I, K. Marie Hoefer, hereby submit this original work as part of the requirements for the degree of Master of Science in Biological Sciences.

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The three-dimensional orientation of gaps has species-dependent effects on bridging performance and gap choice of arboreal snakes

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Abstract

Challenges for moving in arboreal environments include sizable gaps and complex three-dimensional orientations between the discrete destinations created by branches. Especially for elongate animals, different three-dimensional orientations change the mechanical demands of crossing gaps, but these effects on both the maximal gap distance (Gap$_{\text{max}}$) and the choice of destinations are poorly understood despite the large diversity of animals that regularly encounter these circumstances. We tested and compared the effects of three-dimensional gap orientation on the performance of three species of snakes with similar length but moderately stout (Boa constrictor), intermediate (Pantherophis guttatus) or slender (Boiga irregularis) shapes, and we tested for bias in choice of destinations for the latter two species. The effects of both gap orientation and species on Gap$_{\text{max}}$ were highly significant, and the rank order of species from greatest to least Gap$_{\text{max}}$ was often from the most slender to the stoutest species. Although the effects of yaw (horizontal) angles were statistically significant, they were small compared to those of pitch (vertical) angles, which created nearly two-fold variation in the performance within each species with the greatest values when snakes went straight down. Within a horizontal plane, P. guttatus and B. irregularis had similar preferences for choosing gaps with smaller yaw angles. However, when pitch angle was varied, P. guttatus preferred lower destinations, whereas B. irregularis preferred higher destinations. Thus, despite many consistent effects of gap orientation on the performance and torques acting on the animals, some behavioral preferences were species specific.
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Introduction

The gaps between branches, the three-dimensional complexity, and the discrete options for supporting surfaces are just a few of the many demands for animals that move in arboreal environments (Cartmill, ’85). The ability to cross gaps between branches can benefit animals by reducing the length and circuitousness of paths that are confined to branches (Temerin and Cant, ‘83), and the elongate bodies of snakes appear well-suited for reaching considerable distances across gaps. Many species of snakes move in trees (Lillywhite and Henderson, ‘93) where bridging gaps in different three-dimensional directions also seems likely to be ecologically relevant. However, no previous study of gap bridging by snakes (Jayne and Riley, 2007; Lillywhite et al., 2000; Lin et al., 2003; Mansfield and Jayne, 2011; Byrnes and Jayne, 2012) has simultaneously manipulated the three-dimensional orientation of gaps and studied different species with substantial variation in morphology. In addition, data are lacking regarding whether snakes or other animals have bias in the three-dimensional orientation of the gap they choose to cross, even though arboreal animals seem likely to often encounter such options.

Especially for elongate animals such as snakes, the three-dimensional orientation of the body can have profound effects on the mechanical demands of supporting the body as the animal reaches in different directions (Byrnes and Jayne, 2012). For example, the unsupported weight of the animal causes a torque ($\tau_{\text{bend}}$) that could make the body bend or buckle at the end of the supporting surface at the edge of the gap (Fig. 1). Even if the body of a snake can remain rigid as it crawls straight across a horizontal gap, the unsupported weight of the body produces a torque ($\tau_{\text{pitch}}$) that tends to pitch the unsupported anterior portion of the body downward and the posterior portion of the body upward similar to the motion of a see-saw (Fig. 1). In addition, if a
snake turns in a horizontal plane (yaw angle not equal to 0°), then the unsupported portion of the
snake will create a torque (τ\text{roll}) that tends to make the supported portion of the body roll about
the long axis of the supporting perch (Fig. 1A,C).

Variable orientations in a vertical plane (pitch angle) also affect the mechanical demands
of bridging a gap (Fig. 1). For example, a snake moving either straight up or straight down from
the edge of a supporting surface would not have a moment arm that would create a pitching
torque (Fig. 1B). However, potential difficulties of moving straight up are the work required to
lift the weight of the snake and the difficulty of maintaining balance for a situation analogous to
an inverted pendulum. By contrast, while spanning a gap directly below the edge of a supporting
surface, the unsupported weight of the snake should provide a passive, pendulum-like
mechanism for maintaining the body in the position needed to reach the destination. Thus, both
the pitch and yaw angles needed to reach a destination across a gap are important, but with only
one exception (Byrnes and Jayne, 2012), previous studies of gap bridging and cantilevering of
snakes have not manipulated pitch angles.

Although snakes are elongate for their weight compared to many other groups of animals,
different species of snakes vary substantially in their stoutness (Fig. 2), as well as in their axial
anatomy and degree of arboreality. Hence, we compared three species of snakes that readily
climb trees but also had a wide range of morphological variation. When the snout-vent lengths
of our three study species are similar, boa constrictors (Boa constrictor) are the heaviest and
have the shortest tails, corn snakes (Pantherophis guttatus) are intermediate, and brown
treesnakes (Boiga irregularis) are the lightest with the longest tails. Both weight and tail length
have approximately three to four-fold variation between these extreme species (Table 1). The
rank order of boa constrictors, corn snakes, and brown treesnakes also corresponds to having the shortest to longest lengths of semispinalis-spinalis muscle segments (15, 18 and 29 vertebrae, respectively), which are important dorsiflexors of the vertebrae (Jayne, ’88). Many different lineages of specialized arboreal snakes have convergently evolved a combination of attenuate body form, long tails, and long lengths of epaxial muscle segments (Guyer and Donnelly,’90; Lillywhite and Henderson, ‘93; Jayne, ’82; Pizzatto et al., 2007), which suggests that such morphology enhances locomotion on and between the complex three-dimensional networks of branches in trees.

We manipulated the yaw and pitch angles required to traverse a gap to test how these factors affected the maximal gap-bridging distances (Gap$_{max}$) of boa constrictors and corn snakes, and we compared the performance of our two study species with those published previously for the brown treesnake (Byrnes and Jayne, 2012). We expected that the combination of large $\tau_{\text{roll}}$ and $\tau_{\text{bend}}$ when the snakes make a right angle turn in a horizontal plane would cause a large decrease in Gap$_{max}$ compared to other three-dimensional orientations of gaps, and we expected that more attenuate species of snakes would have better gap-bridging performance than stouter species. We also tested whether corn snakes and brown treesnakes had any bias in choice when they encountered a pair of alternative destinations with different three-dimensional orientations across a gap. We expected the snakes to prefer crossing the gap with the three-dimensional orientation that allowed snakes to attain greater gap-bridging performance.
Materials and Methods

Experimental Subjects

We conducted experiments with boa constrictors (*Boa constrictor*), corn snakes (*Pantherophis guttatus*), and brown treesnakes (*Boiga irregularis*) that had snout-vent lengths (SVL) as similar as was practical to obtain (Table 1). The corn snakes were captive-bred individuals obtained from commercial suppliers, whereas the juvenile boa constrictors were born in captivity and raised in a laboratory at the University of Cincinnati (UC) where all of our experiments were conducted. The brown treesnakes used for testing gap-bridging performance by Byrnes and Jayne (2012) were captured in Guam where experiments were conducted, whereas the brown treesnakes that we used for choice tests were caught in Guam and shipped to UC for our experiments. All captive snakes were housed individually in a variety of cages with incandescent light bulbs that allowed them to behaviorally thermoregulate and attain daytime body temperatures from 25 - 33° C. We used juvenile boa constrictors, partly to better match the SVL of the other species and partly because juveniles of this species tend to be more arboreal than adults (Greene, ‘83).

To estimate the longitudinal distribution of mass in the snakes used for performance testing, we used an overdose of sodium pentobarbital to euthanize one boa constrictor (SVL = 84 cm, mass = 375 g) and one corn snake (SVL = 68 cm, mass = 141 g) which had similar overall sizes to the snakes used for testing performance. After determining the masses for increments of 10% SVL and for the tail, we converted these values to percentages of the total mass of the animal. After fixing the sections from these two snakes in 10% formalin, they were used to
quantify the cross-sectional areas of the major epaxial muscles at locations 10 and 50 %SVL posterior to the snout using methods similar to those of Jayne and Riley (2007).

General Experimental Procedures and Apparatus

Several aspects of procedures were used for both the performance tests and the choice experiments. All of the snakes were post-absorptive at the time of the experiments as they had been fed seven or more days prior to the experiment, and we did not use any snakes when their eyes were cloudy as a result of being in the early stages of ecdysis. Prior to an experiment, the snakes were placed in individual cloth bags within a chamber that was 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 similar to the field active body temperatures of these species (Brattstrom, ‘65). To avoid a confounding influence of time, the individuals of each species were split into two batches, and each batch experienced the treatments within an experiment in a different randomized order.

The testing area was 3.4 m X 3.4 m and 3.2 m high, and all four walls were covered with white cloth to provide a uniform visual background. The primary crawling surfaces were polyvinyl chloride (PVC) pipes that were 1 m long and 2.7 cm in diameter and covered with lengthwise strips of 5 cm wide Nashua 394 duct tape (Berry Plastics, Franklin, KY, USA) to provide uniform texture, as described by Astley and Jayne (2007). All of the cylinders were oriented so that their long axes were horizontal. As in Byrnes and Jayne (2012), each cylinder had two rows of pegs in which the individual pegs (3 cm long, 6.4 mm diameter) were perpendicular to the surface of the cylinder, oriented at a 45° angle relative to the horizontal and
located at each end of a 90° arc that was centered on the top of the cylinder. Beginning 1 cm from the end of the cylinder that was closest to the gap bridged by the snakes, the pegs were spaced at 5 cm intervals for a 50 cm portion of the length of each cylinder.

As in Byrnes and Jayne (2012), both of the angles used to describe the orientation of gaps were relative to the top center line (parallel to the long axis) of the cylinder initially supporting the snakes, and the vertex of each angle was the point at the top center location of the end of the initial cylinder that formed the edge of the gap. Yaw angles were in a horizontal plane, and a value of zero indicated a straight trajectory along the long axis of the initial supporting surface (Fig. 1D). Pitch angles were within a vertical plane containing the top center location of the ends of the cylinders that formed the edges of the gap. Positive and negative values of pitch indicated gap orientations that were uphill (Fig. 1B) and downhill, respectively, and values of zero indicated a trajectory within a horizontal plane (Fig. 1D).

**Gap-Bridging Performance and Associated Torques**

For a total of 11 treatments, we determined the maximum gap-bridging distance (Gap$_{\text{max}}$) for all 10 combinations of two yaw angles (0°, 90°) and five pitch angles (0°, ±45°, ±, 90°) and for one treatment with yaw and pitch angles of 45° and 0°, respectively. The lowest cylinder was always at least 1 m above the floor.

We used the following procedures to determine Gap$_{\text{max}}$ for each snake. If a snake successfully crossed a gap within three attempts, then we increased the gap distance by 5 cm and continued to test the snake until it had three unsuccessful attempts to cross a gap or refused to
attempt to cross a gap for five times. After a failure to cross a gap, we decreased the gap distance by 2.5 cm and retested the snake. After the snake had rested overnight, the next day we tested whether it could bridge a gap 2.5 cm greater than was bridged successfully on the preceding day. If the snake successfully bridged that gap distance, then the gap distance was increased by 2.5 cm until the snake had three failed attempts or had five refusals to cross the gap.

We videotaped the performance tests using one Sony DCR-HC42 and one Panasonic PV-GS320 camcorder. One overhead camera had a view that was perpendicular to a horizontal plane, and the other (side-view) camera simultaneously obtained a view that was perpendicular to the vertical plane containing the two points at the top center location of the ends of the cylinders that formed the edges of the gap.

We used Adobe Premiere Pro version 7 to create deinterlaced avi video files (60 images sec$^{-1}$) of the trial in which each snake attained $\text{Gap}_{\text{max}}$. For the digital video image just before the snake contacted the destination, we used MaxTRAQ version 2.2.4.2 (Innovision Systems, Inc., Columbiaville, MI, USA) to determine the two-dimensional coordinates in both views of marks along the mid-dorsal line of the midpoints of 10% SVL increments of the snake. To estimate the mass of each of these segments, we multiplied the total mass of the snake by the percentage of total mass in the homologous segment of the con-specific specimen that was used to determine the longitudinal distribution of mass. Whenever the most posterior part of the unsupported portion of the snake was a fraction of a 10%SVL segment, we corrected for mass and midpoint location based on the proportion of the length of this region compared to that of the complete 10%SVL segment that included this region. We then used all of the midpoint coordinates and masses of each unsupported segment to determine the location of the center of
mass (COM) and the weight of the unsupported portion of the snake as in Byrnes and Jayne (2012).

We followed the conventions and methods of Byrnes and Jayne (2012) for calculating estimates of three torques arising from the weight of the unsupported portion of the snake acting at its COM (Fig. 1A). All three moment arms (r) were in a horizontal plane and formed a right triangle in which \( r_{\text{roll}} \) and \( r_{\text{pitch}} \) were orthogonal components of \( r_{\text{bend}} \) (Fig. 1A). We used the coordinates from the overhead view to determine the length of \( r_{\text{roll}} \) and the coordinates from the side view to determine the lengths of \( r_{\text{pitch}} \) and \( r_{\text{bend}} \). The rolling (\( \tau_{\text{roll}} \)), pitching (\( \tau_{\text{pitch}} \)) and bending (\( \tau_{\text{bend}} \)) torques were the product of the weight of the unsupported potion of the snake times the length of the corresponding moment arm (Fig. 1A).

Choice Tests

For 14 *P. guttatus* and 16 *B. irregularis*, we performed choice tests to determine whether or not any preferences for a particular destination existed within 14 treatments that had pairs of destinations requiring different orientations to cross a gap. The initial supporting surface and the two destinations were cylinders and pegs with the same dimensions and materials as used in the performance tests. With only two exceptions, the gap distances of all of the treatments were 35 cm. For all choice tests, the investigator stood directly behind the end of the initial supporting surface farthest from the gap crossed by the snake.

Five treatments had all of the cylinders confined to a single horizontal plane (pitch = 0°) while yaw angles of the destination varied from 0° to 90°, and two of these five treatments had
ga  

gap distances of 20 and 40 cm for the pair of destinations. Four treatments had one destination 
that was straight ahead and in the same horizontal plane as the initial surface (pitch = 0°, yaw = 
0°) while the alternative destination within each pair had pitch angles varying from straight up 
(90°) to straight down (-90°). The remaining five treatments had different combinations of yaw 
and pitch angles while the gap distance was constant (35 cm).

For a given treatment, each snake within a batch performed three trials in rapid succession. 
After each trial all of the surfaces were cleaned with a paper towel dampened with 70% ethanol 
to reduce odors possibly left by the snakes. After each of the individuals within one batch had 
performed three trials, the tape covering the surfaces was replaced to reduce possible odors left 
by the snakes. When a treatment had destinations with different yaw angles, the left-right 
locations of the alternative destinations were switched before performing another three trials in 
rapid succession for each individual within a batch. Thus, each choice test treatment for each 
individual had six replicates.

We performed the preliminary experiments that were similar to Mansfield and Jayne 
(2011) to determine if odor possibly left by the snake crawling on a surface might create bias in 
the choice between a pair of destinations that were otherwise identical. The initial cylinder and 
the two destination cylinders were all in a horizontal plane. The two destinations were placed 
with a 45° yaw angle to the left and right of the initial surface upon which the snake was placed 
and with gap distances of 35 cm. Before the first trial, all individuals within one species were 
allowed to crawl once along the entire length of one of the destinations. As in the other choice 
tests, three trials were performed in rapid succession for each individual. If a snake contacted the 
destination without snake odor, then the tape covering this destination was replaced before the
next trial. The left-right position of the destinations with and without snake odor was switched before performing the remaining three trials per individual on the following day. Thus, during the course of these experiments, one destination was exposed to progressively greater amounts snake odor than the other destination. Although no significant bias in the choice of destinations was detected for the perches with different odor for either of the two study species, we took the previously-mentioned precautions against unintentional differences in olfactory cues.

Data Analysis

Prior to analyzing the data for the performance tests, we combined our data for *P. guttatus* and *B. constrictor* with those of Byrnes and Jayne (2012) for *B. irregularis*. To correct for the relatively minor differences in the lengths of different snakes, we standardized Gap$_{\text{max}}$ to %SVL or %TL (total length) before performing statistical analyses. We made both of these corrections for overall size because the relative lengths of the tails differ among these three species.

To test for treatment effects on performance and the estimates of torque, we used mixed-model ANOVAs, in which species was a fixed and crossed factor, individual was a random factor nested within species, and both yaw and pitch angles were fixed and crossed factors. We used three-way ANOVAs (factors: individual, species ($N = 3$) and yaw ($N = 3$)) to analyze the data for treatments with all three of the cylinders in a horizontal plane (yaw = 0°), whereas we used four-way ANOVAs (factors: individual, species ($N = 3$), yaw ($N = 2$) and pitch ($N = 5$)) for the data from the treatments with yaw angles of 0° and 90°.
To analyze data from the choice tests, we calculated the percentage of six trials in which one gap was chosen by each individual (Pref1). We subsequently used a two-tailed t-test to determine whether or not the mean value of Pref1 for each treatment and species differed significantly from 50%, which would be the value expected when the choice between a pair of destinations is random.

All mean values are reported ± SE, and we used $P<0.05$ as the criterion for significance for all statistical tests.

**Results**

**Morphology**

From anterior to posterior, the relative masses of the ten body segments and tail segment for *B. constrictor* were 3.7, 6.1, 9.4, 13.0, 13.1, 14.0, 13.5, 11.9, 8.8, 4.7 and 1.8%, and for *P. guttatus*, the corresponding values were 5.0, 7.8, 10.6, 11.3, 10.7, 13.6, 11.4, 11.0, 9.5, 6.4 and 2.5%, respectively. For a *B. irregularis* (SVL = 81 cm) used in Jayne and Riley (2007) and for Fig. 2, these percentages of total mass were 8.8, 5.8, 8.3, 9.4, 10.6, 11.3, 11.5, 10.0, 9.2, 8.5 and 6.7%, respectively. For *B. constrictor* the height, width, and thus mass of the snake at 50% SVL was much larger compared to that at 10% SVL, and this longitudinal disparity in size and weight was greater than that which occurred within the other two species (Fig. 2).

For all three species, the absolute cross-sectional areas of the major epaxial muscles were larger at 50% SVL compared to 10% SVL (Table 2; Fig. 2). The cross-sectional areas of homologous major epaxial muscles were greatest for *B. constrictor* and least for *B. irregularis*
Compared to a *B. irregularis* with similar SVL and at a similar longitudinal location, *B. constrictor* had cross-sectional areas of dorsiflexors (semispinalis-spinalis [SSP-SP] and multifidus [M]) that were approximately 4-8 times larger and the lateral flexors (longissimus dorsi [LD] and iliocostalis [IL]) were approximately 10-30 times larger (Table 2, columns 1,3). Compared to a *B. irregularis*, *P. guttatus* had cross-sectional areas of dorsiflexors and lateral flexors that were approximately 3-8 times larger (Table 2, columns 2,4).

The relative areas of homologous muscles were usually fairly similar at different longitudinal location within each species (Table 2). The relative areas of the SSP-SP, M, LD, and IL at a given longitudinal location within *B. irregularis* were fairly similar (Table 2; Fig. 2), whereas in *B. constrictor* and *P. guttatus* the areas of two most dorsal and medial muscles (SSP-SP, M) tended to be smaller relative to those of the two more ventral and lateral muscles (LD, IL).

**Performance and Torques**

For gaps oriented horizontally (pitch = 0°), yaw angle and its two-way interaction with species had highly significant effects on Gap$_{\text{max}}$ regardless of whether values were adjusted to SVL or total length (Table 3; Fig. 3). For gap orientations within a horizontal plane, the mean values of Gap$_{\text{max}}$ for the 90° yaw angle were less than those for the 0° for all three species (*B. constrictor* 37.9 ± 2.6 vs. 48.8 ± 1.6 %SVL; *P. guttatus* 46.8 ± 1.1 vs. 49.3 ± 1.1 %SVL; *B. irregularis* 45.2 ± 1.1 vs. 51.3% SVL). The decrease in performance associated the 90° yaw angle was substantially more for *B. constrictor* compared to the other two species.
For gap orientations with yaw angles of 0° or 90°, pitch, species, and all of the two-way interaction terms significantly affected performance (Table 4; Fig. 4). The greatest values of $\text{Gap}_{\text{max}}$ for all three species were for the gap orientations straight down and with a yaw angle of 90° (Fig. 4C) ($B. \text{constrictor}$ 60.1 ± 2.2 %SVL; $P. \text{guttatus}$ 82.5 ± 3.2 %SVL; $B. \text{irregularis}$ 96.5 ± 3.4 % SVL). For $B. \text{constrictor}$ and $P. \text{guttatus}$, the differences in performance for pitch angles ranging from -45° to 90° were small compared to $B. \text{irregularis}$, which had a substantial increase in performance when going straight up compared to gaps with pitch angles ranging from -45° to 45° (Fig. 4). Compared to the effect of yaw angle when pitch angle was constant, the effect of pitch angle when yaw was constant was large (Fig. 4).

For the horizontal gap orientations, yaw angle, species, and their two-way interaction terms all had highly significant effects on bending, pitching, and rolling torques (Table 3). For a given yaw angle, the rank order of species from largest to smallest mean torque was $B. \text{constrictor}$, $P. \text{guttatus}$, and $B. \text{irregularis}$ (Fig. 5). Although the bending torques of $P. \text{guttatus}$ and $B. \text{irregularis}$ changed minimally with yaw angle, $\tau_{\text{bend}}$ of $B. \text{constrictor}$ decreased substantially from the yaw angle of 45° to that of 90°, which was congruent with the smaller values of $\text{Gap}_{\text{max}}$ for this species at the 90° yaw angle within a horizontal plane. In fact, the length of the unsupported portion of $B. \text{constrictor}$ bridging the gap with the 90° yaw angle was so small that the rolling torque experienced under for this condition was less than that for the yaw angle of 45° (Fig. 5C).

Across all pitch angles, pitch angle, yaw angle, species, and all of their two-way interaction terms had significant effects on the bending, pitching, and rolling torques (Table 4). Overall, torques were usually greatest for $B. \text{constrictor}$ and least for $B. \text{irregularis}$ (Fig. 6). For
0° yaw, the values of $\tau_{\text{bend}}$ (Fig. 6A) and $\tau_{\text{pitch}}$ (Fig. 6B) were similar to each other for a given species and pitch angle, whereas for 90° yaw, the values of $\tau_{\text{bend}}$ (Fig. 6D) and $\tau_{\text{roll}}$ (Fig. 6F) for a given pitch angle and species were similar to each other. When substantial variation in torque occurred with different pitch angles (Fig. 6 A, B, D, F) the values of torques were nearly zero at the extreme values (-90° and 90°) of pitch angle.

**Gap Choice**

As shown in Table 5, the snakes frequently had a significant bias in choosing a particular gap within a pair as mean Pref1 was significant in 20 of the total of 28 combinations for 14 treatments and two species ($P. guttatus$ and $B. irregularis$). For pairs of gaps within a horizontal plane, both species of snakes strongly preferred to go straight or turn 45° rather than making a 90° turn (Table 5, rows 2-3). In addition, $B. irregularis$ also had a marginally significant preference for a gap with a straight orientation rather than one requiring a 45° turn. For a constant yaw angle (45°), both species preferred the shorter gap (20 cm) rather than the longer gap (40 cm), and the preference for a shorter gap (requiring a turn) apparently can override the preference for going straight (Table 5, row 4).

Of the treatments manipulating pitch angle, four treatments (Table 5, rows 6 - 9) had one destination that was straight ahead while the alternative destination had variable pitch angle while yaw was 0°. Whenever $B. irregularis$ had a significant preference in these four treatments, it was for the destination that was uphill relative to the other, whereas whenever $P. guttatus$ had a preference within these same treatments, it was for the destination that was downhill relative to the alternative. Similarly, for the remaining treatments (Table 5, rows 10 - 14), whenever $B.$
irregularis had a significant preference it was for the destination that was higher, whereas the one significant preference of *P. guttatus* was for the destination that was lower than the alternative.

**Discussion**

**Performance**

The heaviest of the three species we studied, *B. constrictor*, often had the smallest values of $Gap_{max}$, whereas the most slender species, *B. irregularis*, often had the best performance (Fig. 3; Fig. 4). However, when gaps were straight ahead and in a horizontal plane, the performance of our three study species was nearly identical. Another study of the cantilevering ability of snakes (yaw = 0°, pitch = 0°) also found minimal variation in performance (expressed as a proportion of snake length) among 26 non-aquatic species with highly variable ratios of weight relative to length (Lillywhite et al, 2000). Even if different animals have geometrically similar shapes, one would expect the ratio of mass to length to increase with increased length because mass increases as a cubic function of length. However, if either a stouter snake species or a larger individual within a single species is substantially stronger than a more slender or shorter snake, then this could be one mechanism to compensate for demands arising from increased weight when bridging a gap. Thus, accounting for length, weight and the cross-sectional area of the relevant muscles may help explain some of the differences in performance, or lack thereof, among different species.
In caenophidian snakes, the SSP-SP and M have bilateral activity during sidewinding when dorsiflexion of the vertebrae occurs (Jayne '88b); hence, they also seem likely to oppose ventral bending of the body of a snake at the edge of a gap. *B. constrictor* belongs to the henophidian lineage of snakes, which has a dorso-medial tendon that forms a somewhat diffuse but direct connection with the dorsal edge of the neural spines of the vertebrae (Gasc, ’74) rather than forming an indirect attachment via the ventral head of the SSP-SP as in the caenophidian species in our study (*B. irregularis* and *P. guttatus*) (Jayne, ’88a; Jayne and Riley, 2007). Based on their anatomical locations in *B. constrictor*, the SSP-SP and M and perhaps the LD may function as a dorsiflexors, but available electromyographic data for henophidian snakes have not involved behaviors with significant dorsiflexion (Gasc et al., ‘89).

Several slender arboreal caenophidian species have convergently evolved longer anterior tendons of the SSP-SP than those of terrestrial species (24-37 vs. 15-20 vertebrae), and thus the total lengths of the SSP-SP muscle segments (usually 30-45 vertebrae) in these species are often much longer (Jayne, ’82). By contrast, henophidians have more uniformly short (2-7 vertebrae) anterior tendons and total lengths of the SSP-SP segments (10-16 vertebrae) (Jayne, ’82), even though some species that are highly arboreal are very slender compared to their terrestrial relatives (Pizzatto et al, 2007). If the tension of the all tendons and all the contractile tissue crossing a single joint can oppose bending at that joint, then the tendinous elongation of axial muscle segments could increase the amount of contractile tissue that resists bending at a single joint without increasing the cross-sectional area of muscle at a single longitudinal location. For example, a single cross-section of *B. irregularis* only has contractile tissue from five adjacent SSP-SP segments, whereas the tendons of one segment contribute to a total longitudinal span of 29. Consequently, multiplying the cross-sectional area of the SSP-SP from a single cross-section
by a factor of 5.8 (= total span/contractile tissue length) corrects for the possible contribution of contractile tissue that is not in a single cross section (Jayne and Riley, 2007).

Bridging gaps in a horizontal plane usually caused the greatest torques acting on the unsupported portion of the snake (Fig. 6), which often approximated 40-50%SVL in these circumstances. Consequently, the cross-sectional areas of the dorsiflexor muscles at 50% SVL can provide an estimate of the relevant amount of contractile tissue to prevent buckling of the body at the edge of a gap. If one simply calculates a ratio of the combined areas of the SSP-SP and M (Table 2) relative to the mass of the snake, the resulting values for *B. irregularis*, *P. guttatus* and *B. constrictor* are 0.087, 0.086 and 0.079 mm$^2$ g$^{-1}$, respectively. If the LD is included for *B. constrictor*, then this value increases to 0.244 mm$^2$ g$^{-1}$. If one makes a correction for the total spans of the muscle segments crossing the joint of interest, then *B. irregularis*, *P. guttatus* and *B. constrictor* have values of 0.34, 0.29 and 0.41 mm$^2$ g$^{-1}$, respectively. If the LD is included for *B. constrictor*, then the value is 0.58 mm$^2$ g$^{-1}$. Thus, despite the *B. constrictor*, *P. guttatus*, and *B. irregularis* in our study having ratios of weight of approximately 4:2:1, the effective cross-sectional areas of muscle likely to support the body may nearly be sufficient to compensate for these large disparities in weight.

Tendon is very stiff compared to contractile tissue; hence, the cross-sectional area of tendon required to resist a deformation resulting from a given load is very small compared the corresponding amount required for contractile tissue. Consequently, an axial muscle segment of given length can be lighter if a greater portion of it length is tendon (Jayne, '82). Thus, although in some circumstances large cross-sectional areas of muscle may compensate for the greater bending torques encountered by heavier snakes while bridging gaps in certain directions, heavy-
bodied species may be at a disadvantage for crawling on slender branches that would probably bend excessively from the weight of the animal (Lillywhite and Henderson, ‘93). Many of the B. irregularis captured by BCJ in Guam moved in natural vegetation with apparent ease while their entire weight was only supported on several leaf stems with diameters approximating 2-3 mm.

Scaling relationships of muscle cross-sectional areas and gap-bridging performance have only been quantified for B. irregularis (Jayne and Riley, 2007). The scaling exponents of mass (3.42) and cross sectional areas of the SSP-SP, M, LD and IL (range = 2.46-2.68) have a positive allometry, whereas that of Gap\textsubscript{max} (0.82) has a negative allometry with the SVL of B. irregularis. Similar to the negative allometry of performance described for B. irregularis, Lillywhite et. al, (2000) found that juvenile Pantherophis obsoletus (SVL not specified) had significantly greater values than adults for cantilevering performance when expressed as a proportion of snake length. For the mean values of SVL of the P. guttatus (79.5 cm), B. constrictor (86.7 cm) and B. irregularis (96.0 cm) that we used to determine performance, the scaling equation for B. irregularis predicts values of Gap\textsubscript{max} of 47.9, 47.1 and 46.3 %SVL, respectively. Consequently, the relatively minor differences in SVL in our study species seem unlikely to be a significant confounding factor for our comparisons among species.

Compared to B. constrictor, both P. guttatus and B. irregularis had greater relative areas of the two muscles (SSP-SP and M) most likely to be dorsiflexors (Table 2). Whether this reflects an important functional difference or is mainly a result of belonging to different evolutionary lineages is not clear because of the current lack of relevant comparative anatomical and functional data for caenophidian and henophidian snakes. Electromyographic studies would be extremely useful for resolving which of these muscles are most important for supporting the
body and how many adjacent serial homologues have synchronous activity and thus contribute to the effective muscle cross-sectional area.

Given the predicted reduction in all of the torques acting on the unsupported portion of snakes bridging gaps with a pitch angle of 90° (Fig. 1B), the lack of substantially greater performance than when pitch was 0° for \textit{P. guttatus} and \textit{B. constrictor} (Fig. 4) was unexpected. Perhaps this difference among species reflects a behavioral difference rather than different biomechanical constraints in these species.

Unlike \textit{B. constrictor} and \textit{P. guttatus}, \textit{B. irregularis} can support its entire weight with only a fraction of the length of its prehensile tail, whereas we never observed an ability of either \textit{B. constrictor} or \textit{P. guttatus} to support their weight with their tails. Gripping a branch is one mechanism for preventing rolling and pitching (Cartmill, ’85; Byrnes and Jayne, 2012), and a greater capacity to grip with the tail may partly explain why \textit{B. irregularis} had better performance than the other species when the yaw angle was 90° and rolling torques were large (Fig. 4C; Fig. 6F). Another difference between \textit{B irregularis} and the other two species is that it occasionally lunges to bridge a gap, and this ballistic movement used to negotiate the final several cm of a gap avoids the larger moment arm and greater weight associated with holding a posture just before contacting the destination via slowly crawling across a gap (Jayne and Riley, 2007; Byrnes and Jayne, 2012).
Gap choice

The discrete destinations created by branches in arboreal environments make an excellent system for testing the importance of environmental structure and sensory information for influencing where animals go. A non-random choice between alternatives is sufficient to demonstrate that an animal perceives some difference, whereas random choice between alternatives could result either from an inability to perceive a difference or from a lack of response to a perceived difference. The two species of snakes in our study (*P. guttatus* and *B. irregularis*) both had several treatments in which they had a highly significant preference for one of the alternative destinations requiring them to cross gaps with different three-dimensional orientations.

Although comparative data on choosing arboreal destinations are limited, available data do indicate that at least some squamate reptiles can use visual cues to select between alternative destinations. For example, when fleeing from an investigator, arboreal anole lizards in laboratory experiments and in the field usually have a strong bias for selecting the surface that maximizes running speed, as is the case for cylinders with larger diameter (Mattingly and Jayne, 2005; Jones and Jayne, 2012). Unlike their effect on the speed of lizard locomotion, cylindrical surfaces with large diameters reduce the maximal locomotor speeds of snakes (Jayne and Astley, 2007; Jayne and Herrmann, 2011). However, North American rat snakes (*Pantherophis obsoletus* and *P. guttatus*) often prefer destinations on the far side of a gap that are wider, presumably because they create a large target that is easier to land on after crossing a gap (Mansfield and Jayne, 2011). In addition, when the size and shape of the destinations is constant, rat snakes have a strong bias for selecting the shorter gap (Mansfield and Jayne, 2011).
Thus, many of the choices made by the animals in these previous studies are consistent with choosing a destination that enhances some aspect of locomotor performance or increases the ease of accomplishing a task.

Several preferences of the *P. guttatus* and *B. irregularis* in our study for different gap orientations in a horizontal plane were also consistent with selecting a destination requiring less effort as straighter gap orientations were correlated with increased gap-bridging performance. Choosing to cross a gap to a destination with a smaller yaw angle also reduces the tendency to roll about the long axis of the supporting surface. One caveat in our results was that a shorter gap distance in a horizontal plane can override the preference for going straight, which is similar to a finding of Mansfield and Jayne (2011). Moving along the line formed by the initial location of an animal and the location of an averse stimulus also maximizes that rate at which an animal can increase the distance between itself and the averse, stationary stimulus (Howland, ‘74). Indeed, a wide diversity of animals employ the tactic of moving more or less straight away from the location of a threat (Webb, ’86; Irschick and Jayne, ’99; Mattingly and Jayne, 2005).

The preferences of *P. guttatus* for gaps with pitch angles of -45° and -90° rather than 0° also correspond well to preferring destinations requiring less effort as implied by the greater values of performance and lower values of bending and pitching torque for these gap orientations. Similarly, two of the six cases in which *B. irregularis* preferred a gap with a higher pitch angle involved gap orientations with greater performance and lower values of torque.

Some other preferences of *P. guttatus* and *B. irregularis* involving different pitch angles differed from the trend of crossing the gap that was likely the easier of the two alternatives as suggested by the measures of performance. For example, for a given gap distance, the torques
acting on a snake should be the same for uphill and downhill pitch angles with the same magnitude, but *P. guttatus* preferred the gap with a pitch angle of -45° rather than 45°. Although these two situations should have similar torques, the downhill orientation may be somewhat easier from a pendulum-like mechanism that could enhance side-to-side stability. Preference of stability rather than lower energetic cost of locomotion also appears to account for changes in gait dynamics when humans walk on a steep surface (Hunter et al., 2010). However, some of the significant preferences of *B. irregularis* that were for gaps with higher values of pitch angle were unexpectedly for orientations in which performance was lower and maintaining stability would seem to be more problematic (Table 5, rows 12 and 14). Perhaps some of these different tendencies of *P. guttatus* and *B. irregularis* to go down or up without an obvious attendant biomechanical benefit simply reflect different behavioral tactics that are best suited for evading the threats that are most often encountered in their natural habitats.

The strength of some preferences of anoles for choosing different running surfaces diminishes as the ratio of performance between the two alternative surfaces decreases (Jones and Jayne, 2012). Similarly, some of the differences in performance for bridging gaps in different orientations may be trivial compared to a difference that may be required to elicit a significant preference.

Overall we observed a wide variety of significant effects of three-dimensional gap orientations on both gap-bridging performance and behavioral preferences, many of which conformed to expectations based on the varying biomechanical demands imposed by our different treatments. However, some of the species-dependent effects also emphasize the importance and utility of obtaining comparative data and accounting for the influence behavior
when attempting to understand how environment variation affects the form and function of organisms.
Literature Cited


## Table 1. Sizes of snakes used in different experiments.

<table>
<thead>
<tr>
<th>Species</th>
<th>Experiment</th>
<th>N</th>
<th>SVL (cm)</th>
<th>Tail length (cm)</th>
<th>Mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>B. constrictor</em></td>
<td>performance</td>
<td>8</td>
<td>86.7 ± 0.4 (84.5 – 88.0)</td>
<td>10.8 ± 0.3 (9.5 – 11.5)</td>
<td>379 ± 6 (345 – 399)</td>
</tr>
<tr>
<td><em>P. guttatus</em></td>
<td>performance</td>
<td>8</td>
<td>79.5 ± 0.6 (77.0 – 82.0)</td>
<td>14.4 ± 0.5 (12.0 – 16.0)</td>
<td>151 ± 6 (124 – 177)</td>
</tr>
<tr>
<td><em>B. irregularis</em> ¹</td>
<td>performance</td>
<td>10</td>
<td>96.0 ± 1.1 (90.0 – 102)</td>
<td>26.8 ± 0.3 (25.0 – 28.5)</td>
<td>86 ± 4 (70 – 110)</td>
</tr>
<tr>
<td><em>P. guttatus</em></td>
<td>choice</td>
<td>14</td>
<td>96.0 ± 0.7 (93.0 – 100)</td>
<td>17.7 ± 0.6 (13.0 – 21.0)</td>
<td>312 ± 9 (263 – 368)</td>
</tr>
<tr>
<td><em>B. irregularis</em> ¹</td>
<td>choice</td>
<td>16</td>
<td>109.4 ± 1.3 (100.5 – 118.0)</td>
<td>29.1 ± 0.6 (24.5 – 34.0)</td>
<td>175 ± 6 (140 – 203)</td>
</tr>
</tbody>
</table>

Below each mean, the values in parentheses are ranges. ¹ from Byrnes and Jayne (2012).
Table 2. Cross-sectional areas of major epaxial muscles of the three study species.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>B. constrictor</th>
<th>P. guttatus</th>
<th>B. irregularis¹</th>
<th>B. irregularis¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>SVL (cm)</td>
<td>84</td>
<td>68</td>
<td>84</td>
<td>68</td>
</tr>
<tr>
<td>Mass (g)</td>
<td>375</td>
<td>141</td>
<td>67</td>
<td>33</td>
</tr>
<tr>
<td>10% SVL SSP-SP mm²</td>
<td>5.6 (14%)</td>
<td>3.2 (32%)</td>
<td>0.67 (25%)</td>
<td>0.38 (25%)</td>
</tr>
<tr>
<td>10% SVL M mm²</td>
<td>2.7 (7%)</td>
<td>1.4 (13%)</td>
<td>0.60 (23%)</td>
<td>0.33 (22%)</td>
</tr>
<tr>
<td>10% SVL LD mm²</td>
<td>16.0 (40%)</td>
<td>1.7 (17%)</td>
<td>0.53 (20%)</td>
<td>0.30 (20%)</td>
</tr>
<tr>
<td>10% SVL IL mm²</td>
<td>16.0 (40%)</td>
<td>4.0 (39%)</td>
<td>0.85 (31%)</td>
<td>0.50 (33%)</td>
</tr>
<tr>
<td>50% SVL SSP-SP mm²</td>
<td>10 (16%)</td>
<td>3.7 (19%)</td>
<td>1.6 (27%)</td>
<td>0.93 (29%)</td>
</tr>
<tr>
<td>50% SVL M mm²</td>
<td>4.8 (8%)</td>
<td>2.4 (13%)</td>
<td>1.3 (24%)</td>
<td>0.73 (23%)</td>
</tr>
<tr>
<td>50% SVL LD mm²</td>
<td>30.9 (50%)</td>
<td>6.3 (33%)</td>
<td>1.3 (24%)</td>
<td>0.75 (23%)</td>
</tr>
<tr>
<td>50% SVL IL mm²</td>
<td>16.4 (27%)</td>
<td>6.7 (35%)</td>
<td>1.4 (25%)</td>
<td>0.79 (25%)</td>
</tr>
</tbody>
</table>

¹ Values are from the scaling equations in Jayne and Riley (2007). Abbreviations: SVL, snout-vent length; SSP-SP, semispinalis-spinalis muscle; M, multifidus muscle; LD, longissimus dorsi muscle; IL, iliocostalis muscle. The areas of each muscle relative to the total area of the SSP-SP, M, LD and IL are in parentheses.
Table 3. *F*-values from three-way mixed model ANOVAs testing the effects of yaw angle and species on the performance and torques for snakes crossing maximal gap distances in a horizontal plane.

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>ANOVA effects</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Yaw (Y)</td>
<td>Species (S)</td>
</tr>
<tr>
<td></td>
<td>(DF = 2,46)</td>
<td>(DF = 2,23)</td>
</tr>
<tr>
<td>Gapₘₐₓ (%SVL)</td>
<td>23.7**</td>
<td>1.7</td>
</tr>
<tr>
<td>Gapₘₐₓ (%TL)</td>
<td>22.8**</td>
<td>3.3</td>
</tr>
<tr>
<td>τₜₜₑₙᵈ</td>
<td>40.8**</td>
<td>33.8**</td>
</tr>
<tr>
<td>τₚᵢᶜʰ</td>
<td>166.5**</td>
<td>43.1**</td>
</tr>
<tr>
<td>τₗₒᵣᵱ</td>
<td>142.2**</td>
<td>15.0**</td>
</tr>
</tbody>
</table>

Abbreviations: Gapₘₐₓ, maximum gap distance crossed; %SVL, %snout-vent length; %TL, %total length; τₜₑₙᵈ, bending torque; τₚᵢᶜʰ, pitching torque; τₗₒᵣᵱ, rolling torque. 

** P<0.001
Table 4. *F*-values from four-way mixed model ANOVAs testing the effects of yaw angle, pitch angle, and species on the performance and torques for snakes crossing maximal gap distances with 0° or 90° yaw angles.

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>ANOVA effects</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pitch (P) (DF = 4,92)</td>
</tr>
<tr>
<td>Gap_{max} (%SVL)</td>
<td>132.6**</td>
</tr>
<tr>
<td>Gap_{max} (%TL)</td>
<td>133.9**</td>
</tr>
<tr>
<td>τ_{bend}</td>
<td>87.4**</td>
</tr>
<tr>
<td>τ_{pitch}</td>
<td>44.8**</td>
</tr>
<tr>
<td>τ_{roll}</td>
<td>40.0**</td>
</tr>
</tbody>
</table>

Abbreviations are as in Table 3. *P*<0.05; **P*<0.001
Table 5. Effects of gap orientation on gap choice.

<table>
<thead>
<tr>
<th>Gap Pitch; Yaw (distance in cm)</th>
<th>Mean Pref1 ($P$)</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P. guttatus ($N = 14$)</td>
<td>B. irregularis ($N = 16$)</td>
<td></td>
</tr>
<tr>
<td>0°;0° (35)</td>
<td>57 ± 8% (0.388)</td>
<td>61 ± 5% (0.016)</td>
<td></td>
</tr>
<tr>
<td>0°;0° (35)</td>
<td>77 ± 6% (&lt;0.001)</td>
<td>75 ± 5% (&lt;0.001)</td>
<td></td>
</tr>
<tr>
<td>0°;45° (35)</td>
<td>70 ± 5% (&lt;0.001)</td>
<td>72 ± 5% (&lt;0.001)</td>
<td></td>
</tr>
<tr>
<td>0°;90° (20)</td>
<td>77 ± 6% (&lt;0.001)</td>
<td>63 ± 5% (0.027)</td>
<td></td>
</tr>
<tr>
<td>0°;45° (20)</td>
<td>99 ± 1% (&lt;0.001)</td>
<td>81 ± 4% (&lt;0.001)</td>
<td></td>
</tr>
<tr>
<td>0°;0° (35)</td>
<td>92 ± 3% (&lt;0.001)</td>
<td>19 ± 6% (&lt;0.001)</td>
<td></td>
</tr>
<tr>
<td>0°;0° (35)</td>
<td>40 ± 8% (0.263)</td>
<td>20 ± 6% (&lt;0.001)</td>
<td></td>
</tr>
<tr>
<td>0°;0° (35)</td>
<td>21 ± 8% (&lt;0.001)</td>
<td>61 ± 7% (0.132)</td>
<td></td>
</tr>
<tr>
<td>0°;0° (35)</td>
<td>17 ± 6% (&lt;0.001)</td>
<td>70 ± 7% (0.011)</td>
<td></td>
</tr>
<tr>
<td>45°;0° (35)</td>
<td>32 ± 7% (0.025)</td>
<td>80 ± 6% (&lt;0.001)</td>
<td></td>
</tr>
<tr>
<td>90°;0 (35)</td>
<td>44 ± 9% (0.507)</td>
<td>75 ± 7% (&lt;0.001)</td>
<td></td>
</tr>
<tr>
<td>45°;0° (35)</td>
<td>50 ± 10% (1)</td>
<td>55 ± 8% (0.513)</td>
<td></td>
</tr>
<tr>
<td>45°;0° (35)</td>
<td>46 ± 9% (0.687)</td>
<td>65 ± 6% (0.027)</td>
<td></td>
</tr>
<tr>
<td>-45°;0° (35)</td>
<td>46 ± 10% (0.712)</td>
<td>75 ± 8% (0.003)</td>
<td></td>
</tr>
</tbody>
</table>

Pref1, percentage of trials in which gap 1 was chosen. The $P$-values are from two-tailed t-tests comparing Pref1 to 50%.
Fig. 1

A
Pitch = 0°
Yaw = 45°

B
Pitch = 90°
Yaw = 0°

C
Pitch = 0°
Yaw = 90°

D
Pitch = 0°
Yaw = 0°
Fig. 3
Fig. 5

A

\[ \tau_{\text{bend}} (N \cdot m) \]

\[ \tau_{\text{pitch}} (N \cdot m) \]

\[ \tau_{\text{roll}} (N \cdot m) \]

B

C

\( Yaw \ angle \ (\text{degrees}) \)

\[ 0 \quad 45 \quad 90 \]
Fig. 6

(A) 0° yaw
(B) Pitch angle (degrees)

(C) 0° yaw
(D) 90° yaw

(E) Pitch angle (degrees)

(F) 90° yaw


t_{\text{yaw}}(N \cdot m)

\begin{itemize}
\item B.c.
\item P.g.
\item B.i.
\end{itemize}