Received: 6 July 2023 | Revised: 2 February 2024 | Accepted: 9 February 2024

DOI: 10.1002/ajpa.24917

RESEARCH ARTICLE

AMERICAN JOURNAL OF BIOLOGICAL ANTHROPOLOGY
The Official Journal of the American Association of Biological Anthropologists
WILEY

From such great heights: The effects of substrate height and the perception of risk on lemur locomotor mechanics

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Funding information
Division of Behavioral and Cognitive Sciences, Grant/Award Numbers: 1640453, 1640552, 1921135, 1921314, 2316841

Abstract

Objectives: An accident during arboreal locomotion can lead to risky falls, but it remains unclear that the extent to which primates, as adept arborealists, change their locomotion in response to the perceived risk of moving on high supports in the tree canopy. By using more stable forms of locomotion on higher substrates, primates might avoid potentially fatal consequences.

Materials and Methods: Using high-speed cameras, we recorded the quadrupedal locomotion of four wild lemur species—*Eulemur rubriventer*, *Eulemur rufifrons*, *Hapalemur aureus, and Lemur catta* ($N = 113$ total strides). We quantified the height, diameter, and angular orientation of locomotor supports using remote sensors and tested the influence of support parameters on gait kinematics, specifically predicting that in response to increasing substrate height, lemurs would decrease speed and stride frequency, but increase stride length and the mean number of supporting limbs.

Results: Lemurs did not adjust stride frequency on substrates of varying height. Adjustments to speed, stride length, and the mean number of supporting limbs in response to varying height often ran counter to predictions. Only *E. rubriventer* decreased speed and increased the mean number of supporting limbs on higher substrates.

Discussion: Results suggest that quadrupedal walking is a relatively safe form of locomotion for lemurs, requiring subtle changes in gait to increase stability on higher—that is, potentially riskier—substrates. Continued investigation of the impact of height on locomotion will be important to determine how animals assess risk in their environment and how they choose to use this information to move more safely.

KEYWORDS
arboreality, cognition, kinematics, primate locomotion

1 | INTRODUCTION

Arboreal environments are complex matrices of substrates that vary in diameter, obliquity, compliance, and connectedness. Many studies on arboreal locomotion have connected the biomechanical challenges posed by these physical characteristics to potential locomotor and morphological adaptations that increase stability and survival (e.g., Cartmill et al., 2002; Larson, 2018; Larson et al., 2000;

Schmitt, 1999; Shapiro et al., 2014, 2016; Shapiro & Young, 2010; Young & Chadwell, 2020). The present study proposes that adding another physical characteristic of locomotor substrates—their height above the ground—could shed light on the types of information primates gather and process to make locomotion less risky.

Unlike diameter, obliquity, compliance, or connectedness—substrate properties which can be seen and touched—substrate height is only judged visually. "Visual cliff" studies affirm the importance of height perception for safe locomotion (Gibson & Walk, 1960). In these studies, animals are placed on a ledge and encouraged to cross a platform made of glass, or from the subject's perspective, encouraged to step over an apparent cliff. The common pattern of infant and juvenile animals refusing to cross an apparent chasm suggests sensitivity to height is an important conserved trait among various species (Adolph et al., 2014). Indeed, in a visual cliff study done with neonatal rhesus macaques (*Macaca mulatta*), monkeys responded to heights as early as 3 days after birth, a level of precociality that the authors attributed to primate arboreality (Rosenblum & Cross, 1963). This study focuses on how adult primates may respond to perceived risk while traveling at higher points in the tree canopy.

Including approximate height measurements have been standard in primate locomotor studies for decades, but these studies tend to use height to broadly describe different canopy usage of conspecific primate taxa (Cannon & Leighton, 1994; Fleagle & Mittermeier, 1980; McGraw, 1996, 1998; McLean et al., 2016; Off & Gebo, 2005; Palminteri et al., 2012) or the preference for certain forest structures while animals engage in particular locomotor patterns (Cheyne et al., 2013; Fan et al., 2013; Garber & Pruetz, 1995; MacKinnon & MacKinnon, 1980; Walker, 2005). Moreover, such studies are methodologically limited for the purposes of understanding the moment-by-moment interaction of sensory systems, cognition, and locomotor output. Most often, the heights at which different bouts of locomotion occur are visually estimated within a given stratum (e.g., 0–10 m, 11–20 m, etc.; per Richards, 1952), though the use of LiDAR (light detection and ranging) has emerged recently to provide more accurate and detailed information about canopy structure (McLean et al., 2016; Palminteri et al., 2012). Advances in video recording for fine-grained locomotion analysis, coupled with the use of remote measurements of branch morphology, permit careful evaluation of how the perception of risk at increased substrate heights might affect locomotion on a stride-by-stride basis (Dunham et al., 2018).

Falling is the mechanism that makes height a potential selective pressure (Wheatley et al., 2021). The risk of injury or severity of injury should be greater at higher levels in the tree canopy because potential energy (PE) increases linearly with height ($PE = mgh$, where m is the body mass, g is the gravitational acceleration, and h is the height above the ground), but this risk is only actualized in the event of a fall. If a fall does not directly result in death, injuries may affect reproductive fitness of an individual through a loss in rank and reduced capacity for agile locomotion (Lovell, 1991). Fall rates in primates are, to our knowledge, yet to be systematically documented. Researchers studying the sympatric monkeys of Kibale National Park, Uganda, have discussed the contribution of falls to the inventory of injuries they documented (Arlet et al., 2009), and Struhsaker and Leakey (1990) reported witnessing several falls of red colobus monkeys (*Piliocolobus tephrosceles*), including three that were fatal. More substantively, in a study on 1672 primate skeletons, 223 individuals collectively had 300 fractures of their long bones attributed to falls (Jarrell, 2011). Fracture rates were similar across a broad sample of arboreal primates including representative strepsirrhines, platyrrhines, and catarrhines, though larger primates and primates who tend to live higher in the canopy had higher fracture rates of proximal limb elements (humerus or femur) than primates who are smaller or live lower in the tree canopy.

Regardless of the actual risk, animals may adjust their behavior in response to perceived risk. Using forms of locomotion that improve stability on arboreal substrates may reduce fall rates and therefore the risk of such fractures. One strategy to increase stability common among arboreal mammals is to reduce speed on more precarious substrates (e.g., Dunham et al., 2020; Gaschk et al., 2019; Karantanis et al., 2015; Lammers & Biknevicius, 2004; Shapiro et al., 2014; Young, 2023). Adjustments in speed may be variable (Shapiro et al., 2016), and increasing speed may reduce mediolateral fluctuations of the center of mass during locomotion (Young, 2023). Some studies have shown that, controlling for speed, animals may synchronously lengthen strides and decrease stride frequency, which is thought to decrease peak forces exerted on compliant arboreal substrates (Larson et al., 2000, 2001; Schmitt, 1999; Shapiro et al., 2014; Young, 2023), though this is not always consistent (Granatosky & McElroy, 2022; Karantanis et al., 2017; Schapker et al., 2022). Another strategy to improve stability is to increase net contact with the support. In this study, we focus on the mean number of supporting limbs and the constituent limb support configurations that this measure summarizes. The mean number of supporting limbs is a summary measure of the combined proportions of a stride where the body was supported by one, two, three, or four limbs, respectively. This measure is related to other spatiotemporal variables such as duty factor, defined as the relative duration of limb contact, and limb phase, a measure that describes the relative timing of footfalls within a stride. Stability should increase as the mean number of supporting limbs increases (Shapiro et al., 2014; Shapiro & Young, 2012), but where only two limbs are in contact with the substrate, contralateral limb stances should be more stable than ipsilateral ones, as the likelihood that the center of mass tips over the narrow support of a branch should decrease (Cartmill et al., 2002, 2007). Figure 1 depicts four moments in time during a stride captured from *L. catta*, illustrating how limb stances change over time during a gait cycle.

Here, we investigate the effect of substrate height in the canopy—that is, the vertical distance of a branch or liana from the ground—on the quadrupedal locomotion of four lemur species: *Eulemur rubriventer*, *E. rufifrons*, *Hapalemur aureus*, and *Lemur catta*. These lemurs are of similar mass; *H. aureus* is the smallest at a mean body mass of 1.75 kg while *E. rufifrons* is the largest at 2.25 kg (Fleagle, 2013). There are some notable morphological and ecological differences, however *H. aureus* engages in more vertical clinging and leaping as it navigates bamboo forest, and it has relatively longer hind limbs compared with *Eulemur* and *L. catta* (Glander et al., 1992). *L. catta* is more terrestrial than the other species (Ward & Sussman, 1979), but a study comparing *L. catta* and *E. rufifrons* (named

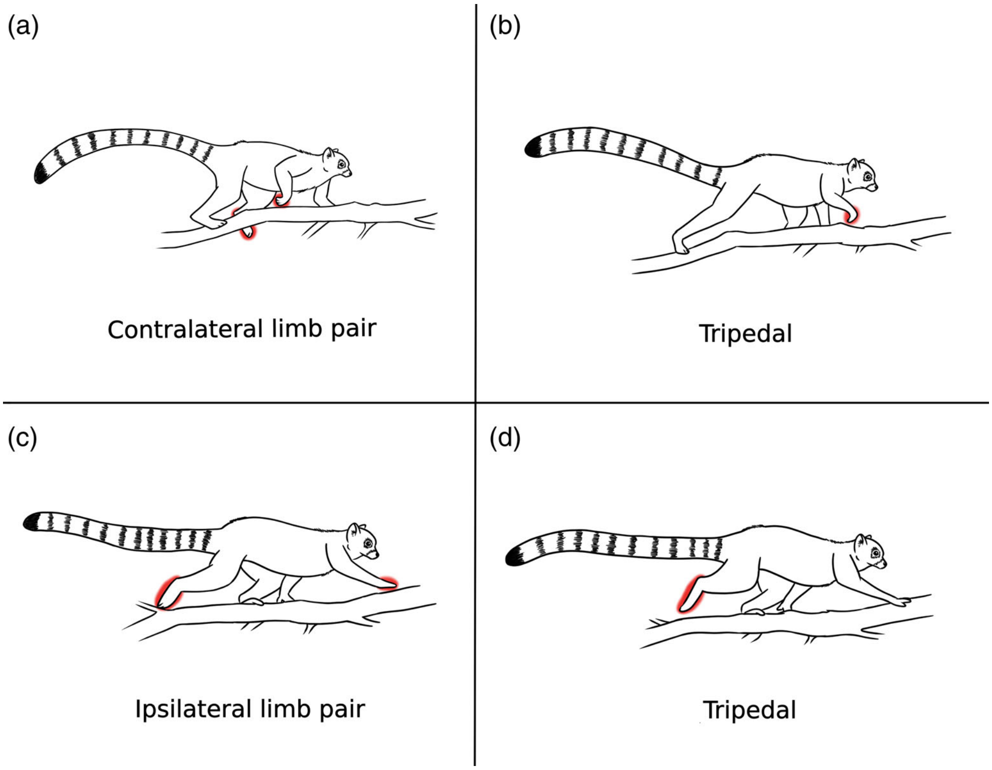

FIGURE 1 An illustrated representation of a video captured of *Lemur catta* walking. The panels sequentially represent the changes in limb stance configurations experienced during a stride. Hands and feet which are in swing phase (i.e., not in contact with the substrate) are highlighted in red for clarity. In this example, *L. catta* started in a contralateral limb pair stance (a). It transitioned to a tripedal stance (b). Next, it was momentarily supported in an ipsilateral limb pair stance (c) before returning to a tripedal stance again (d).

E. fulvus rufus in the study) showed that these two species made similar changes in gait when moving from terrestrial to arboreal substrates (Franz et al., 2005). Despite these differences in morphology and ecology, we predict that all four lemur species should adjust limb kinematics to maximize stability on arboreal substrates and should respond similarly to variation in substrate height.

Following from our hypothesis that lemurs should use more stable gait kinematics as substrate height and its potential for perceived risks increase, we expect the following predicted changes in locomotion. *Prediction 1*: as substrate height increases, lemurs should decrease speed and stride frequency while increasing stride length. *Prediction 2*: as substrate height increases, lemurs should increase the mean number of supporting limbs. Correspondingly, we also expect lemurs to decrease the frequency with which they use single limb stances, and where a pair of limbs support the body, ipsilateral limb pairs should decrease in frequency. *Prediction 3*: if there are differences in response to increasing substrate height among lemur species, *E. rubriventer* and *E. rufifrons* are expected to make the least exaggerated changes in locomotion as they represent more generalized quadrupedal arboreal primates (i.e., not specialized for vertical clinging and leaping, like *Hapalemur*, or terrestrial locomotion, like *Lemur*).

2 | MATERIALS AND METHODS

2.1 | Data collection

Free-ranging *E. rubriventer*, *E. rufifrons*, and *H. aureus* were studied at Ranomafana National Park, Madagascar, and *L. catta* was studied at the Anja Community Reserve, Madagascar. Data were collected from June–August 2022. Data collection methods followed the protocol outlined by Dunham et al. (2018). To summarize, lemur locomotion was recorded using modified Backbone GoPro Hero 10s (Back-bone, Ottawa, Ontario, Canada) equipped with a C-mount Fujinon HD 8–80 mm Vari-Focal CCTV lens (Fujifilm, Tokyo, Japan). Videos were recorded at 120fps and 1080p resolution. We remotely measured branch obliquity (reported relative to a horizontal line perpendicular to the axis of gravity, accuracy: +/− 2.5°) and key measurements needed to calculate branch diameter (accuracy: +/−1.5 mm) using a forestry-grade rangefinder (TruPulse 360R). The rangefinder operates by sending a laser pulse to the object of interest (in this case the branch or liana) and using the time necessary for that light to bounce back to calculate the distance from the instrument. The rangefinder reports the slope distance (the shortest possible distance between two points), as well as the horizontal and vertical distances that compose this vector. The support height above the ground was measured with the rangefinder by either standing directly under the support and adding the height of the measurement-taker (no horizontal distance, so slope and vertical distances are equal), or by recording the vertical distance between support and the ground level (accuracy: +/− 0.2 m). Videos were processed using the custom-developed program ClipStride (Dunham et al., 2018) to isolate single strides ($N = 113$, see Table 1 for strides recorded per species). Strides were identified as the successive touchdowns of a reference limb during a gait cycle. GaitKeeper (Dunham et al., 2018) was used to annotate individual frames, track footfalls, and calculate spatiotemporal gait metrics. Both programs were written in MATLAB (Mathworks, Natick, MA) and are available for download at www.younglaboratory.org. Table 2 summarizes the gait parameters analyzed in this study, their definitions, and the predicted changes as substrate height increases.

TABLE 1 Summary of number of strides and lowest and highest substrate heights recorded for each species.

Species	No. of strides	Lowest recorded substrate height (m)	Highest recorded substrate height (m)	Mean substrate height (m)
E. rubriventer	24	0.9	16.6	6.4
E. rufifrons	37	9.1	22.2	15.7
H. aureus	24	2.1	13.7	6.7
L. catta	28	0.5	9.2	4.0

TABLE 2 Predicted changes in gait in response to increased substrate height.

Gait property	Definition	Expected change on higher substrates
Relative speed	Product of stride frequency and relative stride length	Decrease
Stride frequency	The number of strides per second	Decrease
Relative stride length	The distance traveled between subsequent touchdowns of the reference limb, measured in body lengths	Increase
Mean number of supporting limbs	Average number of limbs contacting the support at any instance during the stride	Increase
Single limb stance	Instances in which the body is supported by only one limb that is contact with the substrate	Decrease
Ipsilateral limb pair stance	Instances in which the body is supported by a hind limb and a forelimb on the same side of the body	Decrease
Contralateral limb pair stance	Instances in which the body is supported by a hind limb and a forelimb on opposite sides of the body	Increase relative to ipsilateral limb pair stances
Tripedal stance	Instances in which the body is supported by three limbs in any configuration	Increase
Quadrupedal stance	Instances in which the body is supported by all four limbs	Increase

2.2 | Statistical analysis

Before statistical analysis, data were Box-Cox transformed to improve normality. First, a mixed effect ANOVA was used to determine if mean substrate heights were different across species. Next, Tukey's honestly significant difference (HSD) tests were run as a post hoc analysis to determine which species' means were statistically different ($\alpha = 0.05$).

We also ran mixed effects models to test whether support height had a significant effect on the defined gait parameters. Data were not pooled across species but instead used for within-species regression analysis only. The random factor for the models was the individual video clip, as individual animals were not identified. Most video clips contained one stride (average number of strides per video clip was 1.3), some had two or three, and the most was seven. In this particular case, the video captured the movements of four lemurs moving on different substrates. Substrate orientation, substrate diameter, and relative speed (except where speed was a dependent variable) were included as covariates. For each test, we first fit the full model, and then we used backward stepwise term elimination to discern which of our independent variables best predicted the variation in the data. Terms were sequentially eliminated until only significant ones remained. Because of increased variability expected in the quantitative analyses of unconstrained locomotion in natural environments, we recognized significance at $p \leq 0.1$. Data were processed and analyzed in R (version 4.2.2; R Core Team, 2022). Packages used to process raw data were plyr (Wickham, 2011) and dplyr (Wickham et al., 2023). Data visualization was done with ggplot2 (Wickham, 2016), and packages used for the linear models were lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017).

Two types of data categorization were used to understand the role of different limb stance types to overall body support. First, substrate heights were categorized as either high or low relative to their position around the median substrate height for that species. Second, in the high and low categories, we recorded the frequency with which strides contained each limb stance. Fisher's exact tests ($\alpha = 0.05$) were used to discern if these limb configurations occurred in different frequencies at these high or low points in the tree canopy.

3 | RESULTS

3.1 | Distribution of support heights

Heights at which individual strides were recorded are summarized in Figure 2. *E. rubriventer*, *H. aureus*, and *L. catta* were recorded at relatively low heights—mean 6.4, 6.7, and 4.0 m, respectively—compared with *E. rufifrons* at a mean height of 15.7 m (Table 1). The results of the Tukey HSD (Table 3) analysis indicate that the mean height of *E. rufifrons* was significantly greater than that of the other species ($p < 0.01$). The mean height of *L. catta* was also significantly lower than either *E. rubriventer* or *H. aureus* ($p \leq 0.024$).

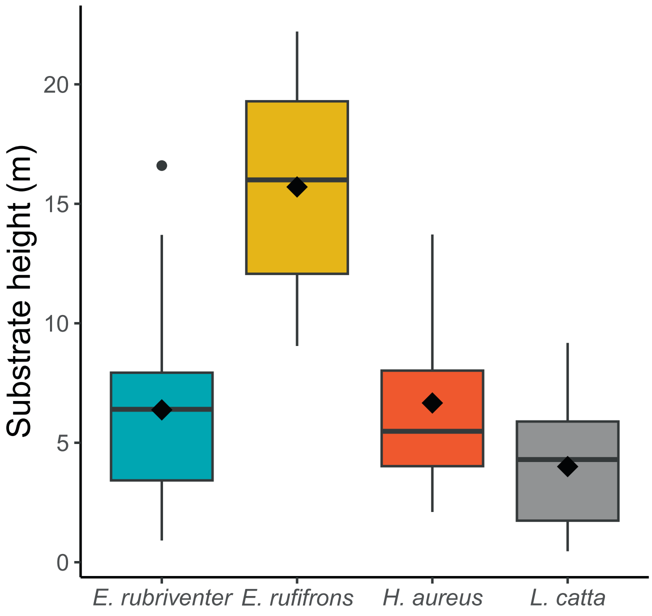

FIGURE 2 Box-and-whisker plot of measured substrate heights from recorded strides of each lemur species. The bolded black line is the median, and the box spans are the interquartile range. The means are indicated by the black diamonds.

TABLE 3 Results of Tukey HSD analysis comparing the mean substrate heights measured for each species.

Species pairwise comparison	Difference [95% CI]	*p*-value
E. rufifrons—*E. rubriventer*	1.4 [1.01, 1.87]	<0.001
E. rufifrons—*H. aureus*	1.3 [0.90, 1.76]	<0.001
E. rufifrons—*L. catta*	1.9 [1.54, 1.95]	<0.001
L. catta—*E. rubriventer*	−0.50 [−0.96, −0.05]	0.024
L. catta—*H. aureus*	−0.62 [−1.08, −0.16]	<0.01
H. aureus—*E. rubriventer*	0.11 [−0.36, 0.59]	Nonsignificant

Note: The mean difference between species is recorded, and the bounds of the 95% confidence interval are reported in brackets.

3.2 | Gait kinematics

3.2.1 | Relative speed

Lemurs changed relative speed in response to substrate properties (Table 4, Figure 3a). *E. rubriventer* decreased speed with increasing height ($p = 0.071$). *L. catta* and *H. aureus*, however, increased relative speed on higher substrates ($p \leq 0.052$) and on broader substrates ($p < 0.01$). Changes in relative speed also correlated with changes in substrate diameter in *L. catta* and *E. rufifrons*. Both increased relative speed on broader supports ($p \leq 0.054$).

3.2.2 | Relative stride length

Only *H. aureus* adjusted relative stride length in response to substrate height, decreasing stride length on higher substrates ($p = 0.042$, Table 5, Figure 3b). The other lemurs did not change relative stride length in response to substrate properties. For all species, relative stride length positively correlated with relative speed ($p < 0.001$).

3.2.3 | Stride frequency

No lemurs significantly adjusted stride frequency in response to substrate height (Table 6, Figure 3c). *E. rubriventer* increased stride frequency on broader substrates ($p = 0.075$), but the other species did not change stride frequency in response to substrate orientation or diameter. For all species, stride frequency positively correlated with relative speed ($p < 0.001$).

3.2.4 | Mean number of supporting limbs

Both *E. rubriventer* and *E. rufifrons* adjusted the mean number of supporting limbs on higher substrates, though they did so in opposing directions (Table 7, Figure 3d). *E. rubriventer* increased the mean number of supporting limbs on higher substrates ($p < 0.001$) whereas *E. rufifrons* decreased them ($p = 0.033$). *L. catta* and *H. aureus* did not adjust the mean number of supporting limbs in response to substrate properties. For all species, the mean number of supporting limbs negatively correlated with relative speed ($p < 0.027$).

3.2.5 | Limb stances

The frequencies of limb stances on low (below median) and high (above median) are reported in Table 8. Though Fisher's exact tests indicated that differences in limb support frequencies are not significant, we nonetheless observed subtle patterns that were in line with predicted responses to increasing substrate height. Contralateral limb pair and tripedal stances were the most common stances, occurring in all strides in the data set (frequency of 1 in Table 8). *E. rubriventer* was the sole species that increased the mean number of supporting limbs on higher substrates, and accordingly, the proportion of strides with single limb and ipsilateral limb pair stances decreased on high substrates while the proportion of quadrupedal stances increased. In *E. rufifrons*, strides containing single limb stances also decreased in frequency on high substrates while quadrupedal stances increased. Ipsilateral limb pair stances increased marginally in *E. rubriventer* on high substrates as well. Single limb stances increased in frequency when *H. aureus* and *L. catta* moved on high substrates, whereas use of ipsilateral limb pair stances decreased. Strides containing quadrupedal stances decreased on high substrates in *H. aureus*, but *L. catta* did not change the frequency with which it used quadrupedal stances.

4 | DISCUSSION AND CONCLUSIONS

Lemurs were recorded at differing heights in the tree canopy, and locomotion of *E. rufifrons* was recorded at mean height nearly 10 m

TABLE 4 Effects of substrate properties on relative speed.

Species	Final model	Estimate	Statistic	*p*-value
E. rubriventer	Substrate height	−0.41	$F_{[1,22]} = 3.64$	0.071
E. rufifrons	Substrate diameter	0.34	$F_{[1,31]} = 4.00$	0.054
H. aureus	Substrate height	0.56	$F_{[1,22]} = 4.74$	0.052
L. catta	Substrate height	0.47	$F_{[1,27]} = 5.19$	0.032
	Substrate diameter	0.59	$F_{[1,27]} = 7.94$	<0.01

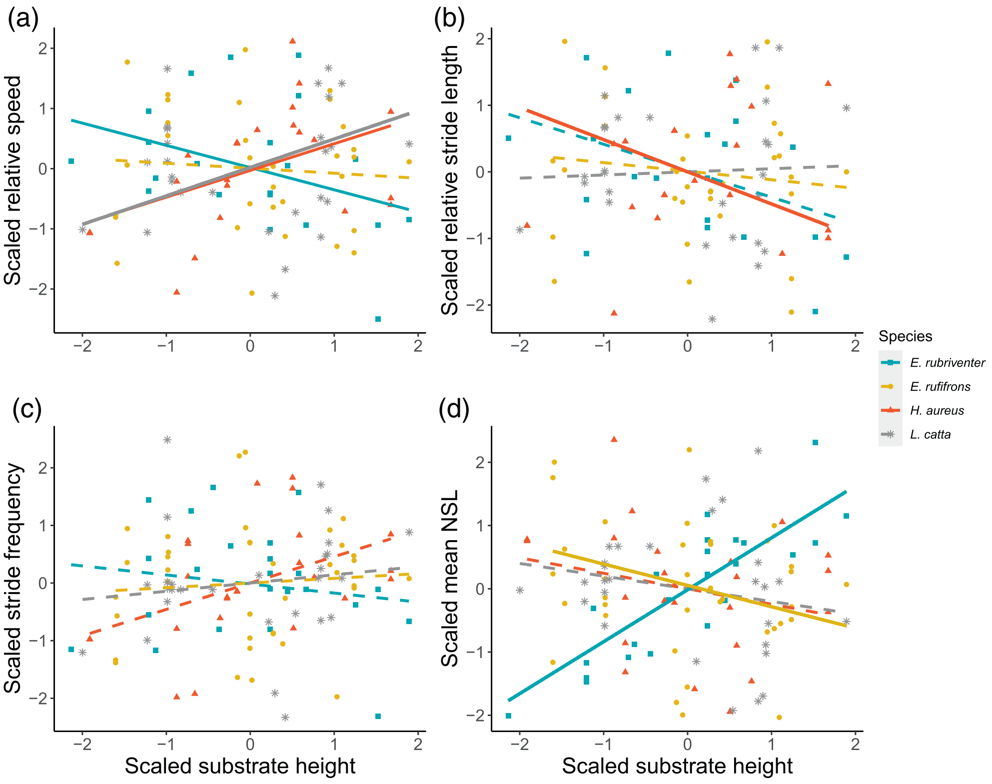

FIGURE 3 Scatterplots of scaled gait parameters—relative speed (a), relative stride length (b), stride frequency (c), and mean number of supporting limbs (NSL, d)—plotted against scaled substrate height, grouped by lemur species. Trend lines indicate reduced maximum likelihood fits from mixed-effects analysis of covariance (ANCOVA) models as reported in Tables 4–7. Dashed lines indicate trends from nonsignificant regressions, whereas solid lines indicate significant trends.

TABLE 5 Effects of substrate properties and relative speed on relative stride length.

Species	Final model	Estimate	Statistic	*p*-value
E. rubriventer	Relative speed	0.090	$F_{[1,22]} = 80.7$	<0.001
E. rufifrons	Relative speed	0.61	$F_{[1,33]} = 30.1$	<0.001
H. aureus	Substrate height	−0.48	$F_{[1,22]} = 5.08$	0.042
	Relative speed	1.4	$F_{[1,22]} = 530$	<0.001
L. catta	Relative speed	0.78	$F_{[1,27]} = 39.7$	<0.001

TABLE 6 Effects of substrate properties and relative speed on stride frequency.

Species	Final model	Estimate	Statistic	*p*-value
E. rubriventer	Substrate diameter	0.26	$F_{[1,19]} = 3.56$	0.075
	Relative speed	0.63	$F_{[1,19]} = 21.6$	<0.001
E. rufifrons	Relative speed	0.63	$F_{[1,33]} = 21.6$	<0.001
H. aureus	Relative speed	0.79	$F_{[1,22]} = 35.2$	<0.001
L. catta	Relative speed	0.80	$F_{[1,27]} = 40.5$	<0.001

greater than the other species. Following basic principles of ballistic physics where all PE is converted to kinetic energy during a fall ($E = mgh = 0.5mv^2$, where v is velocity), *E. rufifrons* would incur the greatest velocities upon impact with the ground. Despite this,

TABLE 7 Effects of substrate properties and relative speed on the mean number of supporting limbs.

Species	Final model	Estimate	Statistic	*p*-value
E. rubriventer	Substrate height	0.82	$F_{[1,19]} = 45.6$	<0.001
	Relative speed	−0.11	$F_{[1,19]} = 13.3$	<0.01
E. rufifrons	Substrate height	−0.34	$F_{[1,30]} = 5.02$	0.033
	Relative speed	−0.52	$F_{[1,30]} = 11.9$	<0.01
H. aureus	Relative speed	−0.82	$F_{[1,22]} = 51.3$	<0.001
L. catta	Relative speed	−0.42	$F_{[1,27]} = 5.56$	0.027

TABLE 8 Proportion of strides containing the given limb stances on low and high substrates (above or below median height).

Limb stance	*E. rubriventer*		*E. rufifrons*		*H. aureus*		*L. catta*	
	Low	High	Low	High	Low	High	Low	High
Single limb	0.13	0	0.15	0.06	0.23	0.36	0.07	0.29
Ipsilateral limb pair	0.44	0.38	0.45	0.47	0.38	0.27	0.79	0.50
Contralateral limb pair	1	1	1	1	1	1	1	1
Tripedal	1	1	1	1	1	1	1	1
Quadrupedal	0.69	0.88	0.80	1	0.92	0.82	0.50	0.50

Note: Single limb, tripedal, and quadrupedal rows indicate the proportion of strides where the body was at least momentarily supported only by one, three, or four limbs, respectively. Ipsilateral limb pair stances occur when the body is supported by a hind limb and a forelimb on the same side of the body. Contralateral limb pair stances occur when the body is supported by a hind limb and a forelimb on opposite sides of the body.

E. rufifrons did not adjust relative speed, relative stride length, or stride frequency in response to higher substrates, and instead they decreased the mean number of supporting limbs as substrate height increased.

In contrast, *E. rubriventer* did increase the mean number of supporting limbs during strides on higher substrates, following our predictions. It appears that this was accomplished by both reducing the frequency that unstable (single limb and ipsilateral limb pair) stances were used while also increasing stable (quadrupedal) stances. Functionally this should mean that over the course of a stride, the limbs are in contact with the substrate more often. This could reduce perturbations of the substrate itself while also allowing more opportunity to exert muscular force to stabilize the body should its trajectory begin to veer from its intended course. In a study conducted in Ranomafana National Park, *E. rubriventer* was observed using strata lower than *E. rufifrons* during travel (Overdorff, 1996), a distinction in canopy use that mirrors our data. It is possible that *E. rufifrons*, in comparison to the closely related *E. rubriventer*, changed locomotion relatively little because they move more habitually at these higher levels, potentially indicating a difference between these two species in perception of risk at increasing substrate heights.

Like *E. rufifrons*, *H. aureus* and *L. catta* also adjusted gait in response to increasing substrate height in manners counter to our predictions. If lemurs were to vary in their response to increasing perceived risk on higher substrates, these two species were expected to make more exaggerated changes to gait given their ecological and/or morphological differences from the arboreal and more generalized *Eulemur* species. However, *H. aureus* and *L. catta* both tended to increase speed on increasing substrate heights, and *H. aureus* also decreased stride length. These changes are thought to reduce static stability on precarious arboreal substrates, but increasing speed can reduce mediolateral fluctuations of the center of mass, thus providing an alternate, dynamic form of stability (Young, 2023). As speed increases, single limb and paired limb support configurations (i.e., a decrease in mean number of supporting limbs) should be more frequent. And indeed, that is what occurred in *H. aureus* and *L. catta*, who shifted to use more limb configurations that we hypothesized would be statically unstable on higher substrates. More data are needed to assess whether adjustments in speed and subsequent adjustments in limb support configurations are responses to substrate height or demonstrations of robust locomotor performance regardless of substrate height.

The observed subtle changes in locomotion suggest that lemurs move their limbs in ways that already ensure safety, and perhaps only small adjustments are needed to account for variation in the arboreal environment. After all, lemurs do possess long, flexed limbs, grasping hands and feet, and long, mobile tails—morphological characteristics that are thought to enhance locomotor performance of primates on arboreal substrates (Larson, 2018; Mincer & Russo, 2020; Schmitt, 2010). Whereas the kinematic changes to gait discussed in the present study are common strategies for stable arboreal locomotion, the most pronounced adjustments to increase stability are found in species that, for instance, may have reduced grasping abilities or otherwise do not share the morphological features of typical primates (Shapiro et al., 2014; Young & Chadwell, 2020). Moreover, lemurs in this study generally performed robustly on substrates of varying physical properties. There were some adjustments in response to variations in substrate diameter: *E. rufifrons* and *L. catta* both tended to use lower speeds on narrower, theoretically more unstable, substrates, while *E. rubriventer* tended to use lower stride frequencies. No lemurs adjusted gait in response to variation in substrate inclination. This contrasts with a study on captive mouse lemurs (*Microcebus murinus*) which described the tendency for individuals to increase contact time on oblique substrates (Shapiro et al., 2016). Another study involving several *Eulemur* species showed that lemurs traveling on inclined supports augment elbow and knee flexion to promote stability (Stevens et al., 2010), and primates joint kinematics typically change more in response to varying substrate orientation than varying diameter (Janisch et al., 2024). Future work on the influence of substrate height on locomotion could include analyses of joint kinematics, nonwalking gaits, or even tail kinematics as possible avenues of investigation.

While subtle changes in locomotion could be interpreted as robust locomotor performance, lemurs alternatively could be trading energetic efficiency for stability (Miller et al., 2019). Table 8 shows that lemurs used tripedal and quadrupedal stances frequently, regardless of their position in the tree canopy. Strides with more tripedal and quadrupedal stances should be less efficient than strides where paired limb stances predominate (Griffin et al., 2004). Studies in baboons (*Papio anubis*) and chimpanzees (*Pan troglodytes schweinfurthii*) indicate that maneuverability and efficiency are traded for stability when moving from terrestrial to arboreal substrates (Druelle et al., 2021; Pontzer & Wrangham, 2004). Even the much smaller squirrel monkey (*Saimiri sciureus*) has been shown to make adjustments to limb phase to increase stability on more precarious substrates (Miller et al., 2019).

There are few previous studies addressing how substrate height might directly influence locomotor patterns in other animals. Ornate lizards (*Urosaurus ornatus*) have been shown to decrease speed on higher arboreal substrates, generally, though they *increase* speed on higher substrates while engaging in display behaviors (McElroy et al., 2007). Orangutans (*Pongo* spp.) do not change positional behaviors at different heights in the tree canopy (Thorpe & Crompton, 2006). A later analysis by this research group of only locomotor behavior kept substrate height in the model that best predicted locomotor mode, but in this case, height had the most predictive power when classified as either core stratum—where there is the most continuity among substrates—or peripheral strata—where substrates are relatively discontinuous (Manduell et al., 2011). The present study focuses on lemur locomotion on individual branches, so the relative continuity of substrates was not tested here.

4.1 | Limitations and future directions

The study presented here is an introductory attempt to incorporate additional aspects of arboreal substrate variation into primate locomotion analysis. However, we acknowledge that not all relevant parameters could be accounted for in our analyses. For example, the structure of the lower canopy and forest floor may attenuate some of the risk of a fall by providing cushion or alternative places to land. In physics terms, this would increase the distance over which the falling lemur would decrease its velocity to zero, reducing the force of impact. Such cases would be more likely in Talatakely, the dense forest area of Ranomafana National Park where we studied *E. rubriventer*, *E. rufifrons*, and *H. aureus*. At the Anja Community Reserve, however, where we recorded *L. catta*, the trees were shorter overall but the underbrush was sparse and the ground rocky. Additionally, substrate height may also correlate with other unobserved environmental features like continuity of the substrates (Manduell et al., 2011).

Studying the locomotion of free-ranging animals provides the opportunity to capture more naturalistic variation in the data; however, this also skewed our data in a manner that is difficult to account for. We recorded *E. rufifrons* on much higher substrates than the other species. While this is reflective of previously recorded differences in habitat use between *Eulemur* species at Ranomafana National Park (Overdorff, 1996), it complicates interpretation. For example, it remains unclear if a relatively terrestrial species like *L. catta* traveling at the same heights as *E. rufifrons* would make the predicted adjustments to gait to improve stability. Furthermore, the studies in lizards (McElroy et al., 2007) and orangutans (Manduell et al., 2011; Thorpe & Crompton, 2006) emphasize the importance of the interacting effects of habitat structure and other behaviors on locomotion. Future work, which incorporates more aspects of habitat structure or other types of behavior beyond walking gaits, may shed light on potential differences in the perception of risk during locomotion in arboreal primates.

4.2 | Conclusions

The response to increasing substrate height varied among lemur species. *E. rubriventer* increased the mean number of limbs used to support its body during a stride on higher substrates, whereas other lemurs either did not respond or responded counter to our predictions. Nevertheless, a holistic understanding of primate arboreal adaptation in primates is incomplete without knowledge of the sensory and cognitive processes that govern their movements. Though subtle, the adjustments to gait observed in one species of lemur suggest that they may be gathering information about their position in the tree canopy and making decisions to reduce risks.

AUTHOR CONTRIBUTIONS

Nicole M. Schapker: Conceptualization (supporting); data curation (lead); investigation (equal); writing – original draft (lead). **Judith Janisch:** Investigation (equal); writing – review and editing (equal). **Lydia C. Myers:** Investigation (equal); writing – review and editing (equal). **Taylor Phelps:** Data curation (supporting); writing – review and editing (equal). **Liza J. Shapiro:** Conceptualization (lead); funding acquisition (equal); writing – review and editing (equal). **Jesse**

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ACKNOWLEDGMENTS

This work was funded by the National Science Foundation (BCS-1921135, BCS-1921314, BCS-1640552, BCS-1640453, and BCS-2316841). All procedures were authorized by NEOMED IACUC (Protocol 15-021) and UT Austin IACUC (Protocol AUP-2022-00002). We would like to thank the many personnel of MICET, Centre ValBio, Ranomafana National Park, and the Anja Community Reserve for making this work possible, and extra special thanks go to field technicians Naina Nirina Paul John and Rasendry Nirina Victor. Additional thanks to Ammon Hottensmith and Ian Barry for their aid in video processing and analysis.

OPEN RESEARCH BADGES

This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at http://doi.org/10.6084/m9.figshare.23571684.v2.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in figshare at http://doi.org/10.6084/m9.figshare.23571684.v2 (Schapker et al., 2023). Original video recordings are shareable upon reasonable request.

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How to cite this article: Schapker, N. M., Janisch, J., Myers, L. C., Phelps, T., Shapiro, L. J., & Young, J. W. (2024). From such great heights: The effects of substrate height and the perception of risk on lemur locomotor mechanics. *American Journal of Biological Anthropology*, e24917. https://doi.org/10.1002/ajpa.24917