

Substrate diameter and compliance affect the gripping strategies and locomotor mode of climbing boa constrictors

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SUMMARY

Arboreal habitats pose unique challenges for locomotion as a result of their narrow cylindrical surfaces and discontinuities between branches. Decreased diameter of branches increases compliance, which can pose additional challenges, including effects on stability and energy damping. However, the combined effects of substrate diameter and compliance are poorly understood for any animal. We quantified performance, kinematics and substrate deformation while boa constrictors (*Boa constrictor*) climbed vertical ropes with three diameters (3, 6 and 9 mm) and four tensions (0.5, 1.0, 1.5 and 2.0 body weights). Mean forward velocity decreased significantly with both decreased diameter and increased compliance. Both diameter and compliance had numerous effects on locomotor kinematics, but diameter had larger and more pervasive effects than compliance. Locomotion on the largest diameter had a larger forward excursion per cycle, and the locomotor mode and gripping strategy differed from that on the smaller diameters. On larger diameters, snakes primarily applied opposing forces at the same location on the rope to grip. By contrast, on smaller diameters forces were applied in opposite directions at different locations along the rope, resulting in increased rope deformation. Although energy is likely to be lost during deformation, snakes might use increased surface deformation as a strategy to enhance their ability to grip.

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Key words: arboreal, locomotion, performance, kinematics, *Boa constrictor*, concertina, gait, posture, prehensile, substrate deformation.

INTRODUCTION

The locomotor performance of animals can affect critically important abilities, such as acquiring food resources, competing for mates and avoiding mortal harm (Turchin, 1998; Nathan et al., 2008), and arboreal habitats pose many functional challenges for locomotion as a result of their narrow cylindrical surfaces, inclines, and discontinuities between branches. Although branch diameters and orientation vary considerably in arboreal habitats, available data suggest that small diameters (median <0.8 cm) and steep inclines (median 67°) dominate (Mattingly and Jayne, 2004). Narrow surfaces and steep inclines in the arboreal environment each provide a unique set of challenges for locomotion. Small diameter substrates might interfere with the ability of an organism to balance or fit on the substrate (Cartmill, 1985), as well as with the ability to apply propulsive or gripping forces. In addition, steep inclines decrease the proportion of the mass of the organism supported passively by the substrate and thus are likely to require added muscular effort to prevent slipping.

Of the many attributes of branches that vary, the effects of branch diameter on locomotion are well studied (e.g. Irschick and Losos, 1999; Lammers and Biknevičius, 2004). However, a correlate of decreased diameter in natural substrates is an increased compliance, which is defined as the amount of deflection of the substrate when loaded. Substrate compliance poses additional challenges, such as effects on locomotor stability and energy damping (Bonser, 1999), which also might affect the mode (Thorpe et al., 2009) and dynamics (McMahon and Greene, 1979; Byrnes et al., 2008) of locomotion. However, no study has explicitly examined the combined effects of substrate diameter and compliance on animal locomotion.

To successfully climb vertical surfaces without structures that allow animals to adhere, sufficient friction must be generated by active gripping to prevent slipping. The ability to grip a substrate depends on the nature of the contact between the animal and the surface (Cartmill, 1985). For example, grip force in humans reaches a maximum at an intermediate diameter proportionate to the dimensions of the hand, with reduced force at both larger and smaller diameters (Edgren et al., 2004). The elongate body plan of snakes allows them considerable ability to modulate the extent of wrapping and the number of gripping regions, but extreme branch diameters might limit the ability of snakes to conform to or grip the branch, which in turn could negatively affect performance (Astley and Jayne, 2007).

Snakes climb cylindrical vertical substrates using concertina locomotion (Astley and Jayne, 2007), characterized by convoluted static regions pressed against the substrate while another portion of the body extends anteriorly (Gray, 1946; Jayne, 1986). The cyclical changes in momentum associated with repeated starting and stopping make concertina locomotion (in tunnels) far more costly energetically than other modes of locomotion for an animal of a given mass (Walton et al., 1990), and narrower tunnels appear to be more demanding than tunnels of a moderate width (Jayne and Davis, 1991). Compared with horizontal locomotion, the energetic costs of climbing vertical surfaces using concertina locomotion should increase because of the additional work done against gravity. Thus, climbing narrow and compliant vertical substrates is presumably a highly demanding task. As a result, studying this behavior facilitates our understanding of how environmental variation affects locomotion.

We studied juvenile boa constrictors; boa constrictors are often found in trees particularly when they are juveniles (Greene, 1983), as indicated in part by the large proportion of passerine birds (>40%) in their diet (Quick et al., 2005). Although many species of arboreal colubrid (Lillywhite and Henderson, 1993) and boid snakes (Pizzatto et al., 2007) have relatively slender bodies, boa constrictors are rather heavy bodied. Greater weight might exacerbate some of the challenges of arboreal locomotion, such as supporting body weight by gripping, the risk of toppling when the mass is not centered above a branch, and the likelihood of deforming thin vegetation. However, just as the large numbers of vertebrae and the short axial muscle segments of boids are likely to enhance their ability to wrap around and grip prey during constriction (Ruben, 1977; Jayne, 1982), these traits could also enhance their ability to grip arboreal surfaces.

The goal of the present study was to determine how the combined influence of diameter and compliance of substrates in arboreal habitats affects locomotor mode and performance. Very narrow substrates might limit the ability of animals to produce the necessary normal forces to grip. Therefore, to produce sufficient force snakes might use a greater extent of their bodies to grip these substrates. This could have a negative effect on locomotor performance by limiting the extent of the body free to move anteriorly during each cycle. In addition, we expected performance to decrease on more compliant substrates, as some of the muscular force produced to grip or propel the animal forward would be lost to deformation of the substrate. Using flexible substrates also allowed us to measure substrate deformation and to resolve some of the forces required for locomotion, which could not otherwise be determined for small diameters.

MATERIALS AND METHODS

Experimental subjects

We used six captive-born juvenile boa constrictors (*Boa constrictor*; Linnaeus 1758). All animals had prior experience climbing rigid cylindrical surfaces as part of a previous experiment. The snakes were individually housed in terraria (52×26×31 cm), with an incandescent bulb overhead establishing a temperature gradient of 27–33°C. The snakes had similar snout-vent length (SVL; mean SVL=68.8 cm, range=66–70 cm), total length (TL; mean TL=77.1 cm, range=74–79 cm) and mass (mean=175.8 g, range=158–192 g). We performed all experiments on post-absorptive animals (>7 days after feeding) to minimize possible postprandial effects on locomotor performance (Garland and Arnold, 1983) and metabolism (Secor et al., 2000).

Experimental protocol

We used vertically oriented, braided nylon ropes (The Lehigh Group, Macungie, PA, USA) with three diameters (3, 6 and 9 mm; 13–39% of mid-body diameter of the snakes) encompassing the median diameter (0.8 cm) of branches in the arboreal environment (Mattingly and Jayne, 2004) and of perch diameters used in the wild by other boid snakes (Henderson and Winstel, 1995; Henderson et al., 1998). Preliminary tests revealed that 3 mm was the smallest diameter the experimental subjects would reliably climb and that a gait change occurred across this range of diameters. To test the effects of substrate compliance, we increased the tension in the rope to reduce compliance. We used four rope tensions, that were scaled to 0.5, 1, 1.5 or 2 body weights. To measure tension (± 0.003 N) in the rope we used a linear load cell (Honeywell Sensotec Model 31, 5 lb., Columbus, OH, USA). The rope was passed through a pulley and attached, via a spring ($k=46\text{ N m}^{-1}$), to the load cell fixed to an

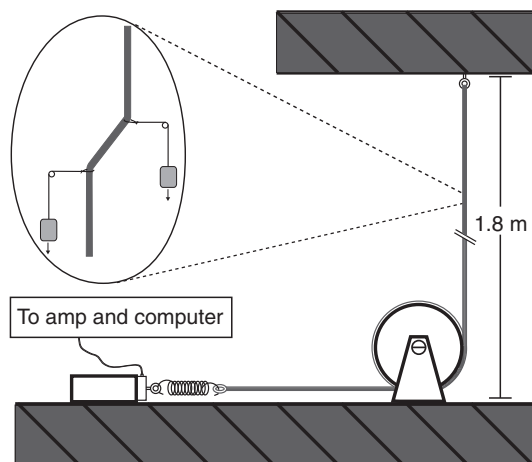


Fig. 1. Schematic illustration of the experimental setup to measure substrate deformation by snakes climbing compliant perches. Snakes were free to climb a 1.8 m rope that passed through the pulley and was coupled to the linear load cell via a spring. Inset shows the experimental setup for determining the normal force required for observed substrate deformations. Equal masses were passed over pivots at a distance similar to the wavelength between gripping regions of the snake.

adjustable mounting block (Fig. 1). To increase the tension, the mounting block was moved farther from the pulley, stretching the spring.

To determine the amount of force required to deform each of the three ropes, we applied known horizontal forces at each tension (0.5, 1, 1.5, 2 mean body weights) using a setup that allowed unopposed forces similar to those the snakes produce (Fig. 1, inset). Two identical masses, ranging from 0–120 g in 10 g increments, were suspended over brass pivots using silk sutures attached to the rope 15 cm apart, and we measured the resulting rope deformations using the load cell.

Preliminary experiments revealed that using a small section of pipe covered at one end to create a dark refuge near the top of the rope was the best method to motivate snakes to climb vertically. The snakes performed three trials for each experimental condition (3 diameters × 4 tensions). Each snake was rested for at least two hours between experimental conditions and the snakes performed no more than two experimental conditions per day. We randomized the order in which diameter and tension were presented to snakes to reduce potential effects of experience on performance. The body temperatures of the snakes were approximately 30°C during all trials, which is within the range of reported field-active body temperatures for this species (McGinnis and Moore, 1969; Montgomery and Rand, 1978).

We recorded each trial at 30 frames s⁻¹ using two synchronized digital video cameras (Panasonic PV-GS320, Secaucus, NJ, USA) positioned orthogonal to the long axis of the rope. We used Adobe Premiere Pro v7 (Adobe Systems, San Jose, CA, USA) to convert the video to AVI files that were imported into MaxTRAQ v2.19 software (Innovision Systems, Columbiaville, MI, USA) for kinematic analysis. Because the snakes were able to wrap around the substrate in any orientation relative to the two cameras, the widest portion of the head was the most practical landmark to use for following the forward progress of each snake. We used the vertical line connecting the ends of the rope in the video frame as the x-axis of our coordinate system.

The force and video data were synchronized using a square wave voltage to illuminate LEDs that were visible in both cameras. The analog signal from the load cell was amplified using Honeywell Sensotec Model UV in line amplifier and acquired digitally at 1 kHz and low-pass filtered with a cutoff frequency of 25 Hz using a Powerlab 8 SP system and Chart 5 software (ADInstruments, Castle Hill, NSW, Australia).

To determine the coefficient of static friction (μ_s), we placed each snake in a natural extended posture on a board (28 × 120 cm) covered in 3 mm nylon rope, such that the long axis of the snake was parallel to the orientation of the rope and the long axis of the board. One end of the board was elevated until the snake began to slide downwards. Boa constrictors began to slide at an average angle of 12.7 deg, corresponding to a μ_s of 0.225 ± 0.003 . Given this measured μ_s , a total normal force of approximately 7.6 N (4.4 body weights) is required to support the body weight of the snake.

Kinematic and kinetic measurements

We analyzed five variables describing the whole-body kinematics and force over each cycle. The cycle duration (t_{cycle}) was the total time from the start of static contact until the end of subsequent sliding contact. The percentage of time in static contact (%stat) was the amount of time during a cycle in which a given point along the body was in static contact with the substrate divided by t_{cycle} . The total height climbed per cycle was Δx . The mean forward velocity (v_x) was Δx divided by t_{cycle} . The maximum change in tension (ΔT_{max}) within each cycle, representing the amount of substrate deformation, was also calculated from the force data.

Six additional variables quantified the posture and movements associated with the snake gripping the substrate and extending the body forward within each cycle. We determined the maximum and minimum vertical (x) length (l_{max} and l_{min}) of the body and tail along the rope. We also determined the maximum and minimum number of simultaneous crossing regions per cycle ($N_{\text{cr,max}}$ and $N_{\text{cr,min}}$), which represent the number of potential gripping regions, and the difference between them (ΔN_{cr}). For each cycle, we also calculated the mean angle of the midline of the body at each crossing region relative to x at the time of the greatest longitudinal extent of static contact (α_{cr}) for locations that were nearly parallel to the plane of focus of the camera.

Statistical analyses

We analyzed each variable for the four fastest cycles for each individual in each experimental treatment ($N=12$) using a three-way mixed-model ANOVA (total $N=288$). Diameter ($N=3$) and tension ($N=4$) were considered fixed, crossed factors, whereas the individual snake used ($N=6$) was considered a random, crossed factor. We also performed a principal component analysis (PCA) on eight kinematic variables to evaluate whether distinct locomotor patterns occurred. We used a mixed-model ANOVA (as above) to test whether the first two principal component scores differed significantly with diameter or tension. All statistics were performed using the Statistics Toolbox in Matlab v7.4 (MathWorks, Natick, MA, USA), and $P < 0.05$ was used as the criterion for significance.

RESULTS

Performance

All snakes successfully climbed all combinations of substrate diameter and compliance, but all climbing velocities were extremely slow (~ 0.5 – 1.0 cm s^{-1}), and seldom greater than 2% SVL s^{-1} (Fig. 2A). Backwards slipping was common on the smallest diameter, especially with higher substrate compliance (Fig. 3A).

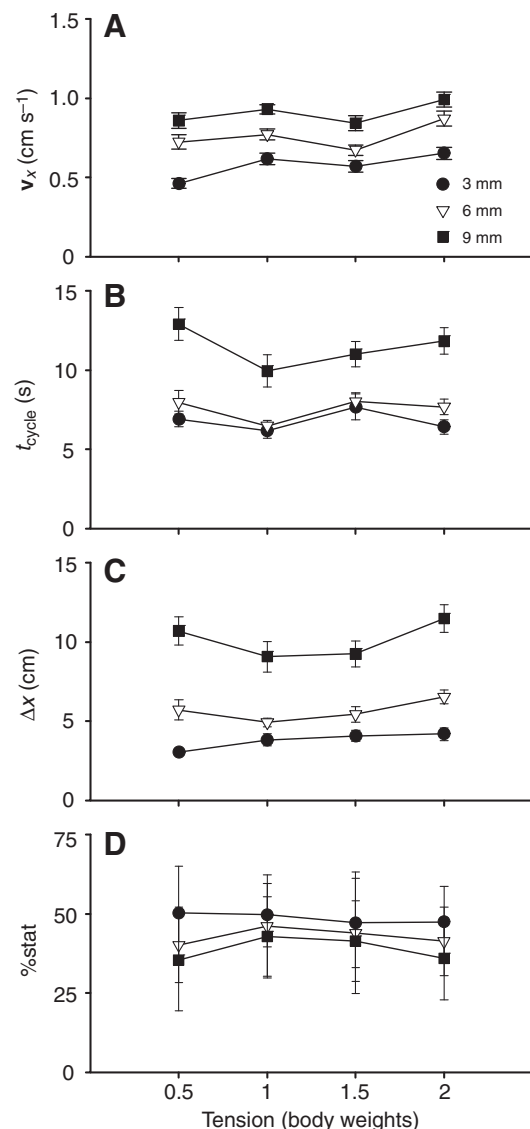


Fig. 2. Mean values (\pm s.e.m.) of whole-cycle variables on the three substrate diameters, 3, 6 and 9 mm, and four tensions. (A) Maximal forward velocity, v_x . (B) Cycle duration, t_{cycle} . (C) Distance traveled per cycle, Δx . (D) Percentage of cycle spent in static contact with substrate, %stat.

Substrate diameter and compliance significantly affected v_x (Table 1; Fig. 2A). Velocities increased approximately twofold from the smallest to the largest diameter, as well as having nearly a 1.4-fold increase with increased rope tension for a given diameter (Fig. 2A).

Locomotor mode

All snakes used a variant of concertina locomotion with periodic starting and stopping along the length of the body, and at no time was the entire length of the body moving simultaneously (Fig. 3). Regardless of diameter or compliance, the snakes climbed using alternating curves to the left and the right, gripping the substrate using medially directed normal forces in regions where the body crossed the rope (Fig. 3). Occasionally, snakes made full helical wraps around the rope, with their tails. On the smaller diameters, the dorsal, lateral and ventral surfaces often contacted the rope, whereas on the largest diameter greater ventral flexion resulted in

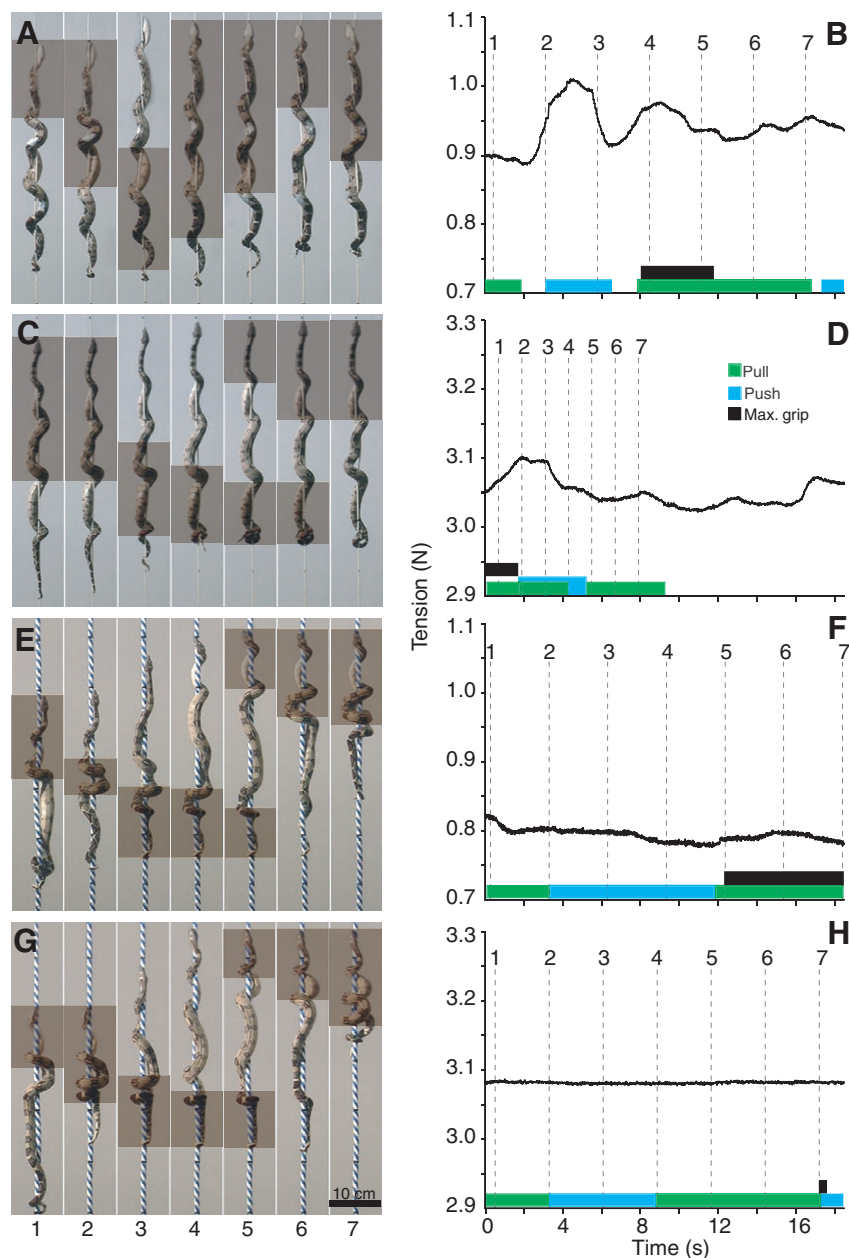


Fig. 3. Video images of movement (A,C,E,G) and the corresponding force profiles (B,D,F,H) for four combinations of substrate diameter and tension: (A,B) 3 mm, 0.5 body weights (BW); (C,D) 3 mm, 2.0 BW; (E,F) 9 mm, 0.5 BW; and (G,H) 9 mm, 2.0 BW. For A, C, E and G, frames were taken at equal time intervals within a cycle. Frames 2–6 correspond to a complete cycle and frame 1 is an equal time interval prior to the start of the cycle. Time intervals in between successive frames were 2.7, 1.2, 3.0 and 2.8 s, respectively, for A, C, E and G. Shaded regions represent areas along the snake in static contact with the substrate. Numbers in B, D, F and H correspond to individual frames in A, C, E and G, respectively. 'Pull' refers to the uphill movement of the posterior body towards a more anterior region of gripping, 'Push' refers to the anterior extension of the anterior body and 'Max. grip' refers to the maximum longitudinal extent of gripping along the substrate. Videos of boa constrictor locomotion on narrow substrates are available in the supplementary material (Movies 1–4).

predominantly ventral scale contact and gripping. On the two smallest diameters, each point on the snake followed nearly the same path along the rope as the snake moved forward (Fig. 3A,C). By contrast, on larger diameters, snakes used a form of concertina locomotion in which extensive portions of the body, corresponding to multiple adjacent gripping loops, were progressively extended anteriorly and did not follow a similar path.

Kinematics and substrate deformation

Diameter significantly affected more kinematic variables than did substrate compliance (11 vs 5 of 11) (Table 1). During climbing, both t_{cycle} (Fig. 2B) and Δx (Fig. 2C) increased with increasing diameter, whereas %stat decreased significantly with increased diameter (Fig. 2D; Table 1). On larger diameters, the potential benefits of the large increase in Δx and the decrease in %stat on velocity were partially offset by longer cycle durations, resulting in only a modest increase in velocity.

Several kinematic variables describing the ability of snakes to both grip the substrate and extend the body anteriorly also changed significantly with both diameter and compliance. The maximum (l_{max}) and minimum (l_{min}) longitudinal extent of the snake along the rope decreased significantly as diameter increased and as substrate compliance decreased (Table 1; Fig. 4A). As diameter increased, both $N_{\text{cr,max}}$ (Fig. 4B) and $N_{\text{cr,min}}$ decreased significantly, whereas ΔN_{cr} (Fig. 4C) increased significantly (Table 1). However, none of these variables describing the number of crossing regions changed significantly with substrate compliance. Both increased diameter and decreased compliance significantly increased α_{cr} (Table 1; Fig. 4D).

Substrate deformation is the result of forces applied to the rope by the snake in opposite directions at different points along the length of the rope, analogous to a moment couple. We will refer to these forces as 'unopposed forces'. Both increased diameter and increased rope tension decreased the amount of rope deformation, as indicated

Table 1. Effects of diameter and tension on performance, kinematics and force

Variable	Effect		
	Diameter (d.f.=2,10)	Tension (d.f.=3,15)	Diameter \times tension (d.f.=6,30)
v_x	44.4 (<0.001)	11.1 (<0.001)	0.5 (0.629)
t_{cycle}	20.5 (<0.001)	2.0 (0.160)	0.4 (0.691)
Δx	57.5 (<0.001)	2.2 (0.134)	1.5 (0.205)
%stat	22.59 (<0.001)	1.31 (0.308)	0.7 (0.644)
l_{max}	31.9 (<0.001)	3.9 (0.030)	0.7 (0.651)
l_{min}	62.8 (<0.001)	9.8 (<0.001)	1.3 (0.307)
$N_{\text{cr,max}}$	49.1 (<0.001)	1.6 (0.227)	1.1 (0.361)
$N_{\text{cr,min}}$	80.1 (<0.001)	2.6 (0.087)	0.7 (0.652)
ΔN_{cr}	6.2 (0.017)	0.9 (0.479)	0.4 (0.871)
α_{cr}	76.3 (<0.001)	4.4 (0.021)	3.0 (0.022)
ΔT_{max}	32.2 (<0.001)	51.1 (<0.001)	4.6 (0.002)

Values are $F(P)$.

v_x , average velocity; t_{cycle} , cycle duration; Δx , distance per cycle; %stat, percentage of cycle static; l_{max} , maximum length along substrate; l_{min} , minimum length along substrate; $N_{\text{cr,max}}$, number of crossing regions at l_{max} ; $N_{\text{cr,min}}$, number of crossing regions at l_{min} ; ΔN_{cr} , change in number of crossing regions; α_{cr} , mean angle of body with rope; ΔT_{max} , maximum change in tension.

by ΔT_{max} , within the locomotor cycle (Table 1; Fig. 3; Fig. 5A). Snakes produced the largest substrate deformations in two ways: increasing the number of gripping regions ($N_{\text{cr,max}}$), which effectively increased the number of unopposed forces applied to the rope, and rapidly extending the anterior body (Fig. 3B,D,F). However, at the combination of highest diameter and lowest compliance, little or no deformation occurred (Fig. 3H).

The first two principal components (PC1 and PC2) accounted for 52% and 16% of the observed variation in the data, respectively. Higher values of PC1 represent greater Δx and α_{cr} , and smaller l_{max} and l_{min} , whereas higher values of PC2 represent larger values of t_{cycle} , $N_{\text{cr,max}}$ and $N_{\text{cr,min}}$ (Table 2). The PCA effectively distinguished the largest and smallest diameters into distinct clusters in the PC space, but both had significant overlap with the intermediate diameter; conversely, different tensions were not easily distinguished (Fig. 6). However, in the mixed-model ANOVA, both diameter ($F=160.6$, $P<0.0001$; d.f.=2,10) and tension ($F=7.7$, $P=0.002$, d.f.=3,15) significantly affected PC1. By contrast, PC2 only changed significantly with diameter ($F=8.8$, $P=0.006$, d.f.=2,10).

DISCUSSION

Understanding variation in locomotor gait or mode provides insights into how motor output changes with changes in environmental demands or speed (Biknevicius and Reilly, 2006). Historically, locomotor gaits or modes have been defined by a variety of continuous kinematic parameters, including duty factor and limb phase (Hildebrand, 1965; Hildebrand, 1968), or by discrete changes, such as in locomotor mechanics (Cavagna et al., 1977; Hedrick et al., 2002) or appendage use (Webb, 1982). Although the definitions of locomotor modes obtained using these different criteria do not always correspond perfectly to one another (Biknevicius and Reilly, 2006), both of these types of information prove useful for identifying novel locomotor modes. In this study, a combination of changes in continuous kinematic variables and a change in the gripping strategy used by boa constrictors suggest that two locomotor modes occurred with varying environmental conditions.

Locomotor mode and performance

No previous study has examined the combined effects of substrate diameter and compliance, and for the snakes in our study both of these salient features of arboreal habitats significantly affected their locomotion. Snakes commonly alter locomotor mode in response to variations in environmental structure (e.g. Gray, 1946; Jayne,

1986), whereas many gait transitions of animals with appendages are associated with changing speed.

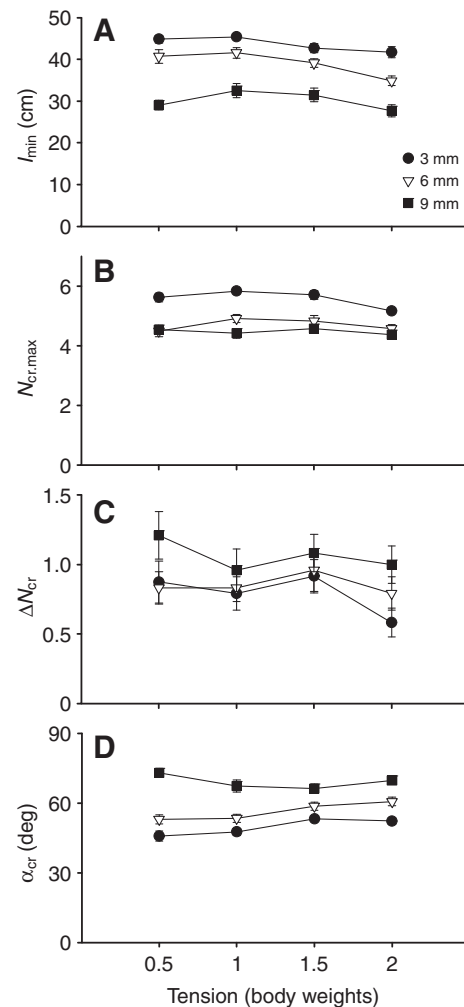


Fig. 4. Mean values (\pm s.e.m.) of postural variables on the three substrate diameters, 3, 6 and 9 mm, and four substrate tensions. (A) Minimum longitudinal extent of the snake's body along the substrate, l_{min} . (B) Maximum number of crossing regions, $N_{\text{cr,max}}$. (C) Change in the number of crossing regions within a cycle, ΔN_{cr} . (D) Angle of the body with respect to the substrate at the minimum longitudinal extent, α_{cr} .

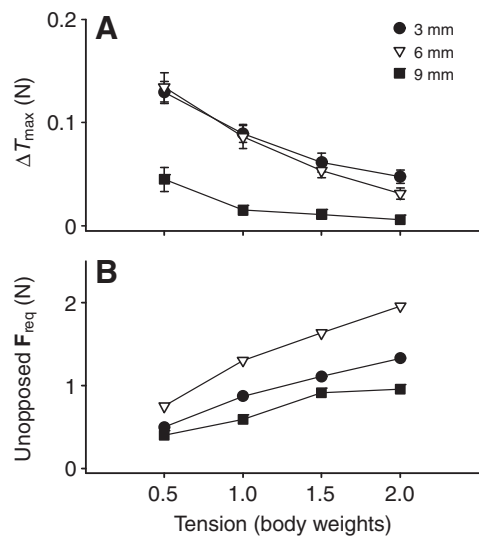


Fig. 5. Mean values (\pm s.e.m.) of force variables on the three substrate diameters, 3, 6 and 9 mm, and four substrate tensions. (A) Change in tension in the substrate due to deformation, ΔT_{\max} . (B) Unopposed normal force required to attain the change in tension (ΔT_{\max}) due to the substrate deformations observed from the snakes shown in A.

On narrow vertical substrates, the snakes in this study used forms of concertina locomotion, with some similarities to the forms of concertina locomotion used by other species in tunnels (Mosauer, 1932; Gray, 1946; Jayne, 1986; Jayne and Davis, 1991) and on rigid cylinders (Astley and Jayne, 2007). On all diameters, movement used alternating curves of the body to the left and the right, periodic stopping, and static contact along some extent of the body. However, climbing on ropes had two differences with tunnel concertina locomotion. First, forces applied to the substrate were always directed medially regardless of rope diameter. Second, on the smallest diameter, the entire body followed nearly the same path as the crossing region at a specific location along the rope, which shifted posteriorly within the body of the snake while the animal ascended (Fig. 3A,C); this is similar to the arboreal concertina locomotion observed during vertical climbing in *Pantherophis* (*Elaphe*) (Astley and Jayne, 2007). By contrast, on the largest diameter, points along the body did not follow a similar path, more closely resembling concertina locomotion in tunnels (Fig. 3E,G). This kinematic difference is one line of evidence for the existence of two distinct variants of arboreal concertina locomotion in *B. constrictor* in response to changes in diameter.

Table 2. Principal components analysis factor loadings

Variable	PC1	PC2
t_{cycle}	0.33	0.42
Δx	0.40	0.30
ΔT_{\max}	-0.28	-0.28
l_{\max}	-0.35	0.12
l_{\min}	-0.44	-0.02
$N_{\text{cr,max}}$	-0.26	0.65
$N_{\text{cr,min}}$	-0.33	0.46
α_{cr}	0.41	0.04

Loadings with a magnitude ≥ 0.35 are marked in bold type. PC1 and PC2, principal components 1 and 2, respectively. See Table 1 for variable definitions.

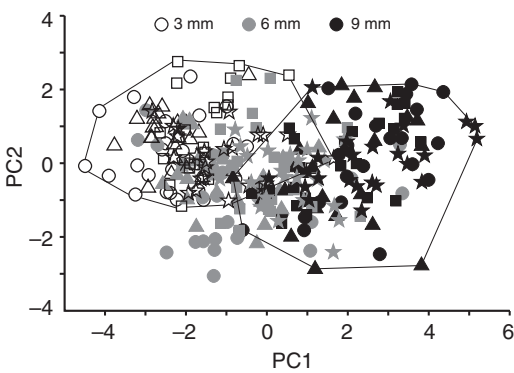


Fig. 6. Principal component 1 (PC1) versus principal component 2 (PC2) from an analysis of eight kinematic variables on the three substrate diameters and four substrate tensions. White, gray and black symbols represent 3, 6 and 9 mm diameters, respectively. Minimum polygons are drawn for 3 and 9 mm. Each tension is given by a different symbol (circle, 0.5 BW; triangle, 1.0 BW; square, 1.5 BW; star, 2.0 BW). Factor loadings are given in Table 2.

As in previous studies of snakes (Astley and Jayne, 2007) and diverse limbed animals (Losos and Sinervo, 1989; Delciellos and Vieira, 2009), substrate diameter had profound effects on locomotor performance. In many lizards (Sinervo, 1991; Losos and Irshick, 1996; Irshick and Losos, 1999) and some mammals (Delciellos and Vieira, 2009), maximum speed decreases with decreased perch diameter. By contrast, Astley and Jayne (Astley and Jayne, 2007) found that for North American rat snakes, moving both horizontally and uphill, speed decreases with increased cylinder diameter. The different ranges of substrate diameters used in these two studies probably explain this discrepancy. We used very small rope diameters (13–39% of the mid-body width of the snake) when compared with those previously used for adult *Pantherophis* (76–1000% of mid-body width) (Astley and Jayne, 2007). Thus, for snakes, performance is probably maximized at an intermediate diameter (Herrmann and Jayne, 2010).

Substrate deformation and grip

Depending on their body plan and behavior, animals use various strategies to closely conform to objects in their environment in order to effectively apply gripping or propulsive forces. Two contrasting ways in which such close contact can be attained are for the animal itself to deform and comply with shapes in the environment or, conversely, to deform the environment so that it complies with the shape of the animal. The snakes in our study successfully employed both of these mechanisms while climbing compliant substrates. Some of the effects of surface compliance on locomotor performance are dependent on the amount of environmental deformation and the rate of energy return. For example, in terrestrial systems, both humans (Ferris et al., 1999) and cockroaches (Spence et al., 2010) can maintain or increase velocity when running on elastic surfaces, whereas, on substrates that yield permanently underfoot, such as sand, the mechanical work required for locomotion increases (Lejeune et al., 1998). Similarly, in arboreal systems, terminal branch compliance increases the costs of leaping across canopy gaps (Alexander, 1991; Demes et al., 1995). However, in rare cases animals can employ branch compliance to their benefit (Thorpe et al., 2007). In our study, increased rope compliance decreased the performance of snakes, and the combination of deformations in the

ropes and in the bodies of the snakes seems likely to have some additional consequences on how the substrate is gripped.

What we observed for the largest diameter rope compared with the two smaller ones suggests a change in gripping strategy, whereas different compliances of the ropes might explain much of the observed variation between the two smallest ropes. Although all ropes were of similar material and weave, our deformations of the ropes with standard weights revealed that compliance decreased with increased rope diameter (see supplementary material Fig. S1). Thus, the nearly identical deformations caused by the snakes on the two smaller diameters (Fig. 5A) with much higher values of unopposed normal forces (F_{req}) are consistent with the decreased compliance of the larger rope. By contrast, the unopposed F_{req} of the 9-mm diameter rope decreased substantially when compared with that of the 6-mm diameter rope (Fig. 5B). Consequently, the near absence of observable deformation of the largest rope by the snakes (Fig. 5A) seems likely to indicate a reduction in unopposed normal forces and a greater reliance on opposing normal forces to prevent slipping. Positioning the body nearly perpendicular to the largest rope in the gripping regions and the greater ventral contact with the rope seem likely to enhance the ability to generate opposing normal forces while minimizing unopposed normal forces.

This mode of gripping observed on the largest rope created large gripping arcs. Similarly, the opposable thumb of primates facilitates gripping larger arcs and hence increasing grip force because frictional gripping arcs of $>180^\circ$ cause the normal forces to push the substrate towards the animal (Cartmill, 1974; Cartmill, 1979).

The observed change from using predominantly opposing grips on the largest diameter to using both gripping strategies on small diameters might result from limits on flexibility or on the ability to produce sufficient normal forces on small diameter substrates using opposing grips. The inability to form a small radius of curvature (r_c) might underlie this change in gripping strategy, and r_c could be affected by increased mobility between adjacent vertebrae, increased numbers of vertebrae per unit distance, the stoutness of the body, or the architecture of the axial muscles. The shorter length of some axial muscle segments in boid species might enhance their force production at small r_c values compared with that of many colubrid species (Ruben, 1977; Jayne, 1982). Some of the similarities of body posture between the colubrid *Pantherophis* on a wide range of diameters (Astley and Jayne, 2007) and the boa constrictors on very small diameters might reflect the need of *Pantherophis* to use a gripping strategy that will compensate for a larger r_c , owing to both a smaller body diameter and longer axial muscle segments.

As a result of these probable anatomical constraints on their gripping ability, snakes could use other methods on smaller diameters to generate the necessary normal force to both support body weight and ascend. Unlike arboreal primates that cope with compliant branches by increasing the number of discrete hand and foot holds (Thorpe et al., 2009), the elongate and flexible bodies of snakes have an exquisite ability to modulate the size of the gripping region, thereby providing additional strategies that snakes could use to increase grip force, including deforming the substrate and helical wrapping.

The frictional force generated can be increased exponentially by increasing the contact angle (an angular measure of arc length) between a flexible substrate and a cylinder as a result of the capstan effect (Meriam, 1980). This principle is used in a variety of mountaineering equipment, creating a convoluted path to retard the sliding of a loaded rope. For snakes on the two thinner ropes, we commonly observed five crossing regions, each of which bent the

rope approximately one-tenth the circumference of the snake, and the resulting contact angle of 180° would create a capstan effect sufficient to support one-half of the weight of the snake. Perhaps snakes applied greater unopposed normal forces at each tension on the 6 mm compared with the 3 mm rope to attain a similar amount of deformation (Fig. 5) and thus facilitate gripping the substrate.

In addition to increasing the frictional force by substrate deformation, helical wrapping can passively increase the normal force applied by the snake on the substrate. By using helical wrapping, twining vines grip their host plant by self-tightening under tension (Silk and Hubbard, 1991; Isnard et al., 2009). Self-tightening of a helix can produce greater normal force with increases in the curvature (decreased diameter), the pitch angle and the number of gyres (Silk and Hubbard, 1991). Many of the changes observed in the posture and helical wrapping for snakes on smaller diameter are consistent with enhancing this effect. If snakes produce normal loads similar to those of twining plants (Silk and Hubbard, 1991), this passive mechanism could support the entire weight of the snake while at rest.

Although previously undescribed, it is likely that other arboreal organisms use similar mechanisms to supplement their ability to grip. For instance, although the gripping postures of tails have not been studied in detail, they seem likely to be subject to similar mechanical demands as those faced by snakes. A common feature of prehensile tails that have evolved convergently in diverse lineages of reptiles (Zippel et al., 1999) and mammals (McClern, 1992; Schmitt et al., 2005) is that they have sufficient length, flexibility and strength to encircle branches and produce normal force.

Despite the likely physical and energetic challenges, the benefits of the ability to move on narrow and compliant substrates might have large ecological implications for animals. Arboreal organisms must often feed or hunt in the terminal branch niche, which requires the ability to move safely on small diameter and compliant substrates. Additionally, because of the discontinuous nature of arboreal habitats, the limits of diameter and compliance on which an animal can safely move determines the length of a detour an animal must make around an impassable gap (Thorpe et al., 2009), which is likely to influence foraging patterns, energy expenditure and exposure to predators.

Diverse substrates place similar functional demands on climbing organisms using frictional grips. These vertical substrates require the ability to produce forces normal to the surface using muscular contraction. However, to climb perches with differing substrate properties, different strategies are used. In boa constrictors, a shift in the locomotor mode of animals climbing on smaller diameter substrates results from both differing kinematics and gripping strategies. Broad comparisons across species of both gripping behavior and the underlying motor control could elucidate the potential mechanisms that underlie these shifts in climbing strategy, and thus could promote a better understanding of the diversity of arboreal forms.

LIST OF SYMBOLS AND ABBREVIATIONS

F_{req}	normal force required to attain observed ΔT_{max}
l_{max}	maximum longitudinal extension of body and tail along the rope
l_{min}	minimum longitudinal extension of body and tail along the rope
$N_{\text{cr.max}}$	number of crossing regions at l_{max}
$N_{\text{cr.min}}$	number of crossing regions at l_{min}
r_c	radius of curvature
t_{cycle}	cycle duration in seconds
v_x	average velocity of a cycle

α_{cr}	mean angle of the body midline with respect to the long axis of the rope at crossing regions during maximal static contact
ΔN_{cr}	change in number of crossing regions
ΔT_{max}	maximum change in tension due to deformation within a cycle
Δx	distance traveled per cycle
μ_s	coefficient of static friction
%stat	percentage of a cycle in static contact with the substrate

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