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RESEARCH ARTICLE

The effect of substrate compliance on the biomechanics of gibbon leaps

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SUMMARY

The storage and recovery of elastic strain energy in the musculoskeletal systems of locomoting animals has been extensively studied, yet the external environment represents a second potentially useful energy store that has often been neglected. Recent studies have highlighted the ability of orangutans to usefully recover energy from swaying trees to minimise the cost of gap crossing. Although mechanically similar mechanisms have been hypothesised for wild leaping primates, to date no such energy recovery mechanisms have been demonstrated biomechanically in leapers. We used a setup consisting of a forceplate and two high-speed video cameras to conduct a biomechanical analysis of captive gibbons leaping from stiff and compliant poles. We found that the gibbons minimised pole deflection by using different leaping strategies. Two leap types were used: slower orthograde leaps and more rapid pronograde leaps. The slower leaps used a wider hip joint excursion to negate the downward movement of the pole, using more impulse to power the leap, but with no increase in work done on the centre of mass. Greater hip excursion also minimised the effective leap distance during orthograde leaps. The more rapid leaps conversely applied peak force earlier in stance where the pole was effectively stiffer, minimising deflection and potential energy loss. Neither leap type appeared to usefully recover energy from the pole to increase leap performance, but the gibbons demonstrated an ability to best adapt their leap biomechanics to counter the negative effects of the compliant pole.

Key words: jumping, *Hylobates*, primate, branch, energy storage.

INTRODUCTION

Animals have long been known to store and recover energy in the elastic structures of the musculoskeletal system (Cavagna et al., 1977; Alexander, 1984; McGowan et al., 2005), economising muscular work and reducing the cost of locomotion (Alexander, 1991; Alexander, 1992). For animals moving on compliant substrates, the external environment represents another potentially useful energy store (see Alexander, 1995; Demes et al., 1995). Indeed, recent studies have shown that orangutans utilise the slow sway of tree trunks to minimise the cost of gap crossing (Thorpe et al., 2007) (see also Chevalier-Skolnikoff et al., 1982; Russon, 1998) and that they control excess branch sway through irregular gait patterns and multiple support limb use (Thorpe et al., 2009). Biomechanics studies of humans show that athletes run faster on tracks with optimum stiffness properties (McMahon and Greene, 1979), whereas spring boards and floors are commonly known to increase the jumping performance of divers and gymnasts (Kooi and Kuipers, 1994; McNitt-Gray et al., 1994; Cheng and Hubbard, 2004). Wild white-headed langurs (*Trachypithecus leucocephalus*) and siamangs (*Hylobates syndactylus*) have been shown to utilise the damping properties of compliant substrates for dissipating energy when landing after vertical descent (Fleagle, 1976; Huang and Li, 2005; Stevens, 2008), reducing impact forces and the risk of injury (Demes et al., 1995; Demes et al., 1999). Despite field studies reporting that "In preparation for a leap, a siamang often acquires momentum by 'pumping in place on a branch'" (Fleagle, 1976), useful elastic energy storage in the substrate by non-human animals during powerful movements such as leaping has not been demonstrated to date. Biomechanical studies on sifaka (*Propithecus* sp., a vertical clinger and leaper) concluded that energy spent deforming the substrate was not recovered on take-off, increasing the metabolic cost of leaping (Demes et al., 1995). Furthermore, tarsiers executing long leaps actively select wider diameter take-off substrates with orientations that best direct the leaping force along the long axis of branches, suggesting that they are actively seeking to avoid branch deflection and energy loss (Crompton et al., 2010).

A probable barrier to utilising substrate compliance during rapid, powerful movements is the stiffness and resonant frequency of the substrate (Alexander, 1991; Cheng and Hubbard, 2004; Ahlborn et al., 2006). When an animal leaps from a compliant substrate, such as a branch, the magnitude of deflection is proportional to the substrate's stiffness. Because the animal is in contact with the substrate, it loses potential energy proportional to the deflection. In a leaping animal, leg extension contributes equal energy to substrate deformation and to centre of mass acceleration, hence stiffer substrates, which deflect less for a given force (i.e. input energy), minimise potential energy loss of the centre of mass. The resonant oscillation frequency of the substrate is dependent on its stiffness and mass moment of inertia (Jeffrey, 2005). An oscillating beam (or substrate) undergoes alternating periods of descent and ascent, where one period of descent and one period of ascent represent one oscillation. In order to most effectively utilise the energy stored in the substrate, leg extension should occur during the second half of the final period of ascent before take-off (when the pole is decelerating in an upward direction) (Cheng and Hubbard, 2004). Therefore, slower oscillations (lower natural frequencies) require longer periods of leg extension and consequently lower forces, hindering leap performance.

The most common natural compliant substrates are living wooden branches and trunks and the animals most likely to encounter such substrates are habitually arboreal. Owing to the fragmented nature of forest canopies, habitually arboreal animals must frequently cross (often large) gaps between trees, which they can do in a number of ways, including tree swaying by larger animals (Thorpe et al., 2009) and gliding and leaping in smaller animals (Demes et al., 1991; Crompton et al., 1993; Byrnes et al., 2008). 'Branch pumping', observed in wild siamangs (Fleagle, 1976) before a leap may be a mechanism to utilise the energy stored in the branch for propulsion. However, most gap-crossing leaps are conducted from fine terminal branches (Fleagle, 1976; Gittins, 1983; Crompton et al., 1993; Sati and Alfred, 2002), with low resonant frequencies (McMahon and Kronauer, 1976) making efficient energy storage and recovery during leaping from terminal branches unlikely (Alexander, 1991). Indeed, wild sifaka were shown to take-off at the 'wrong' time for efficient energy return from thin branches (Demes et al., 1995).

Another significant effect of substrate compliance is unexpected perturbation. Many arboreal animals move rapidly through the forest canopy and presumably lack the time to test the compliance of each branch before use. Branch failures by fracture or buckling have been observed in field studies, e.g. in leaping of *Otolemur crassicaudatus* and *Tarsius bancanus*, respectively (R.H.C., personal observation), but observations are not frequent enough for statistical analysis. Even on familiar routes (during travel arboreal primates often follow specific routes or 'jungle highways') (McClure, 1964), branch material properties may be highly dependent on foliage, water content or interaction with other trees (McMahon and Kronauer, 1976). Because a mistake could result in serious injury or death (Schultz, 1956; Bramblett, 1967; Buikstra, 1975; Lovell, 1987), it seems probable that rapidly moving arboreal animals possess some mechanism(s) for coping with the perturbation effects (unexpected or otherwise) of compliant substrates. Data on arboreal animals dealing with such perturbation is lacking but the problem is undoubtedly real. McClure reported a siamang that "...misjudged the strength of a dead limb [branch]... and it plunged 25 or 30 feet into a crown below and continued without hesitation" (McClure, 1964). Laboratory studies of running guinea fowl suggest that the rapidity of perturbation may require that such responses are passive (i.e. do not require central nervous system activity) (Biewener and Daley, 2007).

In this study we compare the biomechanics of gibbons leaping from stiff and compliant substrates. Although renowned as specialist brachiators (Fleagle, 1974; Bertram et al., 1999), recent studies have highlighted that gibbons possess anatomical adaptations to execute hindlimb-powered movements such as leaping (Channon et al., 2009; Channon et al., 2010a). Gibbons commonly utilise leaping for 20–25% of their locomotor activity (Fleagle, 1976; Gittins, 1983; Sati and Alfred, 2002) and regularly leap from thin terminal branches during travel and feeding (Kappeler, 1984; Sati and Alfred, 2002). Channon et al. (Channon et al., 2010b) demonstrated that leaping is a highly versatile locomotor mode for gibbons, which probably use one of a number of leap types depending on the environment and leap function (i.e. travel, feeding etc.). The authors quantified four distinct leap types on the basis of the orientation of the trunk and the number of feet used during the take-off. It was hypothesised that the two slower leap types (with an orthograde trunk posture executed using one or both feet to push off from the substrate) were probably useful for shorter leaps within one tree, during feeding or playing. Conversely, the more rapid pronograde leaps could be utilised when crossing large gaps along familiar routes. Squat leaps are also likely to be useful for longer leaps, especially when the leap is challenging (unfamiliar or landing site visually obscured, etc.) because the gibbon can take the time to accurately assess the leap before take-off.

This study is the first to investigate the leaping mechanics of gibbons (and hence lesser apes as a whole) from compliant substrates, with specific attention to the role and effect of substrate compliance. We hypothesise that gibbons will not usefully store and recover elastic energy from the substrate but expect that the gibbons will modify their leap biomechanics to cope with substrate compliance. Specifically, we expect that the gibbons will use a larger range of hindlimb joint angles when leaping from the compliant substrate, resulting in a more extended limb, to compensate for the deflection of the substrate. Cheng and Hubbard showed in their human diving study, that the subjects introduced a phase-delayed pattern of joint extension, allowing the useful recovery of elastic energy (Cheng and Hubbard, 2004). We do not expect the gibbons to alter the timing of limb extension and force production between the stiff and compliant substrates. Instead, we expect the gibbons to follow patterns seen in walking primates on compliant substrates, utilising lower peak forces and a lower centre of gravity when leaping from the compliant pole (Schmitt, 1999).

MATERIALS AND METHODS

Voluntary leaps from a stiff (N=16) and compliant substrate (N=16) to a nearby landing pole (~1 m away) by two white-cheeked gibbons [*Hylobates* (*Nomascus*) *leucogenys* (Ogilby 1840), 1 female, 6 years old, weighing 8.7 kg and 1 male, 38 years old, weighing 6.7 kg] were recorded using high-speed video (120 Hz; AOS X-PRI, AOS Technologies, Baden Daettwil, Switzerland). The cameras were positioned orthogonal to each other and recorded lateral and frontal views. The lateral-view camera was used for the two-dimensional (2-D)-biomechanical analysis, and the frontal-view camera was used to ensure that leaps were conducted in the plane perpendicular to the lateral camera. Each pole was mounted atop a strain gauge forceplate (Fig. 1; OR6-7, AMTI, Watertown, MA, USA) and the analogue output signals were digitised by a National Instruments data acquisition module (NI, Austin, TX, USA) and collected at 500 Hz using custom-written software (LabVIEW 8.2, NI). The forceplate recordings were triggered by a synchronisation pulse from the high-speed video cameras, and were thus fully synchronised with the video recordings.

The stiff pole was a cylindrical (80 mm diameter, 1000 mm length) wooden pole, rigidly mounted horizontally to the forceplate. The compliant pole was a stiff horizontal aluminium tube (80 mm diameter, 1000 mm length, 2.3 kg mass), fixed at one end to a pivot, with the other end free (cf. a cantilever). Four parallel springs [stiffness (k) 7.5 N mm^{-1} each, combined 30 N mm^{-1}] were mounted at a distance of 285 mm from the pivot on the underside of the pole and fixed to the forceplate (Fig. 1).

In our analyses the compliant pole was modelled as a massless beam attached to a frictionless pivot. To validate this assumption we compared the pole tip position based on the forceplate readings with the pole tip position as digitised from the high-speed video. We used craniocaudal (CC; where positive forces were propelling the gibbon forward and negative forces were braking forces),

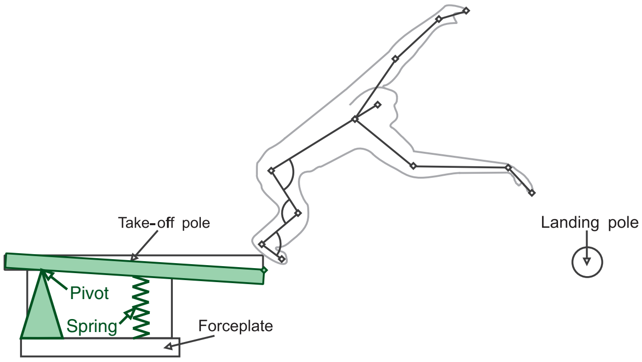

Fig. 1. The experimental setup. Open diamonds show the joint centre digitisation points; filled green diamond shows the pole tip digitisation point. Black outlines show the stiff pole setup; green outlines show the compliant pole setup.

mediolateral (ML) and vertical (V) forces and moments ($\mathbf{F}_{CC}$, $\mathbf{F}_{ML}$, $\mathbf{F}_V$, $\mathbf{M}_{CC}$, $\mathbf{M}_{ML}$, $\mathbf{M}_V$ respectively; the animal moved parallel, from negative to positive, to the *X*-axis of the forceplate, allowing the animal and forceplate to share co-ordinate systems) to calculate the horizontal centre of pressure (CoP_{CC}) position relative to the pivot as:

$$CoP_{CC} = [\mathbf{M}_{ML} + (\mathbf{F}_{CC}\,\alpha)] \,/\, \mathbf{F}_V\,, \qquad (1)$$

where α is a forceplate-specific constant.

The displacement of the spring (S_{DIS}) was calculated as:

$$S_{DIS} = (\mathbf{F}_V\, CoP_{CC}) \,/\, (S_{CC}\, k)\,, \qquad (2)$$

where S_{CC} is the distance between the spring and the pivot and *k* is the spring stiffness.

Displacement at the tip (T_{DIS}) as:

$$T_{DIS} = (S_{DIS} \,/\, S_{CC})\, T_{CC}\,, \qquad (3)$$

where T_{CC} is the beam length (1 m).

We compared the tip displacement of the compliant pole, calculated from forceplate data, and digitised videos for each trial using a linear regression (SPSS 17, Systat Software, Erkrath, Germany). The mean gradient was close to 1 (0.97±0.23; mean ± s.d.), the regression was highly significant (mean R^2=0.95, mean P<0.0005) and the unloaded resonant frequency of the pole was high (~30 Hz), suggesting that our model is sound.

Anatomical landmarks representing the toes, ankles, knees, hips, shoulders, elbows, wrists, fingers and head were digitised manually from the high-speed video (Fig. 1). Hindlimb joint angles were defined as, ankle: the internal angle made by a line joining the toe, ankle and knee (between the dorsum of the foot and the anterior of the shank), knee: the internal angle made by a line joining the ankle, knee and hip joints (between the posterior of the shank and posterior of the thigh), and hip: the internal angle made by a line joining the knee, hip and shoulder (between the anterior surface of the thigh and the anterior surface of the trunk; Fig. 1). Hindlimb joint angles were resampled to the final stance phase before take-off (i.e. 0% stance, when the take-off limb touched the pole, to 100% stance, when the take-off foot left the pole at take-off), using a cubic spline-based interpolation algorithm in LabVIEW.

Forces were resampled to the duration of the final stance before take-off (hereafter: stance) and normalised to body mass, to remove the effect of body size. Mediolateral forces were small, and out of plane with the camera, and were omitted from our analyses (i.e. they were restricted to two dimensions). Horizontal and vertical impulses were calculated separately as the integral of the craniocaudal and vertical force–time curves, respectively, during stance and were normalised to body mass.

Accelerations, resultant velocities ($\mathbf{v}_R$) and centre of mass positions were calculated by dividing force by body mass and double integration of the resulting curve. Boundary (initial) conditions for the integration were attained using a kinematic path-matching technique, where the initial centre of mass position was calculated by combining the positions of the body segments (from digitised video) with published inertial properties (from Isler et al., 2006), and resolving the resulting moments. A more comprehensive description of these commonly used methods can be found elsewhere (McGowan et al., 2005; Daley et al., 2006; Williams et al., 2009; Channon et al., 2010b). Instantaneous centre of mass position was normalised to the landing pole position so that the tip of the landing pole was set at the origin (0, 0).

Potential (E_P) and kinetic energy (E_K) were summed to give mechanical energy (E_M):

$$E_P = m\, g\, h \qquad (4)$$

and

$$E_K = 0.5\, m\, \mathbf{v}_R^{\,2}\,, \qquad (5)$$

where $\boldsymbol{g}$ is gravitational acceleration (9.81 m s^{-2}), *h* is the vertical height of the centre of mass and *m* is body mass.

Mechanical work was calculated as the net change in mechanical energy during the final stance phase before take-off. Power was calculated as the derivative of work over time through stance. Work and power were divided by body mass to yield mass-specific work and power.

As the gibbon travels along the compliant pole, away from the pivot, the moment acting to compress the spring increases and so the combination of pole and spring becomes effectively less stiff. The instantaneous pole stiffness (k_I), was calculated as:

$$k_I = \mathbf{F}_V \,/\, S_{DIS}\,. \qquad (6)$$

Statistical comparisons of biomechanical parameters (listed in Table 1) were made between leaps from the stiff and compliant pole. Because of the limited sample size (both in terms of individuals and number of leaps), we opted to use a non-parametric Kruskal–Wallis test, thus avoiding any assumptions of normality or equal variance, where a *P*-value of 0.05 or less was deemed significant. All statistical calculations were conducted in SPSS 17. Because of the large number of statistical comparisons being made a Bonferroni correction was used to attain a conservatively modified *P*-value (see Table 1).

RESULTS

During this study, the gibbons utilised two distinct leap types: orthograde single-footed and pronograde single-footed leaps (Fig. 2). Because these are biomechanically distinct leap types, they were analysed separately here. Orthograde leaps were conducted with the trunk in a more upright position (>45 deg to the horizontal), using a lower take-off velocity and a less acute take-off angle than pronograde leaps. Qualitatively, orthograde leaps began with the gibbon walking along the pole and the leap was a continuation of that movement with an acceleration during the final push-off phase before take-off. Conversely, during pronograde leaps, the gibbon rapidly moved along the pole with the trunk in a pronograde posture and the leap was conducted as a smooth continuation of this movement, with no visible acceleration during push-off. During pronograde leaps, the gibbon always ‘overleapt‘ the distance, missing the landing pole and opting instead to grasp a nearby rope

Table 1. Statistical comparisons of leap types on stiff and compliant substrates

			Orthograde			Pronograde		
		Fig.	Mean	s.e.m.	*P*-value	Mean	s.e.m.	*P*-value
Peak $\mathbf{F}_{\mathrm{CC}}$ (body weights)	Stiff	3	0.41	0.04	0.71	0.48	0.02	0.21
	Compliant		0.39	0.02		0.41	0.04	
% Stance of peak $\mathbf{F}_{\mathrm{CC}}$	Stiff	3	39.39	11.20	0.39	46.50	14.21	0.82
	Compliant		59.92	5.96		31.00	24.08	
Peak $\mathbf{F}_{\mathrm{V}}$ (body weights)	Stiff	3	1.76	0.07	0.30	1.65	0.06	0.57
	Compliant		1.69	0.05		1.71	0.02	
% Stance of peak $\mathbf{F}_{\mathrm{V}}$	Stiff	3	45.22	6.00	**0.04**	45.07	4.81	0.09
	Compliant		36.31	2.75		22.33	2.35	
Stance duration (s)	Stiff	4A	0.29	0.02	**0.04**	0.21	0.02	**0.03**
	Compliant		0.39	0.06		0.30	0.02	
Horizontal impulse ($\mathrm{N\,kg^{-1}}$)	Stiff	4B	0.64	0.12	0.97	0.85	0.09	0.57
	Compliant		0.59	0.09		0.94	0.03	
Vertical impulse ($\mathrm{N\,kg^{-1}}$)	Stiff	4B	4.31	0.54	**0.00***	3.30	0.27	**0.02**
	Compliant		8.66	0.61		4.83	0.09	
Horizontal centre of mass position at take-off (m)	Stiff	5	–0.81	0.05	**0.00***	–0.70	0.04	0.09
	Compliant		–0.38	0.07		0.55	0.09	
Kinetic energy at 0% stance ($\mathrm{J\,kg^{-1}}$)	Stiff	6	2.21	0.27	**0.00***	3.51	0.26	0.14
	Compliant		0.80	0.15		2.63	0.49	
Kinetic energy at take-off ($\mathrm{J\,kg^{-1}}$)	Stiff	6	3.66	0.20	**0.00***	4.11	0.21	0.43
	Compliant		1.76	0.24		3.63	0.52	
Potential energy at 0% stance ($\mathrm{J\,kg^{-1}}$)	Stiff	6	5.32	0.08	**0.01**	4.97	0.22	0.31
	Compliant		4.10	0.33		5.47	0.31	
Potential energy at take-off ($\mathrm{J\,kg^{-1}}$)	Stiff	6	8.41	0.61	0.19	6.61	0.18	**0.03**
	Compliant		6.71	0.60		8.18	0.54	
Mechanical energy at 0% stance ($\mathrm{J\,kg^{-1}}$)	Stiff	6	7.53	0.25	**0.00**	8.48	0.44	0.31
	Compliant		4.90	0.38		8.10	0.18	
Mechanical energy at take-off($\mathrm{J\,kg^{-1}}$)	Stiff	6	12.07	0.74	**0.01**	11.71	0.39	0.09
	Compliant		8.48	0.76		12.69	0.21	
Mass-specific work ($\mathrm{J\,kg^{-1}}$)	Stiff	7	3.66	0.60	0.84	2.63	0.25	**0.05**
	Compliant		3.74	0.46		3.74	0.16	
Peak mass-specific power ($\mathrm{W\,kg^{-1}}$)	Stiff	8	25.73	2.42	**0.04**	22.32	0.61	0.14
	Compliant		19.08	1.89		20.04	1.41	
% Stance of peak mass-specific power	Stiff	8	60.93	1.09	0.17	64.29	1.91	0.42
	Compliant		57.15	1.72		67.17	3.19	
Hip range of angles (deg)	Stiff	9	97.46	2.65	**0.00***	80.39	3.32	0.31
	Compliant		135.44	5.13		72.97	3.71	
Knee range of angles (deg)	Stiff	9	65.44	3.35	**0.03**	53.93	3.47	0.73
	Compliant		75.55	3.20		52.16	3.64	
Ankle range of angles (deg)	Stiff	9	72.74	3.01	0.23	84.17	5.54	0.73
	Compliant		66.45	4.14		80.68	14.34	

P-value are the significance levels of a Kruskal–Wallis test between substrate types; where a value of 0.05 or less is deemed significant (significant differences are shown in bold). Asterisks denote significance after a Bonferroni correction (Rice, 1989).

[for more detailed comparisons of gibbon leap types see Channon et al. (Channon et al., 2010b)].

The female gibbon conducted both leap types from both substrates (nine orthograde leaps from the stiff pole, two from the compliant pole, seven pronograde leaps from the stiff pole, three from the compliant pole), whereas the male gibbon only conducted orthograde single-footed leaps from the compliant substrate (11 leaps).

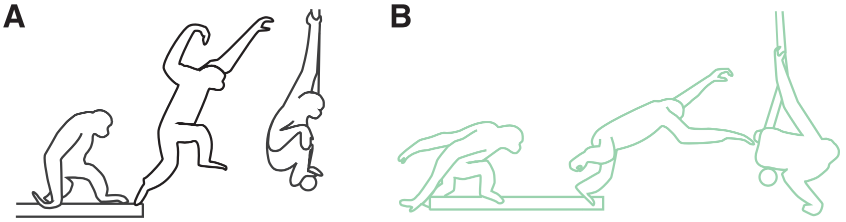

Fig. 2. Schematic representations of the leap types observed. (A) Orthograde single-footed leaps. (B) Pronograde single-footed leaps.

Orthograde leaps: stiff *vs* compliant pole

Orthograde leaps from the compliant pole used peak vertical forces that were not statistically different in magnitude to stiff-pole leaps (P=0.71), but peak force occurred earlier in stance during leaps from the compliant pole [P=0.04, not significant (NS) after Bonferroni correction; Table 1, Fig. 3A]. The vertical ground reaction force component appeared flatter during leaps from the compliant pole than during leaps from the stiff pole. Horizontal forces, conversely, were qualitatively and statistically similar between the pole types. Stance duration for orthograde leaps was significantly longer when leaping from the compliant pole than from the stiff pole (P=0.04, NS after Bonferroni correction; Table 1, Fig. 4A). Vertical impulse during stance was higher in leaps from the compliant pole than from the stiff pole (P<0.005; Fig. 4B, Table 1), whereas horizontal impulse was not significantly different between substrate types. Leap distance (the horizontal distance from the centre of mass at take-off to the landing pole) was shorter (P<0.005) for leaps from the compliant pole (0.38±0.07 m) than from the stiff pole (0.81±0.05 m), as take-off occurred nearer the tip of the compliant pole (Table 1, Fig. 5). Leaps from the compliant pole began more slowly (with less E_{K}, which is proportional to $\mathbf{v}_{\mathrm{R}}^{2}$, P<0.005; Fig. 6, Table 1), with less potential energy (P=0.01, NS after Bonferroni correction; Fig. 6) and less mechanical energy (P<0.005, NS after Bonferroni correction). The centre of mass trajectories (Fig. 5A) were qualitatively similar in shape during the stance period, although at take-off the gibbons appeared to reach more with fore- and hindlimbs during leaps from the compliant pole compared with leaps from the stiff pole (Fig. 5A). The stance phase of leaps from the compliant pole ended (at take-off) with lower velocity (P<0.005) and less mechanical energy (P=0.01; Table 1, Fig. 6). Potential energy at take-off was not significantly different between substrate types (P=0.19; Table 1). Mass-specific work done on the centre of mass during stance phase was similar between substrate types (P=0.84, Fig. 7). Peak centre of mass power during stance was not significantly different between leap types, and occurred at a similar point in stance (57–61% stance, P=0.17; Fig. 8A, Table 1).

The hip and knee joints underwent a wider angular excursion during the stance phase when leaping from the compliant pole (hip: P<0.005, knee: P=0.03, NS for the knee joint after Bonferroni correction; Table 1, Fig. 9), whereas the ankle joint excursion was not significantly different between substrate type. The timing of joint extension was not different between the pole types for any of the hindlimb joints (Fig. 9).

Pronograde leaps: stiff *vs* compliant pole

Peak vertical force was similar in magnitude but occurred at varying points of stance during leaps from the compliant pole (31±24% stance; Table 1, Fig. 3B). The vertical ground reaction force component oscillated during the stance period with a noticeable peak early in stance (before 50%; Fig. 3B), when leaping from the compliant pole. By comparison, the pronograde leaps from the stiff pole had a more ‘typical’ single humped vertical ground reaction force profile. Peak horizontal forces were similar in magnitude and timing for both substrates. Leaps from the compliant pole used a longer stance duration (P=0.03, NS after Bonferroni correction; Fig. 4A), and higher vertical impulse (P=0.02, NS after Bonferroni correction; Fig. 4B), than leaps from the stiff pole. The centre of mass trajectories for both substrate types when pronograde leaping appear qualitatively and statistically similar (Table 1, Fig. 5B), and, in contrast to orthograde leaps, the posture of the gibbons was not noticeably different when leaping from the two substrates. There were no significant differences in potential, kinetic or mechanical energy of the centre of mass at the beginning of stance between substrates (Table 1, Fig. 6), yet the centre of mass had more potential energy at take-off when leaping from the compliant pole. Mass-specific work done on the centre of mass was significantly greater when leaping from the compliant pole than from the stiff pole (P=0.05, NS after Bonferroni correction; Table 1, Fig. 7). Neither peak centre of mass power magnitude or timing were significantly different between substrate types, but there was an additional power ‘peak’ at the beginning of stance (~20%; Fig. 8B) when leaping from the compliant pole, which was not observed during leaps from the stiff pole. Hindlimb joint angular excursions were (statistically) similar between substrate types (Table 1, Fig. 9), and the timing of joint extension was similar for both substrates, during pronograde leaps.

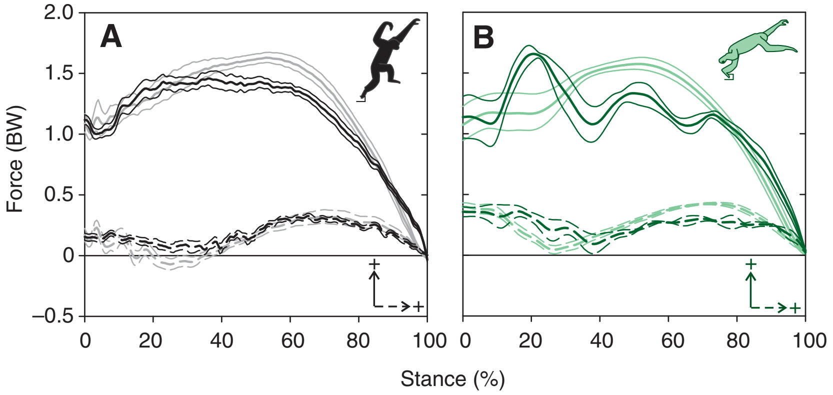

Fig. 3. Ground reaction force traces normalised to body weight (BW) in the vertical (solid lines) and craniocaudal (dashed lines) directions during stance phase. Thick lines show the mean, thin lines show standard error of the mean. Lighter colours (grey and pale green) show the stiff pole condition, Darker colours (black and dark green) show the compliant pole condition for (A) orthograde leaps and (B) pronograde leaps. Positive forces in the craniocaudal direction are propulsive. The gibbon diagrams show body posture at take-off.

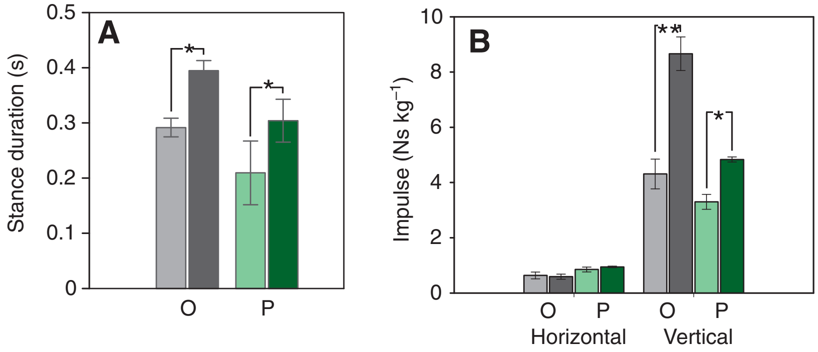

Fig. 4. (A) Stance duration and (B) impulse (normalised to body weight) in the horizontal and vertical directions during stance phase for orthograde (O) and pronograde (P) leaps from the stiff (grey and light green) and compliant (black and dark green) poles. Asterisks denote significant differences (*P<0.05; **P<0.01) see text for statistical calculations.

Peak force occurred earlier in stance during pronograde leaps and so the pole was stiffer at the moment of peak force application during pronograde leaps than during orthograde leaps (P=0.04; Fig. 10, Table 2; see Materials and methods).

DISCUSSION

Leaps from compliant *vs* stiff substrates

The gibbons increased the vertical impulse, without increasing peak force, during both leap types when leaping from the compliant pole. This is advantageous because it minimises pole deflection (which is proportional to instantaneous force) and the associated loss in potential energy of the centre of mass. The minimisation of pole deflection in leaping is reflected by the leap types utilised when taking off from a compliant pole. A previous study on leaping kinematics from stiff substrates (Channon et al., 2010b) showed that gibbons use at least four leap types, of which two were never used on the compliant pole (i.e. orthograde two-footed and squat leaps). These two leap types exhibit higher peak centre of mass powers than the leap types shown here, which points to a preference for low power (and indirectly, force) leap types to minimise the deflection of the substrate. The mechanisms used by the gibbons to maximise impulse without increasing peak force differed between leap types.

The approach taken during orthograde leaps was to leap more slowly, using a (significantly) longer stance time and slower take-off velocity. Pole deflection toward the end of stance during orthograde leaps (Fig. 9A) was compensated for by using a more extended hip joint (Fig. 9), increasing effective leg length and minimising potential energy loss by deflection of the pole. Lowering the centre of mass (E_P is effectively a measure of centre of mass height; Fig. 6) at the beginning of stance was facilitated by increased hip flexion. Flexed hips allow a more 'compliant' gait leading up to the leap, aiding stability and yielding a flatter ground reaction force curve, a mechanism employed by many arboreal primate species (Schmitt, 1994; Schmitt, 1999; Schmitt, 2003; Crompton et al., 1998). A more flexed hip joint also increases the amount of leg extension available before take-off, increasing effective leg length during the push-off phase (see above). Like other leapers, gibbons have relatively long hindlimbs relative to their trunk length (Schultz, 1936; Alexander, 1985; Isler et al., 2006) (although the long forelimbs disguise this in traditional indices such as the intermembral index), which helps to compensate for the downward movement of the pole by allowing force production over a longer time period (Preuschoft et al., 1996), so increasing impulse without increasing peak force. A downside of this tactic is that the extra impulse gained compared with leaps from stiff poles (Fig. 4B) is used in deflecting the compliant pole, and is not used to accelerate the centre of mass (Figs 5, 6 and 7). The increased hip joint excursion also allows the gibbon to effectively reduce the leap distance by maintaining pole contact until the centre of mass is further toward the landing pole (Fig. 5) than when leaping from the stiff pole. This is probably a necessity for safely completing the leap, given the reduced amount of kinetic energy available at take-off.

Although pronograde leaps from the compliant pole used significantly longer stance times than leaps from the stiff pole, the kinetic energy of the centre of mass was similar between substrates:

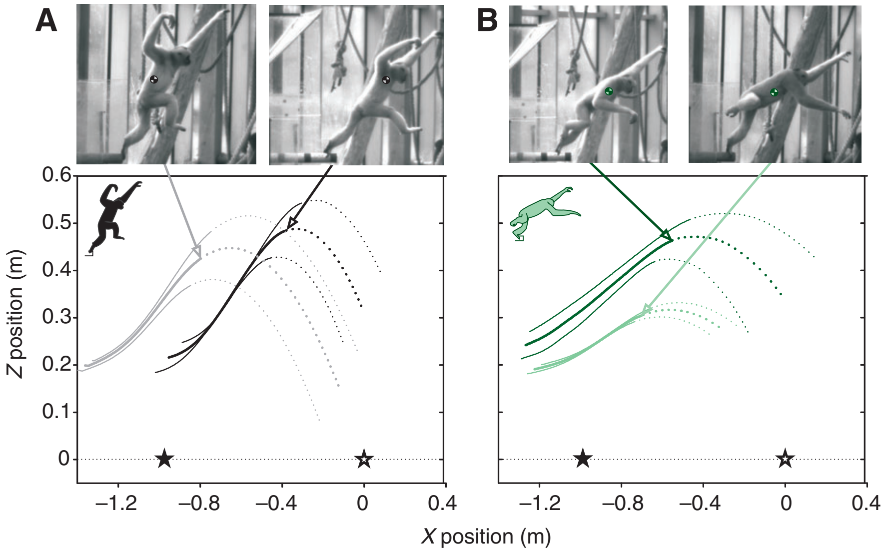

Fig. 5. Centre of mass position during (A) orthograde and (B) pronograde leaps from the stiff (grey and light green) and compliant (black and dark green) poles. Thick lines show the mean, thin lines show the standard error of the mean. Solid lines indicate stance phase, dotted lines show centre of mass position after take-off. Filled stars show the position of the take-off pole; open stars show the position of the landing pole. Centre of mass position was normalised to the position of the landing pole. The gibbon diagrams show body posture at take-off.

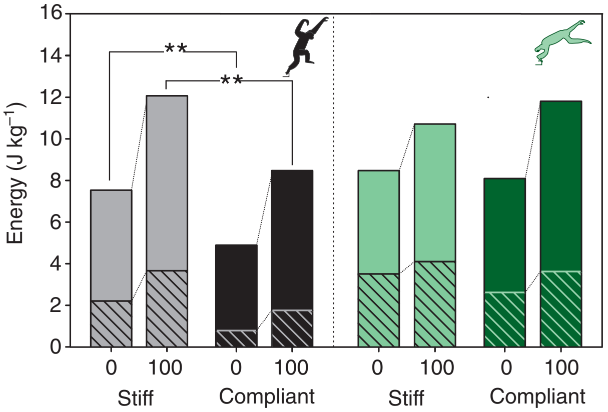

Fig. 6. Potential (plain solid bars) and kinetic (hatched bars) energy of the centre of mass normalised to body mass during orthograde (left) and pronograde (right) leaps from the stiff (grey and light green) and compliant (black and dark green) poles. Numbers show percentage stance phase: 0 denotes the start of stance and 100 denotes take-off. The total bar height represents the mechanical energy of the centre of mass. **Significant differences in mechanical energy ($P<0.01$); see text for statistical calculations. The gibbon diagrams show body posture at take-off.

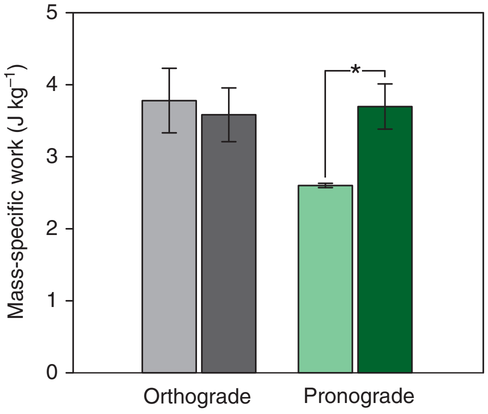

Fig. 7. Mass-specific mechanical work done on the centre of mass during orthograde and pronograde leaps from the stiff (grey and light green) and compliant (black and dark green) poles. *Significant differences in mechanical work ($P<0.05$); see text for statistical calculations.

i.e. the gibbons did not leap more slowly. The power peak early in stance (~20%), accelerated the centre of mass (the peak coincides with peak force; Fig. 3) while it was positioned over a relatively stiff (compared with the orthograde leaps) part of the pole. Powering the leap from a stiffer region of the pole minimises vertical deflection, and hence, potential energy loss, i.e. the extra power, compared with leaps from the stiff pole, is converted into centre-of-mass work (see Fig. 7) and not spent deflecting the pole, as is the case during orthograde leaps from the compliant pole, resulting in a net gain in work.

We believe that this preference for powering the leap from a stiffer section of the pole, as well as actively avoiding leap types with higher centre of mass powers, demonstrates a strategy to optimize leaping performance. During data collection the female gibbon changed her leap type from always conducting orthograde leaps to always conducting rapid pronograde leaps, suggesting some conscious learning while using the pole, and a preference for the stiffer section (closer to the pivot) of the pole from which to power the leap.

Using elastic energy storage in substrates

The pole used here was very lightweight, possessed little rotational inertia and had a high unloaded natural frequency (~30 Hz). These characteristics are more comparable with a springboard that a gymnast might use to vault from than with a cantilever diving board that a diver might use. Reports of ‘branch pumping’ of wild gibbons to store energy in the branch before leaping (Fleagle, 1976) are similar to the latter. In this hypothesis, as the gibbon pumps the branch it stores energy in it, which allows the energy from a number of ‘pumps’ to be released quickly during one leg extension (Cheng and Hubbard, 2004). This technique is reliant on the substrate having more momentum than the accelerating gibbon. Without this prerequisite the substrate is deflected away from the gibbon and potential energy is lost (Alexander, 1991). Conversely, when a gymnast uses a springboard, the kinetic and potential energy of the falling centre of mass is stored as elastic energy in the springs and returned when the gymnast undergoes leg extension, in a much more rapid (single) oscillation (for a review, see Prassas et al., 2006).

The gibbons in this study did not purposefully oscillate the pole before leaping, despite being capable of sitting comfortably on the end of the pole (indicating that the stability of the pole did not prohibit this behaviour). Squat leaps have a stationary start and so seem the most likely leap type to involve ‘branch pumping’ behaviour, but squat leaps from the compliant pole were not observed in this study. Field data from wild gibbons are needed to determine the relationship between leap type and substrate properties.

The increased vertical impulse (which is not converted to centre of mass work), the requirement of a wider range of hip joint angles and the slow take-off speed of the recorded gibbon leaps makes the efficient use of the pole as a gymnastic-style springboard seem unlikely during orthograde leaps. The more rapid pronograde leaps,

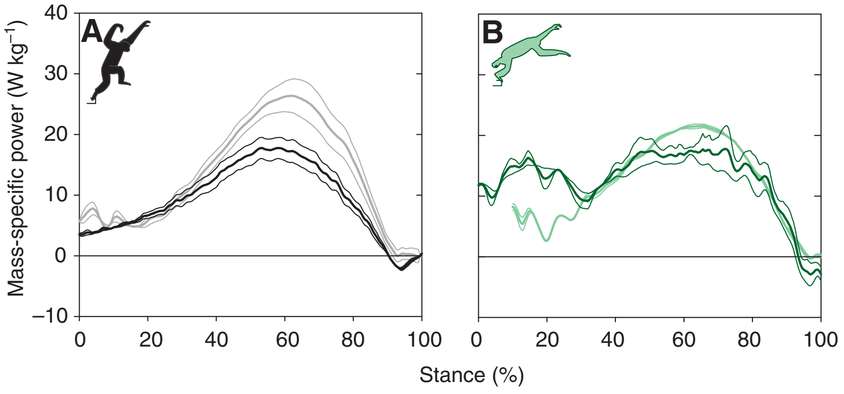

Fig. 8. Mass-specific centre of mass power during stance phase for (A) orthograde and (B) pronograde leaps from the stiff (grey and light green) and compliant (black and dark green) poles. Thick lines show the mean, thin lines show the standard error of the mean. The gibbon diagrams show body posture at take-off.

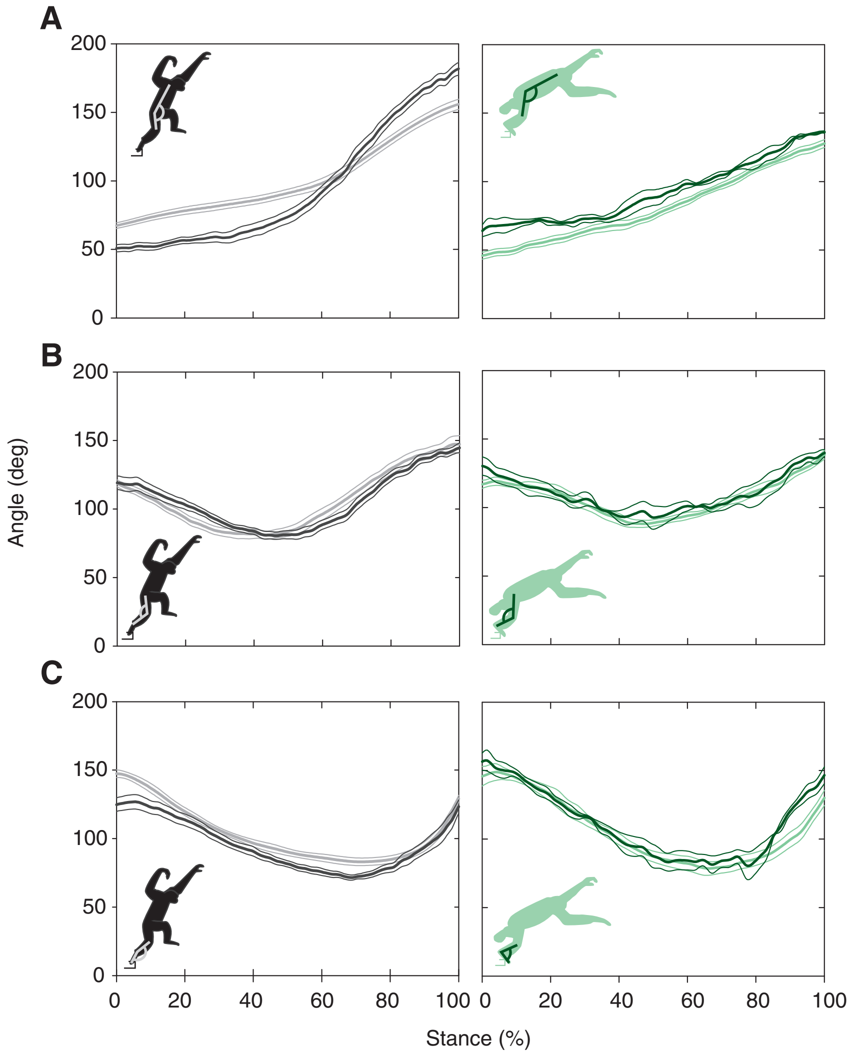

Fig. 9. Hindlimb joint angles during stance at the (A) hip, (B) knee and (C) ankle, for orthograde (left) and pronograde (right) leaps from the stiff grey and light green) and compliant (black and dark green) poles. Thick lines show the mean, thin lines show the standard error of the mean. Angle definitions are described further in the text. The gibbon diagrams show body posture at take-off.

however, do convert additional impulse into increased mechanical work. Yet, if the gibbons were using the pole like a gymnastic springboard, we would expect to see the centre of mass lose gravitational-potential energy through the first part of stance, storing energy in the springs before rising upward until take-off (where energy is returned as kinetic energy) (Kooi and Kuipers, 1994). The centre of mass of the gibbons during pronograde leaping increased in height throughout the stance phase (Fig. 5), ruling out the use of the pole in this manner. Furthermore, there was no increase in kinetic energy at take-off, a major leap performance determinant (Crompton et al., 1993) when leaping from a compliant pole, which makes it improbable that the compliant pole increases leap performance by the storage and recovery of elastic energy, either *via* a branch pumping method or by using the pole as a rapidly recoiling springboard. Finally, if the gibbons were using the pole for energetic gain, we would expect to observe a change in the timing of hindlimb joint extension between substrate types (Cheng and Hubbard, 2004), yet, no such change was observed.

This study is the first to highlight the ability of non-human apes to actively modify leaping biomechanics advantageously when using a compliant *vs* stiff substrate. Furthermore, our findings highlight peak force (and hence, pole deflection) minimisation during leaping as a desideratum in both the leap types used, with differing techniques employed for each leap type to achieve this.

Wild animals using compliant substrates

For leaping animals the ideal substrate to utilise an energy saving or power amplifying mechanism would be either highly compliant, with a low natural frequency (similar to a diving board) or relatively stiff, with a high natural frequency (like a gymnastic springboard).

Table 2. Pole stiffness at the moment of peak force application for each leap type

		Orthograde		Pronograde		
	Fig.	Mean	s.e.m.	Mean	s.e.m.	*P*-value
Pole stiffness at peak force (N mm^{-1})	10B	4.02	0.332	6.04	0.54	**0.03**

P-value denotes the significance of a Kruskal–Wallis test between leap types, where a value of 0.05 or less is deemed significant (the significant difference is shown in bold).

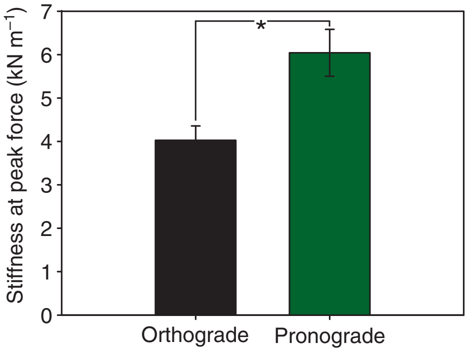

Fig. 10. The instantaneous pole stiffness at the moment of peak force for orthograde and pronograde leaps. *Differences at the $P<0.05$ significance level, see text for statistical calculations.

Tree branches of this nature are likely to be rare because those that are highly compliant are generally very thin and hence lightweight (McMahon and Kronauer, 1976) and branches with a high natural frequency are likely to be too stiff to deflect sufficiently to facilitate useful energy storage.

Like the pole used here, tree branches get progressively less stiff with distance from the trunk, and so there is a possible optimum distance from the trunk from which to execute the leap. Field data from gibbons and langurs suggest that most leaps are conducted tree to tree from the terminal branches (Fleagle, 1976; Gittins, 1983; Sati and Alfred, 2002; Huang and Li, 2005), indicating that such optima are not utilised. This is probably because the energy required to leap the increased distance from the optimum position to the target is greater than the energy required to negate the deflection at the branch terminus. Alternatively, there may be trade-offs between leap cost and safety, where terminal branch leaps allow a better perception of leap distance and potential hazards (predators, obstructions etc.).

The selection of larger-diameter obliquely angled take-off substrates that minimise forces orthogonal to the branch (and hence branch deflection) by tarsiers (*Tarsius bancanus*) indicates avoidance of the undesirable perturbing properties of compliant branches, rather than an attempt at utilising them for energetic gain (Crompton et al., 2010). The gibbons in this study could not avoid the compliant pole, or choose a less compliant alternative. They did, however, modulate the timing of their force production during pronograde leaps to coincide with the centre of mass being positioned over a stiffer region of the pole, again suggesting an active avoidance of the deflection of the pole, rather than using the pole for energetic gain. Together, the two studies suggest that haplorrhine primates, at least, are capable of selecting substrates for leaping according to their gross mechanical properties.

The approaches used by the gibbons to minimise pole deflection in this study are theoretically available to all leapers. The method used when leaping with orthograde posture (wider hip excursion, minimising leap distance and peak force) is probably most useful for short leaps. Our gibbons reduced the effective leap distance from 0.81 m to 0.38 m during orthograde leaping from the compliant pole *vs* the stiff pole. In this case that represents a 43% reduction in leap distance, whereas if the leap was 4 m [mean wild-siamang leap distance (Fleagle, 1976)] instead of the 1 m used here, the leap would be reduced by ~12% [(3.38/3.83)×100]. However, even this reduction could be considered significant when a fall could result in serious injury or death (Schultz, 1956; Bramblett, 1967; Buikstra, 1975; Lovell, 1987).

The extra 'power peak' early in stance during the leaps observed here, could easily be replicated by wild animals moving on compliant branches. A notable limitation of our setup was that the gibbons did not have sufficient distance to 'run up' to the leap. Wild animals can run along the stiffer regions of branches for several metres before take-off, adding substantial mechanical energy to the centre of mass, while minimising branch deflection.

A further probable method by which arboreal animals minimise branch deflection is by sacrificing potential energy during the leap. Our setup was built to study horizontal leaps without loss of height, but field studies of wild gibbons (Fleagle, 1976; Gittins, 1983) and observations of free ranging captive gibbons (A.J.C., personal observation, at Planckendael Wild Animal Park, Belgium, Chester Zoo, UK and Twycross Zoo, UK) indicate that gibbons often simply run off the end of branches or "…(launch themselves) by pulling with the arms." (Gittins, 1983) and "…leaps are always from a higher to a lower level… Although leaps may extend over, 20 m vertically, they rarely cover as far as 10 m horizontally" (Fleagle, 1976). These leaps probably have comparatively low vertical acceleration (Crompton et al., 1993) and hence, branch displacement, yet still reach the lower positioned landing target. This hypothesis is supported by field data suggesting that in gibbons, leaping is mainly used to rapidly cross gaps in the forest canopy, whereas height gains are achieved by climbing (Gittins, 1983).

Conclusions

Our data indicate that the gibbons in this study neutralised substrate deflection rather than utilising its energy-storage capability. The gibbons employed different techniques to minimise substrate deflection depending on leap type and approach speed. Orthograde leaps used a wider hip joint excursion to compensate for the deflection of the pole and increased the effective leg length over which force could be exerted. The increased hip joint motion also reduced the effective distance of the leap, allowing a longer stance time and slower take-off velocity to be used. More rapid pronograde leaps produced power earlier in stance than orthograde leaps from the compliant pole, when the pole is effectively stiffer, minimising deflection and potential energy loss. The gibbons also avoided more powerful orthograde two-footed and orthograde squat leaps, perhaps to minimise pole deflection. Future work investigating maximal leap biomechanics and a wide range of pole stiffnesses would increase our understanding of leap biomechanics and the role of substrate compliance in an arboreal environment.

LIST OF ABBREVIATIONS

CoP_{CC}	craniocaudal position of the centre of pressure
E_K	kinetic energy of the centre of mass
E_M	mechanical energy of the centre of mass
E_P	potential energy of the centre of mass
$\mathbf{F}_{CC}$	craniocaudal force
$\mathbf{F}_{ML}$	mediolateral force
$\mathbf{F}_V$	vertical force
$\boldsymbol{g}$	gravitational acceleration (–9.81 m s^{-2})
h	vertical height of the centre of mass
k	stiffness
k_I	instantaneous pole stiffness
m	mass
$\mathbf{M}_{CC}$	craniocaudal moment
$\mathbf{M}_{ML}$	mediolateral moment
$\mathbf{M}_V$	vertical moment
S_{CC}	distance between the spring and the pivot point
S_{DIS}	vertical displacement of the spring
T_{CC}	distance between the pole tip and the pivot (pole length)
T_{DIS}	displacement at the pole tip
$\mathbf{v}_R$	resultant velocity
α	forceplate specific constant, 0.478

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