

RESEARCH ARTICLE

Perch size and structure have species-dependent effects on the arboreal locomotion of rat snakes and boa constrictors

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SUMMARY

Arboreal habitats create diverse challenges for animal locomotion, but the numerical and phylogenetic diversity of snakes that climb trees suggest that their overall body plan is well suited for this task. Snakes have considerable diversity of axial anatomy, but the functional consequences of this diversity for arboreal locomotion are poorly understood because of the lack of comparative data. We simulated diverse arboreal surfaces to test whether environmental structure had different effects on the locomotion of snakes belonging to two distantly related species with differences in axial musculature and stoutness. On most cylindrical surfaces lacking pegs, both species used concertina locomotion, which always involved periodic stopping and gripping but was kinematically distinct in the two species. On horizontal cylinders that were a small fraction of body diameter, the boa constrictors used a balancing form of lateral undulation that was not observed for rat snakes. For all snakes the presence of pegs elicited lateral undulation and enhanced speed. For both species maximal speeds decreased with increased incline and were greatest on cylinders with intermediate diameters that approximated the diameter of the snakes. The frictional resistances that we studied had small effects compared with those of cylinder diameter, incline and the presence of pegs. The stouter and more muscular boa constrictors were usually faster than the rat snakes when using the gripping gait, whereas rat snakes were faster when using lateral undulation on the surfaces with pegs. Thus, variation in environmental structure had several highly significant effects on locomotor mode, performance and kinematics that were species dependent.

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Key words: arboreal, locomotion, performance, kinematics, *Boa constrictor*, *Pantherophis guttatus*, phylogeny, concertina locomotion, lateral undulation, gait, posture, prehension.

INTRODUCTION

Arboreal habitats create numerous challenges for animal movement (Cartmill, 1985). For example, moving on top of the narrow, cylindrical surfaces of branches increases the risk of toppling sideways, and animals may encounter different branch diameters (Schoener, 1968), inclines (Mattingly and Jayne, 2004) and textures (Mullin and Cooper, 2002) as they move within a single tree or between different trees. Such structural variation in the environment often requires animals to balance or use some sort of adhering (Irschick et al., 1996) or gripping mechanism (Cartmill, 1974). Arboreal animals also must cope with secondary branches that emerge from the primary surfaces on which they move, and depending on size and body plan of an animal and the mode of locomotion, such structures may either impede (Jones and Jayne, 2010) or enhance the ability to move (Astley and Jayne, 2007; Thorpe et al., 2009).

Many phylogenetically diverse animals are arboreal and have evolved a variety of behavioral and morphological specializations, but previous studies on the effects of arboreal habitat structure on vertebrate locomotor function and performance are mainly limited to anole lizards (Irschick and Losos, 1999) and primates (Strasser et al., 1998). Several studies of anoles have quantified the effects of branch diameter on maximal running speeds (reviewed by Irschick and Garland, 2001), but only limited kinematic data are available (Spezzano and Jayne, 2004). By contrast, most studies of

the arboreal locomotion of mammals have focused on kinematics, gait selection and dynamics (Lammers and Biknevicius, 2004; Schmitt, 1998; Schmitt et al., 2006). Hundreds of species of snakes from several phylogenetically distant lineages are arboreal (Lillywhite and Henderson, 1993; Pizzatto et al., 2007), but the effects of branch structure on kinematics, gait selection and locomotor performance are only well known for a single species of rat snake, *Pantherophis guttatus* (Astley and Jayne, 2007; Astley and Jayne, 2009; Gerald et al., 2008).

Despite previous data being limited, they are sufficient to emphasize the primacy of branching structure for affecting both the speed and mode of locomotion of snakes (Astley and Jayne, 2007; Astley and Jayne, 2009). Three factors that allow faster arboreal locomotion by rat snakes are decreased cylinder diameter (from ~10 to ~1 to snake body diameters), decreased slope of the locomotor surface, and the presence of pegs to simulate secondary branches emerging from the surface that snakes crawled upon. In addition, rat snakes moving on smooth cylinders periodically stop to grip the surface using a type of concertina locomotion, whereas when cylindrical surfaces have pegs they use a variant of lateral undulation during which no gripping or static contact occurs.

In addition to considerable ecological and behavioral diversity of more than 2500 extant species of snakes (Greene, 1997), their axial morphologies also vary with phylogeny and specializations in

habits and habitat (Gasc, 1974; Jayne, 1982; Mosauer, 1935; Ruben, 1977). For example, in the species used in this study, the anterior tendon of a major epaxial muscle, the semispinalis-spinalis in the colubrid, *Pantherophis guttatus*, spans 13 vertebrae, which is nearly twice the span, of seven vertebrae, for the homologous tendon in the boid, *Boa constrictor* (Jayne, 1982). Greater numbers of vertebrae and shorter axial muscle segments with longer portions of contractile tissue relative to tendon seem likely to enhance the strength and flexibility of constricting snakes, but this may come with a cost of reducing the speed of terrestrial locomotion (Ruben, 1977). Unlike most terrestrial surfaces, small diameter branches require a snake to make a small radius of curvature to grip them. Consequently, terrestrial locomotor performance may have little predictive value for modes of arboreal locomotor performance that require a gripping gait. Given the differences in axial morphology and motor control during constriction and the large phylogenetic distance between boids and colubrids (Greene and Burghardt, 1978), species from these two lineages seem likely to differ in some aspects of their behavior and performance when moving in arboreal habitats.

To test the hypothesis that the effects of environment may have species-dependent effects on the speed and modes of arboreal locomotion, we manipulated the texture, slope, cylinder diameter and branching complexity of surfaces upon which snakes crawled. Although our two study species, boa constrictors and rat snakes, are distantly related, they both commonly climb trees. We used a very large range of perch diameters (from <0.1 to >5 body diameters) in an attempt to determine the limits of what surfaces were passable for the snakes and test the generality of previous findings suggesting that crawling performance of snakes decreases with increased perch diameter. We also tested whether factors such as frictional resistance, incline and branching complexity have interactive effects on performance and the use of different locomotor modes. We expected decreased frictional resistance, increased incline and an absence of secondary branching to decrease locomotor performance. Although the morphology of the boa constrictors seems likely to enhance their ability to grip smooth surfaces, the predicted consequences of this for climbing performance are not obvious because of the greater mass of this species compared with rat snakes with similar length.

MATERIALS AND METHODS

Experimental subjects

We used seven juvenile boa constrictors (*Boa constrictor* Linnaeus 1758) that were born in captivity ~4 months before our experiments began, and eight juvenile red rat snakes (*Pantherophis guttatus* Linnaeus 1766) that were obtained from a commercial supplier. Boa constrictors, especially juveniles, frequently climb trees (Greene, 1983), and red rat (corn) snakes also readily climb trees although they are not considered arboreal specialists (Wright and Wright, 1957; Conant and Collins, 1991). All snakes were housed individually in a 52×26×31 cm terrarium with an incandescent light bulb that provided a daytime thermal gradient of 27–33°C. All procedures were approved by the Institutional Animal Care and Use Committee of the University of Cincinnati (protocol # 07-01-08-01).

The length of a snake limits what is available to grip cylinders (Astley and Jayne, 2007). Consequently, we chose snakes for which the range in snout–vent length (SVL) within a species was small (~10% or less of the mean value) and the mean values (± s.e.m.) did not differ significantly between the boa constrictors and the rat snakes (60.0±0.6 vs 59.8±0.6 cm; $t=1.25$, d.f.=13, $P=0.23$). The boa constrictors had significantly more body vertebrae than the rat snakes

(242±4 vs 227±3; $t=3.39$, $P=0.004$), whereas the tails of the boa constrictors were significantly shorter (7.5±0.1 vs 9.2±0.6 cm; $t=-2.63$, $P<0.001$) and had significantly fewer vertebrae (56±1.3 vs 71±2; $t=-7.42$, $P<0.001$) than those of the rat snakes. Compared with the rat snakes the boa constrictors were significantly heavier (114±3 vs 65±5 g; $t=14.9$, $P<0.001$), and thus their mean mid-body width was also greater (18.9±0.7 vs 13.3±0.1 mm; $t=6.5$, $P<0.001$; Fig. 1).

Experimental protocol

The cylindrical surfaces used to test performance were 120 cm long and 1.7, 3, 13, 25, 48, 73 or 108 mm diameter, with a total of five surface textures. For the smallest diameter we used both a single-stranded 16 gauge galvanized steel multi-purpose wire (Hillman Group, Inc., Cincinnati, OH, USA) and an 18 gauge multi-stranded copper wire (General Cable, Highland Heights, KY, USA) covered with a soft polyvinyl chloride (PVC) insulating layer that created an outer diameter of 1.7 mm. Similar to Astley and Jayne (Astley and Jayne, 2007), we covered the remaining six cylinder types with length-wise strips of Nashua 394 duct tape (Franklin, KY, USA) to create a standardized uniform surface with a rougher texture than that of the material of the underlying cylinder. For the 25 mm diameter cylinders we also used an uncovered PVC pipe and an uncovered hardwood dowel to create additional variation in texture and the coefficient of friction. To simulate the effects of secondary branching we placed uncovered wooden pegs (diameter, 6 mm; length, 30 mm), spaced at 10 cm intervals, along the top center of all three 25 mm diameter cylinders and the 108 mm diameter cylinder, which preliminary experiments suggested was impassable when inclined and lacking pegs. The long axis of each perch was horizontal or inclined to 45 or 90 deg.

The far (uphill) end of each perch was secured by two 0.3 mm diameter wires, which were in a vertical plane and tightened in opposite directions. To minimize the sagging and movement of the three thinnest perches, we put them under ~40 N of tension along their long axis. Some sagging (~15 mm) and lateral movement (<5 mm) did occur at the middle of the 1.7 mm perches, but no discernible sagging or movements were observed for the thicker perches.

We performed all experiments on post-absorptive animals (>7 days after feeding) to minimize possible effects of recent ingestion on locomotor performance (Garland and Arnold, 1983) and metabolism (Secor et al., 2000). The body temperatures of the snakes during experiments were between 30.5 and 32.0°C. To provide landmarks for digitizing kinematic data, we painted white marks centered on the mid-dorsal line of each snake at ~25, 50 and 75% SVL. For each trial, a snake was placed onto one end of the perch (the downhill end of inclines) and was encouraged to crawl along the perch at maximum velocity by gently tapping the tail with a thin flexible wire or paper towel. We performed three trials in rapid succession for each treatment. We performed no more than three treatments per day and allowed a rest of 3 h between each treatment within a day. The order of the treatments was randomized with respect to diameter, incline and surface. We videotaped dorsal, lateral and anterior views using Panasonic PV-GS320 camcorders (Panasonic, Osaka, Japan) operating at 30 frames s⁻¹.

We estimated the coefficients of static friction for each of the five surfaces by placing each snake (without anesthesia) more or less parallel to the long axis of a board covered with length-wise strips of the material being tested. We did not anesthetize the snakes because preliminary experiments using anesthesia appeared to slightly alter the muscle tone and body shape compared with the

Table 1. The coefficients of static friction of the primary surfaces used for testing locomotor performance

Surface	Boa constrictor	Rat snake
Tape	0.39±0.005	0.28±0.004
Insulated wire	0.35±0.003	0.32±0.005
Wood	0.32±0.015	0.25±0.006
Bare wire	0.29±0.013	0.18±0.006
PVC	0.27±0.007	0.21±0.006

Values are means ± s.e.m. PVC, polyvinyl chloride.

normal condition. The 1.7-mm diameter wires were secured parallel to the long axis of the board using a double-sided tape beneath the wires, and fasteners allowed us to place the wires under tension in order to keep them straight and minimize movement. In a manner similar to Astley and Jayne, we gradually lifted one end of the board (nearest the head of the snake) and used a Smarttool digital level (MD Building Products, Oklahoma City, OK, USA) to determine the angle of the board when the snake first slipped downhill (Astley and Jayne, 2007). The process was repeated three times for each snake on each surface. We calculated the average coefficient of friction for each species using the average values for each individual and surface (Table 1). A three-way ANOVA (factors: species, individual nested within species and surface) revealed highly significant ($P < 0.001$) effects of surface ($F_{4,52}=91.2$), species ($F_{1,13}=125.4$) and the two-way interaction between species and surface ($F_{4,52}=12.0$). For both species the insulated wire and taped surfaces had the two highest values for the coefficient of friction, and the metal wire and PVC pipe had the two lowest values (Table 1). Overall the boa constrictors had higher coefficients of friction than the rat snakes.

Motion analysis

For each snake within each treatment we selected the fastest trial as the one with the shortest elapsed time for the snake to travel 60 cm. We then performed a more detailed analysis of each of these fastest trials using Adobe Premiere Pro version 7.0 (Adobe Systems, San Jose, CA, USA) to create digital video files for frame-by-frame motion analysis using MaxTRAQ 2.13 (Innovision Systems, Columbiaville, MI, USA). We used the long axis of the locomotor surface to define an x -axis, and the y -axis was perpendicular to the x -axis and in the plane of a dorsal view of the snake. When the movements of the reference paint marks on a snake at 25, 50 and 75% were cyclical, we determined the duration (t_{cycle}) and forward displacement (Δx) of each cycle within the fastest trial. For

concertina locomotion we defined a cycle as the time between successive initiations of static contact, whereas for lateral undulation one cycle was the elapsed time between successive times of maximum lateral displacement to one side. For each cycle we calculated the average forward velocity (v_x) by dividing Δx by t_{cycle} . For cyclic locomotion we used a variable sampling rate for frame-by-frame analysis such that we obtained a minimum of 25 evenly spaced images per cycle. For a small number of trials in which the snakes appeared to use a combination of locomotor modes, we calculated v_x for the fastest 10 cm (for irregular movement) traversed by the snake. Our primary measurement of performance was the maximal value of v_x per cycle or 10 cm interval for the fastest trial per individual per treatment. If a snake did not make any forward progress or was unable to hold on to the surface we used a value of 0 for v_x . Thus, we were able to obtain values of v_x for all combinations of individuals, species, surfaces and inclines.

For the four individuals of each species with the greatest grand means of v_x , we measured three additional variables to quantify the posture of the snake for all treatments in which these snakes were able to hold on to a surface or make forward progress. We determined the minimum length of the snake along the x -axis (l_{min}) within each cycle of movement or interval used to measure performance. At the time of l_{min} , which corresponds to the time of maximal gripping area during concertina locomotion (Astley and Jayne, 2007), we also determined the number of regions where the body of the snake crossed the middle of the locomotor surface (N_{cr}), and the average angle of the body relative to the x -axis (α_{cr}) at all of these locations.

For the fastest cycle of locomotion for each of the four fastest snakes per species, we also quantified the percentage of the cycle of concertina locomotion when the point at 50% SVL was in static contact with the substrate (%stat). We only determined values of %stat, Δx and t_{cycle} for trials in which the snakes did make forward progress and used a cyclic pattern of movement.

To better understand some of the oscillations that occurred for boa constrictors on the smallest horizontal diameter, we estimated the height of the center of mass (COM) relative to the wire. To do this we created a lateral-view bitmap, in which the entire background was lightened to provide a high contrast image with a darkened silhouette of the entire the body of the snake. We then used the COM feature of Maxtraq, which calculated the coordinates of the centroid of the dark pixels forming the snake silhouette. Hence, this simplified two-dimensional analysis assumed that the body of the snake was mostly in the vertical plane, and the boa constrictors on the horizontal wire conformed best to these conditions (Fig. 1C).

Table 2. F -values from four-way mixed model ANOVAs performed separately for four variables describing performance and posture from the trials using the highest friction surface for each diameter and surface without pegs

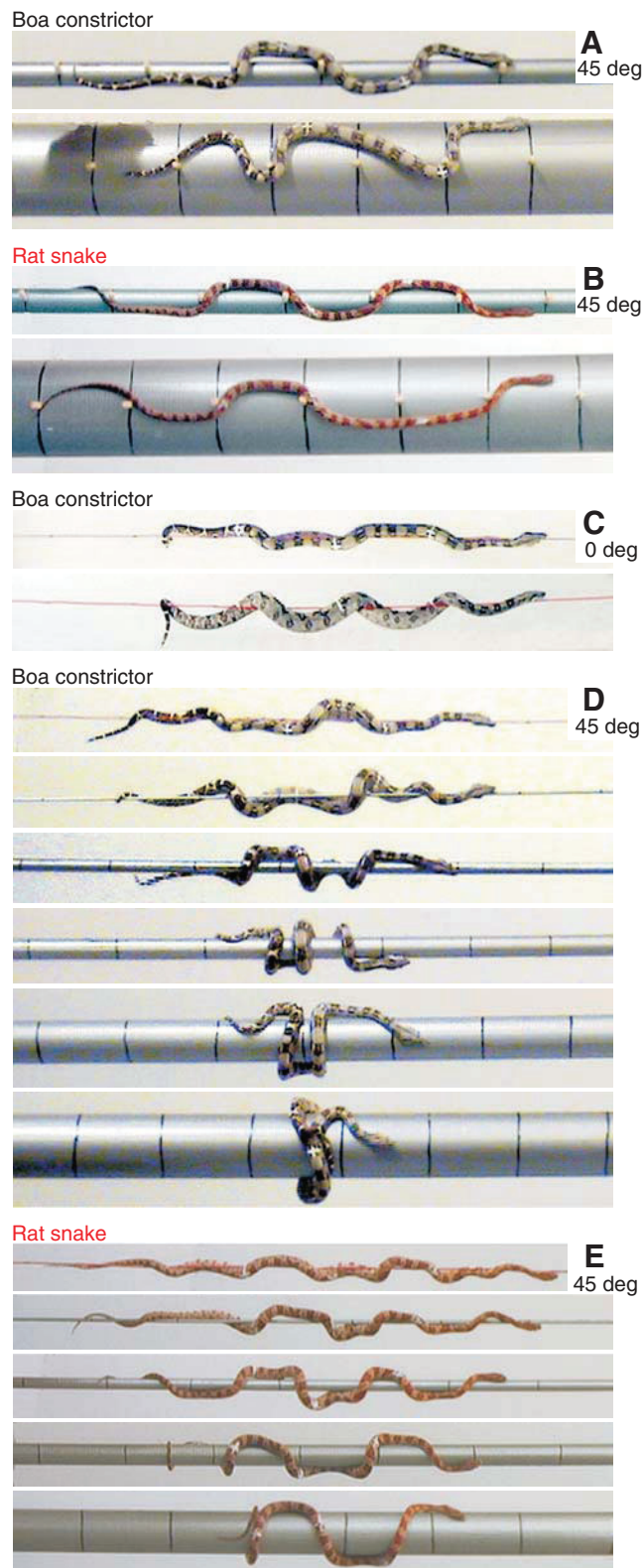
Variable	D	I	Species	$D \times I$	$D \times \text{species}$	$I \times \text{species}$
v_x	83.8**	45.4**	15.9**	3.6*	23.8**	0.8
d.f.	(6,78)	(2,26)	(1,13)	(12,156)	(6,78)	(2,26)
N_{cr}	84.5**	25.0**	66.7**	4.8**	8.1**	1.0
α_{cr}	147.1**	9.5*	35.7*	1.0	5.3*	0.1
l_{min}	110.7**	20.6**	40.2**	0.7	4.3*	0.7
d.f.	(5,30)	(2,12)	(1,6)	(10,60)	(5,30)	(2,12)

D , diameter; I , incline; l_{min} , minimum length of snake from its snout to tail tip along the x -axis; N_{cr} , number of crossing regions at l_{min} ; v_x , average velocity for the fastest cycle or 10 cm; α_{cr} , angle of the body midline with respect to the x -axis from the dorsal view.

* $P < 0.05$; ** $P < 0.001$; degrees of freedom are in parentheses. The F -values for v_{max} include all individuals, diameters and inclines, whereas the F -values for N_{cr} , α_{cr} and l_{min} are only for the four fastest individuals per species on the six smallest diameter cylinders and all inclines for which they were able to make forward progress or hold their position.

Statistical analysis

For all analyses of variance (ANOVAs), species was a fixed and crossed factor, whereas individual was a random factor nested within species. All of the remaining factors describing the simulated arboreal surfaces (diameter, surface and the presence or absence of pegs) were fixed and crossed.



We did not have any missing values of v_x and hence we were able to use the following ANOVAs to analyze values of v_x for all individuals of both species. For the highest friction surfaces without pegs and for all seven diameters and all three inclines we used a four-way mixed-model ANOVA (factors: species, individual, diameter and incline; Table 2). For the 25 mm diameter cylinders with a variety of surfaces with and without pegs we performed a five-way ANOVA [factors: species, individuals, surface ($N=3$), incline ($N=3$), presence of pegs ($N=2$)]. For the values of v_x for all three inclines, we used a four-way mixed-model ANOVA (factors: species, individual, presence of pegs and incline) for the largest diameter surfaces with and without pegs, and another four-way mixed-model ANOVA (factors: species, individual, surface and incline) for the smallest diameter cylinders with bare metal or insulated surfaces.

Additional analyses and descriptive statistics were restricted to the four fastest individuals of both species in order to minimize the occurrence of missing values, better characterize maximal speeds of locomotion and increase logistical feasibility. We analyzed the three variables describing posture (l_{min} , α_{cr} and N_{cr}) using four-way mixed model ANOVAs (factors: species, individual, diameter and incline; Table 2) using only the data from the six smallest diameters because the snakes were unable to hold onto the largest diameter. We provide descriptive statistics for the three variables describing the time course of movement and amplitude modulation (t_{cycle} , $\%stat$ and Δx), but so many values of these variables were missing that an ANOVA for a sizable majority of the treatments was not feasible.

RESULTS

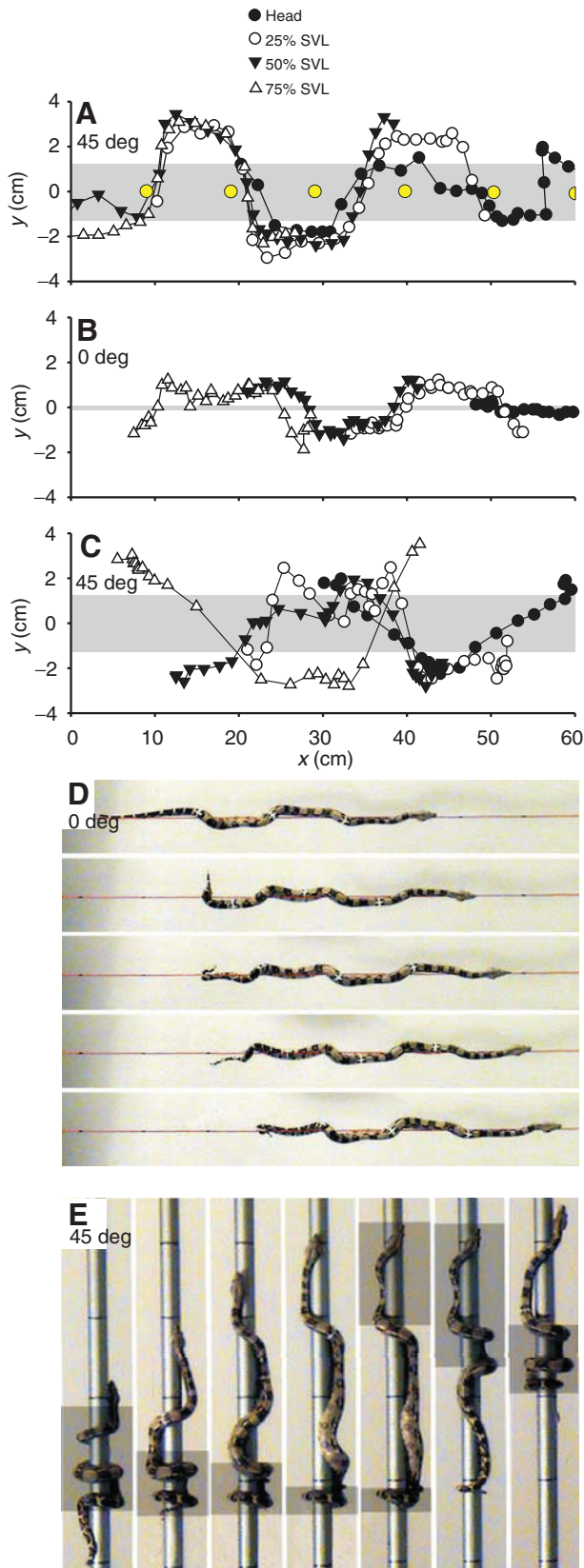
Locomotor modes

The modes of locomotion varied depending on the species, surface and incline. On all of the surfaces with pegs, regardless of incline, both species performed lateral undulation (Fig. 1A,B). During this mode all points along the length of the snakes moved simultaneously and followed a fairly similar path (Fig. 2A). Although the waves of bending were propagated posteriorly along the length of the snake, they were stationary relative to the pegs, which prevented backward slipping.

When the two smallest diameter (1.7 and 3 mm) cylinders without pegs were oriented horizontally, all of the boa constrictors performed lateral undulation, during which different longitudinal locations along the snake followed a similar overall path (Fig. 1C, Fig. 2B,D). This form of lateral undulation was also performed occasionally by boa constrictors on horizontal 12 and 25 mm diameter cylinders without pegs. Unlike conventional terrestrial lateral undulation, the bodies of the boa constrictors on the very narrow surfaces were not

Fig. 1. Effects of species, surface and incline on body posture and locomotor mode of *Boa constrictor* and *Pantherophis guttatus*. (A,B) Both species performed lateral undulation as shown in the dorsal views of the surfaces with pegs. (C) The simultaneous dorsal (top) and lateral (bottom) views of the boa constrictor on the horizontal 1.7 mm diameter wire illustrate another variant of lateral undulation, during which the mid-dorsal surface of the snake sagged considerably below the locomotor surface. (D,E) From top to bottom, the cylindrical surfaces upon which boa constrictors (D) and rat snakes (E) performed concertina locomotion had diameters of 1.7, 3, 12, 25 and 48 mm, and 73 mm (boa constrictor only). All images of concertina locomotion are dorsal views at the time when the maximal amount of gripping occurs and hence the snout-to-tail length is at a minimum (l_{min}). The distance between lines on the cylinders is 10 cm. As the diameter of the cylinders lacking pegs increased, the angle of the crossing and gripping regions increased and became nearly perpendicular to the long axis of the cylinder.

mainly in a horizontal plane because they often sagged well below the supporting surface, and sagging occurred both from anterior to posterior (Fig. 1C) and from side to side (Fig. 3A,B). In addition, the entire snake periodically rotated about the long axis of the



cylinder on the two smallest horizontal surfaces. The frequency and amount of lateral displacement for these pendulum-like movements were greatest for the narrowest of the two surfaces on which this occurred (Fig. 3C,D; supplementary material Movie 1). These long-axis rotations had much faster frequencies (2–3 Hz) than those associated with propagating the wave of lateral bending posteriorly along the length of the snake (0.6–0.7 Hz; Fig. 2D).

The vast majority of locomotion observed for both species of snakes was concertina locomotion (Fig. 1D,E, Fig. 2E, Fig. 4), but the boa constrictors used a different variant of concertina from the rat snakes. Unlike lateral undulation, during concertina locomotion some parts of the body moved while other regions had static contact associated with gripping the cylindrical surface (Fig. 2E). As the snake progressed using this mode, the region of gripping usually shifted from a more anterior to a more posterior location along the length of the snake (Fig. 2E). At a given location along the cylinder the boa constrictors required a space much larger than the cross section of its body because different points along the snake usually traveled along different paths (Fig. 2C,E). Unlike the boa constrictors, different longitudinal locations along the rat snakes performing concertina locomotion usually crossed the top of the cylinder at similar locations and appeared overall to follow a similar path, as described previously for adults of this species (Astley and Jayne, 2007).

On some surfaces individual snakes used more than one mode or different individuals used different modes on a single surface. For example, the boa constrictors used either lateral undulation or concertina locomotion on the 12 and 25 mm diameter cylinders that were horizontal (Fig. 4A). On the largest diameter cylinders without pegs the movements of snakes of both species were often irregular or involved a mixture of locomotor modes (Fig. 4). For example, for the rat snakes on the largest horizontal cylinder, one individual performed only rectilinear locomotion, during which propulsion occurs *via* the ventral skin moving relative to the skeleton rather than by flexing the vertebral column (Lissmann, 1950). A different rat snake performed very slow lateral undulation, another combined rectilinear and concertina locomotion and the others often used a combination of lateral undulation and concertina locomotion. When the largest cylinder was inclined 45 deg, two of the boa constrictors used a combination of rectilinear and concertina locomotion, whereas the others used exclusively concertina locomotion.

Locomotor performance

The maximum speeds attained by the snakes varied significantly with perch diameter, perch incline, species, the presence of pegs

Fig. 2. Modes of locomotion of the boa constrictors. (A–C) Dorsal views of the paths traveled by different longitudinal locations along the mid-dorsal line are shown for a single individual (gray areas indicate the surfaces the snake crawled on). (D,E) Successive dorsal view images showing approximately one cycle of movement. The snake performed lateral undulation on the 25-mm diameter cylinder (A) with pegs (yellow circles) and the 1.7-mm diameter insulated wire (B,D). Concertina locomotion was used on the 25-mm diameter cylinder lacking pegs (C,E). During lateral undulation different points along the body of the snake followed a similar path, whereas during the concertina locomotion of boa constrictors this was not the case. Note that the *y*- and *x*-axes of the plots are not to the same scale and hence lateral movements appear exaggerated. The times between successive points for A–C were 0.53, 0.23 and 0.50 s, respectively. For D and E the times between successive images were 3.3 and 0.5 s, respectively. The snake performing lateral undulation (D) had a steady forward progression unlike the periodic starting and stopping (shaded areas) involved in concertina locomotion (E). The distance between successive lines on the cylinders is 10 cm.

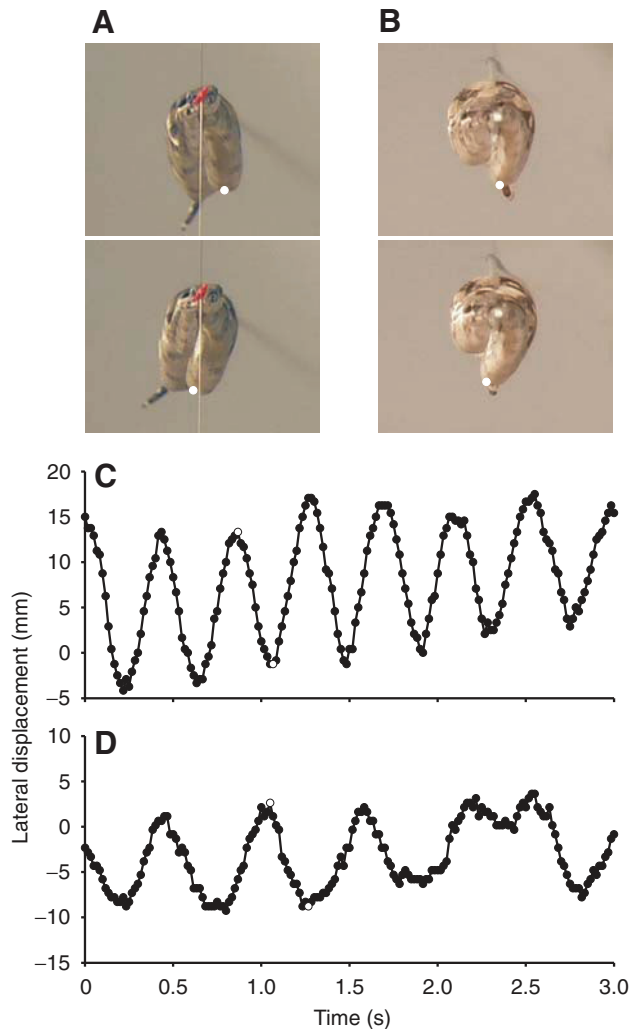


Fig. 3. (A,B) Anterior views of long-axis oscillations of a single boa constrictor performing lateral undulation on the horizontal 1.7-mm diameter insulated wire (A) and the 3-mm diameter taped surface (B). Note that the thin vertical light-colored lines are the wires supporting the far end of the perch rather than the surface that the snake crawled on. A substantial portion of the snake was below the supporting surface. (C,D) Lateral displacement of a point (white circle) along the mid-ventral line of the lowest loop on the left side of the snake during the periodic long-axis rotations shown in A and B, respectively. On the narrower surface both the amplitude and frequency of these lateral displacements increased compared with the wider surface. The successive images in A and B are one-half cycle apart, and the time interval between successive points in C and D is 0.017 s. See supplementary material Movie 1.

and surface textures (Figs 4, 5, 6). Many of these factors also had significant interactive effects on v_x (Table 2).

For the high-friction surfaces (insulated wire or duct-tape covered) without pegs, v_x of both species usually decreased with increased incline, and for a given incline, the greatest values occurred for intermediate diameters that were approximately equal to or less than the diameter of the snakes (Fig. 4). The differences in performance between the two species were highly dependent upon diameter (Table 2), as the rat snakes were slightly faster than the boa constrictors on the smallest diameters, whereas the boa constrictors were substantially faster than the rat snakes on surfaces with

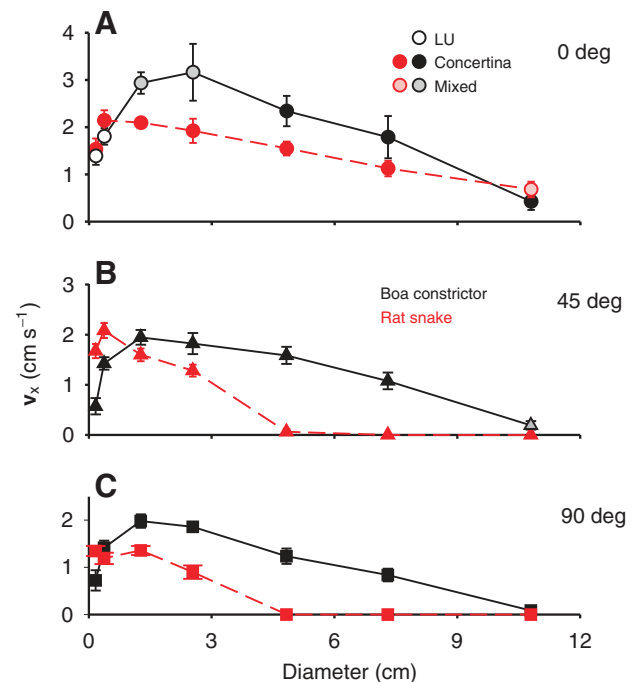


Fig. 4. The effects of species, incline and diameter of cylinders on locomotor performance. (A–C) Forward velocity per cycle (v_x) of boa constrictors (black) and rat snakes (red; dashed line) on the high-friction surfaces (insulated wire and duct tape covering) without pegs and oriented horizontally (A) or with inclines of 45 deg (B) or 90 deg (C). For a given species and incline the fastest speed occurred on an intermediate diameter cylinders. As explained in more detail in the results, a mixture of locomotor modes was used for the extremely small or extremely large diameters, but most locomotion on these surfaces was concertina. LU, lateral undulation. Values are means \pm s.e.m.

diameters ranging from 13 to 73 mm (Fig. 4). On the largest diameter cylinder, none of the rat snakes was able to hold position on either the 45 or 90 deg incline (Fig. 4B,C), whereas all of the boa constrictors were able to either hold their position or make forward progress on the 45 deg ($v_x > 0$ for five individuals) and 90 deg ($v_x > 0$ for two individuals) inclines. On the second and third largest diameters inclined, 45 and 90 deg, all of the rat snakes were at least able to hold their position, but for all these four treatments only a single individual made forward progress (48 mm diameter, 45 deg incline). By contrast, all of the boa constrictors were able to make forward progress on these four combinations of diameter and incline.

For the values of v_x on the 25 mm diameter cylinders with and without pegs (Fig. 5), the main effects of both incline ($F_{1,13}=75.6$, $P < 0.0001$) and the presence of pegs ($F_{2,26}=58.1$, $P < 0.0001$) were highly significant because both species of snakes were slower as incline increased and faster when pegs were present. The main effect of the primary surface ($F_{2,26}=2.79$, $P=0.08$) was not statistically significant. However, surface and the presence of pegs had a significant interactive effect ($F_{2,26}=5.34$, $P=0.011$) as a result of both species having decreased performance with decreased friction of surfaces lacking pegs (Fig. 5) but little regular variation in v_x occurred with the primary surface when pegs were present. Similarly, the main effect of species on performance was not statistically significant ($F_{1,13}=1.53$, $P=0.24$), but a significant interaction occurred between species and the presence of pegs ($F_{1,13}=18.8$, $P=0.0008$) because boa constrictors were faster than rat snakes when

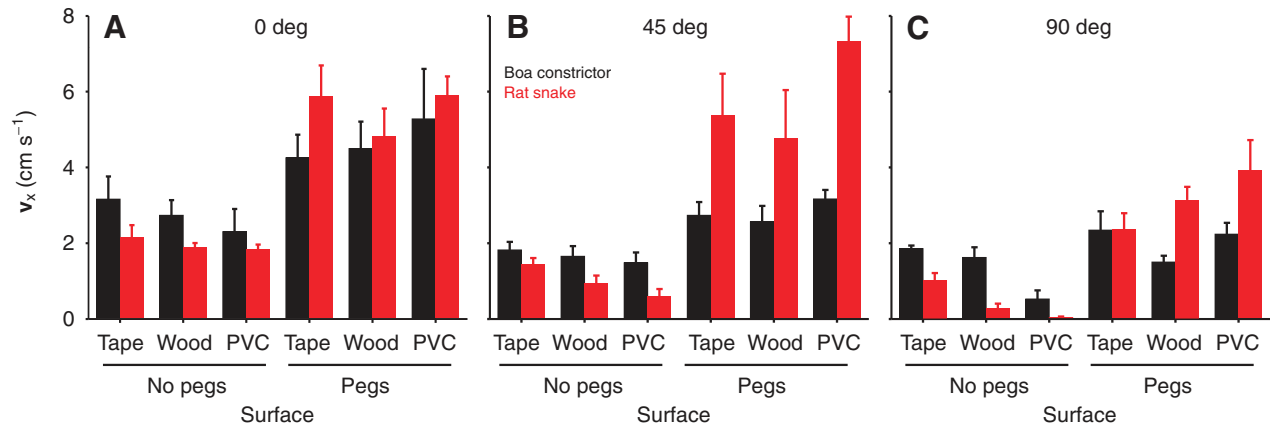


Fig. 5. The effects of species, surface texture, pegs and incline for the locomotor performance of snakes on the 25-mm diameter surfaces with and without pegs for the horizontal (A), 45 deg uphill (B) and vertical uphill (C) surfaces. The boa constrictors usually moved faster than rat snakes on surfaces without pegs, whereas the rat snakes were usually faster than the boa constrictors on the surfaces with pegs.

pegs were absent and rat snakes were faster than boa constrictors when pegs were present (Fig. 5).

For the largest and smallest diameter surfaces either the presence of pegs or differences in the coefficient of friction were sufficient to influence whether the surface was passable (Fig. 6). Although the largest diameter cylinder was impassable for many individuals of both species, the addition of pegs significantly increased the performance of both species ($F_{1,13}=58.7$, $P<0.0001$) and allowed all individuals of both species to make forward progress on all inclines (Fig. 6A). For the largest diameter cylinder the peg treatment also had significant interactive effects both with species ($F_{1,13}=10.6$, $P=0.0063$) and with incline ($F_{1,13}=9.5$, $P=0.0008$) as the vertical incline markedly reduced the benefits associated with the pegs compared with the shallower inclines. In addition, the rat snakes were much faster than boa constrictors on the surfaces with pegs that were horizontal and inclined 45 deg, whereas boa constrictors were faster than rat snakes on the largest vertical cylinder with pegs (Fig. 6A).

Performance on the smallest diameter (Fig. 6B) had significant main effects of incline ($F_{2,26}=14.2$, $P=0.0001$), species ($F_{1,13}=6.7$, $P=0.0224$) and surface ($F_{1,13}=19.9$, $P=0.0006$) and a significant interaction between surface and incline ($F_{2,26}=7.7$, $P=0.0024$). The species by surface interaction effect was marginally significant ($F_{1,13}=5.1$, $P=0.041$), and the species by incline interaction was not significant ($F_{2,26}=2.0$, $P=0.15$). Performance usually decreased with increased incline, and the rat snakes were often slightly faster than the boa constrictors (Fig. 6B). The slipperier surface did not appear to be detrimental for the maximum speeds of horizontal movement, but the lower friction surface did decrease the speeds of uphill locomotion compared with the insulated wire (Fig. 6B).

Kinematics

The variation in speed of the two species on different surfaces was associated with complex combinations of modulating both the frequency and amplitude of movements (Fig. 7). For both species the values of cycle duration were usually lowest and varied little between the three smallest diameters, but cycle duration usually increased with further increases in cylinder diameter (Fig. 7A,B). However, a notable exception to these trends was that the lateral undulation of boa constrictors on the narrowest horizontal surface had very long cycle durations compared with those on intermediate diameters when these snakes started to perform mostly concertina

locomotion (Fig. 7A). For a given diameter and incline the boa constrictors usually had longer cycle durations than the rat snakes (Fig. 7A,B).

The forward movement per cycle for the concertina locomotion of boa constrictors was usually greatest on intermediate diameter cylinders (Fig. 7C), whereas this quantity generally increased with increasing diameter of horizontal surfaces for the rat snake (Fig. 7D). For a given diameter and incline, boa constrictors usually had much greater forward movement per cycle than rat snakes (Fig. 7C,D).

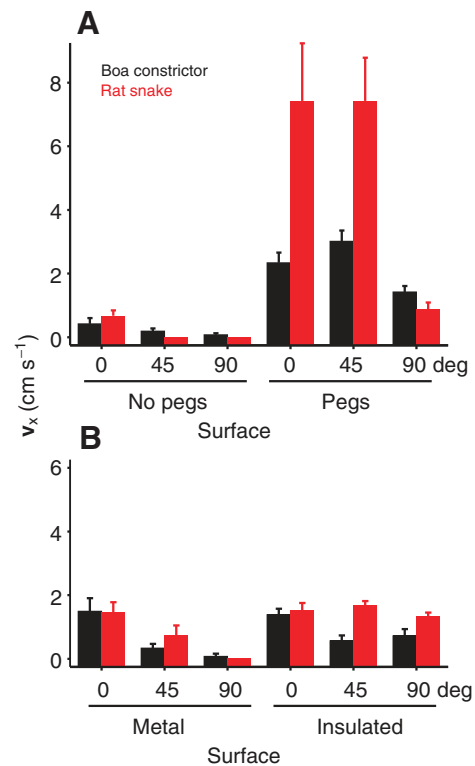


Fig. 6. The effects of species, incline and pegs (A) or surface texture (B) on the locomotor performance of snakes on the 108-mm (A) and 1.7-mm (B) diameter surfaces. Either the addition of pegs (A) or increased friction (B) allowed many snakes to make forward progress when they could not otherwise do so.

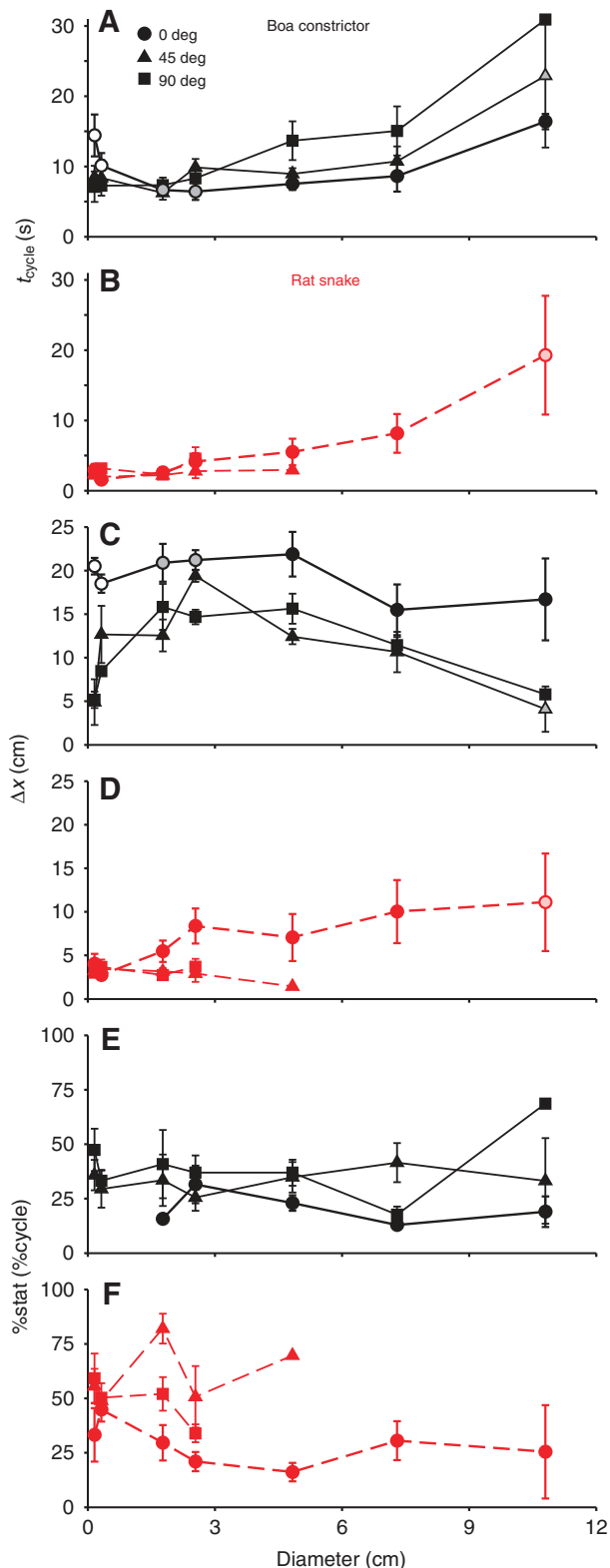


Fig. 7. The effects of species, incline and diameter on kinematics. (A,B) Cycle duration (t_{cycle}). (C,D) Forward movement per cycle (Δx). (E,F) The percentage of a cycle of concertina locomotion in which there was static contact between the snake and the surface (%stat). All values (mean \pm s.e.m.) are for the high-friction surfaces (insulated wire and duct tape covering) without pegs; (A,C,E) boa constrictors and (B,D,F) rat snakes. Missing values indicate surfaces upon which the snakes made no forward progress. The boa constrictors usually moved much farther per cycle than the rat snakes.

Different speeds were thus not attained by a single mechanism of modulating either the frequency or the amplitude of movements. Instead, the increased speed of boa constrictors on the smallest to intermediate diameter cylinders was accomplished primarily by increasing the forward movement per cycle while frequency changed little, and the decreased speed of boa constrictors on the intermediate to largest diameters was associated with simultaneous decreases in the frequency and forward movement per cycle. Although the forward movement per cycle of rat snakes had some increases associated with the increased diameter of horizontal surfaces, the increases in cycle duration were so large that performance still decreased markedly from the intermediate to greatest diameter.

During concertina locomotion both species spent large portions of time in static contact with the substrate when moving on very small diameters (Fig. 7E,F), but for subsequent increases up to the greatest diameter few trends in values of %stat were evident. One notable difference observed for rat snakes was that %stat for inclined surfaces were usually greater than those for the corresponding diameters of cylinders that were horizontal (Fig. 7F).

For the high friction surfaces lacking pegs, N_{cr} , α_{cr} and l_{min} were significantly affected by incline, diameter, species and the two-way interaction between diameter and species (Table 2, Fig. 8). For both species N_{cr} decreased with increased cylinder diameter (Fig. 1C–E) and within each species, for a given diameter, (<30 mm) values of N_{cr} were often greater for the steeper surfaces (Fig. 8A,B). For a given diameter and incline rat snakes usually had greater values of N_{cr} than boa constrictors (Fig. 1, Fig. 8A,B).

For both species α_{cr} increased significantly with increased diameter up to ~ 30 mm, after which little change in α_{cr} occurred (Fig. 1, Fig. 8C,D). For a given diameter the values of α_{cr} for both species were often greater for the steeper inclines, and the boa constrictors usually had greater values than those of the rat snakes (Fig. 8C,D).

As a result of having larger loops and greater portions of the body not oriented along the long axis of the cylinder, the minimum length of the snake along the x -axis decreased for both species with increased cylinder diameter (Fig. 1, Fig. 8E,F). For both species, values of l_{min} were usually lower for steeper inclines for cylinders of a given diameter (Fig. 8E,F). Except when they were performing a lateral undulation on the narrowest horizontal surfaces, the boa constrictors usually had lower values of l_{min} than rat snakes on a given diameter and incline (Fig. 8E,F).

DISCUSSION

To simulate some of the diversity of arboreal habitat structure, our study included a wide variety of cylinder diameters and inclines combined with different surface textures and branching complexity. In addition to affecting the type of locomotion used by snakes, these factors affected whether a surface was passable, how fast the snakes were able to move and several details of the posture of the snakes while moving. The magnitude and nature of these effects on locomotion depended upon the species of snake, and the effects of cylinder diameter and pegs were usually large compared with those of the surface textures (and friction) that we studied.

Modes of locomotion

Much of the diversity of gaits used by a single species of limbed animal is associated with changes in speed, in addition to some gaits being associated with different evolutionary lineages (Hildebrand, 1976). By contrast, most of the variation in the modes of locomotion described previously for snakes is associated with the shape and

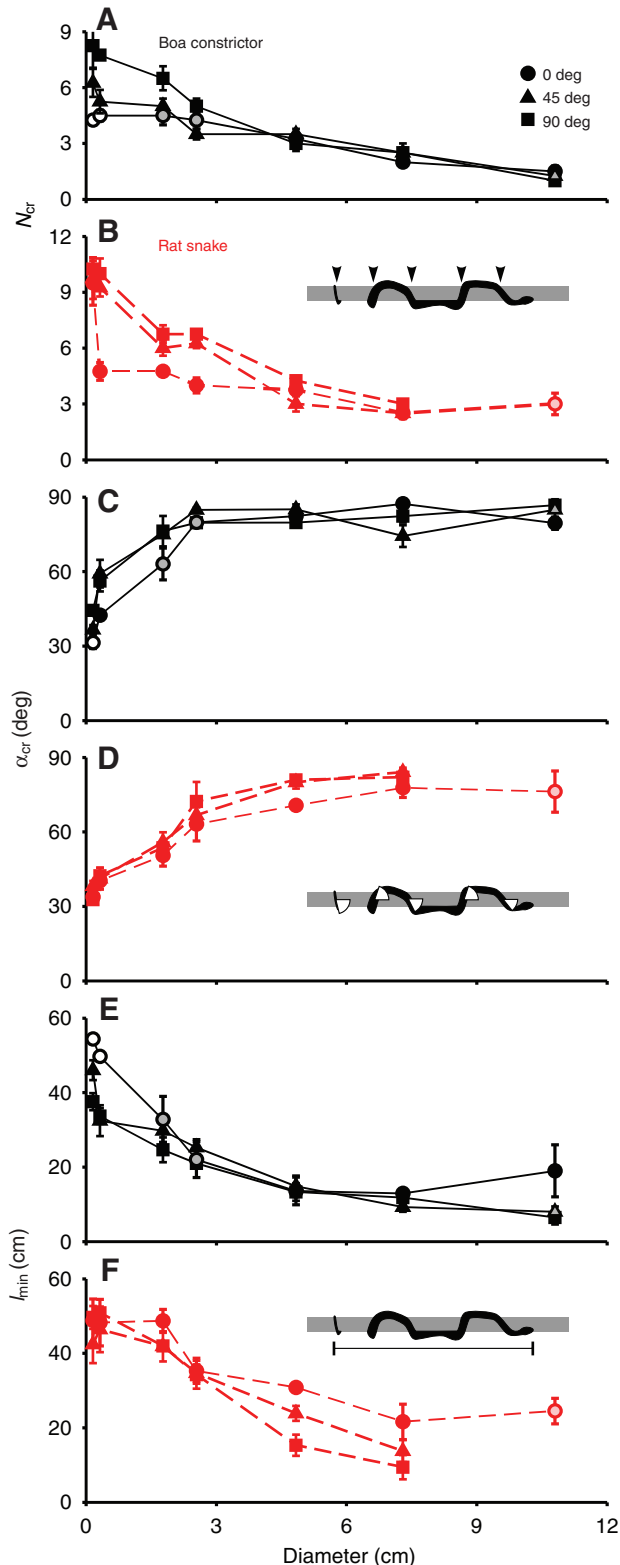


Fig. 8. The effects of species, incline and diameter on kinematics. All values (mean \pm s.e.m.) are for the high-friction surfaces (insulated wire and duct tape covering) without pegs; (A,C,E) boa constrictors and (B,D,F) rat snakes. The number of crossing regions (N_{cr}) for boa constrictors (A) was lower than for rat snakes (B), and the crossing angle (α_{cr}) of the body of boa constrictors (C) was usually higher than that of rat snakes (D). The minimum length of the body (l_{min}) of boa constrictors (E) was often shorter than that of rat snakes (F). The effects of diameter often exceeded those of incline for a given kinematic variable.

frictional resistance of surfaces, and single species of snakes often can perform all major modes of locomotion although the tendency to use a particular mode varies among different evolutionary lineages (Gans, 1974; Gray, 1946; Jayne, 1986; Lissmann, 1950).

A long-held view of terrestrial lateral undulation is that it requires macroscopic surfaces that allow the sides of the snakes to push against them (Mosauer, 1932; Gray and Lissmann, 1950; Gans, 1974). Thus, a noteworthy feature of the lateral undulation of boa constrictors on the narrowest horizontal cylinders was the absence of such surfaces. Recent experiments and simulations indicate that the directionally dependent coefficient of friction for snake skin may allow some snakes to perform lateral undulation on smooth flat surfaces, and the efficiency of this type of lateral undulation might be enhanced if the body of the snake has some localized lifting to localize the distribution of mass (Hu et al., 2009). When the entire length of the snake touches the ground, detecting a non-uniform mass distribution is technically very difficult, and flat surfaces often cause snakes to use sidewinding, during which a snake lifts different sections of its body (Gray, 1946; Gans, 1974; Jayne, 1986). However, the boa constrictors on the narrow horizontal cylinders unambiguously had very localized mass distribution (Fig. 1B), and their lateral undulation on smooth cylinders provides additional support for the mechanism of flat-surface lateral undulation proposed by Hu et al. (Hu et al., 2009).

The selection of different gaits can affect stability. For example, if the COM of a limbed animal is always within a polygon of support formed by the feet contacting the ground, then it is statically stable because it would not topple if its posture were frozen at any instant (Alexander, 2003). Thus, for limbed animals one of many consequences of moving on arboreal surfaces narrower than their normal stance width is that this method for attaining stability probably becomes more difficult (Schmidt and Fischer, 2010). However, depending on factors such as cycle duration and the time it takes for an animal to fall a distance less than the height of its legs, limbed animals can move without falling completely while using gaits that are not statically stable (Alexander, 2003).

One obvious advantage of the limbless snake body plan for moving on flat surfaces is that falling is not a risk, and hence snakes in these circumstances are statically stable. By contrast, for snakes in arboreal environments, a cylindrical body on a cylindrical surface is at great risk of toppling unless a branch has an extraordinarily large diameter or secondary branches (Astley and Jayne, 2009) or unless the long axis of the snake departs from a straight line. The boa constrictors used very symmetric waveforms during lateral undulation on the narrowest horizontal cylinders. Consequently, they were stable in so far as they could stop without gripping and not fall or topple. For most smooth cylinders in our study, the snakes of both species at least transiently had irregular waveforms (Figs 1, 2) that were less stable, and they used increased reliance on gripping to cope with this. For example, when the rat snakes extended forward and had a minimal gripping area on the horizontal wire, they frequently would spin entirely around the wire or topple so that they were temporarily upside down. During uphill concertina locomotion, the boa constrictors were able to grip the smallest diameter, even though it appeared to be difficult to do so. Thus, the use of balancing lateral undulation by boa constrictors on the thin horizontal surfaces appears to reflect a behavioral preference rather than an inability to grip. An additional factor for the different gaits of the boa constrictors moving uphill rather than horizontally on the smallest smooth cylinders is that a grip is required to prevent backward sliding caused by the weight of the snake.

In addition to the probable benefits for stability, boa constrictors may have used lateral undulation on the thin horizontal cylinders to reduce the energetic cost of locomotion. The energetic cost of the conventional terrestrial lateral undulation is substantially less than that of concertina locomotion in tunnels with moderate width (Walton et al., 1990), and the energetic cost of concertina locomotion probably increases with decreased tunnel width (Jayne and Davis, 1991). Arboreal concertina shares the following traits with tunnel concertina movement, which seem likely to make it energetically costly: large and frequent changes in momentum associated with periodic stopping, the need to overcome both sliding and static frictional resistance, and substantial forces perpendicular to the direction of movement in order to prevent slipping (Walton et al., 1990). Horses provide a precedent for an animal selecting a more economical gait when two gaits are possible (Hoyt and Taylor, 1981), but factors other than energetic economy may provide the proximate cue for gait selection (Farley and Taylor, 1991). Thus, the boa constrictors also might select a more economical alternative when more than one gait is possible, but stability could be another important factor or the proximate cue leading to this choice.

For many years the definitions of both limbed (Hildebrand, 1976) and limbless (Gans, 1974; Gray, 1946; Jayne, 1986) gaits have relied primarily on kinematics, but such methodology is not always sufficient to detect important distinctions for how animals move. For example, a recent analysis of force platform data found that some tetrapods with walking and running kinematics (duty factors <50% and >50%, respectively) actually had running or walking mechanics (Reilly et al., 2006). Similarly, aquatic and terrestrial lateral undulation of snakes have continuous posterior propagation of lateral bending but different phase relationships between bending and muscle activity (Jayne, 1988a).

Given the probable diversity of forces and motor pattern, several types of concertina locomotion appear to be distinct gaits. All types of concertina locomotion described in this and other studies (Gans, 1974; Gray, 1946; Jayne, 1986) involve periodic starting and stopping as the body is either pulled toward or pushed away from a convoluted region that functions as an anchor. However, the manner in which the body is anchored depends on the shape of the substratum. On flat surfaces the weight of the convoluted region of the snake appears sufficient to create an anchoring region (Gray, 1946), whereas all other forms of concertina movement probably involve actively pressing the body against surfaces to attain an anchoring region or grip. Electromyograms of snakes performing concertina locomotion in tunnels are consistent with the snakes pressing outward against the vertical sides of tunnels (Jayne, 1988b), whereas moving on cylinders probably requires pressing inward to establish a grip.

Some snakes may have two methods for gripping cylinders. For example, the lack of surface deformation when boa constrictors use concertina locomotion to climb thick ropes suggests they use opposing grips, whereas deformation of thinner ropes suggests these snakes press inward at different locations (Byrnes and Jayne, 2010). The preponderance of ventral contact on thicker cylinders also suggests an important role for muscles that flex the vertebrae ventrally, whereas the more extensive contact between the lateral surfaces of the snakes and the thin vertical cylinders suggests an increased importance of the lateral flexors for gripping (Byrnes and Jayne, 2010). If snakes use two distinct gripping strategies with both path-following and non-path-following kinematics (Fig. 2) (Astley and Jayne, 2007; Byrnes and Jayne, 2010), then this may represent

four distinct patterns of arboreal concertina locomotion from the combined data for only two species.

In addition to these different types of arboreal concertina locomotion, rat snakes moving downhill on smooth cylinders use a unique form of sliding (Astley and Jayne, 2007), and the arboreal lateral undulation of boa constrictors seems likely to be distinct from the mostly planar movements of terrestrial lateral undulation in which the sides of the snakes push against objects. Considering that most traditional schemes recognize only four or five modes of terrestrial snake locomotion (Gray, 1968; Cundall, 1987), this diversity of arboreal gaits found for only two species of snake is noteworthy.

Relating performance to morphology, kinematics and environmental structure

A key reason for comparing boa constrictors with rat snakes was that their axial anatomy differs. Although the snakes in our study had similar SVLs, the boa constrictors were nearly twice as heavy, 40% wider and had 10% more body vertebrae than the rat snakes. In addition, major axial muscles of the boa constrictor differ substantially from those of the rat snakes. For example, the single segments of the semispinalis muscle in boa constrictors and rat snakes span 15 and 18 vertebrae, respectively (Jayne, 1982), and the anterior tendon of this muscle is also much shorter in boa constrictors than rat snakes (7 vs 13). Additional qualitative differences in muscle morphology are correlated with boa constrictors and rat snakes being representative henophidian (booid) and caenophidian (coubroid) snakes, respectively (Gasc, 1974; Jayne, 1982; Mosauer, 1935). In addition to some correlations between axial morphology and phylogeny, constricting snakes usually have more body vertebrae and shorter axial muscle segments than related non-constricting species (Jayne, 1982). Although all henophidian snakes constrict their prey, the constricting habit is not universal and evolved independently several times within the caenophidian snakes (Greene and Burghardt, 1978). Both of the species in our study constrict their prey.

Ruben suggested that the shorter total spans and a greater proportion of contractile tissue per segment typical of boid snakes are well suited for making tight coils and generating high forces during constriction but ill suited for rapid locomotion (Ruben, 1977). Indeed he found that the maximal speeds of terrestrial lateral undulation of a boid (rosy boa) were much slower than those of the slender bodied, non-constricting colubrid (coachwhip snake). Similarly, the colubrid in our study with longer axial muscle segments was faster than the boid when performing lateral undulation on the cylindrical surfaces with pegs. However, for moderate to large diameter cylinders lacking pegs, the boa constrictors were faster than the rat snakes. Thus, unlike Ruben's suggestion that shorter axial muscle segments enhance the ability to constrict to the exclusion of the ability to move fast, the consequences of this morphology for locomotor performance are highly dependent on the mode of locomotion and environmental structure.

The primary constraints for arboreal locomotor performance may differ from those commonly considered for locomotion in other environments. For example, we observed very low frequencies of movement at reasonably warm temperatures (30°C), and thus unlike some lizards running at low temperatures (20°C) (Swoap et al., 1993), the time course of muscle twitch kinetics seems unlikely to be important for our tests of performance. In addition, the capacity of the muscles to produce force useful for propulsion becomes irrelevant if sufficient force is not produced perpendicular to

movement, to create a grip during concertina locomotion. As is the case with the performance of novice ice skaters, the ability to stay upright might trump the potential capacity of the locomotor muscles to produce propulsive force.

Many of the differences in kinematics between species and on different surfaces and inclines reflect these demands of either maintaining balance or generating an effective grip. The somewhat deeper loops of the boa constrictors using later undulation on the horizontal 1.7 mm wire compared with the 3 mm cylinder (Fig. 3) are consistent with the snakes lowering their COM more on perches where balancing is probably more difficult. The strategy of below-branch locomotion is also used by some limbed mammals such as primates and sloths (Wright et al., 2008; Nyakatura and Fischer, 2010), but the factors that cause the transition between moving with the COM above or below the branch are not well understood. Although many limbed animals prefer to move on the top of cylindrical surfaces, with decreased diameters or increased inclines a common strategy is to have a more flexed limb posture, which can decrease the height of the COM as well as having a variety of other effects that may benefit stability (Vilensky et al., 1994; Spezzano and Jayne, 2004; Schmidt and Fischer, 2010). Unlike limbed animals, snakes are able to get their COM below a branch while keeping their head right-side up and above a branch.

A potential disadvantage of a snake such as a boa constrictor having a large body diameter is that on top of a perch its COM will be higher than that of a snake with a smaller body diameter. Perhaps this helps to explain why the boa constrictors on the narrowest horizontal cylinders used a different gait and body posture from those of the rat snakes. If the COM of the boa constrictors on the horizontal wire oscillated with the mechanics of a simple frictionless pendulum, then for the observed frequency ($f=T^{-1}$) of 2.5 Hz the length (L) of the arm of pendulum would be ~ 4 cm [$T=2\pi(Lg^{-1})^{-1/2}$, where g is gravitational acceleration]. Our estimated location of the COM was 7 mm below the wire, which would predict $f=6$ Hz. The observed frequency of long axis oscillation was much greater than the frequency with which the snakes propagated bending posteriorly (<0.1 Hz). Thus, rather than the peculiar long-axis oscillations corresponding simply to the frequency of arboreal lateral undulation, they are more similar to those values expected from pendulum mechanics considering that significant frictional resistance does occur between the snake and the wire. Despite the tension on the wire, the movements of some snakes did cause some sagging and vibration of the wire, which might contribute to the observed oscillating rotations. However, long-axis rotations of snakes also occurred on the 5 mm diameter rod, which appeared to function much better as a rigid surface. Regardless of their causes, the oscillating rotations of the boa constrictors nicely illustrate a remarkable ability of these snakes to maintain balance, whereas the rat snakes often spun completely around the wire while attempting to perform concertina locomotion on top of it.

Another strategy to minimize difficulties associated with balancing and slipping is to move slowly (Lammers, 2009). Highly arboreal limbed animals such as lorises, chameleons and twig anoles often move slowly, but depending on the context for their movement some bursts of faster locomotion may occur (Peterson, 1984; Irschick and Losos, 1998; Nekaris and Stevens, 2007). Similarly the locomotion that we observed for snakes on the thin horizontal cylinders was extremely slow, especially the arboreal lateral undulation of the boa constrictors on the wire. In nearly all other circumstances the speeds of lateral undulation of a particular species of snake greatly exceed those of concertina locomotion (Jayne, 1986). An interesting but largely unresolved question is whether

snakes and other arboreal animals move slowly on cylindrical surfaces simply because they cannot move any faster or whether they are using this as a strategy to reduce the risk of falling.

Gripping can compensate for an inability to balance, but the benefits of gripping depend on the incline of the surface. Gripping a horizontal cylinder can help to prevent toppling by long-axis rotation, whereas the primary problem associated with climbing up a vertical cylinder is preventing backward slipping. Snakes could increase gripping ability by some combination of modulating the muscular force generated at a particular location, changing the orientation of the body so that gripping force is maximized for a given muscular force or using a greater number of gripping areas. However, unlike many limbed animals with prehensile feet, snakes have a direct tradeoff between how much of the body is used to grip and what is available to extend forward from a region of gripping (Astley and Jayne, 2007).

Several observations suggest that the gripping ability of boa constrictors is superior to that of the rat snakes in our study. For a similar diameter, the rat snakes usually had more gripping regions than the boa constrictors. When the boa constrictors were on many of the inclined surfaces they often prevented downward slipping with only a single gripping region (Fig. 2E), whereas this was not observed for the rat snakes in our study or that of Astley and Jayne (Astley and Jayne, 2007). Presumably this ability of the boa constrictors allowed them to traverse much greater distance per cycle and attain faster speeds than the rat snakes on all but the two smallest diameters when moving uphill (Fig. 4B,C, Fig. 7C,D). The boa constrictors were also able to climb some low-friction inclined surfaces that were impassable for the rat snakes (Fig. 4B,C) despite being nearly twice as heavy as the rat snakes.

For a given amount of gripping force generated by the animal, orienting the gripping structures perpendicular to the long axis of the cylinder will maximize the normal forces and resulting friction, and limbed animals with opposable digits such as chameleons and many primates often orient their digits in this manner (Cartmill, 1985; Fischer et al., 2010). Similarly, the angle of the crossing region of both species of snakes in our study approached 90 deg as cylinder diameter increased, and for a given diameter the value was greater for the boa constrictors than for the rat snakes (Figs 1, 8). For boa constrictors climbing vertically, the decreased deformation of larger diameter ropes is correlated with increased crossing angles (Byrnes and Jayne, 2010). Thus, the decreased crossing angles of the rat snakes compared with the boa constrictors seem likely to impede their ability to form opposing grips or reflect the alternative strategy of applying normal forces on opposite sides of the surface at different locations along its length. When climbing, the boa constrictors must produce more gripping force than the rat snakes because they are heavier, and using opposing grips could be one strategy to facilitate this.

Several factors may help to explain why the rat snakes having superior speed to boa constrictors while gripping during uphill concertina locomotion on the two smallest diameters (Fig. 4B,C). The simple fact that boa constrictors have a larger body diameter has important implications for bending and muscle function. For example, the disparity in the arc length of the side of the snake touching and conforming to a curved surface and the arc length of the opposite side increases with increased snake diameter. Consequently, if the muscles responsible for flexing the snake were superficial and oriented longitudinally, then a greater change in length would be required for a snake with a larger diameter to conform to the curvature of a given surface. Extremely short sarcomere length compromises the ability to produce force; however,

at present, neither the *in vivo* muscle strains nor the locations and activity of the relevant muscles are known for this system. The body postures of both species suggest that much of the gripping on the smallest cylinders does not just involve opposing grips, and the rat snake might be more adept at this method of gripping. Both species in our study had similar SVL and their numbers of body vertebrae were not very different; hence, similar curvature of their vertebral columns should involve roughly similar angles of flexion per joint. The extent to which the skeletal system limits the amount of vertebral flexion has not been quantified for any species of snake, but on the smallest diameter surfaces different amounts of skeletal mobility in different directions might be important, as well as the ability to produce force.

The effects of cylinder diameter on locomotor performance are well documented for a wide variety of species with and without limbs. For example, the maximal speeds of anole lizards increases with increased branch diameter although the magnitude of this effect is greater for species that have relatively long limbs (Losos and Sinervo, 1989; Losos and Irschick, 1996). Beyond a certain point, further increases in diameter have little effect on either the performance or limb kinematics of anoles (Spezzano and Jayne, 2004). Astley and Jayne found that, unlike the usually beneficial effect for limbed animals, the maximal speed of large adult rat snakes decreased with increased cylinder diameter, and our study found that maximum locomotor performance occurred on intermediate diameter cylinders (Fig. 4) (Astley and Jayne, 2007). Our different conclusions for rat snakes probably result simply from using different ranges of cylinder diameters. The diameter of cylinders used in our study ranged from 0.13 to 8.1 and from 0.04 to 5.7 times the mid-body width of the juvenile rat snakes and boa constrictors, respectively, whereas these values ranged from approximately 0.76 to 10 for the adult rat snakes used by Astley and Jayne (Astley and Jayne, 2007). In our study the maximal speeds of the stouter boa constrictors usually occurred on a diameter slightly larger than those on which the rat snakes obtained maximum performance (Fig. 4). Thus, the data currently available for snakes suggest that a good predictor for optimal cylinder size may be a diameter similar to that of the snake.

A single measure clearly is not sufficient to indicate the size of an animal. However, to avoid radical differences in the size of our two study species we used snakes with similar SVL, in part because length constrains what is available to grip a cylindrical surface. The distal part of the tails of most snakes is extraordinarily narrow, and for terrestrial locomotion of some species it appears nearly irrelevant (Jayne and Bennett, 1989). The tail of rat snakes is significantly longer than that of boa constrictors, but how important the tail is for arboreal locomotion is still unknown. The diameter of snakes seems likely to have important implications for they are able to fit onto narrow surfaces such as branches, as well as for how the snakes bend. A conspicuous convergent feature of many species of specialized arboreal snakes is a more slender shape than less arboreal species (Pizzatto et al., 2007). The rat snakes were much thinner than boa constrictors in our study, but both of these species are stout compared very light-weight, attenuate arboreal specialists such as vine snakes (*Ahaetulla* spp., *Oxybelis* spp.) and dipsadine snakes, which also have extraordinarily long tails (Lillywhite and Henderson, 1993). A greater cross-sectional area of axial muscles should enhance gripping ability, but the associated increase in the diameter and mass of the snakes may be detrimental for other demands such as moving on extremely thin branches or bridging gaps (Lillywhite and Henderson, 1993; Jayne and Riley, 2007).

For colubroid snakes a correlate of the extremely attenuate shape of many arboreal specialists is that the length and proportion of

tendons in the segments of major axial muscle segments increases. Boid snakes represent another extreme as they are generally stout and have short axial muscle segments with relatively short tendons (Gasc, 1974; Ruben, 1977; Jayne, 1982). Unlike the axial musculature of snakes, few correlations with specialized function are apparent for vertebral morphology (Johnson, 1955). Our results emphasize the importance of accounting for locomotor mode when considering the sum of the consequences of anatomical variation. Some comparisons of performance between colubroid and boid snakes with different axial muscle segment lengths could be confounded by other factors such as the boid snakes being stouter and heavier. However, such tremendous diversity of axial morphology and shape exists within snakes that future comparisons hold great promise for further isolating some of the likely functional consequences of different aspects of this anatomical diversity.

LIST OF SYMBOLS AND ABBREVIATIONS

%stat	percentage of a cycle in static contact with the substrate
l_{\min}	minimum length of snake from its snout to tail tip along the x -axis
N_{cr}	number of crossing regions at l_{\min}
t_{cycle}	cycle duration in seconds
v_x	average velocity for the fastest cycle or 10 cm
α_{cr}	angle of the body midline with respect to the x -axis from the dorsal view
Δx	forward distance traveled per cycle

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