

# Arboreal Habitat Structure Affects the Performance and Modes of Locomotion of Corn Snakes (*Elaphe guttata*)

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**ABSTRACT** Arboreal environments pose many functional challenges for animal locomotion including fitting within narrow spaces, balancing on cylindrical surfaces, moving on inclines, and moving around branches that obstruct a straight path. Many species of snakes are arboreal and their elongate, flexible bodies appear well-suited to meet many of these demands, but the effects of arboreal habitat structure on the locomotion of snakes are not well understood. We examined the effects of 108 combinations of surface shape (cylinder vs. rectangular tunnel), surface width, incline, and a row of pegs on the locomotion of corn snakes (*Elaphe guttata*). Pegs allowed the snakes to move on the widest and steepest surfaces that were impassable without pegs. Tunnels allowed the snakes to move on steeper inclines than cylinders with similar widths. The mode of locomotion changed with habitat structure. On surfaces without pegs, most snakes used two variants of concertina locomotion but always moved downhill using a controlled slide. Snakes used lateral undulation on most surfaces with pegs. The detrimental effects of increased uphill incline were greater than those of increased surface width on maximal velocity. Snakes moved faster in tunnels than on cylinders regardless of whether pegs were present. Depending on the surface width, the addition of pegs to horizontal cylinders and tunnels resulted in 8–24-fold and 1.3–3.1-fold increases in speed, respectively. Thus, pegs considerably enhanced the locomotor performance of snakes, although similar structures such as secondary branches seem likely to impede the locomotion of limbed arboreal animals. *J. Exp. Zool.* 311A, 2009. © 2009 Wiley-Liss, Inc.

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The structure of arboreal habitats creates functional challenges for locomotion often not found in terrestrial and aquatic habitats (Cartmill, '85). For example, animals must fit onto narrow cylindrical surfaces or within narrow spaces (such as within hollow trees or in crevices of bark), and the cylindrical surfaces also require gripping and balancing (Schmitt, 2003; Spezzano and Jayne, 2004; Astley and Jayne, 2007). While moving up or down various inclines, animals must counteract the force of gravity to raise their center of mass or control their speed of descent. Branches emerging from an arboreal locomotor surface may also affect movement, either detrimentally as obstructions or beneficially as additional locomotor surfaces.

Most prior studies of arboreal locomotion have investigated the locomotor performance and gaits of limbed animals such as primates, opossums, and lizards moving on unobstructed cylinders

(Losos and Sinervo, '89; Lemelin et al., 2003; Lammers and Biknevicius, 2004; Stevens, 2008). For limbed animals, decreased perch diameter usually decreases the stride length and the maximal speed of locomotion (Losos and Sinervo, '89; Spezzano and Jayne, 2004; Delciellos and Vieira, 2006). However, decreased diameter increases the maximal speed and the range of inclines that snakes can climb (Astley and Jayne, 2007). Thus, different body plans can alter some of the effects of habitat structure on locomotion.

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Many species and evolutionary lineages of snakes are arboreal (Lillywhite and Henderson, '93; Pizzatto et al., 2007), but the arboreal locomotion of snakes has barely been studied (Astley and Jayne, 2007; Gerald et al., 2008). The elongate and flexible bodies of snakes have several theoretical benefits for moving in arboreal habitats, such as distributing weight evenly across several thin branches, conforming easily to laterally restricted spaces, being able to form variable sizes of frictional grips on cylindrical surfaces, and placing their center of mass closer to the perch than the limbed organisms (Astley and Jayne, 2007).

Snakes are also adept at changing their locomotor gait in response to structural variation in their environment, but these different modes of locomotion have diverse consequences (Gray, '68; Jayne, '86; Walton et al., '90; Jayne and Davis, '91; Secor et al., '92; Astley and Jayne, 2007). For example, in the presence of irregularities in the substrate, snakes usually perform terrestrial lateral undulation, which has intermediate energetic demands and can be quite rapid. The entire body of the undulating snake moves continuously following a nearly identical path, and thus can fit through a hole equal to the cross-sectional area of its body. In contrast, snakes in parallel-sided tunnels usually perform tunnel concertina locomotion during which snakes periodically stop and wedge portions of their body against the sides of the tunnel, with at least one region of static contact at all times. This gait has a very high metabolic cost, a slow maximal speed, and requires a swath of space equal to that of the tunnel width because different portions of the body follow different paths. Some snakes on cylinders use arboreal concertina locomotion, during which the body follows a single path like lateral undulation, but cyclically forms static grips on the cylinder and always retaining at least one grip. Advantages of this gait may include gripping the cylinder while requiring little space for movement and permitting maneuvering around obstacles such as branches (Astley and Jayne, 2007).

Bare cylinders are effective for the experiments designed to isolate the effects of surface width and curvature (Losos and Sinervo, '89; Lammers and Biknevičius, 2004; Astley and Jayne, 2007). However, in natural vegetation, smaller branches arising from large branches pose another ecologically important source of structural variation, which we simulated in this study by using a row of small pegs. Most types of snake locomotion

involve a convoluted path (Gray, '68; Jayne, '86), which could provide snakes with a method of negotiating obstacles that is not available to limbed animals within the narrow confines of many arboreal surfaces. Despite their ecological importance, no prior study of arboreal locomotion has manipulated obstructions such as those created by secondary branches.

To determine the effects of arboreal habitat structure on the performance and patterns of movement of snake locomotion, we manipulated surface shape (cylinder vs. rectangular tunnels), surface width, incline and the presence of pegs. We expected pegs to enhance speed and require the use of either arboreal concertina locomotion or lateral undulation, but very small surface widths might constrain the waveform of snakes and reduce speed. On the inclined surfaces, pegs theoretically can prevent sliding down the surface and facilitate generating forces more directly opposing gravity, which lead us to expect that pegs would allow snakes to traverse inclined surfaces more effectively. Thus, although pegs should create an impassable obstacle for one mode of locomotion (tunnel concertina), they might globally enhance the performance as long as an appropriate gait was used.

## MATERIALS AND METHODS

### *Animals and apparatus*

We used four adult corn snakes (*Elaphe guttata*), which climb well in their natural habitat but are not exclusively arboreal (Conant, '75). Procedures and animal care conformed to NIH guidelines and were approved by University of Cincinnati Institutional Animal Care and Use Committee (IACUC 07-01-08-01). The snakes had similar snout-vent lengths (mean SVL = 113 cm, range = 110–117 cm), total lengths (mean TL = 134 cm, range = 132–140 cm), mid-body lateral widths (mean = 2.1 cm, range = 1.95–2.25 cm), and masses (mean = 443 g, range = 381–485 g).

For two surfaces (perches and tunnels), we used seven cylinder diameters (1.6, 2.9, 4.1, 5.7, 8.9, 15.9, and 21.0 cm) and seven tunnels with widths corresponding to the perch diameters plus two mean mid-body widths (5.8, 7.1, 8.3, 9.9, 13.1, 20.1, and 25.2 cm) to allow similar amounts of lateral displacement. The long axes of our race tracks had three orientations relative to horizontal (0°, 45°, 90°) with snakes ascending and descending inclined tracks for a total of five incline treatments. For select combinations of surface and incline

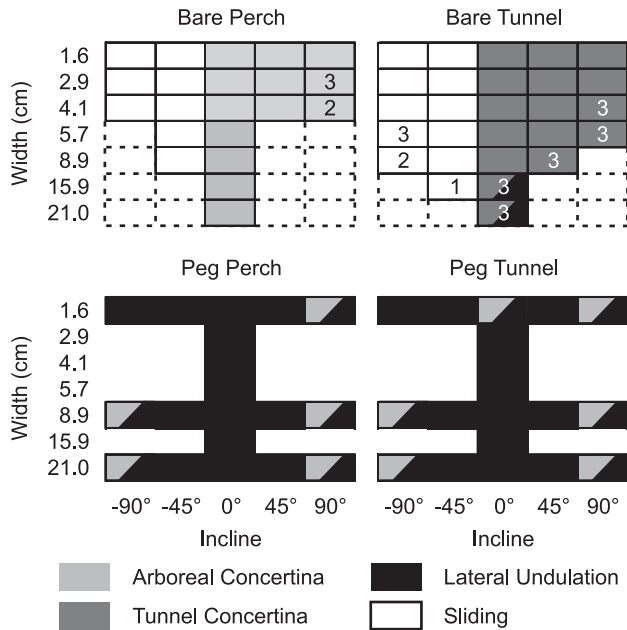


Fig. 1. Capability and mode of locomotion for all tested combinations of width, incline, surface, and peg condition. Cells with two colors indicate two modes were used. Areas with dashed borders indicate that no snake was able to move on a surface that was tested. Numbers within cells indicate how many individuals (out of four) succeeded in moving when some individuals were unsuccessful. Each equivalent width of a tunnel is the width of a perch plus two mid-body widths (4.2 cm).

(Fig. 1) we added a midline row of 0.65 cm diameter pegs that protruded 3.8 cm perpendicular to the surface. Pegs were placed at 10 cm intervals, which is a spacing near that found to facilitate locomotion in a closely related species with similar size (Jayne, '86). Hereafter, all surfaces without pegs shall be preceded by the term “bare” while all surfaces with pegs will be preceded by “peg”.

As described in more detail in Astley and Jayne (2007), we covered all surfaces with Nashua 394 duct tape (Franklin, KY) to provide a uniform texture and one that was rougher than that of the underlying materials. Strips of duct tape were oriented parallel to the long axis of the perches and tunnels, and wrapped circumferentially around pegs.

**Data collection and variables**

We placed each snake onto the surface and lightly tapped its tail to attempt to elicit maximum velocity. We allowed at least 30 min rest between trials, which we limited to fewer than five per day. If the snake did not make forward progress in three trials of 5 min each, we assumed it was

unable to move on that surface. Test conditions were presented to the snakes in random order. In all tests, the body temperatures of the snakes were between 27.8 and 29.4°C. The tunnels were covered with Plexiglass to confine the snakes to the tunnel.

We videotaped (30 images s<sup>-1</sup>) each trial with a Sony Handycam DCR-HC42 digital video camera positioned perpendicular to the long axis of the surface and dorsal to the snakes. We used Adobe Premier Pro (San Jose, CA) to create digital video files for frame-by-frame motion analysis using MaxTRAQ software (Innovision Systems, Columbiaville, MI). White paint marks at 25, 50, and 75% of the SVL provided landmarks for digitizing, and additional paint marks were used to facilitate qualitative visualization of different patterns of movement and preparation of illustrations. The *x*-axis was parallel to the long axis of the surface and the *y*-axis was perpendicular to the *x*-axis and in a horizontal plane.

For each trial with periodic patterns of movement, the mid-body point was digitized for at least five cycles. To calculate speed for nonperiodic patterns of movement, we determined the elapsed time and exact forward displacement for successive images with a cumulative forward displacement that was as close as possible to 5 cm for at least five nonoverlapping intervals. Twenty or more points were digitized at equal time intervals for each cycle or distance interval of nonperiodic motion that was analyzed. For each combination of treatments and individual, the single cycle or distance interval with the greatest forward velocity (*V<sub>x</sub>*) was selected for further analysis. We defined a cycle of lateral undulation as the time during which a point moved from right to left and back. As the concertina locomotion includes periodic stopping and irregular lateral movement (Jayne, '86), a cycle during this mode was the interval between two successive initiations of movement.

For each selected cycle or distance interval, the 25, 50, and 75% locations along the body were analyzed, and the forward displacement per cycle ( $\Delta x$ ), cycle frequency ( $f$  = inverse of cycle duration), and forward velocity ( $V_x = f\Delta x$ ) were averaged between all three points. When concertina locomotion was used, we also calculated the average forward velocity while moving (*V<sub>m</sub>*), but during lateral undulation, *V<sub>m</sub>* was equal to *V<sub>x</sub>*. Postural variables were calculated at the end of the cycle of lateral undulation or at the time of maximal static contact during concertina

locomotion as in (Astley and Jayne, 2007). We determined the total number of bends along the entire length of the snake ( $Nb$ ), the number of bends touching pegs ( $Np$ ), the average angle of all bends ( $\alpha$ ) relative to the  $x$ -axis, and the percentage of pegs contacted that touched the postero-laterally-oriented surfaces of the snake ( $PL$ ). We digitized the location of points on the most lateral extent of each bend, from which we determined the wavelength ( $\lambda$ ) (distance between crests of two successive ipsilateral bends), and we determined the maximum lateral width of the entire snake ( $Y_{max}$ ).

### Statistics

We analyzed each variable using mixed-model ANOVAs (JMP IN 5.1, SAS Institute, Inc., Cary, NC) where individual ( $n = 4$ ) was a random, crossed factor and width ( $n = 7$ ), surface ( $n = 2$ ), pegs ( $n = 2$ ) and incline ( $n = 5$ ) were fixed, crossed factors. Because of numerous blank cells and incomplete replication from failures of snakes to move (Fig. 1), we were unable to perform a single ANOVA on the entire data set. Thus, we performed two more restricted four-way ANOVAs. One ANOVA (factors: individual, pegs, width, surface) only included horizontal surfaces. To assess the effects of incline, we performed another ANOVA (factors: individual, surface, incline, width) only on data for peg surfaces and the three diameters (1.6, 8.9, and 21.0 cm) and equivalent tunnel widths for which data were available for all inclines (Fig. 1). For the one individual that attempted to move in the two largest tunnel widths but failed to make forward progress, we analyzed postural variables and  $f$  and set the values of  $Vx$ ,  $\Delta x$ , and  $Vm$  to zero. To facilitate evaluating the effects of multiple comparisons, we provide tabular summaries of  $F$ -values and their degrees of freedom.

## RESULTS

### Performance

The presence of pegs, surface width, surface incline, and surface shape all affected the ability to move forward (Fig. 1). Out of the total of 108 treatments, 22 combinations of bare surfaces, widths and nonhorizontal inclines could not be traversed by any snake, whereas the addition of pegs allowed all snakes to move successfully on every combination of width, incline, and surface tested (Fig. 1). Without pegs, as incline steepness

increased, the maximum width of perch or tunnel that could be traversed decreased, and the snakes were able to move on a wider range of bare tunnel widths than bare perch diameters at a given incline (Fig. 1).

Forward velocity ( $Vx$ ) was affected less by width than by incline, surface, and pegs (Tables 1 and 2, Figs. 2a and 3a). For a given width, snakes moved significantly faster through tunnels than on perches, and this difference was most pronounced in the absence of pegs (Fig. 2a). For nearly all combinations of surface and width, adding pegs increased  $Vx$  (Table 1, Fig. 2a). On the horizontal perches, snakes increased  $Vx$  on a given diameter from 8- to 24-fold with the addition of pegs, whereas the increase in  $Vx$  from bare to peg tunnels of a given width was only 1.3–3.1-fold (Fig. 2a). For all horizontal surfaces, the maximum speeds observed (for a single snake) were  $0.47 \text{ SVL s}^{-1}$  and  $0.41 \text{ SVL s}^{-1}$  for a 20.1 cm wide peg tunnel and an 8.9 cm diameter peg perch, respectively. A significant width-by-peg interaction term reflected a large decrease in speed for the smallest peg tunnel width without a similar decrease for perches (Table 1, Fig. 2a). On peg surfaces the snakes were faster on the horizontal than any other incline, and they had horizontal velocities from 2.2- to 13.7-fold greater than for corresponding width uphill vertical surfaces. However, for all bare surfaces, descending locomotion was faster than all other inclines (Table 2, Fig. 3a). Some of the decreases in  $Vx$  resulted from snakes stopping periodically, but even when the snakes moved continuously, their average forward

TABLE 1.  $F$ -values from ANOVAs performed separately on each variable for data from all substrate widths

Dependent Variable	Width	Pegs	Surface			
	( $W$ ) (6, 18)	( $P$ ) (1, 3)	$W \times P$ (6, 18)	( $S$ ) (1, 3)	$W \times S$ (6, 18)	$P \times S$ (1, 3)
$Vx$	1.3	23.5*	3.6*	16.7*	0.6	0.7
$\Delta x$	3.2*	255.6**	4.3*	40.4*	1.5	6.8
$f$	5.8*	10.6*	4.0*	22.9*	0.8	0.0
$Vm$	2.6	15.7*	4.8*	19.6*	0.8	3.4
$Nb$	21.6**	6.0	10.2**	0.1	8.2**	16.6*
$\alpha$	13.5**	759.8**	1.3	4.8	3.2**	3.6
$\lambda$	3.2*	13.4*	0.6	1.5	5.3*	21.0*
$Y_{max}$	45.2**	5.4	3.1*	1.9	6.4*	0.4

\* $P < 0.05$ .

\*\* $P < 0.001$ .

Degrees of freedom are indicated in parentheses.  $Vx$ —forward velocity per cycle,  $\Delta x$ —forward displacement per cycle,  $f$ —cycle frequency,  $Vm$ —forward velocity while moving,  $Nb$ —number of bends,  $\alpha$ —angle of bends,  $\lambda$ —wavelength,  $Y_{max}$ —maximal lateral width.

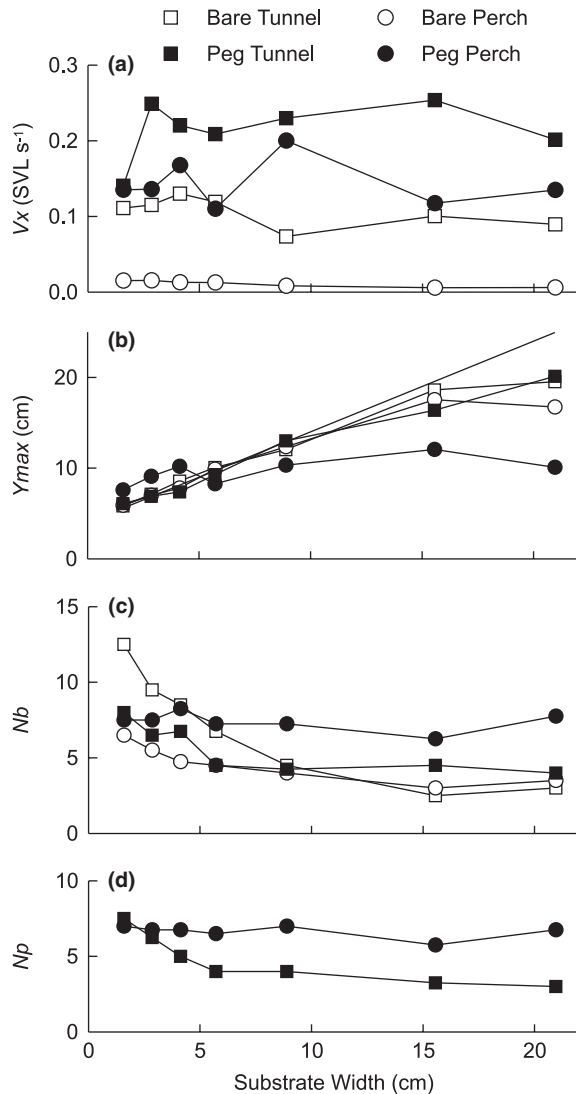


Fig. 2. Mean values ( $n = 4$  individuals) of kinematic variables during horizontal locomotion. (a) Forward velocity,  $V_x$ , (b) maximum lateral width,  $Y_{max}$ , (c) number of bends along the entire length of the snake,  $N_b$ , and (d) number of pegs touched by the snake,  $N_p$ . Tunnel widths are illustrated at the equivalent perch diameters.

velocity while moving ( $V_m$ ) displayed overall changes with habitat structure similar to those of  $V_x$  (Tables 1 and 2).

### Mode of locomotion

The snakes used four distinct modes of locomotion, which depended more upon surface, incline, and pegs than on the width of the surface. In the absence of pegs, all downhill locomotion on perches and in tunnels was a controlled slide (Fig. 1) as described previously (Astley and Jayne, 2007). For all horizontal or uphill locomotion on

bare cylinders, snakes used the arboreal concertina mode, during which all points nearly follow a single path (Astley and Jayne, 2007). Except for the largest widths, nearly all the horizontal and uphill locomotion in bare tunnels was the tunnel concertina mode (Fig. 4b,d), during which different longitudinal locations on the body of the snake follow different paths.

On almost all peg surfaces snakes used lateral undulation, which allowed the body of the snake to nearly follow a single path (Figs. 1 and 4a). On all vertical uphill and most vertical downhill peg surfaces, some snakes used arboreal concertina mode (Fig. 1), as determined by the movement of some portions of the body while other portions were stationary and each point on the body closely following the same path. We never observed the snakes using either tunnel concertina or the sliding mode when pegs were present (Fig. 1).

### Kinematics

Changes in the frequency of movement ( $f$ ) and the amount of forward movement per cycle ( $\Delta x$ ) are the two mechanisms for modulating  $V_x$ , and the presence of pegs often allowed snakes to increase  $\Delta x$  significantly compared with when pegs were absent (Table 1, Fig. 3b). However, in some circumstances, the potential benefits of increased  $\Delta x$  were negated by decreased  $f$  (Fig. 3b, c). Greater  $V_x$  in tunnels compared with perches resulted from increases in both  $f$  and  $\Delta x$  (Table 1, Fig. 3a-c). For many combinations of pegs, surface and width,  $f$ ,  $\Delta x$  and  $V_x$  were all significantly greater on the horizontal than either the uphill or downhill inclines (Table 2, Fig. 3a-c).

Several additional variables related to the space required to move and the configuration of the body of the snake were significantly affected by pegs, surface width, surface, and incline (Tables 1, 2). The width of the entire snake ( $Y_{max}$ ) often conformed closely to that of the surface except for large surface widths (Figs. 2b and 5a). However,  $Y_{max}$  was nearly constant on all peg perches and commonly exceeded the widths of the small (<5 cm) perches (Figs. 2b and 5a).

Snakes consistently had the greatest number of bends ( $N_b$ ) within the narrowest bare tunnel (Fig. 2c). When snakes used concertina locomotion to ascend wide peg tunnels (Fig. 5j), they had many more bends than during lateral undulation (Fig. 5h). The number of pegs touched ( $N_p$ ) coincided closely with  $N_b$  (Fig. 2c, d). Adding pegs to perches had little effect on the wavelength ( $\lambda$ ) of

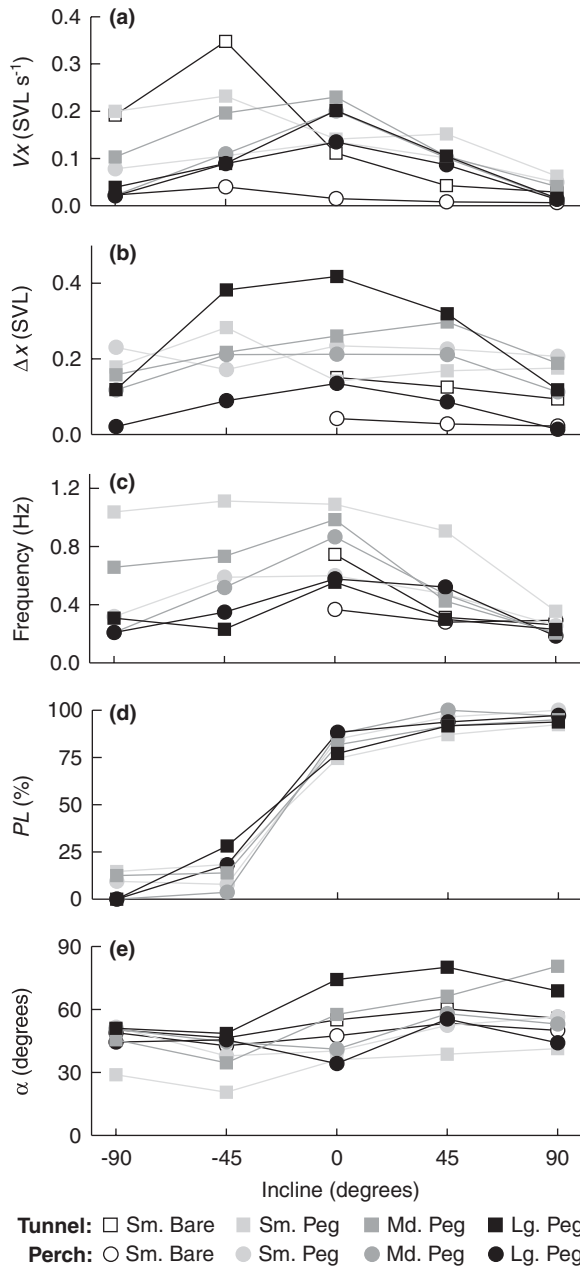


Fig. 3. Mean values ( $n = 4$  individuals) of kinematic variables at selected substrate inclines. Small (Sm.) perches and tunnels are 1.6 and 5.8 cm width, medium (Md.) are 8.9 and 13.1 cm, and large (Lg.) are 21.0 and 25.2 cm. (a) Forward velocity,  $V_x$ . (b) Forward displacement per cycle,  $\Delta x$ . (c) Frequency,  $f$ , of periodic movements. (d) Percentage of pegs that contacted postero-laterally oriented surfaces of the snake's body,  $PL$ . (e) Mean angle of the bends in the body,  $\alpha$ . Downhill bare surface data are not included in (b) and (c) because movements were not periodic.

snakes, whereas adding pegs to tunnels significantly increased  $\lambda$  (Tables 1, 2, Fig. 5c vs. d and g vs. h). The angle of the bends ( $\alpha$ ) increased significantly with both increased surface width

and increased incline (Tables 1 and 2, Fig. 3e). For horizontal and uphill locomotion nearly all of the points of contact with pegs were on the posteriorly directed surfaces of the snakes, whereas during downhill locomotion nearly all of the pegs touched anteriorly facing the surfaces of the snake (Fig. 3d).

## DISCUSSION

The mechanical demands of moving in different habitats can be met by evolving different body plans, modifying morphology within a body plan, and modifying the behavior of how a given morphology is used. Some animals such as fish and bats have different body plans that facilitate moving in their primary habitat but preclude moving in other habitats. The ecomorphs of anole lizards are an excellent example of how quantitative variation within a body plan (limb length) can mediate the effect of habitat structure (perch diameter) on locomotion (Irschick and Losos, '99). The diverse movements we found for snakes in this study nicely illustrate the importance of the behavior for mediating the effects of habitat structure. Testing organismal performance provides a powerful methodology for linking all of these sources of variation to the ecology of organisms (Arnold, '83; Wainwright and Reilly, '94).

To assess the effects of habitat structure, we determined the performance, mode of locomotion, and the extent to which the elongate, flexible body of snakes conformed to habitat structure. We observed large and pervasive effects of pegs on the locomotion of snakes. Not only did pegs enhance performance considerably, they allowed the snakes to move on surfaces and inclines that would otherwise be impassable. Pegs precluded two modes of locomotion (tunnel concertina and sliding), but they permitted lateral undulation, which was an underlying reason for many gains in performance. In addition, pegs often had interactive effects with the other aspects of habitat structure we studied.

We observed a close conformity of snake waveforms with peg locations, which emphasizes the importance of pegs for propulsion. The magnitude and direction of forces that snakes can generate when undulating past pegs depend on both the waveform of the snake's body and the number of pegs contacted (Gray and Lissmann, '50). When pegs are located posteriorly, snakes with bends of the body more nearly perpendicular to the direction of travel should have a higher

TABLE 2. *F*-values from ANOVAs performed separately on each variable for data from 1.6, 8.9, and 21.0 cm substrate widths for all inclines of peg perches and peg tunnels

Dependent Variable	Width ( <i>W</i> ) (2, 6)	Incline ( <i>I</i> ) (4, 12)	<i>W</i> × <i>I</i> (8, 24)	Surface ( <i>S</i> ) (1, 3)	<i>W</i> × <i>S</i> (2, 6)	<i>I</i> × <i>S</i> (4, 12)
<i>V</i> <sub>x</sub>	18.1*	6.9*	3.1*	5.0	2.1	0.9
$\Delta x$	0.3	7.2*	3.9*	31.4*	5.2*	0.9
<i>f</i>	7.5*	4.4*	1.6	7.5	4.5	2.5
<i>V</i> <sub>m</sub>	15.3*	6.7*	3.0*	4.9	3.5	0.8
<i>N</i> <sub>b</sub>	1.9	3.4*	2.0	9.4	11.3*	0.8
$\alpha$	25.5*	13.5**	1.0	1.2	23.3*	10.7**
$\lambda$	0.8	7.4*	2.2	23.4*	4.6	1.7
<i>Y</i> <sub>max</sub>	22.8*	21.8**	2.5*	1.7	11.5*	1.8
<i>N</i> <sub>p</sub>	1.9	1.1	4.0*	182.1**	37.9**	1.1
<i>PL</i>	0.0	289.2**	0.9	0.0	0.2	3.5*

\**P* < 0.05.

\*\**P* < 0.001.

Degrees of freedom are indicated in parentheses. Abbreviations are as in Table 1. *N*<sub>p</sub>—number of pegs contacted, *PL*—percentage of pegs contacted that touched postero-laterally oriented surfaces of the snake.

proportion of reactive force contributing to propulsion. A decreased number of pegs contacted can also enhance the ratio of propulsive force vs. lateral forces, but a minimum of three pegs may be required for a stable balance of lateral forces (Gray and Lissmann, '50). Swimming snakes not constrained by rigid objects usually have only three bends (Gray, '68; Jayne, '85), and snakes approached this minimum number of bends as the width of peg tunnels increased (Fig. 2c). Although a large number of bends did not appear to be detrimental for the speed of snakes over a wide range of conditions in our study, a disproportionate increase in lateral forces with increased numbers of pegs (Gray and Lissmann, '50) may decrease efficiency. The anterior location of pegs allowed the generation of reactive forces to slow the descent of the snake, and was a unique feature of downhill locomotion (Fig. 3d).

Only the narrowest tunnel with pegs (Fig. 5d) appeared to impose severe enough constraints on waveform to have detrimental effects on speed and perhaps efficiency. No conspicuous differences in waveform seemed sufficient to explain the reduced speed on peg perches compared with peg tunnels, but the need to balance on peg perches may have contributed to decreased speed as well as constraining waveform. When pegs were present, surface width became nearly irrelevant above a certain threshold (Fig. 5f, i, j).

Although we used only one spacing between pegs, several previous studies suggest that, for a snake of a given size and species, peg spacing strongly affects maximal speed (Heckrotte, '67;

Bennet et al., '74; Jayne, '86; Kelley et al., '97). Different peg spacing may disrupt some of the relationships that we observed between performance, posture, and our manipulation of habitat structure. However, we chose a distance between pegs within a row that was similar to the distance between pegs in an array that facilitated attaining maximal speed by a congeneric species of snake (Jayne, '86). Furthermore, snakes on peg surfaces often only made contact with a subset of the pegs adjacent to their bodies (Figs. 4a and 5b, f, h), effectively lengthening the peg spacing as needed.

Incline, surface, and surface width all affected the performance of snakes, and these factors can also affect the locomotion of diverse limbed animals. With steeper uphill inclines, speed decreases in snakes as well as some lizards (Huey and Hertz, '82; Irschick and Jayne, '98) and mammals (Lammers et al., 2006). The effect of inclines on the locomotion of animals generally increases with increased mass (Taylor et al., '72), and the masses of snakes in our study (381–485 g) were well over an order of magnitude greater than that of most previously studied lizards but were a similar order of magnitude to some of the previously studied mammals (80–150 g).

Similar to snakes, mammals are usually slower on cylinders than on flat surfaces (Lammers and Biknevicius, 2004; Delciellos and Vieira, 2006), suggesting that the need to balance can impede locomotion for animals with diverse body plans. Some studies suggest that the unusual gaits of primates facilitate balance (Prost, '69; Schmitt and

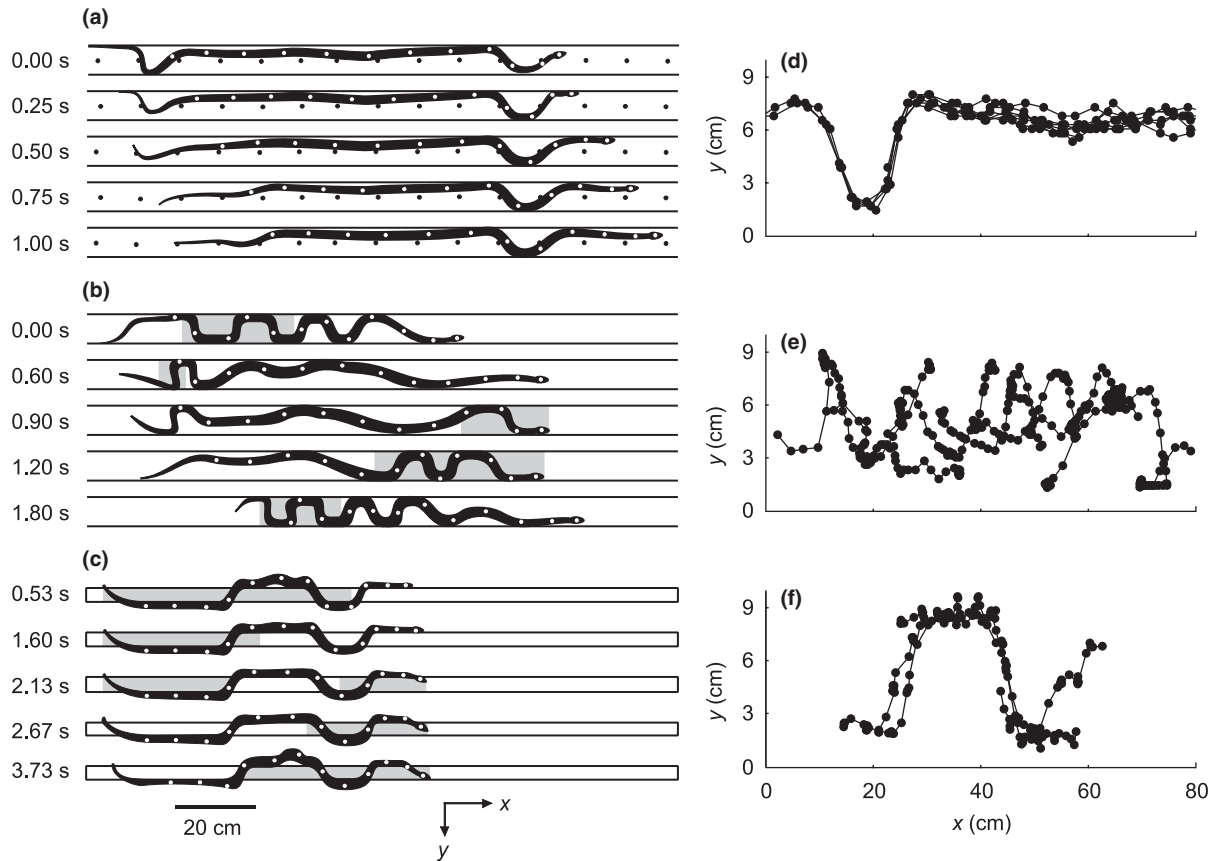


Fig. 4. Lateral undulation and two variants of concertina locomotion. Tracings are of dorsal view videos of a single corn snake during one cycle of movement. Gray areas represent static contact between the snake and the surface. The times of successive images are given to the left of each tracing. Body posture during (a) lateral undulation (b) tunnel concertina locomotion and (c) arboreal concertina locomotion. Paths relative to the substrate are shown for the seven evenly spaced longitudinal locations between 25 and 75% SVL for the same cycle of movement from that the tracings were made. The entire body of the snake follows a nearly identical path during lateral undulation (d) and arboreal concertina locomotion (f), whereas the different paths traveled by different points of the snake performing concertina locomotion in the tunnel require a swath along their path equal to the entire tunnel width (e). Videos can be found at [http://www.artsci.uc.edu/collegedepts/biology/fac\\_staff/jayne/videos.aspx](http://www.artsci.uc.edu/collegedepts/biology/fac_staff/jayne/videos.aspx).

Lemelin, 2002), but other studies dispute this (Vilensky and Larson, '89; Stevens, 2008). Gripping during the arboreal concertina gait of snakes (Astley and Jayne, 2007) and during primate locomotion (Cartmill, '85) on bare cylinders overcomes some of the difficulties associated with balance, and the adhering ability of many arboreal lizards (Irschick et al., '96) should also have similar benefits.

The effects of cylinder diameter on the maximal speed of locomotion are best studied for relatively small (5–10 g) species of highly arboreal anole lizards. The speeds of anoles usually decrease with decreased diameter of bare perches (Losos and Sinervo, '89; Irschick and Losos, '99), but the magnitude of this effect ranges from very large for a long-limbed species (*Anolis gundlachi*:

110–200  $\text{cm s}^{-1}$ ) to little if any effect for a short-limbed species (*A. valencienni*: 105–120  $\text{cm s}^{-1}$ ). Unlike some anoles, the speeds of snakes decrease significantly with increased diameter of bare perches (Astley and Jayne, 2007), but the absolute difference of this nearly three-fold change in speed (1.7–0.6  $\text{cm s}^{-1}$ ) may be too small to be ecologically relevant. The effects of perch diameter on maximal speed of mammals vary across species (Delciellos and Vieira, 2006; Stevens, 2008). These various effects of diameter on performance thus vary both among taxa with different body plans and for anatomical variation within a body plan. Perhaps the body plan of snakes and the path-following gaits they use (Fig. 4) provide a considerable advantage over the generalized tetrapod body plan for moving through increasingly



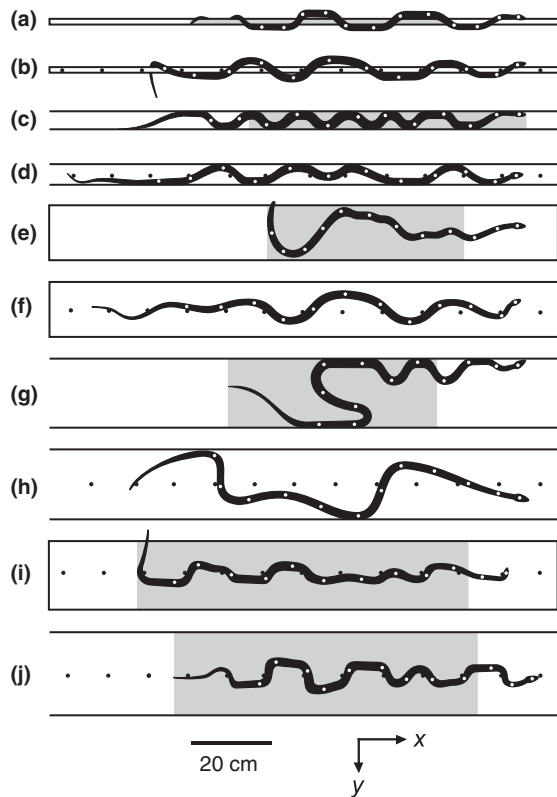


Fig. 5. The effects of pegs, width, surface, and incline on the posture of a single corn snake, illustrated from tracings made from video images. Gray areas represent static contact between the snake and the surface. (a) 1.6 cm bare perch. (b) 1.6 cm peg perch. (c) 5.8 cm bare tunnel. (d) 5.8 cm peg tunnel. (e) 15.9 cm bare perch. (f) 15.9 cm peg perch. (g) 20.1 cm bare tunnel. (h) 20.1 cm peg tunnel. (i) 21.0 cm peg perch. (j) 25.2 cm peg tunnel. (a–h) are horizontal, and (i) and (j) are uphill vertical.

cluttered arboreal habitats as simulated by adding pegs to surfaces.

Bare cylindrical surfaces that are not vertical require animals to use some combination of balancing or gripping, so that they do not slide or topple sideways (Cartmill, '85; Astley and Jayne, 2007). In all but one of our 52 observations of snakes on peg perches that were not vertical, snakes contacted four or more pegs with a series of alternating bends (Fig. 5). Such weaving between pegs will generate medially oriented forces that create a nearly automatic mechanism for preventing toppling off of the cylinder by sliding sideways. In contrast to snakes on bare perches, where the body flexes ventrally to grip the perch (Astley and Jayne, 2007), snakes had remarkably little ventral contact with the large, cylindrical surfaces on which pegs were placed. If ventral flexion is the primary means of gripping a bare perch, such

gripping forces should be maximized for a body angle of  $90^\circ$ , but a body angle of  $90^\circ$  seems unlikely to be optimal for using pegs to prevent sliding sideways off the perch. Some of the observed differences in the body angles were consistent with such a trade-off (Fig. 5). Although arboreal concertina with ventral perch gripping theoretically could be performed with pegs, the absence of this mode on nonvertical perches suggests that the maximizing speed may be favored over maximizing grip.

In addition to snakes being highly proficient at moving on diverse surfaces, widths, and inclines that simulated arboreal habitat structure, some structures that enhanced the performance of snakes, such as secondary branches (simulated by pegs), seem likely to impede limbed animals. However, limblessness by itself may not be advantageous for moving in arboreal habitats. Many lineages of tetrapods, such as caecilians, amphisbaenians, *Amphiuma* salamanders, and many lizards, convergently lost functional limbs, but none of these groups is arboreal. Snakes are exceptional for the diversity of behaviors that may have contributed to them occupying not only arboreal habitats but also a diversity of habitats unparalleled by any of these other groups. Arboreal habitats uniformly demand that animals be able to grip or balance on narrow cylindrical surfaces and negotiate inclines, but snakes and arboreal limbed animals provide a remarkable example of how behavior can enable groups with fundamentally different body plans to accomplish the same task.

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## APPENDIX A: LIST OF SYMBOLS

$\alpha$	angle of body at crossing point relative to $x$ -axis
$\Delta x$	forward displacement per cycle
$f$	frequency of movement
$\lambda$	wavelength of the body of the snake
$N_b$	total number of bends along the entire length of the snake
$N_p$	the number of pegs touching the snake

<i>PL</i>	the percentage of pegs contacted that touched postero laterally oriented surfaces of the snake
<i>SVL</i>	snout-vent length of the snake
<i>V<sub>m</sub></i>	forward velocity only for the portion of the cycle when the snake is moving
<i>V<sub>x</sub></i>	forward velocity for an entire cycle
<i>Y<sub>max</sub></i>	maximum lateral width along the entire length of the snake

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