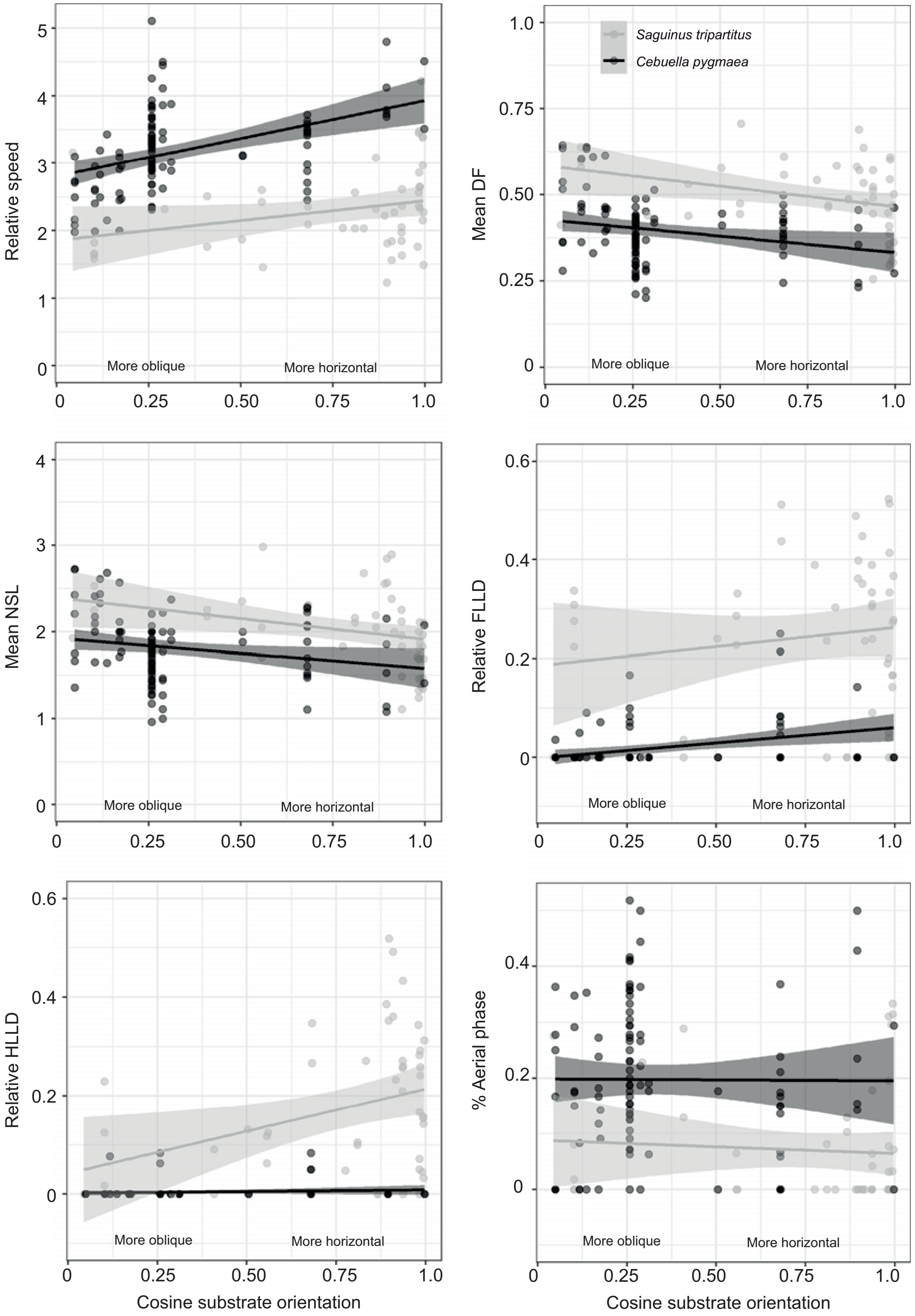

Fig. 6. Variation in callitrichine asymmetrical gait kinematics (*n*=151 strides) in relation to the cosine of substrate orientation (i.e. contrasting oblique versus horizontal substrates).

facilitated more coordinated use of the right and left forelimbs to produce the greater propulsive impulses required to counteract increased gravitational shear on inclined supports (Dunham et al., 2019b). Less is known about how animals adjust gait kinematics on declined substrates (Birn-Jeffrey and Higham, 2014; Hyams et al., 2012; Shapiro et al., 2014), but cautious locomotion characterized by reduced speed and increased DF may be a strategy to exert greater braking impulses during descents (Dunham et al., 2019b), mitigating disruptive gravitational shear while not exacerbating disruptive pitching torques, provided peak accelerations are kept

Table 3. Effects of relative speed, mean DF, mean NSL and relative lead durations on substrate displacement in free-ranging *Saguinus tripartitus* and *Cebuella pygmaea*

	Relative speed			Mean DF			Mean NSL			Relative FLLD			Relative HLLD		
	F-value	d.f.	*P*-value	*F*-value	d.f.	*P*-value	*F*-value	d.f.	*P*-value	*F*-value	d.f.	*P*-value	*F*-value	d.f.	*P*-value
Saguinus tripartitus	0.10	1, 72.5	0.7519	0.17	1, 72.4	0.6780	0.21	1, 70.8	0.6488	0.06	1, 72.7	0.7999	2.89	1, 72.7	0.0933
Cebuella pygmaea	3.12	1, 47.6	0.0835	1.23	1, 75.1	0.2700	0.01	1, 70.8	0.9188	0.85	1, 62.1	0.3592	1.77	1, 78.0	0.1869

low (as would result from applying braking forces over an extended duration via increased DF) (Williams et al., 2009). Captive mouse lemurs were found to utilize more galloping gaits and increase relative HLLD and FLLD on declined substrates (Shapiro et al., 2016). Wild tree squirrels were shown to follow a different strategy from the primates examined thus far, increasing speed, utilizing more bounding gaits and decreasing relative HLLD and FLLD on declined substrates, while preferring half-bounds and gallops on more horizontal and inclined substrates (Dunham et al., 2019b; Schmidt, 2011; Schmidt and Fischer, 2011). This difference in kinematic strategy between squirrels and primates may relate to the hindfoot reversal abilities of sciurid rodents (Jenkins and McClearn, 1984). Hindfoot reversal allows arboreal animals to use the pedal claws in tension to support body weight and slow descent, perhaps obviating the kinematic mechanisms that primates must use to ensure stability on declined supports.

We also assessed how callitrichine gait kinematics affected substrate displacement during locomotor strides. We predicted that higher speeds and increased percent aerial phase would correspond to greater substrate displacement due to elevated forces applied to the substrate. We also predicted that mean DF, mean NSL and relative HLLD and FLLD would show inverse relationships with substrate displacement because these adjustments help to attenuate animal–substrate collisions, thereby decreasing substrate displacement (Young et al., 2016). None of these predictions were supported by our data. The overall lack of congruence between these predictions and our findings may be because small-bodied callitrichines impart relatively low forces to substrates, resulting in minor levels of substrate displacement regardless of asymmetrical gait kinematics. Alternatively, this discrepancy may actually highlight kinematic adjustments to promote stability on more compliant substrates (i.e. compliance is equal to displacement divided by force, the reciprocal of stiffness). For example, it is possible that individuals altered their gait kinematics to prevent/mitigate substrate displacement on more compliant substrates. This is consistent with both callitrichines' tendency to shift gait type to more symmetrical gaits, gallops and/or half-bounds on more narrow substrates rather than using higher impact bounding gaits. Young et al. (2016) found that common marmosets increased DF when moving on compliant substrates in the laboratory but maintained overall speed and center of mass height across both compliant and stable substrates, suggesting that kinematic adjustments helped to reduce displacement of more compliant substrates. Previous studies have shown that substrate compliance affects leaping performance in lizards (Gilman and Irschick, 2013; Gilman et al., 2012) and primates (Channon et al., 2011; Crompton et al., 1993; Demes et al., 1995; Walker, 2005; Warren and Crompton, 1997); however, because we did not directly measure substrate compliance in this study, additional research is needed to better understand how substrate compliance affects quadrupedal gait kinematics (Gosselin-Ildari, 2010; Stevens et al., 2001; Young et al., 2016, 2019).

Symmetrical gaits

This study focused on asymmetrical gait kinematics, but both free-ranging callitrichines also used symmetrical gaits at slow walking speeds. Notably, *S. tripartitus* used predominantly diagonal sequence symmetrical gaits and *C. pygmaea* used lateral sequence gaits for the only two symmetrical strides recorded. These findings are generally consistent with previous studies that found *Saguinus* spp. prefer diagonal sequence gaits, particularly when moving on horizontal and inclined substrates both in laboratory and field settings – although individuals shifted to more lateral sequence gaits on declined substrates (Hesse et al., 2015; Nyakatura and Heymann, 2010; Nyakatura et al., 2008). Schmitt (2003) found that common marmosets (*Callithrix jacchus*) used exclusively lateral sequence walking gaits when moving over horizontal poles in the laboratory – a phenomenon that Schmitt (2003) attributed to the marmosets' retreat from the fine-branch niche and greater propensity for moving on larger substrates including vertical trunks. Because of the paucity of symmetrical gait data in our study, additional data on free-ranging callitrichine symmetrical gaits, particularly for *C. pygmaea* and other marmoset genera, are required to better understand the functional significance of symmetrical gait variation among callitrichines and to what extent diagonal sequence gaits are functionally linked to the fine-branch niche.

Body size and arboreality

As animals decrease in size, arboreal substrates become relatively larger. Thus, smaller bodied arboreal animals are likely to more frequently encounter relatively large substrates (Jenkins, 1974). This trend is evident when comparing callitrichines with larger bodied primates and even within callitrichines. For example, *S. tripartitus* is roughly 3.5 times larger than *C. pygmaea*. Small substrates (i.e. less than half of an individual's trunk diameter) were used for 59.3% of *S. tripartitus* strides but just 5.0% of *C. pygmaea* strides. This disparity is at least partially attributable to differences in feeding ecology and habitat use, with *S. tripartitus* more frequently foraging among small terminal branches and *C. pygmaea* spending more time foraging from large vertical trunks in the forest understory (Garber, 1980, 1984, 1991; Garber and Pruetz, 1995; Youlatos, 1999b, 2009). Regardless, the larger body size and more frequent movement on relatively small substrates in *S. tripartitus* seems to necessitate greater kinematic adjustments. Specifically, we found that *S. tripartitus* altered gait type and all aspects of locomotor kinematics examined in this study (i.e. relative speed, mean DF, mean NSL, relative HLLD and FLLD, and percent aerial phase) to promote stability on small-diameter supports. Kinematic adjustments to changes in substrate diameter were not as evident in *C. pygmaea*, likely because its diminutive body size and propensity to use relatively large substrates did not require significant locomotor adjustments to maintain stability.

Conclusion

The increased affordability and durability of high-speed cameras and remote sensors now allow researchers to record animals moving

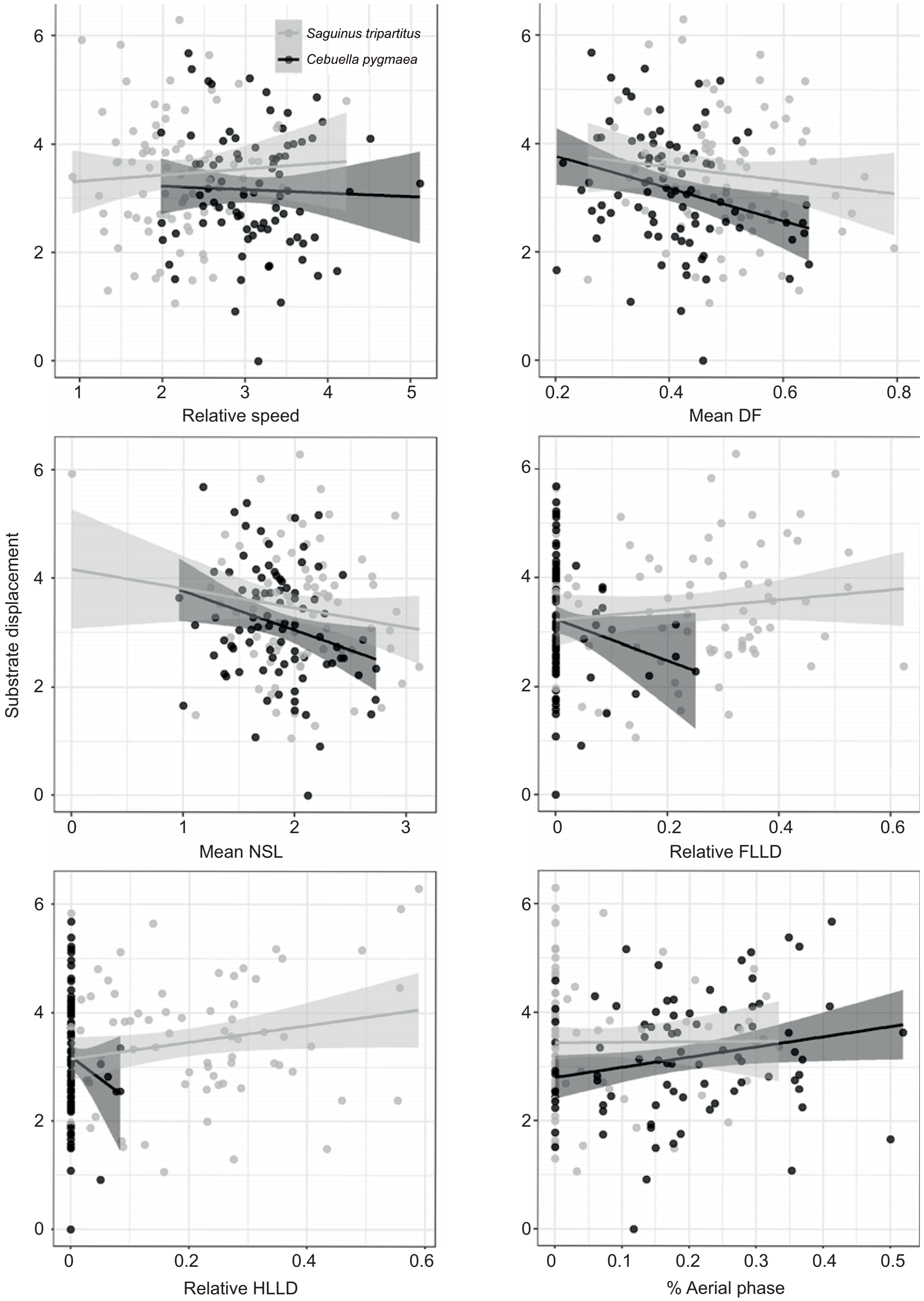

Fig. 7. Variation in substrate displacement in relation to callitrichine asymmetrical gait kinematics (*n*=173 strides). Substrate displacement values were Box–Cox transformed to enhance distributional normality.

in their natural habitats, which ultimately provides more relevant tests of locomotor adaptation (Dunham et al., 2018, 2019a,b; McNamara et al., 2019). Even though the small body sizes characteristic of callitrichines are the result of phyletic dwarfism rather than a retention of a primitive ancestral state (Montgomery and Mundy, 2013), extant callitrichines represent valuable biomechanical analogs for early stages of primate evolution because of their small body size and reduced grasping ability (Nyakatura, 2019). Arboreal quadruped gait research – including laboratory and field studies of callitrichines – has predominantly focused on symmetrical gaits and the functional significance of and potential selective pressures leading to diagonal sequence gaits (Hesse et al., 2015; Nyakatura et al., 2008; Nyakatura and Heymann, 2010; Schmitt, 2003). Regardless of whether diagonal sequence gaits (as opposed to lateral sequence gaits) were the ancestral primate condition or whether these gaits only manifested with later increases in body size, our results highlight that small-bodied callitrichines use primarily asymmetrical gaits when moving through natural environments and adjust asymmetrical gait kinematics in response changes in substrate characteristics. These results combined with those of laboratory studies of other small arboreal mammals (e.g. mouse lemurs: Shapiro et al., 2016; common marmosets: Young, 2009; Chadwell and Young, 2015; Young et al., 2016; tree squirrels: Dunham et al., 2019b) suggest that greater attention should be placed on understanding asymmetrical gait dynamics for insight into hypotheses concerning early primate locomotor evolution.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: N.T.D., A.M., L.J.S., J.W.Y.; Methodology: N.T.D., A.M., L.J.S., T.P., J.W.Y.; Software: J.W.Y.; Formal analysis: N.T.D., L.J.S., J.W.Y.; Investigation: N.T.D., A.M.; Resources: A.M.; Data curation: N.T.D., A.M., T.P.; Writing - original draft: N.T.D.; Writing - review & editing: N.T.D., A.M., L.J.S., J.W.Y.; Project administration: L.J.S., J.W.Y.; Funding acquisition: L.J.S., J.W.Y.

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Data availability

Gait data used in our statistical analyses are available from figshare: https://doi.org/10.6084/m9.figshare.11923122.v1

Supplementary information

Supplementary information available online at http://jeb.biologists.org/lookup/doi/10.1242/jeb.217562.supplemental

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