RESEARCH ARTICLE

Dynamic gap crossing in *Dendrelaphis*, the sister taxon of flying snakes

Mal Graham[1,2,*] and John J. Socha[2]

ABSTRACT

Arboreal animals commonly use dynamic gap-crossing behaviors such as jumping. In snakes, however, most species studied to date only employ the quasi-static cantilever crawl, which involves a whole-body reach. One exception is the paradise tree snake (*Chrysopelea paradisi*), which exhibits kinematic changes as gap distance increases, culminating in dynamic behaviors that are kinematically indistinguishable from those used to launch glides. Because *Chrysopelea* uses dynamic behaviors when bridging gaps without gliding, we hypothesized that such dynamic behaviors evolved ancestrally to *Chrysopelea*. To test this predicted occurrence of dynamic behaviors in closely related taxa, we studied gap bridging locomotion in the genus *Dendrelaphis*, which is the sister lineage of *Chysopelea*. We recorded 20 snakes from two species (*D. punctulatus* and *D. calligastra*) crossing gaps of increasing size, and analyzed their 3D kinematics. We found that, like *C. paradisi*, both species of *Dendrelaphis* modulate their use of dynamic behaviors in response to gap distance, but *Dendrelaphis* exhibit greater inter-individual variation. Although all three species displayed the use of looped movements, the highly stereotyped J-loop movement of *Chrysopelea* was not observed in *Dendrelaphis*. These results support the hypothesis that *Chrysopelea* may have co-opted and refined an ancestral behavior for crossing gaps for the novel function of launching a glide. Overall, these data demonstrate the importance of gap distance in governing behavior and kinematics during arboreal gap crossing.

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

INTRODUCTION

Gap crossing is a critical skill for animals living in the discontinuous arboreal habitat, and many arboreal species can use multiple gap-crossing behaviors (Graham and Socha, 2020). Different behaviors vary in their biomechanics, and this variation, as well as the mechanical features of the environment, influence how an animal crosses a gap. Orangutans and squirrels, for example, alter their locomotor behaviors based on the compliance of branch supports (Casteren et al., 2013; Hunt et al., 2021; Thorpe et al., 2009), and brown tree snakes (*Boiga irregularis*) lunge more often toward wider targets (Jayne et al., 2014). One environmental factor – the size of the gap – is a key determinant of what behavior an animal

[1]Wild Animal Initiative, Inc., Minneapolis, MN 55437, USA. [2]Department of Biomedical Engineering and Mechanics, Virginia Tech, Blacksburg, VA 24061, USA.

*Author for correspondence (mal.graham@wildanimalinitiative.org)

M.G., 0000-0002-4527-5361; J.J.S., 0000-0002-4465-1097

selects, because of distance limitations associated with reaching and jumping. In general, animals face greater biomechanical challenges as they cross greater distances, possibly incurring greater torques, higher landing speeds and increased risk of falling. If a gap is sufficiently large, an animal may not be able to cross at all, representing a physical and biomechanical limit to its ecology.

Despite the importance of distance in the gap-crossing context, thorough investigations of how distance influences the use of different crossing behaviors have only been carried out in a small number of species across groups ranging from insects to primates to birds, and few of these studies have systematically varied gap distance from minimum to maximum crossing ability (but see Blaesing and Cruse, 2004; Gart et al., 2018; Hoefer and Jayne, 2013; Jayne and Riley, 2007). The ways in which distance influences gap-crossing behavior and kinematics have, however, been investigated in the paradise tree snake (*Chrysopelea paradisi*) (Graham and Socha, 2021) and the brown tree snake (Jayne and Riley, 2007). In these species, small gaps are traversed with a slow and steady crawl in a cantilevered body position, congruent with all other snake species that have been investigated (Jayne and Riley, 2007; Lillywhite et al., 2000; Lin et al., 2003; Ray, 2012). Similarly to other snake species, the paradise tree snake and the brown tree snake reach a cantilever limit around 50–60% snout–vent length (SVL), but as gap distance increases, these snakes begin to use dynamic movements (Graham and Socha, 2021; Jayne and Riley, 2007).

At intermediate gap distances, between approximately 30% and 70% SVL, both brown tree snakes and paradise tree snakes utilize above-branch lunges, a dynamic movement in which the snake rises up very slightly and then moves quickly outward and downward onto the target branch (Byrnes and Jayne, 2012; Graham and Socha, 2021; Jayne and Riley, 2007). As gap distance increases further, the paradise tree snake utilizes faster gap-crossing movements with larger vertical and horizontal excursions and changes in body posture, beginning to perform looped movements. As in our previous study (Graham and Socha, 2021), we define looped movements as any dynamic behavior that involves accelerating upward out of a vertically oriented, lateral body bend arranged below the line of the branches (e.g. Fig. 1A,B). For the very largest gaps (approximately 80–120% SVL; Graham and Socha, 2021), these changes culminate in the use of the J-loop jump, which is kinematically indistinguishable from the jump used for launching a glide (Socha, 2006). This pattern suggests that a behavior evolved in one context, gap bridging, could have been co-opted for another, glide launching.

Adding to this evolutionary puzzle is the use of dynamic movements in *Dendrelaphis*, the sister lineage of *Chrysopelea* (Figueroa et al., 2016). Preliminary qualitative video data of a single individual (*D. pictus*; Socha, 2011) suggest that *Dendrelaphis* may exhibit similar dynamic movements to *Chrysopelea*. However, individual behavior may not be representative of a species, and no
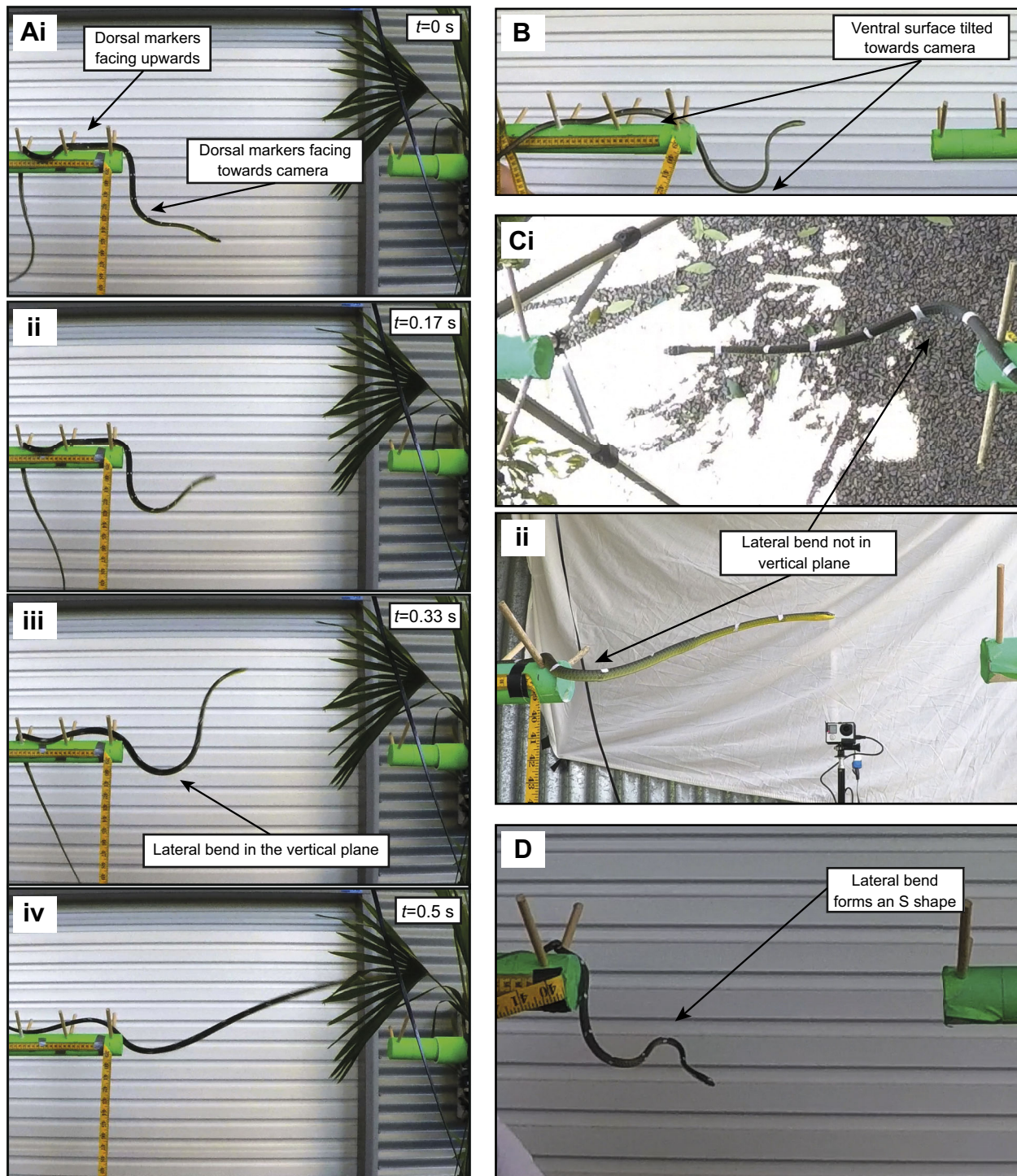
Fig. 1. Illustrations of snake gap-crossing movements with associated special behaviors. (A) A snake (*Dendrelaphis punctulatus*; snout–vent length, SVL 88.9 cm; gap distance 66.3% SVL) forming a lateral bend (Aiii) during a dynamic gap-crossing bout. The snake is utilizing axial twist (Ai) as indicated by the different orientations of the dorsal surface in the gap and on the branch. (B) A second individual (*Dendrelaphis calligastra*; SVL 77.4 cm; gap distance 49.4% SVL) may appear to use axial twist because it is forming a lateral bend in the vertical plane, but it has actually reoriented the whole body: the dorsal surface in the gap and that on the branch both point away from the camera. (C) Snakes can also make lateral bends without axial twist in the horizontal plane, as one individual (*D. punctulatus*; SVL 81.2 cm; gap distance 65.5% SVL) can be seen doing here. (D) Finally, some snakes formed multiple bends to make an 'S' shape (*D. calligastra*; SVL 46.2 cm; gap distance 67.2% SVL).

systematic experimentation or quantitative analysis has been conducted on *Dendrelaphis*. If this sister taxon exhibits similar dynamic behaviors and patterns of usage with gap distance, that suggests that the dynamic movements used by *Chrysopelea* to initiate glides may have been co-opted from gap-crossing behaviors. The hypothesis that jumping evolved prior to gliding has been suggested previously (Jayne and Riley, 2007; Socha, 2006) but has not been explored in any study. As there have been no studies of gap

crossing in *Dendrelaphis*, we effectively know nothing about its gap-crossing behavior, particularly how it responds to increasing gap distance.

In this study, we examined the influence of gap distance on behavior and non-cantilever movement kinematics in two species of *Dendrelaphis*, the green tree snake [*Dendrelaphis punctulatus* (Gray 1826)] and the northern tree snake [*Dendrelaphis calligastra* (Günther 1867)]. We selected these species of *Dendrelaphis* because anecdotal observations from snake catchers in Australia suggested that they might use lunging movements to cross gaps. The study had two aims: first, to determine whether these species use dynamic behaviors to cross gaps, and second, to determine how the kinematics of their non-cantilever gap-crossing movements vary with gap distance. We compared these data with the behavioral repertoire of *Chrysopelea* to provide a preliminary inference of their evolutionary acquisition. We hypothesized that both species of *Dendrelaphis* utilize dynamic movements to cross gaps. Furthermore, as gap distance increases, *Dendrelaphis* should exhibit kinematic and postural changes in these dynamic movements that are similar to those observed in *Chrysopelea*.

MATERIALS AND METHODS
Animals
We studied a total of 20 *Dendrelaphis* snakes from Australia. Of the 16 wild-caught specimens, five [1 male (M), 4 female (F)] were common tree snakes (*D. punctulatus*) and three [2 F, 1 unknown (U)] were northern tree snakes (*D. calligastra*) from in and around the Daintree Rainforest Observatory, Cape Tribulation, QLD, Australia; six were common tree snakes (2 M, 1 F, 3 U) from the Sunshine Coast region, QLD, Australia; and two were wild-caught adult common tree snakes (1 M, 1 F) housed at the Cairns Aquarium, Cairns, QLD, Australia. The remaining four were captive-bred juvenile common tree snakes (2 M, 2 F) from the Cairns Aquarium.

Experimental trials began in the morning once temperatures were above 24°C. Most data collection periods were 3–4 h in a day, although a few lasted as many as 6 h. All snakes were given several minutes of rest between trials, and between 15 and 60 min if the snake showed heavy breathing, shaking potentially due to muscular strain, or refusal to cross a gap several times in a row. All wild-caught snakes (except those housed at the Cairns Aquarium) were returned to their site of capture within 24 h of collection.

If ambient temperatures dropped below 24°C, snakes were placed in a reptile tank with a heating pad between trials to maintain similar body temperatures throughout the study. Temperature was otherwise not controlled in the field, with temperatures in the experimental arena varying from 21.8 to 36.6°C across all trials, and from 22.4 to 36.6°C for non-cantilever trials, specifically (Table S1).

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).

Gap-crossing trials
Setup
Prior to trials, we measured and marked each snake. We took an initial estimate of SVL manually, by gently stretching the snake out along a measuring tape, which was used to determine the gap distances to be presented. For all snakes except those in the Cairns Aquarium, we refined this initial estimate after data collection using

an overhead photograph in a natural curved position, following Astley et al. (2017). Briefly, length was determined in FIJI software (Schindelin et al., 2012) using a spline fit to multiple points on the body. For trials, snakes were marked with white dots (diameter ∼6 mm) using non-toxic, acrylic paint, with 10–17 marks per snake, beginning at the head and ending at the vent. To increase the visibility of the markers from multiple camera views, we marked both the dorsal and lateral surfaces of the snake.

The gap-crossing arena comprised two schedule-40 PVC pipes (outer diameter 48.1 mm, length 80–100 cm) wrapped with green gaffer tape (GaffTac 2 inch keying tape, Rosco, Stamford, CT, USA) to increase the surface roughness. The branches were 138 cm above the ground, and lined with two rows of small wooden dowels (diameter 6 mm, length 10 cm) near the top of the pipe, spaced 10 cm apart and angled radially at 45 deg from the midline. The target branch was decorated with natural vegetation from the surrounding area to provide a refuge, used as a visual cue to encourage the snake to cross the gap. Although available natural vegetation varied with location, we placed the vegetation away from the edge, such that the snake was always landing on the same target.

We conducted work in three regions: far northern Queensland, the only area where *D. calligastra* are present; at the Cairns Aquarium; and in the Sunshine Coast region, where encounters with *D. punctulatus* are more common. In the majority of trials, four cameras (Hero4 Black, GoPro, San Mateo, CA, USA) were set up to record the gap-crossing movements. However, sometimes only two cameras successfully recorded the behavior (resulting from battery- or heat-related malfunctions), and for some trials a fifth camera was available and used. In both northern Queensland and the Sunshine Coast region, the work area was under an open-air shelter with a roof; the six Cairns Aquarium snakes were studied inside the Aquarium building. Camera placements in open-air work areas typically involved three side views and an overhead view. In the Sunshine Coast work area, an additional camera was available, and was used to get a fourth side view. An overhead view was not possible inside the Cairns Aquarium, and cameras were set up along the sides at different vertical heights. Lastly, some trials were conducted outside in the open air, and an overhead view was also not possible in these setups.

Video was recorded at 120 frames s^{-1} with an image size of 1920×1080 pixels. The cameras were typically synchronized with a custom synchronization system designed for GoPro cameras (MewPro 2, Orangkucing Lab, Tokyo, Japan). Additionally, we recorded a flashing light produced by a headlamp (H2R Nova, OLight, 3 flashes s^{-1}) as a backup and/or to confirm synchronization between cameras.

The pipe the snake started on was designated the 'origin branch' and the pipe the snake was crossing towards was designated the 'target branch'. These branches were set up horizontally in a straight line at the same height (Fig. 2, top), with a variable gap between the two branches. Temperature and air speed were recorded at the start of each trial using a digital anemometer (HP-866B, HoldPeak, Zhuhai Jida Huapu Instrument Co., Ltd, Zhuhai, China); trials were not initiated unless wind speed was less than 2 mph (∼3.2 km h^{-1}) in all directions.

Determining the distance at which non-cantilever movements begin
For each snake, we aimed to determine the gap distance at which the snake began to exclusively use non-cantilever movements, and then increased the gap distance to elicit as many additional non-cantilever gap crosses as the snake would perform. We initially attempted to determine each snake's maximum cantilever distance
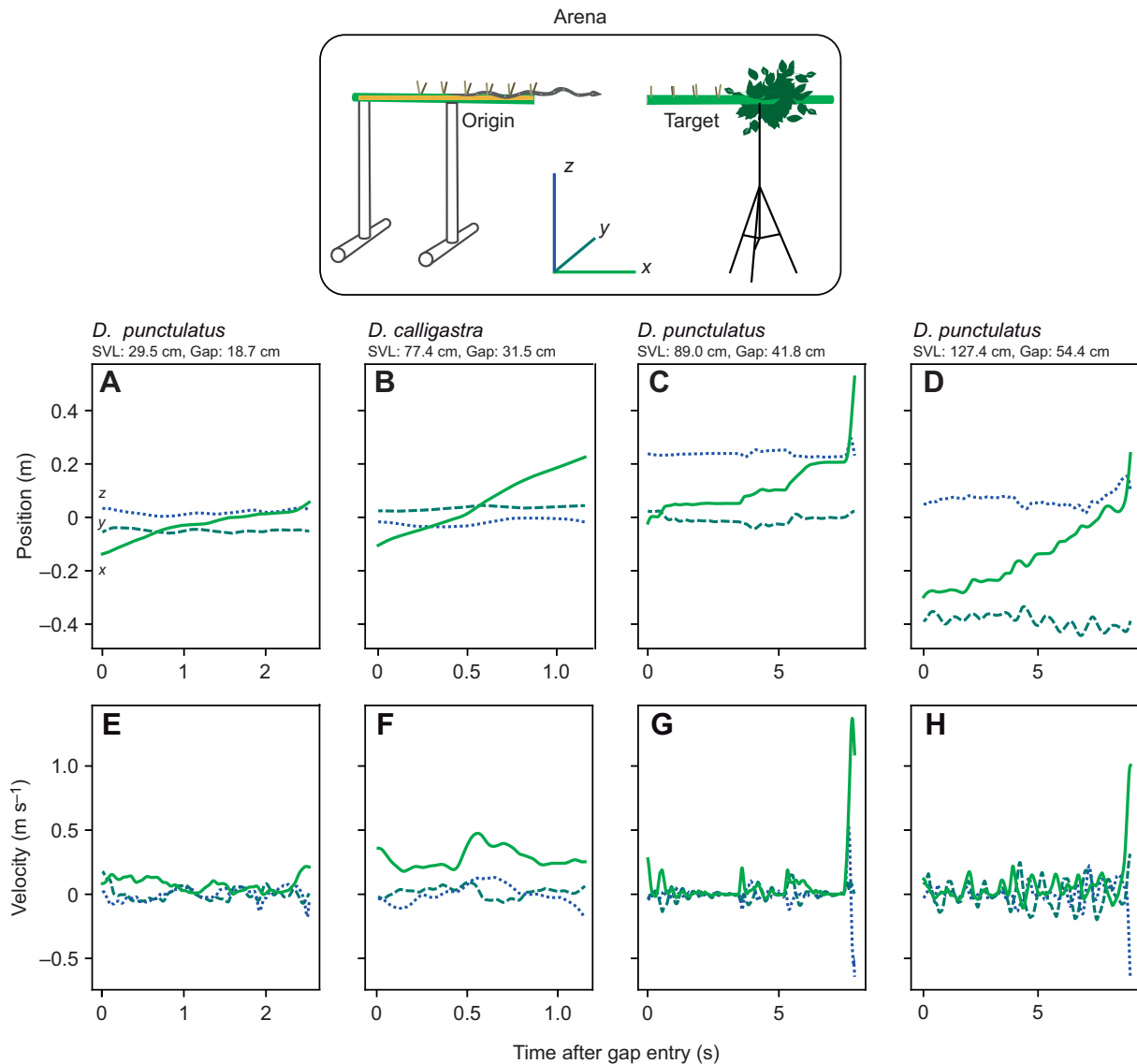
Fig. 2. Kinematics of the head in five representative non-cantilever movements. (A–D) Each panel shows a single trial (each from a different individual) in which the snake crossed the gap using a dynamic movement (none of which involved a loop or axial twisting). The species, SVL and gap distance are indicated above the column. (E–H) The corresponding velocity trajectories for the trial. The diagram of the arena is shown at the top for reference.

by drawing away the target branch from the snake as it crossed until failure was observed, following the method used in some prior studies of gap crossing in snakes (Lillywhite et al., 2000; Ray, 2012). We attempted this method with several snakes, but found that the movement of the target branch led them to either lunge at the target branch or turn back to the origin branch. As such, we reverted to presenting snakes first with a small gap, then gradually increasing the gap distance a few centimeters at a time. From this series of trials, an intermediate gap-size range could be identified, such that the snake always used cantilevers for smaller gaps and always used non-cantilevers for larger gaps. Additional trials were presented within the intermediate range to identify the largest gap distance the snake could cross with a cantilever within increments of 2 cm.

For the first and second snakes, initial gaps presented were approximately 20% SVL. The data from the first two snakes informed our expectations about the species' cantilever abilities, so for subsequent snakes, we began by presenting a fixed-size gap of between 30% and 40% SVL. Gap distances were set using a

measuring tape attached to the origin branch. We found that different individuals responded differently to the same amount of gap distance increase, so we used the snake's behavior to determine how much to increase the gap distance between trials, and sometimes presented smaller gaps if the snake could not or did not successfully cross a presented gap distance. Thus, the gap presentation order and number of events recorded varied between snakes, but we chose to use this approach because it led to the best chance of eliciting larger gap crosses.

Behavior coding

Each successful gap-crossing event was categorized as a 'cantilever' or 'non-cantilever' as in Graham and Socha (2021). Briefly, cantilever movements were characterized primarily by minimal variation from a straight line path of the head and a relatively straight, stiff body posture, along with essentially quasi-static movement, whereas non-cantilever movements did not fit this profile. Additional details of how behaviors were coded are

provided in the Supplementary Materials and Methods. Overall, we recorded kinematic and behavioral data from 92 successful cantilever trials and 121 successful non-cantilever trials. The mass, SVL, number of successful non-cantilever trials and range of distances each snake crossed using a non-cantilever movement are reported in Table S1.

We also examined the video data for the non-cantilever movements at the acceleration frame (the first moment the dynamic movement begins – see below), and categorized the movement as a looped movement if it utilized a single below-branch, vertically oriented body bend to generate the dynamic movement (Fig. 1Aiii). The J-loop used in *C. paradisi* is one type of looped movement, defined using the following criteria: (1) it is a looped movement, (2) the body forms a distinctive 'J' shape in the gap, (3) the loop is formed with a lateral bend that is oriented in the vertical plane through the use of axial twisting, and (4) the snake utilizes a static 'anchor' during acceleration (i.e. some portion of the body on the branch does not move during the acceleration phase) (Graham and Socha, 2021; Socha, 2011).

We examined the *Dendrelaphis* video data to look for the first three of these features in the dynamic trials: whether there was a loop, whether this loop was 'J' shaped, and whether the snake was forming the loop using a combination of a lateral bend and axial twisting. Because our camera views mostly focused on the body within the gap, we could not always identify the presence of a static anchor (which would require views of the on-branch body). To look for the presence of axial twist, we analyzed the acceleration frame to determine whether the portion of the snake's body forming the loop was oriented with the dorsal surface facing to the side, while the dorsal surface of the head or the on-branch portion of the body faced up (as in Fig. 1Aiii).

We examined each non-cantilever behavior for the presence of various other behaviors observed in the brown tree snake and the paradise tree snake. Snakes often begin non-cantilever crossings by extending a significant distance in a cantilever before initiating the dynamic portion of the movement. Then, the snake may either assume a different body position before accelerating, or accelerate upward directly from the cantilevered position. For this study, we refer to the initial cantilever stage as the 'approach phase', the transition into a new body position (if present) as the 'transition phase' and the dynamic portion of the movement as the 'dynamic phase'. In the video, the moment the transition phase begins is the 'transition frame' and the moment the dynamic phase begins is the 'acceleration frame'. The video from each non-cantilever trial was reviewed to identify the presence or absence of these phases, and to subsequently identify the transition and acceleration frames. In some cases, the two frames were the same (e.g. if the snake began accelerating immediately from a cantilevered position, as shown in Movie 1, non-cantilever example 2). Finally, in seven trials, we adjusted the snake's position slightly by tapping in order to get it to finish crossing the gap; if so, we did not record a transition frame, as we had interfered with the transition from cantilever to dynamic movement.

Kinematic analyses of non-cantilever movements

For all trials identified as non-cantilevers, we digitized the position of the head during gap crossing using 3D digitizing software. Most trials were analyzed using the MATLAB (The MathWorks, Natick, MA, USA) package DLTdv8a (Hedrick, 2008). Three trials, filmed in a fisheye mode that increased distortion beyond what DLTdv8a can handle, were analyzed in the program Argus (Jackson et al., 2016), which works similarly but has additional functionality for fisheye lens distortion.

From each trial, the video sequence used for analysis was generally from the frame in which the snake's nose tip crossed the end of the origin branch into the gap ('entry') until the snake landed on the target gap following a successful period of movement ('landing'). If the snake made multiple gap-crossing attempts or had to be removed and reintroduced to the arena, only the final, successful crossing bout was analyzed. Additionally, some individuals paused for long periods in the relevant crossing bout. For these trials, we digitized the position of the head from when the snake appeared to begin moving toward the target. We also digitized the position of the origin branch end, the target branch end and two points along a vertical reference (either a plumb line or a vertical line in the background) to identify the direction of gravity.

To translate the 2D video coordinates of the head position into 3D world coordinates, we digitized endpoints of a wand of known length moving around the experimental arena. These points, along with profiles of the cameras, were used in the Matlab package Easywand (Hedrick, 2008) to generate coefficients to facilitate direct linear transformation. Using these coefficients, DLTdv8a generates 3D positions of digitized points.

We used a custom Python code to transform the data exported from DLTdv8a into a right-hand coordinate system such that the *x*-axis pointed from the origin branch to the target branch, the *y*-axis pointed from side-to-side in the horizontal plane, and the *z*-axis was aligned with gravity, with positive upward. The head trajectory was first smoothed using a global, cross-validatory spline (Woltring, 1986). We then determined an appropriate smoothing parameter by visually comparing the smoothed trajectories with the video data from 10 trials with easily distinguishable features, such as a small head tilt during the dynamic phase, to find a smoothing parameter that would remove apparent noise while preserving features of the movement (Fig. S1). This review led to a smoothing parameter that was 64 times the smoothing value that met the global cross-validatory criteria for that trial. We then plotted the smoothed data on top of the raw data for all trials and reviewed the video for any trials in which there were noticeable differences between the smoothed and raw outputs, and compared peak vertical position values between the smoothed and raw data. The visual comparison appeared appropriate, and the peak vertical position in the smoothed data did not differ from the raw data by more than 1/1000 of a meter, showing that the selected smoothing value preserved all real features of the movement. A selection of representative trajectories can be seen in Fig. 2A–H, and all trajectories can be seen in Fig. S2A.

The digitized position of the branch ends and the position of the snake's head at landing (i.e. in the final frame of the smoothed trajectory) were used to calculate two distances for all non-cantilever trials (Table S1): the true gap distance (NC gap distance) and total distance traveled (DT). The latter metric is defined as the Euclidean distance between the snake's head location at landing and the origin branch end.

From the position time series data, we calculated the horizontal and vertical excursion (Fig. 3Aii,iii) of the movement throughout the gap-crossing event by subtracting the leftmost head position from the rightmost head position, and the vertically highest from vertically lowest head position, respectively. For each dimension, the velocity (*v*) of the head in the *i*th frame was calculated from the smoothed position data (*p*) at neighboring frames using finite differences:

$$v_i = \frac{p_{i+1} - p_{i-1}}{2} \times \text{frame rate.} \tag{1}$$

The resulting raw velocity data were smoothed using a global, cross-validatory spline (Woltring, 1986). The velocity time series for each trial can be seen in Fig. S2B.
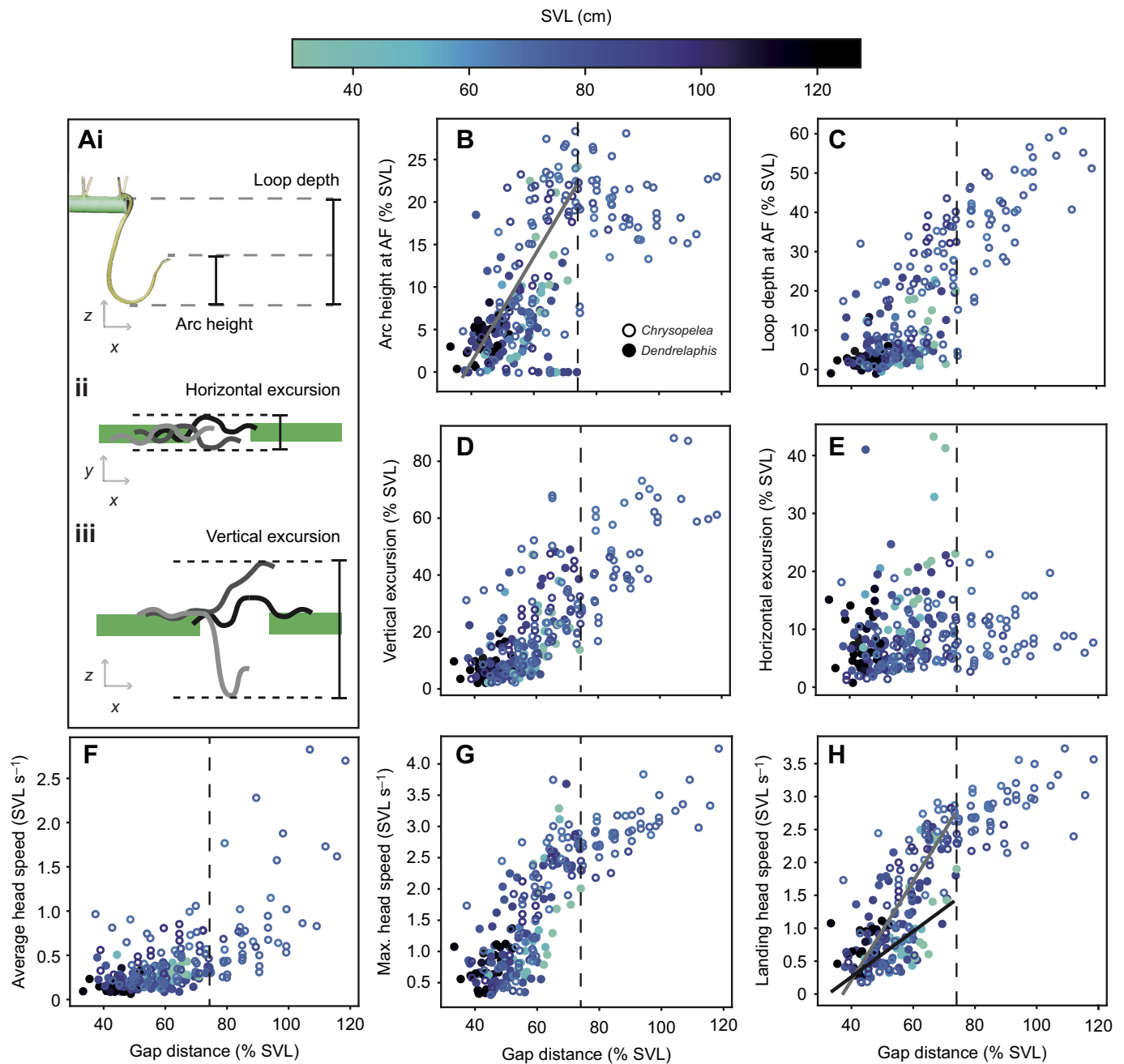
Fig. 3. Comparison with gap crossing in flying snakes. (A) Parameters characterizing the snake's body position: loop depth (the vertical distance from the origin to the trough of the body), arc height (the vertical distance from the head to the trough of the body) and horizontal and vertical excursion. (B) Arc height, (C) loop depth, (D) vertical and (E) horizontal excursion, and (F) average, (G) maximum and (H) landing head speed. AF, acceleration frame. Open circles are data from *Chrysopelea paradisi* (Graham and Socha, 2021); filled circles are those from *Dendrelaphis* (present study). Gray dashed lines indicate the gap distances included for analysis; data from additional trials at larger gap distances (exceeding the maximum gap distances crossed by *Dendrelaphis* in this study) are included for illustration only. Values for all metrics overlapped between the two groups at the smaller gap distances, and no significant differences were detected for excursion (vertical or horizontal) or relative head speed (average, maximum or landing). However, both arc height and loop depth increased more quickly with increasing gap distance in *C. paradisi*. The *C. paradisi* data in each panel represent 137 trials from 6 individuals; the *Dendrelaphis* data in each panel show 118 trials from 18 individuals; 115 trials from 15 individuals were included in statistical analysis.

From the velocity time series, we identified three behaviorally relevant metrics: the landing velocity, the maximum velocity and the average velocity while moving. The landing speed was defined as the speed of the head at landing, calculated as the magnitude of the resultant velocity in the last frame of the velocity time series. The maximum speed, defined as the greatest magnitude of the resultant velocity of the head attained during the trial, was calculated as the maximum value of the magnitude of the resultant velocity time series throughout the movement. The average velocity while moving, defined as the average moving speed of the animal across the whole trial, was calculated by taking the average of the magnitude of the resultant velocities of the head across all frames in which the snake's velocity along the *x*-axis was greater than 0.02 m s^{-1}. This calculation excludes the effects of long pauses or

other movements in which the snake was not actively moving towards the target.

Posture analyses at the acceleration frame

To examine how gap distance influences the starting posture used for dynamic movements, we examined body posture at the acceleration frame and the vertical position of the head, relative to the origin branch. At the acceleration frame, we digitized the position of the markers on the snake that were in the gap, and one additional marker that was the first marker on the origin branch. These marker positions were used to calculate the arc height and the loop depth, as previously defined for *C. paradisi* (Graham and Socha, 2021). Briefly, the arc height quantifies the position of the head relative to the lowest point on the body, and the loop depth quantifies the position of the lowest point on the body relative to the origin branch (Fig. 3Ai).

We also calculated the vertical distance (along the *z*-axis) from the origin branch to the head at two time points: at the acceleration frame and at the peak of the movement. These are referred to as the 'vertical position at acceleration' and the 'maximum vertical position', respectively. Together with the loop depth and arc height, these metrics characterize the postural characteristics of a given behavior.

Comparisons with flying snakes

To make comparisons with flying snakes, we re-analyzed data from our gap-crossing study of *Chrysopelea paradisi* (Graham and Socha, 2021). From these data, we analyzed the same variables and fitted linear mixed models as described above, restricting the dataset to the same relative gap distances observed in *Dendrelaphis*. Because of limited specimen data, body size was not included as a predictor for *C. paradisi*. Additionally, we reviewed the motion-capture data from that study to identify trials in which *C. paradisi* did or did not use looped movements across the range of gap distances at which they used non-cantilever movements. Because the video data from those trials were not sufficiently zoomed in to assess fine differences in body orientation, axial twist was not analyzed for *C. paradisi*.

To better compare the performance of the two groups, we also examined the differences between total distance traveled and gap distance for each trial (Fig. 4A,B), and examined the maximum total distance traveled for each individual (Fig. 4C,D).

Statistical analysis of non-cantilever kinematics

We analyzed the influence of gap distance and body size (SVL) on side-to-side range, vertical range, maximum velocity, average velocity, landing velocity, loop depth at acceleration, arc height at acceleration, vertical position at acceleration and maximum vertical position of non-cantilever movements in both *Dendrelaphis* and *C. paradisi*. Each of these variables was normalized by SVL before fitting a mixed linear regression model. Each *Dendrelaphis* model included SVL (cm) and gap distance (% SVL) as the fixed effects, with individual ID as a random effect interacting with gap distance; because of insufficient size variation in *Chrysopelea*, those models used gap distance only as a fixed effect. We also fitted a mixed logistic regression to the *C. paradisi* data to determine the predicted probability of using a looped movement across gap distances. For this model, gap distance was the predictor, with individual as a random effect.

For the mixed linear models, we tested two random effects structures: one in which both slopes and intercepts were allowed to vary by individual (the random effect) and one in which only the

intercept was allowed to vary. The final random effects structure was selected by comparing the Akaike information criterion (AIC). The lower-AIC model was used, unless the random slopes model became singular, in which case the intercept-only model was used. For all models, we used a bootstrap method to calculate the 95% confidence interval for the fixed effects associated with each predictor. For comparisons between *Dendrelaphis* and *Chrysopelea*, these confidence intervals were compared. Non-overlapping confidence intervals for the slope and intercept of a regression line indicate significant differences in how the two lineages respond to increasing gap distance (in the case of slope) or overall magnitude of the dependent variable in question (in the case of intercept differences).

We were only able to collect data from three specimens of *D. calligastra*, making it difficult to detect differences between the two *Dendrelaphis* species. Because of this limitation, and because the *D. calligastra* data did not visually appear to lie outside the range of the *D. punctulatus* data, we pooled species data and did not include species as a predictor. We also calculated the scaling relationship between mass and length (Fig. S3) for the pooled data (slope: 2.8 [2.6, 3.0], intercept: −8.0 [−8.8, −7.2], adjusted R^2=0.98, $P \leq 2e-16$), and the residual values of mass of *D. calligastra* were within the range of *D. punctulatus* residuals, further supporting the decision to pool the two groups.

The final non-cantilever dataset included 121 trials from 18 *Dendrelaphis* snakes (2 snakes never displayed a non-cantilever movement). Of these 121 trials, six non-cantilever trials were excluded from the statistical analysis for two different reasons. First, 3 trials from 2 snakes that exhibited fewer than 3 non-cantilever trials were not included, as the mixed model approach could not accommodate fewer than 3 data points per individual. This issue resulted in 2 snakes being dropped from the statistical analysis. Second, three trials were excluded because the snake appeared to be exhibiting a stress response upon initial exposure to the arena (see Results). In total, then, the statistical models incorporated 115 non-cantilever trials from 16 individuals.

RESULTS

Behavior and kinematics of *Dendrelaphis*

We observed 14 trials (*n*=7 snakes) in which *Dendrelaphis* formed lateral bends, although these bends were sometimes oriented in the horizontal plane (e.g. Fig. 1C) or used to form 'S' shapes (e.g. Fig. 1D). Looped jumps were only observed in 9 trials in *Dendrelaphis* (*n*=6 snakes), and we never observed a full J-loop (involving a loop, a distinctive 'J' shape, and a single lateral bend oriented vertically through the use of axial twisting).

All *Dendrelaphis* specimens (*n*=20) performed at least one successful cantilever cross, and most (*n*=18) performed at least one successful non-cantilever cross. The average maximum successful cantilever was 44.5±7.6% SVL (mean±s.d.) for *D. punctulatus* and 44.0±8.9% SVL for *D. calligastra*. Snakes used non-cantilever crosses to cross gap distances ranging from 26.4% SVL to 74.0% SVL (Table S1); however, three of the smallest gap distances crossed by non-cantilever movement appeared to be the result of a stress response. In these trials, the two snakes in question used lunging movements for their first, or first and second, gap crosses. The lunge movement was very distinct from other dynamic movements, in that the animal moved very quickly across the gap from the moment of being placed on the origin branch, and there was no distinct approach phase. Both snakes crossed subsequent gaps much more calmly. When these trials were excluded, the range of gap distances crossed by non-cantilever movement changed to 33.3–74.0% SVL.
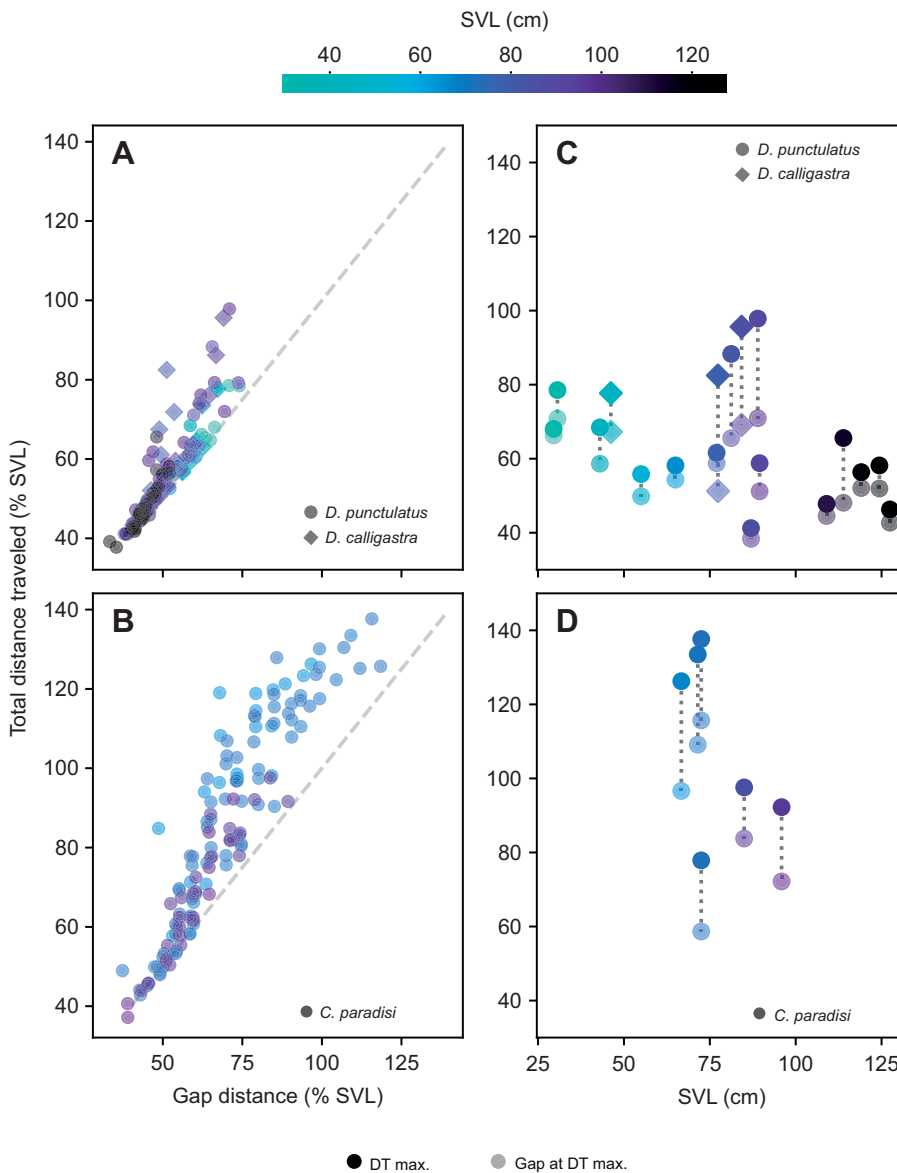
Fig. 4. Total distance traveled does not always match gap distance. Both *Dendrelaphis* (A, n=118 non-cantilever crosses) and *C. paradisi* (B, n=137 non-cantilever crosses) sometimes traveled farther than the gap distance during successful gap crosses; the gray dashed line indicates a 1:1 relationship between gap distance and distance traveled. The largest distance traveled in a single trial is shown for both *Dendrelaphis* (C, n=18 snakes) and *C. paradisi* (D, n=6 snakes). Opaque symbols indicate the maximum distance traveled (DT), whereas translucent symbols indicate the gap distance when this distance was achieved.

The snakes in this study sometimes traveled straight-line distances far exceeding the gap distance during dynamic crosses (effectively 'overshooting' the gap), particularly at intermediate gap distances (Fig. 4A,B). For example, at a gap distance of 70.9% SVL, a snake with a SVL of 89 cm traveled a total distance of 97.8% SVL (87 cm). The average difference between total straight-line travel distance and gap distance was 5.5±5.8% SVL in *Dendrelaphis* (compared with 15.1±12.1% SVL in *C. paradisi*), with 5 *Dendrelaphis* individuals exhibiting travel distances greater than 15% SVL farther than gap distance across 8 trials.

As gap distance increased, *Dendrelaphis* exhibited changes in kinematics associated with the use of increasingly dynamic behaviors, as has been observed in other snake taxa with the ability to use non-cantilever movements. Seven of the nine kinematic variables examined – maximum and landing speeds (Fig. 5B,C), horizontal and vertical excursion (Fig. 6A,B), loop depth (Fig. 6C), and z-position at both the acceleration frame and the maximum (Fig. S4) – changed significantly with gap distance (Table 1). Together, these results show that snakes were moving through greater excursions, going lower beneath the branch at

acceleration and attaining higher peak positions, with increasing speed as gap distance increased.

By contrast, the only influence of body size shown in this study was a slight decrease in average relative head speed as body size increased (0.002 SVL s^{-1} decrease per cm increase in SVL; Table 1 and Fig. 5A). Otherwise, no significant changes with body size were detected in these body-size relative variables.

In addition to the significant fixed effects of gap distance on non-cantilever kinematics, we also found a high degree of inter-individual variation, both in how individuals responded to increasing gap distance (represented by the slope random effect) and, to a lesser extent, in the magnitude of the variable in question (represented by the intercept random effect). Random slopes models were supported for average speed, vertical excursion, arc height, and maximum z-position, with random effect standard deviations being similar in magnitude to the fixed effect size (Table 1). The resulting differences in individual slope estimates are shown in Figs 5A and 6B,D and Fig. S3B. In the case of average speed and arc height, intercept random effect standard deviations were similar in magnitude to the fixed effect as well (Table 1).
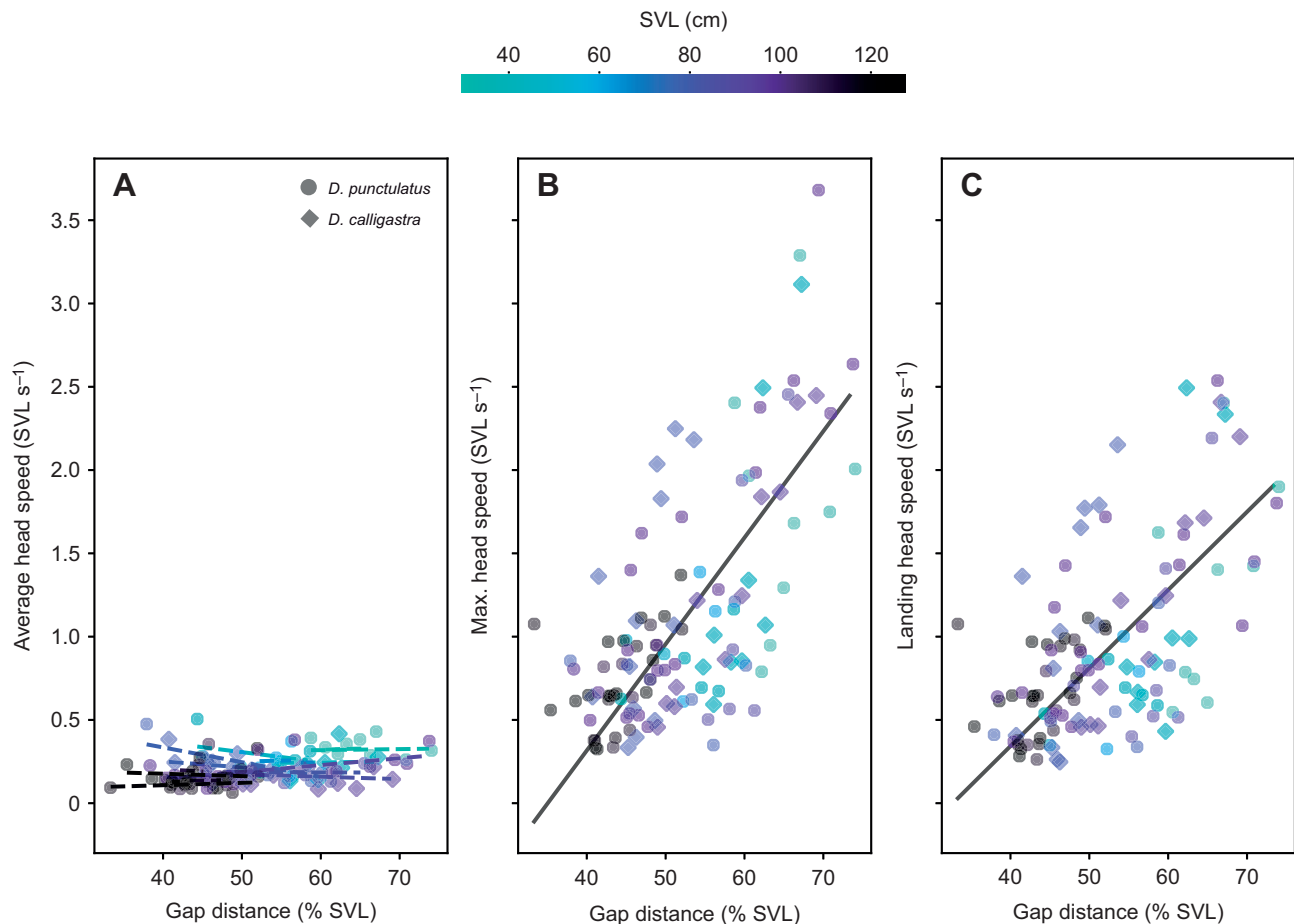
Fig. 5. Effects of gap distance on head speed. (A) Average head speed for each trial (*n*=118 trials, 115 included in statistical analysis). There was no overall effect of gap distance on average head speed in this study, but there was a large degree of inter-individual variation, with individuals responding differently to increasing gap distance. There was a small effect of body size, with large snakes moving relatively slower than small snakes. By contrast, relative maximum (B) and landing (C) head speeds increased with gap distance. Dashed lines in A indicate individual model predictions for the 18 snakes included in the mixed linear model and are shown because a random slopes model was supported for average velocity. Symbol and line color indicates SVL.

Comparisons with *Chrysopelea paradisi*

As mentioned above, we did not observe the full J-loop in *Dendrelaphis*, although we observed each of the component features in various combinations in some trials. Although *C. paradisi* also does not typically use the full J-loop for the distances in this study (<75% SVL), other gap-crossing behaviors involving loops are very common at these distances: across 137 non-cantilever crosses in *C. paradisi*, we observed 98 trials in which the snake utilized a looped movement (Fig. 7B), only some of which fitted the criteria for being a J-loop (Graham and Socha, 2021). The results of the mixed logistic regression show a significant effect of gap distance on the likelihood that *C. paradisi* will use a looped movement, with probability increasing as gap distance increases (Table S2, bottom). Based on the logistic model, *C. paradisi* has a 25% predicted probability of using a looped movement at 50% SVL, and a nearly 100% predicted probability of using a looped movement by 75% SVL (Fig. 7A).

The magnitudes of the various kinematic variables observed in this study were consistent with those found in *C. paradisi* (Figs 3B–H, 4) at similar gap distances; no significant differences in model intercepts were detected (Table S2, top), except for arc height. With regard to how the two groups responded to increasing gap distance, only two significant differences were detected, for landing speed and arc height. In the case of landing speed,

C. paradisi increased speed at a greater rate as gap distance increased. In the case of arc height, *C. paradisi* exhibited a consistent increase in arc height over the gap distance range in question, whereas *Dendrelaphis* did not exhibit any consistent response across individuals (Table 1).

Although the fixed effects (i.e. the consistent response across individuals) were similar for most dependent variables between the two groups, *Dendrelaphis* exhibited a much higher degree of inter-individual variation (Table 1). Random slopes models were only supported for loop depth in *C. paradisi*, whereas random slopes models were supported for four kinematic variables in *Dendrelaphis*, and generally the random effects standard deviation of the intercept was higher for *Dendrelaphis* than for *C. paradisi* (Table 1).

We did not compare distances traveled between the two groups statistically, because the *Dendrelaphis* study was not designed to elicit maximal performance. Nevertheless, comparing gap distances and total travel distances seems illustrative. Both groups of snakes exhibited a pattern of landing quite near the end of the target branch for gaps of ~60% SVL and below (Fig. 4A,B). As gap distance increased, snakes tended to land past the target end, sometimes by a large amount.

In two of the looped trials in *Dendrelaphis*, there was no appearance of axial twisting; instead, the snake formed a lateral bend in the vertical
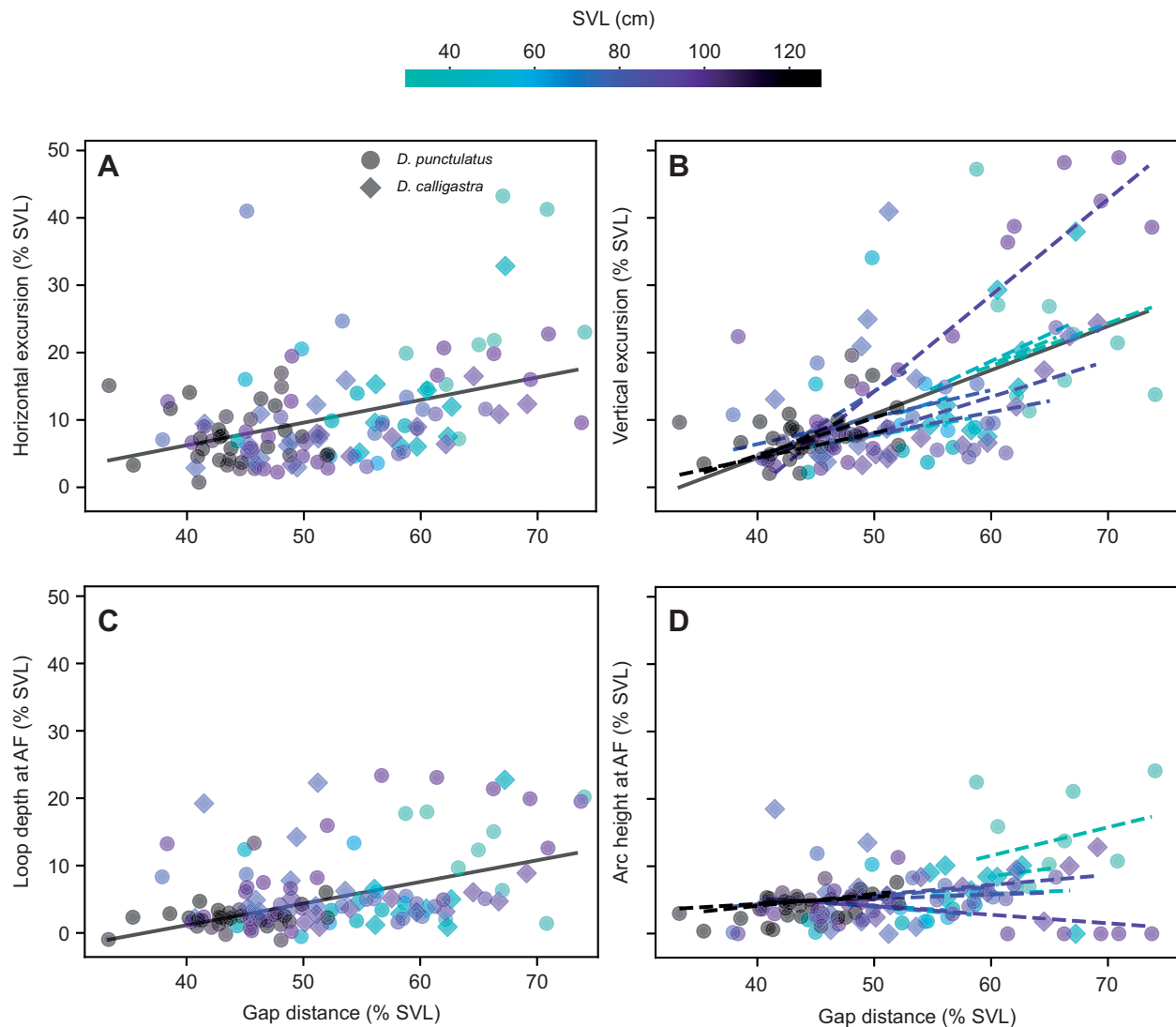
Fig. 6. Postural metrics for dynamic gap crossing movements in *Dendrelaphis*. (A) Relative horizontal excursion, (B) relative vertical excursion and (C) relative loop depth at the acceleration frame increased with gap distance. (D) There was not a significant effect of gap distance on relative arc height at the acceleration frame, although small snakes created relatively larger arcs than large snakes. Dashed lines in B and D correspond to individual predictions from the mixed linear regression. Symbol and line color indicates SVL. For all panels, *n*=118 trials, 115 trials from 18 individuals included in statistical analysis.

plane by positioning its body along the side of the branch, resting on the pegs at an angle to the horizontal (as in Fig. 1B). By contrast, we have invariably seen axial twist in every J-loop we have observed in both launch and gap-crossing contexts in *C. paradisi*. This suggests that usage by *Dendrelaphis* of axial twist may be less frequent.

DISCUSSION
Dendrelaphis utilizes non-cantilever movements that become more dynamic as gap distance increases
This study demonstrates that two species of *Dendrelaphis* snakes, *D. calligastra* and *D. punctulatus*, use dynamic movements to cross gaps. Similar to findings in other snakes (Hoefer and Jayne, 2013; Jayne and Riley, 2007; Lillywhite et al., 2000; Ray, 2012), the distance at which cantilevering stopped being observed was typically around 50% SVL. The use of dynamic movements was observed at gap distances as small as 26.4% SVL, but using dynamic movements for gap distances this small appears to be relatively less common, and may have been observed in this experiment as a stress response. When the non-cantilever trials that

appeared to involve a stress response were removed, the lower bound became 33.3% SVL.

The largest gap crossed using non-cantilever movements by *Dendrelaphis* was 74% SVL. It is possible that these species can cross even larger gaps, but we found that most snakes became much more reluctant to cross at the largest gap distances used in this study. Furthermore, the straight horizontal trajectory utilized in this study is one of the most physically taxing for snakes (Byrnes and Jayne, 2012; Jorgensen and Jayne, 2017). We therefore would predict that Australian tree snakes could reach greater distances when traveling vertically downward or upward. For comparison, the brown tree snake crossed gaps 65% larger in the vertical versus horizontal direction, with extreme performance exhibited in snakes that reached straight downward, crossing gap distances near 100% SVL (Byrnes and Jayne, 2012).

Dendrelaphis calligastra and *D. punctulatus* varied the kinematics of their non-cantilever movements as gap distance increased. Larger gap distances were associated with faster landing and maximum head speeds, greater vertical and horizontal excursions, lower

Table 1. Model parameters for influence of gap distance and body size on kinematic variables in *Dendrelaphis punctulatus*, *Dendrelaphis calligastra* and *Chrysopelea paradisi*

Dependent variable	Fixed effect estimates [95% CI]				Random effects s.d.	
	Gap distance (% SVL)		Body size (cm)		Intercept	Gap distance
Dendrelaphis						
Horizontal excursion*	0.336	[0.158–0.506]	−0.041	[−0.117–0.034]	3.91	N/A
Vertical excursion*	0.652	[0.327–1.014]	0.025	[−0.001–0.001]	5.06	0.402
Loop depth*	0.321	[0.176–0.47]	−0.001	[−0.001–0.001]	2.29	N/A
Arc height	0.069	[−0.092–0.237]	−0.029	[−0.001–0]	2.10	0.197
Vertical position at acceleration*	−0.283	[−0.439−−0.134]	0.060	[−0.001–0]	3.53	N/A
Max. vertical position*	0.460	[0.308–0.616]	0.092	[0–0.001]	2.52	0.161
Average speed‡	−0.001	[−0.004–0.003]	−0.002	[−0.003−−0.001]	0.092	0.004
Max. speed*	0.064	[0.050–0.079]	0.005	[0–0.01]	0.168	N/A
Landing speed*	0.047	[0.035–0.060]	0.005	[0–0.009]	0.138	N/A
Chrysopelea						
Horizontal excursion*	0.147	[0.053–0.242]	–	–	1.16	N/A
Vertical excursion*	0.844	[0.571–1.13]	–	–	8.06	N/A
Loop depth*	0.830	[0.408–1.28]	–	–	11.1	0.51
Arc height*	0.624	[0.481–0.768]	–	–	2.19	N/A
Vertical position at acceleration*	−0.288	[−0.497−−0.079]	–	–	3.09	N/A
Max. vertical position*	0.586	[0.445–0.729]	–	–	3.55	N/A
Average speed*	0.007	[0.002–0.012]	–	–	0.085	N/A
Max. speed*	0.076	[0.064–0.088]	–	–	0.053	N/A
Landing speed*	0.075	[0.064–0.087]	–	–	0.028	N/A

Dendrelaphis punctulatus and *Dendrelaphis calligastra*: 115 trials, 16 snakes (data from this study). *Chrysopelea paradisi*: 90 trials, 6 snakes (re-analyzed from Graham and Socha, 2021). CI, confidence interval; SVL, snout–vent length; AF, acceleration frame. Models that incorporate random slopes with gap distance per individual show the standard deviation in slope in the final column ('gap distance'); models with N/A in this column are random intercept models. Speed is reported in SVL s^{-1}; other variables are reported as % SVL. Asterisks indicate models where the 95% CI did not include zero for gap distance, indicating a significant effect on the corresponding dependent variable; the double dagger indicates a significant effect of body size. Dependent variables for which the 95% CI for the *Dendrelaphis* gap distance or intercept parameter did not overlap with the equivalent parameter in the *Chrysopelea* model are bolded or italicized, respectively. Generally, comparing the magnitude of the random effects standard deviations with the fixed effect parameters illustrates the relative importance of between-individual differences to the effect of gap and body size.

positions below the origin branch at acceleration, and higher peak heights. Taken together, these data show that as gap distance increases, *D. calligastra* and *D. punctulatus* utilize more dynamic movements that deviate increasingly from cantilever movements. By contrast, we found only one small effect of body size on the kinematic parameters.

Similar kinematics but greater inter-individual variation in *Dendrelaphis* compared with *C. paradisi*

In terms of distance, we did not observe as large gap crosses in *Dendrelaphis* as we found in *Chrysopelea* (Graham and Socha, 2021). However, the gap distance ranges reported here should be viewed as a lower bound on maximum ability, as we had much more time to elicit maximum responses in *Chrysopelea* because of the laboratory setting in that previous study. Nevertheless, we observed crossing distances greater than 64% SVL, the largest relative distance spanned by the brown tree snake *Boiga irregularis* (Jayne and Riley, 2007), in six *Dendrelaphis* specimens, including individuals from both *D. calligastra* and *D. punctulatus*, suggesting that *Dendrelaphis* fall between *Boiga* and *Chrysopelea* in ability.

Additionally, the *Dendrelaphis* studied here exhibited straight-line travel distances that were occasionally far greater than the gap distance, suggesting that some individuals may have been capable of crossing much larger gaps. Four snakes (SVL: 77, 84, 81 and 89 cm) exhibited total travel distances greater than 80% SVL, with one snake traveling 97.8% SVL. For comparison, the largest successfully crossed gap distance in *C. paradisi* was 118% SVL, but the largest straight-line travel distances in that species exceeded 130% SVL (Fig. 4B,D). Interestingly, the maximum travel distance did not always occur at the maximum gap distance, particularly for

medium-sized snakes (Fig. 4). There were not enough *C. paradisi* to analyze this potential pattern, but we anecdotally observed that the intermediate-sized *Dendrelaphis* seemed more prone to jump. Future studies might examine willingness to jump, targeting accuracy, size and age for potential biomechanical or ontogenetic explanations of this potential pattern.

Kinematically, the *Dendrelaphis* in this study exhibited many similarities in gap crossing with *Chrysopelea*. At the smallest gap distances for which non-cantilever movements were used, the two groups' movements were indistinguishable, characterized by very small variations from a cantilevered movement. As gap distance increased, both groups increased speed and excursion, and accelerated starting from lower vertical positions. However, their responses were not entirely identical, as indicated by the lack of an arc height response to gap distance in *Dendrelaphis*, the greater increase in landing speeds in *Chrysopelea*, and the much less frequent utilization of looped movements in *Dendrelaphis*. Overall, *Chrysopelea* appear to exhibit more stereotyped and complex gap-crossing behaviors at larger gap distances.

Several individuals in this study did assume postures relatively similar to those of *Chrysopelea* at some point after beginning their acceleration, but had very small (if any) arc height at the acceleration frame (as in the non-cantilever movement illustrated in Fig. 1A). In effect, *Chrysopelea* lift the head upward to form a small arc, whereas these two species of *Dendrelaphis* do not consistently do so. During recording, we also noticed a previously unemphasized feature of loop formation, which is the lowering of the body into the gap while maintaining a relatively fixed body bend during the transition phase. In *C. paradisi*, once the snake begins initiating a loop, the preparation of the pre-launch posture consistently involves the snake maintaining its head position fixed on the target branch while feeding the body forward
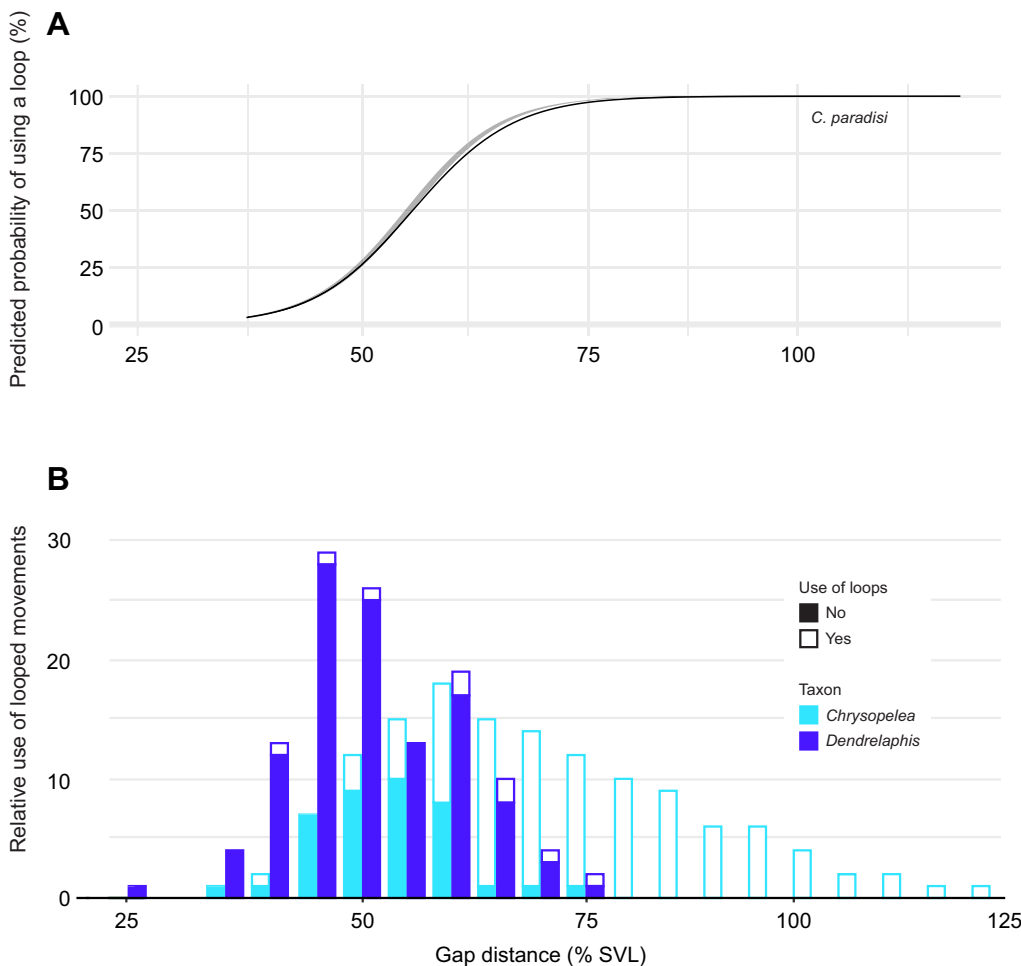
Fig. 7. The use of looped movements in *C. paradisi*, *D. calligastra* and *D. punctulatus*. (A) A mixed logistic model was used to calculate the mean (black line) and upper and lower quartile (gray shading) predicted probabilities of using a looped movement across gap distances in *C. paradisi* (*n*=137 trials, 6 individuals), illustrating an increasing likelihood of using a looped movement from 40% SVL, and near 100% probability by 75% SVL. (B) The relative use of looped movements (filled bars, non-looped; open bars, looped) at different gap distances in the two groups shows that generally *Dendrelaphis* did not use looped movements even at gap distances where *Chrysopelea* was primarily doing so (e.g. 75% SVL).

into the gap, holding a relatively consistent arc height as the loop depth increases, thereby lowering the body. We only observed this type of behavior in 3 individuals (1 *D. calligastra* and 2 *D. punctulatus*). For the other individuals that formed loops, loop formation involved more variability and oscillation up and down, and arc heights at the acceleration frame were comparatively small (as in Fig. 1A).

Although the use of looped movements appeared rare in *Dendrelaphis*, each of the components was observed at least once in many individuals. Thus, while it appears that at least some individuals of both *Dendrelaphis* species are physically capable of all of the components of looped jumps, it was relatively rare to observe each component together to utilize a looped movement for dynamic gap crossing.

In particular, the J-loop jump, used both for crossing gaps and for initiating glides in *C. paradisi*, was not observed in *Dendrelaphis* in this study. Although we observed axial twisting, looped jumps and a 'J' shape separately in many snakes, we never observed all these characteristics together, which suggests a limitation in motor program rather than morphology. However, the bulk of the data in this study correspond to gap distances in the intermediate region observed in prior work on *C. paradisi* (30–75% SVL). At these gap distances, *C. paradisi* use both looped and non-looped dynamic movements (Fig. 7B) but do not typically exhibit the full J-loop (Graham and Socha, 2021). It is possible that the two species of *Dendrelaphis* tested here might exhibit a J-loop to cross sufficiently large distances, but given that they did not use it even when the straight-line travel distance exceeded 90% SVL, we suspect they are not capable of performing it.

Whether this holds true for the more than 40 other species of *Dendrelaphis* is also an open question.

In terms of how these loops are used to generate accelerations, the kinematic data in this study are insufficient to fully analyze the behavior. However, some kinematic notes can be made. Similar to the J-loop launches described for *Chrysopelea*, when *C. paradisi* utilizes a J-loop to cross gaps, there is an initial upward acceleration, and then the point of maximum curvature moves posteriorly along the body (Socha, 2006). However, during looped movements that do not fit the J-loop profile, a range of loop patterns can be observed (Movie 2). In many cases, but not all, the body loop does not straighten during the upward acceleration and instead only straightens out towards the end of the movement, when the snake adds horizontal acceleration toward the target. Additional investigations of the use of traveling and standing waves during looped gap-crossing behaviors, including analysis of muscle activation patterns, is warranted to further explore how the looped body movements are used to generate accelerations.

In particular, the relatively infrequent use of axial twist during looped movements may also be an important factor. By twisting axially, snakes are able to form a loop in the vertical plane with a lateral bend. Previous studies in snakes show that the process of straightening a lateral bend uses all three major epaxial muscles (Jayne, 1988), allowing the snake to exert more force than it could while straightening a dorsoventral bend; therefore, utilizing a lateral bend may enable the snakes to accelerate more vigorously. By orienting the bend in the vertical plane (rather than making large

epaxial bends to the side), the snake may also be reducing the torque on the body during the preparatory phase, as extending large amounts of the body into the gap could easily exceed the cantilevering strength of the snake if held horizontally. Of course, as these data show, *Dendrelaphis* can use lateral bends in the vertical plane without twisting (Fig. 1B) if they can also angle the on-branch portion of the body. It is therefore unclear what advantage twisting axially (as opposed to reorienting the entire body) might have. Additional studies investigating the use of axial twist versus whole body re-orientation, as well as the degree of axial twist different snakes are capable of, may shed light on these questions.

Overall, both the statistical results and the behavioral observations suggest a much higher degree of inter-individual variation in *Dendrelaphis* than in *Chrysopelea*. However, the *Chrysopelea* study involved only 6 individuals of similar size and was conducted in a laboratory context, which may explain some of the difference in variation. Nevertheless, we have observed hundreds of glide launches in the field in other studies with *Chrysopelea*, and every individual we have worked with has exhibited a very consistent J-loop launch that looks identical to the behavior used for the largest gap crosses (M.G. and J.J.S., personal observation). Further analysis is warranted, particularly a study that would examine the genera under the same conditions.

Because of the larger degree of variation in *Dendrelaphis*, it may be worthwhile to pool data in this study with additional observations of gap crossing in more individuals and species, in case small fixed effects are obfuscated by large random effects. Anecdotally, we generally find that the larger looped movements (both the distinctive J-loop and other, more U-shaped loops) are highly stereotyped in *Chrysopelea*, and very recognizable from snake to snake. By contrast, the different looped movements of *Dendrelaphis* were much more variable between individuals.

Based on new data from this study, it is clear that both *Dendrelaphis* and *Chrysopelea* use dynamic movements during gap crossing, providing support for the hypothesis that the use of such dynamic movements for crossing evolved prior to their use for launching glides in the subfamily Ahaetulliinae. Additionally, *Boiga irregularis* uses dynamic movements to cross gaps (Byrnes and Jayne, 2012; Jayne and Riley, 2007) and does not use the J-loop (or, to our knowledge, any looped jumps), and many of the distinctive features of the below-branch loops used for launching glides appeared only infrequently in *Dendrelaphis*. These data suggest that while the use of dynamic movements for gap crossing is ancestral to *Chrysopelea*, the J-loop is a more sophisticated locomotor behavior that has evolved specifically in *Chrysopelea*.

To better understand the evolution of these movements, the gap-crossing behaviors present in the sub-family Ahaetulliinae (comprising *Chrysopelea*, *Dryophiops*, *Ahaetulla*, *Proahaetulla* and *Dendrelaphis*; Mallik et al., 2019) should be surveyed, along with additional species from related lineages (such as species in the sub-family Colubrinae, including *B. irregularis*). However, as the data from this study indicate, the large amount of variation in behavior between individuals and across gap distances suggests that such surveys should examine behavioral data at relatively large gap distances and from many individuals in order to identify the presence or absence of axial twisting, loop formation, body feeding and other hallmarks of the J-loop launch.

Additional observations of juvenile snakes
This is the first study in the sub-family Ahaetulliinae to observe the gap-crossing behavior of juveniles. The two smallest snakes in this study were captured together near where they hatched, suggesting

that they were very young. Nevertheless, these hatchlings also exhibited dynamic gap-crossing movements, and did not exhibit dramatic differences (relative to body size) when compared with much larger adults. These data suggest that the ability to lunge across gaps is not a learned behavior in *D. punctulatus*, conforming to a similar pattern for gliding-related behaviors seen in its sister taxon, *Chrysopelea* (Socha, 2006; Socha et al., 2005). However, we noticed that these two very small snakes appeared to be much more interested in exploring the arena and making multiple attempts to cross gaps, and they also exhibited some behavioral differences from the adults. For example, the smallest snakes sometimes would fail to reach a gap and try again, whereas large snakes that missed a crossing attempt almost invariably returned to the origin and had to be reset on the origin branch facing the target branch before they would attempt to cross again. Additionally, these two juveniles exhibited a landing behavior not seen in others, in which they touched down with only the very tip of their snout and exhibited a wave-like movement of the body to 'scoot' the nose further onto the branch, allowing them to secure purchase. These behavioral differences could be an effect of life stage, or possibly gap crossing requires less metabolic effort in smaller snakes, such that making multiple attempts is less physically taxing.

Implications for gap crossing in other taxa and contexts
Overall, additional studies of the life history and ecology of arboreal snakes would be useful to contextualize the results from this study. Although many studies of forest structure exist, none that we are aware of characterize the size of fine-scale gaps that would present locomotor challenges to arboreal animals. Thus the probability of encountering the gap distances we presented to the snakes is not known, nor are the snakes' specific movement patterns, which may favor certain gap distances. Such variation is important for understanding the ecological relevance of differences in gap-crossing ability in the arboreal environment. For instance, the apparent performance difference between *Dendrelaphis* and *Chrysopelea* may be less ecologically meaningful if most gaps an individual encounters in its environment are smaller than 50% SVL. This data limitation holds for all arboreal animals, not just snakes.

Body size also seems likely to play a key role in the ecology of gap crossing in snakes. Despite the lack of relative changes in kinematics with body size, the absolute performance is dramatically different between large and small snakes. Most snakes that have been studied can cross gaps up to 50% SVL, but 50% SVL for a 30 cm small hatchling is a much smaller actual gap than for a 120 cm adult. It seems likely, then, that small or young individuals are more frequently challenged by their environment than their adults.

It is also possible that small individuals exhibit a broader range of gap-crossing strategies to compensate for size, but it is unknown how habitat exploration or lifestyle varies with ontogeny in these species. There is some evidence of ontogenetic changes in habitat exploration in other arboreal snake species; in *Oxybelis brevirostris*, for instance, larger snakes select higher sleeping perches than smaller snakes (Montgomery et al., 2011). Although no studies to our knowledge have quantified forest density at the relevant resolution to determine how gap distance varies with canopy height, it may be that in some environments these ontogenetic shifts are influenced by gap-crossing ability. For example, in *Anolis carolinensis*, juveniles exhibit both decreased horizontal jumping performance in the lab and a tendency to occupy perches that are closer together in the field (Irschick et al., 2005), suggesting that gap-crossing ability plays a role in habitat selection for this species.

Across a wide range of taxa, the factors influencing behavior selection at distances where two or more behaviors are available have not been well elucidated, and are deserving of further investigation. The data from *Dendrelaphis* snakes provide further support for the hypothesis that animals use less dynamic reaching movements to cross small gaps and more dynamic movements to cross large gaps. However, 8 of the 20 *Dendrelaphis* studied here used non-cantilever behaviors at gap distances smaller than the observed maximum successful cantilever, showing that these snakes do not reserve dynamic movements exclusively for gaps that cannot be crossed by cantilevering. Overall, additional contextual factors beyond gap distance likely play a role in determining locomotor behavioral utilization in arboreal environments.

Data availability
All datasets, processing code and R scripts are available on GitHub: https://github.com/TheSochaLab/DendrelaphisGaps

ECR Spotlight
This article has an associated ECR Spotlight interview with Mal Graham.

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Supplementary Materials and Methods

Snake capture, housing, and transport.

Wild snakes were captured by hand and transported in cloth snake bags to the experimental site. If collected before sunset, trials began immediately upon return to the experimental site. Trials were stopped at sunset and resumed (or began) the following day. Snakes were housed in reptile caging at the experimental site, and provided with natural vegetation for a hide and a water dish.

Crossing distances

The gap distance for each trial was initially measured using a measuring tape during experimentation. To determine the largest gap crossed with a cantilever, we verified this measurement for the trial with the largest recorded gap distance, across all trials successfully crossed with a cantilever for a given individual, and any other trials in which (1) the snake used a cantilever and (2) the gap distance as recorded with the measuring tape was within 2 centimeters of this largest distance. To perform this check, the Euclidean distance between the locations of the branch ends was calculated from the 3D position of the branch ends. The largest such value for each snake is reported ("CMax" in Table S1).

The gap distance was also calculated as above for every trial in which the snake used a non-cantilever behavior ("NC gap distances", Table S1). Additionally, the total distance traveled for each trial was calculated as the Euclidean distance between the snake's head location at landing and the origin branch end (DT, Table S1).
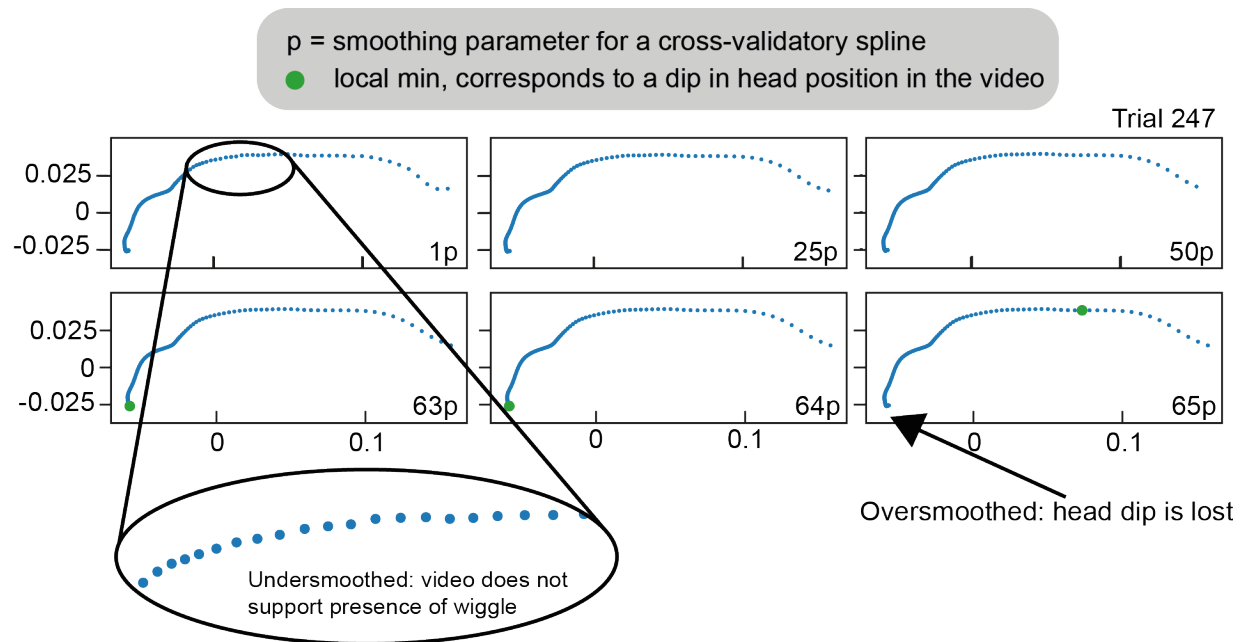
Fig. S1. Illustration of how smoothing changes with smoothing parameter p.
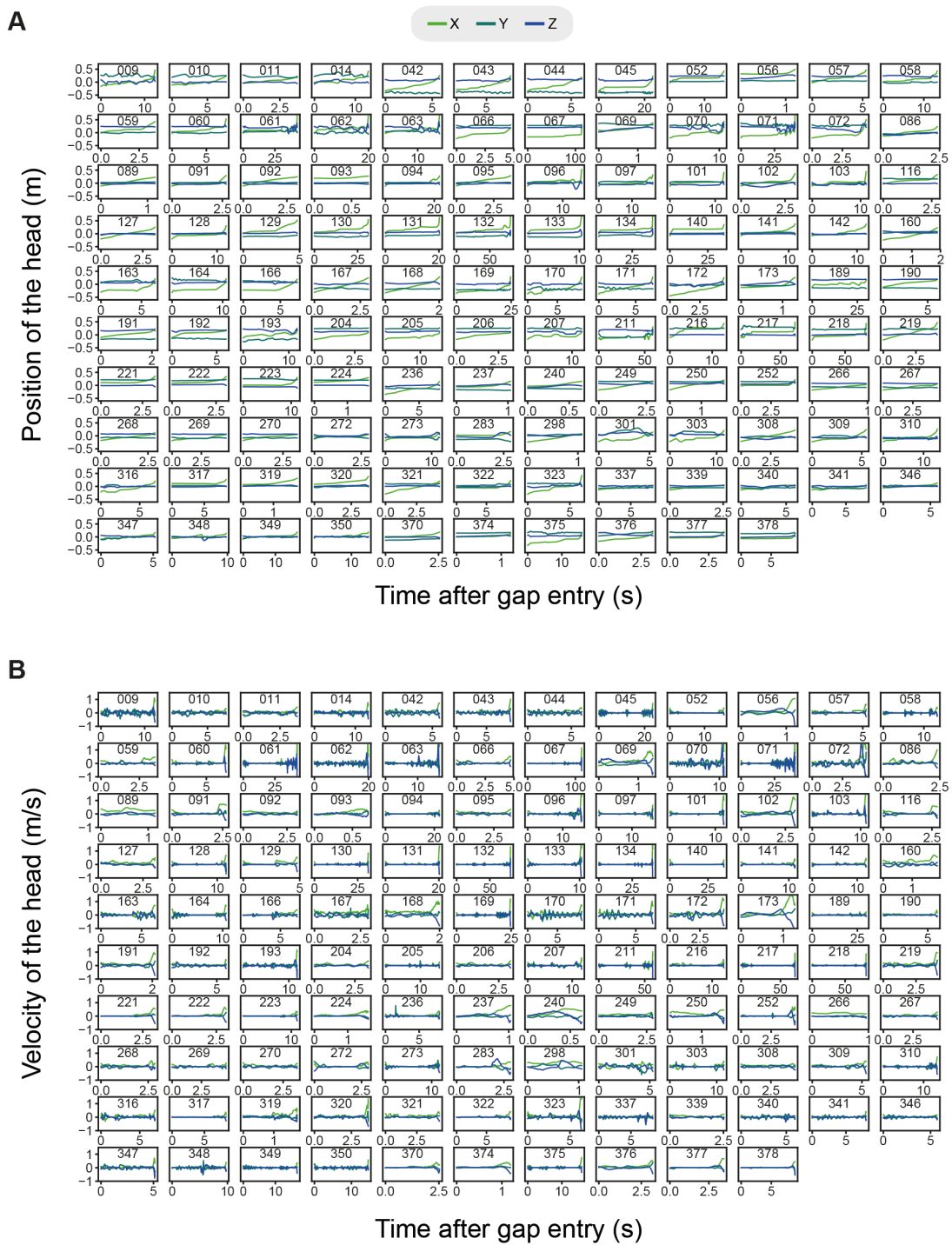
Fig. S2. (A) Smoothed trajectory plots for all 118 non-cantilever trials in *Dendrelaphis*. (B)

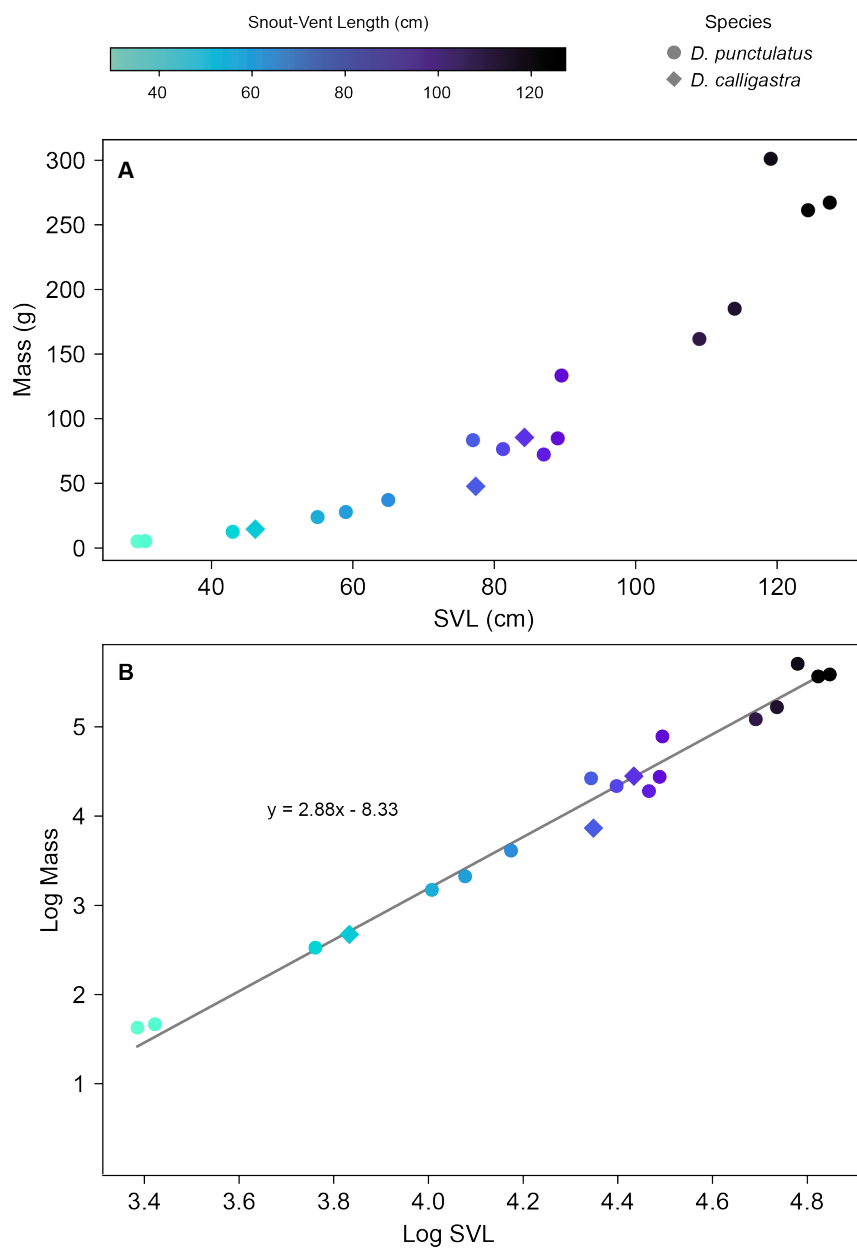Corresponding smoothed velocity plots for all 118 non-cantilever trials in *Dendrelaphi*.

Fig. S3. Body size and scaling in *Dendrelaphis*. Mass and length data from 19 *Dendrelaphis* individuals (mass data was not collected for one of the 20 snakes included in the study) in standard (A) and log-transformed (B) units. The regression on the log-log data included both *D. calligastra* (n = 3 individuals, diamonds) and *D. punctulatus* (n = 16 individuals, circles).
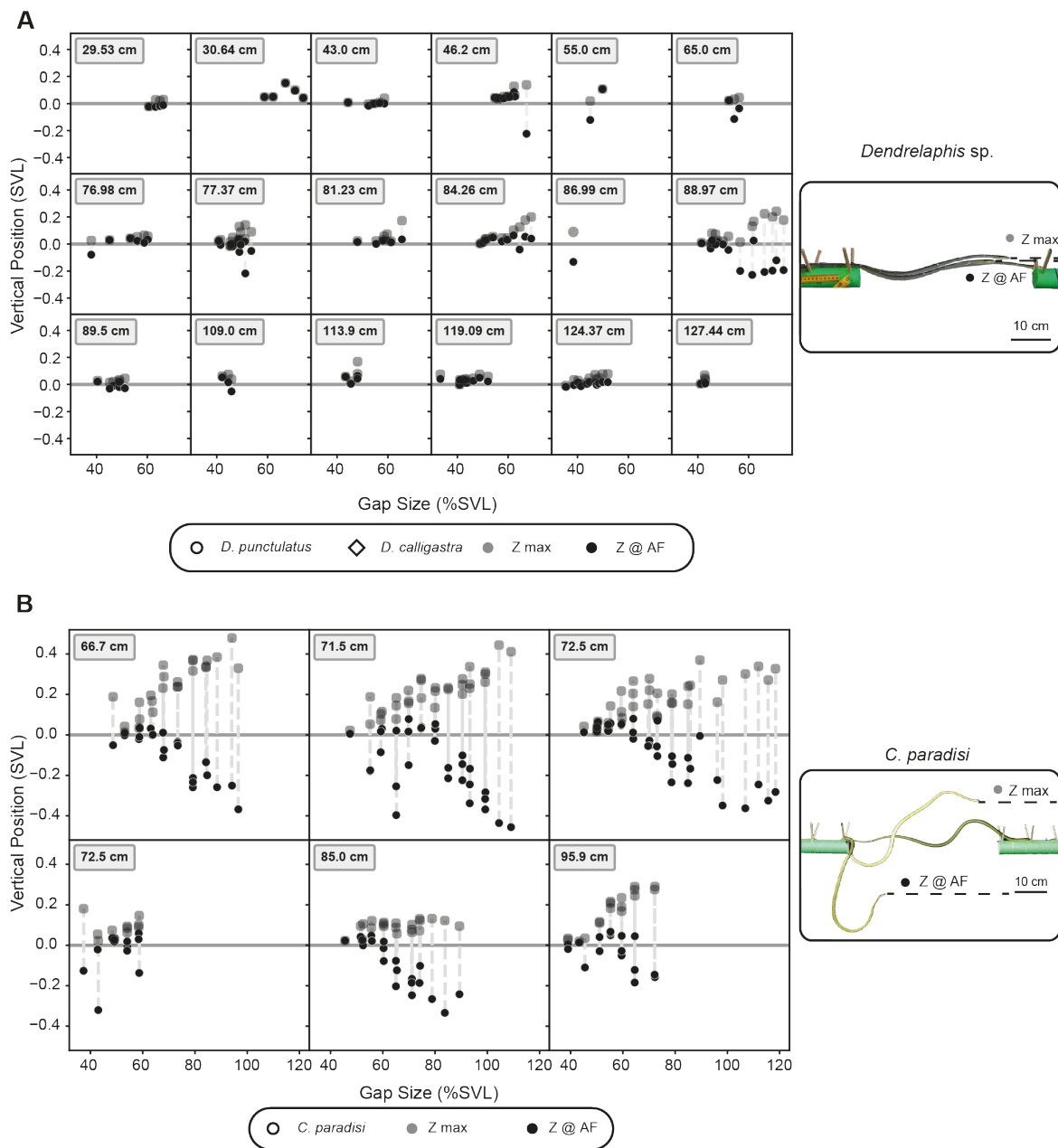
Fig. S4. Vertical head positions relative to the level of the branch (grey horizontal line) are shown at the acceleration frame (black markers) and the maximum position attained after acceleration (gray markers) in 18 *Dendrelaphis* (A) and 6 *C. paradisi* (B). Vertical dashed lines connect data from the same trial. *C. paradisi* often exhibited greater than 20% SVL differences between the acceleration frame and maximum positions, while *Dendrelaphis* generally did not.

Table S1. Body size and amount of non-cantilever data collected for *Dendrelaphis*, by individual.

Species	Type/Location	SVL (cm)	Mass (g)	Temp range (°C)	Cmax, %SVL	# NC Trials	NC gap distances, %SVL	DT, %SVL
Dp	WC, Sunshine Coast	30	5.1	22.6 – 23.6	56.2	4	60.6 - 66.3	60.7 – 68.0
Dp	WC, Sunshine Coast	31	5.3	29.2 – 30.0	57.7	5	58.7 – 74.0	63.0 - 78.5
Dp	CB, Cairns	43	12.5	24.6 - 24.8	39.3	5	44.3 - 58.6	48.2 - 68.4
Dc	WC, FNQ	46	14.5	26.5 - 32.1	52.4	9	54.8 - 67.2	56.7 - 77.7
Dp	CB, Cairns	55	23.9	24.6 - 24.8	41.5	2	45.0 - 49.8	46.8 - 55.8
Dp	CB, Cairns	59	27.8	24.6 - 24.8	54.9	0	-	-
Dp	CB, Cairns	65	37.1	24.6 - 24.8	49.0	3	52.2 - 56.3	52.6 - 58.2
Dc	WC, FNQ	77	47.7	30.7 - 33.6	44.9	15	33.8 - 53.6	42.1 – 82.5
Dp	WC, Sunshine Coast	77	83.4	24.5 – 25.3	51.9	6	37.9 – 60.2	41.1 – 61.6
Dp	WC, Sunshine Coast	81	76.5	23.0 - 29.5	48.2	7	48.0 - 65.5	50.0 - 88.3
Dc	WC, FNQ	84	85.5	27.0 - 36.6	49.8	12	26.4 - 69.1	38.4 - 95.6
Dp	WC, Sunshine Coast	87	72.3	27.0 - 27.0	34.7	1	38.3 - 38.3	41.2 - 41.2
Dp	WC, FNQ	89	84.8	27.6 - 30.2	46.3	15	41.5 - 73.8	47.2 - 97.8
Dp	WC, Sunshine Coast	89	133.4	22.4 - 24.8	45.7	6	40.4 - 51.2	43.7 - 58.8
Dp	WC, Cairns	102	-	24.6 - 24.8	32.5	0	-	-
Dp	WC, Cairns	109	161.7	24.6 - 24.8	41.6	3	42.1 - 45.8	45.4 - 47.8
Dp	WC, FNQ	114	185.1	29.5 - 30.7	39.4	4	43.4 - 48.1	47.3 - 65.6
Dp	WC, FNQ	119	301.1	27.6 – 30.0	42.0	9	33.3 - 52.1	39.2 - 56.4
Dp	WC, FNQ	124	261.3	26.3 - 28.7	37.4	11	35.4 - 51.9	37.8 - 58.2
Dp	WC, FNQ	127	267.2	31.1 – 32.0	38.1	4	41.1 – 43.0	41.8 - 46.3

Snakes are listed in SVL order; *Dp = Dendrelaphis punctulatus; Dc = Dendrelaphis calligastra.* All locations are in Australia; FNQ: far north Queensland (Cairns to Daintree Rainforest area). Cmax: Maximum cantilever extent across all trials. #NC trials: number of trials the snake used a non-cantilever movement. NC gap distances: range of gap distances crossed with a non-cantilever movement. DT: range of distances traveled, all non-cantilever movements. In column 2, WC = wild caught, CB = captive bred.

Table S2. Additional statistical details.

Dependent variable	Model intercept	95% CI	Model intercept	95% CI
	Dendrelaphis punctulatus and *Dendrelaphis calligastra*		*Chrysopelea paradisi* (re-analyzed from Graham and Socha, 2021)	
Horizontal variation	4.10*	-0.058 – 8.15	3.22*	0.438 - 5.89
Vertical variation	-0.386*	-6.07 – 4.76	1.02*	-8.92 - 10.9
Loop depth	-0.553*	-0.364 – 2.53	-6.58*	-17.2 - 3.20
Arc height	*4.08*	1.47 – 6.55	*-3.39**	-7.75 - 0.905
Z position, AF	5.58*	1.89 – 9.14	3.73*	-2.61 - 9.90
Z position, Max	-3.36*	-6.08 - -0.759	-2.14*	-7.14 - 2.76
Average speed	0.216^	0.145 - 0.283	0.255*	0.100 - 0.408
Max speed	-0.108*	-0.408 - 0.190	-0.166*	-0.515 - 0.168
Landing speed	**0.029***	-0.230 - 0.285	**-0.292***	-0.605 - 0.019

Statistical details for the mixed logistic regression.

Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) - N: 137, groups: 6

Family: Binomial

Scaled residuals

Min	1Q	Median	3Q	Max
-6.2866	0.2057	0.0694	0.3121	7.2883

Random effect variance	0.7883	*Random effect Standard deviation*	0.8879	
	Estimate	Standard Error	Z Value	Pr(>|z|)
Fixed effect: intercept	-10.81358	2.38226	-4.539	5.65e-06*
Fixed effect: gap distance	0.18939	0.04002	4.732	2.22e-06*
Correlation of fixed effects	-0.981			

Top: The data was rescaled to align the intercept with the smallest gap distance in the dataset and average *Chrysopelea* body size, so for the *Dendrelaphis* data, this intercept represents the value of the dependent variable at a gap distance of 33.3% SVL for a snake with a snout-vent length of 85.0 cm (body size was not a parameter in the *Chrysopelea* models). No significant differences in intercept between *Chrysopelea* and *Dendrelaphis* were found, based on the overlap of the 95% CIs, except for arc height (italicized). Starred rows represent variables for which the gap distance effect was significant; ^ indicates a significant body size effect in *Dendrelaphis* (see Table 1 in the main text). Bolded rows are those where the gap distance effect differed between *Dendrelaphis Chrysopelea*.

Bottom: Details for the mixed logistic regression, random effect (intercept, by individual). For fixed effects, * indicates significance.
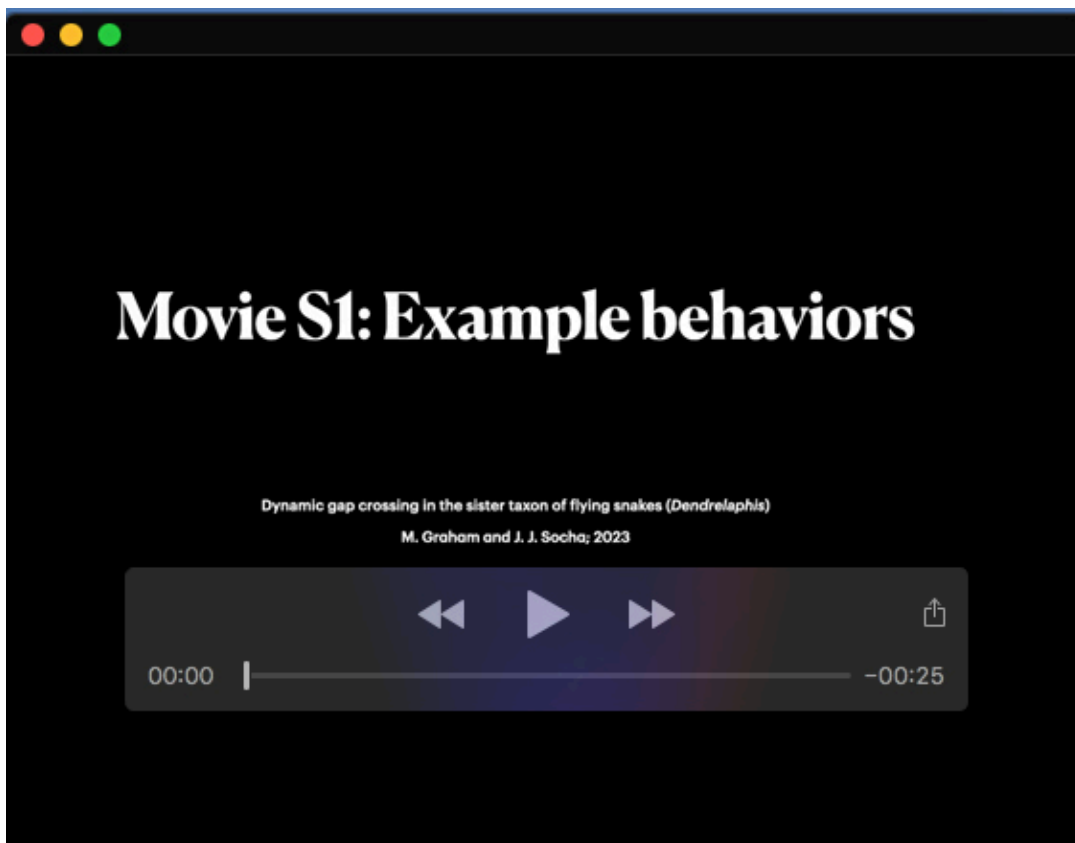
Movie 1. Example behaviors. Illustrations of behaviors used during gap crossing in *Dendrelaphis*, beginning with the cantilever (typically observed at smaller gap distances) and then several different non-cantilever behaviors. For the non-cantilever movements, the transition and acceleration frames are also noted.
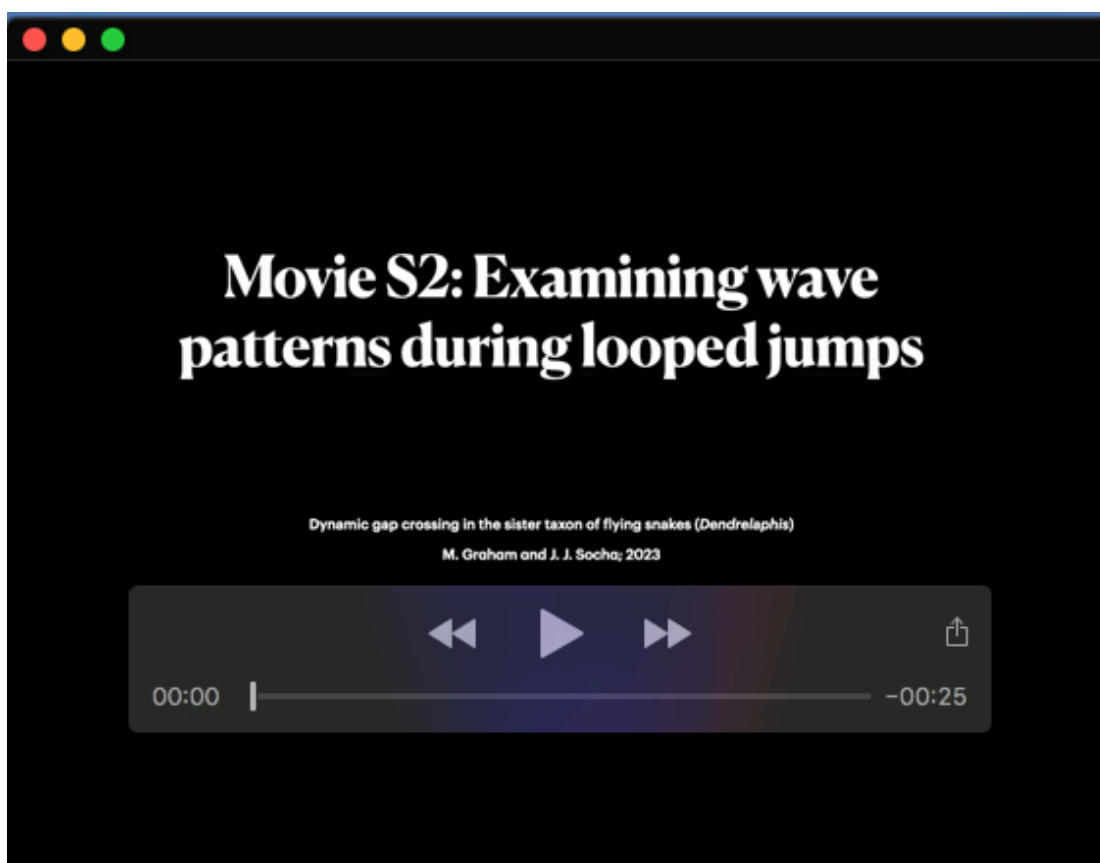
Movie 2. Examining wave patterns during looped jumps. Example gap crossing trials showing that *Chrysopelea* and *Dendrelaphis* sometimes uses multiple waves of bending during non-cantilever jumps. Additional investigations of the use of traveling and standing waves during loop gap crossing behaviors, including analysis of muscle activation patterns, is warranted.