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RESEARCH ARTICLE

Effects of support diameter and compliance on common marmoset (*Callithrix jacchus*) gait kinematics

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ABSTRACT

Locomotion is precarious in an arboreal habitat, where supports can vary in both diameter and level of compliance. Several previous studies have evaluated the influence of substrate diameter on the locomotor performance of arboreal quadrupeds. The influence of substrate compliance, however, has been mostly unexamined. Here, we used a multifactorial experimental design to investigate how perturbations in both diameter and compliance affect the gait kinematics of marmosets (*Callithrix jacchus*; $N=2$) moving over simulated arboreal substrates. We used 3D-calibrated video to quantify marmoset locomotion over a horizontal trackway consisting of variably sized poles (5, 2.5 and 1.25 cm in diameter), analyzing a total of 120 strides. The central portion of the trackway was either immobile or mounted on compliant foam blocks, depending on condition. We found that narrowing diameter and increasing compliance were both associated with relatively longer substrate contact durations, though adjustments to diameter were often inconsistent relative to compliance-related adjustments. Marmosets also responded to narrowing diameter by reducing speed, flattening center of mass (CoM) movements and dampening support displacement on the compliant substrate. For the subset of strides on the compliant support, we found that speed, contact duration and CoM amplitude explained >60% of the variation in substrate displacement over a stride, suggesting a direct performance advantage to these kinematic adjustments. Overall, our results show that compliant substrates can exert a significant influence on gait kinematics. Substrate compliance, and not just support diameter, should be considered a critical environmental variable when evaluating locomotor performance in arboreal quadrupeds.

KEY WORDS: Stability, Fine branch niche, Branch stiffness, Balance, Locomotion

INTRODUCTION

The arboreal habitat is inherently precarious. Because arboreal substrates are heterogeneous in geometry, spatial orientation and material properties, they challenge locomotor stability to a degree not typically encountered in terrestrial environments. Though the precariousness of the arboreal environment fundamentally depends on a complex interplay between the size of the animal and the size of the locomotor substrate (Jenkins, 1974), even very small mammals

have been shown to adjust locomotor kinematics in response to simulated variation in branch diameter and orientation (Shapiro and Young, 2010, 2012; Shapiro et al., 2014; Karantanis et al., 2015). Challenges to stability should be particularly acute during locomotion in the 'fine-branch niche' – the zone of terminal branches found at the edges of tree canopies where supports are both narrow in diameter and compliant.

Locomotion on narrow arboreal substrates increases the likelihood that the animal's center of mass (CoM) will pass laterally beyond the edge of the substrate, inducing disruptive rolling torques (Cartmill, 1985; Preuschoft et al., 1995). Above-branch stability will be compromised unless the animal is able to mitigate such disruptions. Similarly, compliant substrates compromise locomotor stability by complicating the dynamics of the animal–substrate interaction, undermining the animal's ability to kinesthetically estimate body orientation and to use substrate reaction forces to predictably redirect the CoM during locomotion (MacLellan and Patla, 2006). Though narrow supports and compliant substrates impose different mechanical constraints, both perturbations require precise control over CoM movements and force production if stability is to be maintained. Indeed, previous research has shown that when moving on precarious substrates, a variety of animals – including lizards (Hsieh, 2016), marsupials (Shapiro and Young, 2010, 2012; Shapiro et al., 2014), rodents (Schmidt and Fischer, 2010; Schmidt, 2011), carnivores (Lemelin and Cartmill, 2010), quadrupedal primates (Schmitt, 1999; Schmitt et al., 2006; Wallace and Demes, 2008; Young, 2009) and humans (McMahon and Greene, 1979; Ferris et al., 1998; MacLellan and Patla, 2006) – tend to use a set of common strategies to increase stability. Such strategies include limiting the use of whole-body aerial phases, increasing substrate contact duration, more evenly distributing footfalls across a stride, reducing CoM height, mitigating fluctuations in CoM position and reducing the peak magnitude of vertical forces.

In this study, we examined how diameter and compliance independently and interactively influence the gait kinematics of common marmoset monkeys (*Callithrix jacchus* L.) moving over simulated arboreal supports. Marmosets are small-bodied Neotropical monkeys and committed arboreal quadrupeds (Stevenson and Rylands, 1988; Garber, 1992; Rylands and de Faria, 1993; Souto et al., 2007). Through adaptation to facilitate gumnivory on large vertical tree trunks, marmosets have become quite derived relative to other primates (Lacher et al., 1984; Sussman and Kinzey, 1984; Garber, 1992; Hamrick, 1998; Vinyard et al., 2009; Young, 2009; Smith and Smith, 2013). In contrast to most other extant primates, marmosets have claw-like tegulae, rather than flat nails, on all digits except the hallux, and have a relatively short, adducted hallux with diminished intrinsic musculature (Beattie, 1927; Midlo, 1934; Szalay and Dagosto, 1988; Hamrick, 1998). Marmoset gait patterns are also atypical among primates. Though marmosets most frequently use asymmetrical galloping/

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bounding gaits (Young, 2009; Chadwell and Young, 2015), when walking they often use trotting or lateral sequence patterns of coordination (Schmitt, 2003b), versus the diagonal sequence patterns that are typical of most other primates (Hildebrand, 1967). Nevertheless, despite their uniqueness among primates, marmosets and other callitrichines have converged on the general morphotype thought to characterize early euprimate evolution (i.e. a small, agile, arboreal quadruped lacking well-developed grasping extremities; Szalay and Dagosto, 1988; Gebo, 2004; Bloch et al., 2007; Sargis et al., 2007). Data on marmoset locomotion can therefore serve as a baseline against which to evaluate locomotor performance in less-derived primates. Additionally, because marmosets superficially resemble other mammalian arboreal quadrupeds (i.e. sciurids: Garber, 1980; Garber and Sussman, 1984), they can broadly inform our understanding of how unspecialized arboreal mammals respond to balance perturbations.

We tested three predictions. Prediction 1: marmosets will respond to decreased support diameter and increased substrate compliance by: (i) de-emphasizing high-impact bounding gaits in favor of gallops and symmetrical gaits, (ii) increasing duty factors, (iii) increasing the temporal spacing between subsequent footfalls (i.e. relative lead intervals) and (iv) decreasing average CoM height and CoM height fluctuations. Prediction 2: substrate diameter and compliance will have interacting effects on gait kinematics, such that the most pronounced adjustments are required on the smallest, most compliant substrates. Prediction 3: the displacement of the compliant substrate during a locomotor stride will be directly proportional to speed and to the amplitude of CoM displacements, and inversely proportional to overall substrate contact durations.

MATERIALS AND METHODS
Experimental protocol
Data were collected from two adult male marmosets (*C. jacchus*), housed at NEOMED (average body mass: 365 g, range: 354–374 g; and 388 g, range: 375–397 g, respectively). The Northeast Ohio Medical University Institutional Animal Care and Use Committee (IACUC) approved all procedures prior to the beginning of this research (protocol 12-018).

Before each experiment, marmosets were anesthetized with isoflurane and the lateral surfaces of the major limb joints were shaved and marked with retro-reflective tape on both sides of the body, to aid in later kinematic tracking (Fig. 1; Movie 1). Upon recovery from anesthesia, the marmosets were coaxed to cross a 4 m long set of horizontal poles at self-selected speeds. The pole substrates were constructed out of PVC pipes of three different diameters: a 'narrow' 1.25 cm pole, a 'moderate' 2.5 cm pole and a 'broad' 5 cm pole. Given an average hand length of 3.6 cm and an average foot length of 4.2 cm in the marmosets in our sample, the animals would have been able to wrap their extremities completely around the 1.25 cm pole, roughly halfway around the 2.5 cm pole, and roughly 25% around the 5 cm pole. The central 0.6 m of the pole trackway was mounted on interchangeable stable or compliant bases, depending on the experimental condition (see below for details of compliant substrate construction). We recorded locomotor activity using four high-speed cameras (Xcitex XC-2; Xcitex Inc., Woburn, MA, USA), with two cameras located on either side of the animal, positioned at approximately 45 deg to the direction of travel. Videos from the four cameras were recorded synchronously at 150 Hz using ProCapture software (Xcitex Inc.).

From a total of 290 trials collected over the course of 17 experiments (ranging between 5 and 25 trials per animal), we selected 10 strides per animal per experimental condition for further

analyses, excluding trials with obvious changes in speed (i.e. where the animal visibly started or stopped moving in the central portion of the trackway) or in which one or more joint markers was obscured for a substantial portion of time. We also excluded trials where the leading forelimb was the first limb to contact the central portion of the trackway, given that this would have potentially placed the leading and trailing forelimbs on mechanically different substrates (i.e. compliant versus stable). Our final dataset consisted of 120
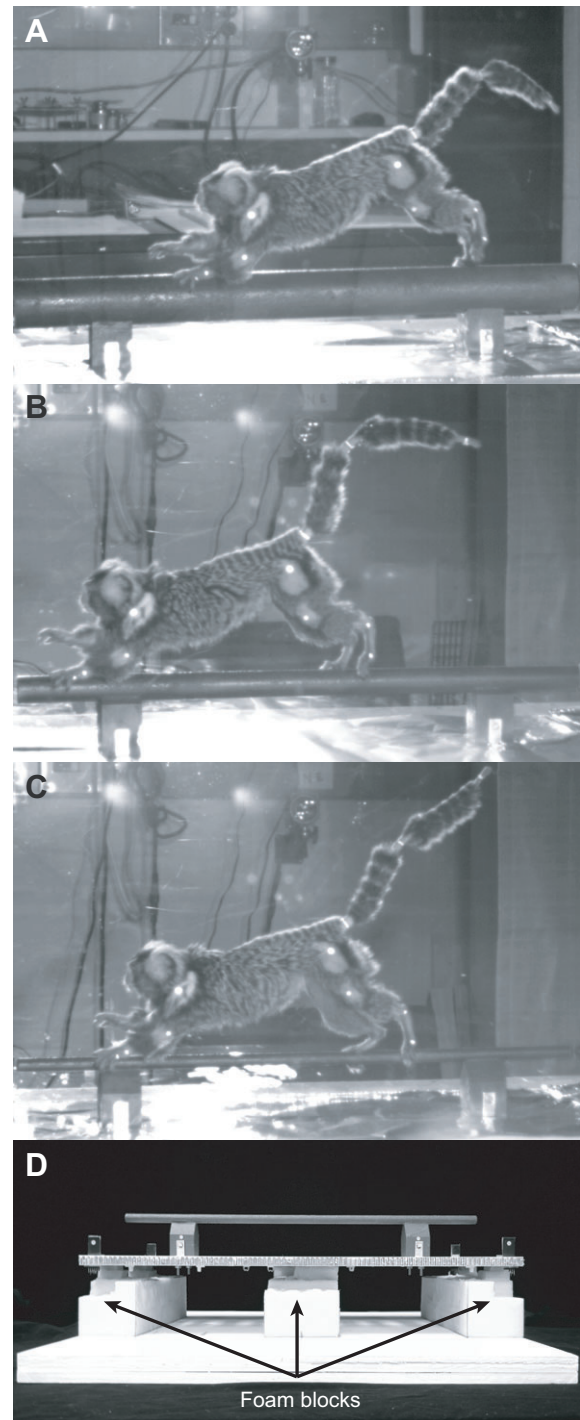
Fig. 1. Experimental apparatus. (A–C) Captured video images of a marmoset crossing the (A) 5 cm, (B) 2.5 cm and (C) 1.25 cm supports. (D) Perpendicular view of the interchangeable central section of the runway, configured for the compliant experimental condition.

strides (i.e. 60 per animal across the six possible experimental conditions).

Substrate construction

The stable base was constructed from a plywood sheet mounted on dense wooden posts, whereas the compliant base consisted of a platform of honeycomb fiberfoam panel (Teklam Corporation, Corona, CA, USA) epoxied to blocks of super-cushioning polyurethane foam (McMaster-Carr Supply Co., Aurora, OH, USA) (Fig. 1D). Both the stable and compliant bases were affixed to heavy wooden baseplates that were clamped to a massive and immobile laboratory bench top. We used an ElectroPuls E3000 material testing machine (Instron, Norwood, MA, USA) to empirically measure the amount of compliant platform deflection (in mm) resulting from a given applied force (in N, i.e. compliance; van Casteren et al., 2013). We measured compliance at the two ends of the platform to better model the material properties the marmosets experienced during their initial contact with the compliant platform at the start of each stride (see Movie 1 for an exemplar stride). We used existing data on marmoset locomotor kinetics (Chadwell and Young, 2015) to select biologically reasonable control parameters, loading the platform linearly at a rate of 3 mm s^{-1} to a maximum force of 11 N. Loading and displacement were linearly related ($R^2 \geq 0.999$). Average compliance of the platform ends over 10 repetitions was 1.39 mm N^{-1} (Table 1), with some variation between the two ends (1.31 versus 1.46 mm N^{-1}). Although no data currently exist on the material properties of locomotor substrates used by wild marmosets, a recent review of branch material properties in a tropical Sumatran rainforest found that locomotor substrates typically used by orangutans had compliances of 0.1–70 mm N^{-1}, with an average compliance of 5.7 mm N^{-1} (95% confidence limits: 3.54 mm N^{-1}, 7.81 mm N^{-1}; van Casteren et al., 2013). Based on available data, the level of substrate compliance used here is therefore of biologically reasonable magnitude for a tropical rainforest.

Dynamically, the platform behaved as a damped harmonic oscillator, such that upon being struck, it vibrated at a relatively constant frequency but with decreasing amplitude. Measured natural frequencies were inversely related to pole diameter (Table 1).

Kinematic calibration and analyses

To quantify the 3D displacement of the animal and the compliant substrate during locomotion, we calibrated the synchronized video images from the four cameras to the same 3D coordinate system using published methods (Standen and Lauder, 2005; Chadwell and Young, 2015). In our final coordinate system, the x-axis was set to be coincident with the long axis of the pole substrate (i.e. the fore–aft direction), the y-axis defined the mediolateral direction and the z-axis defined the vertical direction. The origin of the system was set to the midpoint of the pole trackway's central axis. For each individual stride, axes were then standardized to the predominant direction of animal movement such that positive x-axis displacement was defined as forward (i.e. cranial) movement, positive y-axis displacement was defined as leftward movement (i.e. relative to the central axis of the pole), and positive z-axis displacement was defined as upward movement.

For all 120 strides in the dataset, we used ProAnalyst to digitize hip and shoulder markers on both sides of the body, as well as the reflective markers indicating the pole position for the compliant substrate. Each digitized feature was subsequently fitted to a quintic smoothing spline function (tolerance of 1 mm^2) using a custom-written MATLAB program, allowing us to mitigate digitizing error and interpolate the position of a feature for any frames where the marker was not visible (Walker, 1998).

Smoothed shoulder and hip marker trajectories were then used to estimate instantaneous CoM position throughout the stride, as:

$$\mathrm{mSh} + (\mathrm{mHp} - \mathrm{mSh}) \cdot \mathrm{pCoM}, \qquad (1)$$

where mSh and mHp are the midpoint between the left and right shoulders and hips, respectively, and pCoM is the static position of the CoM, as a percentage of trunk length from the shoulders to the hips (Movie 1). We estimated pCoM empirically for each animal using the reaction board method (Lammers et al., 2006; Larson and Demes, 2011; Young, 2012a,b; Chadwell and Young, 2015). In this procedure, a rigid lightweight board is supported by two nails resting on a platform at one end and a single nail resting on a scale at the other. The scale is zeroed and the anesthetized animal is placed on its side on the board such that the animal's craniocaudal axis is parallel to the board's long axis. Because this system is in mechanical equilibrium:

$$M_\mathrm{b} x_\mathrm{CoM} = R_\mathrm{scl} l_\mathrm{brd}, \qquad (2)$$

where M_b is body mass, x_CoM is the craniocaudal position of the CoM (relative to the two-nail pivot), R_scl is the reaction force measured by the scale and L_brd is the length of the board between the two supports. Rearranging this equation to solve for x_CoM:

$$x_\mathrm{CoM} = \frac{R_\mathrm{scl} L_\mathrm{brd}}{M_\mathrm{b}}. \qquad (3)$$

By taking an overhead photograph of the animal on the board, x_CoM can be related to the position of the animal's shoulders and hips, and thus expressed as a percentage of craniocaudal trunk length (i.e. pCoM). Static CoM position in the two monkeys, across a range of limb, trunk and tail postures (i.e. flexed, extended or neutral), averaged 58.4% (range: 50.8–68.9%) and 58.8% (range: 51.2–64.7%) of trunk length, respectively.

Table 1. Static and dynamic mechanical properties of the compliant pole substrates

Pole diameter (cm)	Compliance (mm N^{-1})	Stiffness (N m)	Natural frequency (Hz)	Period of oscillation (s)	M_eff (g)*
5			8.2	0.12	285
2.5	1.39	722.6	10.2	0.10	204
1.25			11.7	0.092	160

*Following Ferris and Farley (1997), effective mass (M_eff) was estimated as:

$$M_\mathrm{eff} = \frac{k_\mathrm{substrate}}{2\pi f},$$

where $k_\mathrm{substrate}$ is the stiffness of the substrate and f is the natural frequency of the pole segment. The effective mass is a measure of the inertia inherent in the spring system.

In order to quantify the 3D displacement of the compliant pole substrate during locomotion, we tracked four reflective markers at the four corners of the substrate (i.e. at the left and right sides of the proximal and distal ends, relative to the animal). The 3D position of the compliant pole segment midpoint could then be estimated based on the geometry of its construction and the average 3D position of the four digitized points.

To determine the instantaneous height of the animal's CoM above the pole's surface, we first calculated a virtual point, Pole_{CoM}, defined as the point along the central axis of the pole segment directly beneath the estimated position of the monkey's CoM. To calculate Pole_{CoM}, we first defined a pole vector ($\mathbf{V}_{\text{pole}}$) as:

$$\mathbf{V}_{\text{pole}} = (\text{mDist} - \text{mProx})/|\text{mDist} - \text{mProx}|, \qquad (4)$$

where mDist and mProx represent the midpoint between the left and right points at the distal and proximal pole ends, respectively. Pole_{CoM} was then determined by calculating the intersection of the instantaneous pole vector with a transverse (y,z) plane localized at the x-axis projection of the monkey's estimated CoM. We then calculated the height of the CoM above the pole surface as:

$$\text{CoM}_{\text{sub}} = Z_{\text{CoM}} - Z_{\text{pole}} - r, \qquad (5)$$

where Z_{CoM} and Z_{pole} are the z-coordinates of CoM and Pole_{CoM}, respectively, and r is the pole radius. By definition, the Z_{pole} term in Eqn 5 equaled zero during the stable experimental conditions.

Primary outcome measures
Gait type
For all strides in the dataset, we used ProAnalyst to record the timing of the initial touchdown, the subsequent liftoff and the second touchdown of all four limbs. Strides were always chosen to begin with the first forelimb that contacted the stable/compliant central section of the trackway (i.e. the trailing forelimb; see Movie 1). Subsequent gait analyses were all performed in a custom-written MATLAB program.

Temporal data on the phasing of limb support period events were used for subsequent 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. All other strides were categorized as asymmetrical gaits. Asymmetrical gaits were further subclassified based on footfall phasings. Asymmetrical strides in which 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), but forelimb stance periods were temporally staggered, were classified as half-bounds. All remaining asymmetrical strides, where both forelimb and hindlimb touchdowns were temporally staggered, were classified as gallops. Full bounds were never observed. Finally, we also quantified the presence of whole-body aerial phases for each stride in the dataset.

In order to increase overall substrate contact, marmosets moving on narrow supports and compliant substrates should use a greater proportion of symmetrical strides and gallops, reducing the frequency of half-bounds. Additionally, we predicted marmosets moving on precarious substrates would avoid whole-body aerial phases.

Speed
Average speed was defined as the mean of the instantaneous fore–aft CoM velocity (calculated as the first derivative of CoM position). Given that greater speed generally decreases agility (Hyams et al., 2012; Wheatley et al., 2015; Wynn et al., 2015), marmosets should decrease speed on narrow and compliant substrates.

Duty factor
Duty factor was calculated as the quotient of support phase duration and total stride duration. Duty factor was calculated separately for each limb and then averaged across forelimbs and across hindlimbs. Marmosets should increase forelimb and hindlimb duty factor when moving on narrow supports and compliant substrates, thereby increasing periods of substrate contact.

Relative lead interval
Relative lead intervals were calculated as the lag between trailing and leading limb mid-support, scaled to the total contact duration of the limb pair (i.e. the duration between the touchdown of the trailing limb and the liftoff of the leading limb). Relative lead intervals were calculated separately for forelimb and hindlimb pairs. Marmosets should increase relative lead intervals on narrower and more compliant supports, thereby distributing limb contacts more evenly across the stride. More distributed limb contacts attenuate the collision between the animal and the substrate, effectively reducing impact forces and CoM fluctuations.

Relative contact duration
Relative contact duration was calculated as the total contact duration for the limb pair (i.e. the duration between the touchdown of the trailing limb and the liftoff of the leading limb), scaled to stride duration. Relative contact durations were calculated separately for forelimb and hindlimb pairs. Marmosets should increase relative contact durations when moving on narrow supports and compliant substrates, increasing periods of substrate contact.

CoM height
Average CoM height was defined as the average z-axis distance between estimated CoM position and the top surface of the pole support (Eqn 5). We also quantified vertical fluctuations in the CoM position as the peak-to-peak amplitude of CoM height. When moving on precarious supports, marmosets should reduce both CoM height and CoM fluctuations.

Compliant substrate displacement
We calculated resultant substrate displacement as the Euclidean norm of the x, y and z peak-to-peak amplitudes over the stride interval. Substrate displacement should be directly proportional to speed and to the amplitude of CoM displacements, and inversely proportional to overall substrate contact duration. Substrate displacement should also decrease with decreasing substrate diameter, in order to mitigate the combined challenge of moving over narrow and compliant supports.

Statistical methods
We used general linear model (GLM) analyses with Poisson-distributed error terms to test for diameter- and compliance-based differences in the relative frequencies of gait types (half-bound, gallop and symmetrical) and the relative frequencies of aerial phases within asymmetrical gaits. Variation in continuous measures associated with support diameter or level of compliance was assessed using mixed-effects analyses of variance (ANOVA),

analyses of covariance (ANCOVA) or regressions, depending on the categorical or continuous nature of the predictor variables (Doncaster and Davey, 2007). The random factor for all mixed-effects models was individual animal. For each test, we first fitted the full model, including diameter and compliance as main effects, speed as a covariate where appropriate, and all interactions among main effects and covariates (i.e. diameter–compliance, speed–diameter, speed–compliance and speed–diameter–compliance). We then simplified each model by removing non-significant interactions in a hierarchical manner (i.e. by removing three-way interactions first, followed by two-way interactions; Crawley, 2007). In cases where significant main effect or covariate interactions remained in the model, we tested main effects at appropriate levels of the interacting term (e.g. testing for diameter differences within levels of compliance, testing for compliance differences within diameters, or testing for diameter/compliance differences at the minimum and maximum values for the speed range that was common across all experimental conditions). For all tests, continuous variables were log-transformed as necessary to improve normality. Finally, we used a Pearson product-moment correlation and multiple regression procedure to evaluate the association between gait kinematics and compliant substrate displacement. Multiple comparisons within the context of a single test were corrected for alpha-inflation using the false discovery rate method (Benjamini and Hochberg, 1995).

In the Results, we discuss the broad outcomes of each statistical test. Detailed information on each test, including significant P-values and effect sizes for all pairwise comparisons, are presented in Tables S1–S6. Raw data are provided in Table S7. All statistical analyses were performed using R (R Core Team, 2015).

RESULTS
Gait selection
Marmosets used asymmetrical gaits almost exclusively, regardless of support diameter or level of compliance, with asymmetrical gaits making up nearly 90% of the strides in our dataset (i.e. 106/120 strides). Marmosets generally used fewer half-bounds and more symmetrical gaits when moving on narrower supports (P=0.035; Fig. 2A). In contrast, gait selection did not significantly differ between stable and compliant substrates (P=0.73; Fig. 2A).

Marmosets tended to avoid aerial phases when moving on smaller substrates (P<0.001). Whole-body aerial phases were used during 33% of the strides on the 2.5 cm substrate and in only 15% of the strides on the 1.25 cm substrate, versus nearly 50% of the strides on the 5 cm substrate (Fig. 2B). Aerial phase presence did not predictably vary with compliance (P=0.73; Fig. 2B).

Speed
Marmosets moved significantly slower when travelling on the narrowest (1.25 cm) pole versus the two larger poles (all P<0.001; Fig. 3; Table S1). Speed was not significantly associated with substrate compliance (Fig. 3; Table S1).

Duty factor
Forelimb duty factor
Forelimb duty factor significantly decreased with increasing speed (Fig. 4). However, the influence of speed on forelimb duty factor varied among different combinations of support diameter and compliance, as indicated by a significant second-order interaction between speed, support diameter and compliance (P=0.018; Table S2). Specifically, when moving on compliant substrates,
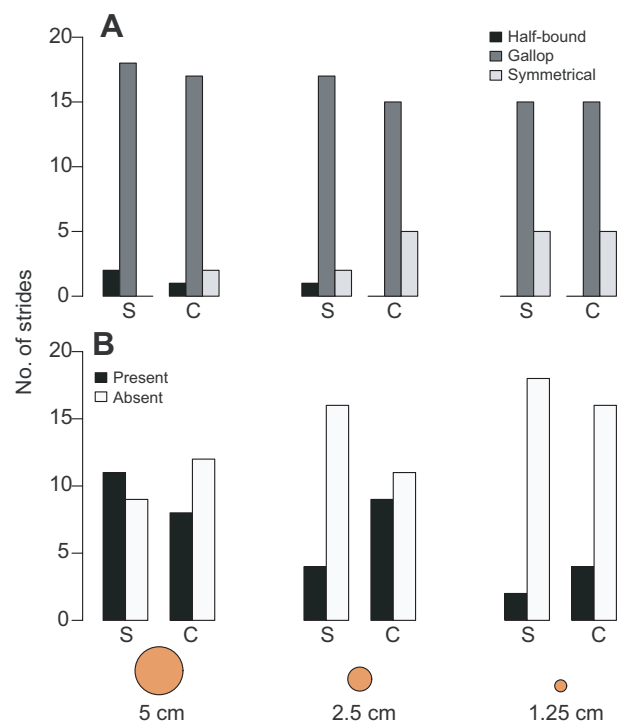

Fig. 2. Influence of substrate diameter and compliance on categorical gait parameters. Bar plots of categorical variation in (A) gait selection and (B) presence of an aerial phase, grouped by support diameter and level of compliance (S, stable; C, compliant).

marmosets used higher duty factors on the 5 cm support when traveling slowly (significant only in comparison to the 2.5 cm support, P=0.044), but lower duty factors than on the two narrower ones when moving quickly (P=0.018). Diameter had no effect on forelimb duty factor during locomotion on stable substrates. Similarly, marmosets used higher forelimb duty factors on compliant versus stable supports when moving on the 5 cm support, and when moving quickly on the 2.5 cm support (P≤0.031). Substrate compliance had no effect on forelimb duty factor during locomotion on the 1.25 cm support.
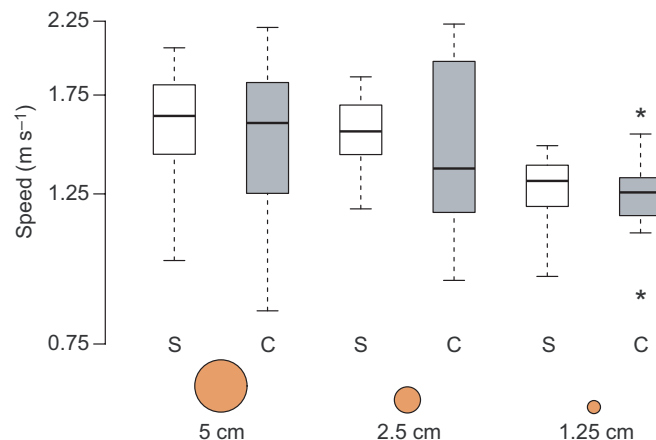
Fig. 3. Box-and-whisker plot of variation in log speed among support diameters and compliance levels. S, stable; C, compliant. In each plot, bold lines represent the median of the distribution, boxes extend across the interquartile range (IQR), and whiskers extend to the extremes of the distribution or to ±150% of the IQR, whichever is smaller. Asterisks indicate outliers >150% of the IQR.
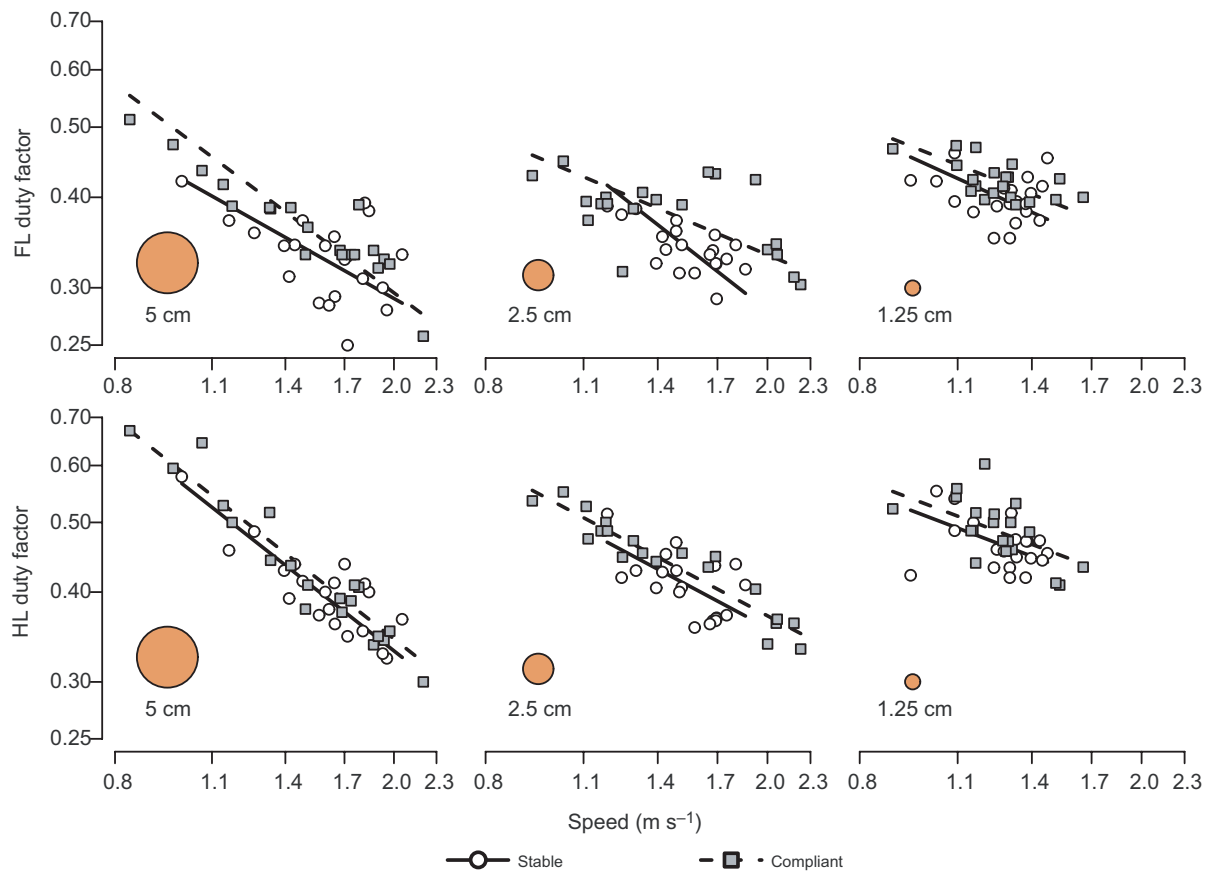
Fig. 4. log–log scatterplots of forelimb and hindlimb duty factor plotted against speed, grouped by support diameter. Top, forelimb (FL); bottom, hindlimb (HL). Trend lines indicate reduced maximum likelihood fits from mixed-effects ANCOVA models.

Hindlimb duty factor

Hindlimb duty factor also decreased with increasing speed (Fig. 4). However, the effects of speed on hindlimb duty factor varied among diameters ($P<0.001$; Table S2), with hindlimb duty factor declining more precipitously with speed on the 5 cm support than on the two narrower ones (Fig. 4). No other covariate or factor interactions were significant. Marmosets used higher hindlimb duty factors on the 5 cm support versus the two narrower ones when moving slowly ($P\leq0.009$), but higher duty factors on the 1.25 cm support versus the two broader ones when moving quickly ($P\leq0.044$). Regardless of support diameter or speed of travel, marmosets used higher hindlimb duty factors when moving on compliant substrates than when moving on stable substrates ($P=0.005$).

Relative lead interval
Relative forelimb lead interval
Relative forelimb lead interval was not significantly related to variation in speed, support diameter or substrate compliance (Fig. 5; Table S3).

Relative hindlimb lead interval
Relative hindlimb lead interval significantly decreased with increasing speed ($P<0.001$), and significantly varied among diameters ($P<0.001$) and levels of compliance ($P=0.011$; Fig. 5; Table S3). Controlling for the effects of speed, marmosets used longer relative hindlimb lead intervals when moving on narrower substrates. However, none of the individual pairwise tests among diameters were significant after correcting for multiple comparisons.

Controlling for the effects of speed, relative hindlimb lead intervals were significantly greater during locomotion on compliant versus stable substrates ($P=0.045$).

Relative contact interval
Relative forelimb contact duration
Relative forelimb contact duration significantly decreased with increasing speed, and significantly varied among diameters and levels of compliance (all $P<0.001$; Fig. 6; Table S4), with no significant interactions. Controlling for the effects of speed, relative forelimb contact duration was significantly greater on the 1.25 cm support relative to the two broader supports ($P\leq0.011$), and significantly greater on compliant substrates relative to stable substrates ($P=0.006$).

Relative hindlimb contact duration
Relative hindlimb contact duration significantly decreased with increasing speed (Fig. 6). However, the effects of speed on relative hindlimb contact duration varied among diameters ($P=0.005$; Table S4), declining more precipitously with speed on the 5 cm support than on the two narrower ones (Fig. 6). *Post hoc* comparisons at minimum and maximum common speeds revealed that diameter had very little influence on relative hindlimb contact duration. When moving slowly, marmosets used relatively greater hindlimb contact durations on the 5 cm versus the 2.5 cm support ($P=0.031$). No other *post hoc* comparisons between diameters were significant (Table S4). Regardless of support diameter, marmosets used higher relative hindlimb contact durations when moving on
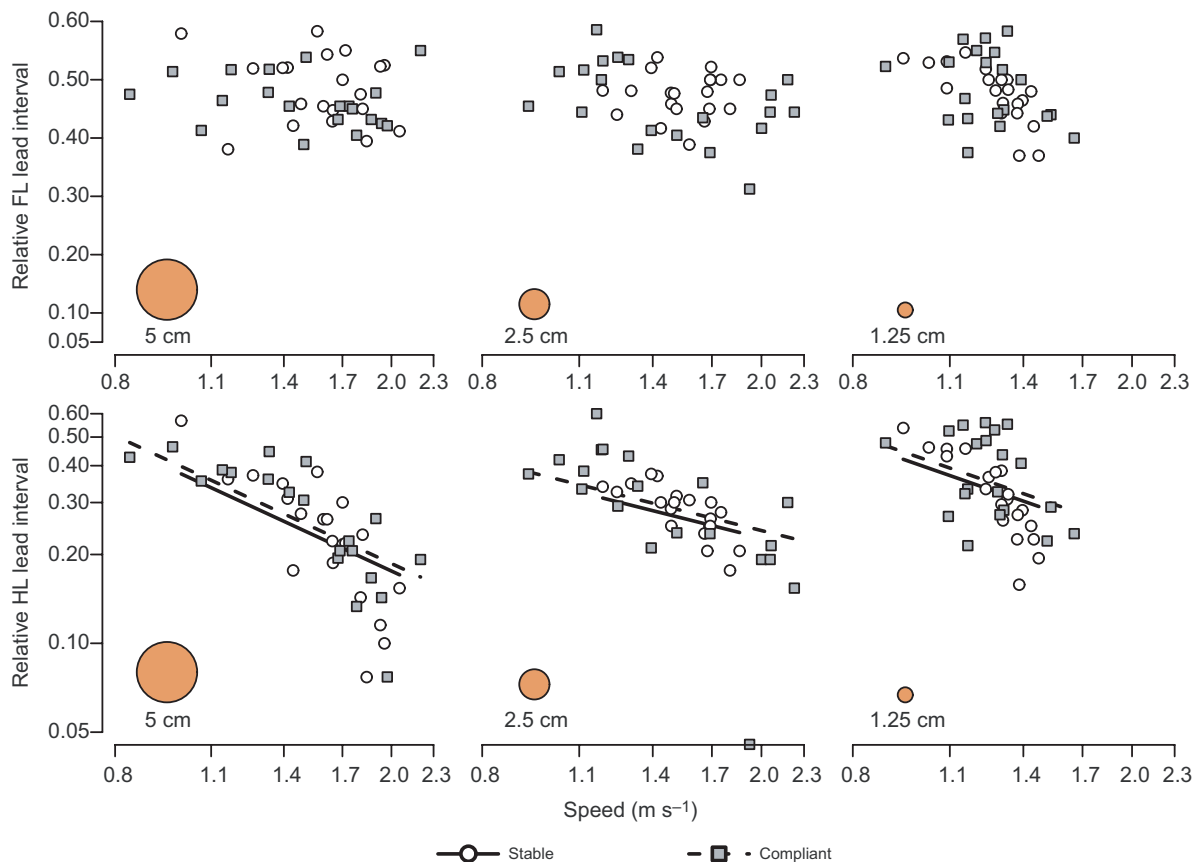
Fig. 5. Scatterplots of relative forelimb and hindlimb lead intervals plotted against logged speed, grouped by support diameter. Top, forelimb (FL); bottom, hindlimb (HL). Relative hindlimb lead intervals are plotted on log–log axes. Trend lines indicate reduced maximum likelihood fits from mixed-effects ANCOVA models. Note that trend lines are not drawn in the relative forelimb lead interval plots because of the non-significant relationship with logged speed (Table S3).

compliant substrates than when moving on stable substrates (P=0.002), after controlling for the effects of speed.

Kinematics of the CoM
The CoM generally followed a sinusoidal path during a stride, with a slight peak at approximately 25–30% of stride duration, followed by a deep nadir at approximately 65–75% of stride duration (Fig. 7). The subtle peak early in the stride corresponds to the period surrounding the touchdown of the leading forelimb, whereas the subsequent nadir corresponds to the period surrounding the touchdown of the leading hindlimb, prior to accelerating and launching the CoM into the next stride (Fig. 7).

Marmosets moved with significantly higher CoM positions when traveling at higher speeds (P<0.001; Fig. 7). However, the influence of speed on average CoM height varied among different combinations of support diameter and compliance (i.e. there was a significant second-order interaction between speed, diameter and compliance; Fig. 7; Table S5). *Post hoc* comparisons indicated that when moving slowly, marmosets typically exhibited lower CoM heights on the 5 cm support versus the two narrower supports (Table S5). When moving quickly, diameter was unassociated with average CoM height. Marmosets exhibited lower CoM heights on compliant versus stable substrates when moving slowly on the 5 cm support and quickly on the 2.5 cm support (P≤0.026). No other *post hoc* comparisons between compliance levels were significant.

CoM height amplitude significantly varied among diameters (P<0.001; Fig. 7), with marmosets exhibiting greater fluctuations in CoM height when moving on the 5 cm support versus the two

narrower supports (P≤0.041 for all *post hoc* comparisons; Table S5). CoM height amplitude was unrelated to either speed or level of compliance.

Compliant substrate displacement
The resultant 3D displacement of the compliant pole midpoint throughout an average stride is plotted separately for each diameter in Fig. 8A. Pole displacement increased throughout the stride, though the increase was not monotonic (Fig. 8A). Displacement peaked first during the loading period immediately after contact of the trailing forelimb, when the animal was likely exerting braking forces to begin redirecting the CoM, and again following contact of the leading hindlimb, when the animal was likely exerting strong propulsive forces to accelerate into the next stride. Across all the diameters, total resultant displacement (i.e. peak-to-peak amplitude) averaged 1.9 mm during a stride (range: 0.7–5.1 mm), equating to 1–5.4% of the average height of the marmoset's CoM above the substrate. Relative to body size, the range of substrate movement amplitudes we observed was comparable to previous data for humans running on compliant surfaces (Ferris et al., 1998), where surface displacements of 2.8–9.9 cm were observed (3–11% of average hip human height).

Total substrate displacement increased with speed (Fig. 8B). Controlling for speed, overall substrate displacement was significantly smaller on the narrowest pole relative to the two broader ones (P≤0.014; Fig. 8B; Table S6). Multiple independent Pearson product-moment correlations showed that, in addition to the positive relationship with speed, substrate displacement was directly
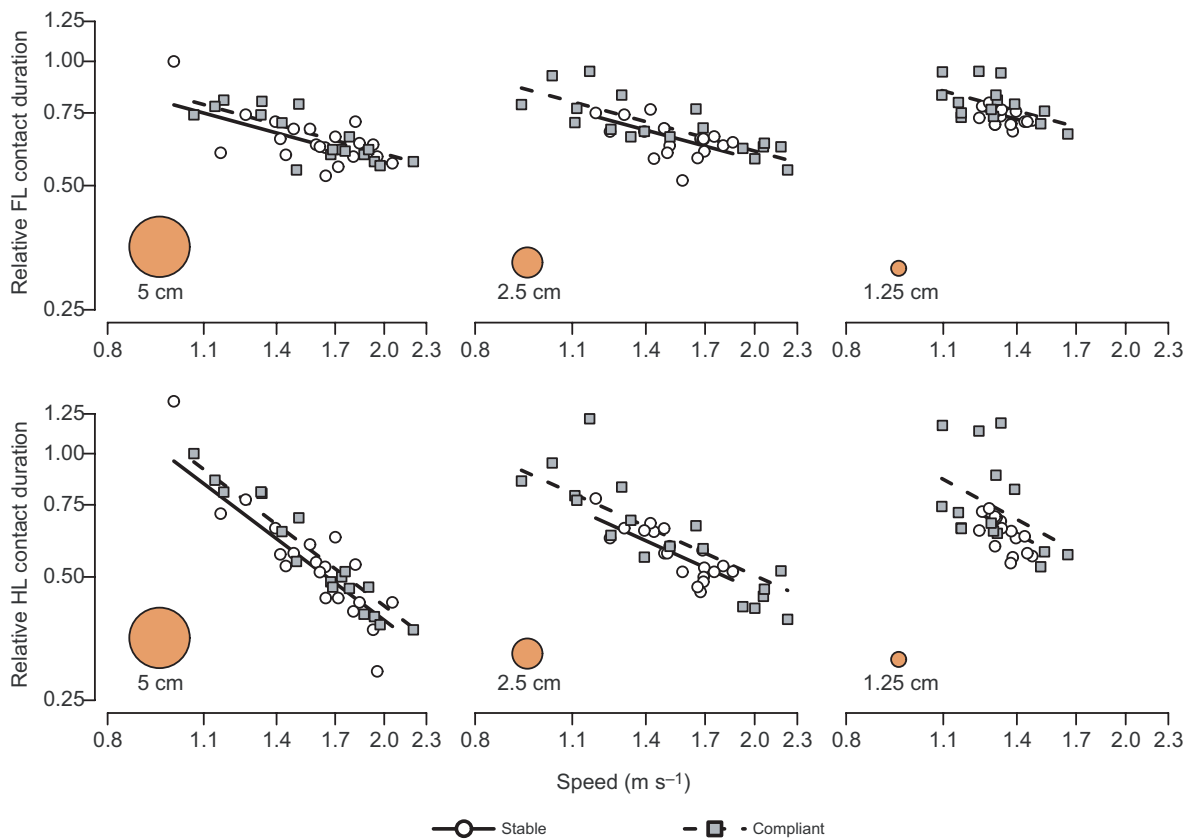
Fig. 6. log–log scatterplots of relative forelimb and relative hindlimb contact duration plotted against speed, grouped by support diameter. Top, forelimb (FL); bottom, hindlimb (HL). Trend lines indicate reduced maximum likelihood fits from mixed-effects ANCOVA models.

proportional to CoM amplitude and inversely proportional to forelimb and hindlimb duty factor, relative lead interval and relative contact duration (Table 2). We used multiple regression analysis to test how well speed, CoM amplitude and relative forelimb and hindlimb contact duration in concert predicted variation in compliant substrate displacement (we did not include duty factors or relative lead intervals in the model to reduce problems of multicollinearity among the predictors). Together, the four included predictor variables explained >60% of the variation in substrate displacement (adjusted multiple R^2=0.629). Controlling for the other predictor variables, substrate displacement was directly proportional to speed, CoM amplitude and relative hindlimb contact duration, and inversely proportional to relative forelimb contact duration (Table 2, Fig. 8C–F). However, the partial regression coefficient for relative hindlimb contact duration was not significantly different from zero (P=0.066) and removing this variable from the model resulted in the lowest rise in AIC (Table 2), indicating that the conditional relationship between relative hindlimb contact duration and substrate displacement was not particularly strong.

DISCUSSION
Influence of support diameter on gait kinematics
When moving on narrow poles, marmosets used fewer high-impact bounding gaits and generally avoided whole-body aerial phases (Fig. 2). Studies of other small-bodied arboreal mammals, including red squirrels (Schmidt, 2011) and mouse lemurs (Shapiro et al., 2016), have also shown a decrease in bounding gaits, and a corresponding increase in gallops, associated with narrow-perch

locomotion. In an analysis of high-speed locomotion in 12 arboreal primates, Schmitt and colleagues (2006) found that primates generally avoided whole-body aerial phases during fast travel, most frequently using 'ambles' (symmetrical running gaits in which at least one limb is always in contact with the substrate throughout the stride) or 'canters' (their term for galloping gaits that lack an aerial phase; see also Howell, 1944). Given that, aside from their use by primates, ambles are also common in large mammals seeking to avoid high loading forces (i.e. elephants and certain breeds of domestic horse: Howell, 1944; Gambaryan, 1974; Hutchinson et al., 2003; Biknevicius et al., 2004, 2006), primates may also avoid aerial phases in order to limit force magnitudes (in this case, though, forces imparted to the substrate, rather than substrate reaction forces imparted to the skeleton). Schmitt et al. (2006) also present a mathematical model showing that the use of more 'grounded' gaits, such ambles and canters, mitigates vertical fluctuations in CoM position. Indeed, in the current study, marmosets both avoided aerial phases and reduced CoM amplitudes on smaller substrates, providing indirect support for this model.

Marmosets significantly reduced speed when moving on the narrowest pole. Though faster speeds may facilitate dynamic stability, particularly in the rolling plane (Bruijn et al., 2009), fast travel also reduces agility (Hyams et al., 2012; Wheatley et al., 2015; Wynn et al., 2015) and increases peak force production (Weyand et al., 2000) – both of which may compromise stability when moving on a precariously narrow support. Indeed, substrate narrowness has previously been shown to be associated with slower travel speeds in many arboreal tetrapods, including tree frogs (Herrel et al., 2013), anoles (Losos and Sinervo, 1989; Losos and Irschick,
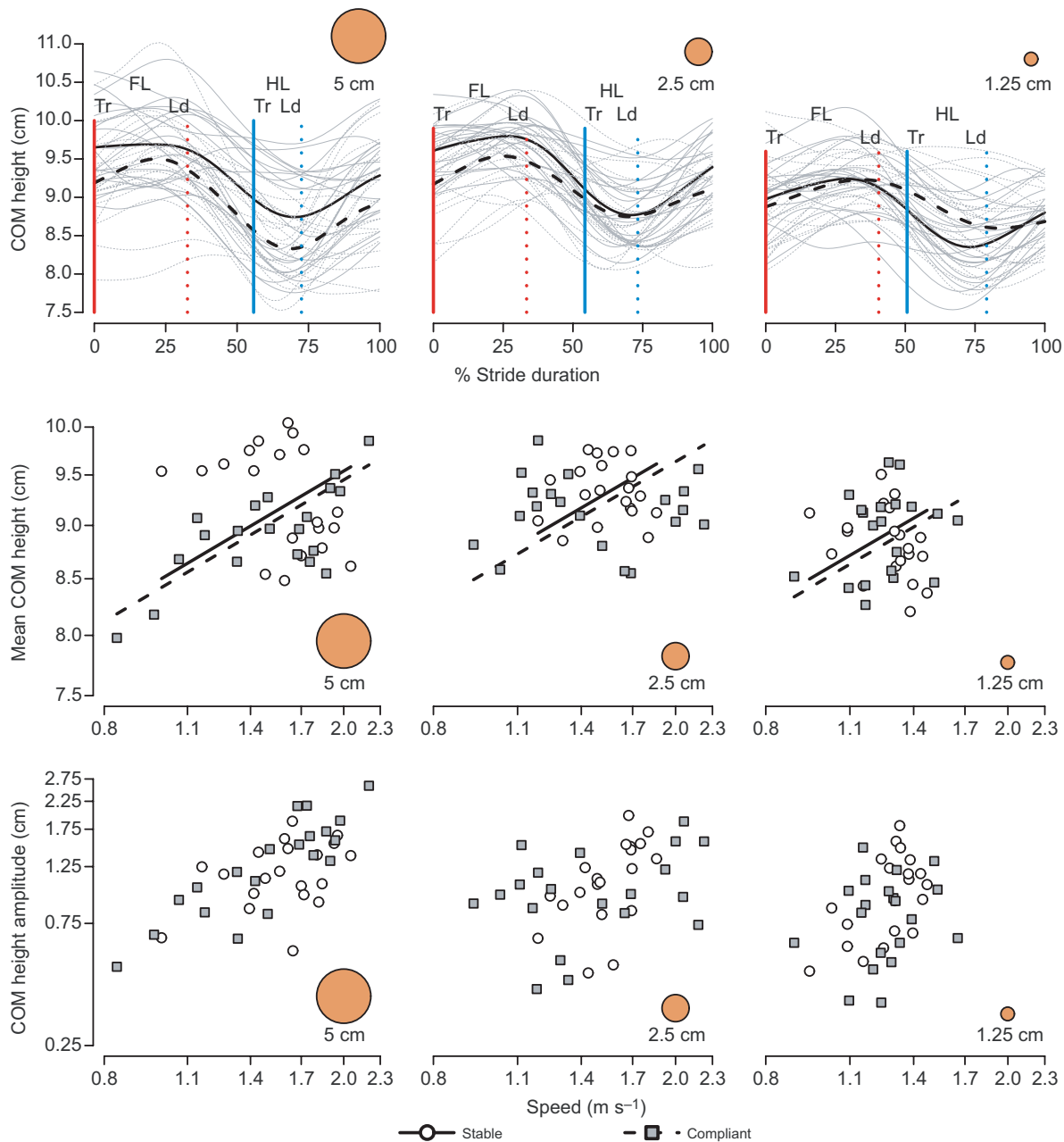
Fig. 7. Effects of substrate diameter and compliance on CoM kinematics. Top, sagittal plane trajectories of the CoM as a function of normalized stride duration, grouped by support diameter. CoM trajectories for individual strides are indicated by the light gray lines, whereas black lines indicate mean trajectories. Vertical lines indicate the mean timing of trailing limb (Tr, solid lines) and leading limb (Ld, dotted lines) touchdown events. Red lines indicate forelimb (FL) events, whereas blue lines indicate hindlimb (HL) events. Middle and bottom, log–log scatterplots of mean CoM height (middle) and CoM height amplitude (bottom) plotted against speed and grouped by support diameter. Trend lines in the mean CoM height plots indicate reduced maximum likelihood fits from mixed-effects ANCOVA models. Note that trend lines are not drawn in the CoM height amplitude plots because of the non-significant relationship with log speed (Table S5).

1996; Mattingly and Jayne, 2004; Hsieh, 2016), fence lizards (Sinervo and Losos, 1991), marsupial gliders (Karantanis et al., 2015), opossums (Lammers and Biknevicius, 2004; Shapiro et al., 2014), mice (Hyams et al., 2012), squirrels (Schmidt, 2011) and strepsirrhine primates (Stevens, 2007). Other gait adjustments were subtler, often displaying a complex interaction with speed. For instance, forelimb/hindlimb duty factor, relative hindlimb contact interval and average CoM height changed more drastically with increasing speed on the 5 cm support than on the 2.5 and 1.25 cm supports – suggesting mechanical constraints may limit kinematic variability on the narrower poles. As a result, kinematic differences

among pole sizes were inconsistent across the range of sampled speeds, showing one trend during slow travel and another when the monkeys were moving quickly (i.e. higher hindlimb duty factors on the 5 cm support at the minimum common speed, but lower duty factors on the 5 cm support at the maximum common speed; Fig. 4, Table S2).

In a previous study, we documented more drastic support-related changes in gait dynamics when marmosets transitioned from a flat trackway to a 3.2 cm diameter pole (Young, 2009). Specifically, marmosets reduced speed, peak vertical force magnitude and CoM displacement, and increased duty factor, relative lead interval and
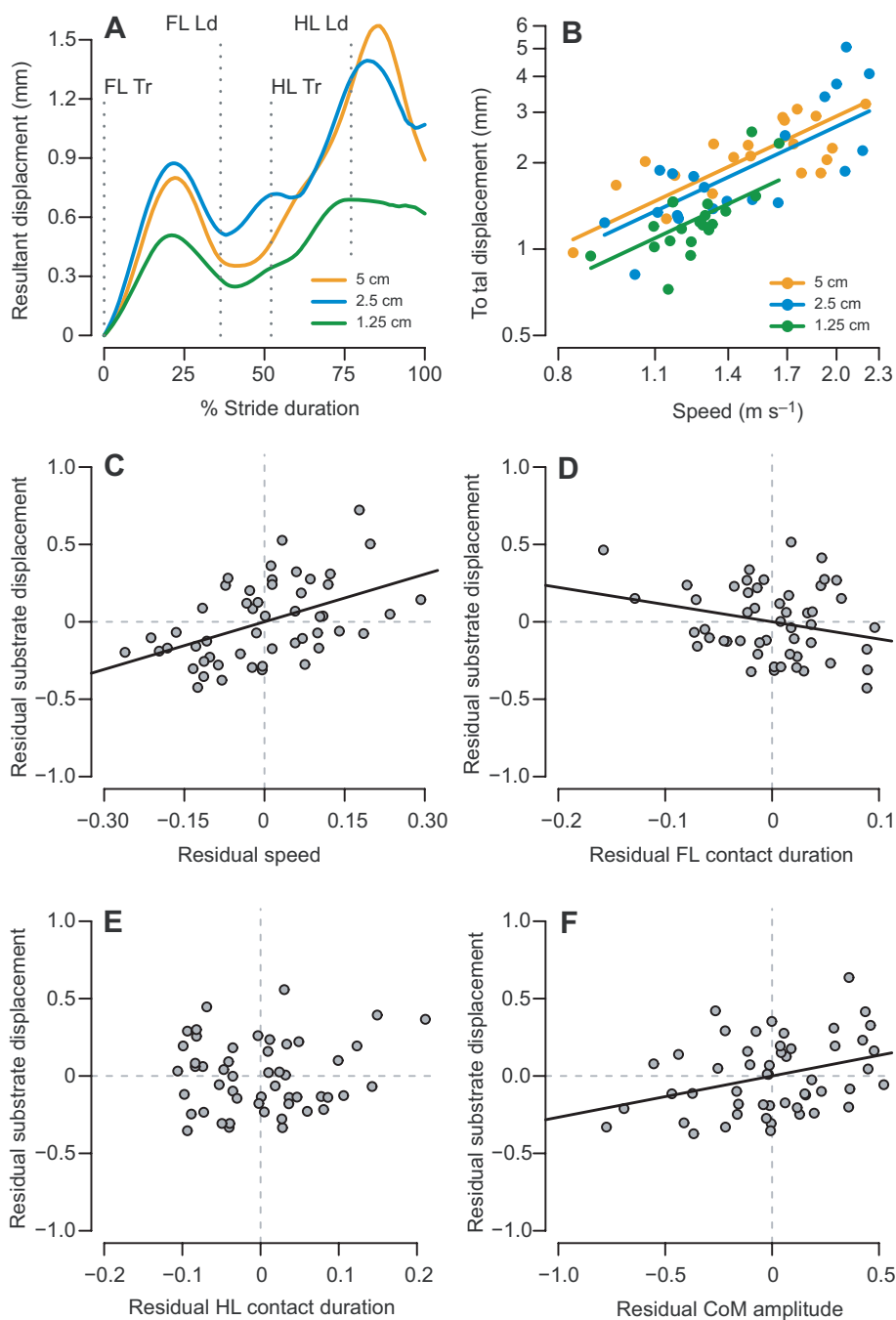
Fig. 8. Determinants of compliant substrate displacement across pole diameters. (A) Average resultant displacement of the compliant pole midpoint as a function of normalized stride duration. (B) log–log scatterplot of total substrate displacement against speed. (C) Partial regression plot of log substrate displacement versus log speed, controlling for log relative forelimb contact duration, log relative hindlimb contact duration and log CoM height amplitude. (D) Partial regression plot of log substrate displacement versus log relative forelimb contact duration, controlling for log speed, log relative hindlimb contact duration and log CoM height amplitude. (E) Partial regression plot of log substrate displacement versus log relative hindlimb contact duration, controlling for log speed, log relative forelimb contact duration and log CoM height amplitude. (F) Partial regression plot of log substrate displacement versus log CoM height amplitude, controlling for log speed, log relative forelimb contact duration and log relative hindlimb contact duration. Trend lines in B–D and F indicate reduced maximum likelihood fits from mixed-effects ANCOVA models.

relative contact duration during locomotion on the pole. Similar kinematic adjustments have been documented in studies of squirrels (Schmidt, 2011) and mouse lemurs (Shapiro et al., 2016) using asymmetrical gaits on flat versus narrow substrates, and several studies have found a general tendency to increase substrate contact duration on cylindrical supports (Schmitt, 1999; Lemelin and Cartmill, 2010; Schmidt and Fischer, 2010; Shapiro and Young, 2012; Shapiro et al., 2014; Karantanis et al., 2015; Hsieh, 2016). In contrast, differences in gait kinematics among variably sized cylindrical substrates are generally subtler (Schmitt, 2003a; Shapiro and Young, 2010; Hyams et al., 2012; Hsieh, 2016) – as was observed in the current study. Overall, changing substrate type (i.e. flat versus cylindrical) appears to require greater adjustment to quadrupedal gait kinematics than changing substrate size within a

type. Nevertheless, understanding the subtle mechanical differences that facilitate differential locomotor performance within arboreal environments is a critical step in structuring hypotheses of adaptive locomotor evolution in primates and other tree-living animals (Cartmill, 1972; Sinervo and Losos, 1991; Orkin and Pontzer, 2011).

Influence of substrate compliance on gait kinematics
Theory and empirical data suggest that branch compliance should have pronounced effects on the mechanics of arboreal locomotion (Alexander, 1991; Bonser, 1999). Specifically, compliant substrates absorb some of the mechanical work that would be otherwise employed to redirect and accelerate the CoM during steady locomotion, and compromise stability by undermining the

Table 2. Influence of gait parameters on compliant substrate displacement

Parameter	Coefficient[1]	ΔAIC[2]	P-value[3]
Pearson product-moment correlations			
log speed	0.767	–	**<0.001**
log forelimb duty factor	−0.680	–	**<0.001**
log hindlimb duty factor	−0.723	–	**<0.001**
log relative forelimb lead interval	−0.377	–	**0.003**
log relative hindlimb lead interval	−0.670	–	**<0.001**
log relative forelimb contact duration	−0.778	–	**<0.001**
log relative hindlimb contact duration	−0.752	–	**<0.001**
log CoM displacement	0.609	–	**<0.001**
Multiple regression model			
log speed	0.923	11.3	**<0.001**
log relative forelimb contact duration	−2.10	4.80	**0.010**
log relative hindlimb contact duration	0.837	1.22	0.066
log CoM displacement	0.244	4.21	**0.019**

[1] Either the correlation coefficient or the partial regression coefficient is shown, depending on the test.
[2] The increase in Akaike information criterion (AIC) is given, relative to the full model. A lower AIC indicates a better model fit for the given dataset.
[3] P-values from correlation tests were adjusted using the false discovery rate method (Benjamini and Hochberg, 1995) to adjust for multiple simultaneous comparisons. Significant tests following adjustment are indicated in bold.

animal's ability to estimate body orientation (MacLellan and Patla, 2006).

Previous research has shown that increasing branch compliance significantly compromises the locomotor performance of leaping primates (Crompton et al., 1993; Demes et al., 1995; Warren and Crompton, 1997; Walker, 2005; Channon et al., 2011) and lizards (Gilman et al., 2012; Gilman and Irschick, 2013), and necessitates numerous postural and locomotor adjustments in orangutans (Thorpe et al., 2009; Myatt and Thorpe, 2011). However, relative to the breadth of research on the effects of substrate diameter, studies of how perch compliance affects quadrupedal gait mechanics are sparse (but see Stevens et al., 2001; Gosselin-Ildari, 2010). Nevertheless, field observations of wild primates indicate that natural substrates are frequently compliant and move during quadrupedal locomotor activity (e.g. Morbeck, 1977; Boinski, 1989).

We predicted that marmosets moving over compliant substrates would make kinematic adjustments in a manner consistent with reducing peak force magnitudes and mitigating fluctuations in CoM position. We found that increased substrate compliance was associated with greater hindlimb duty factor, increased relative hindlimb lead interval and longer overall forelimb and hindlimb contact duration. Similarly, squirrel monkeys moving on branches in the wild use higher duty factors than when moving on similarly sized (stable) substrates in the lab (Shapiro et al., 2011), perhaps as a result of the greater compliance of the branches. Controlling for speed, increasing substrate contact duration will necessarily reduce peak force magnitude (McMahon et al., 1987; Schmitt, 1999), theoretically mitigating substrate displacement and facilitating greater stability. Indeed, we found that total substrate displacement over a stride was inversely proportional to duty factor and relative contact duration (Table 2), suggesting that marmosets were modulating contact times in order to promote stability. However, it is also possible to interpret the relationship between contact duration and substrate displacement in reverse. Given that compliant substrates absorb some of the mechanical work required to move and redirect the CoM (Alexander, 1991; Bonser, 1999), and that marmosets were nevertheless able to

maintain overall speed, increased substrate contact duration may have been required in order to generate sufficient impulse to compensate for the loss of mechanical work. Testing between these interpretations would require quantitative analyses of marmosets moving over stable and compliant substrates instrumented with a series of strain gauge-based force poles.

Differences in substrate compliance had very little effect on CoM kinematics. Marmosets slightly reduced average CoM height when moving on the two larger diameter substrates, though the magnitude of the difference varied according to speed. Fluctuations in CoM height were unrelated to the level of substrate compliance. Similarly, humans hopping and running on unexpectedly compliant surfaces compensate for these perturbations by producing sufficient negative or positive mechanical work to ensure a continuous, unaltered trajectory of the CoM (Ferris and Farley, 1997; Farley et al., 1998; Ferris et al., 1998; Ferris et al., 1999; Kerdok et al., 2002; Moritz and Farley, 2003, 2004, 2006). Curiously, walking humans do not compensate for changes in surface stiffness, allowing the CoM to sink with each successive step on the compliant surface. It may be that the different responses of running humans and walking humans are due to basal differences in the underlying CoM mechanics of the two gaits (i.e. spring-mass mechanics during running versus inverted pendulum mechanics during walking; Marigold and Patla, 2005; MacLellan and Patla, 2006). Inasmuch as inverted pendulum and spring-mass mechanics are common across legged vertebrates (Cavagna et al., 1977; Heglund et al., 1982; Farley and Ko, 1997), quadrupedal animals may also alter CoM trajectories when walking, but not running, on compliant substrates. However, given that the marmosets in this study chiefly used high-speed asymmetrical gaits, we were unable to test this hypothesis.

We found the adjustment to a small number of kinematic parameters (i.e. speed, relative forelimb and hindlimb contact durations and CoM height amplitude) was able to explain >60% of the variance in substrate displacement when the marmosets were moving on the compliant substrate. Substrate displacement decreased when marmosets increased relative forelimb contact duration, dampened CoM fluctuations and moved more slowly. As discussed above, using longer contact durations and decreasing speed should both result in a reduction of peak force magnitude. Given that the compliant platform behaved as a linear spring, reducing applied force should necessarily reduce substrate displacement as well. Curiously, controlling for speed, CoM displacement, and relative forelimb contact duration, we found a slight positive (though non-significant) relationship between relative hindlimb contact duration and substrate displacement. This counterintuitive association may be due to the fact that hindlimb loading occurs during the period near the end of the stride when the substrate is undergoing its greatest displacement (Fig. 8A), most of which is the cumulative effect of mechanical interactions happening prior to hindlimb contact. At this point in the stride, adjusting hindlimb mechanics may have very little effect on substrate movement.

Finally, it is interesting to note that total substrate displacement was significantly lower on the smallest substrate (even controlling for the effects of speed; Fig. 8B), despite the fact that the effective mass of the 1.25 cm diameter substrate was 22% lower than that of the 2.5 cm substrate and 44% lower than that of the 5 cm substrate (Table 1). The lower effective mass of the small substrate equates to less inertia and, provided loading magnitudes are unchanged, greater displacement. The reduced movement of the small support therefore suggests an interaction between support size and compliance, indicating that marmosets were actively adjusting

gait mechanics to limit perturbations on the most precarious substrate.

Limitations

The sample size for this study was necessarily limited by the logistical difficulties of obtaining and housing non-human primates. Though we made efforts to generate a robust sample of strides (i.e. N=60/individual), the low number of individuals has the potential to bias results, particularly in cases where the two individuals differed in their response. Intraclass correlation coefficients (ICCs – the proportion of total variance accounted for by interindividual differences) were generally low in our dataset, with most values falling below 0.5 (i.e. 6/10), and a median ICC of 0.3685 across all the variables tested (see Tables S1–S6). Nevertheless, ICCs for some variables, such as speed and CoM height, were quite high (0.638 and 0.786, respectively). As discussed in Materials and methods, 'Statistical methods', we explicitly used hierarchical mixed-effects modeling as a means of controlling for interindividual variance when testing our fixed effects. In this respect, our analyses were equivalent to a repeated measures design, testing how substrate diameter and compliance influenced the locomotor performance of each individual monkey. Future studies should carry out similar analyses in arboreal taxa that are more readily sampled (e.g. *Anolis* lizards). Nevertheless, for questions about arboreal adaptation in quadrupedal mammals, primates – a radiation defined by their nearly ubiquitous exploitation of the arboreal habitat – are arguably the most appropriate group to study.

Conclusions

The goal of this study was to investigate the independent and interacting influence of support size and support compliance on marmoset gait kinematics. We found some similarities in how marmosets responded to perturbations in diameter and compliance. For instance, narrowing diameter and increasing compliance were both associated with increased substrate contact duration. Adjustments to substrate contact duration were more pronounced for the hindlimb than the forelimb, perhaps because of the greater role of the hindlimbs in impulse production and propulsion during asymmetrical gaits (Hildebrand, 1980; Bertram and Gutmann, 2009). However, there were also significant differences in the marmosets' responses to perturbations in diameter and compliance. Overall, kinematic adjustments to changes in substrate compliance were more consistent than those associated with changes in diameter. In response to narrowing substrate diameter, many of the adjustments to substrate contact variables were inconsistent across changes in speed and of limited significance in *post hoc* pairwise analyses. Conversely, adjustments to CoM kinematics were more salient in response to changing diameter than changing compliance levels.

As discussed above, whereas several previous studies of locomotor performance in arboreal quadrupeds have concentrated on the effects of support diameter, the effects of support compliance have received very little attention. In this study, we showed that (1) increased perch compliance necessitates several adjustments to marmoset gait kinematics and (2) in many cases, these adjustments are independent of, and more consistent than, adjustments associated with narrowing perch diameter. Furthermore, we showed that compliance exerts a significant influence on gait kinematics despite a rather conservative level of perturbation. Further studies employing substrates with greater levels of compliance may find even more drastic adjustments are required.

Future studies of arboreal locomotor performance, particularly those concentrating on the biological role of purported locomotor 'adaptations' – whether morphological (e.g. grasping hands and feet) or behavioral (e.g. the use of distinctive footfall phasings, or patterns of weight support) – should consider the functional importance of support compliance, rather than simply diameter. This is particularly true for functional studies investigating models of primate locomotor evolution. Because the fine-branch environment has often been cited as the fundamental niche of early primates (e.g. Cartmill, 1972; Rasmussen, 1990; Sussman et al., 2013), investigating the precise mechanical demands of moving on supports that are both narrow and compliant is critical to understanding primate locomotor adaptation and evolution.

Author contributions
J.W.Y. and B.A.C. designed the experiment and collected the data; B.A.C. and B.M.S. analyzed the data; J.W.Y. and B.A.C. drafted the manuscript.

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Table S1. Influence of support diameter and substrate compliance on log-transformed speed.

Term	Mean Difference	Statistic	*P*-value
Overall ANOVA			
Diameter	--	$F_{[2,115]} = 23.9$	**<0.001**
Compliance	--	$F_{[1,115]} = 2.54$	NS
Diameter-Compliance interaction	--	--	NS
Within-individual intraclass correlation	--	0.638	--
Pairwise comparisons - Diameter			
5 cm – 2.5 cm	0.023 ms^{-1}	$t_{[115]} = 0.722$	NS
5 cm – 1.25 cm	0.197 ms^{-1}	$t_{[115]} = 6.31$	**<0.001**
2.5 cm – 1.25 cm	0.174 ms^{-1}	$t_{[115]} = 5.59$	**<0.001**

To control for multiple simultaneous comparisons, *p*-values for post hoc comparisons were adjusted using the false discovery rate method (Benjamini and Hochberg, 1995). Significant tests following adjustment are indicated by bold typeface**.**

Table S2. Influence of support diameter and substrate compliance on log-transformed duty factor, including log-transformed speed as a covariate.

Term	Mean Difference	Statistic	*P*-value
Forelimb Duty Factor			
Overall ANOVA			
Diameter	--	$F_{[2,107]} = 1.19$	NS
Compliance	--	$F_{[1,107]} = 7.13$	**0.009**
Speed	--	$F_{[1,107]} = 32.1$	**<0.001**
Diameter-Compliance interaction	--	$F_{[2,107]} = 3.04$	NS
Speed-Diameter interaction	--	$F_{[2,107]} = 1.56$	NS
Speed-Compliance interaction	--	$F_{[1,107]} = 2.67$	NS
Speed-Diameter-Compliance interaction	--	$F_{[2,107]} = 4.20$	**0.018**
Within-individual intraclass correlation	--	0.539	--
Pairwise comparisons - Diameter			
Minimum common speed – Stable substrate			
5 cm – 2.5 cm	-0.127	$t_{[107]} = -1.53$	NS
5 cm – 1.25 cm	-0.041	$t_{[107]} = -0.628$	NS
2.5 cm – 1.25 cm	-0.086	$t_{[107]} = -1.08$	NS
Maximum common speed – Stable substrate			
5 cm – 2.5 cm	-0.003	$t_{[107]} = -0.141$	NS
5 cm – 1.25 cm	-0.097	$t_{[107]} = -2.17$	NS
2.5 cm – 1.25 cm	-0.093	$t_{[107]} = -2.09$	NS
Minimum common speed – Compliant substrate			
5 cm – 2.5 cm	0.110	$t_{[107]} = 2.48$	**0.044**
5 cm – 1.25 cm	0.076	$t_{[107]} = 1.51$	NS
2.5 cm – 1.25 cm	-0.034	$t_{[107]} = -0.71$	NS
Maximum common speed – Compliant substrate			
5 cm – 2.5 cm	-0.063	$t_{[107]} = -2.56$	**0.018**
5 cm – 1.25 cm	-0.112	$t_{[107]} = -2.75$	**0.018**
2.5 cm – 1.25 cm	-0.049	$t_{[107]} = -1.21$	NS
Pairwise comparisons - Compliance			
Minimum common speed – 5 cm diameter			
Stable - Compliant	-0.152	$t_{[107]} = -2.58$	**0.011**
Maximum common speed – 5 cm diameter			
Stable - Compliant	-0.052	$t_{[107]} = -2.18$	**0.031**
Minimum common speed – 2.5 cm diameter			
Stable - Compliant	0.086	$t_{[107]} = 1.14$	NS
Maximum common speed – 2.5 cm diameter			
Stable - Compliant	-0.111	$t_{[107]} = -4.37$	**<0.001**
Minimum common speed – 1.25 cm diameter			
Stable - Compliant	-0.035	$t_{[107]} = -0.606$	NS
Maximum common speed – 1.25 cm diameter			
Stable - Compliant	-0.067	$t_{[107]} = -1.23$	NS

To control for multiple simultaneous comparisons, *p*-values for post hoc comparisons were adjusted using the false discovery rate method (Benjamini and Hochberg, 1995). Significant tests following adjustment are indicated by bold typeface.

Table S2 (continued). Influence of support diameter and substrate compliance on log-transformed duty factor, including log-transformed speed as a covariate.

Term	Mean Difference	Statistic	P-value
Hindlimb Duty Factor			
Overall ANOVA			
Diameter	--	$F_{[2,112]} = 5.44$	**0.006**
Compliance	--	$F_{[1,112]} = 8.28$	**0.005**
Speed	--	$F_{[1,112]} = 198$	**<0.001**
Diameter-Compliance interaction	--	--	NS
Speed-Diameter interaction	--	$F_{[2,112]} = 9.33$	**<0.001**
Speed-Compliance interaction	--	--	NS
Speed-Diameter-Compliance interaction	--	--	NS
Within-individual intraclass correlation	--	0.015	--
Pairwise comparisons - Diameter			
Minimum common speed			
5 cm – 2.5 cm	0.112	$t_{[112]} = 2.81$	**0.009**
5 cm – 1.25 cm	0.132	$t_{[112]} = 3.22$	**0.005**
2.5 cm – 1.25 cm	0.020	$t_{[112]} = 0.490$	NS
Maximum common speed – Compliant substrate			
5 cm – 2.5 cm	-0.028	$t_{[112]} = -1.60$	NS
5 cm – 1.25 cm	-0.095	$t_{[112]} = -3.15$	**0.006**
2.5 cm – 1.25 cm	-0.067	$t_{[112]} = -2.21$	**0.044**
Pairwise comparisons - Compliance			
Stable - Compliant	-0.038	$t_{[112]} = -2.88$	**0.005**

To control for multiple simultaneous comparisons, *p*-values for post hoc comparisons were adjusted using the false discovery rate method (Benjamini and Hochberg, 1995). Significant tests following adjustment are indicated by bold typeface.

Table S3. Mixed-effects analysis of the influence of support diameter and substrate compliance on relative lead interval, including log-transformed speed as a covariate.

Term	Mean Difference	Statistic	*P*-value
Relative forelimb lead interval			
Overall ANOVA			
Diameter	--	$F_{[2,100]} = 0.263$	NS
Compliance	--	$F_{[1,100]} = 1.43$	NS
Speed	--	$F_{[1,100]} = 0.410$	NS
Diameter-Compliance interaction	--	--	NS
Speed-Diameter interaction	--	--	NS
Speed-Compliance interaction	--	--	NS
Speed-Diameter-Compliance interaction	--	--	NS
Within-individual intraclass correlation	--	0.328	--
Relative hindlimb lead interval			
Overall ANOVA			
Diameter	--	$F_{[1,100]} = 12.0$	**<0.001**
Compliance	--	$F_{[2,100]} = 6.70$	**0.011**
Speed	--	$F_{[1,100]} = 19.0$	**<0.001**
Diameter-Compliance interaction	--	--	NS
Speed-Diameter interaction	--	--	NS
Speed-Compliance interaction	--	--	NS
Speed-Diameter-Compliance interaction	--	--	NS
Within-individual intraclass correlation	--	0.533	--
Pairwise comparisons - Diameter			
5 cm – 2.5 cm	-0.022	$t_{[100]} = -1.47$	NS
5 cm – 1.25 cm	-0.033	$t_{[100]} = -1.71$	NS
2.5 cm – 1.25 cm	-0.011	$t_{[100]} = -0.583$	NS
Pairwise comparisons - Compliance			
Stable - Compliant	-0.026	$t_{[100]} = -2.04$	**0.045**

To control for multiple simultaneous comparisons, *p*-values for post hoc comparisons were adjusted using the false discovery rate method (Benjamini and Hochberg, 1995). Significant tests following adjustment are indicated by bold typeface**.**

Table S4. Influence of support diameter and substrate compliance on log-transformed relative contact duration, including log-transformed speed as a covariate.

Term	Mean Difference	Statistic	*P*-value
Relative forelimb contact duration			
Overall ANOVA			
Diameter	--	$F_{[2,100]} = 31.1$	**<0.001**
Compliance	--	$F_{[1,100]} = 11.9$	**<0.001**
Speed	--	$F_{[1,100]} = 92.8$	**<0.001**
Diameter-Compliance interaction	--	--	NS
Speed-Diameter interaction	--	--	NS
Speed-Compliance interaction	--	--	NS
Speed-Diameter-Compliance interaction	--	--	NS
Within-individual intraclass correlation	--	0	--
Pairwise comparisons - Diameter			
5 cm – 2.5 cm	-0.016	$t_{[100]} = -0.786$	NS
5 cm – 1.25 cm	-0.076	$t_{[100]} = -3.35$	**0.004**
2.5 cm – 1.25 cm	-0.060	$t_{[100]} = -2.73$	**0.011**
Pairwise comparisons - Compliance			
Stable - Compliant	-0.047	$t_{[100]} = -2.82$	**0.006**
Relative hindlimb contact duration			
Overall ANOVA			
Diameter	--	$F_{[2,98]} = 36.6$	**<0.001**
Compliance	--	$F_{[1,98]} = 18.2$	**<0.001**
Speed	--	$F_{[1,98]} = 105$	**<0.001**
Diameter-Compliance interaction	--	--	NS
Speed-Diameter interaction	--	$F_{[2,98]} = 5.62$	**0.005**
Speed-Compliance interaction	--	--	NS
Speed-Diameter-Compliance interaction	--	--	NS
Within-individual intraclass correlation	--	0.258	--
Pairwise comparisons - Diameter			
Minimum common speed			
5 cm – 2.5 cm	0.218	$t_{[98]} = 2.62$	**0.031**
5 cm – 1.25 cm	0.115	$t_{[98]} = 0.998$	NS
2.5 cm – 1.25 cm	-0.104	$t_{[98]} = -0.955$	NS
Maximum common speed			
5 cm – 2.5 cm	-0.074	$t_{[98]} = -2.32$	NS
5 cm – 1.25 cm	-0.087	$t_{[98]} = -1.28$	NS
2.5 cm – 1.25 cm	-0.013	$t_{[98]} = -0.193$	NS
Pairwise comparisons - Compliance			
Stable - Compliant	-0.080	$t_{[98]} = -3.111$	**0.002**

To control for multiple simultaneous comparisons, *p*-values for post hoc comparisons were adjusted using the false discovery rate method (Benjamini and Hochberg, 1995). Significant tests following adjustment are indicated by bold typeface.

Table S5. Influence of support diameter and substrate compliance on average log-transformed CoM height and total COM height amplitude, relative the substrate surface, including log-transformed speed as a covariate.

Term	Mean Difference	Statistic	P-value
CoM height			
Overall ANOVA			
Diameter	--	$F_{[1,107]} = 19.2$	**<0.001**
Compliance	--	$F_{[2,107]} = 9.40$	**0.003**
Speed	--	$F_{[1,107]} = 73.8$	**<0.001**
Diameter-Compliance interaction	--	$F_{[2,107]} = 4.80$	**0.010**
Speed-Diameter interaction	--	$F_{[2,107]} = 0.535$	NS
Speed-Compliance interaction	--	$F_{[1,107]} = 9.75$	**0.002**
Speed-Diameter-Compliance interaction	--	$F_{[2,107]} = 12.8$	**<0.001**
Within-individual intraclass correlation	--	0.786	--
Pairwise comparisons - Diameter			
Minimum common speed – Stable substrate			
5 cm – 2.5 cm	0.109	$t_{[107]} = 3.21$	**0.004**
5 cm – 1.25 cm	0.082	$t_{[107]} = 3.10$	**0.004**
2.5 cm – 1.25 cm	-0.027	$t_{[107]} = -0.833$	0.407
Maximum common speed – Stable substrate			
5 cm – 2.5 cm	-0.025	$t_{[107]} = -2.50$	**0.041**
5 cm – 1.25 cm	0.011	$t_{[107]} = 0.629$	NS
2.5 cm – 1.25 cm	0.037	$t_{[107]} = 2.02$	NS
Minimum common speed – Compliant substrate			
5 cm – 2.5 cm	-0.086	$t_{[107]} = -4.75$	**<0.001**
5 cm – 1.25 cm	-0.070	$t_{[107]} = -3.42$	**0.001**
2.5 cm – 1.25 cm	0.016	$t_{[107]} = 0.811$	NS
Maximum common speed – Compliant substrate			
5 cm – 2.5 cm	-0.013	$t_{[107]} = -1.27$	NS
5 cm – 1.25 cm	-0.020	$t_{[107]} = -1.18$	NS
2.5 cm – 1.25 cm	-0.007	$t_{[107]} = -0.414$	NS
Pairwise comparisons - Compliance			
Minimum common speed – 5 cm diameter			
Stable - Compliant	0.149	$t_{[107]} = 6.22$	**<0.001**
Maximum common speed – 5 cm diameter			
Stable - Compliant	0.011	$t_{[107]} = 1.13$	NS
Minimum common speed – 2.5 cm diameter			
Stable - Compliant	-0.046	$t_{[107]} = -1.51$	NS
Maximum common speed – 2.5 cm diameter			
Stable - Compliant	0.024	$t_{[107]} = 2.28$	**0.026**
Minimum common speed – 1.25 cm diameter			
Stable - Compliant	-0.003	$t_{[107]} = -0.128$	NS
Maximum common speed – 1.25 cm diameter			
Stable - Compliant	-0.020	$t_{[107]} = -0.903$	NS

To control for multiple simultaneous comparisons, *p*-values for post hoc comparisons were adjusted using the false discovery rate method (Benjamini and Hochberg, 1995). Significant tests following adjustment are indicated by bold typeface**.**

Table S5 (continued). Influence of support diameter and substrate compliance on average log-transformed CoM height and total COM height amplitude, relative the substrate surface, including log-transformed speed as a covariate.

Term	Mean Difference	Statistic	*P*-value
CoM height amplitude			
Overall ANOVA			
Diameter	--	$F_{[2,114]} = 11.2$	**<0.001**
Compliance	--	$F_{[2,114]} = 1.75$	NS
Speed	--	$F_{[1,114]} = 2.07$	NS
Diameter-Compliance interaction	--	--	NS
Speed-Diameter interaction	--	--	NS
Speed-Compliance interaction	--	--	NS
Speed-Diameter-Compliance interaction	--	--	NS
Within-individual intraclass correlation	--	0.409	--
Pairwise comparisons - Diameter			
5 cm – 2.5 cm	0.153 cm	$t_{[114]} = 2.18$	**0.046**
5 cm – 1.25 cm	0.272 cm	$t_{[114]} = 3.36$	**0.003**
2.5 cm – 1.25 cm	0.119 cm	$t_{[114]} = 1.51$	NS

To control for multiple simultaneous comparisons, *p*-values for post hoc comparisons were adjusted using the false discovery rate method (Benjamini and Hochberg, 1995). Significant tests following adjustment are indicated by bold typeface.

Table S6. Influence of substrate diameter on the log-transformed displacement of the compliant substrate displacement during a stride, including log-transformed speed as a covariate.

Term	Mean Difference	Statistic	*P*-value
Overall ANOVA			
Diameter	--	$F_{[2,55]} = 7.17$	**0.001**
Speed		$F_{[1,55]} = 68.4$	**<0.001**
Speed-Diameter interaction	--	--	NS
Within-individual intraclass correlation	--	0	--
Pairwise comparisons - Diameter			
5 cm – 2.5 cm	0.082 mm	$t_{[55]} = 1.07$	NS
5 cm – 1.25 cm	0.297 mm	$t_{[55]} = 3.69$	**0.002**
2.5 cm – 1.25 cm	0.215 mm	$t_{[55]} = 2.70$	**0.014**

To control for multiple simultaneous comparisons, *p*-values for post hoc comparisons were adjusted using the false discovery rate method (Benjamini and Hochberg, 1995). Significant tests following adjustment are indicated by bold typeface**.**

Table S7.

Click here to Download Table S7

Movie S1. High-speed video and animated reconstruction of an exemplar stride of marmoset locomotion over the compliant 5 cm diameter support (slowed to 3% of actual speed). In the animated reconstruction, the compliant pole segment is indicated in yellow. The red star in the center of the wireframe model of the marmoset indicates the estimated position of the center of mass.