

## RESEARCH ARTICLE

# Incline and peg spacing have interactive effects on the arboreal locomotor performance and kinematics of brown tree snakes, *Boiga irregularis*

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### SUMMARY

Many animals move using lateral undulations, but snakes are noteworthy for using this type of locomotion in an unusual diversity of environments, including trees in which both the spacing and orientation of branches vary considerably. Despite branches providing discrete locations for snakes to generate propulsive forces during lateral undulation, the consequences of branch spacing for the locomotion of snakes are poorly understood. Hence, we determined maximal speeds and kinematics of an arboreal snake (*Boiga irregularis*) crawling on horizontal and vertical cylinders with pegs that simulated different spacing between secondary branches. Peg spacing, perch orientation and their two-way interaction term had widespread, significant effects on both performance and kinematics. For the horizontal surfaces, maximal locomotor speed occurred with intermediate peg spacing, and it was nearly twice as fast as for both the smallest and largest peg spacings. By contrast, the locomotor speed of snakes on the vertical surfaces was unaffected by peg spacing, and was uniformly slower than that for the horizontal surfaces. For both perch orientations, the number of pegs touched by the snake decreased as peg spacing increased, and while touching only one peg the snakes crawled with apparent ease and steady speed. The snakes crawled vertically with only one peg as quickly as they did using 2–10 pegs. Pegs on a horizontal cylinder are probably important both for propulsion of snakes and prevention of long-axis rolling, whereas pegs protruding from vertical cylinders and those protruding from horizontal planar surfaces are probably used almost exclusively for propulsion.

Key words: locomotion, biomechanics, balance, lateral undulation, axial, squamata.

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### INTRODUCTION

Many phylogenetically diverse lineages of animals use axial bending for propulsion (Gray, 1968). However, compared with most other taxa that use axial bending, snakes have a remarkable ability to traverse a greater variety of habitats, which is enhanced by having several different modes of locomotion that use axial bending (Gray, 1946; Gans, 1974; Jayne, 1986). The most common mode of snake locomotion is lateral undulation, which occurs in effectively all species and is often the most common mode within a species. During lateral undulation, waves of lateral bending propagate posteriorly and push against objects in the environment, and the entire body of the animal has sliding contact with the supporting surfaces as each point along the animal follows a nearly identical path (Gray, 1946; Gans, 1974; Jayne, 1986). Despite underlying qualitative similarities for this mode, the speed and waveform of snakes using lateral undulation vary substantially depending on the surfaces encountered and the species of snake.

Terrestrial lateral undulation usually requires surfaces against which the sides of the body can push to produce anteromedial propulsive forces (Gray and Lissmann, 1950; Gans, 1974). Consequently, the number and spacing of such points of force application (points d'appui) are key features for understanding how structural variation of the environment can affect limbless locomotion. Several decades ago, a series of classic experiments with snakes moving on a smooth, flat surface and with a single row of peg-like objects established that the lateral forces decrease

substantially with a decreased number of points of force application until effectively all of the reactive force is directed forward for movement past a single peg, but the forward-directed forces remain nearly constant (Gray and Lissmann, 1950). However, the speed of snakes crawling through large arrays of evenly spaced pegs on planar surfaces appears to be maximized when peg spacing is intermediate (Heckrotte, 1967; Bennet et al., 1974; Kelley et al., 1997). Furthermore, some review articles on snake locomotion have variously suggested that either two (Gans, 1962) or three (Gans, 1974) points of force application are required for terrestrial lateral undulation.

Although previous work has clearly established the importance of the number and spacing of points of force application for lateral undulation, several issues remain unclear. For example, maximal speed occurring with intermediate peg spacing seems at odds with a presumably optimal relationship between forward and lateral forces with only a single point of force application. This apparent contradiction could simply reflect the limited ranges of peg spacing that have been used, or perhaps larger lateral forces for a given forward force are more relevant for energetic economy than for maximal speed. Previous studies that have determined performance and manipulated peg spacing also have not quantified the number of pegs actually touched by snakes, although snakes do seem likely to touch more pegs as the distance between pegs decreases. The irregular direction of travel and irregular waveforms that often occur when snakes move through arrays of pegs on a planar surface

complicate measurement of speed as well as the angle of the body relative to the overall direction of travel, and this latter variable is related to the direction of forces generated during undulatory locomotion.

The effects of peg spacing also have considerable ecological relevance for animals in arboreal habitats because secondary branches have a peg-like shape and they create conspicuous, discrete sites for force application with highly variable spacing (Mattingly and Jayne, 2004). Although many species of phylogenetically diverse snakes move in trees (Lillywhite and Henderson, 1993; Pizzatto et al., 2007; Hampton, 2011), the effects of branch (and peg) spacing on locomotor performance are known only for a few species of arboreal limbed vertebrates (Hyams et al., 2012; Jones and Jayne, 2012). For snakes, adding pegs (with constant spacing) to a cylindrical surface is known to: (1) elicit lateral undulation, (2) increase the maximal speed of locomotion and (3) reduce the tendency to roll about the long axis of the supporting surface (Astley and Jayne, 2009; Jayne and Herrmann, 2011). Manipulating peg spacing along a cylindrical surface also has some practical advantages for clarifying the effects on waveform and speed because snakes on such surfaces often move with straighter overall trajectories than when they traverse wide arrays of pegs on planar surfaces.

We manipulated both peg spacing and the incline of the primary cylindrical surface to test how both of these factors affect the locomotor performance and kinematics of a highly arboreal species of snake (*Boiga irregularis*) that commonly uses lateral undulation. We used a very large range of peg spacing with one extreme that transiently allowed contact with only a single peg. Two alternative hypotheses seemed equally plausible for the expected effects of peg spacing on performance. Previous force data suggest that speed might be greatest when contacting only a single peg, whereas the results from snakes crawling through arrays of pegs suggest intermediate spacing is optimal for speed. For movement on cylindrical surfaces, the dual function of pegs for generating propulsive force and balancing could complicate these expectations. However, as the weight of the snake on a vertical cylindrical surface does not cause long-axis roll, comparing locomotion on vertical and horizontal surfaces can provide a useful test of whether different needs for balancing affect performance and aspects of posture such as how far the crests of waves are located from the supporting surface. The requirement for animals to lift their entire weight when climbing up a vertical surface led us to expect decreased maximal speed for snakes on the vertically inclined surfaces compared with the horizontal surfaces, with similar numbers of pegs, but if the prevention of long-axis rolling on horizontal surfaces is overwhelmingly difficult, the reverse could be the case.

## MATERIALS AND METHODS

### Experimental subjects

We used nine brown tree snakes, *Boiga irregularis* (Merrem 1802), captured in Guam. All of the experiments were performed in a laboratory at the University of Cincinnati. The snakes were housed individually in cages with incandescent light bulbs that allowed them to behaviorally thermoregulate and attain daytime body temperatures from 25 to 33°C. The snakes had values of snout–vent length (SVL, mean  $\pm$  s.e.m. 110 $\pm$ 1.9 cm, range 101–118 cm), total length (TL, mean  $\pm$  s.e.m. 140 $\pm$ 2.4 cm, range 130–152 cm) and mass (mean  $\pm$  s.e.m. 174 $\pm$ 7.9 g, range 141–203 g) that were as similar as was practical to obtain. All experiments were performed at least 1 week after the snakes had been fed. White paint marks at 25%, 50%, 75% and 100% SVL provided landmarks for motion analysis. The care

of animals and all procedures were approved by the Institutional Animal Care and Use Committee at the University of Cincinnati (protocol no. 07-01-08-01).

### Experimental apparatus and procedures

We tested the locomotor performance of all snakes on five perches consisting of a metal cylinder (diameter 2.4 cm, length 273 cm) with pegs (diameter 6 mm, length 4 cm) oriented perpendicular to the long axis and arranged in a single row along the top center of the cylinder (Fig. 1). We used five different distances between adjacent pegs (10, 20, 30, 40 and 80 cm). The long axis of the perches had two orientations (horizontal and vertical). To encourage the snakes to crawl along the perch, we attached a cylinder (diameter 7.5 cm, length 15 cm) with a blackened interior at the end of the perch opposite where the snakes were placed initially. To provide a standardized surface with a sufficient amount of friction and texture (Astley and Jayne, 2007), we applied strips of duct tape (Nashua 394, Franklin, KY, USA) along the long axis of all the cylindrical surfaces forming the perch. As explained in more detail elsewhere (Astley and Jayne, 2007), the frictional resistance of this tape with snake skin and the texture created by the rectangular array of fibers embedded in the tape seemed more likely to resemble natural branches than the extraordinarily smooth surfaces (metal pipe and manufactured hardwood pegs) that the tape covered. However, we also deliberately avoided using a surface for the cylinder with overly large projections, which could render the pegs largely irrelevant for the locomotion of the snakes.

Prior to an experiment, the snakes were placed in individual cloth bags within a chamber held at 30–31°C. During experiments, we used a PE-1 infrared temperature gun (Pro Exotics, Littleton, CO, USA) to verify that all snakes had body temperatures between 29 and 31°C, which is within the range of field active body temperatures for this species (Anderson et al., 2005). For each treatment, we performed three trials in rapid succession by placing a snake onto the perch and gently touching the snake near the tail to encourage it to move at maximum velocity. Two or fewer treatments were performed per snake on each day, except for one day on which three treatments were carried out per snake. Whenever a snake performed more than one treatment per day, 3 h of rest were provided between

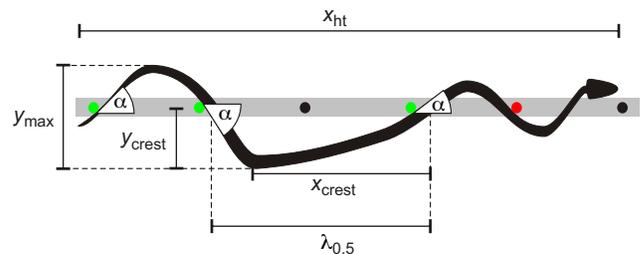


Fig. 1. Schematic illustration of methods used for analyzing kinematics. The gray rectangle represents the primary cylindrical surface of the perch. Black, green and red circles indicate pegs that were not touched by the snakes, pegs that were touched and useful for propulsion, or pegs that were touched but were not likely to be useful for propulsion, respectively. In this example, the number of crossing regions ( $N_{cr}$ ) was 5, and the number of propulsive ( $N_{peg,prop}$ ) and non-propulsive pegs ( $N_{peg,non-prop}$ ) touched was 3 and 1, respectively. Each white wedge indicates the angle ( $\alpha$ ) between the tangent of the body of the snake at a propulsive peg and the x-axis. The overall length of the snake from head to tail along the x-axis is  $x_{ht}$ . For each half-wave, the length along the x-axis ( $\lambda_{0.5}$ ) and the lateral amplitude ( $y_{crest}$ ) were recorded. The maximum width of the snake ( $y_{max}$ ) was the sum of the greatest magnitudes of  $y_{crest}$  for half-waves to the left and right. Values of  $x_{crest}$  were expressed as a proportion of  $\lambda_{0.5}$ .

successive treatments. To minimize confounding influences of time and experience, the snakes were assigned to two groups, and each group experienced the treatments in a different randomized order.

### Image acquisition and analysis

We videotaped simultaneous dorsal and lateral views of the snakes at 30 images  $s^{-1}$  using a two-camera (Basler piA640, Ahrensburg, Schleswig-Holstein, Germany) video system with MaxTraQ version 2.13 software (Innovision Systems, Columbiaville, MI, USA). A 30Hz square-wave voltage was used as an external trigger to synchronize the images of the two cameras. The cameras were positioned perpendicular to the long axis of the perches, and the mid-way point along the perch was near the center of the field of view of both cameras. The top-center line along the long axis of each perch contained the origin and the  $x$ -axis for our coordinate system. The  $y$ - and  $z$ -axes were both perpendicular to the long axis of the perch. The  $z$ -axis was in the plane containing the pegs, whereas the  $y$ -axis was perpendicular to this plane.

For all of the nine snakes, we quantified the average forward velocity ( $v_x$ ) of the landmark at 50% SVL for 20 cm of forward movement ( $x$ -direction) immediately prior to this landmark passing the middle peg of each perch and another 20 cm interval immediately after this landmark passed the middle peg of the perch. The locomotor performance of each snake ( $v_{x,max}$ ) was the single greatest value of all these velocities (for 20 cm of forward movement) from the three trials per treatment. We chose the largest value of peg spacing so that the snakes would have some locomotion using only one peg, and depending on the snake length and how convoluted the snake was, this usually occurred when the location at 50% SVL was within 20 cm of the peg at the middle of the long axis of the perch. Occasionally the snakes paused during the performance trials, but choosing only a 20 cm interval usually allowed us to obtain locomotion without pausing. We consistently used a 20 cm interval to determine maximal speed of all of our treatments because the values of maximal speed usually decrease with an increase in the distance used to make this measurement.

For the five snakes with the greatest grand mean of  $v_{x,max}$  across all treatments, we also quantified several variables describing the contact points and posture of the snake on the perch at the time when the mid-body landmark was at the middle peg along the length of the perch in the 20 cm interval used to determine  $v_x$ . Four variables quantified the number and nature of locations where the body of the snake interacted with solid surfaces and hence where significant forces were likely to occur. We counted the number of regions in which the dorsal midline of the snake crossed the  $x$ -axis (Fig. 1,  $N_{cr}$ ). Rather than merely assuming that snakes contacted more pegs when the space between successive pegs was smaller, we determined the number of pegs touched by the snake simultaneously at all locations ( $N_{peg,all}$ ) and for locations likely ( $N_{peg,prop}$ ) or unlikely ( $N_{peg,non-prop}$ ) to be useful for propulsion (Fig. 1).

If we could not discern a gap between the body of the snake and a peg, then this was classified as a peg that had been touched. Our video images and methods were not able to clarify additional details such as how hard the snakes pressed against a peg or whether the body wall had a curvature different from the mid-dorsal line as has been described for the terrestrial locomotion past pegs of some other species of snakes that are much heavier than the snakes in our study (Gasc et al., 1989; Moon and Gans, 1998). Thus, whether a peg was considered a 'propulsive' peg was based only on its position relative to the body of the snake and the direction of movement (Fig. 1). For example, if a peg was located on the trailing edge of a half-wave so that a normal reactive force arising from it could

have a forward-directed component parallel to the overall direction of movement (Fig. 1, green dot), then this was considered a propulsive peg. By contrast, pegs that touched the leading edge of a half-wave (Fig. 1, red dot) or precisely at the crest of a half-wave were considered non-propulsive pegs.

For each of the propulsive pegs, we determined  $\alpha$ , the angle between the tangent through the midline of the snake where the body of the snake touched the peg and the  $x$ -axis (Fig. 1). This angle has strong implications for the orientation and proportion of forces that ultimately contribute to propulsion when snakes undulate past solid objects (Gray and Lissmann, 1950). To obtain an overall indicator of how convoluted the snake was, we measured the total distance between the head and tail of the snake ( $x_{ht}$ ) along the  $x$ -axis (Fig. 1), and we expressed this as a proportion of the TL of the snake. In addition to  $x_{ht}$  clarifying the amount of longitudinal space required for the snakes to move, this variable also allowed us to directly compare the effect of peg spacing in our study with effects observed in the most detailed previous study of peg spacing and locomotor performance (Kelley et al., 1997).

We determined the lateral amplitude ( $y_{crest}$ ) for each half-wave ( $\lambda_{0.5}$ ), and the  $x$ -distance from the anterior node to the crest of the half-wave ( $x_{crest}$ ) was measured and expressed as a proportion of the half-wavelength (Fig. 1). We determined the maximal width of the snake ( $y_{max}$ ) by adding the largest amplitudes of half-waves to the left and right of the snake (Fig. 1). For each half-wave that was visible in the lateral view camera, we determined the  $z$ -distance between the top-center line of the perch and the most ventral portion of the half-wave. For each individual and treatment we determined the maximal ( $z_{max}$ ) and mean ( $z_{crest}$ ) value for these measurements of half-wave depth. Collectively, these remaining variables further determine the extent to which the shape of the snake conformed to the shape and locations of the objects traversed by the snake. For example, a snake could theoretically use the same large amplitude, large wavelength undulations when pegs are far apart as when pegs are closer together if it simply failed to touch each successive peg. Different locations of the crests of waves also have different implications for stability. For example, when moving on horizontal cylindrical surfaces, lowering the crest of a wave beneath the cylinder is a mechanism for increasing stability by lowering the center of gravity and functioning like a pendulum, whereas a large lateral excursion can be disadvantageous because it could generate a torque that causes long-axis rotation about the supporting cylinder (Jayne and Herrmann, 2011).

### Data analysis

Each quantity describing either performance or kinematics was used as the dependent variable in a three-way mixed-model ANOVA. The independent variables (factors) in each ANOVA were peg spacing ( $N=5$ ), incline ( $N=2$ ) and individual, and all three of these factors were fully crossed. In each ANOVA, incline and peg spacing were fixed factors, whereas individual was a random factor. Data from all nine snakes were used in the ANOVA for performance, whereas data from only the five fastest individuals were used in each ANOVA of a kinematic variable. For dependent variables such as maximum speed and some kinematic variables such as the total number of pegs touched, we had only one observation per treatment per individual, whereas for each of the kinematic variables ( $\alpha$ ,  $y_{crest}$ ,  $x_{crest}$ ,  $z_{crest}$ ,  $\lambda_{0.5}$ ) with multiple observations along the length of a snake within a single treatment, we calculated a mean value per treatment. Thus, in each ANOVA, each individual had only one value of the dependent variable for each combination of incline and peg spacing. We used  $P<0.05$  as the criterion for statistical

significance. To facilitate evaluating the effects of multiple comparisons (Moran, 2003), we provide exact *P*-values. All mean values are reported  $\pm$ s.e.m.

## RESULTS

For all of the trials used to quantify locomotor performance, the locomotion of the snakes conformed to previous definitions of lateral undulation. Waves of bending were propagated posteriorly along the body of the snake, but the waves formed a standing pattern relative to the supporting surface as the pegs prevented backwards slipping (Fig. 2). All points along the snake moved simultaneously, with continuously sliding contact with the supporting surface. Different points along the length of the snake more or less followed the same path, but this was less evident for the larger distances between pegs (Fig. 2B) compared with the surfaces with smaller distances between pegs (Fig. 2A).

A noteworthy feature of the lateral undulation that we observed, especially when snakes were moving vertically, was how loosely the body was draped across the cylinder, which often contributed to sizable gaps between the body and the cylinder that were evident in a dorsal view (Figs 2, 3). This body posture at the crossing regions during arboreal lateral undulation differs substantially from the tight wrapping and greater encirclement that has been described for the arboreal concertina locomotion of snakes (Astley and Jayne, 2007; Jayne and Herrmann, 2011). Surprisingly, some snakes in our study also occasionally climbed vertically with a sizable gap between their ventral scales and the cylinder at the base of a peg that they were pushing against. Thus, no appreciable active gripping of the cylinder appears to occur for the type of arboreal lateral undulation involving pegs that we observed.

A three-way ANOVA revealed that both peg spacing ( $F_{4,32}=4.2$ ,  $P=0.008$ ) and incline ( $F_{1,8}=19.3$ ,  $P=0.002$ ) had significant effects on locomotor performance, but the effect of peg spacing was highly dependent upon the incline (incline $\times$ spacing  $F_{4,32}=6.2$ ,  $P=0.001$ ). For the horizontal surfaces, the mean value of  $v_{x,max}$  was greatest for the 40 cm peg spacing ( $17.8\pm 2.4$  cm s $^{-1}$ ) which was nearly twice as large as the values for the 10 cm ( $10.5\pm 1.6$  cm s $^{-1}$ ) and 80 cm ( $10.9\pm 1.4$  cm s $^{-1}$ ) peg spacing (Fig. 4). The mean values of  $v_{x,max}$  (grand mean 6.5 cm s $^{-1}$ ) for locomotion up the vertical surface were not much more than one-half the lowest values observed for snakes on the horizontal surfaces. Two-way ANOVA (factors: peg spacing, individual) performed separately for data from the two different inclines confirmed that peg spacing lacked a significant effect on  $v_{x,max}$  for the vertical surfaces ( $F_{4,32}=0.4$ ,  $P=0.8$ ) but had a highly significant effect for the horizontal surfaces ( $F_{4,32}=8.3$ ,  $P=0.001$ ).

In addition to affecting performance, peg spacing and incline commonly affected kinematics. For example, the number and nature of the contact regions between the snake and the supporting surfaces also varied considerably among the different treatments (Figs 3, 5; Table 1). The number of regions where the midline of the snake crossed the midline of the supporting surface decreased significantly with increased distance between adjacent pegs, and for a given peg spacing the snakes usually had fewer crossing regions when moving up the vertical surface than when moving horizontally (Fig. 5A; Table 1). The total number of pegs (Fig. 5B) and the number of propulsive pegs (Fig. 5C) touched by the snakes also decreased significantly with increased distance between pegs (Table 1), but incline did not have a significant effect on these variables (Table 1). Peg spacing and incline had a significant interactive effect on  $N_{peg,non-prop}$  (Table 1) as a result of snakes commonly touching one or two non-propulsive pegs while moving on the horizontal surfaces with the two smallest values of peg spacing, but in most other

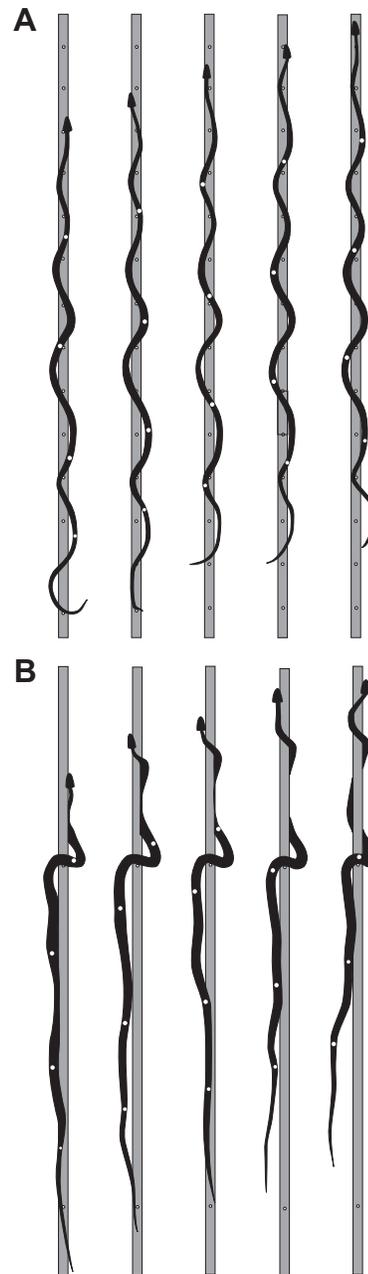


Fig. 2. Tracings from dorsal-view video images of a single snake performing lateral undulation on surfaces with different inclines and peg spacing. The small white circles represent the pegs. (A) A horizontal surface with pegs every 10 cm. (B) Locomotion up a vertical surface with pegs every 80 cm. The time between successive images in A and B was 0.3 and 1.2 s, respectively. This snake had snout-vent length (SVL) and total length (TL) of 108 and 137 cm, respectively. The white marks on the snake indicate locations of  $\sim$ 25%, 50%, 75% and 100% SVL.

circumstances nearly all of the pegs touched by the snakes were propulsive pegs (Fig. 5D).

The waveforms created by the bodies of the snakes also commonly showed substantial variation among the different surfaces (Fig. 3). Especially on the horizontal surfaces with peg spacing  $<30$  cm, the waves of lateral bending of the snakes closely resembled a sinusoidal function, whereas with increased distance between pegs many of the waves resembled a square wave with an amplitude that was small compared with the wavelength (Fig. 3). The waveforms

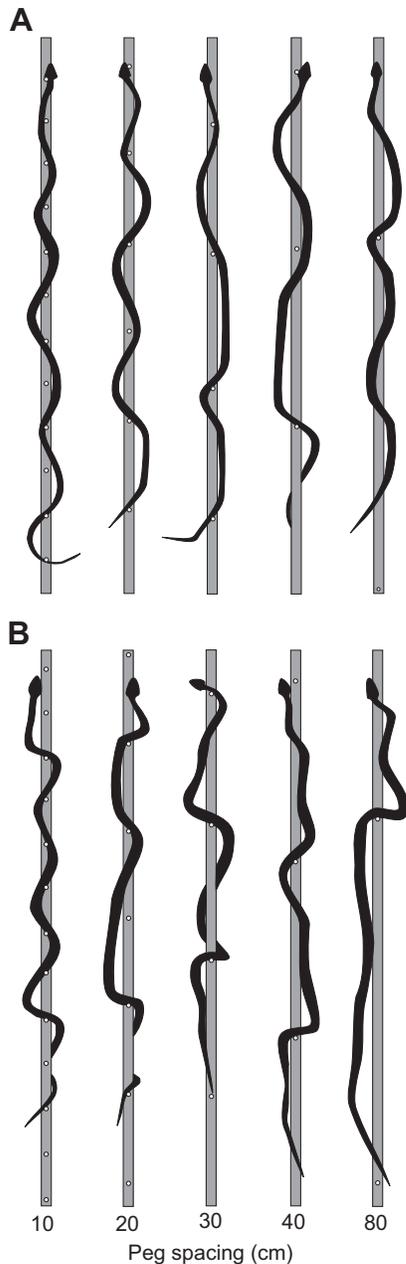


Fig. 3. Tracings from dorsal-view video images showing the body posture of a single snake while crawling on all 10 combinations of incline (A, horizontal; B, vertical) and peg spacing that were used to test performance. The small white circles represent the pegs. The number of waves increased as the number of pegs increased, and the waveforms on the horizontal surfaces were often more regular and symmetric than those when the snake was climbing the vertical surface.

of snakes on the vertical surfaces (Fig. 3B) were often less regular than those observed for snakes on the horizontal surfaces (Fig. 3A).

All four of the variables ( $y_{\max}$ ,  $z_{\max}$ ,  $y_{\text{crest}}$  and  $z_{\text{crest}}$ ) describing the lateral and ventral measurements of the half-waves varied significantly with peg spacing, but they all lacked a significant peg spacing  $\times$  incline interaction effect (Table 1). For both inclines, the maximum width (Fig. 6A) and mean lateral amplitude (Fig. 6C) of the snake increased from the 10 cm to the 20 cm peg spacing but changed little with further increases in peg spacing. The values of  $y_{\max}$  and  $y_{\text{crest}}$  were also significantly greater for movement up the

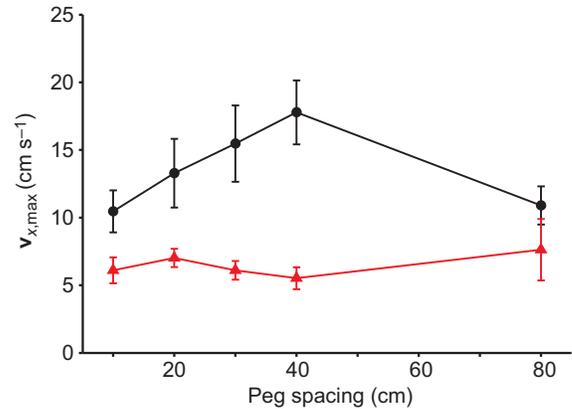


Fig. 4. The effects of peg spacing and incline on the mean values of maximum locomotor performance ( $v_{x,\max}$ ).  $N=9$  individuals. The black circles and red triangles indicate mean values for the horizontal and uphill vertical treatment, respectively. For the horizontal surface, an intermediate peg spacing maximized performance, whereas peg spacing lacked a significant effect on performance for snakes crawling up the vertical surface.

vertical surface than for movement on the horizontal surface (Fig. 6A,C; Table 1). For  $y_{\max}$ , the greatest mean value ( $11.8 \pm 1.1$  cm) occurred for locomotion on the vertical surface with the 20 cm peg spacing. Both the maximum (Fig. 6B) and mean (Fig. 6D) ventral locations of the wave crests increased from the 10 to the 40 cm spacing, but few differences were apparent between the two different inclines. For  $z_{\max}$ , the greatest mean value ( $5.8 \pm 2.0$  cm) occurred with the horizontal surface with 40 cm peg spacing, which indicates that the greatest amount of ventral sagging coincided with the conditions that optimized speed.

The angle of the body of the snake at the point of contact with the propulsive pegs showed highly significant variation with peg spacing and its two-way interaction with incline (Table 1; Fig. 7C). On the vertical surface,  $\alpha$  had the smallest values when peg spacing was smallest ( $41 \pm 2.6$  deg), and  $\alpha$  increased asymptotically with increased spacing up to a maximum value of nearly 90 deg ( $89 \pm 1.4$  deg). By contrast, for the horizontal surface the value of  $\alpha$  had little regular variation with peg spacing, and the grand mean was 36 deg (Fig. 7C). For both inclines, half-wavelength was often greater for locomotion on the vertical surface (Fig. 7B), but incline did not have a statistically significant effect on this variable (Table 1). The value of  $x_{\text{crest}}$  was usually near 0.5, indicating many of the half-waves were fairly symmetrical (Fig. 7A). However, for the largest peg spacing and the vertical surface, the mean value of  $x_{\text{crest}}$  ( $0.73 \pm 0.08$ ) indicated that the crests of the waves were often shifted posteriorly and in the downhill direction (Fig. 3B). The head-to-tail distance lacked variation that was clearly significant (Table 1), but  $x_{\text{ht}}$  was often greatest with the smallest peg spacing and slightly smaller for the vertical compared with the horizontal surface (Fig. 7D).

## DISCUSSION

The inclines of surfaces and the spacing of branches are two features of natural arboreal habitats that vary considerably (Mattingly and Jayne, 2004), and the brown tree snakes in Guam that we observed and collected moved on branches with a wide range of both slopes (from horizontal to vertical) and spacing between secondary branches. Both slope and branch spacing had widespread effects on

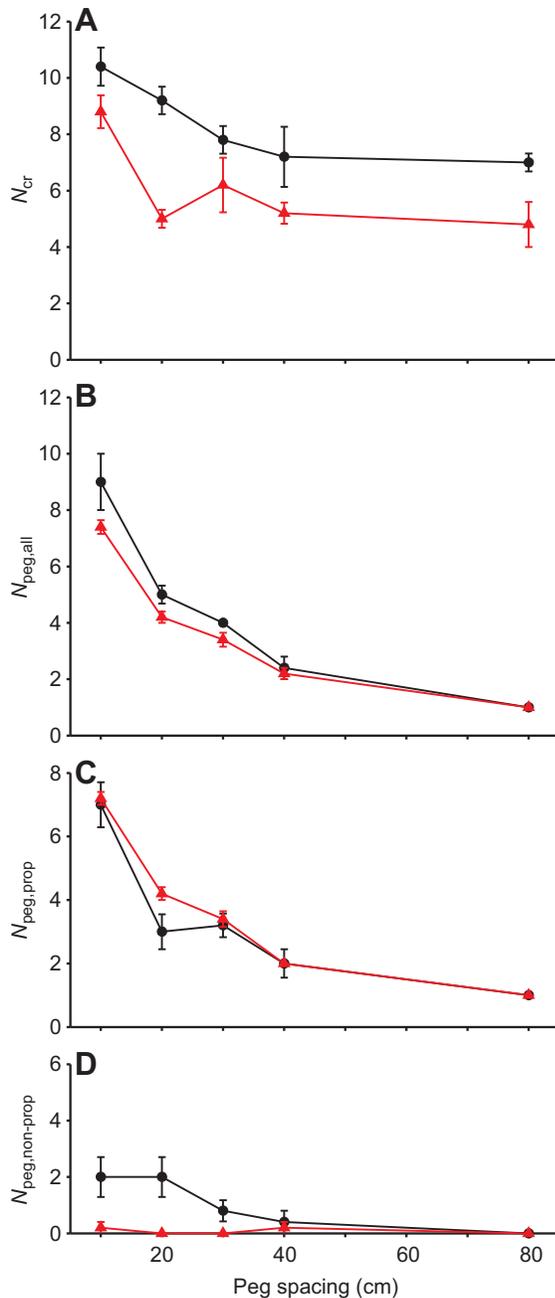


Fig. 5. The effects of peg spacing and incline on the mean values associated with contact points between the snake and the surfaces.  $N=5$  individuals. The black circles and red triangles indicate mean values for the horizontal and uphill vertical treatment, respectively. (A) The number of crossing regions ( $N_{cr}$ ). (B) The total number of pegs touched by the snake ( $N_{peg,all}$ ). (C) The number of propulsive pegs touched ( $N_{peg,prop}$ ). (D) The number of non-propulsive pegs touched ( $N_{peg,non-prop}$ ). When the distance between successive pegs was large, the snakes were more likely to cross the primary supporting surface without touching a peg ( $N_{cr} > N_{peg,all}$ ). When snakes crawled up the vertical surface, the pegs touched by snakes were almost always located posterior to the body of the snake, whereas snakes crawling on horizontal surfaces with the smallest distance between pegs often touched one or two pegs anterior to the body.

the locomotion of the snakes in our study. However, peg spacing had more pervasive effects on the kinematics of the snakes than did incline. The interactive effects of peg spacing and incline on the locomotor performance (Fig. 4) and body angle (Fig. 7C) of brown

tree snakes were especially striking. Two unexpected findings were the apparent ease with which snakes moved when touching only a single peg and the lack of a significant effect of peg spacing on the locomotor performance of snakes climbing up the vertical surface.

Key features of environmental structure are the coarseness and regularity of how objects are spatially distributed, but compared with some resources such as food, data are limited for the effects of the spatial distribution of the objects involved in the locomotion of animals (Kelley et al., 1997; Mattingly and Jayne, 2004; Goodman, 2009). Variation in the size, orientation and spacing of branches in arboreal habitats (Mattingly and Jayne, 2004) creates an interesting amount of complexity, and all of these attributes of branches can be readily simulated. However, previous experimental manipulations of branch spacing to determine effects on locomotion are limited to only a few arboreal limbed vertebrates such as anole lizards (Jones and Jayne, 2012) and mice (Hyams et al., 2012). For the arboreal locomotion of snakes, the presence or absence of pegs has been manipulated (Astley and Jayne, 2009; Jayne and Herrmann, 2011), but our study is the first to manipulate peg spacing. Consequently, most previous insights regarding the effects of peg spacing on snake locomotion must be derived from experiments using variable peg spacing for snakes crawling horizontally on planar surfaces (Gray and Lissmann, 1950; Heckrotte, 1967; Bennet et al., 1974; Jayne, 1986; Kelley et al., 1997).

The effects of objects such as pegs and secondary branches on locomotion depend on the body plan of the animal. For limbed animals moving horizontally, vertically oriented objects such as pegs impede locomotion unless the animal has sufficient space to detour around such objects without taking an overly circuitous route (Hyams et al., 2012; Jones and Jayne, 2012). By contrast, peg-like objects that are perpendicular to the surface supporting the ventral surface of the animal can facilitate the lateral undulation of limbless animals such as snakes by providing suitably oriented surfaces for applying posterior–laterally directed forces to generate thrust (Gray and Lissmann, 1950). At one extreme, pegs spaced less than a body width could also create a barrier for a limbless animal, and at the other extreme, pegs more than a body length apart could not be used continuously to generate propulsive forces for undulatory locomotion. However, additional variation in peg spacing between these extremes can also affect snake locomotion.

A long-standing suggestion has been that three lateral points of force application are needed for terrestrial lateral undulation (Gans, 1974). The body posture and performance of snakes in this study moving past a single peg may suggest otherwise, but regions of the body other than the location touching the peg may help to obtain the balance of forces necessary for stable forward motion, especially when such regions touching the cylinder are flexed ventrally. However, additional circumstances have been described when snakes may use lateral undulation without any obvious points of lateral contact such as when boa constrictors move on very slender, cylindrical, horizontal surfaces (Jayne and Herrmann, 2011) or when rat snakes move on very smooth planar surfaces (Hu et al., 2009).

Our study and some previous studies of terrestrial snake locomotion found large effects of peg spacing on performance (maximal speed). For example, juvenile garter snakes crawling through arrays of pegs on a flat surface have mean speeds with a peg spacing of 8% TL that are ~50% and 25% greater than those for peg spacings of 21% TL and 6% TL, respectively (Kelley et al., 1997). For peg spacing from 5% to 18% TL (Jayne, 1986), rat snakes and water snakes are fastest with the largest peg spacing. For another species of North American rat snake, the speed of locomotion with a peg spacing of 19% TL exceeds that for a spacing of 43% TL

Table 1. Effects of peg spacing and incline on kinematics

Dependent variable	ANOVA effect		
	Spacing (d.f.=4,16)	Incline (d.f.=1,4)	Spacing × incline (d.f.=4,16)
$N_{cr}$	8.9 (0.001)	35.8 (0.004)	1.6 (0.225)
$N_{peg,all}$	97.6 (<0.001)	4 (0.115)	2.2 (0.11)
$N_{peg,prop}$	126.2 (<0.001)	1.4 (0.306)	1 (0.455)
$N_{peg,non-prop}$	4.3 (0.015)	8.7 (0.042)	3.7 (0.025)
$y_{crest}$	3.8 (0.024)	77.8 (0.001)	0.2 (0.948)
$z_{crest}$	7.9 (0.001)	10 (0.034)	1.6 (0.223)
$y_{max}$	5.9 (0.004)	48.3 (0.002)	0.1 (0.991)
$z_{max}$	5.8 (0.004)	0.1 (0.803)	1 (0.448)
$\lambda_{0.5}$	3.1 (0.044)	6.3 (0.066)	0.9 (0.508)
$x_{crest}$	2.4 (0.098)	11.3 (0.028)	2.9 (0.055)
$\alpha$	49.4 (<0.001)	473.5 (<0.001)	9.9 (<0.001)
$x_{ht}$	3.2 (0.043)	7.2 (0.055)	0.2 (0.926)

Values are  $F(P)$ .

$N_{cr}$ , number of crossing regions;  $N_{peg,all}$ , total number of pegs touched by the snake;  $N_{peg,prop}$ , number of propulsive pegs touched by a snake;  $N_{peg,non-prop}$ , number of non-propulsive pegs touched by a snake;  $y_{crest}$ , lateral amplitude of a half-wave;  $z_{crest}$ , depth of a half-wave;  $y_{max}$ , maximum width of a snake;  $z_{max}$ , maximum depth of half-waves;  $\lambda_{0.5}$ , half-wavelength;  $x_{crest}$ , location of wave crest;  $\alpha$ , angle of snake body at point of peg contact;  $x_{ht}$ , head-to-tail distance.

(Bennet et al., 1974). Thus, peg spacing from ~10% to 20% TL often appears well suited for snakes to attain high speeds of terrestrial lateral undulation. In our study, peg spacing ranged from a mean value of  $7 \pm 0.1\%$  TL to  $57 \pm 1\%$  TL, and the maximal value of speed for brown tree snakes on the horizontal surfaces, which occurred with a spacing of  $28 \pm 0.5\%$  TL, was nearly twice the value for both the smallest and largest peg spacing. Similar to some of the previous studies of terrestrial lateral undulation through arrays of pegs with a limited range of spacing (Bennet et al., 1974; Jayne, 1986), our results would have suggested that speed simply increases with increased peg spacing rather than being optimized at an intermediate value if we had not included the largest peg spacing.

In addition to affecting speed, peg spacing also can affect the number of waves, waveform, body posture and number of pegs touched by undulating snakes. For example, the number of undulations decreases with increased distance between pegs for both garter snakes (Kelley et al., 1997) and the brown tree snakes in our study. For the peg spacing that maximizes speed, both garter snakes and brown tree snakes commonly have four to six half-waves. Previous illustrations of terrestrial locomotion show that the angle of the body of snakes ( $\alpha$ ) often increases with increased distance between pegs [see fig. 6 of Gray and Lissmann (Gray and Lissmann, 1950) and fig. 5 in Kelley et al. (Kelley et al., 1997)], and we observed this for the uphill locomotion of the brown tree snakes but not for their horizontal locomotion (Fig. 3, Fig. 7A). The number of pegs touched by the snakes in our study decreased more rapidly with increased peg distance than the number of crossing regions (Fig. 5). Consequently, even though the brown tree snakes touched an average of only two pegs for the conditions that maximized speed on the horizontal surface, nearly half of the nodes between undulations were not associated with a peg. Unfortunately, previous studies of locomotor performance for snakes crawling through arrays of pegs have not systematically quantified the number of pegs touched.

The effects of peg spacing on lateral displacement (wave amplitude) differ for the terrestrial lateral undulation of garter snakes compared with the arboreal undulation of brown tree snakes. With increased peg distance the amplitude of lateral undulations of garter snakes nearly doubles [see fig. 5 in Kelley et al. (Kelley et al., 1997)], whereas that of the brown tree snakes was nearly constant for all but the smallest peg spacing used in

our experiments (Fig. 6C). The large increase in wave amplitude for garter snakes results in their  $x_{ht}$  decreasing from ~70% TL to 50% TL with increased peg distance, whereas that of the brown tree snakes was usually larger and nearly constant (~80% TL). Increased wave amplitude usually correlates well with increased wavelength both for undulations of a snake in different environments and for undulations at different longitudinal locations within the snake in a given environment (Gray and Lissmann, 1950; Jayne, 1985; Jayne and Davis, 1991; Kelley et al., 1997), whereas the small wave amplitudes that we observed for the arboreal locomotion of the brown tree snakes were nearly independent of wavelength (Fig. 3A, Fig. 6C). Such small wave amplitudes could reduce the tendency for long-axis rolling during horizontal locomotion by decreasing the amount of unsupported weight and decreasing the length of the lever arm that contributes to the rolling torque acting on each half-wave. For a given peg spacing, the brown tree snakes also had undulations with very similar shape along the lengths of their bodies when moving horizontally, and if the rolling torques acting on each undulation to the left and right are equal, then maintaining balance should be easier.

Variable body orientations and numbers of contact points can have important consequences for the orientation and magnitude of forces that are relevant for undulatory propulsion (Gray and Lissmann, 1950). For the snakes in our study, the values of body angle,  $\alpha$ , can provide a good estimate of the orientation of the reaction forces arising from pressing against the peg after making a correction for the frictional resistance between the snake and the peg (Fig. 8). For the surfaces that we used, the coefficient of static friction for snake skin is 0.28 (Astley and Jayne, 2007), which would cause a difference of ~16 deg between the orientation of the normal force and the resultant reaction force (Fig. 8). Sliding friction is less than static friction, which would reduce the value of this correction. The grand mean of  $\alpha$  for brown tree snakes moving on the horizontal surfaces was 36 deg, which suggests that the angle of the reaction forces against the pegs commonly approximated 45 deg and thus the ratio of the magnitude of the forward and lateral components of force should be ~1:1 (Fig. 8).

The only experimental data for the reaction forces of snakes performing lateral undulation past a series of pegs are those of Gray and Lissmann (Gray and Lissmann, 1950), who observed a snake

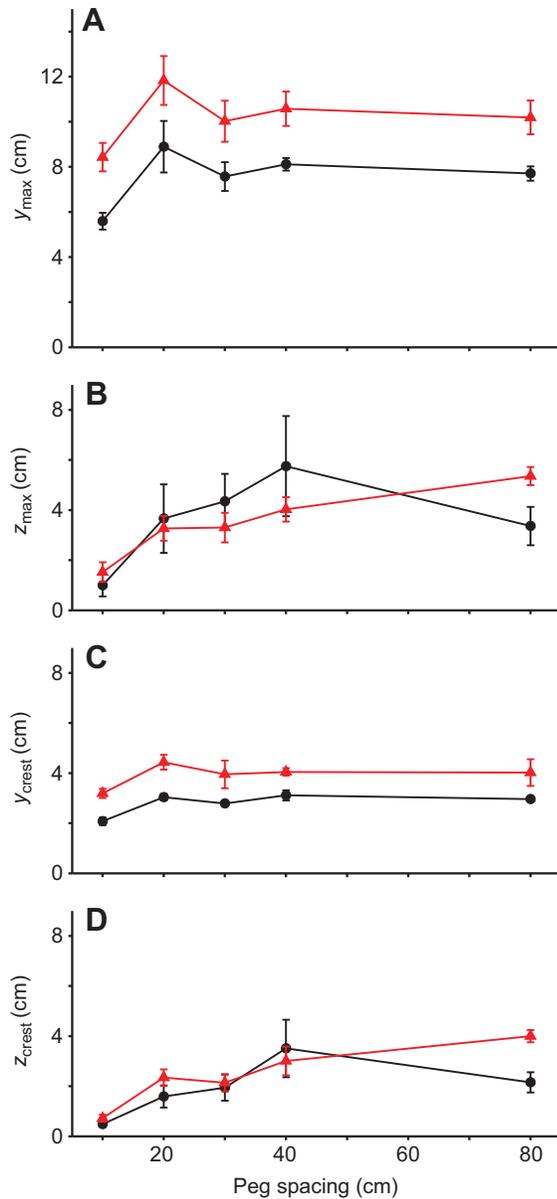


Fig. 6. The effects of peg spacing and incline on the mean values of lateral and vertical location of wave crests.  $N=5$  individuals. The black circles and red triangles indicate mean values for the horizontal and uphill vertical treatment, respectively. (A) The maximum width of the snake ( $y_{max}$ ). Snakes climbing up vertical surfaces often used more lateral space. (B) The maximum depth of a wave crest ( $z_{max}$ ). (C) The lateral amplitude of half-waves was greater for vertical locomotion ( $y_{crest}$ ). (D) The depth of half-waves ( $z_{crest}$ ).  $z_{crest}$  of snakes crawling up the vertical surface was greater than that with the horizontal surface for the largest distance between pegs, and for horizontal locomotion the greatest mean value coincided with the conditions that maximized performance.

crawling on planar horizontal surfaces for five treatments with a range of one to nine contact points. The spacing between successive contact points (pendulums) for these treatments with two, three and four contact points was  $\sim 17\%$  TL, whereas that of the treatment with nine pendulums was approximately one-half that value. From the least to most contact points, the ratios of the total lateral to longitudinal components of the reaction force were 0, 0.12, 0.94, 1.39 and 2.27, respectively, and these values correspond to average angles of the reaction force relative to the direction of forward travel

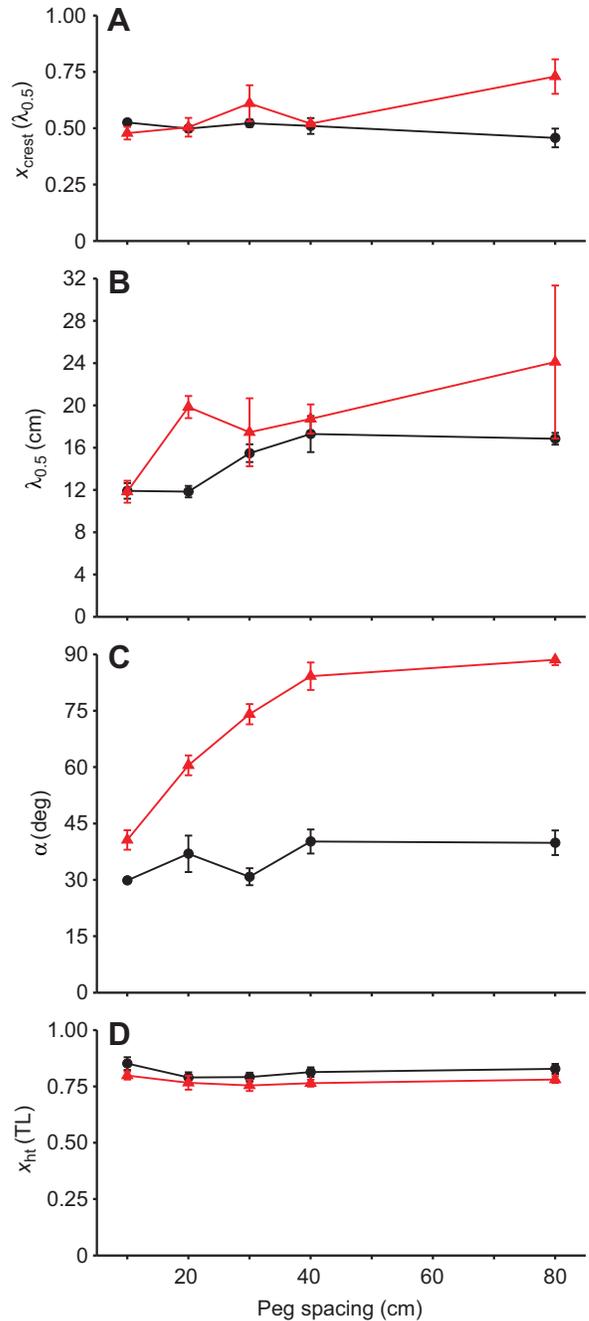


Fig. 7. The effects of peg spacing and incline on the mean values of waveform and overall posture.  $N=5$  individuals. The black circles and red triangles indicate mean values for the horizontal and uphill vertical treatment, respectively. (A) Wave crest location ( $x_{crest}$ ). Asymmetric half-waves were most common for snakes crawling up the vertical surface with the largest distance between pegs. (B) Half-wavelength ( $\lambda_{0.5}$ ). (C) The angle ( $\alpha$ ) of the body of the snake at the point of contact with the pegs. For snakes climbing up the vertical surface,  $\alpha$  increased asymptotically to a value of 90 deg as peg spacing increased, whereas peg spacing for the horizontal surface had little effect on  $\alpha$ . (D) The head-to-tail distance of the snakes ( $x_{ht}$ ).

of  $\sim 0, 7, 43, 54$  and  $66$  deg, respectively. The corresponding average values of body angle thus ranged from  $\sim 90$  deg for treatment with a single pendulum to less than 30 deg for the largest number of contact points. Thus, even when the spacing between contact points was constant, the ratio of sideways to forward forces increased with

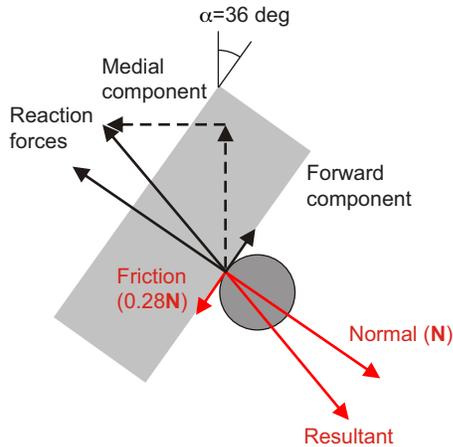


Fig. 8. A schematic diagram of the orientation of forces acting on a peg. The gray rectangle represents the body of the snake oriented relative to the peg (gray circle) with the value of  $\alpha$  observed for all peg spacings for the horizontal surface. The red arrows show how a given normal force applied by the snake against a peg generates a frictional force that opposes the movement past the peg, and the resultant sum of these two vectors is oriented postero-medially (Gray and Lissmann, 1950). The black arrows indicate the corresponding reaction forces with a resultant that is oriented antero-medially, and black dashed arrows indicate the magnitudes of the forward (propulsive) and sideways components of the reaction force in this example are approximately equal. Note that frictional resistance against the peg causes the resultant reaction force to be oriented closer to the overall direction of travel ( $\sim 16$  deg) compared with the orientation of the normal reaction force.

increased number of contact points, and the two treatments with the most contact points support the conclusion that the ratio of lateral to forward components of forces also increases with decreased distance between peg-like contact points. Although forces were quantified in this study (Gray and Lissmann, 1950), neither speed nor locomotor mode was determined.

Variation in the ratio of the lateral- to forward-directed reaction forces seems unlikely to account for all of the differences in performance that we observed for the brown tree snakes moving on the horizontal surfaces because  $\alpha$  was nearly constant regardless of peg spacing (Fig. 7C). Perhaps the greater number of changes in the direction of momentum associated with a greater number of undulations contributed to decreased speed when the space between pegs was small. Unlike pegs protruding from a planar surface, pegs on a cylindrical surface seem likely to have the dual function of providing sites for generating propulsive force as well as preventing long-axis roll of the snake about the cylinder supporting its weight. Large values of  $\alpha$  could enhance the ratio of propulsive to lateral force, but the nearly constant body orientation of  $\sim 45$  deg at the pegs on the horizontal cylinder further suggests the primacy of maintaining balance rather than generating thrust on these surfaces. Consequently, the decrease in performance when moving on the surface with the largest distance between pegs may have arisen primarily from the difficulties associated with maintaining balance.

Several factors suggest that the constraints on speed of the snakes climbing vertically differ substantially from those for the snakes moving horizontally. For example, when climbing vertical cylinders, the direction of the weight vectors for alternating loops of the snakes are parallel to the cylinder and thus should not contribute directly to long-axis rolling. Indeed, we observed very little long-axis rolling

for snakes in these circumstances despite the snakes having consistently larger values of lateral displacement than were observed for horizontal locomotion (Fig. 6C). Despite little apparent need to counteract long-axis rolling, the maximal speeds during vertical climbing were slower than those for the horizontal surface, and the maximal vertical speeds lacked any clear pattern of change with peg spacing. The large values of  $\alpha$  for snakes crawling vertically while touching only one or two pegs (Fig. 3B, Fig. 7C) should reduce the magnitude of laterally directed forces, and this may have increased the ease of dealing with these forces and helped to prevent a decrease in performance similar to that which occurred for the largest peg spacing when snakes crawled horizontally. The ventral curvature of the snake interacting with the underlying cylinder provides another potential mechanism for balancing left and right lateral forces in addition to modulating the orientation of the body at the pegs.

Some additional effects of body weight also differ for snakes climbing vertically *versus* those moving horizontally. For example, snakes climbing vertically must apply sufficient force to lift their entire weight,  $\mathbf{W}$ , whereas the weight of snakes moving horizontally produces a ventral frictional resistance equal to  $\mu\mathbf{W}$ , where  $\mu$  is the coefficient of friction (Gray and Lissmann, 1950). Snakes climbing vertically should have a negligible amount of ventral friction. For both vertical and horizontal lateral undulation, the snakes will also encounter a lateral frictional resistance where the body contacts the pegs, and this should be greater for vertical movement as the snakes should have to press harder against the pegs to overcome their weight rather than primarily the (lesser) ventral frictional resistance when the snake moves horizontally. Consequently, the force required to move vertically should exceed that required to move horizontally by more than  $(1-\mu)\mathbf{W}$ . Thus, generating propulsive force seems more likely to limit vertical climbing speed, whereas horizontal arboreal lateral undulation may be limited more by factors involving coordination and balance.

The different body orientations that we observed for snakes climbing vertically could result from the snakes actively controlling their body posture to optimize the orientations of forces, or the increased values of  $\alpha$  (Fig. 3B) could also arise from greater amounts of passive bending resulting from fewer pegs being used to generate the same total amount of propulsive force. Most vertebrates with elongated body plans have acquired them *via* increased numbers of body segments (Ward and Mehta, 2010), and if the mobility per joint is constant, then an increased number of joints per unit length can enhance the flexibility of the body. Snakes are certainly a noteworthy group for having both large numbers of vertebrae (Hoffstetter and Gasc, 1969) and an ability to bend readily, but variation in the morphology of muscles is also likely to have consequences for axial flexibility and how it is controlled. For example, the number of vertebrae spanned and length of tendon relative to the length of contractile tissue within certain major axial muscle segments of specialized arboreal colubroid snakes, such as the species we studied, are greater than those for nearly all groups of snakes that are not arboreal (Jayne, 1982). Not only is tendon stiff but also when there are greater proportions of tendon in individual axial muscle segments, a greater amount of length change in the contractile tissue will be required to accommodate the same amount of axial bending as in a different species with a higher proportion of contractile tissue per axial muscle segment. Hence, this morphological specialization may facilitate the enhancement of axial stiffness, which may in turn facilitate supporting the body of arboreal snakes in between branches (Hofer and Jayne, 2013) or be well suited for moving using a minimal

number of contact points (Ruben, 1977). Such long tendons also might enhance the ability of these snakes to cope with the large and very localized loads that occur when they climb vertically using undulation past only one or two points of support.

Many aspects of the shape of the brown tree snakes did change with peg spacing, but some details of waveform and body shape did not conform strictly to either peg spacing or some other features of the supporting surfaces. For example, with the smallest peg spacing the snakes commonly did not contact each successive peg as they often used a larger waveform than would be possible if they did this (Fig. 3). Similarly, the ventral curvature of the snakes was usually far less than the tight conformity to the circumference of a cylindrical surface that is probably required to generate an effective frictional grip, as has been described for arboreal concertina locomotion (Astley and Jayne, 2007; Jayne and Herrmann, 2011). Nonetheless, the amount of ventral curvature and total dorso-ventral displacement that we observed for arboreal lateral undulation does seem likely to exceed that which occurs during lateral undulation on natural terrestrial surfaces even though many of them can deviate substantially from a simple horizontal plane.

The extent to which the ventral curvature of snakes on arboreal surfaces is caused actively or passively poses an interesting area for future work. Ventral curvature when the snakes climbed vertical surfaces seems quite likely to be caused by active ventral flexion of the snake, but for snakes moving horizontally on a cylindrical surface, ventral curvature could be caused solely by the weight of the snake. In this latter case, activity of the most dorsal muscles might occur bilaterally to prevent or modulate the amount of sagging in a fashion similar to how these muscles arch the back of snakes during sidewinding locomotion with a motor pattern that deviates from that of terrestrial lateral undulation (Jayne, 1988). Modulating the depth and width of the waves of snakes while on cylindrical surfaces could also serve as an important mechanism for enhancing the stability of arboreal snake locomotion. Hence, all of these factors could cause arboreal lateral undulation to deviate substantially from some of the major features of terrestrial lateral undulation while retaining many of the kinematic similarities including a posteriorly propagated wave, all points following a similar path and continuous sliding contact.

Many studies have quantified maximum speeds of diverse species of animals (Irschick and Garland, 2001). However, much remains to be learned regarding what factors generally limit speed and the extent to which the constraints on speed vary with physiology, animal body plan, environmental structure and interactions between these factors. For example, under some conditions the limbs of some small lizards have stride frequencies close to those predicted based on the time course of force development and relaxation of a single muscle twitch (Marsh and Bennett, 1985), but the frequencies of undulation of snakes observed in this and other studies are so slow that this factor is irrelevant to their maximal locomotor speeds. Our results also provide a striking example of how different aspects of environmental structure can have interactive effects on locomotor performance and can create some circumstances where force production may limit speed and other circumstances where balance and coordination may be the primary constraints on performance. Although the need for balance may seem most obvious for animals moving on narrow branches, investigating the rich complexity of additional natural habitats (Tucker and McBrayer, 2012) seems likely to hold much additional promise for identifying factors besides muscle force production (Higham et al., 2011) that may limit locomotor performance.

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## AUTHOR CONTRIBUTIONS

B.C.J. conceived the main ideas and experimental design, wrote and revised drafts of the entire manuscript, performed statistical analyses, revised the figures and interpreted the findings. J.T.B. executed the experiments, obtained measurements from videos and wrote a draft of the methods section and created initial versions of the figures. G.B. executed experiments, interpreted the findings and wrote and revised portions of the manuscript.

## COMPETING INTERESTS

No competing interests declared.

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