RESEARCH ARTICLE

The effects of three-dimensional gap orientation on bridging performance and behavior of brown tree snakes (*Boiga irregularis*)

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SUMMARY

Traversing gaps with different orientations within arboreal environments has ecological relevance and mechanical consequences for animals. For example, the orientation of the animal while crossing gaps determines whether the torques acting on the body tend to cause it to pitch or roll from the supporting perch or fail as a result of localized bending. The elongate bodies of snakes seem well suited for crossing gaps, but a long unsupported portion of the body can create large torques that make gap bridging demanding. We tested whether the three-dimensional orientation of substrates across a gap affected the performance and behavior of an arboreal snake (*Boiga irregularis*). The snakes crossed gaps 65% larger for vertical than for horizontal trajectories and 13% greater for straight trajectories than for those with a 90 deg turn within the horizontal plane. Our results suggest that failure due to the inability to keep the body rigid at the edge of the gap may be the primary constraint on performance for gaps with a large horizontal component. In addition, the decreased performance when the destination perch was oriented at an angle to the long axis of the initial perch was probably a result of the inability of snakes to maintain balance due to the large rolling torque. For some very large gaps the snakes enhanced their performance by using rapid lunges to cross otherwise impassable gaps. Perhaps such dynamic movements preceded the aerial behavior observed in other species of arboreal snakes.

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INTRODUCTION

Arboreal habitats are characterized by a discontinuous matrix of cylindrical supports with varying orientations and diameters, and to forage or evade predators in trees, animals often must move on these narrow supports as well as cross the open spaces between them. An important benefit of having the ability to cross gaps within the crown of a single tree or between adjacent tree crowns is the avoidance of the longer and more circuitous routes that are necessary when uncrossable gaps are present (Temerin and Cant, 1983; Thorpe et al., 2009).

Two major strategies for crossing gaps are leaping and reaching, and their use depends on the gap distance and the behavior and morphology of the animal. To cross large gaps, legged animals commonly leap (Demes et al., 1995; Channon et al., 2011) and gliding can greatly enhance the distance traveled between different branches and trees (McGuire and Dudley, 2005; Byrnes et al., 2008). However, as body size increases, some animals such as primates tend to rely less on leaping and more on reaching to cross gaps (Fleagle and Mittermeier, 1980; Cannon and Leighton, 1994; Thorpe et al., 2009). Many phylogenetically diverse species of snakes are arboreal, and they rely mainly on extending their bodies to reach across gaps (Lillywhite et al., 2000; Lin et al., 2003; Jayne and Riley, 2007), although the combination of leaping and gliding of snakes in the genus *Chrysopelea* provides a spectacular exception (Socha, 2006). Compared with limbed animals, the bodies of all snakes are greatly elongated, and within snakes many arboreal specialists have independently evolved a more attenuate body shape

than their non-arboreal relatives (Lillywhite and Henderson, 1993; Pizzatto et al., 2007). Such elongate bodies appear especially well suited for reaching across gaps and crawling on fine terminal branches without breaking them. Despite the complex three-dimensional structure of arboreal habitats, all previous data for snakes bridging gaps are for destinations confined to the horizontal plane (Lillywhite et al., 2000; Lin et al., 2003; Jayne and Riley, 2007; Mansfield and Jayne, 2011) even though this type of gap represents only a tiny subset of all of the gap orientations that occur in nature.

Crossing gaps by cantilevering poses many physical challenges, and the three-dimensional trajectory traveled across a gap has profound effects on the nature of the associated mechanical demands. Similar to a cantilevered beam, a snake moving straight across a horizontal gap must withstand a large torque at the point of support (Fig. 1A). This torque, τ, equals $m\boldsymbol{g}r$, where m is the mass of the unsupported portion of the snake, $\boldsymbol{g}$ is gravitational acceleration, and r is the length of the moment arm from the center of mass (COM) of the unsupported portion of the animal to the edge of the gap. Increasing the distance of horizontal gaps creates the dual challenges of increasing the amount of unsupported mass as well as increasing the length of the moment arm, which results in a quadratic increase in torque with increased gap distance. To prevent this torque (resulting from gravity acting at the COM) from causing failure by localized bending at the edge of the gap, the axial muscles of some snakes may be operating near their limit for generating isometric force while the snake is crossing large horizontal gaps (Jayne and

A
0 deg pitch
0 deg yaw

Side view

B
90 deg pitch
0 deg yaw

Side view

C
0 deg pitch
90 deg yaw

End-on view

D
0 deg pitch
45 deg yaw

r_{pitch}

r_{roll}

Roll τ_{roll}

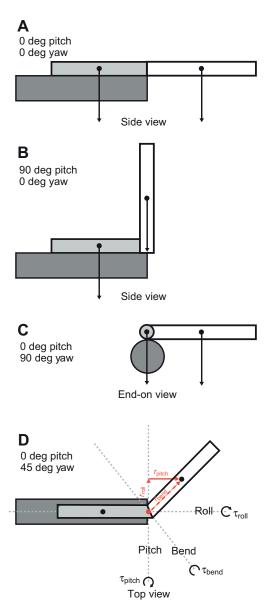Pitch   Bend

τ_{bend}

τ_{pitch}
Top view

Fig. 1. Schematic representations of the effects of bridging gaps with different three-dimensional orientations. The supporting surface is dark gray, and the supported and unsupported portions of the cylindrically shaped snake are light gray and white, respectively. The arrows indicate the forces arising from the weight of these regions acting at their center of mass (COM). (A) 0 deg yaw and 0 deg pitch orientation. Snakes will experience negligible rolling torque (τ_{roll}), but pitching torque (τ_{pitch}) and bending torque (τ_{bend}) will be large because the COM of the unsupported region is far from the supporting surface. (B) 0 deg yaw and 90 deg pitch orientation. The COM of the unsupported region is directly above the support; therefore, τ_{pitch}, τ_{roll} and τ_{bend} should be negligible. (C) 90 deg yaw and 0 deg pitch orientation. The COM of the unsupported body is far from the supporting surface and should cause high values of τ_{roll} and τ_{bend}, but τ_{pitch} should be negligible. (D) Schematic representation of the moment arms and torques acting on a snake as it crosses a gap with 0 deg pitch and 45 deg yaw. *r* is the length of the moment arm from the COM of the unsupported portion of the animal to the edge of the gap.

Riley, 2007). Even if a body is perfectly rigid, another problem could arise when the torque resulting from the unsupported body exceeds that of the supported body. At this point the unsupported portion of the body would pitch in a downward direction, lifting the supported body off the substrate. However, in reality, snakes counter this tendency by producing a counter-torque by gripping or placing a portion of the body or tail beneath the supporting surface (Jayne and Riley, 2007).

Although the effects of these torques are absent when an elongate body moves straight up (pitch=90 deg) at the edge of a gap (Fig. 1B), an animal must perform work to lift the COM of the unsupported body against gravity. Furthermore, if the COM of the raised portion of the body deviates from a position directly above the perch during upward movement, then the high COM could increase the tendency to topple, but this too could be countered by some active mechanism such as grasping the supporting perch (Cartmill, 1985). By contrast, an orientation straight down should be easy to maintain by a passive mechanism similar to a pendulum returning to its lowest position. If a snake must make a right-angle turn (yaw=90 deg) within the horizontal plane (pitch=0 deg) while crossing a gap, the unsupported portion of the body will create a large a torque that could cause long-axis rotation (roll) of the supported portion of the body off the perch (Fig. 1C). An added difficulty when making large yaw turns is that the body on the supporting perch is poorly positioned to counterbalance this roll-inducing torque and maintain balance because there is effectively no moment arm between its COM and the edge of the gap (Fig. 1C).

We quantified the effects of different three-dimensional gap orientations on the bridging performance of the brown tree snake, *Boiga irregularis*. Our study species has derived features of its axial anatomy that resemble many other highly specialized arboreal snakes (Jayne, 1982), and its capacities to climb and reach have probably contributed greatly to the difficulty of preventing its spread and reducing its economic impact where it was accidentally introduced (Rodda et al., 1999). To test whether the three-dimensional orientation affected the distance that snakes could traverse across a gap, we manipulated the yaw and pitch angles of a gap by varying the location of a destination across a gap. We expected the largest gap distance to be for orientations that required the snake to move straight down (pitch=–90 deg, yaw=0 deg). We expected the lowest performance for gap orientations in the horizontal plane (pitch=0 deg) because torques are maximized for a given gap distance. Although a right-angle turn within a horizontal plane (pitch=0 deg, yaw=90 deg) eliminates the pitching torque, the combination of large bending and rolling torques seems likely to result in the poorest gap-bridging performance. Understanding the limits to the performance of brown tree snakes crossing gaps can inform applied and conservation biology efforts to reduce the negative impacts of this invasive species.

MATERIALS AND METHODS
Experimental subjects

We used 10 brown tree snakes, *B. irregularis* (Merrem 1802) captured in Guam, and we conducted all experiments within 3 weeks of their capture. Similar to other specialized arboreal snakes, the brown tree snakes are relatively light for their length, have proportionately long tails and have exceptionally long tendons for the most dorsal and medial epaxial muscle, which probably has an important role in supporting the suspended portion of the body (Jayne and Riley, 2007). The animals were housed individually in 19 l containers in a temperature-controlled (~27°C) room with a 12 h:12 h light:dark cycle during the course of the experiments. The snakes had similar snout–vent length (SVL, mean 95.4 cm, range 90–102 cm), total length (TL, mean 121.9 cm, range 115–130.5 cm) and mass (mean 83.4 g, range 70–110 g). To provide landmarks on the bodies of the snakes, we painted white marks on the snakes at

intervals of ~10% SVL. The care and experimental procedures were approved by the Institutional Animal Care and Use Committee at the University of Cincinnati (protocol no. 07-01-08-01).

Experimental protocol

All experiments were conducted in an open-air garage within the Guam National Wildlife Refuge, near Dededo, GU, USA. We kept the animals in their individual containers in the shade of the garage until they equilibrated to ambient temperatures, which averaged 30.0±1.3°C during the experiments. The experimental apparatus consisted of two horizontal PVC pipes (28 mm diameter). We covered the pipes with length-wise strips of 5 cm wide duct tape (Nashua 394, Franklin, KY, USA) in order to provide a rougher texture and higher coefficient of friction than the underlying PVC pipe. Each of the pipes serving as perches had two length-wise rows of wooden pegs (25 mm length, 4 mm diameter) placed at 5 cm intervals and inclined ~45 deg relative to the horizontal. To simulate some of the diversity of the three-dimensional gap orientations occurring in natural vegetation, we placed the two perches in a total of 11 orientations such that the angle of the vector between the top center location at their ends nearest the gap varied in both the pitch (vertical) and the yaw (horizontal) planes. For each of two yaw angles (0 and 90 deg) we used five pitch angles (–90, –45, 0, 45 and 90 deg), and the remaining orientation had pitch=0 deg and yaw=45 deg. The initial perch was 1.5 m above the ground for all treatments other than those with a 90 deg pitch angle, for which the height was 1.2 m. To minimize possible confounding effects of time and experience, the 11 treatments were presented in different randomized order for each of two groups of five snakes.

Gap distance was measured as the three-dimensional distance from the top center of the supporting perch to the top center of the destination perch. The initial gap distance presented to snakes was ~50% SVL. If the animal successfully crossed a gap within three attempts, we then increased the gap distance by 5 cm until the gap could no longer be crossed. Once a snake had either three failed attempts or five refusals to cross a given distance, the gap distance was reduced by 2.5 cm and the snake was retested. The resulting maximum gap distance that was crossed (Gap$_{max}$) was converted to percentage SVL.

Anatomical measurements

At the conclusion of the experiments, experimental subjects were killed with an overdose of sodium pentobarbital. Before preservation, we measured the SVL, tail length and total body mass of the intact snake. We then cut the body and tail into 10 and two pieces, respectively, at the locations of the painted marks. The lengths (±5 mm) and masses (±0.1 g) of these sections were used to estimate the location of the center of mass along the unsupported length of the snake (COM$_{gap}$) as previously described (Jayne and Riley, 2007).

Kinematics and torque

We recorded dorsal and lateral views of each trial at 30 frames s^{-1} using two synchronized digital video cameras (Panasonic PV-GS320, Secaucus, NJ, USA; Sony DCR-HC42, New York, NY, USA). We used Adobe Premiere Pro v7 (Adobe Systems, San Jose, CA, USA) to create AVI files, which were subsequently imported into MaxTRAQ 2D v2.19 software (Innovision Systems, Columbiaville, MI, USA) for kinematic analysis. The three-dimensional coordinates were based on measurements within the two orthogonal camera views. A linear calibration was used in the two orthogonal camera views. Both the x- and y-axes were within the vertical plane containing the straight-line trajectory between the ends of the two perches, with the x-axis parallel to the long axis of the supporting perch and the y-axis oriented vertically. The z-axis was oriented perpendicular to the vertical plane containing the x- and y-axes such that +z followed the right-hand rule.

Two potential sources of error for the coordinates that were used to calculate the positions and moment arm lengths involved in estimating torques are image distortions from the optics of our cameras and digitizing errors. To estimate the magnitude of these errors, we videotaped a 1×1 m square grid (similar to the area containing the images of the snakes bridging gaps) that was centered within the field of view with an object-to-camera distance (3 m) and total image size (154×115 cm) similar to those used in our experiments. The grid had lines every 10 cm, which was similar to the distance between the successive landmarks along the length of the snake that were used for the calculations of torque. From the resulting digital video image, we digitized the vertical and horizontal coordinates of all 121 points where the lines forming the grid intersected. We then calculated all of the 220 vertical and horizontal distances between successive vertical and horizontal coordinates of these points, respectively. The resulting measurements from the video image were all within 4% of the actual distances within the grid.

To describe the trajectory of the head, the path of the snout was digitized at 1 Hz throughout the suspended phase of gap crossing. To describe the lunges that were occasionally used to complete gap crossing, we digitized the lateral-view coordinates of each painted landmark along the unsupported length of the body in each field of deinterlaced images (60 Hz) during these movements. To minimize the effect of digitizing errors on subsequent kinematic variables, we filtered these coordinates with a low-pass Butterworth filter with a cutoff frequency of 10 Hz in Matlab v7.4 (The Mathworks Inc., Natick, MA, USA).

We used two variables to describe the unsupported portion of the snake for each gap orientation just prior to touching the destination perch. To determine the length of the unsupported body of the snake extending into the gap (l_{gap}), we totaled the lengths of the body segments between the painted landmarks, and we estimated the length of the most posterior, incomplete segment as the three-dimensional distance between the most anterior point of support and the unsupported painted landmark closest to the origin. This method of estimation introduces little error to the calculated l_{gap} because the length of only the single incomplete segment nearest the perch is estimated. For example, in the extreme case in which an entire 10 cm segment makes a 90 deg arc, the actual segment length and estimated segment length will differ by only ~1 cm (1% SVL). To determine the extent to which the unsupported portion of the snake exceeded the straight-line distance between the two perches (l_{excess}), we divided l_{gap} by maximum gap distance and expressed this as a percentage.

We used a total of 11 variables to describe the kinematics of lunges primarily for a point on the snout at the following three times: (1) the start of the lunge, (2) the highest point and (3) the end of the lunge just prior to the head or body of the snake making first contact with the destination on the far side of the gap (Fig. 2). Three variables describing the initial position were: the horizontal (x_1) and vertical (y_1) distances from the snout to the top-center edge of the destination and the angle of a vector from the origin of the coordinate system to the snout relative to the straight-line trajectory from the edge of the supporting perch to the destination (θ_1). Positive values of y_1 indicate that the snout was initially above the destination perch. Two changes in vertical displacement described the height gained during the lunge (Δy_{2-1}) and the vertical drop from the crest
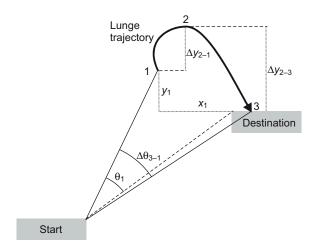
Fig. 2. Methods used to quantify the kinematics of lunging. The gray rectangles represent the starting and destination surfaces, and the thick curved arrow indicates the trajectory of the snout. Locations 1, 2 and 3 are at the start of the lunge, the greatest height of the snout and just prior to initial contact with the destination, respectively. The height and horizontal distance from the snout to the top edge of the destination at the beginning of the lunge are y_1 and x_1, respectively. The height gained from the start to the highest point of the trajectory and the vertical drop from the highest point to the first contact with the destination are Δy_{2-1} and Δy_{2-3}, respectively. The angle between a vector from the edge of the supporting surface to the snout and the straight-line trajectory between the top edges of the starting and destination perches is θ_1, and $\Delta\theta_{3-1}$ is the change in this angle from the beginning to the end of the lunge.

of the trajectory to the destination (Δy_{2-3}). The distance between the origin and the position of the snout at the crest of the trajectory equaled the radius (R) of an arc that would be followed if the snake fell passively from this point as a rigid pendulum. Five additional variables described the movement of the animal during each lunge. From the beginning to the end of the lunge, two additional variables quantified the changes in the angle θ ($\Delta\theta_{3-1}$) and in the anatomical length (Δl_{gap}) of the body that extended beyond the edge of the perch. Finally, the peak velocity of the snout along the x ($v_{x,max}$) and y ($v_{y,max}$) axes, as well as the peak resultant velocity ($v_{r,max}$) were calculated by dividing the difference between successive positions from the filtered data by the intervening time interval (0.017s).

For the last image prior to contact with the destination perch, the midpoint between each of the painted landmarks, which we assumed to be the segment COM, was digitized in the two camera views. From the position of these points and the known segment masses, we estimated the three-dimensional location of the overall COM of the suspended portion of the snake (COM$_{gap}$). We then calculated three relevant torques resulting from gravity acting at COM$_{gap}$ (Fig. 1D): (1) the torque about the long axis of the perch causing the tendency to roll off the perch (τ_{roll}), (2) the torque about the axis orthogonal to the long axis of the perch in the horizontal plane causing the unsupported body to pitch downward at the edge of the gap (τ_{pitch}), and (3) the torque causing the body to bend (flex ventrally) at the edge of the gap (τ_{bend}). Although the moment arm for τ_{bend} is the resultant of the moment arms for the other two torques (Fig. 1D), it is functionally important as it acts about an axis perpendicular to the axis of the unsupported body (Fig. 1D) and must be overcome by muscles acting to keep the body rigid at the edge of the gap. For cases in which snakes lunged, we calculated these three torques both in the last image prior to contact and the first

frame prior to the start of the lunge. We confined our analysis to torques about the first point of support because it was not possible to measure the forces necessary to understand how the complex gripping behavior of the supported portion of the body opposed the torques generated by gravity acting on the unsupported body.

To determine whether the snake fell passively after reaching the vertical peak of the trajectory during lunges, we compared the observed kinematics with the prediction from a model of passive motion of an inverted pendulum (Hibbeler, 2007). We assumed the snake to be a slender rigid rod of uniform density rotating about its end such that $I=1/3mR^2$ where I is the moment of inertia, m is the mass of the unsupported region of the snake and R is the straight line distance between the origin and the snout at the crest of the lunge. The equation used to describe the angular acceleration of the snout is therefore:

$$\dot{\omega} = (3g\sin\theta)/2R, \qquad (1)$$

and Eqn 2:

$$\dot{\omega}d\theta = \omega d\omega, \qquad (2)$$

is the differential relationship between $\dot{\omega}$, ω and θ, where θ is the angle with respect to the vertical, $\dot{\omega}$ is the angular acceleration, ω is the angular velocity and g is the acceleration due to gravity. We solved these equations numerically using the modified Euler method at discrete time points with a time resolution that was four times our imaging frequency to determine position and linear velocity at each time point corresponding to the measured kinematic data for each lunge.

Statistical analysis

For all of the trials with yaw angles of 0 and 90 deg, we analyzed each variable for the maximum gap crossed for each individual using a three-way mixed-model ANOVA, in which yaw angle ($N=2$) and pitch angle ($N=5$) were fixed, crossed factors and individual ($N=10$) was a random, crossed factor. For data from the 0 deg pitch treatments we performed a two-way mixed-model ANOVA in which yaw angle ($N=3$) was a fixed, crossed factor and individual ($N=10$) was a random, crossed factor.

We used two-sample t-tests to compare the kinematics of all the lunges (successful and unsuccessful) that occurred for pitch angles of 45 and –45 deg, using no more than three values per pitch angle per gap distance per individual. To examine the effects of lunging behaviors on the torques associated with crossing gaps, the torques were compared immediately prior to and following each successful S-shaped lunge at Gap$_{max}$ ($N=9$) using paired t-tests. We also used paired t-tests to compare the velocity along each axis predicted by the model of the passive pendulum to the actual velocity just prior to contact with the destination perch for lunges with 45 deg pitch ($N=7$).

All statistics were performed using the Statistics Toolbox in Matlab v7.4 (Mathworks, Natick, MA, USA), and $P<0.05$ was used as the criterion for significance. All mean values are given ±s.e.m.

RESULTS
Gap-bridging performance

All of the snakes successfully crossed gaps with all combinations of pitch and yaw angles, but these factors significantly affected the values of Gap$_{max}$ (Fig. 3A), which ranged from 38 to 115% SVL. For gaps within a horizontal plane (pitch=0 deg), the mean values of Gap$_{max}$ for yaw angles of 0, 45 and 90 deg were 51.3±1.3, 47.4±0.9 and 45.2±1.1% SVL, respectively, and this decrease with increased yaw angle was highly significant ($F_{2,18}=15.3$; $P<0.001$).
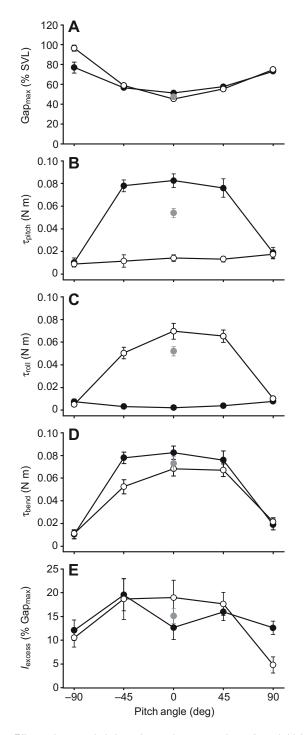
Fig. 3. Effects of yaw and pitch angles on the mean values of gap-bridging performance and the associated variables. (A) Maximum gap distance (Gap_{max}), (B) τ_{pitch}, (C) τ_{roll} and (D) τ_{bend}. (E) Length of the unsupported portion of the body in excess of the straight-line distance between the edges of the supporting and destination surfaces (l_{excess}). Black, gray and white symbols represent data for trajectories with 0, 45 and 90 deg yaw angles, respectively. The 45 deg yaw angle was only used with 0 deg pitch. Error bars show ±s.e.m.

Table 1. Effects (from ANOVA) of gap orientation on gap-bridging performance and associated variables

	Yaw angle	Pitch angle	Yaw × pitch
Variable	(d.f.=1, 9)	(d.f.=4, 36)	(d.f.=4, 36)
Gap_{max}	8.1 (0.019)	67.2 (<0.001)	10.7 (<0.001)
τ_{bend}	19.5 (0.002)	118.1 (<0.001)	6.3 (<0.001)
τ_{pitch}	109.7 (<0.001)	33.7 (<0.001)	33.0 (<0.001)
τ_{roll}	103.0 (<0.001)	43.2 (<0.001)	67.1 (<0.001)
l_{excess}	0.06 (0.51)	4.7 (0.004)	2.3 (0.08)

Values are F (P).
Gap_{max}, maximum gap distance crossed (% snout–vent length, SVL); τ_{bend}, bending torque; τ_{pitch}, pitching torque; τ_{roll}, rolling torque; l_{excess}, body length (% Gap_{max}) exceeding that which was required to cross the gap.
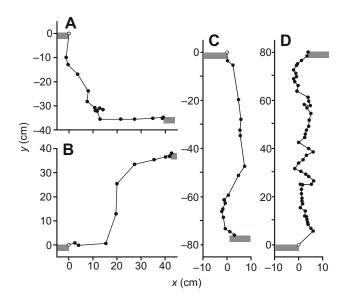
both yaw angles, gap-bridging performance increased with increasing magnitude of both positive and negative pitch angles and was least for the orientations with 0 deg pitch (Fig. 3A). For example, the greatest mean value of Gap_{max} was for –90 deg pitch and 90 deg yaw (96.5±3.1% SVL), and the mean values of Gap_{max} were also large for –90 deg pitch and 0 deg yaw (77.0±5.5% SVL) and 90 deg pitch at both 0 deg (73.2±1.4% SVL) and 90 deg yaw (74.8±2.0% SVL). Thus, for the 90 deg yaw the gap-bridging performance going vertically downhill was more than twice as large as for the horizontal orientation, and the values of performance for the three remaining vertical orientations were ~50% greater than for their respective horizontal orientation. Perhaps the most impressive trial was the one in which a snake successfully crossed a gap vertically upward that was 82% SVL, during which slightly more than 90% SVL was unsupported just before reaching the destination (see supplementary material Movie 1).

Gap-bridging behaviors
In 90% of the 110 trials with the maximum gap distance, the snakes simply crawled across the gap by continually extending the anterior body across the gap. In these situations the head of the snake commonly followed a trajectory that deviated substantially from the most direct route (Fig. 4). However, in the remaining 10% of trials the snakes used dynamic lunging behaviors to complete crossing the gap after initially crawling much of the distance towards the destination and then briefly stopping (Fig. 5; see supplementary material Movie 2). In every trial, regardless of gap orientation or lunging behavior, all snakes used their tail to grip or wrap the perch to overcome the tendency to pitch downward into the gap.

The snakes had two distinct types of lunging behavior (Fig. 5). When the destination perch was elevated or horizontal, the unsupported portion of the snake nearest the supporting perch was flexed dorsally, whereas the portion of the snake nearest the destination perch was flexed ventrally (S-shaped) (Fig. 5A). When the destination perch was below the supporting perch, the unsupported portion of the snake nearest the supporting perch was flexed ventrally, whereas the portion of the snake nearest the destination perch was flexed dorsally (inverted S-shaped) (Fig. 5B). For both types of lunge, the suspended portion of the body was nearly confined to a vertical plane with little or no discernable lateral flexion (Fig. 5).

Six of the 10 snakes lunged at least once, and five of these individuals had at least one successful lunge. Collectively, we observed a total of 23 lunges, of which 11 were successful and 12 were unsuccessful. All of the successful lunges occurred at Gap_{max}, whereas all of the unsuccessful lunges occurred at gap distances 2.5–5 cm greater than Gap_{max}. Both of the lunges at the 0 deg pitch

For the 10 combinations of the five pitch angles and the 0 and 90 deg yaw angles, the values of Gap_{max} were significantly affected by the main effects of the pitch and yaw angles of the gap orientation as well as their two-way interaction term (Table 1). For
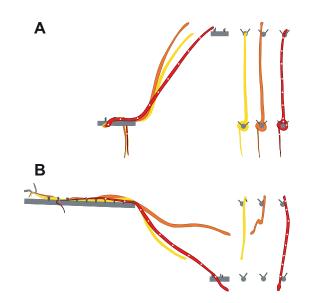
Fig. 4. Lateral views of paths traveled by the head of the snake in the plane of movement for different pitch angles with 0 deg yaw in representative trials. (A) –45 deg pitch, (B) 45 deg pitch, (C) –90 deg pitch and (D) 90 deg pitch. The white symbols indicate the initial position of the head. The time between successive points is 1 s. The path of the head deviated considerably from a straight-line trajectory, and the movement of the head often slowed just before contacting the destination.

Fig. 5. Body position during two types of lunges in lateral (left) and posterior (right) views. (A) An upward S-shaped lunge for a gap with 0 deg yaw, 45 deg pitch. (B) A downward inverted S-shaped lunge for a gap with 0 deg yaw and –45 deg pitch. The yellow, orange and red silhouettes depict the start, highest point and end of the lunge, respectively. Note the near absence of lateral flexion during the lunges and the extent to which the head is momentarily higher than the destination. For the last image within each panel the white dots denote intervals of 10% snout–vent length (SVL).

angle were successful. Only one of the seven lunges (14%) at the –45 deg pitch angle was successful, whereas 7 of the 13 lunges (54%) at the 45 deg pitch angle were successful. For all of the unsuccessful lunges nearly equal proportions were off target as a result of errors in lateral position (54%) or lack of sufficient distance (46%).

Torque
The orientation of the gap significantly affected all of the estimated torques (Fig. 3B–D). For increased yaw angles in the horizontal plane, τ_{bend} ($F_{2,18}=6.3$; $P=0.008$) and τ_{pitch} ($F_{2,18}=71.6$; $P<0.001$) decreased significantly and τ_{roll} increased significantly ($F_{2,18}=83.8$; $P<0.001$). For the 10 combinations of pitch and yaw angle, both of these main effects and their interaction term significantly affected τ_{bend}, τ_{pitch} and τ_{roll} (Table 1). In all cases, the values of τ_{bend} were by far the smallest for vertical orientations (both +90 and –90 deg pitch) (Fig. 3D). Similar to τ_{bend}, the values of τ_{pitch}, for 0 deg yaw and τ_{roll} for 90 deg yaw were extremely small for both vertical orientations (±90 deg pitch) and very large for the pitch angles ranging from –45 to 45 deg (Fig. 3B,C). By contrast, the values of τ_{pitch} for 90 deg yaw and τ_{roll} for 0 deg yaw were extremely small and varied little for the entire range of pitch angles, which was reflected in the highly significant pitch × yaw interaction term for both of these variables (Table 1). The greatest mean values of τ_{bend}, τ_{pitch} and τ_{roll} all occurred with horizontal orientations (Fig. 3B–D).

For the subset of all trials with a successful S-shaped lunge at the maximum gap distance ($N=9$), the values of τ_{bend} just prior to contact with the destination perch (post-lunge) were significantly greater than those immediately prior to the lunge (pre-lunge) (paired $t_8=-11.95$; $P<0.001$; Fig. 6A). In addition, the post-lunge values of τ_{bend} were significantly greater than those for the remaining trials ($N=21$) of the same orientations that did not involve lunging behavior (two-sample $t_{28}=-3.3$; $P=0.001$; Fig. 6B).

Kinematics
In addition to the head not traveling along a straight line (Fig. 4), the unsupported portion of the snake was substantially longer than the straight-line distance of Gap_{max}, but the amount of this discrepancy (l_{excess}) changed significantly with the pitch angle of the gap (Table 1; Fig. 3E). The mean value of l_{excess} for the gap vertically up with a 90 deg yaw angle was 4.8% Gap_{max}, whereas for the other three vertical trajectories this variable ranged from 10.5 to 12.6% Gap_{max} (Fig. 3E). The remaining values of l_{excess} for pitch angles from –45 to 45 deg were between 12.6 and 19.5% Gap_{max} (Fig. 3E).

For both types of lunges the paths traveled by different points along the length of the snake depended on their longitudinal location. The location of the body at the edge of the supporting perch at the beginning of a lunge and locations immediately posterior to this more or less followed a similar path towards the destination, as the body on the supporting perch often had ~10 cm of translational movement along the length of the supporting perch (Fig. 7; Table 2, Δl/gap). However, the unsupported portion of the body also had rotational motion within the vertical plane containing the gap, resulting in curved paths for each kinematic marker, and thus the head of the snake traveled farther than the more posterior locations that were closer to the pivotal point for the rotational movements (Fig. 7). Regardless of the gap orientation, the initial rotational movement was opposite to a subsequent rotational movement that ultimately allowed the snake to bridge the gap (Figs 5, 7). Additional details of our kinematic analysis of lunges focused primarily on the most distal point (snout) of the snake (Fig. 8).

Eight of the 11 variables describing the kinematics of lunges differed significantly between upward S-shaped and downward inverted S-shaped lunges (Table 2). Neither the initial horizontal
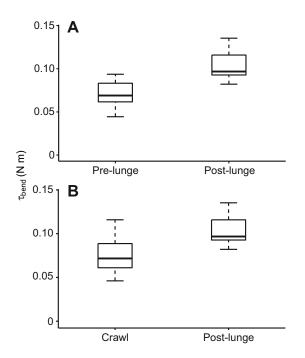
Fig. 6. Comparisons of τ_{bend} for S-shaped lunges. (A) Mean τ_{bend} just prior to lunge initiation (pre-lunge) and just prior to contact with destination perch (post-lunge) for successful lunges across all gaps with both 0 and 90 deg yaw and 0 and 45 deg pitch (N=9). (B) Comparison of τ_{bend} for all non-lunging (crawl, N=21) and lunging (post-lunge, N=9) trials with both 0 and 90 deg yaw and 0 and 45 deg pitch. The boxplots show mean and the quartiles. Whiskers show minimum and maximum.

Fig. 7. Paths traveled by different longitudinal locations along the snake during the two types of lunges. (A) An upward S-shaped lunge for a gap with 90 deg yaw and 45 deg pitch. (B) A downward inverted S-shaped lunge for a gap with 0 deg yaw and −45 deg pitch. The white symbols indicate the positions at the start of the lunge, and the different colors are for the snout and intervals equal to 10% SVL. Note that the different longitudinal locations followed different paths. The portion of the body on the starting perch had substantial translational motion, and the anterior, unsupported portion of the snake had substantial rotational movement. The sample rate for these data was 60 Hz.

(x_1) nor the initial vertical (y_1) distances between the snout and the destination perch differed significantly between these two types of lunges (Table 2), which usually began with the head more than 10 cm from the destination perch. The mean value of y_1 for upward lunges was small as a result of the head of the snake being slightly below or of very similar height relative to that of the destination, whereas the mean value of y_1 for the downward lunges was small as a result of a wide range of negative and positive values (−16.4 to 11.4 cm), indicating starting positions substantially below and above the perch, respectively. The mean values of relative body angle at lunge initiation (θ_1) differed significantly as a result of the snout usually being below or above the straight-line trajectory to the destination for the upward and downward lunges, respectively (Table 2). The change in the height of the head relative to the destination was significantly greater for the downward lunges than for the upward lunges for both the upward (Δy_{2-1}) and downward (Δy_{2-3}) portions of the trajectory (Fig. 7; Table 2). Consequently, significantly greater vertical and resultant maximal velocities occurred for the downward lunges. The initial radius for the downward pivoting motion was significantly greater for the upward than for the downward lunges (Table 2). None of the 11 kinematic variables differed significantly between successful and unsuccessful upward lunges.

DISCUSSION
Limits to gap-bridging performance
Understanding the effects of environmental variation on performance can lead to insights into what factors limit performance in a variety of taxa and locomotor tasks (Altshuler and Dudley, 2003; Byrnes and Jayne, 2010; Channon et al., 2011; Daley and Biewener, 2003). Two common and important features of arboreal habitats are the
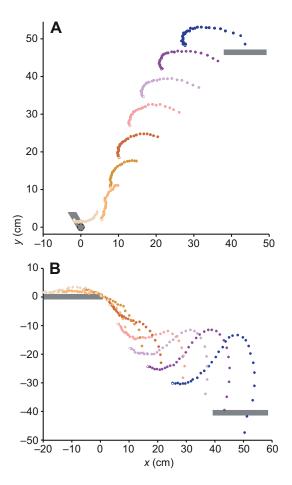
gaps between solid surfaces and the highly variable three-dimensional trajectories that may be required to move or reach from one location to another. Therefore, crossing such gaps by extending unsupported portions of the body is paramount to an arboreal lifestyle for both locomotion and resource acquisition. The performance of these tasks in different directions, whilst seemingly simple, has a profound potential to alter the relevant mechanical demands, but data on this topic remain quite limited despite how commonly this may occur for arboreal animals. For example, some arboreal primates use reaching to cross up to 50% of the gaps they encounter in the environment (Cannon and Leighton, 1994). Sometimes animals must also suspend their bodies across space to reach food located on the fine terminal branches of trees, and, similar to gap bridging, the orientation of reaching should alter the mechanical demands, thus affecting performance. For example, feeding squirrels are able to reach food a greater distance from a support perch in a vertical than in a horizontal direction (Ando et al., 1985), likely as a result of the increased torques associated with horizontal reaching.

Table 2. Mean values and comparisons between the kinematics of upward (*S*-shaped) and downward (inverted-*S*) lunges

Variable	Pitch angle (deg)			45 deg *versus* −45 deg
	0 (*N*=2)	45 (*N*=13)	−45 (*N*=7)	
x_1 (cm)	4.7±0.4	9.1±1.4	14.8±3.3	1.85 (0.054)
y_1 (cm)	1.0±0.1	−1.3±0.8	1.7±3.4	1.00 (0.330)
θ_1 (deg)	8.2±3.0	9.4±1.4	−9.7±4.9	4.82 (<0.001)
R (cm)	51.0±0.3	58.3±1.6	42.3±2.2	5.96 (<0.001)
Δy_{2-3} (cm)	5.7±1.2	5.5±0.9	27.8±5.9	5.03 (<0.001)
Δy_{2-1} (cm)	5.5±2.2	5.2±0.7	25.4±5.3	5.15 (<0.001)
$\Delta\theta_{3-1}$ (deg)	−6.8±2.9	−10.4±5.0	7.1±5.0	0.64 (0.528)
Δl_{gap} (cm)	9.8±4.6	5.6±0.7	10.9±3.2	2.15 (0.046)
$\mathbf{v}_{x,max}$ (cm s^{-1})	49±0.02	78±9	53±6	1.98 (0.063)
$\mathbf{v}_{y,max}$ (cm s^{-1})	50±19	50±8	142±12	6.76 (<0.001)
$\mathbf{v}_{r,max}$ (cm s^{-1})	70±15	93±10	153±15	3.55 (<0.001)

Values for 45 deg *versus* −45 deg are *t*(*P*).
For definitions of variables, see List of symbols and abbreviations.

The length of the structure used to reach imposes an upper limit on reaching distance, and hence the elongate body of snakes seems very well suited for the task of reaching. For example, the snakes in our study had mean values of mass, SVL and tail length of 83 g, 95 cm and 27 cm, respectively, whereas an 80 g mammal such as a slender squirrel (*Sundasciurus tenuis*) has body and tail lengths of only roughly 15 cm and 12 cm, respectively (Medway, 1978). In addition to snakes being elongate compared with limbed tetrapods of similar mass, diverse evolutionary lineages of arboreal snakes have independently evolved relatively low mass per unit length compared with more terrestrial species of snakes (Lillywhite and Henderson, 1993; Pizzatto et al., 2007). For example, terrestrial snakes such as pine snakes (Himes et al., 2002) and diamondback rattlesnakes (Klauber, 1972) may be more than 5 or 10 times heavier, respectively, than brown tree snakes of similar total length. Within limbed vertebrates the monkeys and apes are noteworthy for their elongate grasping forelimbs, which in the case of gibbons may approximate the distance from the shoulder to the ground when the animal is upright. Further, possessing a prehensile tail can extend the reach of an animal, increasing the maximum gaps that can be crossed by reaching. For example, both chameleons (Peterson, 1984) and some primates (Dunbar and Badam, 2000; Lawler and Stamps, 2002) use prehensile tails to aid in gap crossing. Similarly, we observed brown tree snakes using their prehensile tail to wrap or grip the supporting perch while crossing gaps.

In our study the only case in which the length of the snake appeared to impose a direct limit to gap-bridging distance was when the snakes moved straight down, although the gap-bridging performance in *B. irregularis* was significantly affected by both the yaw and pitch angles of the gap orientation. Perhaps there is a torque 'envelope' that limits gap-bridging performance in most directions. If such an envelope exists, we would expect that gap-bridging performance would be minimized in horizontal (0 deg pitch) trials in which nearly all of the length of the unsupported body contributes to τ_{bend}. Similarly, we would expect slightly better performance in trials with pitch angles of ±45 deg in which a large portion of the unsupported body contributes to the moment arm (*r*), and the best performance for the ±90 deg trials in which *r* is very small. Our data on τ_{bend} support this view (Fig. 3D). For a subset of the data with pitch angles from −45 to 45 deg, a three-way ANOVA revealed that although Gap$_{max}$ changed significantly with pitch angle (pitch main effect: $F_{2,18}$=12.98; P<0.001), τ_{bend} did not ($F_{2,18}$=0.98;
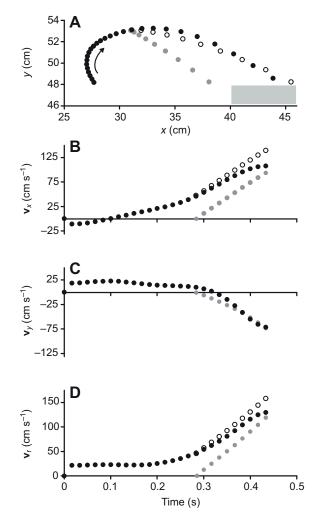

Fig. 8. Observed and predicted values for the kinematics of the snout during an upward *S*-shaped lunge for a gap with 0 deg yaw and 45 deg pitch. (A) Vertical and horizontal position of the snout in the plane of movement throughout the lunge. The arrow shows the direction of movement. (B) Horizontal velocity ($\mathbf{v}_x$). (C) Vertical velocity ($\mathbf{v}_y$). (D) Resultant velocity ($\mathbf{v}_r$). In all panels the black symbols show the observed movement of the head, whereas the gray symbols show the movement of the head predicted by passive pendular dynamics beginning from the crest of the lunge, and the open symbols show the prediction of the pendular model including the initial $\mathbf{v}_x$ (46.2 cm s^{-1}) at the crest of the lunge. In C the open symbols are overlaid by the gray symbols.

P=0.396). This constancy of τ_{bend} with variable Gap$_{max}$ suggests τ_{bend} may be the primary limiting factor for performance over a wide range of conditions. Such a limit may result from the maximum muscular force that can be exerted (Jayne and Riley, 2007) by the semispinalis–spinalis (SSP) and multifidus (M) muscles, which are the primary dorsal flexors in snakes (Jayne, 1988). Three observations suggest that τ_{pitch} does not play a dominant role in determining maximum performance: (1) for orientations where torques were greatest, 50% or more of the total length of the body remained on the supporting perch to act as a counterweight, (2) snakes used their body or tail to wrap the perch or pegs, offsetting any tendency to pitch, and (3) all observed failures were the result of localized bending of the body rather than rigid-body pitching off the end of the perch. Our data show that τ_{roll} might also be a determinant of performance in cases in which the trajectory of gap bridging includes a significant yaw angle (Fig. 3C). However,

because performance is decreased during high yaw orientations compared with 0 deg yaw orientations, it suggests that τ_{bend} could determine the ultimate envelope of performance.

Further evidence that performance could be limited by τ_{bend} comes from the transition of gap-bridging behaviors at extreme gap distances. Animals began using dynamic lunging behaviors to attempt gap crossings as gap distance increased. In many instances, unsuccessful lunges were attempted at gap distances beyond what was ultimately bridged successfully. In addition, the torques that would need to be sustained just prior to contact were greater than those both prior to lunging (Fig. 6A) and during crawling across gaps (Fig. 6B), suggesting that dynamic behaviors allow snakes to cross gaps for which they would not otherwise be able to create enough force to sustain the torques required. Analogous dynamic movements, referred to as 'dynos', allow human rock climbers to reach new holds they would not otherwise be capable of reaching (Long, 2004).

In addition, we often observed brown tree snakes using intentional lunging behaviors that allowed them to escape to the ground, or in rare cases to the destination perch during testing, suggesting that aerial behaviors in this species could also be an anti-predator behavior. *Chrysopelea* also use a 'jumping behavior' when crossing large gaps (Socha, 2011). These observations may give insight into the evolution of the gliding behavior of *Chrysopelea* (Socha, 2002; Socha, 2006) as a development from a pre-existing behavior for success in the discontinuous matrix of arboreal habitats (Jayne and Riley, 2007; Socha, 2011). These dynamic behaviors observed in *Chrysopelea* could possibly be both a means of similarly circumventing the large torques associated with crawling across large gaps and a mechanism for predator evasion.

Comparison of lunges to an inverted pendulum

Upward lunges theoretically could use only passive pendular mechanics after the anterior body is lifted to sufficient height. To meet the expectations of a passive falling pendulum, the unsupported portion of the snake should not lengthen and each point along the snake should fall through a similar arc angle. Further, the velocity of the snout of the snake should be similar to that predicted by the pendular mechanics of a rod falling by rotating about its end (Eqns 1 and 2). The first two conditions clearly are not met (Fig. 7A). Instead, the unsupported region of the body increases by a mean Δl_{gap} of more than 5 cm (Table 2), and the paths of different longitudinal locations on the snake do not move through equal arc angles (Fig. 7A).

Unlike the early portion of an upward lunge that clearly deviates from the motion expected for an inverted pendulum, several longitudinal locations superficially appear to move through a similar arc angle after the crest of the lunge. Therefore, it is possible that these lunges have two distinct phases: an extension to maximal height and a subsequent passive pendular fall. However, even during the portion of the lunge after its crest the kinematics of the head do not support this view (Fig. 8). The path of the head of the snake from the crest of the lunge to contact does not follow the path predicted by pendular mechanics (Fig. 8A). One possibility for this discrepancy is that the head of the snake has an initial velocity along the x-axis at the crest. However, whether this initial velocity is included or not, there are significant differences between the component velocities of the head at contact compared with a pendulum model (Fig. 8B–D). If this initial forward velocity is not included, the mean observed value of $\mathbf{v}_y$ ($-41.6\pm5.6\,\mathrm{cm\,s}^{-1}$) at contact is significantly less than predicted ($-67.7\pm5.5\,\mathrm{cm\,s}^{-1}$; $t_6=3.33$, $P=0.01$); however, the mean observed values of $\mathbf{v}_x$ ($80.5\pm7.5\,\mathrm{cm\,s}^{-1}$;

$t_6=1.06$, $P=0.32$) and $\mathbf{v}_r$ ($91.0\pm8.7\,\mathrm{cm\,s}^{-1}$; $t_6=-0.48$, $P=0.65$) are not. If this initial velocity is included, all three observed velocities at contact are significantly lower than that of a passive falling pendulum ($\mathbf{v}_x$: $t_6=-4.62$, $P<0.01$; $\mathbf{v}_y$: $t_6=3.33$, $P=0.01$; $\mathbf{v}_r$: $t_6=-4.62$, $P<0.01$). For example, the mean observed value of $\mathbf{v}_r$ is more than $50\,\mathrm{cm\,s}^{-1}$ slower than predicted by the model, suggesting the snake is actively slowing its fall.

During predatory strikes many snakes reach maximum velocity and then begin slowing down prior to impact (Alfaro, 2002; Kardong and Bels, 1998; Vincent et al., 2005), and this deceleration may be a mechanism to reduce the potential for injury from the impact with the prey (Cundall and Greene, 2000; Kardong and Bels, 1998). However, peak velocities during strikes can be 2–3 times greater than the lunge velocities observed in this study (Greenwald, 1974; Young et al., 2001). Thus, a more likely explanation for why *Boiga* slow their lunges is not to avoid injury, but to maintain a grip upon contact with the destination perch without limbs, using primarily ventral flexion of the braincase relative to the trunk.

Implications of performance space for barrier design

Since its introduction to Guam, an island in the Pacific Ocean, the brown tree snake has caused considerable damage to both the ecology and economy of the island (Rodda et al., 1999). As a result, substantial resources have been expended to control the population of snakes on Guam and prevent their introduction to other islands. One mechanism by which the spread of snakes is limited is by placing barriers around facilities with cargo or vessels destined for other locations (Campbell, 1999). Data from this study of the performance of brown tree snakes crossing gaps can inform the design and maintenance of barriers to exclude snakes.

One of the crucial findings from this study is the asymmetry of performance based on the orientation of the gap. Brown tree snakes are capable of crossing vertically oriented gaps that are 165% the span of the maximum horizontal gaps that they can bridge. Brown tree snakes on Guam can attain lengths greater than 3 m (Rodda et al., 1999). Given that snakes in this study can cross horizontal gaps and vertical gaps that require up to 58% SVL and 90% SVL, respectively, to be unsupported, if these large snakes can cross gaps equivalent to those in this study, Gap_{max} would approach 1.5 and 2.2 m for horizontal and vertical gaps, respectively. Therefore, vegetation should be trimmed to ensure a gap at least this large adjacent to barriers meant to exclude snakes. Further, barrier walls would need to be at least 2.2 m tall because snakes can likely extend vertically an even greater distance if the wall is supporting a portion of their body. This study highlights the importance of understanding the effects of environmental variation on performance, as this not only leads to insights into what physical factors limit locomotor performance but also can provide useful information for both applied and conservation biologists.

LIST OF SYMBOLS AND ABBREVIATIONS

COM	center of mass
COM_{gap}	center of mass of the unsupported region of the snake
g	acceleration due to gravity
Gap_{max}	maximum gap distance as a percentage of SVL
I	moment of inertia
l_{excess}	l_{gap} divided by maximum gap distance, expressed as a percentage
l_{gap}	length of the unsupported body of the snake in the gap at contact
m	mass of the unsupported region of the snake
r	length of the moment arm from the COM of the unsupported portion of the snake to the edge of the gap

R	distance between origin and snout at maximum height
SVL	snout–vent length
TL	total length
$v_{r,max}$	maximum resultant velocity
$v_{x,max}$	maximum velocity in x
$v_{y,max}$	maximum velocity in y
x_1	distance from snout at lunge initiation to top center of destination in x
y_1	distance from snout at lunge initiation to top center of destination in y
Δl_{gap}	change in length of the unsupported body during a lunge
Δy_{2-1}	vertical displacement of snout from start to crest of a lunge
Δy_{2-3}	vertical displacement of snout from crest of a lunge to position at contact
$\Delta \theta_{3-1}$	change in the angle of the vector between the origin and snout during a lunge
θ	angle with respect to vertical
θ_1	angle with respect to straight line between the two perches at lunge initiation
τ_{bend}	bending torque
τ_{pitch}	pitching torque
τ_{roll}	rolling torque
ω	angular velocity
$\dot{\omega}$	angular acceleration

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