RESEARCH ARTICLE

The effect of substrate diameter and incline on locomotion in an arboreal frog

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SUMMARY

Frogs are characterized by a unique morphology associated with their saltatory lifestyle. Yet, arboreal species show morphological specializations relative to other ecological specialists allowing them to hold on to narrow substrates. However, almost nothing is known about the effects of substrate characteristics on locomotion in frogs. Here, we quantified the 3D kinematics of forelimb movement for frogs moving across branches of different diameters (1 and 40 mm) and two different inclines (horizontal and 45 deg uphill). Our results show that grip types differ while moving across substrates of different diameters and inclines. The kinematics of the wrist, elbow and shoulder as well as the body position relative to the substrate also showed significant effects of individual, diameter and incline. Kinematic differences involved duration, velocity of movement and angular excursions. Differences were most pronounced for the proximal joints of the forelimb and effects for substrate diameter were greater than for incline. Interestingly, the effects of diameter and incline on both grip type and kinematics are similar to what has been observed for lizards and primates, suggesting that the mechanics of narrow substrate locomotion drive the kinematics of movement independent of morphology and phylogeny.

Key words: kinematics, movement, fine branch milieu, grasping, walking.

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INTRODUCTION

Despite the huge advances conferred by studies of locomotion in controlled conditions, more and more researchers are beginning to understand the value of investigating locomotion in ecologically pertinent contexts (Irschick and Garland, 2001; Biewener, 2002; Daley and Biewener, 2006). In nature, variation in surface characteristics is ubiquitous and these variations are non-negligible, especially for small animals where even seemingly minor obstacles or variations in substrate properties may affect locomotion (Irschick and Jayne, 1999; Vanhooydonck et al., 2005; Hyams et al., 2012). For arboreal animals, variation in substrate diameter and incline are two obvious sources of variation that are known to affect locomotor performance and may have profound effects on performance and fitness (e.g. Higham and Jayne, 2004; Spezzano and Jayne, 2004; Foster and Higham, 2012). For example, variation in morphology associated with habitat use as the result of selection on locomotor performance on branches of different diameters (Losos and Sinervo, 1989; Vanhooydonck et al., 2006) has driven the unique fourfold radiation of ecomorphs on the islands of the Greater Antilles (Losos, 2009). Similarly, it has been demonstrated that chameleons living in habitats characterized by different substrate diameters show different morphologies and levels of performance (Herrel et al., 2011; Herrel et al., 2013). Effects of incline have also been investigated in some detail and the majority of studies have indicated significant effects of incline on the kinematics of locomotion in a variety of taxa (e.g. Irschick and Jayne, 1998; Irschick and Jayne, 1999; Spezzano and Jayne, 2004). These differences are often related to the need of an animal to move against gravity when moving up an incline, thus soliciting the forelimbs to a greater degree in producing propulsive forces (Zaaf et al., 2001a; Zaaf et al., 2001b; Foster and Higham, 2012).

Despite the wealth of information available for the effects of substrate characteristics on locomotion in lizards and mammals (e.g. Schmitt, 2003; Higham and Jayne, 2004; Isler, 2005; Renous et al., 2010), hardly anything is known about the effects of the substrate on locomotion in frogs. Although this may not seem surprising at first, given that the bauplan of frogs is highly specialized for jumping (Lutz and Rome, 1994; Shubin and Jenkins, 1995; Nauwelaerts et al., 2007; Prikryl et al., 2009), many frogs live in arboreal habitats and need to deal with variation in substrate diameter, incline and texture. Moreover, arboreal frogs are extremely diverse and have radiated independently in many different lineages (Frost et al., 2006). Among arboreal frogs many ecological specialists exist, with some species of tree frogs being fine branch specialists and showing a walking-type gait rather than jumping from branch to branch (Manzano et al., 2007; Manzano et al., 2008). Species of the genus *Phyllomedusa* are of special interest given their known ability to move across branches of narrow diameter and the fine motor control they appear to have over their fingers, allowing them to perform a precision grip (Burton, 1998; Herrel et al., 2008). Moreover, many of these arboreal species are known to use their forelimbs in contexts other than locomotion yet requiring great dexterity such as prey capture and manipulation (Gray et al., 1997; Sustaita et al., 2013), nest building (Kenny, 1966; Biju, 2009), and the wiping behaviour where frogs spread lipids over their body (Lillywhite et al., 1997; Barbeau and Lillywhite, 2005).

In the present study, we focused on the effects of substrate diameter and incline on the kinematics of the forelimb in a fine branch specialist, *Phyllomedusa azurea*. We concentrated on the forelimb given its implication in generating traction and propulsion during locomotion on inclines and the general paucity of data on forelimb kinematics in non-mammalian vertebrates. In addition, we investigated how animals grip substrates varying in diameter and incline, and compared these data with previously published data for mammals. We predicted that both incline and substrate diameter will affect locomotion, with the effects of diameter being stronger, as has been observed for lizards (Foster and Higham, 2012), because of the constraints of narrow diameter locomotion on stability likely necessitating profound changes in kinematics. Moreover, we predicted that, in analogy with what has been observed for lizards (Foster and Higham, 2012), kinematic changes will be more pronounced for proximal limb segments. Finally, we predicted that frogs will keep their body closer to the substrate when walking on narrow dowels to improve stability.

MATERIALS AND METHODS
Study animals

Four captive adults of the species *P. azurae* Cope 1862 were used for this study. This species is native to Central America and is a hylid twig specialist (Caramaschi, 2006; Frost et al., 2006; Wiens et al., 2010). Individuals were maintained in the Function and Evolution Laboratory of the National Museum of Natural History in vivaria with a temperature of 25°C during the day and ambient temperature at night. Frogs were misted daily and were fed every other day with crickets. Snout–vent length (SVL) was measured using digital callipers (Mitutoyo, Kawasaki, Japan). For every individual, eight measurements were taken and averaged (SVL means ± s.e.m. for each individual: 34.5±0.5, 36.7±0.5, 40.9±0.4 and 42±0.9 mm). Coloured patches on the inside of the left thigh allowed us to identify each animal individually.

Experimental set-up

For this study a Perspex box (1500×250×250 mm) was built that allowed the attachment of substrates with different diameters (1, 4 and 40 mm). To standardize substrate compliance and texture, all substrates were put under tension to avoid bending and adhesive tape was added to all substrates. Substrate diameter selection was randomized to avoid habituation effects. Two substrate orientations (horizontal and 45 deg) were used.

Video recording

The animals were filmed using five synchronized high-speed cameras (ProSilica GE680, 200 Hz, pixel resolution 640×480) while walking across each substrate. Four cameras were focused on the central part of the substrate and one recorded an overview in dorsal view. Thus, the anatomical points of interest were visible in at least three of the four views during the whole sequence recorded. Cameras were calibrated and scaled using a DLT routine (Hartley and Sturm, 1995) based on the digitization of a 10×10 cm black-and-white checkerboard composed of 1×1 cm squares. Illumination was provided by three custom-made ultra bright red LED arrays. The red lights were used as these animals are nocturnal and were not inclined to move under daylight conditions. The recording sessions consisted of 10 s of recording. In total, five good sessions (i.e. sessions where animals walked straight and continuously through the field of view of the camera) were recorded for each individual on each diameter (1 and 40 mm) and each incline (0 and 45 deg). In addition, we filmed a set of locomotion trials on a substrate of intermediate diameter (4 mm) to quantify hand postures during locomotion.

Video analyses

The posture of the hand was quantified for three substrate diameters (1, 4 and 40 mm) and two inclines (horizontal and 45 deg). To explore whether individuals used different grasp types depending on substrate diameter and orientation, the three first grasps of the left hand during a locomotion sequence were analysed for the five filming sessions obtained for each individual at each diameter at both orientations. To extract kinematic data, a custom-written Matlab routine (Loco 3.3; P.-A. Libourel) was used to digitize anatomical landmarks on multiple synchronized views for five complete steps of each animal on each substrate and for each substrate orientation. Each step came from a different recording session. This allowed us to calculate the screen coordinates of the following landmarks on the left forelimb (Fig. 1): snout, shoulder, elbow, wrist, finger, the ventral most point on the belly of the frog and a point on the substrate directly opposite to this point. A fourth order zero-phase shift Butterworth low-pass filter (Winter, 2004) implemented in Microsoft Excel by Sam Van Wassenbergh (University of Antwerp, Belgium) was used to smooth the raw trajectories and angles. The filtering frequencies used were 3 Hz for the snout and shoulder and 8 Hz for the elbow, wrist and hand. The angular data were smoothed at a frequency of 9 Hz and a filter of 5 Hz was applied on data describing the distance between the body and the substrate. The screen coordinates were transformed into metric units, allowing us to obtain measures of velocity, angle and distance for each recording session. The maximum linear velocities were extracted for each joint as well as the snout. Maximal and minimal shoulder, elbow and wrist angles were recorded in addition to the time required to reach the peak angular excursion. Finally, the body height relative to the substrate (maximum, minimum) was recorded for each trial.

Statistical analyses

To test the effect of the substrate incline and diameter on the type of grasping used by each individual, a Fisher exact test was used. This test is appropriate here because the individual sample is relatively small (15 grasps by individual, by situation). Next, a χ^2
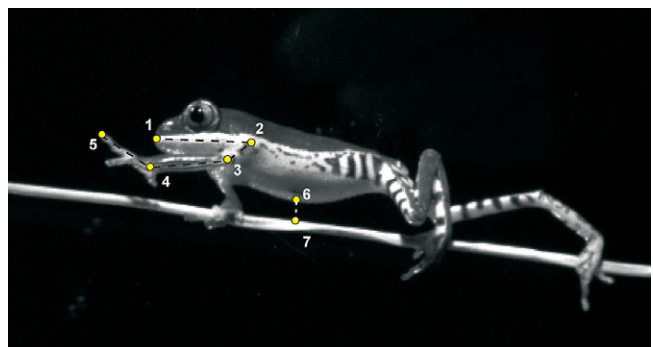

Fig. 1. Illustration of the landmarks digitized on each frame and the angles and distances measured. The shoulder angle was defined as the angle subtended by landmarks 1, 2 and 3; the elbow angle was defined as the angle subtended by landmarks 2, 3 and 4 and the wrist angle as the angle subtended by landmarks 3, 4 and 5. Landmark 1 was used to calculate overall velocity and landmarks 6 and 7 were used to calculate the height of the body above the substrate. All landmarks were digitized on each of the five camera views.

test allowed us to test the effect of the substrate incline and diameter on the grasp type used for all individuals combined (*N*=4).

A factor analysis with a Varimax rotation of the factors was performed on the log$_{10}$-transformed kinematic variables to reduce the dimensionality of the data set. Four factors with eigenvalues greater than one were extracted based on the Kaiser criterion, and retained for subsequent analyses. The factor data being normally distributed, a multivariate analysis variance was performed with incline, substrate diameter and individual as fixed factors. This MANOVA was coupled to a univariate analysis of variance to highlight the specific effects of the substrate properties on the forelimb kinematics in this species. Finally, we conducted a MANCOVA to test whether kinematic differences existed when taking to account differences in overall movement velocity. All analyses were performed using IBMSPSS V. 20.

RESULTS
Grip types
Three grip types were observed: D23, where the substrate is gripped between fingers two and three; D34, where the substrate is gripped between fingers three and four; and D234, where the substrate is gripped between fingers two and four, with finger three aligned with the substrate (Fig. 2, Table 1). Differences in diameter and incline were significant for most individuals (Table 2). Substrate diameter

Table 1. Percentage of grip types observed on each substrate and inclination

	D23		D34		D234	
Diameter (mm)	Horizontal	Inclined	Horizontal	Inclined	Horizontal	Inclined
1	35%	63%		15%	60%	21%
4		12%	40%		50%	83%
40		25%	60%	13%	40%	62%

D23, grip between fingers two and three; D34, grip between fingers three and four; D234, grip between fingers two and four with finger three aligned with the branch. Note that on narrow substrates (1 and 4 mm), animals occasionally (5% on the 1 mm horizontal and 1% on the 1 mm inclined substrate; 10% on the 4 mm horizontal and 5% on the 4 mm inclined substrate) used grips that could not be clearly identified as one of the three main grip types.

(χ^2=72.7, *P*<0.001) and incline (χ^2=37.9, *P*<0.001) also affected the type of grip used at the group level. On the horizontal, frogs never used grip D34 when moving on a 1 mm substrate. In contrast, on a 4 and a 40 mm wide substrate, grip type D23 was never used (Table 1, Fig. 2). Other grip types were used in similar proportions (Table 1). On the incline, grip type D234 dominated for wider substrates (Fig. 2, Table 1) but grip type D23 dominated on the narrowest substrate (1 mm, Table 1).

Forelimb kinematics
Differences in forelimb kinematics and overall locomotion were striking for locomotion on different substrates. Frogs moved at much greater speed when moving across wider substrates (Figs 3–6) taking less than half (horizontal) or even a quarter (inclined) of the time needed to move across narrow substrates. Kinematic patterns were generally similar on different substrate diameters and inclines but showed some distinct features related to diameter and incline. Whereas on the narrow substrate the elbow showed only a single flexion–extension cycle, for example, on the wide substrate a double-humped profile becomes apparent, with an initial extension followed by a flexion–extension cycle (Figs 3–6). This effect of substrate diameter was especially pronounced for locomotor trials at a 45 deg angle. The wrist angle variation through the cycle also showed, distinct differences depending on substrate diameter with the profile being single humped for wide substrates, yet double humped and more variable on narrow diameters. Finally, movements were generally faster and more secure when moving on inclined substrates (Figs 3–6).

The factor analyses extracted four factors that jointly explained 70% of the total variation in our data set (Table 3). The first factor explained nearly 41% of the overall variation in kinematics and was highly correlated with velocity. The second factor explained another 12% of the variation and represents the variation in the height of the body above the substrate. The third and fourth factors explained 10% and 8% of the overall variation, respectively, and are kinematic
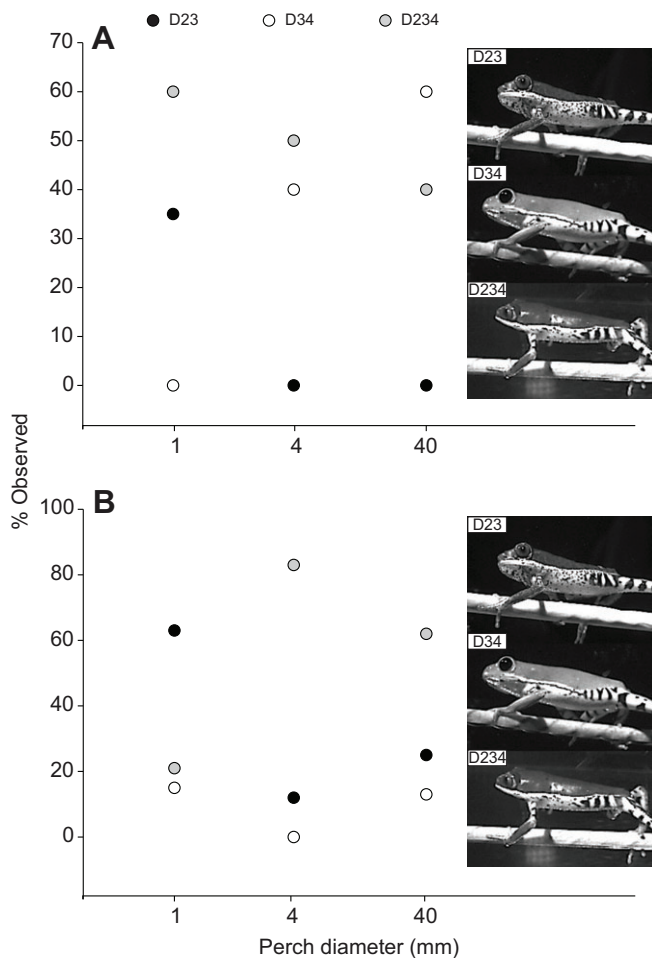

Fig. 2. Figure summarizing the different grip types used by the frogs on different substrates and inclines. (A) Horizontal substrate, (B) inclined substrate (45 deg). Images to the right illustrate the different grip types: D23, D34 and D234 (see Results).

Table 2. Results of the Fisher exact tests for effects of substrate and incline on the grip types used by each individual

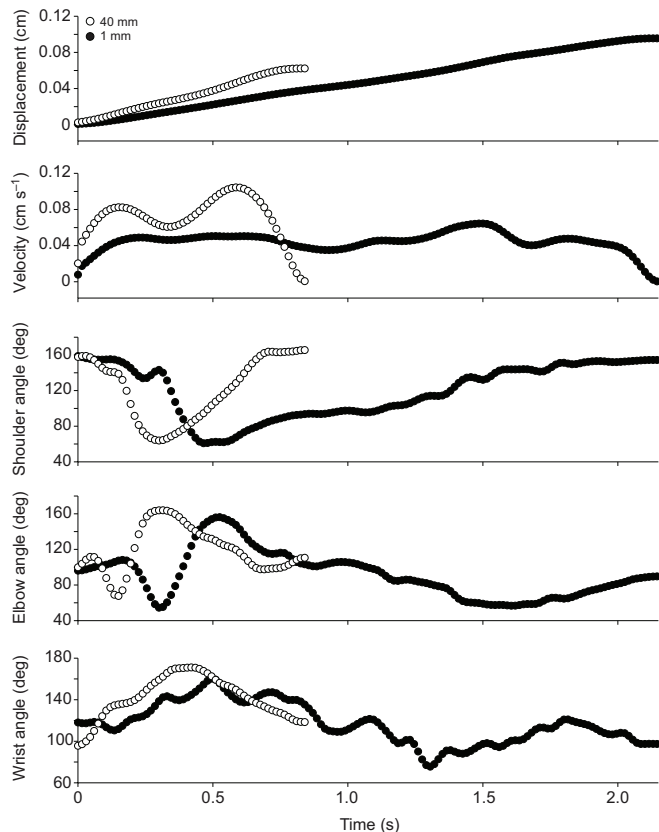| Individual	Diameter	Incline
1	<0.001	0.41
2	<0.001	0.032
3	0.0024	<0.001
4	0.0015	<0.001

Table entries are *P*-values.

Fig. 3. Representative locomotor cycle illustrating changes in forelimb angle during locomotion on a horizontal substrate. Open circles represent locomotion on wide dowels (40 mm) and filled circles represent locomotion on narrow dowels (1 mm). From top to bottom, the graphs indicate the overall displacement, velocity, and shoulder, elbow and wrist angle for a single individual.
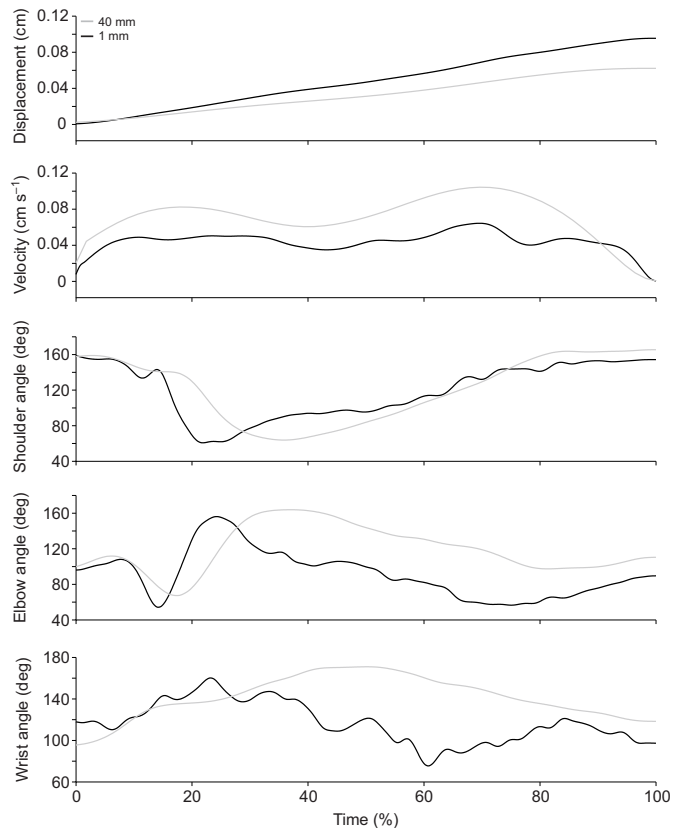

Fig. 4. Representative locomotor cycle illustrating changes in forelimb angle during locomotion on a horizontal substrate. The black line represents locomotion on a narrow dowel (1 mm) and the grey line locomotion on a wide dowel (40 mm). Cycle length has been standardized to 100%.

descriptors of forelimb movement. The third factor was most highly determined by the minimal shoulder angle and the time to the peak elbow angle, with positive scores on this factor being related to animals maintaining large shoulder angles throughout the cycle and long times to maximal elbow excursion. The fourth factor is determined by the maximal shoulder angle, with individuals showing high scores on this factor showing large shoulder angles.

A MANOVA executed using the factor scores showed significant effects of individual (Wilks' λ=0.34, $F_{12,161}$=161.7; P<0.001), diameter (Wilks' λ=0.13, $F_{4,61}$=98.4; P<0.001) and incline (Wilks' λ=0.41, $F_{4,61}$=22.3; P<0.001) on the forelimb kinematics. All interactions were also significant (all P<0.005) suggesting that each individual changes its kinematics differently depending on both substrate diameter and incline. Subsequent univariate ANOVA indicated that individual effects were significant on factors one ($F_{3,64}$=15.0; P<0.001) and three ($F_{3,64}$=15.0; P=0.014), substrate diameter effects on factors one ($F_{1,64}$=99.1; P<0.001), two ($F_{1,64}$=6.2; P=0.006) and four ($F_{1,64}$=37.7; P<0.001), and incline effects on factors one ($F_{1,64}$=15.9; P<0.001), three ($F_{1,64}$=6.3; P=0.015) and four ($F_{1,64}$=56.2; P<0.001). Interactions between individual and diameter were significant on factor four only ($F_{3,64}$=4.0; P=0.011) suggesting a relatively homogeneous response of frogs to changes in substrate diameter. Individual by incline effects were significant on factors two ($F_{3,64}$=3.2; P=0.03), three ($F_{3,64}$=4.1; P=0.01) and

four ($F_{3,64}$=4.9; P=0.004), suggesting that variation in incline has strong subject-specific effects on the kinematics of the forelimb. The interaction between diameter and incline was significant for factors two ($F_{1,64}$=5.8; P=0.019) and three ($F_{1,64}$=8.2; P=0.006), and the three-way interaction for factor one only (i.e. variation in movement velocity; $F_{3,64}$=4.0; P=0.011). When using speed as a co-variate, effects of individual (Wilks' λ=0.54, $F_{12,159}$=3.45; P<0.001), diameter (Wilks' λ=0.65, $F_{4,60}$=8.21; P<0.001) and incline (Wilks' λ=0.71, $F_{4,60}$=6.21; P<0.001) remained significant. Subsequent univariate ANOVA showed, however, that effects of diameter and incline were only significant on factor four (diameter: $F_{1,63}$=7.93; P<0.001; incline: $F_{1,63}$=2.88, P=0.008), showing that kinematic variation independent of speed is most pronounced in the shoulder angle with locomotion on narrow substrates being characterized by greater shoulder angles in general. Moreover, inclined substrates were associated with greater shoulder angles than horizontal substrates.

DISCUSSION
Locomotion and grip types
Our observations of frogs walking along the different substrates show that they generally used slow symmetrical walks ranging from a walking trot on the widest substrates to a lateral sequence walk on the narrower ones. Only on the narrowest substrate (1 mm) did animals deviate from this footfall pattern, with sequences becoming more
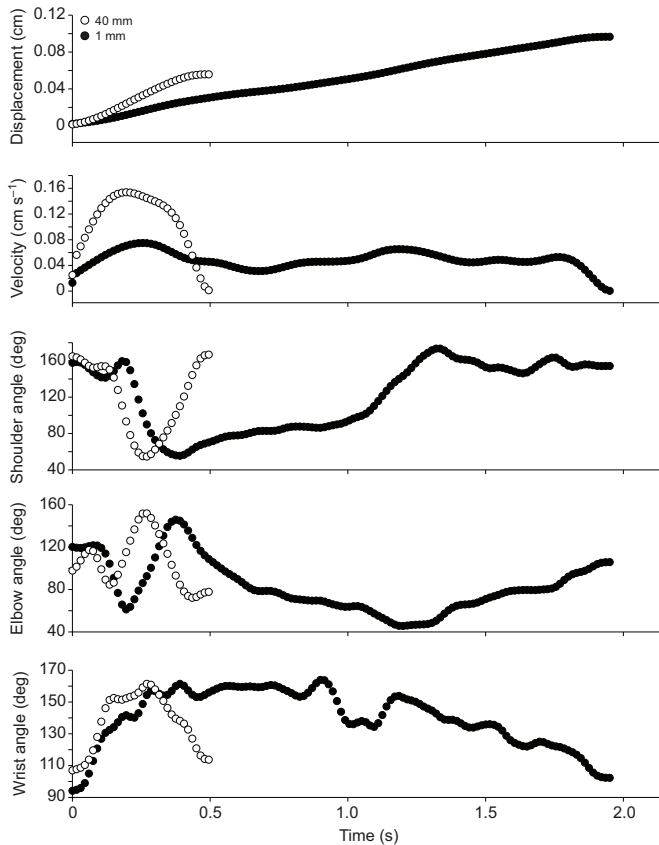
Fig. 5. Representative locomotor cycle illustrating changes in forelimb angle during locomotion on an inclined substrate (45 deg). Open circles represent locomotion on wide dowels (40 mm) and filled circles represent locomotion on narrow dowels (1 mm). From top to bottom, the graphs indicate the overall displacement, velocity, and shoulder, elbow and wrist angle for a single individual.
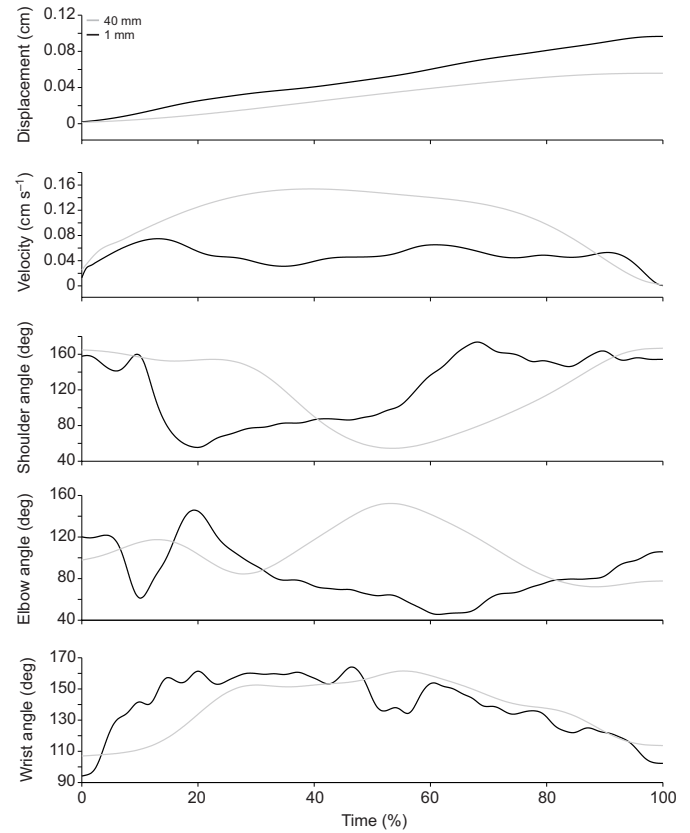

Fig. 6. Representative locomotor cycle illustrating changes in forelimb angle during locomotion on an inclined substrate (45 deg). The black line represents locomotion on a narrow dowel (1 mm) and the grey line locomotion on a wide dowel (40 mm). Cycle length has been standardized to 100%.

irregular. Although animals predominantly used one of three grip types, in some cases irregular grip types were observed on the narrower diameter substrates (Table 1). Grip D23, characterized by a grip between digits two and three, typically observed on the narrowest substrate, allows an alignment of the hand with the long axis of the substrate and as such this grip may help stabilize the animal. Moreover, its more frequent use on inclined *versus* horizontal substrates suggests that it may facilitate traction on the substrate. On wider substrates this grip type is utilized much less frequently, independent of the substrate orientation. These results are similar to data obtained for the gray mouse lemur (Reghem et al., 2012) as well as other arboreal mammals for which the use of this type of grip is reduced on wider substrates (Hershkovitz, 1977; Sargis, 2001). The grip type D34 is most common on wide, horizontal substrates and is nearly absent on inclined substrates. The morphology of the hand with well-developed flexor (flexor indicis superficialis proprius) and extensor muscles (extensor indicis brevis superficialis) associated with the first digit (Manzano et al., 2008) may partly explain this result. Indeed, grip forces are likely to be diminished when the branch is gripped between digits 3 and 4, not allowing the use of the powerful first digit because of rotation at the wrist induced by this grip type. Thus, this type of grip appears less suited for generation traction on inclined substrates. The mesaxonic grip with an axial position of the third digit (D234) is the most common grip type in *P. azurea*. Its use is diminished as the diameter of horizontal substrates increases, as

Table 3. Summary of the factor analysis performed on the kinematic data

	Factor 1	Factor 2	Factor 3	Factor 4
% Variance	40.82	12.40	10.62	8.04
Speed	**0.874**	0.258	−0.088	−0.035
Max. shoulder angle	−0.026	−0.042	−0.152	**0.870**
Min. shoulder angle	−0.157	−0.151	**−0.827**	−0.250
Time to max. shoulder	−0.671	0.03	−0.164	0.465
Max. elbow angle	0.336	0.127	0.675	
Min. elbow angle	0.542	0.363	0.224	0.196
Time to max. elbow	−0.145	−0.028	**0.733**	−0.309
Max. wrist angle	−0.406	0.115	−0.274	0.160
Min. wrist angle	0.354	−0.117	−0.084	−0.287
Time to max. wrist	−0.659	−0.171	0.192	0.378
Max. body height	0.183	**0.912**	−0.001	0.065
Min. body height	0.234	**0.881**	0.158	−0.156
Max. velocity shoulder	**0.845**	0.232	0.025	−0.083
Max. velocity elbow	**0.857**	0.083	0.100	−0.057
Max. velocity wrist	**0.951**	0.102	0.129	0.018
Max. velocity hand	**0.960**	0.113	0.107	−0.010

Values in bold indicate loadings greater than 0.7. Max., maximum; min., minimum.

has also been observed for the gray mouse lemur (Reghem et al., 2012). The use of this grip probably permits the animal to increase its stability when walking on very narrow substrates, needed for an efficient movement. Interestingly, on the incline, wider substrates invoke an increase in the use of this grip, potentially because of its better position to generate traction while maintaining adhesion with the substrate through the frictional forces generated by the toe pad of the third digit positioned flat and in line with the substrate (Endlein et al., 2013). Our results generally confirm those for primates in suggesting that hand positions and grip types are more dependent on substrate than on intrinsic anatomy, with animals changing their grip to optimize the interaction with the substrate (Lemelin and Schmitt, 1998; Reghem et al., 2012).

Kinematics

The most striking difference revealed by our kinematic analyses is an effect on movement velocity. The slowest movements were observed on the narrow (1 mm) horizontal substrate for all individuals, suggesting that this context imposes the strongest mechanical constraints on locomotion. However, strong inter-individual differences in the speed of movement can be observed. This difference is probably at least partly explained by differences in size between the different individuals, with larger animals showing slower movements. Indeed, larger individuals with a greater body mass are probably more constrained to maintain their equilibrium on narrow substrates than are the smaller individuals. In addition to substrate diameter, incline also affected the velocity of movements, with animals being generally faster on an incline for a given diameter. Similar effects were observed for the lizard *Polychrus acutirostris*, another fine branch specialist, where an increase in substrate diameter and incline invoke an increase in movement speed (Renous et al., 2010).

Another striking result was that animals uniformly lowered the height of the body on narrower substrates, thus conferring greater stability to the animal. This is in accordance with data for primates (Cercopithecidae), where the height of the shoulder was diminished on narrower substrates (Schmitt, 2003). This observed lowering of the centre of mass on narrow substrates corresponds to an increase in the time to peak elbow angle and a decrease in the minimal shoulder angle observed due to a greater limb extension on the narrow substrate. The maximal shoulder angle also increases on narrow substrates, confirming the greater overall extension movement of the upper arm. This is probably caused by the fact that the hands need to be placed further in front of the body to grip the narrow substrate, whereas on the wider substrate the limbs are placed closer to the body. Changes in incline did not, however, affect the height of the body above the substrate yet did affect the forelimb kinematics. Similar to what is observed during locomotion on narrow substrates, locomotion on an incline involved a greater extension of the elbow and a reduced flexion of the shoulder, which remains more extended throughout the entire cycle. To optimize traction on the substrate, frogs probably need to place their hands further forward and, as such, extensions are greater. The much greater implication of the proximal limb segments such as shoulder and elbow was also observed in lizards (Foster and Higham, 2012) and primates (Schmitt and Lemelin, 2002; Stevens et al., 2011).

In conclusion, the effects of diameter and incline on both grip type and kinematics are similar to what has been observed for lizards and primates, suggesting that the mechanics of narrow substrate locomotion drive the kinematics of movement independent of morphology and phylogeny. Given the multiple independent origins of fine branch specialists among frogs, this may be an excellent

model to better understand the role of the fine branch milieu in the origin of skilled forelimb movements (Iwaniuk and Whishaw, 2000; Sustaita et al., 2013).

AUTHOR CONTRIBUTIONS

All authors contributed to the writing of the paper. A.H., V.A., A.M. AND E.P. designed the study. M.P. and T.D. filmed the animals and analysed the data.

COMPETING INTERESTS

No competing interests declared.

REFERENCES

Barbeau, T. R. and Lillywhite, H. B. (2005). Body wiping behaviors associated with cutaneous lipids in hylid tree frogs of Florida. *J. Exp. Biol.* **208**, 2147-2156.

Biewener, A. A. (2002). Future directions for the analysis of musculoskeletal design and locomotor performance. *J. Morphol.* **252**, 38-51.

Biju, S. D. (2009). A novel nesting behaviour of a treefrog, *Rhacophorus lateralis* in the Western Ghats, India. *Curr. Sci.* **97**, 433-437.

Burton, T. C. (1998). Are the distal extensor muscles of the fingers of Anurans an adaptation to arboreality? *J. Herpetol.* **32**, 611-617.

Caramaschi, U. (2006). Redefinição do grupo de *Phyllomedusa hypochondrialis*, com redescrição de *P. megacephala* revalidação de *P. azurea* descrição de una nova espécie (Amphibia, Anura, Hylidae). *Arq. Mus. Nac.* **64**, 159-179.

Daley, M. A. and Biewener, A. A. (2006). Running over rough terrain reveals limb control for intrinsic stability. *Proc. Natl. Acad. Sci. USA* **103**, 15681-15686.

Endlein, T., Ji, A., Samuel, D., Yao, N., Wang, Z., Barnes, W. J. P., Federle, W., Kappl, M. and Dai, Z. (2013). Sticking like sticky tape: tree frogs use friction forces to enhance attachment on overhanging surfaces. *J. R. Soc. Interface* **10**, 20120838.

Foster, K. L. and Higham, T. E. (2012). How forelimb and hindlimb function changes with incline and perch diameter in the green anole, *Anolis carolinensis. J. Exp. Biol.* **215**, 2288-2300.

Frost, D. R., Grant, T. R., Faivovich, J., Bain, R. H., Haas, A., Haddad, C. F. B., De Sa, R. O., Channing, A., Wilkinson, M., Donnellan, S. C. et al. (2006). The amphibian tree of life. *Bull. Am. Mus. Nat. Hist.* **297**, 1-291.

Gray, L. A., O'Reilly, J. C. and Nishikawa, K. C. (1997). Evolution of forelimb movement patterns for prey manipulation in anurans. *J. Exp. Zool.* **277**, 417-424.

Hartley, R. I. and Sturm, P. (1995). Triangulation. In *Computer Analysis of Images and Patterns: 6th International Conference, CAIP '95 Prague, Czech Republic, September 6–8, 1995 Proceedings* (ed. V. Hlaváč and R. Šára), pp. 190-197. Berlin: Springer.

Herrel, A., Schaerlaeken, V., Ross, C. F., Meyers, J. J., Nishikawa, K. C., Abdala, V., Manzano, A. and Aerts, P. (2008). Electromyography and the evolution of motor control: limitations and insights. *Integr. Comp. Biol.* **48**, 261-271.

Herrel, A., Measey, G. J., Vanhooydonck, B. and Tolley, K. A. (2011). Functional consequences of morphological differentiation between populations of the Cape dwarf chameleon (*Bradypodion pumilum*). *Biol. J. Linn. Soc. Lond.* **104**, 692-700.

Herrel, A., Tolley, K. A., Measey, G. J., da Silva, J. M., Potgieter, D. F., Boller, E., Boistel, R. and Vanhooydonck, B. (2013). Slow but tenacious: an analysis of running and gripping performance in chameleons. *J. Exp. Biol.* **216**, 1025-1030.

Hershkovitz, P. (1977). *Living New World Monkeys (Platyrrhini): With An Introduction To Primates*. Chicago, IL: University of Chicago Press.

Higham, T. E. and Jayne, B. C. (2004). Locomotion of lizards on inclines and perches: hindlimb kinematics of an arboreal specialist and a terrestrial generalist. *J. Exp. Biol.* **207**, 233-248.

Hyams, S. E., Jayne, B. C. and Cameron, G. N. (2012). Arboreal habitat structure affects locomotor speed and path choice of white-footed mice (*Peromyscus leucopus*). *J. Exp. Zool. A* **317**, 540-551.

Irschick, D. J. and Garland, T., Jr (2001). Integrating function and ecology in studies of adaptation: studies of locomotor capacity as a model system. *Annu. Rev. Ecol. Syst.* **32**, 367-396.

Irschick, D. J. and Jayne, B. C. (1998). Effects of incline on speed, acceleration, body posture and hindlimb kinematics in two species of lizard *Callisaurus draconoides* and *Uma scoparia. J. Exp. Biol.* **201**, 273-287.

Irschick, D. J. and Jayne, B. C. (1999). A field study of the effects of incline on the escape locomotion of a bipedal lizard, *Callisaurus draconoides. Physiol. Biochem. Zool.* **72**, 44-56.

Isler, K. (2005). 3D-kinematics of vertical climbing in hominoids. *Am. J. Phys. Anthropol.* **126**, 66-81.

Iwaniuk, A. N. and Whishaw, I. Q. (2000). On the origin of skilled forelimb movements. *Trends Neurosci.* **23**, 372-376.

Kenny, J. S. (1966). Nest building in *Phyllomedusa trinitatis* Mertens. *Caribb. J. Sci.* **6**, 15-22.

Lemelin, P. and Schmitt, D. (1998). The relation between hand morphology and quadrupedalism in primates. *Am. J. Phys. Anthropol.* **105**, 185-197.

Lillywhite, H. B., Mittal, A. K., Garg, T. K. and Agrawal, N. (1997). Integumentary structure and its relationship to wiping behaviour in the common Indian tree frog, *Polypedates maculatus*. *J. Zool. (Lond.)* **243**, 675-687.

Losos, J. B. (2009). *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. Berkeley, CA: University of California Press.

Losos, J. B. and Sinervo, B. (1989). The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *J. Exp. Biol.* **145**, 23-30.

Lutz, G. J. and Rome, L. C. (1994). Built for jumping: the design of the frog muscular system. *Science* **263**, 370-372.

Manzano, A. S., Fabrezi, M. and Vences, M. (2007). Intercalary elements, treefrogs, and the early differentiation of a complex system in the Neobatrachia. *Anat. Rec.* **290**, 1551-1567.

Manzano, A. S., Abdala, V. and Herrel, A. (2008). Morphology and function of the forelimb in arboreal frogs: specializations for grasping ability? *J. Anat.* **213**, 296-307.

Nauwelaerts, S., Ramsay, J. and Aerts, P. (2007). Morphological correlates of aquatic and terrestrial locomotion in a semi-aquatic frog, *Rana esculenta*: no evidence for a design conflict. *J. Anat.* **210**, 304-317.

Prikryl, T., Aerts, P., Havelková, P., Herrel, A. and Rocek, Z. (2009). Pelvic and thigh musculature in frogs (Anura) and origin of anuran jumping locomotion. *J. Anat.* **214**, 100-139.

Reghem, E., Byron, C., Bels, V. and Pouydebat, E. (2012). Hand posture in the grey mouse lemur during arboreal locomotion on narrow branches. *J. Zool. (Lond.)* **288**, 76-81.

Renous, S., Hofling, E. and Da Rocha, P. L. B. (2010). Effect of the substrate on the locomotion behavior of the South American iguanian lizard *Polychrus acutirostris*. *Ital. J. Zool. (Modena)* **77**, 216-226.

Sargis, E. J. (2001). The grasping behavior, locomotion and substrate use of the tree shrews *Tupaia minor* and *T. tana* (Mammalia, Scandentia). *J. Zool. (Lond.)* **253**, 485-490.

Schmitt, D. (2003). Substrate size and primate forelimb mechanics: implications for understanding the evolution of primate locomotion. *Int. J. Primatol.* **24**, 1023-1036.

Schmitt, D. and Lemelin, P. (2002). Origins of primate locomotion: gait mechanics of the woolly opossum. *Am. J. Phys. Anthropol.* **118**, 231-238.

Shubin, N. H. and Jenkins, F. A., Jr (1995). An early jurassic jumping frog. *Nature* **377**, 49-52.

Spezzano, L. C., Jr and Jayne, B. C. (2004). The effects of surface diameter and incline on the hindlimb kinematics of an arboreal lizard (Anolis sagrei). *J. Exp. Biol.* **207**, 2115-2131.

Stevens, N. J., Ratsimbazafy, J. H. and Ralainasolo, F. (2011). Linking field and laboratory approaches for studying primate locomotor responses to support orientation. In *Developments in Primatology: Primate Locomotion* (ed. K. D'Aout and E. E. Vereeke), pp. 311-333. New-York, NY: Springer.

Sustaita, D., Pouydebat, E., Manzano, A., Abdala, V., Hertel, F. and Herrel, A. (2013). Getting a grip on tetrapod grasping: form, function, and evolution. *Biol. Rev. Camb. Philos. Soc.* **88**, 380-405.

Vanhooydonck, B., Andronescu, A., Herrel, A. and Irschick, D. J. (2005). Effects of substrate structure on speed and acceleration capacity in climbing geckos. *Biol. J. Linn. Soc. Lond.* **85**, 385-393.

Vanhooydonck, B., Herrel, A. and Irschick, D. J. (2006). Out on a limb: the differential effect of substrate diameter on acceleration capacity in Anolis lizards. *J. Exp. Biol.* **209**, 4515-4523.

Wiens, J. J., Kuczynski, C. A., Hua, X. and Moen, D. S. (2010). An expanded phylogeny of treefrogs (Hylidae) based on nuclear and mitochondrial sequence data. *Mol. Phyl. Evol.* **55**, 871-882.

Winter, D. A. (2004) *Biomechanics and Motor Control of Human Movement*. New York, NY: John Wiley and Sons.

Zaaf, A., Van Damme, R., Herrel, A. and Aerts, P. (2001a). Spatio-temporal gait characteristics of level and vertical locomotion in a ground-dwelling and a climbing gecko. *J. Exp. Biol.* **204**, 1233-1246.

Zaaf, A., Van Damme, R., Herrel, A. and Aerts, P. (2001b). Limb joint kinematics during vertical climbing and level running in a specialist climber: *Gekko gecko* (Lacertilia: Gekkonidae). *Belg. J. Zool.* **131**, 173-182.