Effects of perch diameter and incline on the kinematics, performance and modes of arboreal locomotion of corn snakes (*Elaphe guttata*)

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Summary

Animals moving through arboreal habitats face several functional challenges, including fitting onto and moving on cylindrical branches with variable diameters and inclines. In contrast to lizards and primates, the arboreal locomotion of snakes is poorly understood, despite numerous snake species being arboreal. We quantified the kinematics and performance of corn snakes (*Elaphe guttata*) moving on seven cylinders (diameters 1.6–21 cm) with five inclines (horizontal, ±45° and ±90°) and through horizontal tunnels of corresponding widths. When perches were inclined at either 45° or 90°, snakes were unable to move uphill or downhill on the larger diameters. None of the locomotion on perches conformed to any previously described mode of limbless locomotion. On horizontal and uphill perches snakes performed a variant of concertina locomotion with periodic stopping and gripping. When moving downhill, snakes often slid continuously while grasping the perch to reduce their speed. Mean forward velocity decreased both with increased incline and with increased perch diameter, contrary to the beneficial effect of increased diameter on the speeds of lizards. Both tunnel width and perch diameter had widespread and similar effects on kinematics. When perches and tunnels were narrower, the snakes had more lateral bends at shallower angles. The numerous effects of perch diameter on kinematics and the similarity to tunnel concertina locomotion emphasize the importance of fit as a limitation in arboreal locomotion of snakes. However, the slower speeds on horizontal perches compared to tunnels also suggest that balance and grip may further limit locomotor performance.

Key words: arboreal, locomotion, performance, kinematics, snake, *Elaphe*, grip, balance, posture, concertina, perch, diameter, incline, speed, climbing, tunnel, primates, gait.

Introduction

Arboreal locomotion provides an excellent example of how environment affects behavior and function. Animals moving in arboreal habitats face numerous functional demands arising from variable surface diameters and inclines and the need to traverse gaps, to grip and balance on cylindrical perches and to fit onto the perch (Cartmill, 1985). The diameter of perches has numerous and important consequences for gripping and fitting onto the perch during locomotion, and progressively steeper inclines increase the influence of the animal's weight parallel to the direction of forward movement. Within vertebrates, arboreal locomotion is best studied for primates and lizards (Cartmill, 1974; Losos and Sinervo, 1989), in which the effects on limb kinematics (Higham and Jayne, 2004; Larson and Stern, 2004; Schmitt, 1998; Spezzano and Jayne, 2004) and locomotor performance (Losos and Irschick, 1996; Losos and Sinervo, 1989; Sinervo, 1991) are well known. Large diameters generally allow faster forward locomotor speed when lizards are moving on top of the perch (Losos and Sinervo, 1989). Although many species of snake are arboreal and have convergently evolved anatomical specializations for arboreal life (Jayne, 1982; Lillywhite, 1987; Lillywhite and Henderson, 1993), no previous study has determined how any species of snake moves on cylindrical surfaces that typify the branches found in arboreal habitats.

The arboreal locomotion of snakes is interesting for several reasons. The limbless form of snakes provides a conspicuously different body plan in which to examine the effects of various aspects of arboreal habitat structure, with the variation in behavior and kinematics giving insights into the general principles underlying all arboreal locomotion. The flexible, elongate bodies of snakes may allow them to fit onto and conform easily to different sizes of perches and to use a wide range of postures and movements. However, such a variety of movements will be restricted by the need to fit on branches. Similar to primates, snakes use a frictional grip, the strength of which depends upon the extent to which the grip encircles the perch (Cartmill, 1974; Cartmill, 1985). Unlike limbed animals, whose grasp on a given diameter perch is limited by finger or arm span, snakes can change the length of their body that encircles the perch. This ability to modify gripping arc length may allow snakes to increase the grip force they can apply, but increased gripping arc has the potential cost of decreasing the number of grips due to the limited length of the snake and increasing the lateral distance that must be moved.

Additionally, snakes commonly change modes of locomotion

in response to different physical attributes of the environment (Jayne, 1988a; Jayne, 1988b). For example, snakes use concertina locomotion in the laterally restricted spaces of tunnels (Gray, 1946; Mosauer, 1932), which resemble the narrow spaces available on perches. Fitting to narrow surfaces may create many similar demands for snakes moving in tunnels and on cylindrical perches despite differences on perches such as the curvature of the surface and medially directed gripping forces.

Concertina locomotion can be an extremely demanding mode of locomotion and hence is well suited for gaining insights into how environmental variation affects organismal performance and musculoskeletal function. Snakes using concertina locomotion in tunnels periodically form alternating lateral bends that press against the sides of the tunnel to create a static frictional anchor point, after which a portion of the body straightens and moves anteriorly (Gans, 1974; Gray, 1946; Jayne, 1986). Overcoming both sliding and static friction and the numerous changes in momentum during concertina locomotion probably contribute to decreased endurance and a high energetic cost, which is almost seven times that of terrestrial lateral undulation of snakes and of limbed locomotion for an animal of equal mass (Walton et al., 1990). Decreased tunnel width reduces the endurance of snakes using concertina locomotion (Jayne and Davis, 1991), emphasizing that narrower spaces can have important functional consequences.

The overall goal of the present study was to determine how inclines, spatial constraints and shapes of surfaces representative of arboreal environmental structure affect organismal performance and the modulation of movement. Narrow spaces potentially limit the ability of an animal to modulate the amplitude of its propulsive movements during locomotion compared to those that are anatomically and physiologically possible on open ground. In addition, the narrow surfaces of both perches and tunnels led us to hypothesize that snakes on cylindrical perches would use a form of concertina locomotion similar to that used in tunnels. If locomotion on perches resembles that in tunnels, then increased perch diameter would increase both cycle duration and forward displacement per cycle with little change in forward velocity (Jayne and Davis, 1991). Additionally, increased perch diameter would result in fewer bends of the body that are oriented increasingly perpendicular to the long axis of the perch. We also expected that the mean velocity would decrease when moving up steep inclines because of the increased work needed to raise the center of mass.

Materials and methods
Experimental subjects

We used four adult corn snakes (*Elaphe guttata*) (Linnaeus 1766), which were acquired from a commercial supplier. This species climbs well in its natural habitat, although it is also commonly found on the ground (Conant, 1975). The snakes were housed individually in cages ($57 \times 59 \times 26$ cm), with an incandescent light bulb creating a temperature gradient of 27–37°C. The animals had similar snout–vent lengths (mean SVL=106 cm, range=100–110 cm), total lengths (mean TL=125 cm, range=120–133 cm), mid-body lateral diameters (mean=2.1 cm, range=1.95–2.25 cm) and masses (mean=421 g,
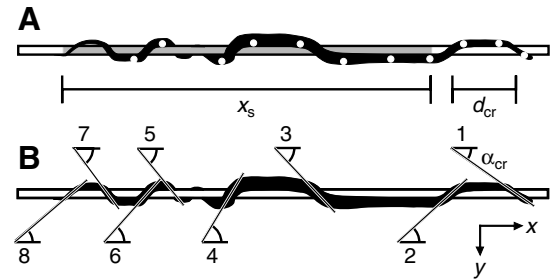

Fig. 1. Methods for kinematic analysis. Anterior is to the right. (A) White dots indicate the locations of mid-dorsal paint marks that were digitized. x_s and d_{cr} denote the length of the region of static contact and the distance between adjacent crossings, respectively. (B) The convention for measuring crossing angles, α_{cr}. A helical loop around the perch occurs between the fourth and sixth crossing regions.

range=369–455 g). All tests were on postabsorptive animals (7 days after feeding). White paint marks on the head and at 20 vertebrae intervals along the mid-dorsal line of the body provided landmarks to facilitate digitizing kinematic data from video images (Fig. 1A).

Experimental protocol

We used perches with seven diameters (1.6, 2.9, 4.1, 5.7, 8.9, 15.9 and 21.0 cm) and tunnels with seven widths corresponding to the perch diameters plus two mean mid-body diameters (5.6, 6.9, 8.1, 9.7, 12.9, 19.9 and 25.0 cm), which allows similar amounts of lateral displacement. The long axes of the perches were oriented at 0°, 45° and 90° relative to horizontal, whereas the tunnels were all horizontal.

To provide a standardized surface with sufficient friction and greater roughness than the underlying material, we covered all surfaces with strips of duct tape (Nashua 394, Franklin, KY, USA) parallel to the long axis of the perches and tunnels. The fibers in the duct tape created a grid of ridges approximately 1.5×3.0 mm. The shorter and more prominent (~0.1 mm high) ridge within the tape was perpendicular to the long axis of the apparatus. To determine the ventral coefficient of static friction, μ_s, we placed eight live *E. guttata* (including all of the experimental animals) on a flat surface covered with duct tape and tilted the surface uphill or downhill (three times per snake) until the stationary snake slipped. Values of μ_s [tangent of the angle relative to the horizontal when the animal slipped (Cartmill, 1979)] did not differ significantly between uphill and downhill trials ($F_{1,7}=3.74$, $P=0.09$), and the grand mean of 0.28 ($N=48$; s.e.m.=0.005; range 0.23–0.39) is similar to previous values for snakes on surfaces with a large range in roughness (Gray and Lissmann, 1950).

We placed each snake onto the perch or into the tunnel and encouraged it to move at maximum velocity by gently tapping the snake near the tail or using the presence of a visual target such as the dark area created by holding cupped hands just out of reach of the snake. The snakes rested for more than 30 min between trials, with individuals performing no more than four trials per day. The order in which perch diameters and inclines were presented was randomized. During tests, the body temperatures of the snakes were approximately 28°C, which is similar to the mean field active body temperature of congenerics

from a similar climate (*Elaphe obsoleta*) (Brattstrom, 1965). The top of the tunnel was covered with a sheet of Plexiglas to contain the snakes.

We videotaped each trial at 30 frames s^{-1} with a JVC GR-DVL-9800 (JVC, Yokohama, Japan) digital video camera positioned perpendicular to the long axis of the perches and tunnels and dorsal to the snakes. We converted the video sequences to AVI files using Adobe Premier Pro version 7 (Adobe Systems, San Jose, CA, USA) and then used MaxTRAQ software (Innovision Systems, Columbiaville, MI, USA) to perform frame-by-frame motion analysis with a minimum of 30 images at equal time intervals within each cycle. In each video image, points were digitized at all visible paint marks (Fig. 1A). Additionally, pairs of points were digitized to determine the angle of the body relative to the perch or tunnel during static contact at each crossing region (Fig. 1B). Crossing regions were defined as either where the body crossed the midline of the perch (Fig. 1B) or the portion of the snake between successive contact points with the right and left walls of the tunnel. The coordinates of crossing regions were digitized where they intersected the midline of the perch or tunnel. Angles were determined with a line tangential to the midpoint, with 0° representing parallel to the perch. If crossing regions were obscured by the perch, we estimated their location at the intersection of the perch midline and a line between the closest visible portions of the body on either side. Five cycles per visible paint mark per diameter–incline combination were digitized for each snake. The *x*-axis was parallel to the long axis of the perch or tunnel and the overall direction of travel, and the *y*-axis was perpendicular to the *x*-axis and in a horizontal plane (Fig. 1).

Kinematic measurements

We analyzed seven variables describing the motion of individual paint marks, and the values for each variable were averaged across all paint marks for each cycle. Durations of events included those of each cycle (t_{cycle}), the time moving per cycle (t_m) and the time of static contact per cycle (t_s) for locomotion that involved periodic stopping, where a cycle was the interval between two successive initiations of movement. The percentage of time in static contact (%stat) was t_s divided by t_{cycle}. The forward displacement per cycle (Δx) was the distance moved during one cycle. Values of %stat and Δx are analogous to the duty factors and stride lengths, respectively, in limbed locomotion. The mean forward velocity per cycle (V_x) and mean forward velocity while moving ($V_{x,m}$) equaled Δx divided by t_{cycle} and by t_m, respectively.

Within each cycle we quantified the maximum lengths of the zones of movement and static contact (Fig. 1A), denoted by subscripts of m and s, respectively. These zone lengths were expressed in terms of the anatomical length of the body of the snake (% SVL) within a zone (l_s, l_m) and the length of the zone along the *x*-axis (x_s, x_m).

Six variables were calculated from the crossing regions. We determined the maximum and minimum number of simultaneous crossing regions ($N_{cr,max}$ and $N_{cr,min}$) during a cycle, which indicates the number of potential grips, and the difference between them (ΔN_{cr}). For each crossing region over the same time interval used to calculate V_x, we recorded its *x* position and calculated its mean velocity ($V_{x,cr}$). For concertina

locomotion in tunnels, $V_{x,cr}$ could not be calculated because crossing regions completely straightened and reformed between cycles. To describe the waveform of the lateral bending of the snakes, we calculated the mean distance between pairs of successive crossing regions (d_{cr}) and the angle of the body (α_{cr}) midline relative to the long axis of the perch (Fig. 1B). We also noted the presence of helical wrapping, when the snake's body encircled 360° of the perch between two successive visible crossing regions without changing the direction of wrapping (Fig. 1B).

Some methods used for concertina locomotion had to be modified or could not be used for downhill locomotion, when the snakes did not have distinct cyclic starting and stopping. Consequently, these sequences were analyzed for the time interval taken for the mid-body paint mark to move 5 cm. The cumulative duration within this time interval in which the snake stopped moving was divided by the total interval duration to give %stat. We measured α_{cr} at the end of each time interval, but l_s, x_s, l_m and x_m could not be calculated for this type of continuous movement. For the two widest tunnels, some snakes used lateral undulation, which was analyzed in cycles defined by the maximum lateral movement of body points.

Statistical analyses

We analyzed each variable for five cycles per combination of individual, diameter, surface (tunnel or perch) and incline (total $N=20$ for all four individuals except uphill and downhill 45° at 4.1 cm, where total $N=18$ and 19, respectively), using three different, mixed-model ANOVAs. Individual ($N=4$) was considered a random, crossed factor whereas diameter, surface and incline were considered fixed, crossed factors. The variables determined by individual paint marks or crossings were averaged to give a single value per cycle.

Because of numerous blank cells and incomplete replication for all combinations of perch diameter and incline, we were unable to perform a single ANOVA on the entire data set. Thus, we performed one two-way ANOVA (with diameter and individual as factors) for all diameters during horizontal movement and another two-way ANOVA (with incline and individual as factors) for all perch inclines at the smallest diameter (Tables 1, 2). Neither distance per cycle nor cycle duration was analyzed in the latter ANOVA because of the lack of distinct cycles during downhill locomotion.

To determine the effects of moving in tunnels *vs* on horizontal perches, we performed a three-way ANOVA (with width, individual and surface as factors). For the ANOVA, we analyzed only the smallest five tunnel widths and perch diameters because two individuals used lateral undulation in the largest two tunnel widths and another individual failed to move forward.

Results
Locomotor mode

The snakes moved on perches with different inclines using two different modes of locomotion, both of which involved a series of alternating left and right bends, occasionally interspersed with a helical wrap (Fig. 2). While moving on the horizontal and uphill perches, the snakes used a mode of locomotion with many similarities to concertina locomotion in

tunnels (Jayne, 1986). In this arboreal variant of concertina locomotion, each point on the snake cyclically moved and stopped (Fig. 3B,C), but some backwards slipping occurred on steep uphill inclines (Fig. 3B). The initiation of the movement and the static phases proceeded from anterior to posterior, resulting in posteriorly shifting or expanding zones of movement and static contact that were commonly 0.25 SVL or more (Fig. 2A,B). On horizontal and uphill perches, each point along the body nearly followed the path of the points anterior to it (Fig. 2, Fig. 4B,C).

When moving downhill, the snakes used a controlled slide (Fig. 2C, Fig. 4D, Fig. 5E), in which each point slid downwards continuously with limited lateral movement (Fig. 3D). As the steepness of the downhill inclines increased, the snakes slid downwards with progressively less posterior propagation of lateral bending and with different points on the snake following different paths (Fig. 2C, Fig. 4D).

For the five smallest tunnel widths, snakes used concertina locomotion as described in previous work (Jayne, 1986) (Fig. 3A). As in arboreal concertina locomotion (Fig. 2A,B), the zones of movement and static contact in tunnels expanded posteriorly, but unlike arboreal concertina locomotion, each point did not follow the same path of the snake's body (Fig. 4A). In tunnels, the crossing regions did not persist between cycles, but rather they were straightened and re-formed at different locations after each moving phase. In the two widest tunnels, only one snake used concertina locomotion whereas two others used lateral undulation with substantial backwards slipping of the waves, although forward movement was achieved.
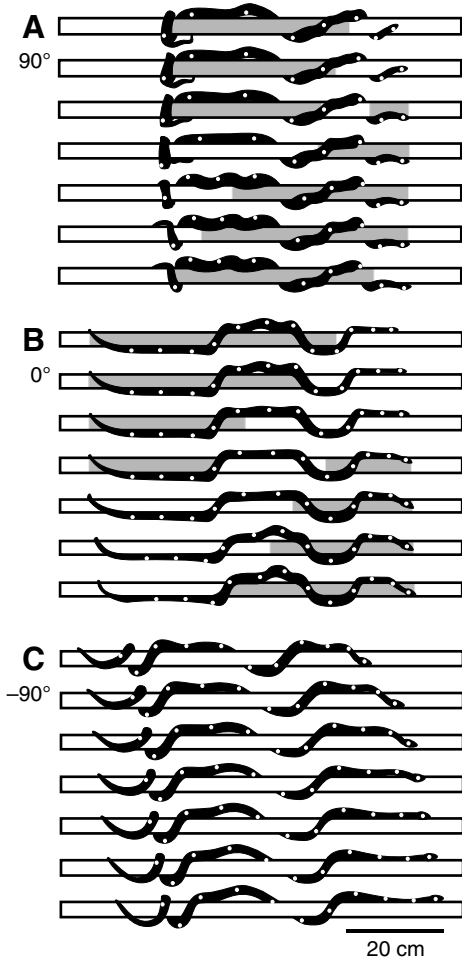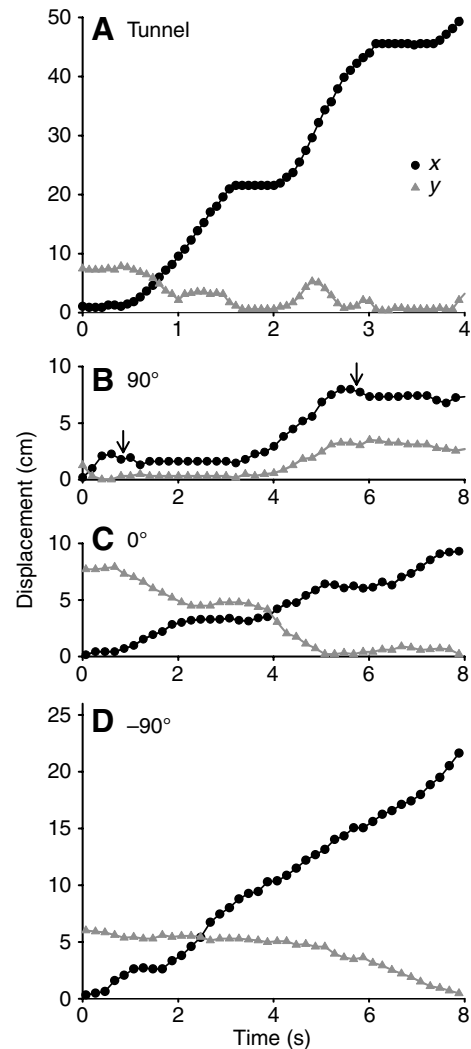

Fig. 2. The effects of perch incline on locomotor mode and movement. The tracings are from dorsal view videos of a corn snake (SVL=102 cm, mass=400 g, 4.1 cm perch) and show seven consecutive images at equal time intervals within a single cycle of concertina locomotion (A,B). The downhill sequence (C) is for the same total time as A. The shaded areas indicate static contact with the perch. (A) Uphill 90°. (B) Horizontal. (C) Downhill 90°. The times between successive images of B and C are 0.53 s, and 0.7 s for A.

Fig. 3. The effect of incline on forward (*x*) and lateral (*y*) displacement of a single longitudinal point over time. All graphs are of a mid-body point on the same individual moving on a 4.1 cm perch and equivalent tunnel width (8.1 cm). Twice as much time is shown for the perches (B–D) compared to the tunnel (A). The arrows in B indicate backwards slipping. A, B and C illustrate approximately two, one and two complete cycles, respectively, and D displays non-cyclic downward sliding. (A) Tunnel. (B) Uphill 90° perch. (C) Horizontal perch. (D) Downhill 90° perch.
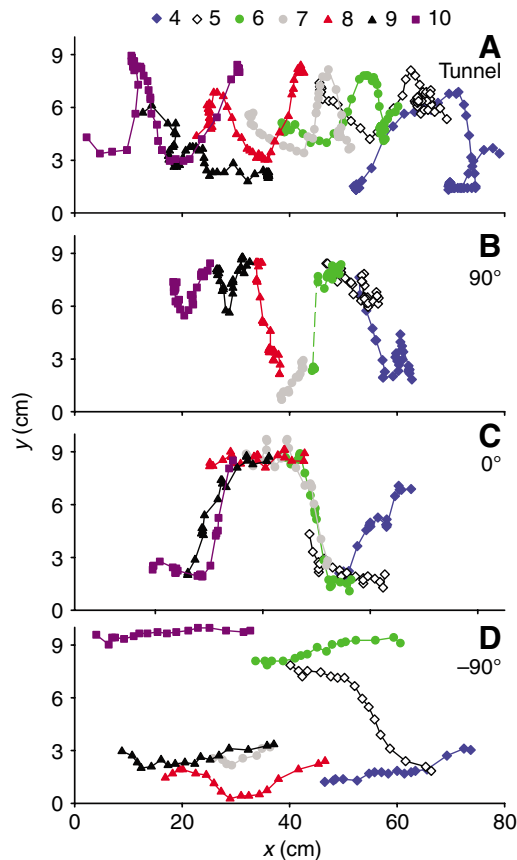
Fig. 4. Dorsal views of the paths traveled by different longitudinal points on a single snake (SVL=102 cm, mass=400 g) in tunnels and on perches at three inclines. Broken lines indicate when points were obscured by the perch. All perches had a diameter of 1.6 cm, and the tunnel had an equivalent width (5.6 cm). The longitudinal points are numbered from anterior to posterior (head=1) at 20-vertebrae intervals. (A) Tunnel. (B) Uphill 90° perch. (C) Horizontal perch. (D) Downhill 90° perch. For all perches (B–D), symbols are placed every 0.5 s. For the tunnel, symbols are placed every 0.03 s. Note that the entire body of the snake follows a nearly identical path in B and C but not in A and D.

Performance

Increased steepness decreased the ability of snakes to move on larger diameter perches. All four snakes were able to move forward on all seven of the perch diameters when they were horizontal, the smallest five diameters at downhill 45°, and the smallest three diameters vertically downhill and 45° uphill. On the vertical uphill perch, four, three, two and no snakes climbed the diameters of 1.6, 2.9, 4.1 and ⩾5.7 cm, respectively. In some of the failures, the snakes used concertina locomotion but had a net backward movement due to slipping. The only failure to move forward in the tunnels was a single animal that did not move in either of two largest tunnel widths. Forward velocity (V_x) decreased significantly with increased perch incline (Table 1, Fig. 5D).

The locomotion in all tunnels and on all perches was relatively slow, with velocities rarely exceeding 10% SVL s^{-1}. The most conspicuous differences in V_x were between tunnels and perches (surface factor in ANOVA), as snakes in tunnels
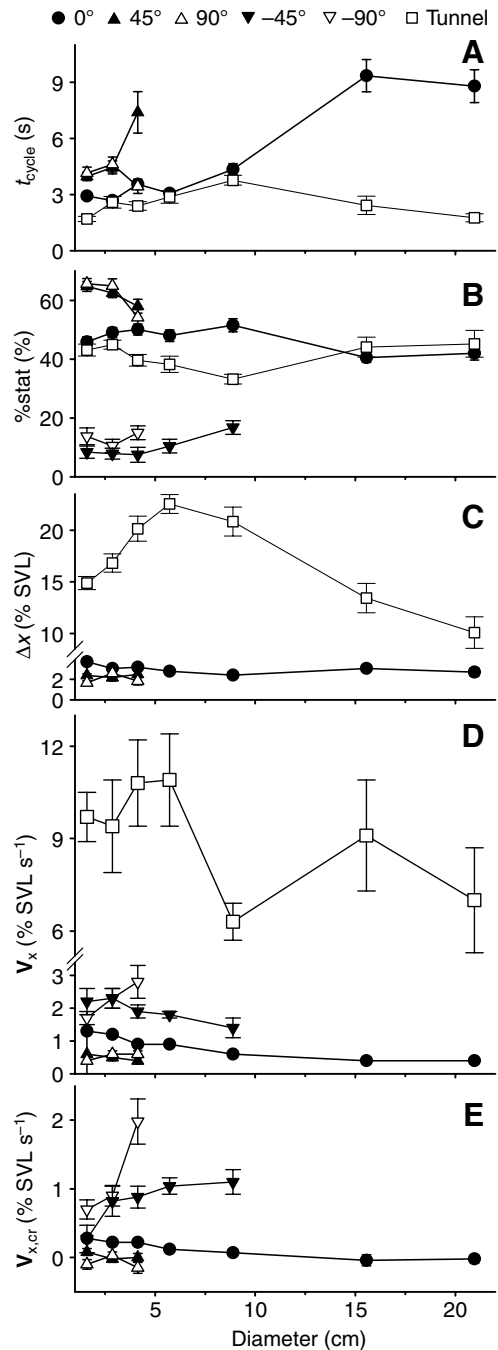

Fig. 5. Mean values (± s.e.m) of kinematic variables. (A) Cycle duration, t_{cycle}. (B) Percent of time in static contact, %stat. (C) Forward displacement per cycle, Δx. (D) Mean forward velocity, V_x. (E) Forward velocity of crossing points, $V_{x,cr}$. The downhill data were omitted from A–C because snakes did not stop periodically. Values for the largest two tunnel widths in A, B and C are only from the single individual who performed concertina locomotion, whereas D includes values from two additional individuals that performed lateral undulation.

moved as much as 12 times faster than snakes on the matching perch diameter (Table 1, Fig. 5D). V_x decreased significantly with increased perch diameter but was unaffected by tunnel width (Table 1, Fig. 5D).

Table 1. *Results of ANOVAs performed separately on each timing, speed and zone length variable*

Variable	2-way, 0° (perch) Diameter d.f.=6,18	2-way, 1.6 cm (perch) Incline d.f.=4,12	3-way (perch and tunnel)		
			Surface d.f.=1,3	'Diameter' d.f.=4,12	Surface × diameter d.f.=4,12
t_{cycle}	13.0 (<0.001)		1.1 (0.372)	8.5 (0.002)	1.41 (0.289)
t_m	10.1 (<0.001)	2.3 (0.124)	0.1 (0.763)	8.5 (0.002)	1.5 (0.256)
t_s	14.6 (<0.001)	13.3 (<0.001)	2.9 (0.188)	4.2 (0.023)	3.5 (0.042)
%stat	2.7 (0.048)	109 (<0.001)	11.2 (0.044)	0.9 (0.482)	2.9 (0.066)
Δx	1.0 (0.464)		142 (0.001)	5.1 (0.012)	5.3 (0.011)
V_x	19.0 (<0.001)	5.6 (0.009)	11.9 (0.041)	1.8 (0.188)	1.4 (0.286)
$V_{x,m}$	20.0 (<0.001)	1.3 (0.338)	16.4 (0.027)	2.3 (0.122)	1.7 (0.213)
l_m	1.7 (0.189)	13.3 (0.006)	74.3 (0.003)	2.1 (0.149)	0.8 (0.537)
x_m	1.8 (0.158)	6.5 (0.032)	6416 (<0.001)	10.8 (0.001)	1.6 (0.239)
l_s	3.2 (0.025)	1.3 (0.347)	9.6 (0.053)	9.8 (0.001)	6.2 (0.006)
x_s	3.8 (0.013)	4.3 (0.068)	30.1 (0.012)	17.5 (<0.001)	3.0 (0.064)

Values are F (P). Variables beginning with t, V_x, l and x are durations, forward velocities, anatomical length and length along the x axis, respectively. Subscripts m and s indicate the moving and static portions within a cycle, respectively. Prefix Δ indicates change within one cycle. For the ANOVA of perch inclines at 1.6 cm diameter, the d.f. for l_m, x_m, l_s and x_s is 2,6.

Kinematics of locomotion on perches

The diameter of horizontal perches significantly affected more kinematic variables than the incline of the smallest perch (12 of 17 *vs* 8 of 15) (Tables 1, 2). For concertina locomotion on perches, t_{cycle} usually increased with increased diameter (Table 1, Fig. 5A). Both t_m and t_s increased significantly with increasing diameter, but little change in %stat was evident among different diameters (Table 1, Fig. 5B). Diameter did not significantly affect Δx (Table 1, Fig. 5C). Thus, the animals on larger diameters were slower as a result of taking longer to cover roughly the same distance per cycle. Increased incline resulted in increased t_s (Table 1) and increased %stat (Fig. 5B). $V_{x,m}$ decreased with increased perch diameter but was unaffected by incline (Table 1). Hence, the decrease in forward speed with increased incline was mainly associated with longer times of static contact rather than changes in the speed while moving.

The lengths of the static zones (l_s, x_s) decreased significantly with increased perch diameter but were unaffected by incline (Table 1, Fig. 6B). The lengths of the moving zones (l_m, x_m) were not significantly affected by diameter (Table 1, Fig. 6A).

Both diameter and incline of the perch had many significant effects on variables related to the shape of the body and the path traveled during locomotion (Table 2). As diameter increased, the maximum and minimum number of crossing regions ($N_{cr,max}$ and $N_{cr,min}$) decreased significantly (Fig. 6C), but the difference between them (ΔN_{cr}) was constant (Fig. 6D). The angle of the body at the crossing regions (α_{cr}) became nearly perpendicular to the long axis of the perch as diameter increased (Fig. 6E, Fig. 7), which may facilitate gripping *via* ventral flexion.

The values of $V_{x,cr}$ indicated that the crossing regions were nearly stationary for horizontal and uphill locomotion on a perch, whereas the crossing regions slipped progressively more
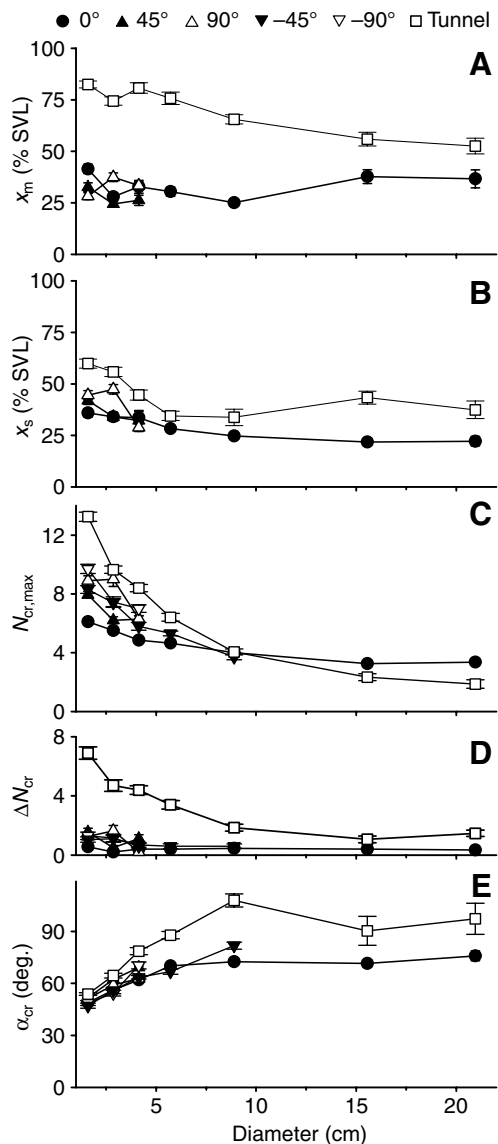

Fig. 6. Mean values (± s.e.m.) of kinematic variables. (A) Maximum x length of moving zone, x_m. (B) Maximum x length of static zone, x_s. (C) Maximum number of crossings, $N_{cr,max}$. (D) Change in the number of crossings during a cycle, ΔN_{cr}. (E) Mean angle of crossings, α_{cr}. The downhill data were omitted from A and B because snakes did not stop periodically.
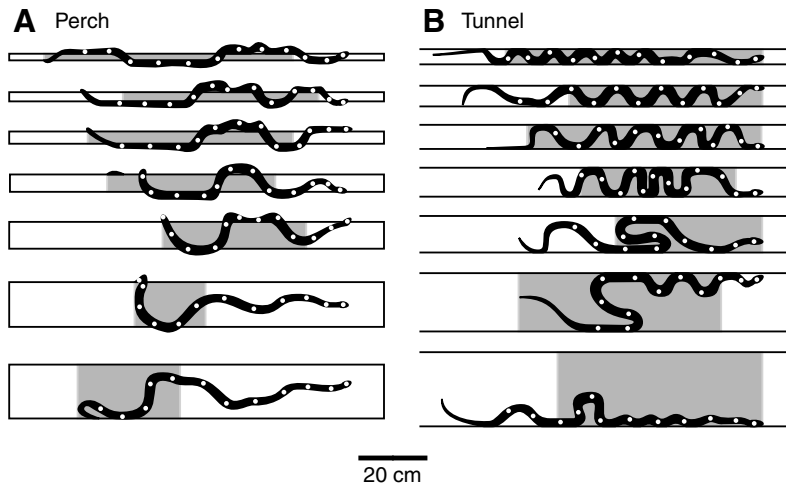
Fig. 7. The effects of perches *versus* tunnels and width on posture of a corn snake (SVL=102 cm, mass=400 g). (A) Horizontal perches of all seven diameters (1.6, 2.9, 4.1, 5.7, 8.9, 15.9 and 21.0 cm). (B) Horizontal tunnels of all seven corresponding widths (5.6, 6.9, 8.1, 9.7, 12.9, 19.9 and 25.0 cm). The shaded areas indicate the regions of static contact with the surface. In the 19.9 and 25.0 cm tunnels, only a single snake moved using concertina locomotion, and in the 25.0 cm tunnel it did so without any crossing regions. All images are for the time within a cycle when the region of static contact is longest. Videos of locomotion described in this paper can be found at http://bioweb.ad.uc.edu/faculty/jayne/videos.htm.

with steeper downhill slopes and larger perch diameters (Fig. 5E). As the perches became steeper, the number of potential gripping regions ($N_{cr,min}$ and $N_{cr,max}$) increased (Fig. 6C) and the half-wavelength of the lateral bends (d_{cr}) decreased (Fig. 2), but ΔN_{cr} and α_{cr} were unaffected by incline (Fig. 6D,E).

Incline had a large effect on the prevalence of helical wraps compared to diameter. For horizontal perches, 0–25% of the sequences analyzed for different diameters had helical wrapping, whereas helical wrapping occurred in 75–100% of the sequences of vertical uphill and downhill locomotion.

Kinematics of locomotion on perches vs. tunnels

For concertina locomotion on perches *versus* in tunnels of similar width (smallest five widths) t_{cycle}, t_m, and t_s (Table 1, Fig. 5A) were all similar. The values of %stat for the five smallest widths were significantly greater for perches than for tunnels (Table 1, Fig. 5B). The forward movement per cycle (Δx) in tunnels and the resulting velocity while moving ($V_{x,m}$) were significantly greater than those for perches with similar diameters (Table 1, Fig. 5C), and all zone lengths except l_s were significantly longer in tunnels than on perches (Fig. 6A,B).

Both $N_{cr,max}$ and ΔN_{cr} were significantly greater in tunnels (Fig. 6C,D) compared to perches of equivalent diameter. Unlike the movement on perches, much of the body periodically straightened during locomotion in tunnels, resulting in larger

values of ΔN_{cr} for tunnels compared to perches, in addition to significant decreases with increased tunnel width (Table 2, Fig. 6D). Compared to the values for perches with equivalent diameter, d_{cr} was smaller (Fig. 7) and α_{cr} was larger for tunnels (Fig. 6E). Thus, the lateral bends used on perches had longer wavelengths relative to their amplitudes compared to those in equivalent width tunnels (Fig. 7). The snakes commonly used lateral bends resembling square waves rather than simple sinusoidal waves, as indicated in part by many values of α_{cr} approaching 90° (Fig. 6E, Fig. 7).

Discussion

No previous study has examined the locomotion of snakes either on inclines or on branches, both of which were ecologically relevant structural attributes of the environment that profoundly affected how the snakes moved. We observed an unexpected variety of movements for snakes on cylinders with an interesting diversity of variation in continuous variables as well as some qualitative differences. Whether gaits and different modes of locomotion are best conceptualized as discrete categories or merely abutting regions along a continuum of variation remains a matter of active debate (Biknevicius and Reilly, 2006). Definitions of gaits relying on the presence or absence of a trait (such as a suspended phase or not for a run *vs* a walk) are likely to emphasize categorical variation, whereas categories arising from quantitative descriptors may be quite arbitrary. Most

Table 2. *Results of ANOVAs performed separately on each crossing region variable*

Variable	2-way, 0° (perch) Diameter d.f.=6,18	2-way, 1.6 cm (perch) Incline d.f.=4,12	3-way (perch and tunnel)		
			Surface d.f.=1,3	'Diameter' d.f.=4,12	Surface × diameter d.f.=4,12
$N_{cr,max}$	19.3 (<0.001)	9.4 (0.001)	208 (<0.001)	108 (<0.001)	45.6 (<0.001)
$N_{cr,min}$	26.7 (<0.001)	7.9 (0.002)	4.5 (0.124)	28.0 (<0.001)	6.2 (0.006)
ΔN_{cr}	0.7 (0.676)	2.5 (0.098)	78.0 (0.003)	27.1 (<0.001)	21.3 (<0.001)
$V_{x,cr}$	3.1 (0.030)	1.6 (0.236)			
d_{cr}	1.1 (0.418)	5.7 (0.008)	33.9 (0.010)	1.3 (0.337)	5.6 (0.009)
α_{cr}	16.5 (<0.001)	2.2 (0.134)	43.7 (0.007)	141 (<0.001)	14.3 (<0.001)

Values are F (P). Subscript cr denotes crossing regions, and N, V_x, d and α are the number, mean forward velocity, distance and angle of crossing regions, respectively. Prefix Δ indicates change within one cycle. max and min denote maximum and minimum values observed within a cycle.

schemes for classifying modes of limbless locomotion have relied on the presence or absence of traits rather than creating categories from continuous variation (Gans, 1974; Gray, 1946; Jayne, 1986; Mosauer, 1932).

Locomotor modes and performance

A key feature described previously for snake locomotion is the extent to which snakes modify locomotor mode in response to structural features of the environment. For example, in the presence of solid surfaces with irregularities that provide anterio-medially directed surfaces, snakes usually perform terrestrial lateral undulation, whereas in the presence of closely spaced, parallel vertical surfaces, such as within the confines of a tunnel, snakes perform concertina locomotion (Gans, 1974; Gray, 1946; Jayne, 1986; Mosauer, 1932). In terrestrial lateral undulation, lateral bending and muscle activity are propagated posteriorly with a constant speed (Jayne, 1988a), the body only has sliding contact with the locomotor surface, and effectively all of the points along the length of the snake during lateral undulation travel along the same path (Gans, 1974; Gray, 1946; Jayne, 1986; Mosauer, 1932). No previous study of concertina locomotion in tunnels found any posterior propagation of lateral bending, and different longitudinal locations along the length of the snake during this mode follow different paths (Gray, 1946; Jayne, 1986; Jayne, 1988b; Jayne and Davis, 1991).

Much of the locomotion of snakes on perches that we observed did not conform simply to any previously described mode of limbless locomotion. Snakes on perches had three qualitative features resembling tunnel concertina locomotion: alternating bends to the left and right, stopping periodically, and some portion of the body always having static contact with the substrate. Two additional features did not conform to concertina locomotion within a tunnel. First, different longitudinal locations along the lengths of snakes on perches commonly followed the same path (Fig. 4B,C). Second, regions of vertebral flexion propagated posteriorly while the snake was moving (Fig. 2). Both of these features resemble terrestrial lateral undulation; however, the periodic stopping disrupts the steady posterior propagation of a particular bend, which differs from terrestrial lateral undulation. To avoid a proliferation of terms, we refer to these movements on horizontal and uphill perches as 'arboreal concertina locomotion', but we emphasize this is a combination of qualitative traits equally distinct as those used previously to describe other modes of limbless locomotion..

When all points of the snake follow a single path, the entire snake can fit through an opening equal to its largest cross-sectional area, whereas other types of movement require a larger area. For example, snakes performing concertina locomotion in tunnels use a swath equal to the width of the tunnel. Consequently, if this tunnel pattern of movement were used on a perch from which branches emerge, then the branches would obstruct forward movement. By contrast, using a mode of concertina that follows a single path readily avoids such potential obstructions.

In addition to obstructions created by branches that arise from a perch, the unobstructed space available for movement may be reduced by impinging vegetation. Clearance within arboreal habitats has received less attention than how fast animals move and fit onto a single perch. For example, within arboreal lizards,

occurrence on narrower perches commonly correlates with limbs that are shorter (Williams, 1983). However, even on a narrow unobstructed cylinder, longer-limbed species usually run faster than shorter-limbed species with similar overall size (Irschick and Losos, 1999; Losos, 1990). Thus, an overlooked benefit of reduced limb length may be simply to reduce the cross-sectional area needed to move along a perch in cluttered natural arboreal environments (Spezzano and Jayne, 2004). Similarly, a key advantage of the limbless body plan and behaviors used by snakes in cluttered arboreal habitats may be the small cross-sectional area required for moving.

Although tunnel width barely affected the maximal speeds of concertina locomotion in this and other studies (Jayne and Davis, 1991), perch diameter and incline had widespread effects on the locomotor performance of the snakes in our study, as is the case for diverse limbed animals (Delciellos and Vieira, 2006; Huey and Hertz, 1982; Lammers et al., 2006; Losos and Sinervo, 1989; Sinervo et al., 1991). One of our most conspicuous findings was that increased incline reduced the maximum size of the perch diameters that snakes could traverse. Even when snakes were able to move on many different surface widths and inclines, the large variation in the forward speeds attained while doing so created large differences in the 'performance spaces' (Bennett, 1989; Wainwright, 1987) that were associated with different environments (Fig. 5D).

Perch diameter affects the maximal speed of locomotion of both snakes and limbed animals, but the directionality of these effects differs. The maximal speeds of most lizards have large decreases with decreasing perch diameter (Irschick and Losos, 1999; Losos, 1990; Losos and Irschick, 1996; Sinervo, 1991), but the effects of perch diameter and round perches *versus* flat surfaces for the speeds of mammals are variable (Delciellos and Vieira, 2006; Lammers and Biknevicius, 2004). In lizards, kinematic changes associated with decreased perch diameter include decreased stride length, which may contribute to decreased maximal speed (Spezzano and Jayne, 2004). Unlike lizards, the maximal speeds that we observed for the arboreal concertina locomotion of snakes increased with decreased perch diameter. When the diameter of horizontal perches decreased for snakes performing concertina locomotion, Δx, which is analogous to stride length, did not change significantly, but an increase in frequency of movement was sufficiently large so that speed increased. Since snakes performing arboreal concertina locomotion follow a path, a decreased perch diameter allows snakes to travel a less circuitous route, which is also advantageous for attaining a greater forward speed.

For both limbed and limbless animals, certain ranges of perch diameters may have little or no consequence for locomotion. For example, the maximal speed and several kinematic variables of some arboreal lizards change asymptotically rather than linearly with increased perch diameters such that values for large-diameter perches resemble those for a flat surface (Spezzano and Jayne, 2004). As in lizards, the smallest incremental change in maximal speed that we observed for snakes occurred between the two largest horizontal cylinders. The maximal speeds of some species of mammals are effectively constant across a wide range of perch diameters, and some species also have little discernable differences in speed between moving on cylinders

and flat surfaces (Delciellos and Vieira, 2006). Above some threshold value of diameter, snakes could not traverse a large range of inclined perches.

Balance and grip

In addition to coping with the laterally restricted spaces of perches, snakes as well as limbed animals moving along the length of cylinders must counter the tendencies to topple and to slide (Cartmill, 1974). Problems related to balance seem likely to explain the reduced speeds of snakes on horizontal perches compared to in tunnels with similar width. The shape and posture of the animal, the curvature of the cylinder, the orientation of the long axis of the cylinder relative to gravity, and the coefficient of friction all affect the ability of an animal to balance on a perch.

Sideways toppling is a problem for any perch that is not vertical (Fig. 8), and pitching and sliding down the length of the perch are problems for perches that are not horizontal. Sideways toppling may occur for two major reasons. Without sufficient friction between the animal and a round perch, the animal will simply topple by sliding circumferentially on the perch unless its center of mass (COM) is located precisely over the center of the perch (Fig. 8B). With sufficient friction, if the animal's COM is lateral to its most lateral point of attachment with the

perch, then it will topple by pivoting sideways unless something is done to counteract this movement (Fig. 8A). The tendency to pitch backwards on inclined perches resembles that of toppling by pivoting sideways; however, the long axis of the animal functions as an analog of the width of support during sideways toppling (Cartmill, 1974; Cartmill, 1979).

A lower COM relative to the perch (Fig. 8A) will decrease the tendencies to topple sideways and pitch backwards (Cartmill, 1974; Cartmill, 1985), and the tendency to topple sideways over a pivot also can be reduced by increasing the lateral distance (Fig. 8A) from the COM to the pivot. However, this lateral distance, L, can be limited by either perch diameter or anatomy. With $h L^{-1}$ approximating one for many species (where h is the height from the COM to the pivot point when the animal is upright on a horizontal surface), snakes have a much lower COM than limbed animals of the same mass (Fig. 8C).

Both limbed animals and snakes have postural variation that is also associated with maintaining balance and altering the location of COM on perches. With increased perch diameter, the lateral extent of support, L, commonly increases in snakes (Fig. 7) as well as some mammals (Cartmill, 1974) and lizards (Spezzano and Jayne, 2004). Limbed mammals commonly adopt a more crouched posture when moving on top of cylinders compared to flat surfaces, as well as when moving on cylinders with smaller diameters (Schmitt, 1999; Schmitt, 2003). However, such reductions in height are often small (~7%), and values of $h L^{-1}$ may be as high as 30 for monkeys (Schmitt, 2003). When values of $h L^{-1}$ are large (>10), even a substantial reduction in h has a barely noticeable effect on toppling angle, which illustrates some of the limitations common to limbed body plans (Fig. 8C).

The alternating loops of snakes on cylinders had wave crests that were much longer than in tunnels (Fig. 7), which increased the amount of the snake's body below the top of the perch and hence lowered the COM. Snakes bridging gaps and launching themselves to glide have large loops that position their COM below the perch (Jayne and Riley, 2007; Socha, 2006), and this mechanism could also enhance stability of moving on top of perches. The only manner in which arboreal mammals can attain this stable posture where the COM is below the perch is to use some form of suspensory locomotion (Cant, 1992; Cartmill, 1985; Fleagle and Mittermeier, 1980; Napier, 1967). By wrapping around inclined perches, snakes are also theoretically able to place the COM at the center of the perch, and wrapping around perches became more common as incline increased. This mechanism for eliminating pitching is not a possibility for limbed animals.

Friction between the animal and the perch is directly related to both balance and grip. As friction increases, the tendencies to topple by sliding and to slip down an inclined perch both decrease, and the ability to grip will increase for a given grip force. Without actively generating any gripping force, the weight of the animal can create frictional resistance, but the magnitude depends upon the orientation of the contact surface. The alternating loops formed by snakes on perches crossed the top centerline of the perch, which ensures that all of the snake's weight will contribute to the normal force on the perch, whereas the feet of limbed animals commonly are placed lateral to the
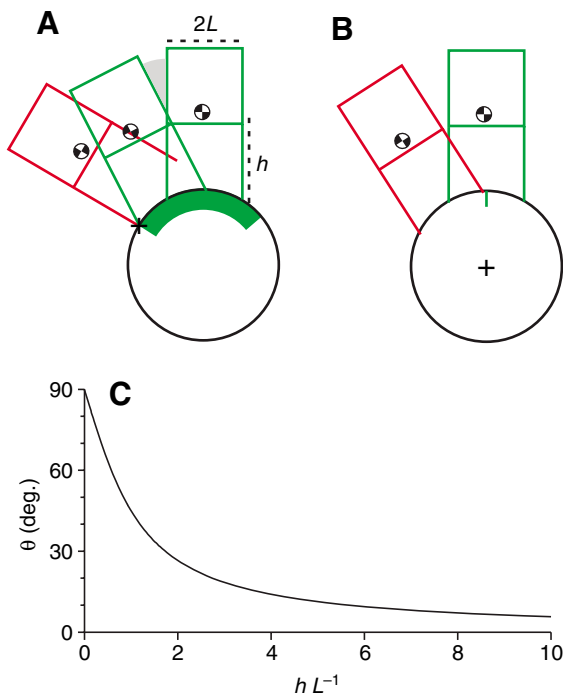

Fig. 8. Modes of sideways toppling failure. (A) Toppling by pivoting over a static contact point. (B) Toppling by slipping on the perch surface. The maximum angular deviations from vertical before toppling and the stable regions on the perches are green. For both toppling failures, the red image indicates the rotational movement about the axis indicated by +. (C) The angle, θ, relative to vertical at which pivot toppling (A) occurs as a function of animal shape ($h L^{-1}$), where h and L are the height and lateral distance, respectively, from the center of mass to the pivot point when the animal is upright on a horizontal surface.

top centerline of the perch (Cartmill, 1974; Spezzano and Jayne, 2004).

Both snakes and primates use frictional gripping rather than claws or adhesion (Autumn et al., 2000; Cartmill, 1985; Emerson and Diehl, 1980); therefore, generating forces normal to the locomotor surface is important in these taxa. Increasing grip force always increases normal force. However, for grips encircling more than 180°, grip forces also push the cylinder towards rather than away from the surface of the animal, as would be the case for grips encircling less than 180°. Consequently, an animal will always be able to squeeze a cylinder harder with gripping arcs of >180° than those <180°, assuming it has the physiological capacity to do so (Cartmill, 1979). The opposable thumb of primates increases the ability to encircle a perch, which can increase gripping force and normal force (Cartmill, 1974). Regardless of incline, snakes commonly used gripping arcs of over 180° for all but the largest diameters (Fig. 7), and the tendency to completely encircle the perch with helical wraps increased with increased incline. Thus, many aspects of the postures that we observed for snakes involved creating opposable grips, which are most vital on steep inclines where weight contributes little or nothing to frictional resistance while creating a tendency to slide downwards. Another advantage of greater encirclement of steep perches is that the gripping forces can oppose pitching moments.

Unlike the fixed grip-span of limbed animals such as primates, we observed an impressive capacity of snakes to modulate the length of the body used for gripping (Fig. 7A) as well as the number of grips (Fig. 6C). The ventral surface of snakes, which was the primary contact surface of the gripping regions, is extremely smooth (Gans, 1974), whereas the volar pads of primates have surface features and mechanical properties well suited for maximizing friction. Unlike the locomotion of primates, for which reduced slippage is beneficial, high friction would impede the most common modes of snake locomotion that use sliding contact with the substrate. Thus, the skin of arboreal snakes faces a tradeoff not found in primates.

Although snakes and primates are both highly reliant on frictional gripping and face similar demands for moving in arboreal habitats, snakes had several unique and unanticipated responses to perches with varying inclines and diameters. Overall, increased perch diameters impeded the forward speed and the ability of snakes to balance and grip. Snakes on perches used some unique modes of locomotion, including sliding down steep inclines and a form of concertina locomotion that differed significantly from that used in tunnels. Sideways toppling by pivoting poses a significant problem for primates, but snakes on perches seem more likely to topple by sliding as a result of their smooth skin and low COM. Unlike most tetrapodal vertebrates, snakes have elongate bodies that can conform readily to structures in the environment and change their distribution of mass, both of which enhance their ability to move proficiently in arboreal habitats.

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