

## Scaling of the axial morphology and gap-bridging ability of the brown tree snake, *Boiga irregularis*

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### Summary

Networks of branches in arboreal environments create many functional challenges for animals, including traversing gaps between perches. Many snakes are arboreal and their elongate bodies are theoretically well suited for bridging gaps. However, only two studies have previously investigated gap bridging in snakes, and the effects of size are poorly understood. Thus, we videotaped and quantified maximal gap-bridging ability in a highly arboreal species of snake (*Boiga irregularis*), for which we were able to obtain a large range in snout-vent length (SVL=43–188 cm) and mass (10–1391 g). We expected smaller snakes to bridge relatively larger gaps than larger individuals because of their proportionately higher ratio of muscle cross-sectional area to mass. The maximal length of the gaps spanned by *B. irregularis* had negative allometry, indicating that smaller snakes could span a greater proportion of their length than larger snakes. The greatest relative gap distance spanned (64% SVL) was by the smallest individual. The majority of snakes (85%) simply

crawled slowly to cross a gap. Most of the suspended portion of the body and the path traveled by the head were below the perch that supported the posterior body, which may decrease the tendency of the snake to roll. Some (15%) of the snakes used another behavior in which the neck inclined as much as 45° and then rapidly lunged towards the anterior perch, and this enabled them to cross larger gaps than those using the crawling behavior. Perhaps the launching behavior of the gliding tree snakes (*Chrysopelea* sp.) evolved from an ancestral behavior of lunging to bridge gaps analogous to that of the brown tree snakes. An estimate of the muscle strain required to prevent the body of the snake from buckling suggests that, despite being light-bodied, brown tree snakes bridging a gap may be at the limit of the physiological capacity of their epaxial muscles.

Key words: locomotion, scaling, axial, morphology, allometry, snake, arboreal, cantilever, muscle, reaching, affordance, gap.

### Introduction

The size and shape of animals can have profound effects on musculoskeletal function, partly as a result of mass increasing more rapidly than the ability of muscles to produce force as the overall size of animal increases (McMahon, 1984; Vogel, 2003; Wainwright et al., 1976). The effects of increased size can be particularly important during locomotion because the entire mass of an animal moves and the entire weight of a terrestrial animal must be supported (Alexander, 2003; Biewener, 2003; Schmidt-Nielsen, 1977). Many insights into the effects of size and the limits of musculoskeletal performance have been gained by studying the demands of rapidly accelerating or steady high-speed locomotion, which are usually very large compared to those required only to support the animal's weight (Biewener, 2005; Dutto et al., 2004; Marsh, 1988; McGowan et al., 2005; Olson and Marsh, 1998; Weyand and Davis, 2005). However, the functional demands for supporting the weight of an animal may vary depending on the relationships between an

animal's mass and its shape, how the body is oriented relative to gravity and where the body is supported by the environment.

Among vertebrates, snakes have one of the most extreme body plans with respect to length and mass since their elongate bodies have such low mass for their length. For example, a 40 g garter snake, which is neither a particularly thin nor stout snake species, can have a mass only 1/100 of that of a domestic cat with a similar (50 cm) body length (Jayne and Bennett, 1990; Nowak, 2005). The elongate body plan of snakes may partly explain why so many species of snakes can move with apparent ease in arboreal habitats. Theoretical advantages of an elongate body for arboreal locomotion include facilitating the ability to drape across many slender branches without bending them excessively or breaking them (Lillywhite and Henderson, 1993), to cross large gaps between branches without having to jump, and to wrap around branches and grasp them. Several different evolutionary lineages of snakes considered arboreal specialists appear to have convergently evolved an

extraordinarily thin body (Lillywhite and Henderson, 1993), which further suggests that low weight per unit length conveys benefits for certain types of limbless arboreal locomotion.

Snakes presumably face some tradeoffs between reducing weight per length *versus* retaining sufficient axial muscle mass to generate locomotor forces and prevent excessive sagging of the suspended portions of the body in arboreal habitats. Spanning a horizontal gap between branches can create a large moment arm between the point of support to the center of mass of the suspended portion of the body, and thus a large torque could result that would tend to buckle the body of the snake despite its light weight. Thus, unlike most situations in terrestrial habitats, where supporting the weight of a stationary animal appears to be relatively trivial, supporting the weight of the body crawling across a gap may pose a formidable functional challenge for snakes. With the remarkable exception of the few species of southeast Asian snakes in the genus *Chrysopelea* (Socha and LaBarbera, 2005) that jump from branches, most snakes use a cantilevering behavior to cross gaps. However, only two studies (Lillywhite et al., 2000; Lin et al., 2003) have previously examined cantilevering behavior, despite its ecological relevance, common occurrence in snakes, and the potential to tax the performance of the musculoskeletal system. Consequently, the ability of specialized species of arboreal snakes to traverse gaps and the effects of size are still poorly known.

The present study investigates the scaling relationships of morphology and gap-bridging ability of the highly arboreal brown tree snake *Boiga irregularis* (Merrem 1802), which belongs to a genus that has independently evolved some features of its axial anatomy that are convergent with those of other highly arboreal snakes (Jayne, 1982). Since its introduction to Guam, an island in the Pacific Ocean, *B. irregularis* has caused substantial ecological and economic damage (Rodda et al., 1999), partly because of its renowned ability to traverse formidable obstacles. A large size range (10 to >1000 g) and its ecology thus make *B. irregularis* well-suited for gaining insights into the biomechanical problems and solutions involved in spanning gaps in locomotor surfaces.

The first purposes of this study were to determine how the gap-bridging performance scales with the size of brown tree snakes and what behaviors are used to bridge gaps. We expected negative allometry (scaling exponent <1) for maximal gap distance *versus* snake length, because weight increases approximately as a cubic function of length whereas the scaling of muscle cross-sectional area usually approximates only a quadratic function of length. We also determined the cross-sectional areas of axial muscles that are likely to be important for supporting the weight of the snakes over the gap in order to test whether or not some of the inter-individual variation in muscle size was correlated with gap-bridging ability. Finally, we combined data on axial muscle anatomy with estimates of torques experienced by the snake to examine whether this important locomotor task of an arboreal animal seems likely to be taxing the limits of its musculoskeletal performance.

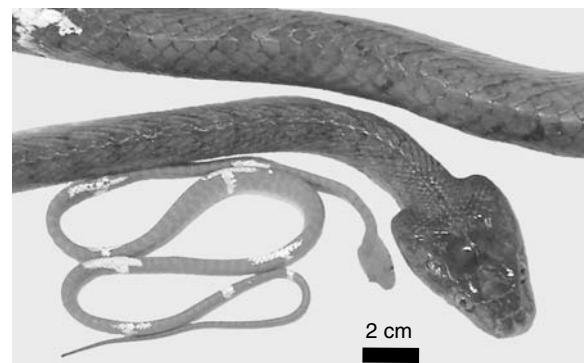


Fig. 1. The smallest ( $SVL=43$  cm, mass=9.9 g) and second largest ( $SVL=184$  cm, mass=1137 g) brown tree snakes used to determine the scaling of anatomy and gap-bridging performance. The smaller snake is near the size of a hatchling.

## Materials and methods

### Experimental subjects and protocol

We tested the gap-bridging performance of 27 brown tree snakes *Boiga irregularis* (Merrem 1802) with a large range in size ( $SVL=43\text{--}188$  cm; mass 10–1391 g; Fig. 1). The five largest snakes ( $SVL>164$  cm) were long-term captives, but all remaining snakes were tested within 2–3 weeks of being captured. None of the snakes had eaten 5 days prior to being tested. All experimental procedures were in compliance with and overseen by the Institutional Animal Care Use Committee of the University of Cincinnati (protocol number 03-12-22-02).

All performance tests were conducted in Guam National Wildlife Refuge, near Dededo, GU, USA, in a shaded outdoor area during the afternoon. The body temperatures of the snakes during the tests averaged  $29.6\pm0.2^\circ\text{C}$ . The testing apparatus was two horizontal PVC pipes (41 mm diameter) 1.5 m above the ground. Each pipe had two rows of 4 mm diameter pegs placed at 5 cm intervals and inclined approximately  $45^\circ$  relative to the horizontal (Fig. 2). We were not always able to align the PVC pipes precisely along a straight horizontal line, but the vertical deviation between the ends of the two pipes and the orientation of each pipe relative to the horizontal never exceeded  $4^\circ$ . The first gap presented to each snake was approximately 50%  $SVL$ . If the snake failed to cross this first gap, we decreased the gap distance by approximately 2 cm until the snake successfully crossed a gap, whereas if the snake successfully traversed the first gap, we increased the gap distance by approximately 2 cm until the snake failed to cross a gap. Thus, for each snake we obtained a maximum gap distance that was crossed ( $\text{Gap}_{\max}$ ) as well as a trial with at least one gap of the next larger size.

### Anatomical measurements

We used an overdose of anesthetic (sodium pentobarbital) to euthanize 25 of the 27 snakes used for performance testing. After euthanasia and prior to preservation (fixation with 10% formalin and storage in 70% ethanol), we measured the

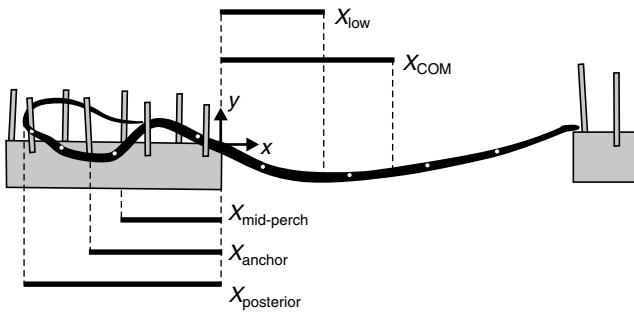


Fig. 2. Methods used to quantify the posture of the snake one frame before bridging a gap. The image is a tracing of a right lateral view of a video of a snake with  $SVL=57$  cm crossing a 30 cm gap. The pegs in the large horizontal cylinder are inclined approximately 45° relative to the horizontal plane, and the tips of those in the foreground were oriented towards the camera. The origin of the coordinate system used for kinematic analysis was the top center end of the perch upon which the snake was initially placed. The longitudinal positions were measured or calculated for the most posterior location of the snake ( $X_{\text{posterior}}$ ), mid-way between the end of the initial perch and  $X_{\text{posterior}}$  ( $X_{\text{mid-perch}}$ ) and the most anterior location of the snake that was underneath part of the initial perch or one of its pegs (third right peg from the edge in this example) so that upward forces could be applied ( $X_{\text{anchor}}$ ). The  $x$  and  $y$  coordinates were digitized for the lowest location of the mid-dorsal line and center of mass (COM) for the portion of the body suspended in the gap between the two perches.

snout–vent length (SVL), tail length and total mass of the intact snake. We then cut the body and the tail into ten and two pieces, respectively. The lengths ( $\pm 5$  mm) and masses ( $\pm 0.1$  g) of these pieces were used to estimate the location of the center of mass (COM) measured from the snout of a straight snake (COM-straight). From cross sections through the preserved pieces at 10% and 50% SVL, we also measured cross-sectional areas of major epaxial muscles that in terrestrial snakes (Jayne, 1988) are dorsiflexors or lateral flexors (M=multifidus, SSP-SP=semispinalis-spinalis) or primarily lateral flexors (LD=longissimus dorsi, IL=iliocostalis). To facilitate comparing the cross-sectional areas among the four epaxial muscles within all individuals, relative cross-sectional areas (%) were calculated by dividing the cross-sectional area of a single muscle by the total cross-sectional area of the four muscles within each individual. To determine the origins and insertions of these axial muscles, we dissected two large ( $SVL>1.5$  m) preserved specimens.

#### Kinematics

We used two digital camcorders (Sony DCR-HC42; New York, NY, USA; 30 images s $^{-1}$ ) to videotape dorsal and lateral views of the performance of 24 individuals, but three additional individuals were only videotaped in lateral view because of a malfunction in the dorsal view camera. After each video sequence was deinterlaced and every other video field was saved as an avi video file using Adobe Premiere Pro version 7, we digitized coordinates from the avi files using

MaxTRAQ version 1.89 (Innovision Systems, Inc., Columbiaville, MI, USA). The origin of the three-dimensional coordinate system used for kinematic analyses was at the top edge at the center of the initial perch adjacent to the gap (Fig. 2). The  $x$ -axis was parallel to the long axis of the horizontal pipes, and the  $y$  and  $z$  axes were in the vertical and horizontal planes, respectively.

Seven variables described the posture of the snake from the lateral view one image before the snake touched the perch on the far side of the gap being crossed. After digitizing points at approximately 5–10 mm intervals along the dorsal midline of the snake from its snout to the point of contact with the initial perch at the edge of the gap, we used the two-dimensional distance formula to estimate the anatomical length of the portion of the snake that was suspended. To estimate the location in the  $x$ - $y$  plane of the center of mass of the portion of the body suspended over the gap (COM-gap), these mid-dorsal coordinates were integrated with the length and mass data of the ten body sections of the snake that were measured prior to preservation. For the sake of simplicity, we assumed that the center of mass of each 1/10 section of the snake was on the mid-dorsal line and midway between its two ends. By combining the locations and masses of the complete 1/10 body sections that were suspended, and interpolating data for the portion of the snake's body between the edge of the gap and the posterior end of the last complete 1/10 body section, we estimated the  $x$  ( $X_{\text{COM}}$ ) and  $y$  ( $Y_{\text{COM}}$ ) positions of the center of mass of the snake over the gap (COM-gap). From these mid-dorsal coordinates just before crossing the gap, we also determined the  $x$  ( $X_{\text{low}}$ ) and  $y$  ( $Y_{\text{low}}$ ) coordinates of the lowest point of the suspended portion of the snake's body (Fig. 2). Three longitudinal distances measured from the edge of the initial perch included: the most anterior point where the snake was able to press up against the initial perch or one of its pegs ( $X_{\text{anchor}}$ ), the most posterior part of the snake ( $X_{\text{posterior}}$ ), and the midpoint between the edge of the perch and the posterior end of the snake ( $X_{\text{mid-perch}}$ ) (Fig. 2).

To describe the trajectory of the head of the snake as it crossed the gap, we also digitized the  $x$ ,  $y$  and  $z$  coordinates of the snout of the snake. We digitized most data at 100 ms intervals, but the end of a few sequences with rapid movement were digitized every 33 ms. We calculated the percentage of the time taken to cross the gap during which the snout of the snake was below ( $T_{\text{below}}$ ) or above ( $T_{\text{above}}$ ) the top edge of the horizontal pipes. We also determined the maximum ( $Y_{\text{max}}$ ) and minimum ( $Y_{\text{min}}$ ) height of the path traveled by the head as well as the  $x$  locations where these values occurred ( $X_{y\text{max}}$  and  $X_{y\text{min}}$ , respectively). The vertical ( $\Delta Y$ ) and lateral ( $\Delta Z$ ) excursions of the entire path traveled by the head were the differences between the maximum and minimum values of the  $y$  and  $z$  coordinates, respectively. To clarify whether the path of the snake narrowed as it approached the destination perch, we calculated values of  $\Delta Z$  for the first ( $\Delta Z_1$ ) and second ( $\Delta Z_2$ ) halves of each sequence. To facilitate pooling data from different individuals,  $Y_{\text{max}}$ ,  $Y_{\text{min}}$ ,  $\Delta Y$  and  $\Delta Z$  were converted to percentages of  $\text{Gap}_{\text{max}}$  for each snake.

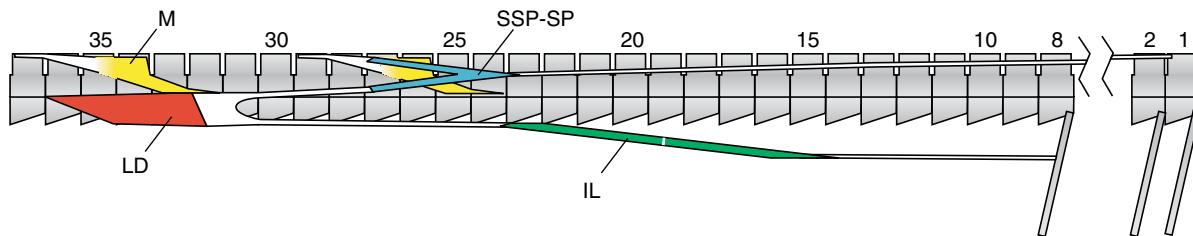


Fig. 3. Schematic right lateral view of the major epaxial muscles of the brown tree snake at mid-body. SSP-SP, semispinalis-spinalis muscle; M, multifidus muscle; LD, longissimus dorsi muscle; IL, iliocostalis muscle. The colored areas indicate contractile tissue, the tendons are white, and the skeletal structures are gray. Vertebrae are numbered beginning at the anterior attachment site of a single segment of the SSP-SP, and five vertebrae (3–7) are not shown. The thin horizontal line represents the shelf formed by the pre- and postzygapophyses.

### Statistical analysis

We used SYSTAT version 9 to perform statistical analyses. We log<sub>10</sub>-transformed all data before using least-squares regressions to determine the scaling relationships of morphology and performance. One of our major reasons for calculating the scaling regressions was to use them to determine if a snake performed unusually well (or poorly) or was unusually muscular for its size by calculating the residual values (difference between the observed and predicted values) and using them for additional analyses. When the primary goal of a regression analysis is prediction, least-squares regressions are often viewed as most appropriate (Sokal and Rohlf, 1995). In addition, the high values of  $r^2$  for most of our data suggest that the differences between using reduced major axis and least-squares regression for our data would be minor. All values are means  $\pm$  s.e.m., unless stated otherwise.

## Results

### Anatomy

The longitudinal columns of the major axial muscles consisted of discrete segments that had a 1:1 ratio with the numbers of underlying vertebrae, but individual axial muscle segments spanned several vertebrae (Fig. 3). The most dorsal muscles for which cross-sectional areas were quantified were the semispinalis-spinalis (SSP-SP) and the multifidus (M) (Fig. 4). A distinct triangular-shaped tendon gave rise to the fibers of the more dorsal head (spinalis) of the SSP-SP on its lateral surface, and the fibers of the multifidus arose mainly from the medial and anterior surface of this tendon. Most of the fibers of the multifidus inserted onto the lateral surface of the neural spine three vertebrae anterior to its origin and the lateral surface of the neural arch four vertebrae anterior to its origin (Fig. 3). A few additional fibers of the multifidus inserted onto the lateralmost portion of a neural arch five vertebrae anterior to its origin (Fig. 3). The length of the contractile tissue of the ventral (semispinalis) and dorsal (spinalis) heads of the SSP-SP both spanned 4–5 vertebrae, and the length of the long anterior tendon of the SSP-SP spanned 20–24 vertebrae. Thus, from origin to insertion a single segment of the SSP-SP could span as many as 29 vertebrae.

The fibers of the longissimus dorsi segments arose from the

prezygapophysis of a vertebra and extended anteriorly 4–5 vertebrae, whereupon they attached to a distinct tendinous arch (Fig. 3). The dorso-medial portion of the tendinous arch gave rise to a distinct tendon that connected to the semispinalis head of the SSP-SP as well as some diffuse connective tissue that contributed to a septum between the LD and SSP-SP and a connective tissue sheath that covered the superficial lateral surface of the SSP-SP. The ventral portion of the tendinous arch of the LD gave rise to a distinct tendon 7–8 vertebrae long that connected posteriorly to the dorsal head of the iliocostalis (IL). The more ventral and anterior head of the IL had contractile tissue approximately the same length as the posterior head (approximately 5 vertebrae), and its fibers were

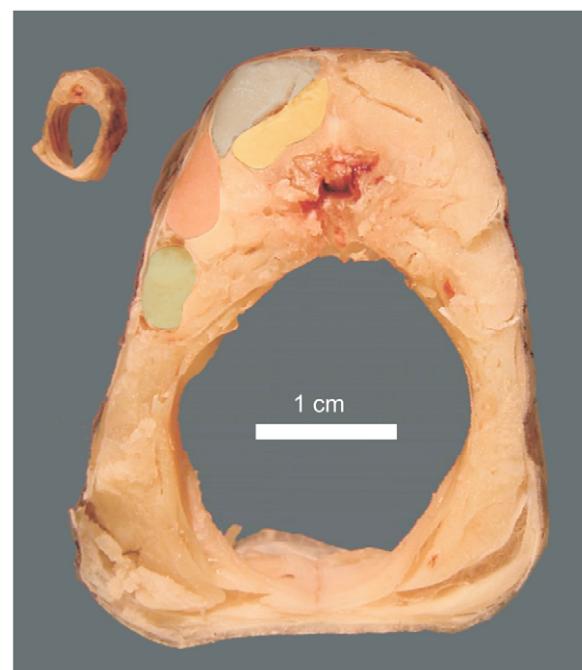


Fig. 4. Cross-sections at mid-body of the smallest ( $SVL=43$  cm) and largest ( $SVL=188$  cm) snakes. On the large section the major epaxial muscles for which cross-sectional area were determined are tinted blue (semispinalis-spinalis), yellow (multifidus), red (longissimus dorsi) and green (iliocostalis).

discernable from the posterior head only by a faint constriction and very small length of connective tissue. The IL extended anteriorly for another 7–8 vertebrae *via* another very distinct but thin tendon that attached to the rib approximately one-third of its length from where it articulated with the vertebra. Thus, from the tendinous arch of the LD to the anterior attachment of the IL, 23–24 vertebrae were spanned by a single muscular segment. The ventral portion of the tendinous arch of the LD also contributed to diffuse connective tissue that formed a septum between the LD and IL.

At mid-body the mean values of relative cross-sectional areas were similar for the SSP-SP ( $27.8 \pm 0.9\%$ ), M ( $23.5 \pm 0.8\%$ ), LD ( $24 \pm 0.7\%$ ) and IL ( $24.7 \pm 0.6\%$ ) (Fig. 4). At 10% SVL the mean relative cross-sectional area of the IL ( $31.3 \pm 0.7\%$ ) was relatively large, that of the LD was relatively small ( $19.9 \pm 0.6\%$ ), and those of the SSP-SP ( $25.4 \pm 0.8\%$ ) and M ( $23.4 \pm 0.6\%$ ) were similar to each other. The diameter of the neck of brown tree snakes is small compared to that at mid-body (Fig. 1). Consequently, the cross-sectional areas of the axial muscle at 10% SVL were much smaller than those at 50% SVL, as indicated by mean values of the area at 10% SVL divided by those at 50% SVL of  $46.8 \pm 3.0\%$ ,  $51.2 \pm 3.5\%$ ,  $42.0 \pm 2.7\%$  and  $63.0 \pm 3.0\%$  for the SSP-SP, M, LD and IL, respectively.

The muscle cross-sectional areas at 50% SVL and total mass of the snakes had scaling coefficients with SVL greater than those expected from geometric similarity (Table 1). COM-straight of large snakes was slightly but significantly more

posterior than that of smaller snakes, as indicated by a scaling coefficient greater than one.

#### Gap-bridging behaviors

The snakes used two major behavioral modes to cross the maximal gap distances. Most commonly (85% of the trials) the snakes crawled across the gap by moving with little or no stopping as the anterior portion of the snake appeared nearly straight in a dorsal view (Fig. 5A). During this crawling behavior the portion of the body on the initial perch moved continuously in a pattern similar to the lateral undulatory mode of terrestrial snake locomotion (Jayne, 1986). The speeds of forward progression during the crawling mode were rather slow as the time to cross the gap commonly exceeded a few seconds. During the latter stages of crossing the gap, the body of the snake usually had a shallow S-shape in lateral view (Fig. 5A).

An alternative mode used by some (15%) of the snakes to cross the gap was performing a rapid lunge (Fig. 5B). Prior to performing a lunge, these snakes used lateral undulatory locomotion of the posterior portion of the body to extend a considerable length of the anterior body over the gap. Subsequently, the snakes flexed the suspended portion of the body into a series of conspicuous left and right bends, and the long axis of the suspended portion of the snakes was oriented upward at an angle as much as  $45^\circ$  relative to the horizontal (Fig. 5B). The snakes then rapidly propelled the head upward and forward by straightening the anterior region as the posterior portion of the body on the initial perch remained nearly

**Table 1.** Least-squares regression parameters of the scaling equations for  $\log_{10}$ -transformed values of anatomy and performance versus snake size

y	N	Slope $\pm$ 95% CL	Intercept $\pm$ 95% CL	$r^2$
Mass (g)	27	$3.427 \pm 0.268$	$-4.766 \pm 0.539$	0.965
Tail length (cm)	27	$0.862 \pm 0.097$	$-0.370 \pm 0.195$	0.930
COM-straight (cm)	25	$1.086 \pm 0.034$	$-0.441 \pm 0.068$	0.995
Vertebral height (cm)	25	$1.149 \pm 0.134$	$-2.659 \pm 0.267$	0.923
Muscle area at 10% SVL ( $\text{cm}^2$ )				
SSP-SP	25	$2.730 \pm 0.322$	$-7.428 \pm 0.641$	0.930
M	25	$2.900 \pm 0.306$	$-7.800 \pm 0.611$	0.944
LD	25	$2.681 \pm 0.396$	$-7.437 \pm 0.791$	0.895
IL	25	$2.528 \pm 0.284$	$-6.933 \pm 0.568$	0.936
Muscle area at 50% SVL ( $\text{cm}^2$ )				
SSP-SP	25	$2.457 \pm 0.357$	$-6.535 \pm 0.712$	0.898
M	25	$2.671 \pm 0.476$	$-7.031 \pm 0.951$	0.854
LD	25	$2.677 \pm 0.462$	$-7.031 \pm 0.923$	0.862
IL	25	$2.619 \pm 0.371$	$-6.902 \pm 0.742$	0.903
Area SP+M at 10% SVL ( $\text{cm}^2$ )	25	$2.815 \pm 0.297$	$-7.309 \pm 0.593$	0.944
Area SP+M at 50% SVL ( $\text{cm}^2$ )	25	$2.571 \pm 0.389$	$-6.488 \pm 0.778$	0.890
X <sub>COM</sub> (cm)	21	$0.818 \pm 0.125$	$0.297 \pm 0.252$	0.903
Torque (N m)	21	$4.099 \pm 0.419$	$-9.191 \pm 0.845$	0.957
Gap <sub>max</sub> (cm)	27	$0.818 \pm 0.128$	$0.026 \pm 0.258$	0.873
X <sub>posterior</sub> (cm)	21	$1.108 \pm 0.337$	$-0.564 \pm 0.680$	0.713
X <sub>anchor</sub> (cm)	20	$1.439 \pm 0.871$	$-1.751 \pm 1.744$	0.401

Regression coefficients are for the scaling equation  $\log_{10}y = \text{slope} \times \log_{10}\text{SVL} + \text{intercept}$ ;  $P < 0.001$ , except for  $X_{\text{anchor}}$  ( $P = 0.002$ ).

SVL, snout-vent length; COM, center of mass; CL, confidence limits; SSP-SP, semispinalis-spinalis muscle; M, multifidus muscle; LD, longissimus dorsi muscle, IL, iliocostalis muscle.

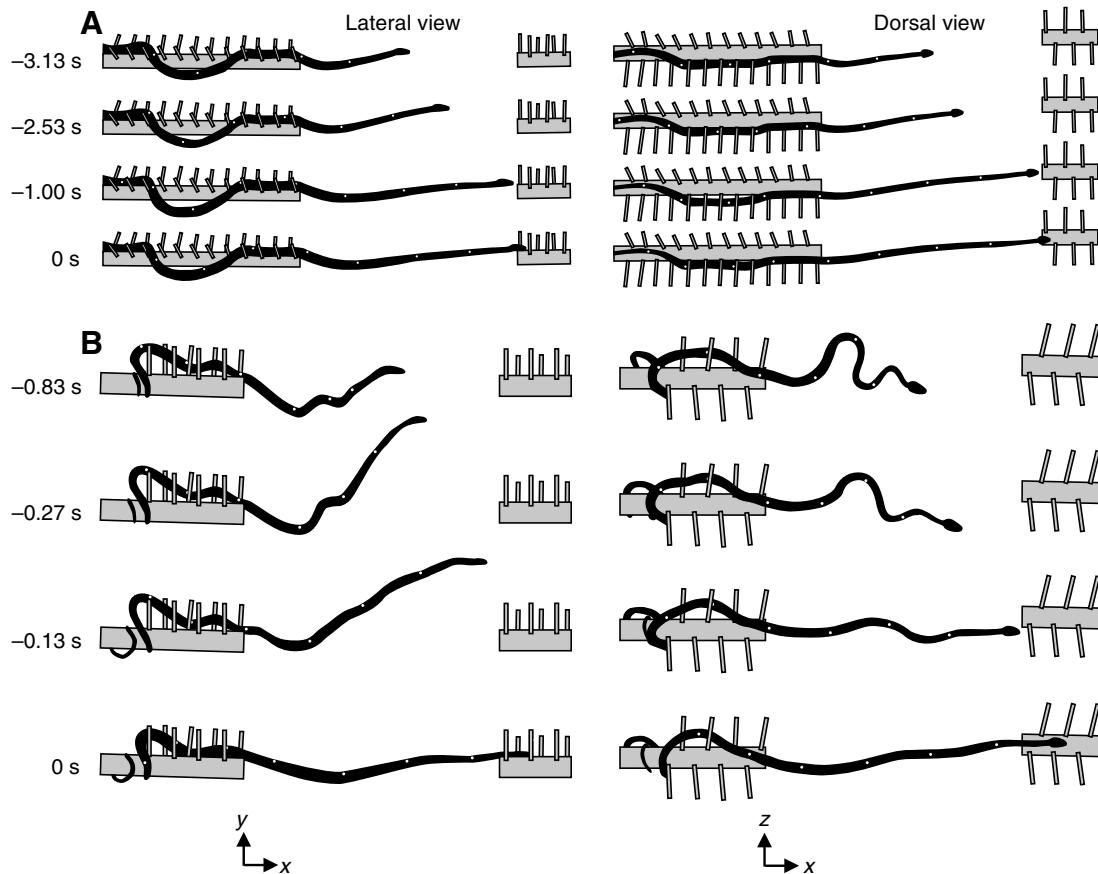


Fig. 5. Tracings from videotapes showing lateral (left) and dorsal (right) views of different gap-bridging behaviors. (A) Crawling behavior of a snake with  $SVL=136$  cm crossing a 67 cm gap. (B) Lunging and tail wrapping behaviors of a snake with  $SVL=106$  cm crossing a 52 cm gap. The most anterior anchor points in A and B are the fifth right peg and the third left peg from the edge of the initial perch, respectively. The white marks indicate intervals approximately one-eighth  $SVL$  along the body of the snake. The times before contacting the destination perch are to the left of each figure. The portion of the snake spanning the gap was nearly straight during crawling, whereas early in the lunge the body had several lateral bends that were later straightened. Videos of these behaviors can be viewed at <http://bioweb.ad.uc.edu/faculty/jayne/videos.htm>.

stationary. Thus, unlike the crawling mode during which the portion of the body on the initial perch propelled the head forward, during the lunging mode most of the head movement resulted from changing the configuration of the suspended portion of the body in a manner similar to how snakes perform defensive and predatory strikes.

When bridging maximal gap distances, all but two of the snakes had at least one location beneath the initial perch or its side branches against which upward forces could be exerted (Figs 2, 5). Only four of the 27 snakes encircled the central portion of the initial perch by wrapping their tail more than  $360^\circ$  around it, and half of these individuals that did so also performed a lunge (Fig. 5B). Two additional individuals wrapped their tail around the initial perch as they used the crawling mode to cross the gap.

During the trials in which the snakes were confronted with a gap approximately 2 cm larger than their maximal gap distance, five individuals performed a lunge but only one of those individuals had performed a lunge when crossing its maximal gap distance. Thus, 30% of the snakes performed a

lunge at least once for the successful and unsuccessful trials combined, and the probability of performing a lunge increased with increased gap distance. For these uncrossable gaps, the heads of all the individuals moved a minimum and average horizontal distance of 60% and  $92 \pm 3\%$   $Gap_{max}$ , respectively. Ten individuals traversed a distance  $\geq 100\%$   $Gap_{max}$ , but they slipped or bounced off the destination perch and hence were unable to cross the gap with their entire body.

#### Scaling of gap-bridging performance

The maximum distances of the gap traversed scaled with negative allometry (Fig. 6, Table 1). The largest relative and absolute gap distances bridged were 64%  $SVL$  ( $SVL=43$  cm) and 81 cm ( $SVL=165$  cm), respectively. The size-corrected (residual) values of  $Gap_{max}$  with either a tail wrap or lunge ( $N=6$ ) were significantly greater than those for crawling only (Fig. 6;  $t=4.22$ , d.f.=16, two-tailed  $P<0.001$ ). Five snakes (all  $<75$  cm  $SVL$ ) spanned gaps exceeding their values of COM-straight. The two snakes ( $SVL=135$ , 178 cm) that lacked a conspicuous anchor point on the initial perch, against which

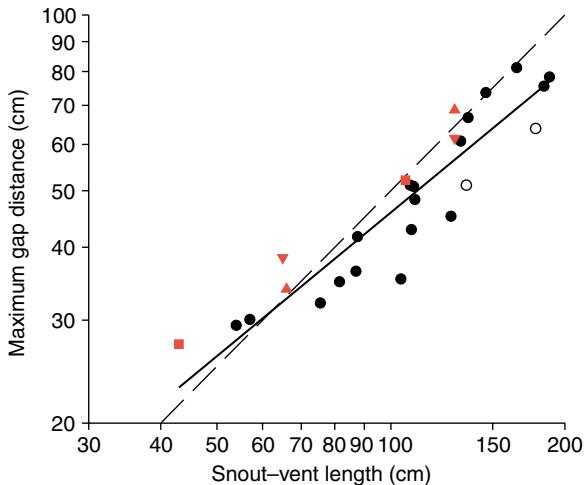


Fig. 6. The scaling of maximal gap distance crossed *versus* snake size. The solid line is the least-squares regression for  $\log_{10}$ -transformed data, and the broken line indicates a 1:1 ratio of snake SVL and gap distance. Each symbol represents one snake. Circles indicate the crawling behavior (see Fig. 5A); triangles, lunging behavior; inverted triangles, tail-wrapping behavior. Squares indicate a lunge while the tail was wrapped around the initial perch (Fig. 5B). A solid symbol indicates that the snake had a conspicuous anchor point on the initial perch against which upward forces could be applied (Fig. 2), whereas a hollow symbol indicates the lack of such a point. See Table 1 for regression statistics.

they could push upward, had two of the lowest five values of size-corrected gap-bridging performance (Fig. 6). The residuals of  $\text{Gap}_{\max}$  (predicted from SVL) were not significantly correlated with mass residuals ( $r=0.28$ , one-tailed  $P=0.079$ ), but they did have some significant positive correlations with mid-body values of residual areas of individual epaxial muscles SSP-SP ( $r=0.25$ ,  $P=0.114$ ), M ( $r=0.48$ ,  $P=0.008$ ), LD ( $r=0.44$ ,  $P=0.014$ ) and IL ( $r=0.46$ ,  $P=0.011$ ), and the combined area of the dorsi-flexors, SSP-SP+M ( $r=0.40$ ,  $P=0.24$ ).

#### Kinematics

The initial forward speed with which snakes crawled across the gap was relatively steady, and then in most trials (20 of 23) the snakes moved very slowly for the last 1–2 s before contacting the destination perch (Fig. 7A). The head was beneath the top of the horizontal cylinder upon which the snake was crawling for on average  $80\pm4.8\%$  of the time taken to crawl across the gap. The low point of the path traveled by the head ( $Y_{\min}$ ) averaged  $24.7\pm4.4\%$  of  $\text{Gap}_{\max}$  below the tops of the horizontal cylinders, and  $X_{y\min}$  was near the midpoint ( $50.7\pm3.9\%$ ) of  $\text{Gap}_{\max}$ .

The lateral component of movement for the path of the head while crawling across the gap was highly variable (Figs 7, 8). Alternating movements to the left and right were often visible, but both the wavelength and amplitude of these excursions varied considerably (Fig. 8). The values of  $\Delta Z$  over the entire path of the head while crossing the gap averaged  $20.1\pm2.8\%$  of  $\text{Gap}_{\max}$ . The average lateral excursion for the first ( $\Delta Z_1$ ) and

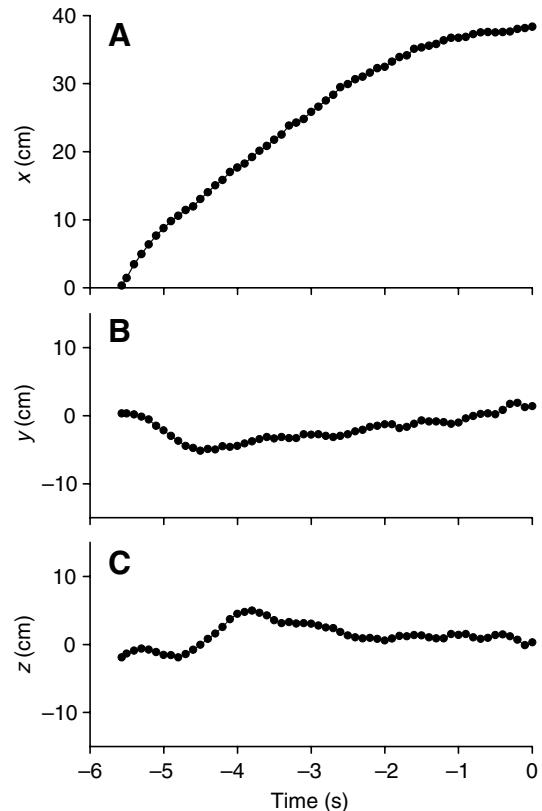


Fig. 7. The kinematics of a snake using the crawling behavior to cross a gap. (A) Forward (B) vertical and (C) lateral displacement of the snout of the snake *versus* time. The time intervals between successive points are all 100 ms. The snake touched the perch on the far side of the gap at 0 s. After moving forward with a nearly constant speed ( $-4.5$  to  $-2.5$  s), the snake gradually slowed before reaching the destination perch. Gap distance, 38 cm; snake SVL, 65 cm.

second ( $\Delta Z_2$ ) halves of the path traveled by the head across the gap were  $15.7\pm2.4\%$  and  $12.3\pm1.9\%$  of  $\text{Gap}_{\max}$ , respectively, and a paired  $t$ -test on these quantities supported the observation that the lateral excursion often decreased significantly as the snakes approached the destination perch (one-tailed  $t=1.79$ ,  $P=0.043$ ,  $N=24$ ). In a few cases the head of the snake deviated remarkably little from a straight line, as seen in dorsal view (Fig. 8F).

Although the body of the snakes sagged noticeably below the perch (Figs 2, 4), this vertical distance ( $Y_{\text{low}}$ ) was only a small fraction ( $7.9\pm1.5\%$ ) of  $\text{Gap}_{\max}$ . The location of the low point of the mid-dorsal line of the snake just prior to bridging the gap was closer to the initial perch than to the destination perch (mean  $X_{\text{low}}=38.2\pm2.5\%\text{Gap}_{\max}$ ).

The observed lunges occurred after a failed attempt to use the crawling behavior to cross the gap. Thus, discontinuous forward movement was common before a lunge (Fig. 9A), and the snakes often made a loop as the head dipped down and then was repositioned for another attempt (Fig. 9C). For the head the average values of  $\Delta Y$  and  $Y_{\max}$  during lunges were  $63.6\pm15.0\%$  and  $16.7\pm6.3\%$  of the gap distance, respectively.

For the lunge with the greatest value of  $Y_{\max}$  (Fig. 9), the head moved down 15.1 cm in the 0.2 s prior to touching the destination perch, and the vertical velocity during the last 33 ms before contacting the destination perch was 133 cm s<sup>-1</sup>. These values were a sizable fraction of those predicted for a freely falling object being accelerated by gravity for the same amount of time (19.6 cm, 196 cm s<sup>-1</sup>, respectively). Consequently, the lunging snakes either did little or were minimally effective in counteracting the acceleration due to gravity. Unlike the conspicuous vertical acceleration during a lunge, the forward velocity could be nearly constant over a substantial portion of the final downward trajectory. For example, in Fig. 9 the forward velocity at the top of the trajectory was 62 cm s<sup>-1</sup> and 133 ms later (over a 33 ms

interval) it was 65 cm s<sup>-1</sup>, while the homologous vertical velocities more than quadrupled. Thus, some aspects of the kinematics of a lunge resembled those of a ballistic trajectory, and the head of the snake could hit the destination perch with sizable forward and vertical velocities.

#### Distribution of mass and torque

The following variables describe how the mass of the snake was distributed just prior to bridging the gap when the torque resulting from the weight of the suspended portion of the snake is likely to be the greatest (Fig. 2). The mass of the suspended

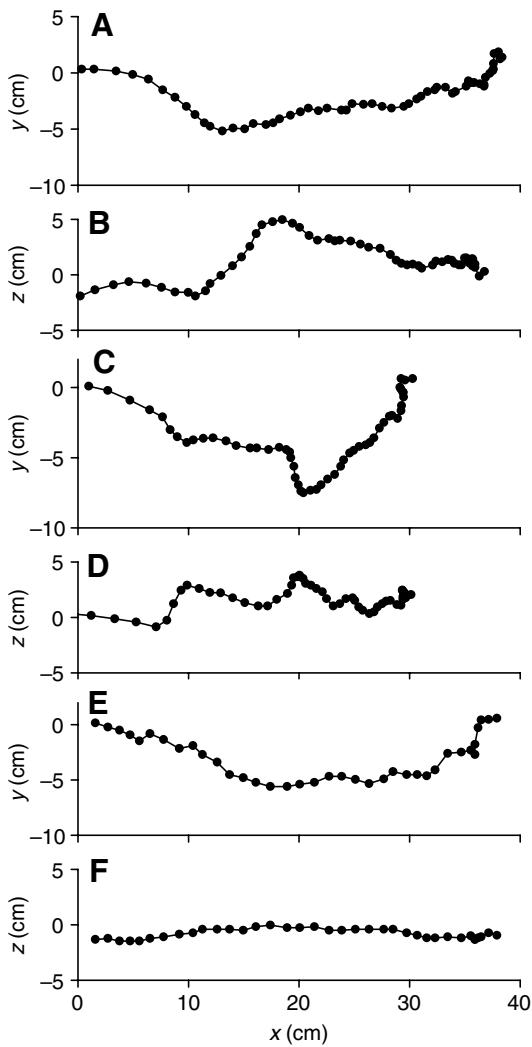


Fig. 8. Variation in the paths traveled by the snout of snakes while crawling across a gap. (A,C,E) Lateral views and (B,D,F) overhead views. (A,B) Snake  $SVL=65$  cm, gap distance=38 cm; (C,D)  $SVL=54$  cm, gap distance=30 cm; (E,F)  $SVL=87$  cm, gap distance=38 cm. The time intervals between successive points are all 100 ms. The end and top center of the initial perch are at the origin of the  $x$ ,  $y$  and  $z$  axes.

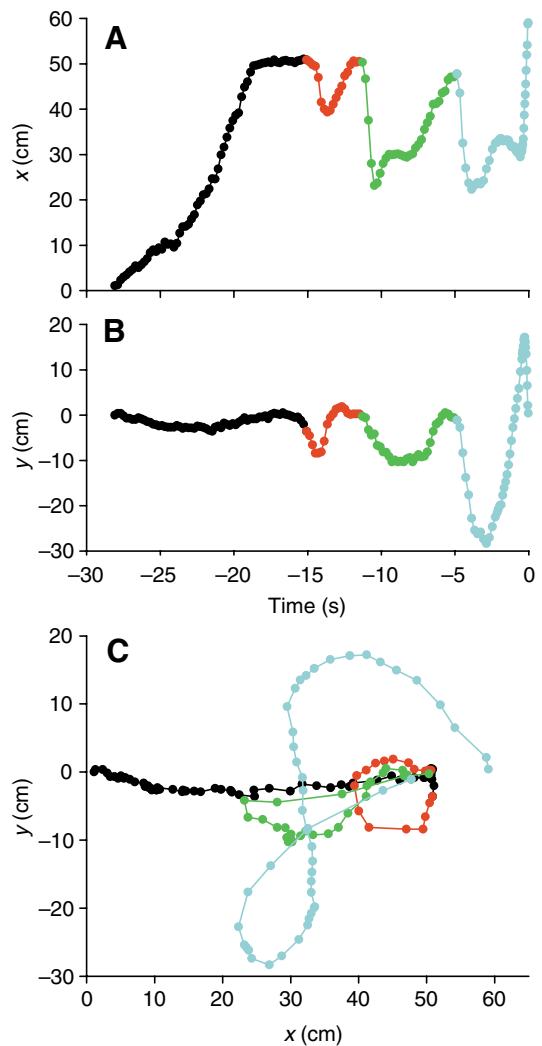


Fig. 9. The kinematics and the path traveled by a snake using the lunging behavior to cross a gap. (A) Forward and (B) lateral displacement *versus* time, and (C) a lateral view of the path traveled by the snout of the snake ( $SVL=106$  cm) while crossing a 52 cm gap. The times between the last thirteen successive points are 33 ms; all other time intervals between successive points are 200 ms. The snake touched the perch on the far side of the gap at 0 s. Different colored symbols indicate four attempts to bridge the gap, for which only the last was successful. The rapid forward and vertical velocities (slope) within the last 0.5 s indicate when the snake lunged. The end and top center of the initial perch are at the origin of the  $x$ ,  $y$  and  $z$  axes.

portion of the snake ranged from 5 g ( $SVL=43.5$  cm) to 477 g ( $SVL=188$  cm), and the mass of the suspended portion of the snakes ranged from 38% to 140% of the mass of the snake that was on the initial perch. All three of the snakes for which the suspended mass exceeded the mass on the perch performed the lunging behavior, and after excluding all lunging snakes, the suspended mass divided by the mass on the perch averaged  $69\pm3.9\%$  ( $N=21$ ).

For the snakes not performing lunges, the torques resulting from the weight of the suspended portion of the snakes (times  $X_{COM}$ ) ranged from 0.005 to 1.67 N m, and the scaling coefficient of these torques with  $SVL$  was almost exactly 4 while  $X_{COM}$  scaled with negative allometry (Table 1). The average locations of the COM-gap in the  $x$  and  $y$  directions were  $48.1\pm0.7\%$  and  $-5.6\pm1.0\%$  of  $Gap_{max}$ . The location of the COM of the suspended portion of the snake was only above the surface of the perch in two of 25 trials, and these two values were both less than 1 cm above the perch.

For the portion of the snake on the initial perch (Fig. 2), neither the scaling coefficient of  $X_{anchor}$  nor that of  $X_{posterior}$  was significantly different from the value of 1 expected from isometry (Table 1). The values of  $X_{posterior}$  exceeded those of gap distance in 61% of the trials. For snakes that crawled across the gap with an anchor point on the initial perch and for which COM was determined ( $N=20$ ), the average mechanical advantages of  $X_{anchor}$  and  $X_{mid-perch}$  relative to  $X_{COM}$  were  $0.77\pm0.11$  and  $1.07\pm0.06$ , respectively, and most of these quantities lacked high correlations with both  $SVL$  ( $r=0.48$ ,  $P=0.032$ ;  $r=0.27$ ,  $P=0.256$ , respectively) and the size-corrected values of  $Gap_{max}$  ( $r=0.02$ ,  $P=0.43$ ;  $r=0.02$ ,  $P=0.28$ , respectively). Thus, extending the body more posteriorly along the initial perch did not appear to facilitate gap-bridging performance.

A direct method for accurately determining the center of mass of the snake on the initial perch was not available because the bodies of the snakes in this region usually had complicated three-dimensional configurations. Thus,  $X_{mid-perch}$  was used as a crude estimate of the COM of the snake on the initial perch, and this was multiplied by the weight of the snake's body on the initial perch to estimate the torque that may be available to prevent the snake from pitching downward as it crossed the gap. The resulting ratio of this quantity to the torque calculated for the suspended portion of the body averaged  $171\pm17\%$ , and it had only a marginally significant positive correlation with  $SVL$  ( $r=0.38$ , one-tailed  $P=0.045$ ). This ratio was more than 100% in 17 of the 21 snakes that crawled across the gap and for which COM could be determined. Thus, the weight of the snake on the initial perch often may be sufficient to serve as a counterweight to prevent the snakes from pitching downward as they cantilever while crossing a gap.

## Discussion

### Limits to performance

To cantilever the body when crossing a gap, the snakes must prevent buckling of the body from the torque created by the

weight of the suspended portion of the body. The anatomical data can be used with estimates of the torque on the suspended portion of the snake to estimate the force and muscular stress required to prevent excessive ventral flexion of the vertebrae at the edge of the initial perch. Electromyographic studies of other colubroid snakes have found that both the multifidus (M) and semispinalis-spinalis (SSP-SP) muscles can dorsiflex the vertebral column (Jayne, 1988). The longest lever arm through which these muscles are likely to act is the dorso-ventral distance from the dorsal edge of the neural spine where they attach via a common tendon and the centrum of the vertebra (see scaling equation for vertebral height in Table 1). Assuming that all of the tendons of the SSP-SP can transmit tension longitudinally within the cable-like structure that they form, then the contractile tissue at remote longitudinal locations could contribute to the longitudinal forces that oppose ventral flexion of the vertebrae. A cross-section through a single location along the length of the snake only includes the contractile tissue from five adjacent SSP-SP segments, whereas the tendons contribute to a total longitudinal span of 29 vertebrae for a single SSP-SP segment (Fig. 3). Thus, multiplying the cross-sectional area of the SSP-SP from a single cross-section by a factor of 5.8 corrects for the potential contribution of contractile tissue not in that cross section, and the analogous correction factor for the multifidus cross-sectional area is 1.67.

The following example uses the assumptions above to illustrate the calculation of muscular stress for the longest snake, which had  $SVL=188$  cm and suspended 477 g (4.67 N) over the gap with its COM located 36 cm from the initial perch. The resulting torque of 1.67 N m divided by a vertebral height of 1.02 cm yields a longitudinal input force of 164 N. The areas of the SSP-SP and M on one side of a single cross section were 0.13 and  $0.17\text{ cm}^2$  (Fig. 3), respectively, and their combined area for the left and right sides (assuming bilateral activity) and corrected for segmental lengths was  $2.08\text{ cm}^2$ . Thus, the estimated stress on the SSP-SP+M for this individual was  $791\text{ kN m}^{-2}$ .

For the 21 snakes that crawled across the gap and for which muscle cross-sectional areas were measured, the average estimated stress of the SSP-SP+M was  $728\pm50\text{ kN m}^{-2}$ . The size-corrected values of maximal gap bridging distance were positively correlated with the estimates of muscle stress ( $r=0.55$ , one-tailed  $P=0.005$ ). Although the contractile physiology of the epaxial muscles of snakes is poorly known, *in vitro* measurements of the maximal isometric stress during tetanic contraction of fast twitch glycolytic limb muscles of lizards at  $30^\circ\text{C}$  are approximately  $200\text{ kN m}^{-2}$  (Marsh and Bennett, 1985; Marsh and Bennett, 1986).

The biologically unrealistic values of muscle stress estimated for the gap bridging of brown tree snakes could be the result of several possible reasons. First, if the input lever arm used to calculate the longitudinal input force is too short, then the estimate of input force and stress would be inflated. However, using the entire height of the vertebra seems likely to overestimate rather than underestimate the relevant lever

arm length. Second, if muscles besides the SSP-SP and M resist ventral flexion of the vertebrae, then the resulting underestimate of cross-sectional area would inflate the estimate of muscle stress. However, the only available EMG data suggest that the SSP-SP and M are the primary dorsiflexors of snakes (Jayne, 1988). Additionally, even if the LD and IL could contribute directly to the force needed to oppose ventral flexion, this would only increase the cumulative effective cross-sectional area by a factor of approximately 1.5, which is still too small to obtain a realistic value of muscle stress. Third, if the vertebrae were maximally flexed, then the ligaments and skeleton could bear the load without muscle activity. However, substantial ventral flexion was usually not apparent in the body of the snake at the edge of the initial perch (Figs 2, 5), and preliminary observations manipulating the body of intact, anaesthetized, relaxed brown tree snakes revealed that a 90° ventral arc can occur with only ten vertebrae. Fourth, if snakes moved continuously over the edge of the initial perch, then force production could be enhanced as a result of activating SSP-SP and M muscles as they lengthen, rather than only activating the muscle isometrically. However, many snakes were nearly stationary before they contacted the destination perch. Finally, perhaps the axial muscles could generate longitudinal compression, which might press the flat articulating surfaces of the vertebrae against each other in such a way that vertebral mobility is limited compared to that of a relaxed snake. Even if accounting for all of these factors reduced the estimate of muscle stress to one-third of that calculated from simplistic modeling, the resulting value would still suggest that this system may be performing near a physiological maximum.

Two observations besides the estimates of muscle stress suggest that supporting the weight during the gap bridging may be taxing the physiological capacity of the brown tree snakes. First, many snakes trembled noticeably during the final stages of bridging a gap. Second, the overall size (SVL) by itself accounted for a very large fraction (87%) of the variance observed in maximal gap distance, which suggests that the behavioral motivation of the snakes was not appreciably decreasing the predictive value of size and physiological capacity for this measure of whole animal performance.

Besides the body needing to be sufficiently rigid to prevent buckling, the snakes must balance the suspended portion of the body with the posterior portion of the body on the initial perch to prevent pitching down into the gap. The posterior part of the snake that is supported by the initial perch may often suffice to serve as a passive counterweight to balance the suspended portion of the snake. In four of the trials, however, the weight of the snake and its location on the initial perch were unlikely to create a sufficient counterweight. Some simple and widely performed behaviors such as passing the body beneath the side branches of a perch or wrapping the tail around the initial perch (Fig. 5) are active mechanisms by which snakes could generate additional vertical forces. Thus, bridging gaps can create the additional demands on the axial muscles of pushing up against

branches or gripping them in order to balance the snake from fore to aft.

The mechanical demands of static loading during the gap bridging of arboreal snakes seem severe and likely to present an interesting contrast to terrestrial limbed animals, for which supporting the weight under static conditions appears trivial compared to the loads that are encountered during high speed locomotion or jumping (Biewener, 2005; Dutto et al., 2004; Marsh, 1988; McGowan et al., 2005; Olson and Marsh, 1998; Weyand and Davis, 2005). The system of snakes bridging gaps is also intriguing for the very direct tradeoffs that may be present between the benefit of increasing the amount of muscle to generate sufficient force to support the body of the snake while balancing the cost of increasing the load from the weight of the snake that must be supported. The brown tree snakes increased epaxial muscle size appears to enhance gap-bridging performance since some of the residual values of muscle-cross-sectional areas were positively correlated with maximum gap distance. However, the interindividual variation in stoutness within brown tree snakes is small compared to that among different species. For example, for an ecologically and phylogenetically diverse assemblage of 21 neotropical snake species including boas, pit vipers and colubrids, the mass of snakes after correcting for length varies by more than twentyfold (Guyer and Donnelly, 1990).

All snakes are light for their length compared to limbed animals, but brown tree snakes are even lighter for their length compared to many species of snakes such as rattle snakes, semi-arboreal vipers and some colubrids (Rodda et al., 1999). However, some arboreal genera of snakes such as *Imantodes* and *Oxybelis* that are even more attenuate than *Boiga* have anterior tendons of the SSP-SP as long as 37 vertebrae (Jayne, 1982). If these arboreal snakes do indeed activate all of the SSP-SP muscles with anterior tendons that cross a joint in such a manner that prevents excessive sagging, this represents an interesting architecture in which serially homologous muscles may contribute to the effective cross-sectional area of muscles without increasing the bulk of the snake at a given longitudinal location.

Besides bridging gaps, *Boiga* use their anterior body to kill large prey by constricting them, which is unlike some of the most attenuate groups of arboreal snakes such as *Imantodes*, *Oxybelis* and *Ahaetulla*. In contrast to these very light-bodied arboreal groups of snakes, most snakes that constrict their prey have robust axial musculature and short tendons that may facilitate generating large longitudinally localized amounts of force and forming the tight coils needed during constriction (Jayne, 1982). Some of the features of axial morphology that enhance constriction also may facilitate gripping perches firmly. Different reliance on weight reduction and draping loosely across thin branches versus great strength and firmly gripping perches may partly explain the lack of uniform vertebral shape and other anatomical features of arboreal specialists (Johnson, 1955). Several constricting species of terrestrial and semi-arboreal snakes have cantilevering abilities that compare favorably with those with highly arboreal snakes

(Lillywhite et al., 2000). Perhaps some of the requirements for effective constriction and gripping have constrained the evolution of light weight to length, tendinous elongation in the axial muscles and the shape of vertebrae of *Boiga*.

When using lunging to bridge a gap, another important task is grasping the destination perch, and the brown tree snakes were very adept at doing this by forming a distinct ventral bend just posterior to the head. One unanticipated feature of the axial anatomy of the brown tree snakes was that the anterior IL had a much greater size than the other major epaxial muscles at 10% SVL. Unfortunately, the limited studies on the sizes of the epaxial muscles of snakes have not described longitudinal variation in muscle size, nor do they permit clear generalizations regarding differences between constricting and non-constricting snakes (Jayne, 1985; Lourdais et al., 2005; Ruben, 1977), but an electromyographic study found that the SSP-SP, LD and IL are all active during constriction (Moon, 2000). Perhaps the large anterior IL serves the dual function of increasing force during constriction as well as creating a strong hook-like structure that catches branches after spanning a gap.

#### *Evolution of gap bridging and gliding behaviors of snakes*

One of the most spectacular locomotor behaviors of arboreal snakes is that of snakes in the genus *Chrysopela*, which launch themselves from branches and either glide to the ground or land on other branches (Socha, 2002; Socha, 2006; Socha and LaBarbera, 2005; Socha et al., 2005). One puzzling feature regarding the evolution of this behavior is what circumstances might prompt an animal high in the canopy to propel itself from a supporting branch when it still does not have the ability to glide. The lunging behavior of the brown tree snakes crossing large gaps may be just such a circumstance. Using momentum can allow the snakes to bridge a gap that would probably not be possible if the snake only used a cantilevering behavior in which it was capable of briefly maintaining its balance in a static position. This switch in behavior is akin to human rock climbers using dynamic moves to reach a hand hold that would otherwise be impossible to reach (Long, 2004).

Although the trajectory of the head in some lunges of the brown tree snakes closely resembled a ballistic trajectory, lunges that failed to reach the destination perch usually had a sufficient grip on the initial perch so that the snake did not fall to the ground. Thus, brown tree snakes accrue the benefit of traversing a larger gap by performing a lunge, without an attendant risk of falling after a failed attempt. Another interesting functional and evolutionary transition is that point at which a snake may completely release its hold and use a ballistic trajectory of its entire body to cross a gap. Besides jumping from branches to initiate a glide (Socha, 2006), *Chrysopela* species jump across large horizontal gaps (J. J. Socha, personal communication), but they simply crawl across smaller gaps (B.C.J., personal observation). A rule of thumb for brown tree snakes may be to use lunges when the mass of the body needed to span a gap exceeds the mass of the body on the initial perch, and it would be very interesting to

determine if *Chrysopela* species perform jumps to cross horizontal gap under similar circumstances.

The lunge of the brown tree snakes resembles the generalized predatory and defensive striking behaviors of terrestrial snakes, which are initiated by forming a left and right lateral bend that are subsequently straightened. In contrast to the brown tree snakes, the most common jumping behavior of *Chrysopela* involves one major lateral bend of the snake. Although the loop formed by the body of *Chrysopela* prior to jumping is in a vertical plane, the loop is made by lateral flexion rather than dorso-ventral flexion (Socha, 2006). Thus, the motor pattern used by brown tree snakes seems unlikely to be novel, although the context in which it is being performed is novel, whereas *Chrysopela* appears to have evolved a novel motor pattern that is associated with its novel ballistic mode of locomotion. Although different in the details, the use of lateral flexion and straightening rather than dorso-ventral movements for propulsion during ballistic behaviors of both *Boiga* and *Chrysopela* may be a result of the need to maximize power by recruiting the large lateral flexor muscles (Fig. 3) and bending the vertebral column in a direction that can maximize the strain of these muscles.

*Chrysopela* and brown tree snakes must also counteract the tendency of the body to topple by rolling (rotating) about the long axis of the branch supporting the snakes as they suspend a large portion of the body in preparation for a jump or lunge. Prior to jumping, effectively all of the suspended portion of *Chrysopela* consistently forms a J-shaped loop that is below the perch, whereas the amount of the body of the brown tree snake prior to a lunge that was below the supporting perch was highly variable. Perhaps the laterally oriented branches on the perches that we used facilitated the ability of the brown tree snakes to avoid toppling over. In contrast to the posture used by the brown tree snakes in preparation for a lunge, during crawling across gaps the vast majority of the body, the COM and the path traveled by the head were all below the perch that was supporting the snake. Thus, in some circumstances, both *Chrysopela* and brown tree snakes appear to use body positions that enhance the stability for long axis rotation, and moving with the COM below a perch is a strategy that is used in other arboreal vertebrates such as sloths and brachiating primates.

#### *Integrating sensory information with motor control*

For an animal to traverse obstacles successfully, sensory information must be integrated with motor control. Thus, an arboreal snake encountering a gap between perches needs to detect sensory information indicating whether the gap is crossable given the snake's length and its physiological capacities. Most of the large body of research on the perception of actions that are possible in an environment (affordances) involves humans (Gibson, 1986). Some examples of the many affordances that humans can perceptually determine include the largest crossable gap in a locomotor path (Mark et al., 1999), what is reachable and what is not (Carelio et al., 1989), the smallest openings through which walking is possible

(Warren and Whang, 1987), and even visually perceiving stair heights that are that are energetically optimal (Warren, 1984). The limited data available on the affordances of non-human species suggest that several other phylogenetically diverse species, such as toads (Lock and Collett, 1979) and praying mantis (Iwasaki, 1991), are equally sensitive to critical animal–environment relations that limit possible actions. Thus, many of the affordances perceived by animals are more complex than simply the size of the animal relative to some dimension in the environment.

If an animal perceives that some obstacle is not crossable, then it simply may not initiate a movement or it may move away from an impassable obstacle, as toads do when confronted by a variety of gaps (Lock and Collett, 1979). The behavioral mode may also change for different types of crossable obstacles. For example, toads walk into and out of shallow gaps, whereas they hop across deeper gaps (Lock and Collett, 1979). When confronted by a gap that was uncrossable by only 2 cm, the brown tree snakes usually moved a considerable distance across the gap instead of refusing to move. However, we did not expose most of the snakes to a gap considerably larger than could be crossed.

When confronted with a gap in the locomotor surface, animals commonly perform a variety of exploratory behaviors such as head movements and visually scanning the gap (human) (Mark et al., 1999) or moving the legs and antennae in the gap (walking stick insects) (Blaesing and Cruse, 2004). Regardless of whether the intent of the brown tree snake is to explore or to initiate crossing, the initial movements of the snakes into the gap can provide additional sensory information about whether or not the gap is crossable. For brown tree snakes, the importance of visual information *versus* proprioceptive information for determining crossability is presently unknown. Large eyes in snakes are correlated with both nocturnal habits and arboreal habitats (Caprette, 2005). *Boiga* species have large eyes and are strongly nocturnal (Rodda et al., 1999), but their visual acuity may not be particularly high compared to some other snake species (Caprette, 2005). For the crawling behavior, brown tree snakes might simply extend their bodies horizontally until they are no longer able to do so, which would suggest a relatively greater influence of proprioceptive than visual information.

The need to integrate sensory information with motor control does not end once a snake detects a crossable gap. The head and anterior portions of the snake must be controlled precisely to contact the next perch, which is often a small target (41 mm diameter in our study). Under variable performance conditions such precise levels of control usually cannot be achieved without using sensory feedback. When moving with high speed and approaching a surface on which an animal intends to land (such as a perch) or with which the animal intends to collide (such as a prey), many species appear to exploit optical variables that specify time-to-contact with the surface and related variables that specify the severity of the impending contact with the surface (Lee and Reddish, 1981; Lee et al., 1991; Wagner, 1982). The time-derivative of

the optical variable *tau* (*tau-dot*), which is the ratio of the optical angle subtended by a surface or object to the rate of optical expansion of the surface or object, is an example of the latter kind of optical variable (Lee, 1976). Moving so that *tau-dot* is slightly greater than 0.5 ensures a ‘softer’ collision (i.e. colliding while decelerating) with the object or surface. Research on humans indicates that when running (Wann et al., 1993) or reaching (Hopkins et al., 2004) towards a target, the final deceleration phases of the movement that result in homing in on the target are controlled using a ‘*tau-dot* strategy’. Similarly, the head of rattlesnakes decelerates substantially before contacting the prey during a rapid predatory strike (Kardong and Bels, 1998). Somewhat unexpectedly, the head of the brown tree snake barely decelerated during some lunges, suggesting a sensory-control strategy different than a *tau-dot* strategy.

### Conclusions

In summary, for well over a 100-fold range of mass, the maximum distance of horizontal gaps bridged by brown tree snakes scaled with negative allometry, but snakes of all sizes were still able to cross gaps that were a large fraction (>40%) of their snout–vent length. The behaviors of lunging across the gap and/or wrapping the tail around the initial supporting perch were correlated with significantly greater size-corrected values of maximum gap bridging performance. When the snakes simply crawled across the gap slowly without a lunge, most of the suspended portion of the snake was below the supporting perch, which seems likely to enhance the stability of the snake. Even though the body of brown tree snakes is light per unit length, the torque resulting from the weight of the suspended portion of the snake was very large as a result of the large moment arm created by holding the body almost horizontally. Thus, unlike most terrestrial limbed animals, the mere act of supporting the weight of the snake seems likely to be taxing the physiological capacity of the epaxial muscles needed to prevent the body of the snake from buckling. The lunging behavior of brown tree snakes, during which the snake retains a hold on the initial perch, may be analogous to one of the key evolutionarily innovations involved in the evolution of the remarkable launching and gliding behaviors of snakes belonging to the genus *Chrysopelea*.

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