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BRIEF COMMUNICATION

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Pump and sway: Wild primates use compliant supports as a tool to augment leaping in the canopy

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Abstract

Objectives: Despite qualitative observations of wild primates pumping branches before leaping across gaps in the canopy, most studies have suggested that support compliance increases the energetic cost of arboreal leaping, thus limiting leaping performance. In this study, we quantified branch pumping behavior and tree swaying in wild primates to test the hypothesis that these behaviors improve leaping performance.

Materials and Methods: We recorded wild colobine monkeys crossing gaps in the canopy and quantitatively tracked the kinematics of both the monkey and the compliant support during behavioral sequences. We also empirically measured the compliance of a sample of locomotor supports in the monkeys' natural habitat, allowing us to quantify the resonant properties of substrates used during leaping.

Results: Analyses of three recordings show that adult red colobus monkeys (*Piliocolobus tephrosceles*) use branch compliance to their advantage by actively pumping branches before leaping, augmenting their vertical velocity at take-off. Quantitative modeling of branch resonance periods, based on empirical measurements of support compliance, suggests that monkeys specifically employed branch pumping on relatively thin branches with protracted periods of oscillation. Finally, an additional four recordings show that both red colobus and black and white colobus monkeys (*Colobus guereza*) utilize tree swaying to cross large gaps, augmenting horizontal velocity at take-off.

Discussion: This deliberate branch manipulation to produce a mechanical effect for stronger propulsion is consistent with the framework of instrumental problem-solving. To our knowledge, this is the first study of wild primates which quantitatively shows how compliant branches can be used advantageously to augment locomotor performance.

KEYWORDS
arboreality, cognition, instrumental problem-solving, primate locomotion

1 | INTRODUCTION

Arboreal substrates are often discontinuous, and gaps must be crossed between trees while traveling (Graham & Socha, 2020). Such gaps typically lie between narrow and compliant terminal branches and may be of particular concern for arboreal leapers, given the need for high push-off forces (Alexander, 1991; Bonser, 1999; Crompton et al., 1993). Most studies that have investigated the impact of substrate compliance on arboreal leaping have found that compliant supports absorb mechanical energy during push-off, negatively impacting leaping performance (Crandell et al., 2018; Demes et al., 1995; Gilman et al., 2012; Gilman & Irschick, 2013; Hunt et al., 2021). For instance, both leaping tree frogs and doves lost mechanical energy to perch deflection when jumping, reducing take-off velocity, and compromising leaping performance (Crandell et al., 2018; Reynaga et al., 2019). Given the cost of leaping from compliant supports, wild tarsiers, platyrrhine monkeys, and green anoles have been shown to avoid leaping from compliant terminal branches (Berles et al., 2022; Crompton et al., 2010; Gilman et al., 2012; Gilman & Irschick, 2013; Walker, 2005).

So far, only a few, mostly anecdotal, observations have suggested that wild arboreal taxa could benefit from branch compliance. Wild langurs (*Trachypithecus leucocephalus*), siamangs (*Hylobates syndactylus*), and strepsirrhines used substrate compliance to reduce impact forces and injuries during landing (Demes et al., 1995, 1999; Fleagle, 1976; Huang & Li, 2005). Large-bodied orangutans (*Pongo abelii*) used the momentum created by rocking their body mass to sway compliant tree trunks, permitting them to cross large gaps in the canopy without leaping (Thorpe et al., 2009). Some primates have been observed using a similar behavior, called "branch pumping," in which fore- and hind limb flexion and extension is used to impart vertical momentum to the support, oscillating the branch and possibly gaining energy for leaping (Dunbar, 1989, 2017; Fleagle, 1976; Hunt et al., 1996). The goal-directed use of body weight and compliant substrates to safely overcome a specific obstacle, such as the crossing of a large gap in the canopy, is an example of instrumental problem-solving (Fragaszy & Liu, 2012; Fragaszy & Mangalam, 2018) and highlights the cognitive challenges of living in such a complex environment.

To our knowledge, it has yet to be quantitatively demonstrated that arboreal animals are able to use tree compliance to enhance leaping performance during push-off. In this study, we quantified different strategies used by the species studied to cross large gaps in their natural environment, including branch pumping and tree swaying, and tested whether such strategies allowed the animals to gain kinetic energy before leaping. Because leaping performance (e.g., distance traveled) depends primarily on vertical/horizontal velocity at take-off (Emerson, 1985), we predicted that they harness the resonant properties of arboreal supports during branch-pumping to augment vertical velocity and during tree swaying to augment horizontal velocity at take-off.

2 | METHODS

Data were collected January–February 2022 at the Makerere Biological Field Station, Kibale National Park, Uganda on red colobus monkeys (*Piliocolobus tephrosceles*; mean body mass: 8.4 kg, Smith & Jungers, 1997) and black and white colobus monkeys (*Colobus guereza*; mean body mass: 11.4 kg, Smith & Jungers, 1997), as part of a larger project studying the locomotor behavior of the eight monkey species at the site. Opportunistic recordings took place during their daily peak activity hours. Given that videos were recorded opportunistically, our sample size is necessarily limited. Specifically, the primary focus of data collection efforts during the 8 weeks of field work spent at Kibale National Park was to record other aspects of primate locomotor kinematics in the wild (primarily quadrupedal locomotion). Though we observed several other instances of branch pumping and tree swaying, commensurate with previous reports in the field of primatology literature (Dunbar, 2017; Fleagle, 1976; Hunt, et al., 1996), we were not able to collect more quantitative data on these events due to the competing data collection priorities. Nevertheless, after the field season was complete, we noticed several instances of branch pumping/tree swaying behaviors in our video database. We specifically identified 18 leaps that indicated possible evidence of the branch pumping and/or tree swaying behaviors. However, we ultimately had to discard all but seven leaps from our final dataset due to additional behaviors that would have confounded our analysis (e.g., the monkey running into the leap, rather than depending solely on substrate rebound to power the leap), resulting in our final dataset for analysis (Table 1). Locomotion was recorded at 120 Hz with modified GoPro cameras (Back-Bone, Ottawa, Ontario, Canada) with attached zoom lenses. We focused on videos in which the camera was positioned approximately orthogonal to the primate's parasagittal plane and the vertical image axis was approximately coincident with gravity. We analyzed three videos of branch pumping behavior (i.e., primate moves branch along the vertical axis, Figure 1a,d, Video S3), and four videos of tree swaying behavior (i.e., primate moves tree trunk along the horizontal axis, Figure 1b,e, Video S2), and compared them to four videos of static leaps, where no preparatory substrate loading took place (Figure 1c; Video S1). Videos were digitized in 2D using DLTdv8a (Hedrick, 2008) in MATLAB R2022b (Mathworks, Natick, MA). For branch pumping videos, we continuously tracked two points on the launching branch, one at the tip and another more proximal along the length of the branch. For tree swaying videos, we continuously tracked a point near the top of the trunk and a lower point. In all videos, we continuously tracked the tip of the primate's nose and the base of their tail. Points were tracked prior to the initiation of movement until a few frames following take-off. We identified the push-off phase of the leap as beginning with hind limb extension and ending when the feet no longer touching the support (i.e., take-off). Two stable reference background points (e.g., landmarks on a large tree) were tracked to compensate for camera movement if necessary. Compensation for camera movement was only required for two videos in our dataset. In these videos, the angular position of the stable points, relative to the global *y*-axis, only varied by 1.7°–8.9° over the course of

TABLE 1 Overview of leaps in our dataset.

Subjects	Static leap	Branch pump	Tree sway	Age	Landing point	Launching tree species
C. guereza #1	1			Adult	Lower	*Prunus africana*
C. guereza #2			1	Adult	Lower	*Prunus africana*
P. tephrosceles #1			1	Adult with infant	Horizontal	Unknown
P. tephrosceles #2		1		Adult with infant	Lower	Unknown
P. tephrosceles #3		1		Adult with infant	Lower	Unknown
P. tephrosceles #4		1		Adult with infant	Lower	Unknown
P. tephrosceles #5	1			Adult	Lower	*Prunus africana*
P. tephrosceles #6	1			Adult	Lower	*Prunus africana*
P. tephrosceles #7	1			Adult with infant	Lower	*Prunus africana*
P. tephrosceles #8			1	Adult	Horizontal	Unknown
P. tephrosceles #9			1	Adult	Horizontal	Unknown
Total leaps by type	4	3	4			

the trial, indicating camera movement was principally translational, not rotatory.

Two-dimensional coordinate data were processed using a custom MATLAB script. First, for the two videos in which the camera moved, we subtracted the instantaneous x–y coordinates of the stable reference midpoint from all other coordinates to control for camera movement. Next, coordinate data were fit to a quintic smoothing spline function (MATLAB function "spaps"; tolerance of 5 pixels^2), allowing us to mitigate digitizing error and interpolate feature positions for frames where the marker was not visible across gaps of ≤100 ms (Walker, 1998). Instantaneous horizontal and vertical velocities were calculated as the first derivative of smoothed x- and y-coordinates, respectively (MATLAB function "fnder"). The net position and velocity of the monkey was calculated as the midpoint of instantaneous nose and tail base positions/velocities. Finally, we calculated four summary outcome variables: the horizontal and vertical velocity of the monkey at the start of push-off and the net change (Δ) in the horizontal and vertical velocity of the monkey during push-off. All calculated velocities were normalized to the instantaneous trunk length of the monkey (i.e., magnitude of the nose to tail base position vector), rendering variables in body length units. Note that due to landmarks occasionally being obscured or out of frame (Figure 1c–e), not every outcome variable could be calculated for every sequence.

To investigate the resonant properties of the compliant supports, we first empirically measured the period of support oscillation by marking the frames in which the branch/trunk reached zenith or nadir before changing direction. Oscillation periods were estimated as twice the average duration between apex events. Second, to estimate the natural oscillation period of launching supports, we empirically measured the stiffness and diameter of a broad sample of branches at the field site that were representative of those typically used by *P. tephrosceles* during locomotion ($n = 89$ samples), following the procedures of Dunham et al. (2018). Natural oscillation period (i.e., t_0; in seconds) was then calculated as:

$$t_0 = \frac{2\pi}{\sqrt{\frac{k}{m}}}, \quad (1)$$

where k is branch stiffness (in N m^{-1}) and m is effective mass (set to 8.4 kg, the mean body mass for *P. tephrosceles*). Because we were unable to estimate resonance properties for the tree trunks used during tree swaying behaviors, we only discuss the implications of natural oscillation periods for branch pumping.

Outcome variables were imported into R (Version 4.2.3, R Core Team, 2023) for analysis and plotting. Given our small sample size, we describe central tendency (i.e., median) and spread (i.e., range) in our quantitative measures of leaping, but eschew inferential statistical testing. All data are publicly available at Janisch et al. (2023a, 2023b).

3 | RESULTS

Outcome variables are summarized in Table 2 and Figure 1c–i. Colobus monkeys used branch pumping to augment their vertical velocity at the start of the leap (Figure 1d,f). During branch pump leaps, median vertical velocity at the start of push-off was greater than during tree sway leaps or static leaps. Monkeys also had positive vertical velocity at the start of tree sway leaps (Figure 1e), whereas vertical velocity was close to zero at the start of static leaps (Figure 1c). Moreover, due to branch deformation, monkeys tended to lose, rather than gain, additional vertical velocity during the push-off phase of branch pump leaps (Figure 1g), such that most of the vertical velocity needed to power the leap at take-off was due to branch recoil alone. Monkeys gained vertical velocity during the push-off phase of tree sway leaps, whereas they both gained and lost vertical velocity during the push-off phase of static leaps, depending on branch deformation.

At the start of tree sway leaps monkeys had greater horizontal velocity than during static leaps, though they also showed positive horizontal velocity at the start of branch pump leaps (Figure 1d,e,h).

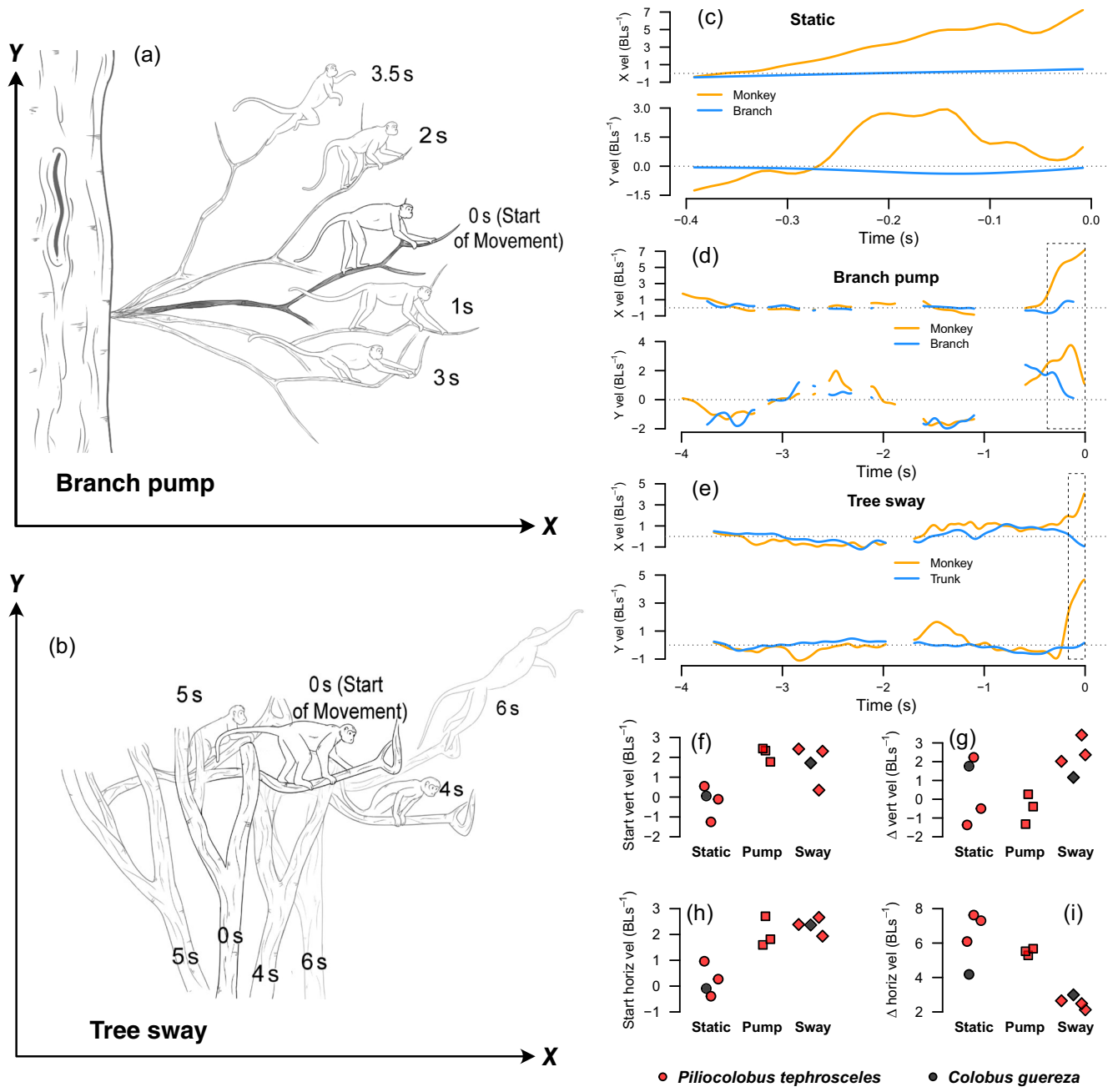

FIGURE 1 Kinematics of leaping in wild colobus monkeys (*Piliocolobus tephrosceles* and *Colobus guereza*). Illustrations of branch pumping (a) and tree swaying (b) behaviors. Time points indicate the sequencing of events from start ($t = 0$ s) to take-off. Axes indicate coordinate system used when digitizing leaps. Exemplar instantaneous velocities of the monkey and support during a static leap (c), a branch pump leap (d), and a tree sway leap (e). Whereas only the push-off period of the leap is plotted in (c), the entire movement period is plotted in (d) and (e), terminating in push-off (dashed rectangle). Missing data indicate that one or more kinematic landmarks were obscured. (f–i) Strip charts of outcome variables during static, branch pump, and tree sway leaps. Plots represent starting vertical velocity at push-off (f), the net change in vertical velocity during push-off (g), starting horizontal velocity at push-off (h), and the net change in horizontal velocity during push-off (i).

As a result, monkeys gained less horizontal velocity during the push-off phase of tree sway leaps than during the other two leap styles (Figure 1i), and a greater percentage of the horizontal velocity used to power the leap came from the swaying momentum of the tree.

Colobus monkey branch pumping and tree swaying push-off durations were 5%–33% of the observed oscillation periods (Figure 2a). Therefore, the duration of push-off was less than half the period of support oscillation, resulting in the support and the monkey moving in the same directions during the push-off phase of the leap. The calculated natural oscillation periods of locomotor supports decreased as a power function of their diameter, such that narrow branches (i.e., those with diameter <5 cm) had relatively long oscillation periods (Figure 2b). Observed oscillation periods during branch

TABLE 2 Summary of kinematic values for static leaps, branch pump leaps, and tree sway leaps in wild colobus monkeys (*Piliocolobus tephrosceles* and *Colobus guereza*).

Leap type	Starting vertical velocity (BLs^{-1})[a]	ΔVertical velocity (BLs^{-1})	Starting horizontal velocity (BLs^{-1})	ΔHorizontal velocity (BLs^{-1})
Static	−0.03	0.63	0.09	6.70
	−1.251	−0.137	−0.392	5.523
	0.546	2.229	0.962	2.778
Branch pump	2.34	−0.39	1.82	5.52
	1.773	−1.325	1.596	5.285
	2.442	0.263	2.705	5.673
Tree sway	2.01	2.19	2.38	2.78
	0.630	1.161	1.930	2.113
	2.420	3.195	2.386	2.992

[a]Top values in each row indicate the median of the distribution, followed by the minimum and maximum values below.

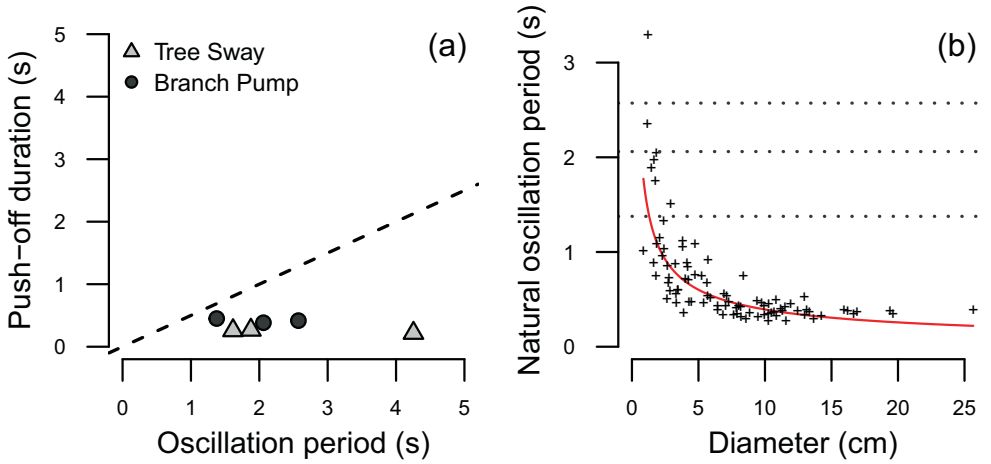

FIGURE 2 Evidence that colobus monkeys consider the natural resonant period of compliant supports. (a) Duration of leaping push-off versus the observed oscillation periods of the supports, both in seconds. The dashed line has a slope of 0.5 and an intercept of zero, indicating where push-off durations equal 50% of the matching oscillation period. (b) Estimated natural oscillation period (calculated from empirically measured branch stiffness and mean *Piliocolobus tephrosceles* body mass) versus diameter for branches used during colobus monkey locomotion. Oscillation periods decreased as a power function of diameter ($y = 0.486x^{-0.614}$, $R^2 = 0.682$). Horizontal dashed lines indicate observed oscillation periods of branches used during branch pumping leaps. Relatively long oscillation periods suggest the monkeys explicitly chose thin, compliant branches for branch pumping leaps.

pumping (indicated by horizontal dashed lines in Figure 2b) suggest that branch pumping occurred on relatively narrow launching branches.

4 | DISCUSSION

To our knowledge, this is the first evidence showing that colobus monkeys use tree compliance to enhance leaping performance by augmenting vertical and horizontal velocity at take-off (Figure 1). The data suggest that the monkeys could exploit the natural spring-like resonant properties of the supports from which they leapt (Thorpe et al., 2007). Doing so would require the duration of push-off to be less than half the period of support oscillation—as shown by our data—otherwise, the support and the monkey could be moving in opposite directions during the leap (Figure 2a). Moreover, empirical data on the relationship between natural oscillation periods and branch diameter suggested that the monkeys may have specifically employed branch pumping on relatively thin branches (as found in the terminal canopy), as such supports allow for long oscillation periods (Figure 2b). Finally, because the oscillation period increases exponentially with mass (see Equation 1), body size is likely an important determinant of primates' ability to beneficially exploit branch compliance. Colobus monkeys are among the largest quadrupedal arboreal primates (Rose, 1973), and we noted that mainly large adult individuals and adults carrying infants displayed branch pumping behaviors. Conversely, red-tailed monkeys (*Cercopithecus ascanius*), a smaller sympatric species at the site (mean body mass: 3.3 kg, Smith & Jungers, 1997), were never observed using branch pumping or tree swaying behaviors during leaping. During our field work, we

occasionally observed adults pumping branches for juveniles to help them cross gaps if the juveniles were too light to deform the branch themselves, emphasizing the importance of body size when utilizing branch compliance.

The observed branch pumping and tree swaying behaviors suggest that colobus monkeys can judge affordances for movement on the compliant supports in their environment. Such behavior fits into the framework of instrumental problem-solving (Fragaszy & Liu, 2012; Fragaszy & Mangalam, 2018)—goal-directed behaviors that display actions to overcome a specific obstacle. Branch pumping likely involves unique cognitive challenges, particularly given that every wrong attempt could be fatal. Such behaviors require the ability to mentally represent the consequences of the action prior to its execution, compare the actual consequences of the actions to the anticipated consequences, and alter subsequent action based on experience with prior executions. Goal-directed behavior therefore requires a functional characterization of the behavior, interrelating the behavior with the observed effects and the hypothetical intended effects (Reynolds, 1982). Further in-depth studies of branch pumping and tree swaying in larger samples of wild primates will help refine our understanding of these complex behaviors, including how frequently they are used and how they are learned and practiced ontogenetically.

This study provides an example of how primates can utilize the arboreal environment to their advantage, and further research in this area has the potential to improve our understanding of the cognitive capacities of wild primates. Because our data collection was opportunistic, our sample size was necessarily small. In future, more widespread studies are needed to establish the overall prevalence of branch pumping and tree swaying behaviors in our focal species, and other primates more broadly. Nevertheless, our study provides the first quantitative evidence that primates can use tree compliance to augment leaping performance, promoting the need for further investigation of the role support compliance plays in the evolutionary adaptations underlying arboreal locomotion. More in-depth studies should focus on identifying the underlying cognitive mechanisms of branch pumping and tree swaying, the ontogeny of these behaviors, and their possible use among other primate species.

AUTHOR CONTRIBUTIONS

Judith Janisch: Conceptualization (equal); data curation (equal); formal analysis (supporting); methodology (equal); writing – original draft (lead); writing – review and editing (equal). **Lydia C. Myers:** Data curation (equal); writing – review and editing (equal). **Nicole Schapker:** Data curation (equal); writing – review and editing (equal). **Jack Kirven:** Formal analysis (equal). **Liza J. Shapiro:** Conceptualization (equal); funding acquisition (equal); methodology (equal); project administration (equal); supervision (equal); writing – review and editing (equal). **Jesse W. Young:** Conceptualization (equal); formal analysis (equal); funding acquisition (equal); methodology (equal); project administration (equal); software (equal); supervision (equal); writing – original draft (equal); writing – review and editing (equal).

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DATA AVAILABILITY STATEMENT

All data used in the analyses presented here are available on Figshare.com (Janisch et al., 2023a, 2023b).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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