© 2026. Published by The Company of Biologists | Journal of Experimental Biology (2026) 229, jeb251396. doi:10.1242/jeb.251396

RESEARCH ARTICLE

Torque limitations on cantilevering in *Dendrelaphis* snakes

Mal Graham[1,2], Henry C. Astley[3], Christofer J. Clemente[4,5] and John J. Socha[2,*]

ABSTRACT

Arboreal animals face potentially substantial torques when reaching across gaps, which may limit the size of the gap they can cross with non-dynamic behaviors. Snakes can experience particularly large torques during gap crossing, because they must counteract both pitching and buckling torques while extending into the gap in a cantilever-like posture. Pitching and buckling limits may impose different constraints on gap-crossing locomotion, but their relative importance remains unclear. To investigate this problem, we analyzed kinematic and morphological data related to gap crossing in *Dendrelaphis* snakes, complemented by data from their sister taxon, *Chrysopelea*, to test predictions from a theoretical model of cantilever failure. Specifically, we evaluated whether the existing model of buckling predicts maximum observed cantilever performance in these snakes, and compared those predictions with pitching limits estimated from body mass distributions. The buckling model produced estimates far below observed cantilever extents, even across plausible ranges of tendon ratio and multi-articular span, indicating that the current model does not yet capture the mechanics of buckling in cantilevering snakes. By contrast, snakes switched to dynamic movements close to their theoretical pitching limit, supporting the idea that pitching torques constrain cantilever abilities. These results suggest that pitching torque is a major constraint on cantilever-based gap crossing, while also identifying the need for improved buckling models with higher anatomical fidelity. More broadly, this study shows how testing mechanical models against behavior can reveal both the limits shaping locomotor performance and the limitations of existing models.

KEY WORDS: Snakes, Gap crossing, Kinematics, Biomechanics, Locomotion

INTRODUCTION

Arboreal animals exhibit a variety of behaviors while crossing gaps, including reaching, jumping and aerodynamic movements (Graham and Socha, 2020). Although animals may choose different gap-crossing behaviors for many reasons, mechanical factors play a role. To ensure they successfully make it from their starting point to their desired target, an animal must select behaviors based on its own abilities and morphology, as well as features of the gap (such as the compliance, orientation or structure of the supports; Thorpe et al., 2009; Byrnes and Jayne, 2012; Jayne et al., 2014; Mauro and Jayne, 2016; Hunt et al., 2021). However, few studies have explicitly investigated the biomechanical factors that might lead to the failure of some gap-crossing behaviors in certain contexts.

One factor known to lead to failure in reaching behaviors is distance. This limitation has perhaps been most explicitly tested in snakes. Most arboreal snakes use a cantilever behavior to cross gaps (Lillywhite et al., 2000; Jayne and Riley, 2007; Byrnes and Jayne, 2012), in which the animal extends its body nearly straight off the end of one branch to make contact with another (Figs 1A and 2); animals utilizing this behavior appear to be biomechanically constrained to maximum distances of around 50–60% snout–vent length (SVL) for level gaps (Lillywhite et al., 2000; Jayne and Riley, 2007). However, some species can also use dynamic gap-crossing movements to overcome this constraint (e.g. *Boiga*: Jayne and Riley, 2007; *Chrysopelea*: Graham and Socha, 2021; *Dendrelaphis*: Graham and Socha, 2023). The ability to modulate behavior in response to increasing gap size makes such snakes a suitable subject for investigating the mechanical drivers of behavioral transitions during gap crossing.

There are multiple potential explanations for such behavioral transitions, but torque constraints have been hypothesized to represent an important biomechanical factor that limits the ability of snakes to use cantilever movements. When an animal crosses a gap with a reaching behavior, suspending some portion of their body from a base of support toward a target support, they are subject to potentially high torques owing to gravity (Jayne and Riley, 2007; Graham and Socha, 2020). The animal must both keep the extended body stiff, countering buckling torques, and maintain contact with the origin support, countering pitching torques. For cantilevering snakes, buckling occurs when the snake is no longer strong enough to maintain a stiff body position, and the body bends at a particular body region. The second type of torque failure, whole-body pitching, occurs when the torque due to gravity on the suspended portion of the body is greater than the torque acting on the supported portion (because of a combination of gravity and grip force).

Although both failure modes are caused by torque, the distance at which they occur may scale differently with body size because the forces resisting bending and the gravitational loads acting on the body scale differently with size (Jayne and Riley, 2007; Alexander, 2003; Astley, 2020). In the case of pitching, if snakes are geometrically similar, we would expect snakes to experience passive pitching at the same relative point on the body (assuming gripping does not occur). By contrast, the distance the snake can extend before buckling is more complex, as it depends on factors of internal morphology that vary widely amongst snake species. Each of these types of torque represents a constraint on gap-crossing performance. Although it is not clear if snakes possess mechanisms to help surpass constraints of internal morphology, they can use behavioral mechanisms to counter the effects of passive pitching (e.g. increasing grip by wrapping around the origin branch).

Theoretical models provide a way to predict where these torque-related failures should occur. For pitching, predictions can be made

[1]Renaissance Philanthropy, 2000 Florida Ave NW FL 5, Washington, DC 20009, USA. [2]Department of Mechanical Engineering, Virginia Tech, Blacksburg, VA 24061, USA. [3]Departments of Biology and Polymer Science, Biomimicry Research and Innovation Center, The University of Akron, Akron, OH 44325, USA. [4]University of the Sunshine Coast, School of Science, Technology, and Engineering, Sippy Downs, QLD 4558, Australia. [5]The University of Queensland, School of Biomedical Sciences, Brisbane, QLD 4072, Australia.

*Author for correspondence (jjsocha@vt.edu)

M.G., 0000-0002-4527-5361; H.C.A., 0000-0003-0136-1433; C.J.C., 0000-0001-8174-3890; J.J.S., 0000-0002-4465-1097

Received 7 August 2025; Accepted 17 July 2026

Journal of Experimental Biology (2026) 229, jeb251396. doi:10.1242/jeb.251396

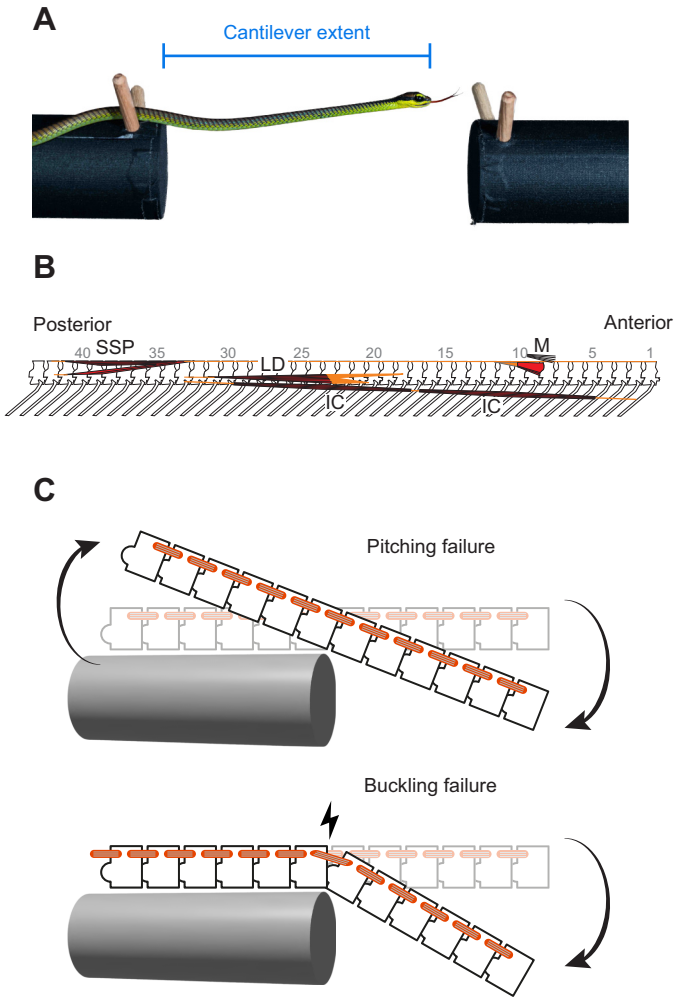

Fig. 1. Musculoskeletal mechanics of a cantilevering snake. (A) A representative snake (*Dendrelaphis formosus*, not used in this study) cantilevering across a horizontal gap. 'Cantilever extent' is the distance a snake extends while holding its body stiffly in a relatively straight configuration. The image background has been removed for clarity. (B) Diagram of snake trunk anatomy, illustrating the concept of multi-articular muscles and tendons. Muscle is red with lines, and tendon is orange. One set of muscles corresponds to each vertebral/rib unit (numbered); the majority of the muscle is not shown. The depicted muscles are: semispinalis-spinalis (SSP), multifidus (MF), longissimus dorsi (LD), and iliocostalis (IC). The specific number of segments for each muscle are taken from a dissection of *Dendrelaphis formosus* (Table 1). (C) Conceptual depiction of two modes of cantilevering failure by torque, by pitching and buckling. In pitching, the torque resulting from extended body weight exceeds the torque resulting from the weight of the body on the perch. In buckling, the muscle fails to produce the countertorque required to hold the weight of the extended body.

using the distribution of body mass along the snake: passive pitching should occur when the torque produced by the suspended portion of the body exceeds the counter-torque produced by the supported portion (Graham and Socha, 2020). For buckling, predictions are more difficult because they depend on complex internal morphology, including muscle cross-sectional area, muscle lever arms, vertebral geometry and the architecture of multi-articular muscle–tendon systems (Astley, 2020).

A recent theoretical model (Astley, 2020) provides an anatomically informed prediction for snakes, estimating the number of articular units (defined per vertebra) a snake could extend before buckling. The model treats the snake as a series of identical segments and predicts that the cantilever distance at which buckling would occur depends on the cross-sectional area of the relevant muscle, the shape of the vertebrae, the number of vertebrae spanned by a major tendon–muscle complex (the semispinalis-spinalis, SSP), and what portion of that span is tendon versus muscle. Snakes with a greater number of vertebral units spanned by the muscle and a higher ratio of tendon to muscle in the complex are predicted to have a greater cantilever ability, although these characteristics also restrict range of movement. When appropriate morphological variables are inserted, the model can be used to estimate the precise number of vertebral units that can be extended before the snake will buckle. However, this estimate has never been tested against real cantilever performance.

Predicting the distance at which a snake would pitch requires detailed measurements of how mass varies along the length of the snake. Because such data are available for only a few species, and even fewer of those also have experimentally determined cantilever limits, only one previous study of cantilever distance has compared maximum cantilever distances to the cantilever distance at which the snake would be expected to passively pitch (Jayne and Riley, 2007). While gripping can counteract pitching torques (Jayne and Riley, 2007; Byrnes and Jayne, 2012), the magnitude of grip force needed increases with increasing pitching torque, and thus even with behavioral adjustments, this mechanism still provides a constraint on cantilever distance.

An alternative to the quasi-static cantilevering behavior is to use a more dynamic movement, taking advantage of momentum. Four snake species (*Chrysopelea paradisi*, *Dendrelaphis punctulatus*, *Dendrelaphis calligastra* and *Boiga irregularis*) have been observed using dynamic movements to cross gaps beyond their cantilever limit (as described in Graham and Socha, 2021 and Jayne and Riley, 2007). Of these, three are in the sub-family Ahaetullinae (Figueroa et al., 2016), which includes the flying snakes (*Chrysopelea*). When using dynamic movements, the paradise tree snake (*C. paradisi*) experiences decreased torques compared with their maximum cantilevers (Graham and Socha, 2021), suggesting that at least one advantage of using dynamic movements might be to reduce torque demands. If so, we might expect that the maximum cantilevers observed in flying snakes and their relatives would be close to the pitching or buckling distances predicted by theoretical models.

In this study, we used behavioral and morphological data to test predictions of pitching and buckling failure during cantilevering. We sought to determine whether snakes would exhibit cantilever failure at the extent predicted by the models, and whether the transition to using non-cantilever movements occurs at or before this limit. To do so, we used morphological data from *Chrysopelea* and *Dendrelaphis* to generate appropriate pitching distance estimates, and data from *Dendrelaphis* to estimate buckling distances in that genus. We then tested these estimates against experimentally observed cantilever extents. Thus, this study has two related goals: to determine whether observed behavioral transitions are consistent with pitching or buckling limits, and to evaluate whether the existing model of buckling produces realistic predictions when applied to empirical snake morphology. Overall, these data improve our understanding of how mechanisms of biomechanical failure influence the gap-crossing behavior of snakes and help us to elucidate the potential factors influencing the selection of dynamic versus reaching behaviors in the arboreal environment.

Journal of Experimental Biology (2026) 229, jeb251396. doi:10.1242/jeb.251396

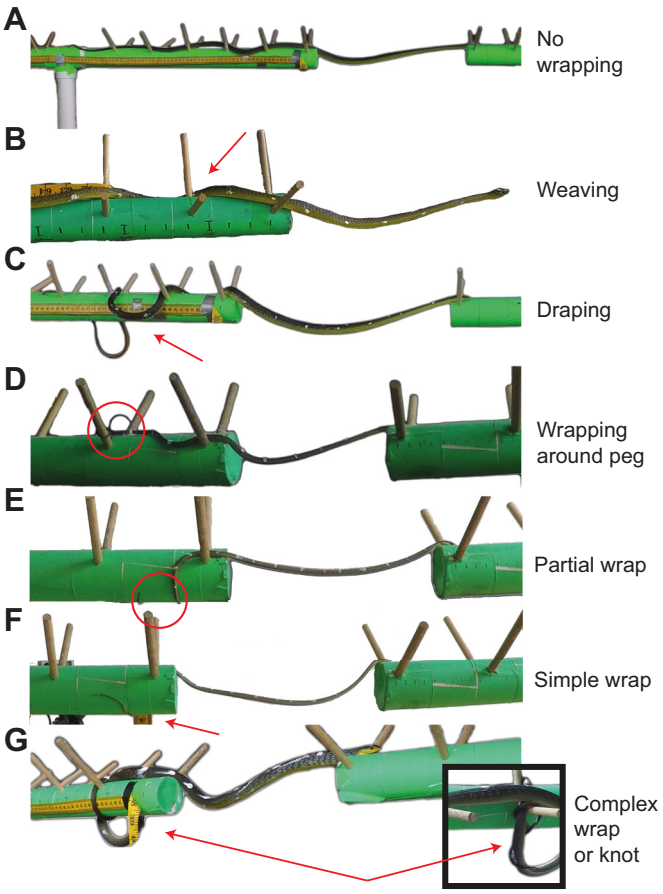

Fig. 2. Tail positioning observed in Australian tree snakes. Snakes in this study positioned the posterior body in several ways. The positions illustrated in A–C were not counted as 'tail wrapping', as it was not clear if the snake was gripping when positioned in this manner. The positions illustrated in D–G were all counted as tail wraps. Snake ID, mass and SVL: (A,C) 2018DP03, 84.8 g, 89.0 cm; (B) 2019DP15, 72.3 g, 87.0 cm; (D) 2019DP18, 5.1 g, 29.5 cm; (E,F) 2019DP19, 5.3 g, 30.6 cm; (G) 2019DP16, 83.4 g; 77.0 cm.

MATERIALS AND METHODS

Data collection

This study includes analysis of cantilever extent and behavior in three species: *Chrysopelea paradisi* Boie 1827, *Dendrelaphis punctulatus* (Gray 1826) and *Dendrelaphis calligastra* (Günther 1867). The data for *C. paradisi* and *Dendrelaphis* spp. are from an analysis of gap-crossing data reported previously (Graham and Socha, 2021, 2023). Briefly, snakes (six captive *C. paradisi*, three wild-caught *D. calligastra*, and six captive and 11 wild-caught *D. punctulatus*) were presented with gaps of increasing size until they began to consistently use a non-cantilever movement. *C. paradisi* were filmed using a motion capture system (Vicon Motion Systems, Oxford, UK). Snakes were filmed with multiple video cameras (Hero4 Black, GoPro, San Mateo, CA, USA) to facilitate three-dimensional reconstruction of their body position.

For both datasets, gap-crossing tests were conducted on an arena comprising two PVC branches wrapped in gaffer's tape (GaffTac 2 inch keying tape, Rosco, Stamford, CT, USA). The PVC branches were drilled with holes at 10 cm intervals, and pairs of 10 cm long wooden dowels were inserted at 45 deg angles to provide an analog to secondary branches in the arboreal habitat. The two PVC supports were placed in a single line at the same vertical level with a gap of variable distance in between the ends of the origin and target supports.

For *C. paradisi*, snakes were presented with the increasing gap sizes in 5% SVL increments, starting with a gap of approximately 40% SVL, until the snake either refused to continue crossing or a failure limit was reached. For *Dendrelaphis*, snakes were presented with gap sizes that increased a few centimeters at a time until the snake began using a non-cantilever movement. Once this distance was established, we attempted to re-test the snake on gap sizes approximately 2 cm smaller and larger to determine the transition gap size with greater confidence.

All procedures were approved by the Virginia Tech Institutional Animal Care and Use Committee under protocol 16-154 and the University of the Sunshine Coast Animal Ethics Committee under protocol ANA18133. Snakes were collected under permits from the Queensland Department of Environment and Science (Permit to Take, Use, Keep or Interfere with Cultural or Natural Resources; permit number PTU18-001432 and Scientific Purposes Permit, permit number WA0010696).

Definitions of cantilevering-related terms

We use a number of terms relating to the cantilevering process throughout this paper.

Drop: a behavior in which the snake appears to be attempting to cross the gap, but suddenly the anterior body rapidly drops/sags vertically, hinging at the edge of the supporting branch.

Buckling: failure of the musculature holding up the cantilevered body.

Cantilever failure: a specific observed event indicating apparent inability to cross gap successfully. Cantilever failure includes drops, but also apparent pitching failures and a behavior in which the snake is extending out seemingly intending to cross but then rapidly pulls back into an S-shape (potentially to prevent pitching).

Cantilever limit: the snake's maximum overall cantilevering limit, whether due to reaching the physiological maximum, volitional behavior, or something else.

Physiological maximum: the maximum distance the snake could extend before physiologically being incapable of going further. The behavioral limit observed as the cantilever limit could be shorter than this distance.

Maximum cantilever extent

We defined cantilever extent as the distance a snake extends in a relatively straight body configuration, measured from the tip of the snout to the location of the terminus of the support it rests upon (Fig. 1A). The snake reaches a biomechanical limit in cantilever extent when it extends to the point of failure due to torque. In this study, we probe this limit by comparing cantilever extents during multiple behavior types, using the procedure below. First, we analyzed the trial with the largest gap across all successful cantilever crosses performed by a given individual. Given that snakes largely proceeded in a straight line from the origin to the target for successful cantilever crosses, we assume that distance extended at contact with the target branch was the greatest cantilever extent for that trial. In practice, we calculated the Euclidean distance from the snake's snout to the point of contact on the origin branch at the moment any part of the snake's body touched down upon the target branch.

The species in this study also use dynamic movements to cross gaps and often begin such movements with a period of cantilevering. Following our previous studies (Graham and Socha, 2021, 2023), the end of the 'approach phase' is defined as the 'transition frame', the video frame in which the snake begins to transition from a straight, cantilevered position (see example in

Movie 1). We identified the onset of dynamic movements by visually identifying the moment the snake began to either: (1) form a loop by lowering a section of body downward into the gap while maintaining a relatively steady head position; or (2) rear upwards while simultaneously feeding the posterior body into the gap. After observing that a snake had used a dynamic movement by watching the video, we stepped the video or motion capture data backward frame by frame until the moment the relevant body section began its upward or downward trajectory. For all non-cantilever trials analyzed, if the trial had an approach phase, the Euclidean distance from the snake's snout to the point of contact with the origin was calculated, and the largest of these distances for each individual was recorded.

Finally, we also reviewed cantilever extent at any moment in which the snake appeared to possibly be experiencing or nearing a cantilever failure. Qualifying moments were those in which the snake: (1) was in an approximately cantilevered body position and (2) appeared to have reached or be nearing a cantilever distance it would not be able to muscularly support. We designated three kinds of events as potential indicators that a snake had reached or was nearing a cantilever failure. These included events where the snake appeared to exhibit one of the following behaviors. (1) Drop: the anterior body of the snake swung downward into the gap while the supported body maintains contact with the origin. (2) Pitch: the posterior body of the snake visibly lifted off the origin support. (3) Pull-back: the snake pulled its head back toward the origin rapidly, often from a straight line into an S-shape. This pull-back behavior was included because it may have indicated that the snake was nearing a torque limit and behaviorally responding to avoid cantilever failure. Data reviewed for this analysis included motion capture and video data from our previous studies of gap crossing in *Chrysopelea* sp. (Graham and Socha, 2021) and *Dendrelaphis* sp. (Graham and Socha, 2023), including successful crossings using either cantilever or non-cantilever behaviors, as well as incomplete crossings (as non-cantilever and incomplete crossings often begin with a cantilever phase).

For each trial that included these potential failure moments, the video data were examined to determine the potential failure moment in which the snake appeared to have the greatest cantilever extent. The Euclidean distance of the snout to the point of contact with the origin at this moment was recorded by analyzing the relevant frame following the same method as in Graham and Socha (2023). If an individual had multiple trials with such potential failure moments, the largest cantilever extent during potential failure was used.

Tail wrapping and axial reorientation observations

During video analysis, we observed that some snakes exhibited behaviors at or near contact with the target branch that could be relevant to their cantilever performance. The first of these behaviors was tail wrapping, in which the snake wraps its tail around the branch or a peg. The second of these behaviors is axial reorientation, in which the snake positions its body on the origin branch such that the body is oriented with a lateral surface up and the ventral surface lateral, and thus a lateral bend is formed in a more vertical plane. To examine the possible effects of these behaviors on cantilever ability, we examined every event of interest (target contact for successful cantilevers, moment of failure for incomplete gap-crosses, moment of transition for non-cantilever crosses) and recorded whether the snake appeared to be axially reoriented or had its tail wrapped around the branch.

Movements where the snake's tail was wrapped around a peg or around the branch counted as tail wrapping. These movements included both those in which the snake fully encircled the branch ('simple wrap', Fig. 2F) or peg ('peg wrap', Fig. 2D), as well as those in which the snake made only a partial wrap around the branch, either not meeting its body or turning the tail back the other direction ('partial wrap', Fig. 2E). Finally, we included movements in which the tail made a knot-like pattern ('complex wrap', Fig. 2G). Because the branch was not instrumented to detect forces, we could not determine whether the snake was producing countertorques except by visual estimation. Thus, we did not consider weaving of the body through the pegs (Fig. 2B) or movements where the body was looped to either side of the branch (Fig. 2C) as tail wrapping. By contrast, behaviors included as tail wrapping always clearly involved a portion of the snake's body being placed beneath a surface, and therefore more evidently could have been used to produce countertorques.

Morphological data

Vertebral morphology of *D. punctulatus*

The equation for buckling failure generated by the model developed by Astley (Astley, 2020) is:

$$\frac{-pL + L + L\sqrt{\frac{(p-1)^2}{2} + \frac{8aP_0\mathrm{CSA}_{\max}}{mgL(1-t)}}}{2}, \quad (1)$$

where a is the lever arm of the SSP muscle complex, L is the length of a vertebral unit, m is the mass of a vertebral unit, $\mathrm{CSA}_{\max}$ is the cross-sectional area of the SSP, p is the multi-articular span (the number of vertebral units spanned by the SSP muscle-tendon complex, overall), t is the tendon ratio (the number of vertebral units spanned by the tendon, in particular, involved in the SSP muscle–tendon complex), P_0 is the peak isometric muscle stress ($\sim$30 N cm^{-2} in vertebrates) and $\boldsymbol{g}$ is the acceleration due to gravity (9.8 m s^{-2}). This equation assumes the following: (1) the snake is in a static (or quasi-static) posture; (2) only the SSP is involved, with other potential dorsiflexors ignored; (3) all intervertebral joints are frictionless; (4) there is strictly a one-to-one matching of muscle to vertebra; and (5) all segments are equal in length, mass and muscle lever arm.

We dissected one preserved *D. punctulatus* to measure these morphological variables. The specimen was provided by the Queensland Museum. Because other specimens of *D. punctulatus* were not readily available for study, we also dissected a specimen of a related species (*Dendrelaphis formosus*), which had died of natural causes in an author's lab colony. We included this specimen to provide comparative context for the morphology of *Dendrelaphis* spp., while recognizing that species-specific values may differ. Photographs were taken of the sections to facilitate later photogrammetric analysis using FIJI software (Schindelin et al., 2012). We estimated the relevant variables as follows (Fig. 3). (1) Lever arm: the distance from the vertebral condyle to the centroid of the SSP muscle bundle, measured in FIJI. For multiarticular muscles, the effective moment arm depends on both the position of the muscle-tendon unit relative to the vertebral joint and the orientation of the force vector across multiple joints; therefore, this measurement should be interpreted as an approximate anatomical lever arm rather than as the maximum distance from the joint to the dorsal margin of the neural spine (Tingle et al., 2023). (2) Length of a vertebral unit: measured in FIJI by measuring the length of ten ventral scales in a photograph of the underside of the snake at three locations along the body and dividing by ten. (3) Mass of a vertebral unit: calculated as the average density of the individual

Journal of Experimental Biology (2026) 229, jeb251396. doi:10.1242/jeb.251396

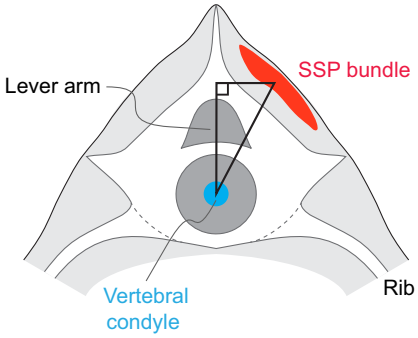

Fig. 3. Schematic diagram of an axial section from the midbody region of *Dendrelaphis punctulatus* used for estimating SSP cross-sectional area and lever arm. Only the dorsal portion of the snake is depicted, showing the vertebra and ribs in white and epaxial musculature in gray. The SSP lever arm was estimated as the distance from the vertebral condyle to the centroid of the SSP bundle, following the effective moment-arm approximation for multiarticular snake muscles described by Tingle et al. (2023). The SSP bundle shown was estimated to contain four muscular units.

excluding the tail, multiplied by the length of the vertebral unit. (4) The cross-sectional area of the SSP: measured in FIJI by drawing an outline of the relevant muscle and calculating the area on a photograph of an axial section. Because vertebral morphology varies with body region in this genus (Nicodemo, 2012), these measurements were taken from the region extended when a snake was cantilevering, specifically the anterior half of the snake caudal to the neck (at approximately 25% SVL). The specimen was not sufficiently preserved to allow for precise measurements of the tendon ratio or multi-articular span.

Mass distribution of *D. punctulatus* and *C. paradisi*

To estimate the mass distribution along the length of the body, we calculated the % mean linear density of the snake. For *D. punctulatus*, a single specimen was sectioned into 43 pieces of roughly equal length (29.1±9.8 mm, mean±s.d.) using a scalpel. The mass of each section was recorded on a digital scale (SF-718, Suofei, Jiangsu, China; resolution, 0.01 g) and a photograph was taken of all the sections with a length reference. Using the photographs, the section lengths were measured using FIJI. Mass distribution data for *C. paradisi* were taken from a previous study (Yeaton et al., 2020), presented as a pooled mass distribution from three individuals.

Predicted pitching and buckling limitations

Pitching

We used mass and length data from the 43 sections of the dissected snakes to determine how mass is distributed along the length of the body and fitted a function to this data to estimate the location of the center of mass. The sections were separated into three groups: the head, the body and the tail. The head region corresponded to a single section. The body region and tail regions were separately linearly interpolated using a custom Python script to generate a mass value every 0.1 mm; this value reflects the numerical intervals of the model (not the resolution of the center of mass). The body section on the specimen in question included a section that had been partially crushed; therefore, the data from that section was averaged with data from the sections on either side before interpolation. A quadratic function was fitted to each set of the resulting data points, one for the body and one for the tail. The resulting body and tail mass and length points were appended to the head point to create a curve of mass against length.

Using these mass–length distributions, we calculated the center of mass, the location at which the torque on the suspended body would be greater than the torque on the supported body if the snake extends out in a perfectly straight line. In other words, the center of mass represents the tipping point. We assumed that the snake's body is a straight line and that the snake exerts no gripping or adhesion on the branch, so the only external force acting on the snake is gravity. We calculated the torque acting on the suspended and supported portions of the snake using:

$$\vec{\tau}_i = \vec{r}_i \times \vec{F}_g \quad \text{or} \quad \vec{\tau}_i = m_i(\vec{r}_p \times \vec{g}), \tag{2}$$

where $\vec{r}_i$ is the distance vector pointing from the end of the origin to a point on the snake's body, $\vec{g}$ is the gravitational vector, and m_i is the mass at that point. The resultant torque is the sum of the torques along the body for the portion of the snake's body in question:

$$\vec{\Gamma}_{\text{sus}} = \sum_{i=\text{head}}^{\text{origin}} \vec{\tau}_i \text{ and } \vec{\Gamma}_{\text{supp}} = \sum_{i=\text{origin}}^{\text{tail}} \vec{\tau}_i. \tag{3}$$

Using a Python script, we calculated $\vec{\Gamma}_{\text{sus}}$ and $\vec{\Gamma}_{\text{supp}}$ assuming the snake extended to a particular distance. This distance was set first at 0 mm, and then increased in 0.1 mm increments until $\vec{\Gamma}_{\text{sus}}$ exceeded $\vec{\Gamma}_{\text{supp}}$, providing a 0.1 mm resolution estimate of the location of the center of mass.

Buckling

We used the morphological values from the single dissected specimen of *D. punctulatus* to estimate those of the snakes studied in the cantilever tests using equations of isometric scaling (see 'Scaling' below). We entered these values into the equation for maximum cantilever distance from equation 17 in Astley (2020). This equation proposes that several morphological factors influence cantilever distance, often in non-linear terms. Increased lever arm, force per unit cross-section area and muscle cross-sectional area all increase cantilever distance, whereas increased mass decreases it. The relationship between segment length and cantilever distance is complex, with increased length improving cantilever distance by improving distance per segment up to some threshold distance, then decreasing beyond that limit owing to disproportionately increased loading. Increasing multi-articular span alone improves performance. However, if total muscle mass remains constant, this imposes a trade-off between multi-articular span and cross-sectional area, resulting in a slightly negative relationship. Increasing the ratio of tendon to contractile muscle alleviates this trade-off and correspondingly increases cantilever distance.

We used the tendon ratio and multi-articular span values from another *Dendrelaphis* species (*D. pictus*, Nicodemo, 2012) to generate a point estimate of buckling failure distance from the equation. Given that the true values of tendon ratio and multi-articular span for *D. punctulatus* are unknown, we provide both a point estimate for buckling failure and a range. The range reflects the range of buckling failure values predicted for every combination of the following values: (1) multi-articular span: 9–36 (by integer); (2) tendon ratio: 0.41 to 0.93 increasing by 0.04.

The values for tendon ratio and multi-articular span were chosen by examining all available measurements of the spinalis muscle for snakes in the same sub-family (Ahaetullinae) in the literature (Jayne, 1982; Nicodemo, 2012) and setting the minimum and maximum values of the multi-articular span and tendon

Journal of Experimental Biology (2026) 229, jeb251396. doi:10.1242/jeb.251396

ratio ranges to cover the full range of measured values from other species.

Our analyses of buckling and pitching both assume that the extended portion of the snake is oriented in a straight and horizontal posture. We made this assumption for a variety of reasons beyond simplicity. Horizontal posture shows the highest bending load compared with the equivalent posture tilted upwards or downwards (specifically, bending load would be the cosine of the angle relative to horizontal). Lateral bends either reduce the cantilever distance if the proportion of suspended body is held constant or increase the cantilevered mass if the cantilever distance is held constant. Although lateral bends may alter the joint loading by allowing the bony joint facets to bear some of the load (specifically, the pre- and post-zygapophyses and the zygosphene–zygantrum joint), thereby reducing needed muscle force to meet the total bending load, it is unlikely that this benefit is outweighed by the reduced distance or increased total bending load. Finally, we observed that snakes tended to adopt a straight or nearly straight posture when approaching the limit of their cantilevering ability.

Adjusting for body size

As described above, adapting the morphological data from the dissected specimens into estimates for the individuals studied relies on the assumption that *D. punctulatus* and *C. paradisi* scale isometrically. The literature supports this assumption in the case of *C. paradisi* (Socha and LaBarbera, 2005): across 20 snakes, the regression line between logMass and logSVL was found to have a slope of 3.16, with a 95% CI of 2.99–3.35 and an r^2 value of 0.989. For *D. punctulatus*, we examined how mass, head width, midbody depth, midbody width and width at the vent varied with SVL across 18 specimens in this study. We did not examine how tail length varied with body size because many individuals had partially shortened tails, presumably due to injury. Each of the width and depth metrics was measured on the day of experimentation using digital calipers. The mass was recorded using a digital scale (CJ4000, J-scale, HBI International, Phoenix, AZ, USA; resolution, 0.01 g). The SVL values are taken from Graham and Socha (Graham and Socha, 2023). Linear regressions were then conducted in R (r-project.org) between log SVL and the log of each of the other metrics. For the mass/length comparison, we also included the mass and length data from all *D. punctulatus* specimens reported in Fearn and Trembath (2011).

RESULTS

Scaling across body size in *Dendrelaphis punctulatus*

The scaling factors for mass (Fig. 4), midbody width, and midbody depth did not differ significantly from predictions of isometric scaling (3, 1, and 1, respectively) in *D. punctulatus*. Larger snakes, however, have relatively narrower heads and taper more at the vent: the scaling factor for head width was 0.67 (95% CI: 0.52, 0.81) and the scaling factor for width at the vent was 0.81 (95% CI: 0.68, 0.94).

Pitching predictions

The torque on the suspended portion of the snake's body, based on our mass distribution and discrete model, is expected to exceed the torque acting on the supported portion of the snake's body at 57.3% SVL for *D. punctulatus* (Fig. 5A) and at 53.2% SVL for *C. paradisi* (Fig. 5B). As no preserved specimens of *D. calligastra* were available for dissection, we assumed a similar mass distribution and subsequent pitch point for this species as *D. punctulatus*.

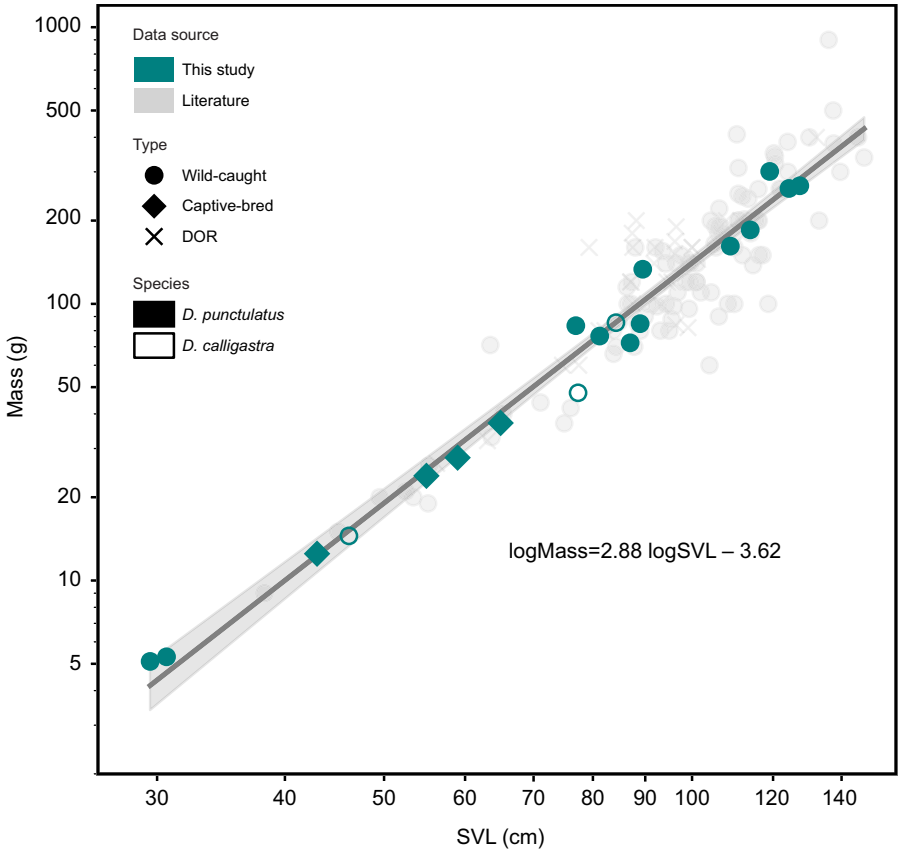

Fig. 4. Scaling of mass and length in two *Dendrelaphis* species. Log–log plot of 16 *D. punctulatus* and three *D. calligastra* documented in this study (green) and 127 *D. punctulatus* documented in Fearn and Trembath, 2011 (gray). Shape indicates whether the snake was wild caught, captive bred, or found dead on the road (DOR). Fill represents *D. punctulatus* whereas empty represents *D. calligastra*. The gray line represents the line of best fit for all the data, with the 95% CI of the slope indicated as gray shading [2.71, 3.06].

Journal of Experimental Biology (2026) 229, jeb251396. doi:10.1242/jeb.251396

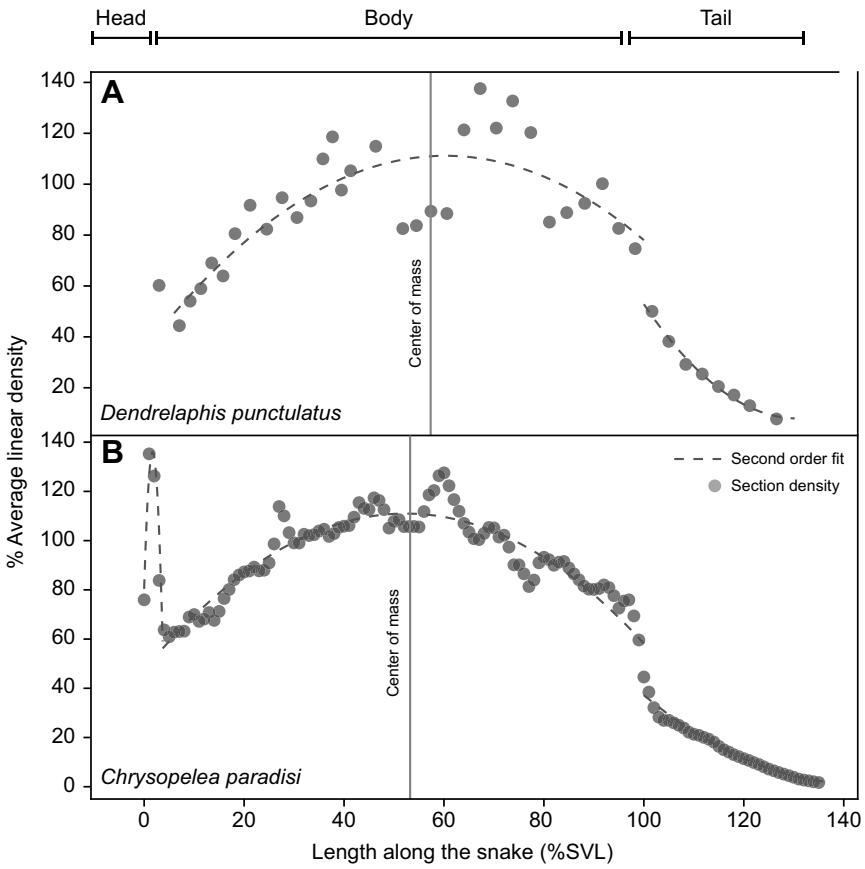

Fig. 5. Mass distribution in *Dendrelaphis punctulatus* and *Chrysopelea paradisi*. The % mean linear density (% mass per unit length) from each section against its position along the body (dots) from a single specimen of *D. punctulatus* (A) or pooled from three specimens of *C. paradisi* (B; data from Yeaton et al., 2020). Data from *D. punctulatus* were obtained using the same sectioning method as by Yeaton et al. (2020). Separate second order fits were conducted for the body and tail segments and the head segments in *C. paradisi* (B). There was only one section for the head for *D. punctulatus* so no curve was fitted. The center of mass (black line) represents the point along the snake at which it would begin to passively pitch.

Buckling predictions

Using calculated values for morphological variables measured during the dissection and subsequent image analysis (Table 1), the point predictions for buckling failure were between 7.2% SVL and 18.1% SVL across the 19 specimens of *Dendrelaphis* for which mass and length data were collected (Table 2). These values are far smaller than the distances at which pitching would be expected and the cantilever extents observed in this study. Using the most generous possible values for multi-articular span and tendon ratio produced at most a prediction of 21.9% SVL in one individual.

Maximum cantilever extent

Analyzed events

We analyzed previously collected gap-crossing data from *Dendrelaphis* and *C. paradisi* to identify the farthest cantilever extent observed in each species. The data for *Dendrelaphis* (Graham and Socha, 2023) comprise 92 successful cantilever crosses, 121

Table 1. Morphological variables and constants used to estimate buckling extent

	Dendrelaphis punctulatus	***Dendrelaphis formosus***	***Dendrelaphis pictus***	***Ahaetulla prasina***	***Ahaetulla prasina***	***Chrysopelea paradisi***	***Chrysopelea ornata***
Source	Dissected	Dissected	Nicodemo, 2012	Nicodemo, 2012	Jayne, 1982	Nicodemo, 2012	Jayne, 1982
Mass (g)	**138.6**	24.0	–	–	–	–	–
SVL (mm)	**983**	891	–	–	–	–	–
Vertebral length, *L* (mm)	25%: 3.16 50%: **5.12** 75%: 3.99	25%: 4.45 50%: 4.59 75%: 3.94	–	–	–	–	–
SSP CSA (mm^2)	**1.16**	0.46	–	–	–	–	–
SSP lever arm (mm)	**3.40**	2.1	–	–	–	–	–
Multi-articular span, *p*	–	**42**	Ant: 14 Mid: 34	Ant: 11 Mid: 36	Mid: 36	Ant: 9 Mid: 24	Mid: 26
Tendon span, *n*	–	33	Ant: 6 Mid: 31	Ant: 5 Mid: 30	Mid: 32	Ant: 5 Mid: 20	Mid: 22
Tendon ratio, *t*=*n*/*p*	–	0.78	Ant: 0.43 Mid: 0.91	Ant: 0.45 Mid: 0.83	Mid: 0.89	Ant: 0.56 Mid: 0.83	Mid: 0.85

We provide values from across the sub-family Ahaetullinae using both our own dissections and literature values. For dissected specimens, muscle/tendon values were measured from the region roughly at 25% SVL. The bolded values from the dissected specimens were used to create the point estimate. To address the fact that the tendon values may be inaccurate for *D. punctulatus*, we used an additionally dissection of *D. formosus* and the full range of values from the literature: multi-articular span, 9–42; tendinous span, 5–33; corresponding tendon ratios 0.43–0.91.

Journal of Experimental Biology (2026) 229, jeb251396. doi:10.1242/jeb.251396

Table 2. Predicted buckling distances for 19 *Dendrelaphis* snakes

Snake ID	Snake mass (g)	Snake SVL (cm)	Prediction (%SVL)	Lower bound (%SVL)	Upper bound (%SVL)
2019DP18	5.1	29.5	17.7	3.7	21.5
2019DP19	5.3	30.6	18.1	3.8	21.9
2019DP12	12.5	43.0	16.2	3.1	19.9
2019DC07	14.5	46.2	16.1	3.1	19.8
2019DP13	23.9	55.0	14.6	2.6	18.3
2019DP11	27.8	59.0	14.5	2.5	18.2
2019DP10	37.1	65.0	13.6	2.2	17.3
2018DC04	47.7	77.4	14.5	2.5	18.2
2019DP15	72.3	87.0	12.9	2.0	16.5
2019DP17	76.5	81.2	11.3	1.4	14.9
2019DP16	83.4	77.0	9.8	1.0	13.4
2018DP03	84.8	89.0	11.9	1.6	15.5
2018DC05	85.5	84.3	11.0	1.3	14.6
2019DP20	133.4	89.5	8.7	0.6	12.2
2019DP09	161.7	109.0	10.1	1.0	13.6
2018DP01	185.1	114.0	9.7	0.9	13.3
2018DP06	261.3	124.4	8.6	0.6	12.1
2018DP02	267.2	127.4	8.8	0.6	12.3
2019DP08	301.1	119.1	7.2	0.1	10.7

Predicted values are given in %SVL. Data are sorted by snake mass. For absolute values, see Table S1. Note that data from one individual were missing.

successful non-cantilever crosses and 54 events (across 24 trials) in which an individual exhibited a behavior that could have indicated some kind of cantilever failure (the snake pulling back, dropping from the perch, or pitching forward). For *C. paradisi*, the dataset (Graham and Socha, 2021) comprises 45 successful cantilever trials and 137 successful non-cantilever trials.

We observed only seven unsuccessful crossing attempts in *C. paradisi*, all from a single individual (described as 'recovery events' in Graham and Socha, 2021). Other individuals did sometimes turn back to the origin branch, but such movements always maintained the cantilevered body position while turning around, suggesting that the snakes had not reached a cantilever failure. Of the seven events in which the snake clearly attempted a crossing and failed, the initial crossing attempt was a non-cantilever movement in five trials. Therefore, only two trials involved a cantilever failure.

The maximum cantilever extent was not consistently found within one behavioral context. In *C. paradisi*, two snakes exhibited their largest cantilever extent during a successful cantilever, three exhibited their largest cantilever extent during non-cantilever transition and one during non-cantilever failure (Fig. 6C).

Similarly to *C. paradisi*, around half the *Dendrelaphis* (11/20) exhibited a larger cantilever distance during some event of interest (transition into a non-cantilever movement or potential failure) than their maximum successful cantilever crossing distance (Fig. 6B). For three *Dendrelaphis*, the maximum cantilever extent was experienced during a potential failure, and for eight, it was during a non-cantilever transition. Absolute and relative values of cantilever extent in each context, as well as the maximum observed for each individual, are presented in Table 3.

Comparisons with predicted pitch and buckling distances

No *C. paradisi* exhibited a cantilever extent exceeding their expected pitching limit. For the one snake that did exhibit cantilever failure, the failure occurred at a cantilever extent of 38.15 cm, compared with the estimated pitch point of 38.32 cm. The other snakes' largest successful cantilevers were between 79.8% and 96.7% of their predicted pitching limit.

In *Dendrelaphis*, four snakes appeared to experience pitch failure; in each case, the cantilever distance at apparent failure was within a few centimeters of the expected pitch point. In contrast to *C. paradisi*, two hatchling *D. punctulatus* – probably from the same clutch – extended out to a cantilever distance exceeding their expected pitching limit. In contrast to the pitching estimates, maximum cantilever distances for all cantilever types were well above the predictions from the buckling equation.

Use of other behaviors

In general, axial reorientation was somewhat uncommon in *Dendrelaphis* and was not observed in any successful cantilever. Although the motion-capture data collected for *C. paradisi* provided no information on axial reorientation, anecdotally, the behavior appeared more common in that species, exhibited with most looped behaviors (pers. obs., M.G.). Axial reorientation was observed at the transition frame to a non-cantilever movement 13 times (in 119 trials) and in 17 of 54 potential failure events.

Dendrelaphis snakes did not use tail wrapping at the transition into a non-cantilever movement in 76 trials. These snakes used tail wrapping in only 21 trials: a simple wrap in eight trials, a partial wrap in eight trials, a peg wrap in four trials, and a combination of a peg wrap and partial wrap in one trial. For ten trials there was no clear transition point, as the snake initiated a non-cantilever movement immediately, and in 23 trials the tail could not be clearly seen.

Only eight snakes exhibited tail wrapping at target contact for successful cantilevers. Three of these eight snakes used tail wrapping for their largest successful cantilever. Overall, *Dendrelaphis* did not use tail wrapping at target contact in 53 successful cantilever trials, and the tail could not be clearly seen for 15 trials. In 13 trials the snake in question used a tail wrap (peg: 2; partial: 2; simple: 8; complex: 1).

Tail wrapping was similarly uncommon during potential failure events. Out of 54 potential failure events from 10 snakes, the snake had its tail wrapped in 15. Interestingly, none of these events were pitching failures; every time a snake exhibited apparent pitching failure, the tail was not wrapped.

DISCUSSION

Maximum cantilever extent typically exceeds maximum successful cantilever

The maximum observed cantilever extent corresponded to the maximum successful cantilever in only half the snakes studied, demonstrating that these animals are capable of cantilevering greater distances than they generally chose to for successful crosses. It seems that it is common for the snakes to initiate dynamic movements before reaching their physiological cantilever maximum. Nevertheless, the difference between the maximum successful cantilever extent and the maximum cantilever extent observed overall was generally quite small (0.86–6.4 cm, 1.2–14.8% SVL). It is possible, then, that snakes may stop using cantilevers to cross gaps quite close to their physiological limits. Because snakes that reach a torque limit might be required to perform a potentially energetically costly and time-consuming set of movements to avoid falling, they might choose to transition to another locomotor mode before reaching this limit.

We observed wide variation in how often a given individual reached a failure limit during gap crossing. Of 54 observed failure events, 40 were from three individuals. For example, 14 failure events were observed in a hatchling snake. These events were

Journal of Experimental Biology (2026) 229, jeb251396. doi:10.1242/jeb.251396

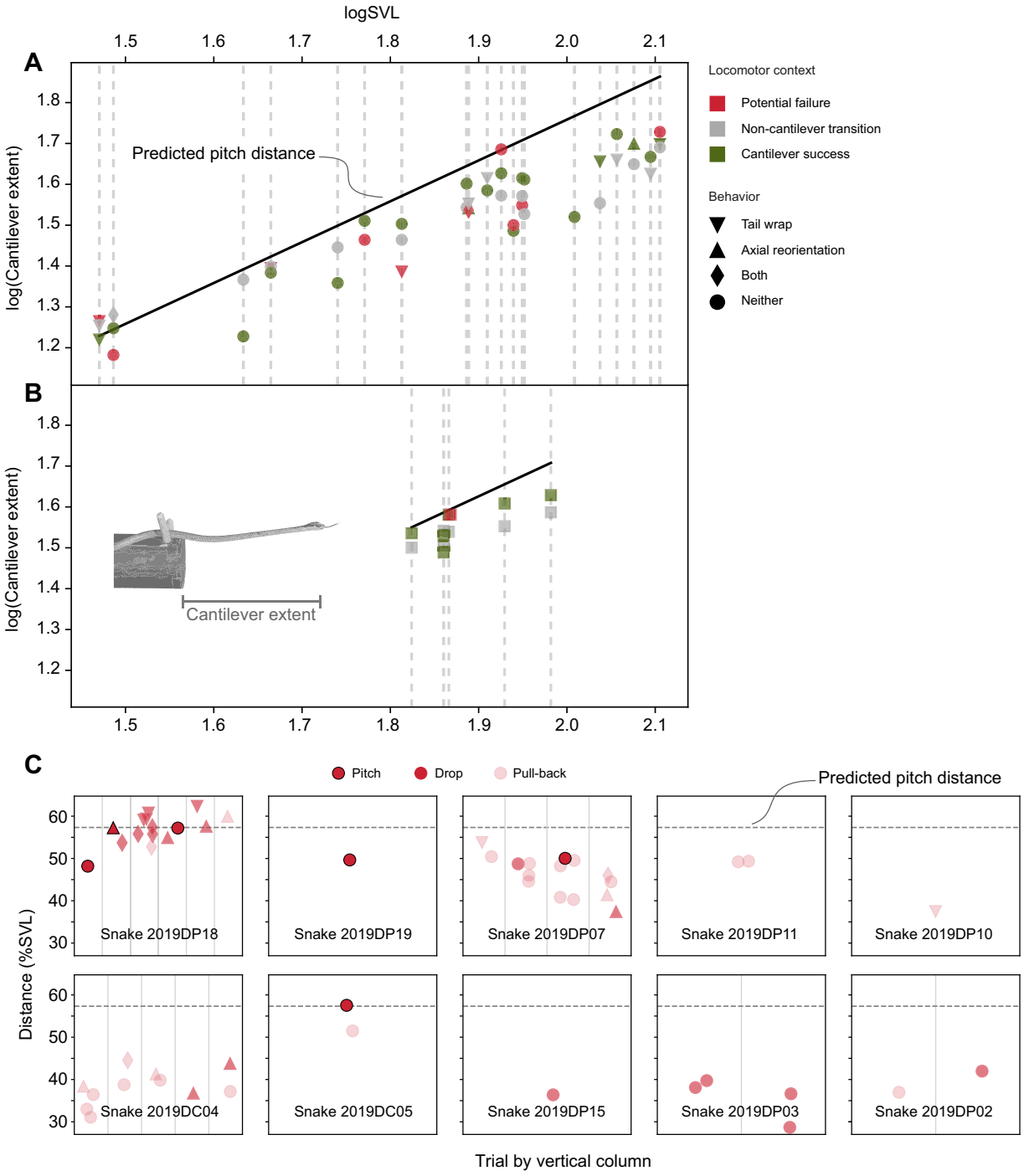

Fig. 6. Maximum cantilever extents. Maximum cantilever distances observed in *Dendrelaphis* species (A) and *C. paradisi* (B) plotted by body size. The colors of the points indicate the locomotor context and their shapes indicate behaviors used during the event. The dashed vertical lines are used to help differentiate data from different individuals. The predicted pitching distance is indicated as the black sloped line. (C) Ten *Dendrelaphis* snakes exhibited some type of potential failure event: either a pull-back (lightest red), drop (medium red) or pitch (darkest red, outlined in black). The shape of the symbols indicates behaviors used during the event, as in A and B. The *x*-axis indicates separate trials, separated by gray vertical lines. Spread in the *x*-axis is jittered to enable viewing of individual points and is therefore not biologically meaningful. Some snakes exhibited multiple failures in a single trial. Note that any failure events in which the snake's cantilever extent meaningfully exceeded the pitch estimate involved the use of a possible anti-torque behavior (tail wrapping, down triangle markers; axial reorientation, up triangle; or both, diamond). Owing to the use of motion capture instead of video, we were not able to document these behaviors in *C. paradisi*.

observed across six trials, as the snake made multiple attempts in a given trial to reach the target, often failing multiple times before succeeding. By contrast, a second hatchling, captured together with the first near where they hatched (thus it possible that they were littermates), extended to cantilever failure only once, despite being presented with a nearly identical experimental procedure.

If snakes attempt to avoid cantilever failure, an important factor governing a snake's decision to cantilever or use a dynamic

Journal of Experimental Biology (2026) 229, jeb251396. doi:10.1242/jeb.251396

Table 3. Maximum cantilever distance compared with predicted pitch point for all snakes

			Distance (%SVL)			
	Snake ID	SVL (cm)	Transition to NC	Potential failure	Successful cantilever	Predicted pitch
Dendrelaphis (*N*=20)	2019DP18	29.5	61.0	**62.4**	56.3	57.3
	2019DP19	30.6	**62.4**	49.7	57.8	57.3
	2019DP12	43.0	**54.2**	–	39.3	57.3
	2019DC07	46.2	**54.3**	53.7	52.4	57.3
	2019DP13	55.0	**50.7**	–	41.5	57.3
	2019DP11	59.0	–	49.3	**54.9**	57.3
	2019DP10	65.0	44.8	37.4	**49.1**	57.3
	2019DP16	77.0	45.3	–	**51.9**	57.3
	2018DC04	77.4	**46.1**	44.6	45.0	57.3
	2019DP17	81.2	**50.7**	–	47.4	57.3
	2018DC05	84.3	44.4	**57.5**	50.3	57.3
	2019DP15	87.0	–	**36.3**	35.2	57.3
	2018DP03	89.0	41.9	39.8	**46.3**	57.3
	2019DP20	89.5	37.7	–	**45.7**	57.3
	2019DP14	102.0	–	–	**32.5**	57.3
	2019DP09	109.0	32.8	–	**41.6**	57.3
	2018DP01	113.9	40.1	–	**46.4**	57.3
	2019DP08	119.1	37.4	–	**42.0**	57.3
	2018DP06	124.4	33.9	–	**37.4**	57.3
	2018DP02	127.4	38.5	**42.0**	39.2	57.3
Chrysopelea (*N*=6)	95	66.7	47.5	–	**51.5**	53.2
	85	72.5	**48.0**	–	46.7	53.2
	89	72.0	48.1	**53.0**	52.9	53.2
	90	72.5	**44.2**	–	42.5	53.2
	94	85.0	42.0	–	**47.8**	53.2
	88	95.9	40.3	–	**44.4**	53.2

The snake ID and SVL are presented alongside maximum cantilever distances observed during the transition to a NC movement, a potential failure event, or successful contact with the target during a cantilever cross. The maximum of these three distances is bolded for comparison with the predicted pitch distance. Distances are in %SVL. Absolute values are provided in Table S2.

movement is its perception of its biomechanical limits. It is not known precisely what sensory modalities these snakes use to assess gap size and their associated cantilever limits, but the data presented in two previous studies (Graham and Socha, 2021, 2023) provide some clues. Both *C. paradisi* and the Australian tree snakes transition to using a non-cantilever movement after an approach phase. For large gaps, the snakes do not reach their maximum cantilever extent during this phase, often initiating a dynamic movement after extending only a small percentage of the gap distance. Given that all three species considered here exhibit head wagging during gap crossing (Socha, 2006; Graham and Socha, 2021), they are likely to be utilizing motion parallax (Kral, 2003; Zamore et al., 2020; Hataji et al., 2021) to assess gap size and thereby determine that they will need to use a dynamic movement. They may also be using proprioception to sense when they are nearing their maximum cantilever extent (Jayne and Riley, 2007; Hoffmann et al., 2026), which could include the sense of where on their body the edge of the origin branch is located, or the sense of how much torque they are experiencing prior to buckling failure.

Beyond the mechanism the snake uses to assess gap size when nearing a cantilever limit is what the snake understands about that information. A snake that has never previously neared its cantilever limit may not be aware that such a limit is nearing, whereas snakes that regularly cross gaps may learn this information. Other species of snake have exhibited evidence of learning in the gap-crossing context: the brown tree snake (*Boiga irregularis*) has a learned preference for rigid over compliant branches over the course of only three trials (Mauro and Jayne, 2016). If snakes are able to learn when they experience failure, snakes that more frequently attempt large gap crosses may not exhibit cantilever failure as often.

A snake's habitat may also have an important impact on its gap-crossing experience and performance. We collected the *Dendrelaphis* snakes in this study from a variety of locations – pristine rainforest, mangrove forests, suburban areas – which will differ in the availability and geometry of suitable gaps. Garter snakes (*Thamnophis elegans*) in mechanically different habitats show population differences in vertebral count and locomotion (Kelley et al., 1997), indicating localized selection is possible. Another species, the Australian tiger snake (*Notechis scutatus*), exhibits a preference for, and increased locomotor performance in, habitats that are similar to those they encountered in early life experiences (Aubret and Shine, 2008), raising the possibility of learning or phenotypic plasticity. If individual *Dendrelaphis* similarly tend to stay consistently within a particular habitat type, individuals collected from different habitats may have experienced different levels of gap-crossing requirements, which could help explain inter-individual differences in performance.

The potential relevance of life history to gap-crossing behavior points to the importance of a better understanding of the fine-scale structure of the local habitat for understanding and contextualizing data regarding locomotor performance. When living in a low-connectivity environment, a snake may regularly encounter large gaps, and thus have more experience with gap crossing. Alternatively, a snake in a highly connected environment may rarely need to test its biomechanical limits to move efficiently through the trees. Snakes may also behaviorally avoid the constraints associated with gap crossing, even in less connected environments, by locomoting on the ground: Stephens' banded snakes (*Hoplocephalus stephensii*), for example, rest in trees but navigate between shelters on the ground (Fitzgerald et al., 2002). Overall, the interaction between ecological needs, locomotor

capability and habitat structure are relevant for understanding locomotor performance and any evolutionary pressures acting on that performance.

Pitch predictions versus buckling predictions

One goal of this study was to test whether theoretical predictions of pitching or buckling limits explain observed cantilever performance during gap crossing. The pitching estimates performed well: observed apparent pitching failures occurred close to the predicted pitch point. By contrast, the buckling model produced predictions far below observed cantilever extents. Thus, the main outcome of the buckling analysis was not a realistic estimate of buckling limits, but a demonstration that the current model omits important anatomical and mechanical features needed to predict buckling in cantilevering snakes.

Pitching estimates informed by morphological data appeared to be relatively good predictions. In the one snake that exhibited a failure event in *C. paradisi*, the cantilever extent at the moment of failure was within a centimeter of the predicted pitch limit. Similarly, failure events observed near the 98.3 cm SVL of the dissected *D. punctulatus* specimen were also within a few centimeters of the predicted limit.

The pitch limit in *Dendrelaphis* may have been a slight underestimate for the smallest snakes, which had a mass of only a few grams and SVL less than 40 cm. It is possible that mass distributions of juveniles are different from the larger snakes, which include many adults. More morphological data from additional specimens across a range of sizes would be useful to predict differences in pitch limit with body size.

In contrast to the pitching estimates, buckling estimates were a large underestimate of the observed cantilever extents. These predictions are based on a model created to examine the effects of multiarticular muscle–tendon systems (Astley, 2020), but this model has several significant simplifications and limitations. First, the model assumed constant morphological parameters along the body length (i.e. the first segment has the same geometry and mass as the *i*th). However, multi-articular span and tendon ratio vary to a great degree along the length of the body, and *D. pictus* exhibits fused tendons (Nicodemo, 2012), which if present in the species included in this study, may serve to increase cantilever ability. Yet, even using the most generous possible combinations of multi-articular span and tendon ratio, the equation predicted values that were well below those observed. Furthermore, in contrast to the series of identical segments in the model, the body geometry and mass of snakes varies along the body axis, with body segments closer to the head generally having smaller linear dimensions and lower mass than those at mid-body (Hoffstetter and Gasc, 1969; Jayne, 1982; Yeaton et al., 2020). This anatomical pattern in snakes has the beneficial result during cantilevering of reducing the mass of the most anterior segments (which have the highest lever arm for imposing external moments) while increasing the muscle area and lever arm of the most posterior segments (which must counteract the highest accumulated external moment). To address the former possibility, we calculated the external moments along the body for two 100-joint cantilever snakes with equal mass and length, with one consisting of identical joints and the other consisting of segments of increasing length and mass such that the 100th joint is 2× the length and 8× the mass of the first (see https://github.com/TheSochaLab/Torque-limitations-on-cantilevering-in-Dendrelaphis-snakes). This simple modification reduces the external moment at the 100th joint by 20%, despite bearing the same mass and length of cantilevered body. A corresponding increase in lever arm may reduce the muscular stress further (if scaled to vertebral size, lever arm would increase by 1/3rd relative to the equal-size configuration), though the consequence of a graded increase is beyond the scope of this simulation. Uncertainty in SSP lever-arm estimation may also contribute to uncertainty in the buckling predictions, because the true effective moment arm of a multiarticular muscle depends on both anatomical position and force orientation across multiple joints. Tingle et al. (2023) found that simple distance-based estimates generally approximated cross-product estimates for snake epaxial muscles, but also showed that individual differences can occur; therefore, the SSP lever arm used here should be interpreted as approximate rather than as a precise reconstruction of three-dimensional force geometry.

Another factor may be that the model for buckling considers only the strength of the SSP muscle complex. However, snakes have another dorsiflexor muscle, the multifidus, which probably contributes to anti-buckling action (Gasc, 1981; Jayne, 1988; Jørgensen and Jayne, 2017). Furthermore, additional muscles are active during cantilevering, specifically the iliocostalis and the longissimus dorsi, although the former may only be stabilizing prior to contact with the destination perch (Jørgensen and Jayne, 2017). Unfortunately, cross-sectional area for these muscles is available for few snake species, and for lever arms for only one, the corn snake (*Pantherophis guttatus*), a generalist colubrid (Tingle et al., 2024). However, this study reveals that the SSP complex, multifidus and longissimus dorsi all have similar cross-sectional area, and the pitch lever arms for the former two are similar, whereas the longissimus dorsi have approximately half the pitch lever arms of the former two. While the complexities of this system are beyond the scope of this paper, a rough estimate would be that the available torque may be approximately 2.5× what is estimated above if *Dendrelaphis* and *Chrysopelea* have similar anatomies. Applying this estimate to the equation used to predict buckling failure (by increasing the cross-sectional area by 2.5×) provides estimated cantilever distances of approximately 45% SVL, far closer to what is observed. This effect may be further accentuated by potential positive allometric scaling of muscle cross-sectional area, as was observed in corn snakes (Tingle et al., 2024). Overall, these inferences suggest that the model of Astley (Astley, 2020) would benefit from a revision that incorporated all three major dorsiflexor groups, providing a more accurate model for buckling for future studies. Other types of models may also be useful. For example, a 3D model reconstructing the morphology of the snake could be used, in concert with a dynamic model of the action of the muscles during cantilevering, to predict buckling distances.

Use of specialty behaviors

Several *Dendrelaphis* specimens exhibited the use of tail wrapping or axial reorientation during cantilevering at least once, but across trials these behaviors were relatively rare. By contrast, such behaviors were more commonly observed in previous experiments with *C. paradisi*. The reasons for this difference are unclear. One possibility is that the evolution of J-loop jumping, used both for crossing gaps and initiating glides in *Chrysopelea*, required greater grip strength or mobility of the tail for control of the jump. Generally, tail wrapping could assist with cantilevering by allowing the snake to produce counter-pitching torques. However, even when not using tail wrapping, the snakes could use other aspects of body positioning to counteract torques due to gravity. Snakes sometimes weaved through the pegs or dropped portions of their body to either side of the branch, which could have also created counter-torques (albeit at the cost of shifting the mass distribution forward and

exacerbating pitching failure). All trials in which the snakes exceeded the predicted pitching limit involved tail wrapping, suggesting that tail wraps were used to create counter-torques.

We used the term 'axial reorientation' to encompass a range of positioning behaviors that might change the active anti-torque muscles from dorsiflexors to lateral flexors. Axial reorientation includes both behaviors in which the whole body is oriented at an angle, and axial twisting, in which portions of the body are angled (achieved via combined vertical and lateral bending) and others are in a normal configuration (dorsal surface up). Axial twisting has been observed in both *Dendrelaphis* (Graham and Socha, 2023) and *Chrysopelea* (Graham and Socha, 2021), and *Chrysopelea* also use axial twisting during active launches that initiate glides (Socha, 2006). Axial twisting is one mechanism for achieving axial reorientation of the suspended portion of the body during a cantilever. However, *Dendrelphis* can also accomplish axial reorientation without twist by placing the entire body at an angle, resting between the pegs and the main body of the branch (Graham and Socha, 2023).

Axial reorientation does not seem likely to have a significant effect on pitching limitations, but it could extend cantilever ability compared with a dorsal-surface-up body configuration, if the animal's lateral flexors have larger cross-sectional area and/or greater lever arms than its dorsiflexors. Furthermore, if the muscles driving lateral motion have a lower proportion of tendon relative to muscle, this will increase the range of motion and consequently may improve work output for dynamic behaviors such as non-cantilever gap crossings and the launch of *Chrysopelea*. This idea is consistent with the use of axial twisting by *C. paradisi* to launch glides: the species forms a lateral bend to make a J-shape, but orients the J in the vertical plane (Socha, 2006). If lateral flexion provides an advantage during dynamic gap crossing, it may help to explain how the behavior evolved in this family. Additional studies should examine other species in the sub-family and in *Dendrelaphis* for the presence of axial reorientation during gap crossing, as well as axial twisting in particular.

Two *D. punctulatus* exhibited axial reorientation in trials in which they exceeded cantilever distances observed in other contexts, suggesting that lateral flexion may be a mechanism for extending cantilever ability. Future studies should examine this possibility in more detail by attempting to restrict the use of axial reorientation, such as by having snakes cross gaps between flat surfaces instead of curved ones and examining the effect on maximum cantilever extent.

The brown tree snake (*Boiga irregularis*) is the only other species of snake known to have the ability to use dynamic movements to cross gaps (Jayne and Riley, 2007; Byrnes and Jayne, 2012; Hoefer and Jayne, 2013; Jayne et al., 2014). This species is also in the family Colubridae, although it is much more distantly related than *Dendrelaphis* is to the *Chrysopelea* (Figueroa et al., 2016; Zheng and Wiens, 2016). In the brown tree snake, tail wrapping is used almost always when lunging, and the species often extends a large portion of its observed maximum cantilever before initiating a lunge. In our previous study (Graham and Socha, 2021), only one of six *C. paradisi* exhibited cantilever failure, whereas 10 of 20 *Dendrelaphis* did so here. Thus, there may be interspecific differences between the brown tree snakes, the Australian tree snakes, and the flying snakes in terms of ability to avoid their cantilever limit, awareness of their cantilever limit, propensity to use dynamic movements, or all three. Such differences may reflect differences in evolutionary history of the behavior, life history traits or morphology; additional studies of gap crossing in these animals will help address these possibilities.

Future directions for understanding torque constraints on reaching behaviors

The interplay between pitching limitations, buckling limitations and environmental structure are important for understanding the evolutionary pressures on arboreal gap crossers. First, a better understanding of the fine structure of forests, so that we may understand the sizes of gaps commonly encountered by different species, is critical to understanding how performance capabilities correspond to behaviors in the wild. If an animal is able to typically find relatively straight, well-connected routes where the gap sizes are not more than its reaching ability, it does not seem that there would be an evolutionary pressure to develop a greater cantilever ability or an alternative behavior. By contrast, if the arboreal structure requires that an animal needs to use dynamic movements or more circuitous routes to navigate, there may be evolutionary pressure to improve the dynamic ability or increase the reaching ability.

Given that cantilever abilities in many snake species have been tested without finding evidence of dynamic gap crossing, dynamic movements for gap crossing appear to have evolved relatively infrequently. It is possible that the evolution of dynamic gap crossing has occurred only a few times in snakes, documented conclusively in the sub-family Ahaetullinae to which *Dendrelaphis* and *Chrysopelea* belong (Graham and Socha, 2021, 2023) and in the brown tree snake (Jayne and Riley, 2007; Byrnes and Jayne, 2012). If it is difficult to evolve dynamic movement abilities, and gap sizes in the local environment present a challenge to the cantilevering snake, it would seem to be evolutionarily advantageous to develop a greater cantilever ability. If so, the question of whether buckling or pitching torques are a greater constraint becomes highly relevant, as the solution to each problem is different.

In the case of pitching being the greater limitation, selection for increased cantilever ability would favor snakes with a weight distribution shifted toward the posterior of the snake, the use of tail wrapping or other behavioral or anatomical modifications to increase grip, perhaps via changes in the microstructure of ventral scales to increase the friction coefficient (Rieser et al., 2021). However, if buckling is the greater limitation, there could be selection pressure to increase the size of the midbody musculature, which would support anti-buckling forces. These potential pressures are made more complex to tease apart by the possibility that torque constraints scale differently with body size, resulting in one type of torque being constraining for small snakes while the other is more constraining for large snakes. And, of course, it is also possible that there are trade-offs between avoiding one or the other type of torque, such as if anti-pitching favors placing weight toward the posterior of the snake but anti-buckling favors greater musculature (and therefore weight) toward the middle of the snake.

The importance of torque as an influence on reaching behaviors does not only apply to snakes. Animals holding up a limb or cantilevering their body out from a branch while gripping will also face the same torques (Graham and Socha, 2020), one associated with maintaining bodily stiffness and one associated with preventing pitching into the gap. In every case, an improved understanding of the evolution of gap crossing will require that we understand how different torque limitations might have favored certain approaches to improving reaching ability, whether the fine-scale habitat provides a challenge to its reaching ability, and how any dynamic movements may or may not avoid these limitations.

Although in some cases in this study it appeared evident that a pitching limit had been reached, the snake often stopped attempting

to cantilever when pitching began, creating the appearance of buckling and making it hard to ascertain whether pitching or buckling was occurring (or both). Additionally, several movements that appeared to be failures might instead merely have been the snake choosing to stop cantilevering. Future work can experimentally validate the predictions of the improved model described above by reducing the ability of the snake to experience one type of cantilever failure in order to examine the other type. For example, placing weights on the rear body of the snake could prevent pitching and allow for the identification of the buckling limit.

Overall, identifying the biomechanical limits to gap crossing is not easy in the experimental context. We attempted to use several methods to elicit such a maximum without finding a method that consistently elicited cantilever failures across all individuals. However, the presence of some potential failure events suggests that the observed values were relatively close to the biomechanical maximum. Despite these limitations, this study allows us to examine the relative importance of distinct failure modes of an ecologically relevant behavior in challenging arboreal environments, potentially offering insights into the selective pressures driving arboreal adaptations in snakes as well as inspiration for similar studies on other taxa.

Acknowledgements
The authors would like to thank Richie Gilbert and the Sunshine Coast Snake Catchers, the people of Cape Tribulation, Kiely Glass, Cassandra Duncan, Jordan Di Cicco and Mela Coffey for assistance with snake acquisition; Dr Michele Schiffer and the crew at the Daintree Rainforest Observatory, Alex Cheesman, Ramon Barbos and Aaron Hopper for facilities and experimental assistance; and Alexia Anous, Allison Henry, Tyler Ellis and Abraham Rowe for assistance with digitizing. We would also particularly like to thank the Jabalbina Yalanji Aboriginal Corporation for permission to enter the Daintree National Park during the field work (permit number PTU18-001432). Portions of all sections of this paper are reproduced from the PhD thesis of Mal Graham (Graham, 2023).

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: M.G., J.J.S.; Data curation: M.G., J.J.S.; Formal analysis: M.G., H.C.A., J.J.S.; Funding acquisition: M.G., J.J.S.; Investigation: M.G., J.J.S.; Methodology: M.G., H.C.A., C.J.C., J.J.S.; Project administration: M.G., J.J.S.; Resources: C.J.C., J.J.S.; Supervision: J.J.S.; Visualization: M.G.; Writing – original draft: M.G., J.J.S.; Writing – review & editing: M.G., H.C.A., C.J.C., J.J.S.

Funding
This work was supported by the National Geographic Society (EC-52215R-18), The Company of Biologists (Travelling Fellowship 180820) and the Virginia Tech Graduate Student Association (Graduate Research Development Program award) to M.G., and the National Science Foundation (1351322, 2027523 to J.J.S. and 2045581 to H.C.A.).

Data and resource availability
Processing code is available on GitHub: https://github.com/TheSochaLab/Torque-limitations-on-cantilevering-in-Dendrelaphis-snakes. All other relevant data and details of resources can be found within the article and its supplementary information.

References
Alexander, R. M. (2003). *Principles of Animal Locomotion*. Princeton, NJ: Princeton University Press.
Astley, H. C. (2020). The biomechanics of multi-articular muscle–tendon systems in snakes. *Integr. Comp. Biol.* **60**, 140-155. doi:10.1093/icb/icaa012
Aubret, F. and Shine, R. (2008). Early experience influences both habitat choice and locomotor performance in tiger snakes. *Am. Nat.* **171**, 524-531. doi:10.1086/528969
Byrnes, G. and Jayne, B. C. (2012). The effects of three-dimensional gap orientation on bridging performance and behavior of brown tree snakes (*Boiga irregularis*). *J. Exp. Biol.* **215**, 2611-2620. doi:10.1242/jeb.064576
Fearn, S. and Trembath, D. F. (2011). Natural history of the common tree snake, *Dendrelaphis punctulatus* (Serpentes: Colubridae), in the wet–dry tropics of north Queensland. *Aust. J. Zool.* **58**, 384-389. doi:10.1071/ZO10059
Figueroa, A., McKelvy, A. D., Grismer, L. L., Bell, C. D. and Lailvaux, S. P. (2016). A species-level phylogeny of extant snakes with description of a new colubrid subfamily and genus. *PLoS ONE* **11**, e0161070. doi:10.1371/journal.pone.0161070
Fitzgerald, M., Shine, R. and Lemckert, F. (2002). Spatial ecology of arboreal snakes (*Hoplocephalus stephensii*, Elapidae) in an eastern Australian forest. *Austral. Ecol.* **27**, 537-545. doi:10.1046/j.1442-9993.2002.01214.x
Gasc, J. P. (1981). Axial musculature. In *Biology of the Reptilia*, Vol. 11 (ed. C. Gans and T. S. Parsons), pp. 355-435. Academic Press.
Graham, M. R. (2023). Dynamic gap-crossing movements in jumping and flying snakes. *PhD thesis*, Virginia Tech. https://vtechworks.lib.vt.edu/handle/10919/110868Google Scholar
Graham, M. and Socha, J. J. (2020). Going the distance: the biomechanics of gap-crossing behaviors. *J. Exp. Zool. Part Ecol. Integr. Physiol.* **333**, 60-73. doi:10.1002/jez.2266
Graham, M. and Socha, J. J. (2021). Dynamic movements facilitate extreme gap crossing in flying snakes. *J. Exp. Biol.* **224**, jeb242923. doi:10.1242/jeb.242923
Graham, M. and Socha, J. J. (2023). Dynamic gap crossing in *Dendrelaphis*, the sister taxon of flying snakes. *J. Exp. Biol.* **226**, jeb245094. doi:10.1242/jeb.245094
Hataji, Y., Kuroshima, H. and Fujita, K. (2021). Motion parallax via head movements modulates visuo-motor control in pigeons. *J. Exp. Biol.* **224**, jeb236547. doi:10.1242/jeb.236547
Hoefer, K. M. and Jayne, B. C. (2013). Three-dimensional locations of destinations have species-dependent effects on the choice of paths and the gap-bridging performance of arboreal snakes. *J. Exp. Zool. A Ecol. Genet. Physiol.* **319A**, 124-137. doi:10.1002/jez.1777
Hoffmann, L. A., Bryde, P., Davenport, I. C., Prasath, S. G., Jayne, B. C. and Mahadevan, L. (2026). Postural control in an upright snake. *J. R. Soc. Interface* **23**, 20250314. doi:10.1098/rsif.2025.0314
Hoffstetter, R. and Gasc, J.-P. (1969). Vertebrae and ribs of modern reptiles. In *Biology of the Reptilia*, Vol. 1 (ed. C. Gans, A. d'A. Bellairs and T. S. Parsons), pp. 201-310. London: Academic Press.
Hunt, N. H., Jinn, J., Jacobs, L. F. and Full, R. J. (2021). Acrobatic squirrels learn to leap and land on tree branches without falling. *Science* **373**, 697-700. doi:10.1126/science.abe5753
Jayne, B. C. (1982). Comparative morphology of the semispinalis-spinalis muscle of snakes and correlations with locomotion and constriction. *J. Morphol.* **172**, 83-96. doi:10.1002/jmor.1051720108
Jayne, B. C. (1988). Muscular mechanisms of snake locomotion: an electromyographic study of the sidewinding and concertina modes of *Crotalus cerastes*, *Nerodia fasciata* and *Elaphe obsoleta*. *J. Exp. Biol.* **140**, 1-33. doi:10.1242/jeb.140.1.1
Jayne, B. C. and Riley, M. A. (2007). Scaling of the axial morphology and gap-bridging ability of the brown tree snake, *Boiga irregularis*. *J. Exp. Biol.* **210**, 1148-1160. doi:10.1242/jeb.002493
Jayne, B. C., Lehmkuhl, A. M. and Riley, M. A. (2014). Hit or miss: branch structure affects perch choice, behaviour, distance and accuracy of brown tree snakes bridging gaps. *Anim. Behav.* **88**, 233-241. doi:10.1016/j.anbehav.2013.12.002
Jørgensen, R. M. and Jayne, B. C. (2017). Three-dimensional trajectories affect the epaxial muscle activity of arboreal snakes crossing gaps. *J. Exp. Biol.* **220**, 3545-3555. doi:10.1242/jeb.164640
Kelley, K. C., Arnold, S. J. and Gladstone, J. (1997). The effects of substrate and vertebral number on locomotion in the garter snake *Thamnophis elegans*. *Func. Ecol.* **11**, 189-198. doi:10.1046/j.1365-2435.1997.00077.x
Kral, K. (2003). Behavioural–analytical studies of the role of head movements in depth perception in insects, birds and mammals. *Behav. Process.* **64**, 1-12. doi:10.1016/S0376-6357(03)00054-8
Lillywhite, H. B., LaFrentz, J. R., Lin, Y. C. and Tu, M. C. (2000). The cantilever abilities of snakes. *J. Herpetol.* **34**, 523-528. doi:10.2307/1565266
Mauro, A. A. and Jayne, B. C. (2016). Perch compliance and experience affect destination choice of brown tree snakes (*Boiga irregularis*). *Zoology* **119**, 113-118. doi:10.1016/j.zool.2015.12.002
Nicodemo, P. (2012). Longitudinal variation in the axial muscles of snakes. *Masters thesis*. University of Cincinnati.
Rieser, J. M., Li, T.-D., Tingle, J. L., Goldman, D. I. and Mendelson, J. R. (2021). Functional consequences of convergently evolved microscopic skin features on snake locomotion. *Proc. Natl. Acad. Sci. USA* **118**, e2018264118. doi:10.1073/pnas.2018264118
Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B. et al. (2012). Fiji: an open-source platform for biological-image analysis. *Nat. Methods* **9**, 676-682. doi:10.1038/nmeth.2019
Socha, J. J. (2006). Becoming airborne without legs: the kinematics of take-off in a flying snake, *Chrysopelea paradisi*. *J. Exp. Biol.* **209**, 3358-3369. doi:10.1242/jeb.02381
Socha, J. J. and LaBarbera, M. (2005). Effects of size and behavior on aerial performance of two species of flying snakes (*Chrysopelea*). *J. Exp. Biol.* **208**, 1835-1847. doi:10.1242/jeb.01580

Tingle, J. L., Jurestovsky, D. J. and Astley, H. C. (2023). The relative contributions of multiarticular snake muscles to movement in different planes. *J. Morphol.* **284**, e21591. doi:10.1002/jmor.21591

Tingle, J. L., Garner, K. L. and Astley, H. C. (2024). Functional diversity of snake locomotor behaviors: a review of the biological literature for bioinspiration. *Ann. N. Y. Acad. Sci.* **1533**, 16-37. doi:10.1111/nyas.15109

Thorpe, S. K. S., Holder, R. L. and Crompton, R. H. (2009). Orangutans employ unique strategies to control branch flexibility. *Proc. Natl. Acad. Sci. USA* **106**, 12646-12651. doi:10.1073/pnas.0811537106

Yeaton, I. J., Ross, S. D., Baumgardner, G. A. and Socha, J. J. (2020). Undulation enables gliding in flying snakes. *Nat. Phys.* **16**, 974-982. doi:10.1038/s41567-020-0935-4

Zamore, S. A., Araujo, N. and Socha, J. J. (2020). Visual acuity in the flying snake, *Chrysopelea paradisi*. *Int. Comp. Biol.* **63**, 209-222. doi:10.1093/icb/icaa143

Zheng, Y. and Wiens, J. J. (2016). Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Mol. Phylogenet. Evol.* **94**, 537-547. doi:10.1016/j.ympev.2015.10.009