

RESEARCH ARTICLE

Dynamic movements facilitate extreme gap crossing in flying snakes

Mal Graham* and John J. Socha

ABSTRACT

In arboreal habitats, direct routes between two locations can be impeded by gaps in the vegetation. Arboreal animals typically use dynamic movements, such as jumping, to navigate these gaps if the distance between supports exceeds their reaching ability. In contrast, most snakes only use the cantilever crawl to cross gaps. This behavior imposes large torques on the animal, inhibiting their gap-crossing capabilities. Flying snakes (*Chrysopelea*), however, are known to use dynamic behaviors in a different arboreal context: they use a high-acceleration jump to initiate glides. We hypothesized that flying snakes also use jumping take-off behaviors to cross gaps, allowing them to cross larger distances. To test this hypothesis, we used a six-camera motion-capture system to investigate the effect of gap size on crossing behavior in *Chrysopelea paradisi*, and analyzed the associated kinematics and torque requirements. We found that *C. paradisi* typically uses cantilevering for small gaps (<47.5% snout-vent length, SVL). Above this distance, *C. paradisi* were more likely to use dynamic movements than cantilevers, either arching upward or employing a below-branch loop of the body. These dynamic movements extended the range of horizontal crossing to ~120% SVL. The behaviors used for the largest gaps were kinematically similar to the J-loop jumps used in gliding, and involved smaller torques than the cantilevers. These data suggest that the ability to jump allows flying snakes to access greater resources in the arboreal environment, and supports the broader hypothesis that arboreal animals jump across gaps only when reaching is not mechanically possible.

KEY WORDS: Kinematics, *Chrysopelea*, Biomechanics, Locomotion

INTRODUCTION

Animals use a wide variety of behaviors to cross gaps in the physical environment, including reaching, jumping and flying (Graham and Socha, 2020). Gibbons, for example, can use reaching, leaping or brachiation to move between tree branches (Cannon and Leighton, 1994), and the Japanese giant flying squirrel can reach, jump or glide (Stafford et al., 1994). In general, the choice of gap-crossing behavior is influenced by biomechanical factors, with gap distance playing a major role in behavioral choice (Graham and Socha, 2020). Most snakes, however, only use one behavior to cross gaps, making them an exception to this general principle. Specifically, snakes use the cantilever crawl (hereafter, ‘cantilever’), in which the

animal holds itself stiff while extending its anterior body outward from the origin support into the air, moving forward in a relatively straight line until it contacts the target support. Animals with access to both reaching and more dynamic behaviors, such as gibbons and macaques (Cannon and Leighton, 1994) and dormice (Arkley et al., 2017), typically reach across small gaps, and lunge or jump across larger gaps. This pattern is familiar to humans, who might step over a small puddle but jump over a large one.

In keeping with this pattern, animals that cannot jump have reduced gap-crossing capacity, particularly for horizontal and upward gap-crossing movements in the arboreal environment. The slow loris, for example, does not jump, and cannot cross gaps if the horizontal distance between supports is greater than the maximally extended length of its body (Dykj, 1980; Sellers, 1996). In contrast, jumping primates can overcome this constraint; for example, a captive gibbon (*Hylobates lar*) with an approximate extended body length of 2 m was observed to leap 5.2 m from a horizontal pole (Channon et al., 2010). In snakes for which cantilevering is their only gap-crossing mode, the distance limitations of cantilevering serve as a limiting factor for gap-crossing performance.

In addition to the limitations of maintaining contact with the origin, the limbless, cylindrical body plan of snakes dictates that they must hold up increasingly large portions of their bodies as the distance to the target increases. The farther a snake extends horizontally into a gap, the more of its body is unsupported, which increases the lever arm from the end of the origin to the unsupported portion’s center of mass, thereby increasing the torque acting on the suspended snake. Across various gap orientations, snakes exert the greatest amount of muscular activity when crossing horizontal gaps (Jorgensen and Jayne, 2017), in which torque effects are more pronounced compared with those in vertical trajectories. These torque limitations result in most snakes being unable to cross gaps of greater ~50% of their snout-vent length (SVL) (Hoefer and Jayne, 2013; Jayne and Riley, 2007; Lillywhite et al., 2000; Ray, 2012), which constrains their ability to access resources, interact with conspecifics, avoid predators or pursue prey.

Of the snakes that have been studied in such conditions, only the brown tree snake (*Boiga irregularis*) uses an additional behavior to cross gaps, known as ‘lunging’, in which the snake rears upward from a cantilevered position to rapidly propel the head forward (Byrnes and Jayne, 2012; Jayne and Riley, 2007). On average, a brown tree snake’s maximal lunge is 7.9% greater than their maximum cantilever (Jayne et al., 2014), and a maximum horizontal gap of 64% SVL has been observed in one snake (Jayne and Riley, 2007). Though small, this performance increase could be ecologically important if it enables a successful crossing.

Similar to the pattern discussed above for dynamic behaviors in other species, brown tree snakes transition from cantilevering to lunging at large gap distances, suggesting that lunging helps to overcome a biomechanical limitation. In fact, torque seems to serve as trigger for the initiation of dynamic movements in brown tree

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snakes: lunges are only observed at or past the maximum cantilever crossing distance, and brown tree snakes proceed through the majority of the gap before initiating the lunge (Jayne and Riley, 2007; Byrnes and Jayne, 2012). Comparing the torques experienced just before lunging with those they would theoretically experience if they had cantilevered across the gap shows that brown tree snakes enjoy considerable reductions in maximum torque experienced by using these dynamic movements (Byrnes and Jayne, 2012). Despite these advantages, lunging appears to be rare: besides the brown tree snake, the only documented instances of a snake lunging to cross gaps are preliminary data from a single individual (*Dendrelaphis pictus*; Socha, 2011).

One other group with known use of arboreal dynamic movements, albeit in a different locomotor context, are the flying snakes (genus: *Chrysopelea*), who use a J-loop jump to launch their glides (Socha, 2006). During these J-loop take-offs, flying snakes travel in an upward arc that enables them to reach a horizontal distance of one full body length ($98.9 \pm 17.1\%$ SVL, range 70.9–126.0%) in the plane level with their launch location (Socha, 2006). If flying snakes can use this same behavior to cross gaps to a target, this range would represent a substantial increase in distance over the cantilever or lunge. Studying how an additional behavioral mode influences the gap-crossing ability of these snakes could therefore help shed light on how novel behaviors can confer mechanical advantages.

In this study, we addressed three key questions concerning gap crossing in flying snakes. First, do flying snakes switch from reaching to more dynamic behaviors such as lunging and jumping as gap size increases? Second, does the use of non-cantilever behaviors confer an advantage for gap crossing? And finally, does torque provide a ‘trigger’ for the transition to non-cantilever behaviors, the way it appears to in the brown tree snake? Based on mechanical considerations and the behaviors of other jumping animals, we hypothesized that flying snakes will reserve dynamic movements for gaps too large to cross by cantilevering, enabling them to match their performance during jumping take-offs ($\sim 100\%$ SVL). We also hypothesized that, similar to the brown tree snake, flying snakes will extend to their maximum cantilever distance before initiating dynamic movements.

To address these hypotheses, we recorded snakes crossing horizontal gaps of varying sizes between two artificial branches (Fig. 1). Snakes were simultaneously filmed with video and motion-capture cameras, allowing us to analyze the 3D body position of the

animal. Using these data, we examined the pattern of crossing behavior with gap size, analyzed the kinematics of the different gap-crossing behaviors, and estimated the torques experienced by the snake during gap crossing. The data in this study contribute to a larger body of knowledge about gap crossing in animals, particularly in understanding patterns of behavior use in animals that employ multiple modes of gap crossing.

MATERIALS AND METHODS

Animals

Six captive *Chrysopelea paradisi* Boie 1827 were used for this study. All snakes were acquired in 2012 from Malaysia. Snakes were kept in individual, vertically oriented mesh housing (Reptibreeze, $16 \times 16 \times 30$ cm) with a heat lamp, UV lamp, water and a hide box. Each cage contained a climbing structure made of PVC pipe ‘branches’ with fake foliage attached. Snakes were fed approximately once per week, typically frozen/thawed mice. No snake was tested on the day of, or the day after, eating, and any snake that participated in two trial days in a row was rested for at least one day before experimentation resumed. The snakes had a mass of 70.4 ± 30.4 g (mean \pm s.d.; range 33.9–114.6 g), SVL of 77.4 ± 10.9 cm (66.7 – 95.9 cm), tail length of 24.5 ± 7.0 cm (12.6 – 32.4 cm) and a mass/length ratio of 0.89 ± 0.28 g cm $^{-1}$ (0.51 – 1.35 g cm $^{-1}$).

All experimental procedures were approved by the Virginia Tech Institutional Animal Care and Use Committee under protocol 16-154.

Experimental arena

We constructed a gap-crossing arena (Fig. 1) to be consistent with recent studies of gap crossing in snakes (e.g. Hoefer and Jayne, 2013; Jayne and Riley, 2007). The branch structures comprised two identical supports, composed of wood and aluminum T-slot structural framing (10 series, 80/20 Inc., Columbia City, IN, USA), with ‘branches’ made of 1.5 inch PVC pipe (outer diameter 1.9 inches). Small wooden dowels (length 10 cm, diameter 6.4 mm) were inserted into drilled holes in the PVC every 10 cm along the branch; these pegs were set at an angle of 45 deg from the vertical on either side to form a V-shaped peg formation along the branch. The PVC pipe was wrapped in green gaffer tape (GaffTac 2 inch Keying Tape, Rosco, Stamford, CT, USA) to provide the snakes with more grip than the smooth PVC alone (Hoefer and Jayne, 2013).

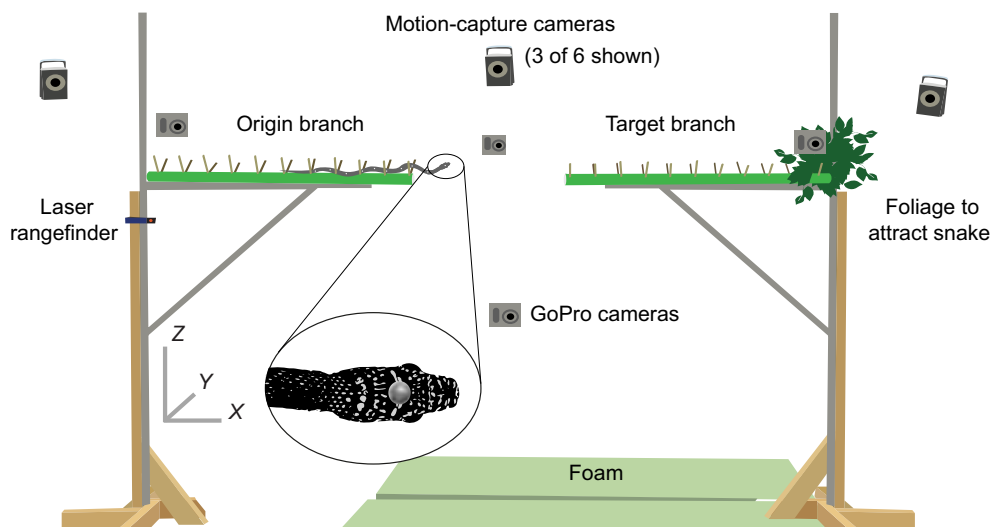


Fig. 1. Experimental setup. Snakes were placed on the origin and crossed the gap to the target. Three additional motion-capture cameras (not shown) were placed in positions mirroring the illustrated cameras. Snakes were marked with 10 motion-capture markers on the dorsal midline; the pop-out shows the appearance and placement of the head marker.

One branch was designated as the ‘origin’ and the other as the ‘target’. The branches were arranged such that the branch ends were at the same height and their long axes in-line and parallel, presenting a straight horizontal path for the snake to cross. An arrangement of fake foliage behind the target was used to help visually motivate the snake to cross the gap. Foam pads were placed beneath the branches to protect the snakes from falls.

3D motion capture and video recording

Gap-crossing trials were recorded with a six-camera motion-capture system (T-series cameras, Vicon Motion Systems Ltd, Oxford, UK; 100–150 Hz) and with three commercial-grade video cameras (Hero4 Black, GoPro, San Mateo, CA, USA; 120 frames s⁻¹, 1920×1080 pixels). The motion-capture cameras were arranged roughly in an oval around the experimental arena (Fig. 1). Two video cameras were placed in the arena, one on the target facing toward the gap, and one to the side of the arena, with the optical axis aimed perpendicularly to the axis of the two branches. The third camera was alternately placed beneath the gap pointing upwards, on the origin branch facing the gap, or to the side of the arena pointing down for an overhead view.

To enable motion capture, snakes were marked with half-dome infrared-reflective markers (MCP1125, OptiTrack, Corvallis, OR, USA; diameter 3 mm). Ten markers were placed on the dorsal midline, spaced approximately evenly from head to vent, with the first marker between the eyes and the last at the vent location.

The motion-capture arena was calibrated and the *X*, *Y* and *Z* directions set using a level, with positive *X* in the direction of the target, positive *Y* to the snake’s left and positive *Z* upward.

After the main experiment, an additional set of videos of two snakes (#89, 65.1 g, 73.5 cm SVL; #85, 53.3 g, 72.5 cm SVL) was recorded to help illustrate behaviors of interest. These videos were recorded in lateral view using a high-speed camera (100–200 frames s⁻¹, 1/1000 shutter, 1280×1024 pixels; Edgetronic SC1, Sanstreak Corp., San Jose, CA, USA), with no markers placed on the snakes.

Morphological data

SVL and tail length were measured on the first day of experiments by gently pulling the snake straight until it was lying flat on a measuring tape. The mass of the snake was determined via measurement in a snake bag using a digital scale (CJ4000, J-scale®, HBI International, Phoenix, AZ, USA) on each experimentation day.

Gap crossing

For each snake, we started by presenting the animal with a small gap, equivalent to 30–40% of its SVL. We began trials by placing the snake on the origin facing the target. If the snake was reluctant to cross, we encouraged it by some combination of moving around/waving behind the snake, tapping the tail and/or body, and holding the snake close to the target and then moving it back to the origin. In some cases, reluctant snakes were first presented with a reduced gap size, which they were more likely to cross; the gap would then be increased in subsequent trials until reaching the specified gap size. In general, snakes became more reluctant to cross as the gap size increased.

We attempted to elicit three successful crosses per gap distance before increasing the distance by approximately 5% SVL. To change the distance, the target was moved by hand. The distance between branches was first determined using a measured string and was then confirmed using a laser range-finder (Bosch Professional

GLM30, Bosch, Gerlingen, Germany) attached to the gap-crossing structure for higher accuracy. The final reported gap distance was determined from the motion-capture data using two IR-reflective spheres (Pearl hard marker, Vicon Motion Systems, Ltd, Oxford, UK; diameter 7 mm) placed at the end of the branches. These gap sizes were then normalized to body size by dividing by the SVL of each snake, and rounded to the nearest 5% SVL in order to pool replicate trials. Differences between the intended and measured gap sizes are available in the Supplementary Materials and Methods.

Snakes were given a rest period between trials of at least 5 min, with longer rest periods given if the snake appeared to be breathing heavily or repeatedly refused to cross. Snakes performed no more than 20 trials in a day, and were not tested more than two days in a row. When resuming trials on a new day, snakes were typically presented with a relatively small gap to acclimate them to the setup before returning to the desired gap. We then continued to increase the gap size until the snake failed to cross, typically by falling to the ground during a gap-crossing attempt (i.e. missing the target). However, three of the six snakes refused to attempt to cross at gap sizes that appeared to be short of their physical limits, as determined by the range of their farthest-reaching non-cantilever crosses. Owing to the difficulty of getting snakes to cross the largest gap sizes, in some cases we were only able to record one trial per gap size for the larger gaps (Fig. S1). In total, we ran 289 trials, and used 182 of these for analysis. Additional details of data inclusion/exclusion are provided in the Supplementary Materials and Methods.

Data analysis

3D coordinates

The raw output of the motion-capture system is unlabeled 3D coordinates of each marker on the snake. To identify points consistently, we used commercial software (Nexus version 1.8.5, Vicon Motion Systems, Ltd, Oxford, UK) to associate each marker (1–10) by position along the snake’s body from head to vent. We performed this labeling in every frame of a sequence, beginning when the snake began to move across the gap and ending when the snake successfully contacted the target. We then exported the 3D positions of each marker through time in a .csv file for each trial.

The 3D data were prepared for kinematics analysis using a custom-written Python script. First, the data were cropped to cover the period beginning when the snake’s snout crossed the end of the origin and ending when the snake landed on the target. The moment of landing was identified by visual inspection of the Nexus data. Second, small sections (<0.2 s) in which the motion-capture system did not successfully record the position of a given marker were estimated using linear interpolation. These temporary drop-outs resulted from occlusion due to the wooden pegs, a problem that was only discovered after experiments were complete. Longer drop-outs also occurred, but were not interpolated (Fig. S2). Third, the data were rotated using a coordinate transformation to align the *X*-axis with the vector pointing from the origin end to the target end. Finally, sections of continuous data were smoothed by fitting a global, cross-validatory spline (Woltring, 1986). This package provides two functions, one (GCVSmoothedNSpline) which uses the generalized cross-validation criteria (Wahba, 1979) to generate an appropriate smoothing parameter (*p*’, see Eqn 1, below; Woltring, 1986), and another (SmoothedNSpline) which allows the user to manually set a value for this parameter. For each section of continuous data, we first used GCVSmoothedNSpline to generate the cross-validatory value for *p*, and then multiplied this value by a pre-factor to increase the smoothing. The pre-factor was selected by

gradually increasing the pre-factor from 1 until obviously non-physical spikes were removed from all trials, but other features remained consistent with the original data, which we found to occur with a pre-factor of 10,000.

Spline fitting

We calculated cubic splines to estimate the body position between the recorded points on the snake. Specifically, a natural cubic spline was interpolated either for every time frame in the trial or in a particular frame of interest (depending on the analysis), resulting in 1000 points fit along the pathway determined by the body marker positions.

Behavior determination, body posture and position deviation

Using observations of the motion-capture and video data, we categorized the movements the snakes used to cross gaps as ‘cantilevers’ or ‘non-cantilevers’. Cantilever crosses were characterized by the snake moving in a straight-line path across the gap with steady movement and a stiffened anterior body. Non-cantilever crosses were defined as any that did not fit that profile, and involved a dynamic component. Additional details regarding the behavioral determinations are available in the Supplementary Materials and Methods.

In some trials, the snake made a second crossing attempt immediately after an initial failure to secure purchase. The snake would approach the target, attempt either a cantilever or a small dynamic movement, fall downward while maintaining grip on the origin, and finally make a successful cross using a larger dynamic movement (e.g. Movie 3). Because there was either no cantilever attempt or the cantilever attempt was not successful, we coded such ‘recovery’ events as non-cantilever movements.

To determine how the straightness of the body changed with gap size and behavior, we analyzed the difference in length between the snake’s curved body and a straight line connecting the head to the last body marker for every frame in each trial. To do so, we calculated the difference between two distances in each frame of the trial: the straight-line distance between the first and last marker, and the sum of the known marker spacings between those markers. The maximum of these differences was then recorded for each trial. In addition, we also report the *Y* variation and the *Z* variation: the overall variation in the differences in the *Y* (side-to-side) and *Z* (vertical) dimensions, averaged across each marker.

Kinematic analyses

Velocity values were calculated from the smoothed position data using a custom-written Python script. In each frame of each continuous section of the smoothed position data, the velocity in the *i*th frame was calculated from the neighboring position using the following formula:

$$v_i = \frac{p_{i+1} - p_{i-1}}{2} \times \text{frame rate}, \quad (1)$$

where frame rate is in Hz. Three speed metrics were calculated from the velocity data: maximum head speed, average head speed and landing head speed. The head was selected to represent the overall speed for two reasons: the data quality was highest for the head marker, and most of the body marker speeds did not vary much from that of the head for most behaviors. Maximum head speed was defined as the maximum resultant velocity of the head in all frames from start to landing. Average head speed is the average speed of the head in a given trial, taken from frames in which the snake was moving toward the target. Landing head speed is the speed of the head as it approached and landed on the target. Additional details of

how these values were calculated are provided in the Supplementary Materials and Methods and Fig. S3.

Frames of interest: transition, low point, high point and landing

Four points of interest were selected from the time series: transition, low point, high point and landing. The transition and landing frames were visually identified from a frame-by-frame analysis of the motion-capture data. Landing is defined as the frame in which the snake contacted the target and thereafter successfully secured purchase on that branch. Transition is defined as the frame in which the snake initiated a more dynamic, non-cantilever movement. As non-cantilever behaviors can involve movements of the head upward (creating an arch) or movements of the midbody downward (creating a loop), the transition could be either when the head began to move up or when the midbody began to move downwards, respectively (Fig. 2). For the trials in which a recovery event occurred, transition is defined as the frame in which the snake fell downward during its first crossing attempt.

To examine both take-off and mid-behavior body posture, we selected two specific frames from the region of data between the transition and landing. The first was the frame in which the snake’s head reached its highest position (the maximum *Z* value; the ‘high point’) and the second was the frame in which the snake’s body (excluding the head) was at its lowest position after entering the gap (the minimum *Z* value; the ‘low point’). These two frames were identified by analyzing the marker positions using a custom-written Python script.

Loop depth, arc height, overshoot and distance traveled

To quantify the body posture of the snake before and after initiation of the dynamic component of a non-cantilever cross, we quantified arc height and loop depth (Fig. 2) for all non-cantilever trials. Arc height is the vertical distance from the snake’s head to the lowest point on its body in a particular frame. Loop depth is the vertical distance from the origin marker to the lowest point on the snake’s body.

In both the low point and the high point, we calculated these postural metrics by fitting a spline to the recorded marker positions, following the methods described above. In practice, arc height was calculated as the vertical (*Z*) distance from the head to the lowest body point on the spline, and loop depth is the vertical distance (*Z*) from the origin marker to the lowest body point on the spline. Values were normalized by SVL for comparison.

Two additional distances were recorded from the head trajectory: the overshoot and the distance traveled. Overshoot quantifies the difference between the total straight-line distance traveled by the head, from entry (into the gap) to landing, and the size of the gap. Distance traveled quantifies the straight-line distance traveled by the head from its position at the low point to its position at landing.

Torque analysis

To explore the role of torque in gap crossing, we quantified the torque due to gravity acting on the snake’s body at two points: at landing for cantilever crosses and at transition for non-cantilever crosses. For each measure, we fitted a spline to the snake in the relevant frame. Using previously recorded average density data from three sectioned snakes (Yeaton et al., 2020) and the mass of the snake as measured on the day of the trial, a mass value was assigned to each point along the spline. Using the marker at the end of the origin, the torque for each point was calculated as:

$$\vec{\tau}_p = \vec{r}_p \times \vec{F}_g$$

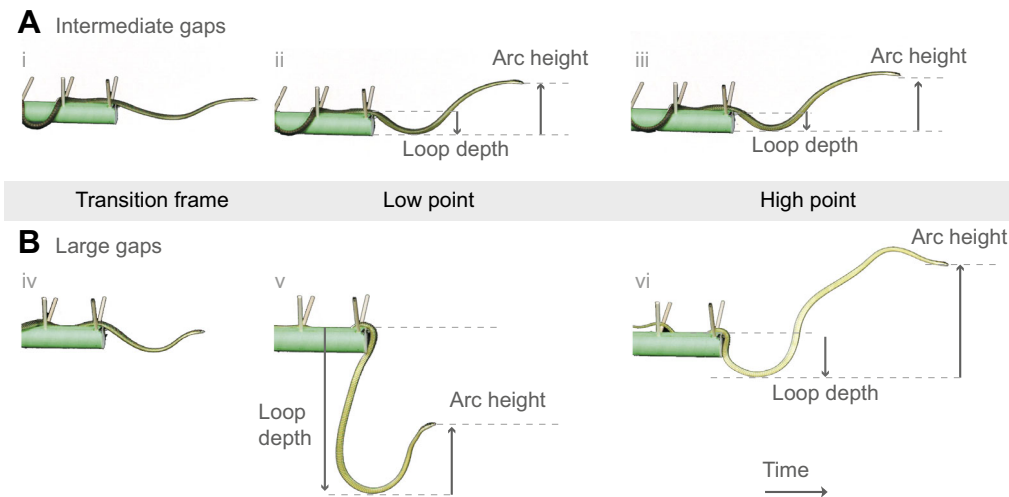


Fig. 2. Body posture at specific time points selected for analysis. We identified three critical time points in a given non-cantilever behavior. The transition (i, iv) occurs when the snake first begins to initiate a bend, changing from a relatively straight, cantilevered position. These transitions most commonly involved moving the head upward into an arch (A) or dropping a loop downward (B). Between transition and landing, we measured two parameters characterizing the snake's body position: the vertical distance from head to the trough of the body (the arc height), and the vertical distance from the origin to the trough of the body (the loop depth). We made these measurements at two time points using the motion-capture data: the low point (ii, v), or the time at which the snake attains its lowest vertical position (measured across all markers besides the head), and the high point (iii, vi), the time at which the snake's head is at its highest vertical position before landing. Example A is more typical of intermediate gap sizes. Example B is typical of the largest gap sizes.

or

$$\vec{\tau}_p = m_p(\vec{r}_p \times \vec{r}_g), \quad (2)$$

where \vec{r}_p is the distance vector pointing from the end of the origin to the spline point, \vec{r}_g is the unit vector in the direction of the force of gravity, and m_p is the mass at that point. The resultant torque is the sum of the torques along the spline for the suspended portion of the snake's body:

$$\vec{\Gamma}_{\text{res}} = \sum_{p=\text{head}}^{\text{origin}} \vec{\tau}_p. \quad (3)$$

To account for differences in body size, we also calculated a normalized torque by dividing the resultant torque by the snake's total weight (where M_{snake} is snake mass) and SVL:

$$\vec{\tau}_{\text{norm}} = \frac{\vec{\Gamma}_{\text{res}}}{g \cdot M_{\text{snake}} \cdot \text{SVL}_{\text{snake}}}. \quad (4)$$

Comparison with J-loop launches

The mean and standard deviation for low arc height and low loop depth during J-loop glide launches are $5 \pm 5\%$ SVL and $55 \pm 8\%$ SVL, respectively (Socha, 2006). Based on these criteria, we chose a subset of the data in this study to compare with J-loop glide launches; namely, all trials in which both the low loop depth and low arc height were within 2 s.d. of the mean values reported for J-loop launches. For the 10 trials in which low loop depth and arc height were not able to be determined (owing to error in the motion-capture data or no defined transition frame), we watched the GoPro video for the trials and judged visually, based on the marker positions, whether these criteria were met. We also ruled out three recovery movements, as the overall movement was not similar to a J-loop launch. The resulting subset comprised eight trials from three snakes.

For this subset, we made comparisons between the following variables, following Socha (2006): preparation time (s), vertical acceleration time (s), maximum and landing velocities in both the vertical and horizontal dimensions (SVL s^{-1}), distance traveled (SVL) and height gained (SVL). In the case of the distance traveled and landing metrics, we compared metrics measured at landing in this study with launch values measured at the moment the snake's head became vertically level with the origin, while travelling downward (0 m values in table 1 of Socha, 2006). The two datasets were compared statistically using a Mann–Whitney U -test.

Statistics

Logistic regression

A mixed-effect, binomial logistic regression was used to analyze the effect of gap size (%SVL) on behavior, with 1 representing a non-cantilever behavior and a 0 representing a cantilever behavior. The regression was conducted using R software (version 3.6.2; <http://www.R-project.org/>) using the lme4 package (Bates et al., 2015), with individual as a random factor influencing the intercept.

Linear mixed-effects modeling

Linear mixed-effects modeling fitted by the restricted maximum likelihood (REML) method was used for statistical analysis of the relationship between the following variables and gap size (all using the lme4 package in R): transition torque, Y variation, Z variation, average head speed, arc height (at the high point), loop depth (at low and high points), head position at transition, and distance traveled by the head from low point to landing. In each model, variables were transformed if necessary to garner an approximately normal distribution and reduce heteroscedasticity. In each case, the named variable was included as a fixed effect, and snake ID was included as a random effect.

After determining the random effects structure using a model-fitting procedure (Burnham and Anderson, 2004; Zuur et al., 2009), the strength of the relationship was assessed by examining the 95% confidence intervals (CI) for the fixed effects.

Breakpoint analysis

Two features, arc height at the high point and overshoot, displayed an inverted U-shaped relationship with gap size. To identify the gap size at which these features changed relationship with gap size, we conducted a breakpoint analysis using the function `segmented.lme` (Muggeo et al., 2014) in R. This function uses a likelihood-based framework to fit segmented models in which change points and slopes are allowed to vary with a random factor (here, snake ID).

Non-linear mixed-effects modeling

Non-linear mixed-effects models were used to analyze relationships between several factors and gap size: maximum head speed, landing head speed and straight-line deviation. For each analysis, the functional form of the model was a sigmoid curve:

$$\text{Response} = \frac{L}{1 + e^{-k \times (\text{Predictor} - x_0)}} + b. \quad (5)$$

Models were fitted using a two-stage process in Python and R. First, a sigmoid curve was fitted using a fixed-effects model from the `SciPy` package in Python (Virtanen et al., 2020), using the curve fit function from the 'optimize' module. The initial parameter guess used $L = \max(\text{response})$, $k = 1$, $x_0 = \text{median}(\text{response})$, and $b = \min(\text{response})$. The parameters returned by this method were then used for the initial parameter guess in R, where the final parameters were estimated using the `nlme` package (Pinheiro et al.,

2021). The final model was fitted using individual ID as a random factor, with the parameter L interacting with the random effect.

RESULTS

The use of non-cantilever movements

Flying snakes predominantly used cantilever movements to cross small gaps, characterized by low maximum head speeds (Fig. 3), low variation in vertical and side-to-side movement (Fig. 4A,B), and low variation from a straight-line posture (Fig. 4C). To cross larger gaps, flying snakes used behaviors that deviated from the cantilever profile, although not always in the same way. Of 182 trials included in this study (15–42 trials per snake), the snake cantilevered across the gap in 45 trials, and crossed with a non-cantilever movement in 137 trials (Fig. 5, bars).

The non-cantilever category included a range of movements that were visually distinct from each other. All were characterized by higher speeds and/or highly curved body configurations compared with cantilever crosses. Based on the mixed-effects logistic regression (Fig. 5, line), the gap size at which snakes would be as likely to use a cantilever as a non-cantilever was 47.5% SVL (mean predicted probability of using a non-cantilever: 50.06% [lower quartile: 25.3%, upper quartile: 65.3%]), although one individual was able to cross a 55% SVL gap using a cantilever.

Individuals displayed some differences in behavior usage at a given gap size (Fig. S1). Two snakes (#88 and #90) used both

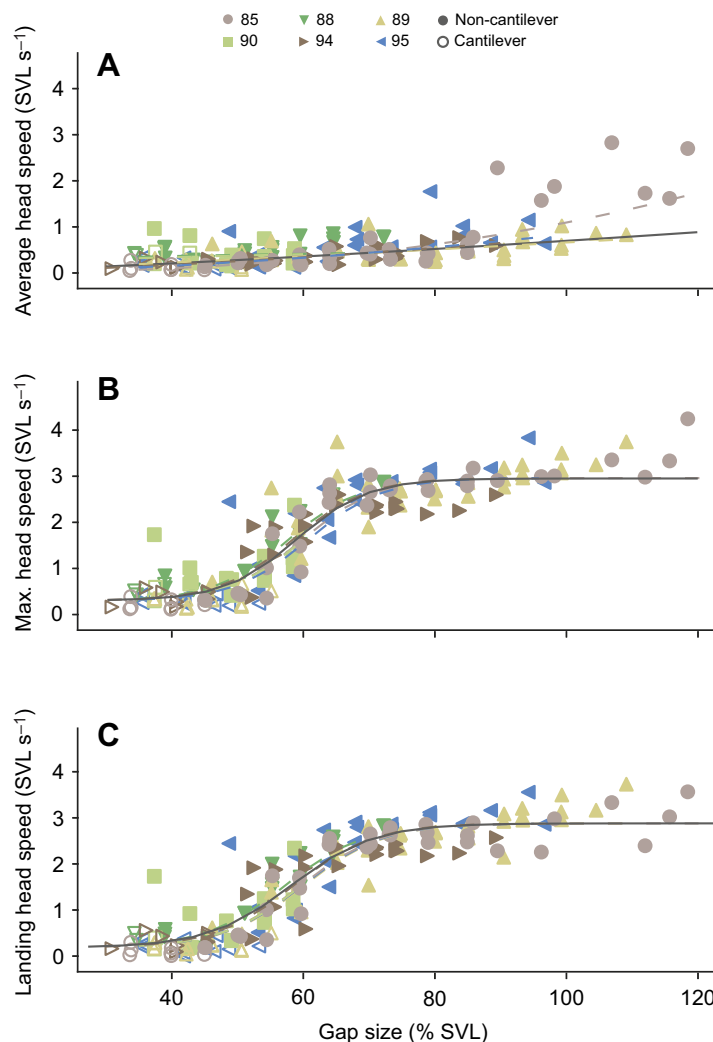


Fig. 3. Head speed versus gap size. Symbol color/shape combinations indicate individual snakes; fill indicates whether the behavior was a cantilever (open) or not (filled). The resultant velocity of the head was generally greater for larger gaps. Average speed (A) of the head only increased slightly, even as maximum (B) and landing (C) head speeds showed sigmoidal increases with gap size, demonstrating that large peak speeds did not always correspond to faster times across the gap. SVL, snout-vent length.

cantilever and non-cantilever behaviors to cross gaps of less than 45%, whereas the other four primarily used cantilevers. All snakes used a non-cantilever behavior at least once by 50% SVL, and for gaps of 70% and above, no snake attempted a cantilever cross (Fig. 5; Fig. S1).

Only one snake (#89, which has a shortened tail) exhibited a recovery movement, which occurred in seven gap-crossing trials (Movie 3). These events occurred at a similar gap size (~55–65% SVL) to where non-cantilever crosses became more frequent in other snakes. In each of these trials, the snake attempted to cross the gap with either a cantilever (3 instances) or a non-cantilever behavior (4 instances), failed to secure contact with the target, and subsequently successfully crossed on a second, more dynamic, attempt. The snake had primarily used cantilevers to cross gaps smaller than those presented in these seven trials, and used non-cantilever behaviors exclusively to cross larger gaps. Although other snakes in this study typically extended a small portion of the body in a cantilevered position before

initiating a dynamic movement, they never exhibited cantilever collapse.

Torques experienced during cantilevers and non-cantilevers

For cantilevers, we estimated the torque due to gravity acting on the suspended portion of the snake when at landing, which we assume is the maximum torque experienced during the crossing. During cantilevers, snakes typically held the body straight and landed with their head very close to the end of the target. As a result, these torques increased linearly with gap size (Fig. 6A, open symbols).

For non-cantilever behaviors, we examined the torque due to gravity experienced by the snake at transition. The log of the transition torques decreased linearly with gap size (Fig. 6A, 95% CI: -0.03 , -0.01), indicating that the maximum static torque experienced by the snakes was increasingly small compared with the theoretical maximum cantilever torque for a gap of the same size. The largest transition torques were very similar to the largest cantilever torques, and occurred for gaps between 43% and 55% SVL

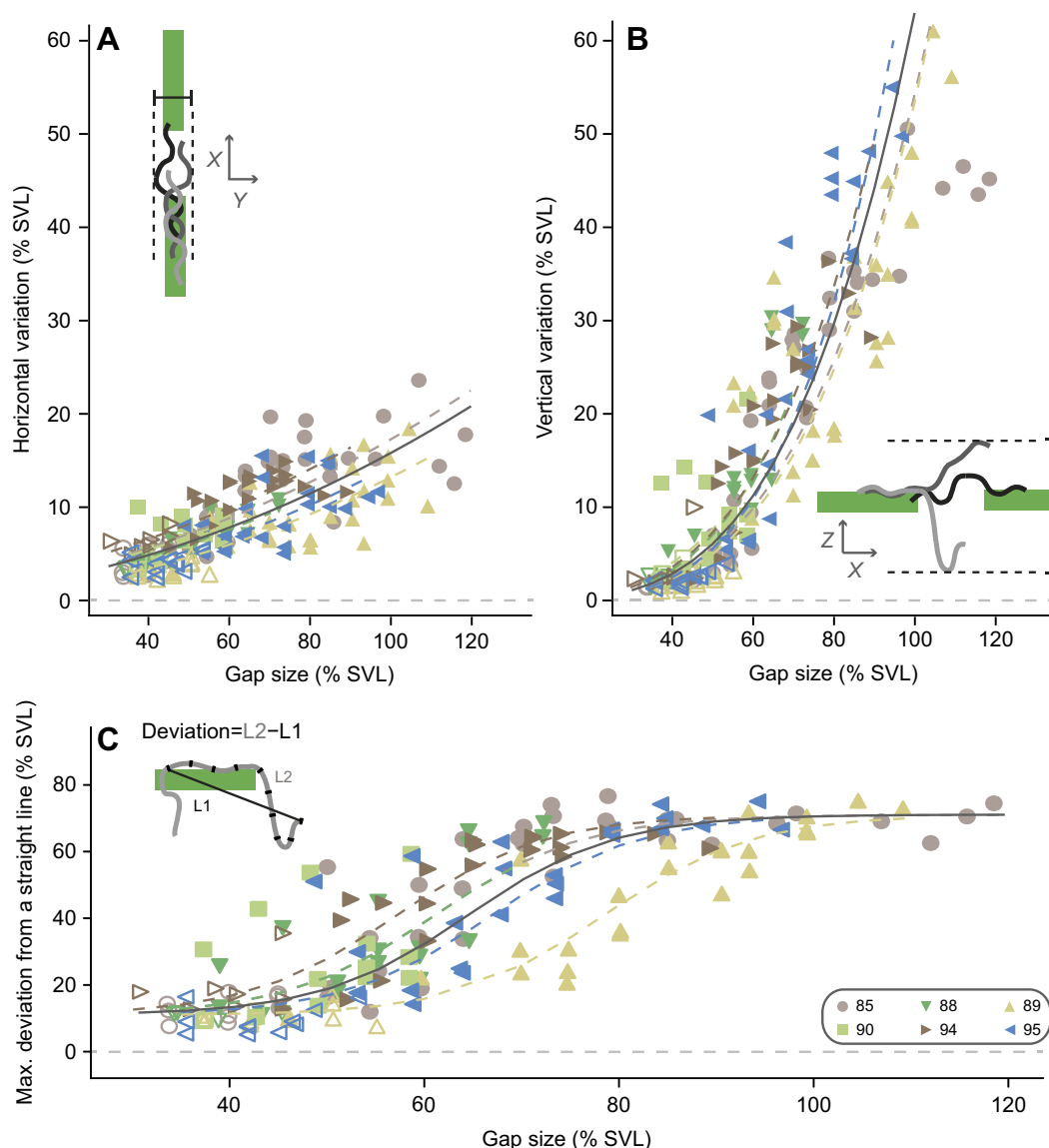


Fig. 4. Positional variation versus gap size. Snakes showed increasing variation in horizontal (A) and vertical (B) position as gap size increased, while the maximum deviation from a straight line (C) showed a sigmoidal relationship with gap size. These changes illustrate the transition from straight-bodied cantilever postures to more dynamic and curved postures for non-cantilever movements.

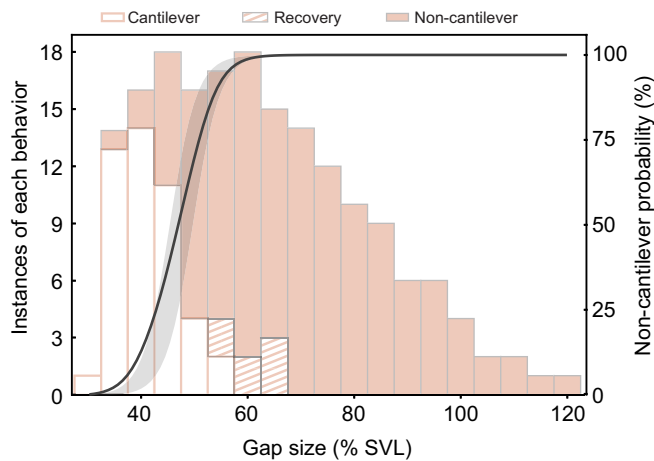


Fig. 5. Likelihood of using specific locomotor behaviors across gap sizes. We categorized behaviors as cantilevers, non-cantilevers or recovery. The bar graph (left axis) shows the number of instances of each behavior type at a given gap size, across 6 snakes. The line graph (right axis) shows the mean predicted probability of a snake choosing a non-cantilever behavior at a given gap size, as determined by a mixed-effects binomial regression. For this analysis, recovery movements are coded as non-cantilevers. The shaded region on the line graph represents the interquartile range of the predicted probability.

(Table S1). In contrast, the torques at transition for the largest gap sizes were generally much smaller, although there was variation between individuals (Fig. S4, top row). Correspondingly, the head position of the snakes at transition was closer to the origin as gap size increased (Fig. 6B, 95% CI: -0.032 , -0.022). Together, these results illustrate that snakes initiate dynamic movements relatively earlier as gap size increases, experiencing decreasing torques as a result.

Maximum, landing and average head speed

Both maximum and landing head speeds exhibited a sigmoidal relationship with gap size (Fig. 3). Low-speed gap sizes corresponded to those in which cantilevers were used, high-speed gap sizes corresponded to those in which non-cantilevers were used, and the transition between the two regions corresponded to gap sizes (40–60% SVL) in which the snakes were using either cantilevers or non-cantilevers that gradually increased in speed with gap size.

There was a positive linear relationship between the log of average head speed and the log of gap size (fixed-effect estimate of 1.29, 95% CI: 0.46, 2.10), although the increase in average head speed was not particularly dramatic. This result indicates that flying snakes do not necessarily experience shorter crossing time for large gaps, even while using movements with higher maximum and landing speeds. However, there were large differences in this relationship between individuals (Fig. S4, 2nd row), with some individuals displaying greater increases in head speed with gap size than others.

We also compared cantilever to non-cantilever landing head speeds at the five gap sizes in which both behavior types were used. The landing head speeds at these gap sizes for non-cantilevers were greater, on average, than those of cantilever movements (Table 1).

Variations in movements with gap size

Across behavior types, square root of Y variation (lateral displacement) increased with gap size (Fig. 4A, 95% CI: 0.026, 0.033). The log of Z variation (vertical displacement) increased with the log of gap size (Fig. 4B, 95% CI: 2.88, 3.79). Together, these results indicate that flying snakes deviate increasingly from the

straight-line positions associated with cantilevers as gap size increases. Snakes also demonstrated a non-linear increase in maximum deviation from a straight line (Fig. 4C), indicating that although the non-cantilever behaviors generally get ‘curvier’ as gap size increases, they reach a limit around 80% SVL.

Within the non-cantilever behaviors, increasing gap size led to large changes in arc height at the low point, arc height at the high point, and loop depth at the low point (Fig. 7). Initially, deviations from a cantilever behavior involved increasing values of arc height at both the low point and high point, whereas loop depth at the low point remained small, giving the snakes’ motion the appearance of a large upward arch. As gap size continued to increase, the snakes began to create U-shaped loops (Movie 2), in which the low point arc height and loop depth were approximately the same size. For the largest gap sizes, the low point loop depth continued to increase while arc height did not, leading to J-shaped loops (Movie 2).

At the high point, there was minimal variation in loop depth associated with increasing gap size (95% CI: -0.073 , 0.018), but arc height increased linearly with gap size (fixed-effect estimate: 0.48, 95% CI: 0.39, 0.56), indicating that in-air peak postures involved greater excursions of the head above the branch without much change in midbody positioning. At the low point, loop depth increased linearly with gap size (fixed-effect estimate: 0.81, 95% CI: 0.67, 0.95), whereas arc height showed an inverted-U-shaped relationship with increasing gap size in most individuals (two snakes included in the analysis did not show this pattern as clearly within the range of gap sizes they crossed; Fig. S4, third row). Based on the linear mixed-effects breakpoint analysis, the breakpoint for the relationship was 69.5% SVL (95% CI: 61.40%, 77.66%), with a difference in slope of -0.85 (95% CI: -1.10 , -0.60). This breakpoint indicates where the transition from U- to J-shaped loops begins: at this gap size, arc height and loop depth are both low; beyond the breakpoint, arc height subsequently decreases while loop depth continues to increase.

In addition to changes in body posture, the distance the snake traveled from low point to landing increased with gap size (Fig. 8A). The fixed-effects estimate for the slope of this relationship was 1.83 (95% CI: 1.62, 2.03), indicating that the distance travelled increased at a greater rate than the gap size. The amount of overshoot (in % SVL) generally increased with gap size up to a certain point (Fig. 8C), beyond which the relationship varied substantially between snakes (Fig. S4, bottom row). Based on the linear mixed-effects breakpoint analysis, the change point for the relationship was 61.2% SVL (95% CI: 50.9%, 71.5%) with a difference in slope of -1.04 (95% CI: -0.59 , -1.50), indicating that this gap size is where many snakes hit a limit in overshoot, subsequently experiencing similar or decreasing amounts of overlap with the target at landing as gap size increases.

Comparisons of J-loop crosses with glide launches

J-loop jumps used in gap crossing were similar to those used by snakes initiating a glide in a previous study (Socha, 2006). Specifically, J-loop crosses did not vary significantly from J-loop launches in terms of preparation time, acceleration time, maximum or landing speed, or height gained. The sole difference was in distance traveled: snakes crossing gaps traveled slightly farther horizontally at the level of the origin (Table S2).

DISCUSSION

Behavior use varies with gap size

This study establishes that *C. paradisi* uses both cantilever and non-cantilever behaviors to cross horizontal gaps. As gap size increases,

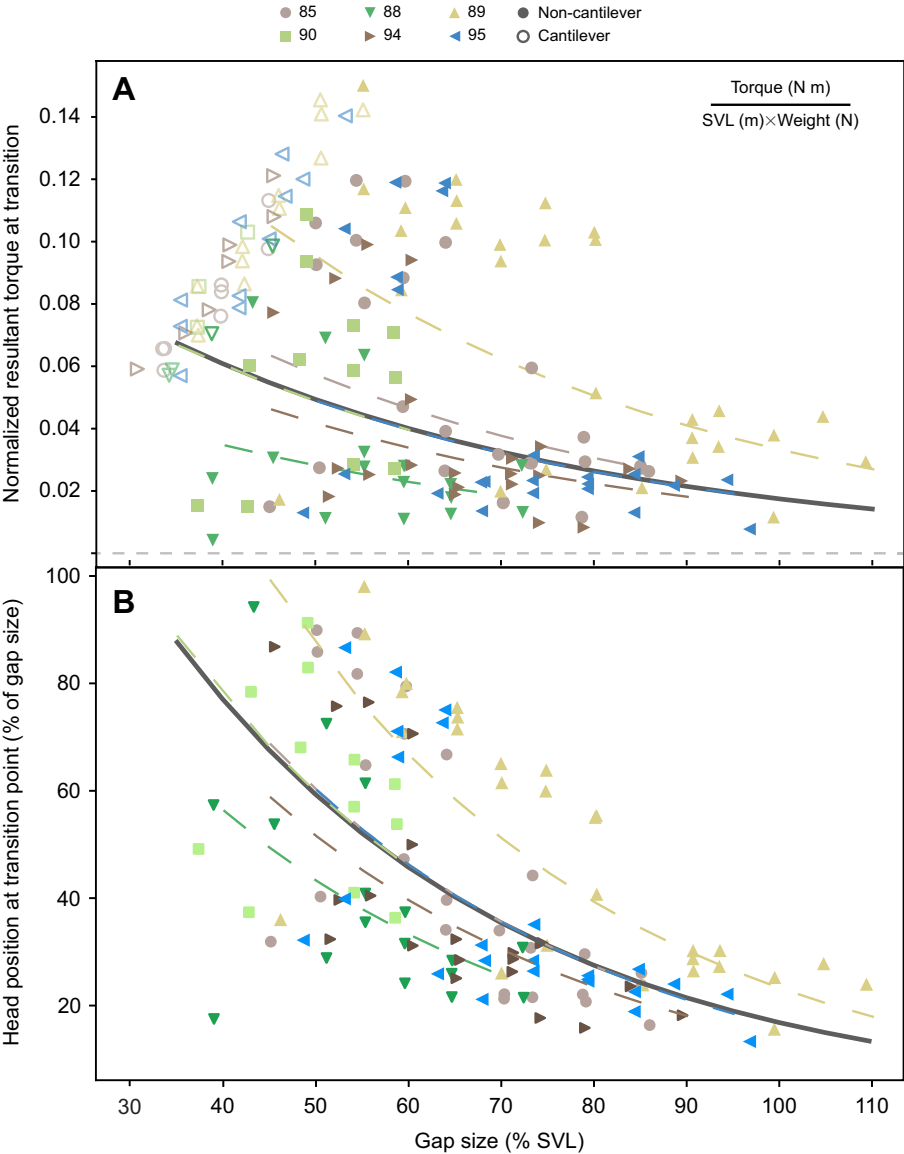


Fig. 6. Torque and relative head position at the transition from a cantilevered position versus gap size. (A) The normalized resultant torque experienced by the snakes at each non-cantilever trial is shown against gap size, measured at transition (filled symbols). Torque (N m) was normalized by SVL (m) and weight (N). Cantilever torques at landing (open symbols) are shown for comparison. The highest torque values at transition were experienced for intermediate gap sizes, and were rarely greater than those experienced during the longest cantilevers. Lines show the results of a mixed-effects model linear regression between gap size and log-transformed torque, reverse-transformed to present on the untransformed axis. (B) The head position at transition, in terms of distance along the X-axis from the origin branch, is shown as a percentage of gap size. Snakes initiated dynamic movements relatively earlier as gap size increased.

flying snakes vary their movements, including changing their body posture and speed. In particular, *C. paradisi* exhibited three behavioral regimes: a predominantly cantilever regime for small gaps (<40% SVL), a transition regime for intermediate gaps (40–60% SVL) in which snakes used both cantilevers and non-cantilevers, and a predominantly non-cantilever regime for large gaps (>60% SVL). This pattern, in which an animal uses a reaching behavior for small gaps and more dynamic behaviors for large gaps, is consistent with behavior–gap size relationships displayed in

several other non-snake species (Graham and Socha, 2020), and supports the hypothesis that flying snakes reserve dynamic movements for gaps larger than those they cantilever across.

For small and intermediate gap sizes, flying snakes do not exhibit behaviors substantially different from those of other snakes. The cantilever of *C. paradisi* is characterized by steady movements and a relatively straight body posture (Movie 1), also typical of other snake species (Hoefer and Jayne, 2013; Lillywhite et al., 2000; Ray, 2012). Some of the non-cantilever behaviors used at intermediate gap sizes also do not appear to be unique to flying snakes. Although the brown tree snake occasionally uses horizontal, S-shaped, lateral bends to lunge (Jayne and Riley, 2007) – a behavior never observed in *C. paradisi* – the primary lunging movement of the brown tree snake (Byrnes and Jayne, 2012) appears to be very similar to some of the non-cantilever behaviors described here.

However, flying snakes use additional types of non-cantilever behavior to cross gaps, which can primarily be distinguished by changes in loop depth and arc height at the low point of the movement. At intermediate gaps, where the behavior appears most similar to that of the brown tree snake, non-cantilever behaviors are characterized primarily by acceleration of the head upward and

Table 1. Landing head speed comparisons between non-cantilever and cantilever crossing events, at the five gap sizes for which both behavior types were performed

Gap size (% SVL)	Average cantilever landing speed (SVL s ⁻¹) (N)	Average non-cantilever landing speed (SVL s ⁻¹) (N)
35	0.275 (13)	1.73 (1)
40	0.195 (14)	0.531 (2)
45	0.249 (11)	0.398 (7)
50	0.225 (4)	0.893 (12)
55	0.359 (2)	1.23 (15)

N, number of trials.

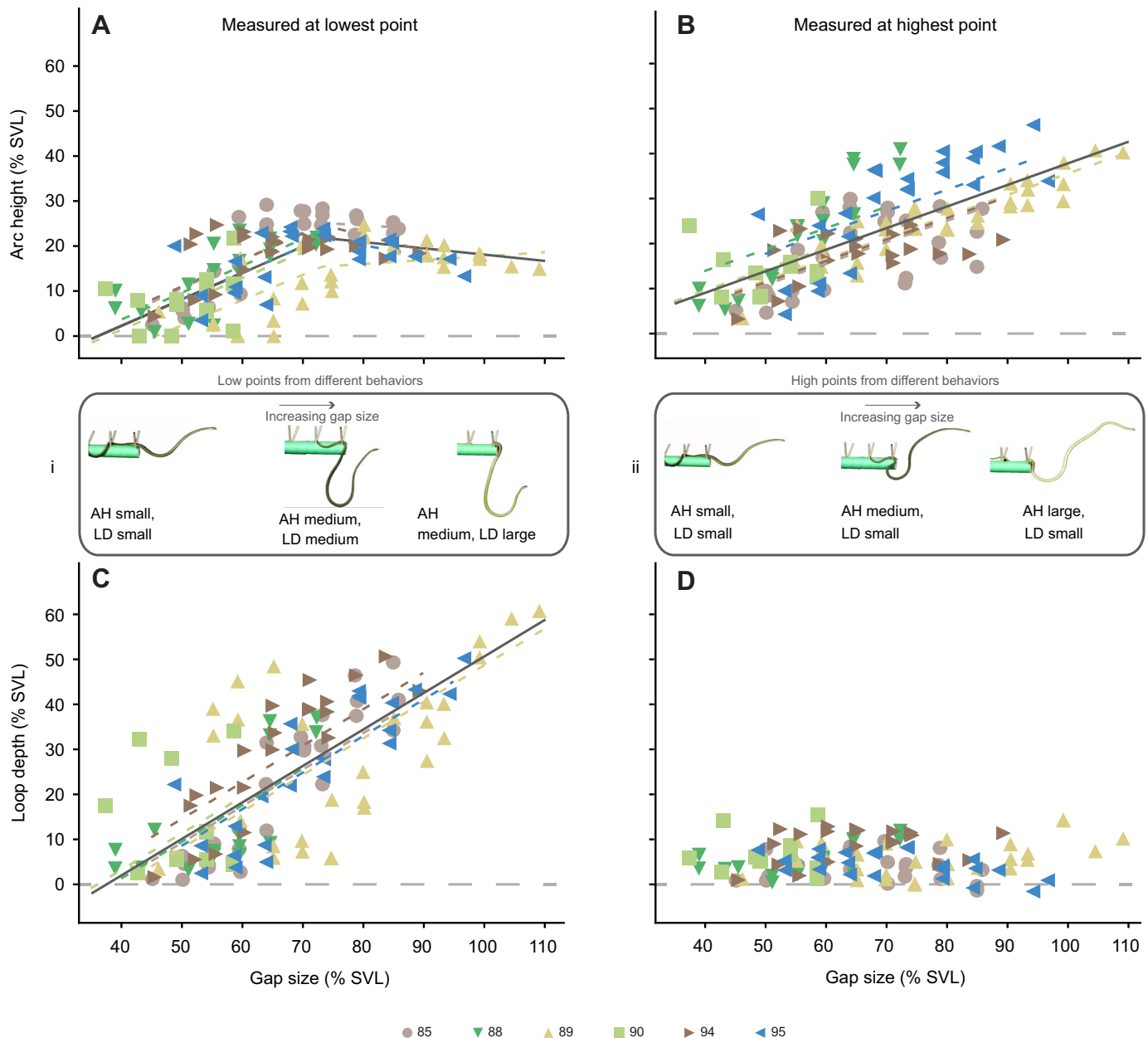


Fig. 7. Snakes use different pre-launch postures for intermediate and large gaps. Arc height at the low point (A) showed two distinct relationships to gap size in most snakes, increasing up to a breakpoint of 69.5% SVL (95% confidence interval, CI: 61.40%, 77.66%), and then decreasing as gap size increased. Paired with increasing loop depths (C), the low point posture generally changed from a U-like to a J-like shape as gap size increased (i), although the relationship varied slightly between snakes (A, dashed lines). Loop depth at the low point (C) and arc height at the high point (B) increased linearly with gap size, reflecting the deeper loops and more dynamic movements required to cross larger gaps. In contrast, loop depth at the high point (D) did not vary as much with gap size between intermediate and large gaps, and was generally small. AH, arc height; LD, loop depth.

outward (Fig. 9, intermediate gap silhouettes). These ‘arching’ lunges involve only very small below-branch loops, if any. As gap size increases, so too does the size of the below-branch loop, until the pre-launch posture resembles first a ‘U’ for gaps around 50–70% SVL, and then primarily a ‘J’ for gaps of 80% SVL and above (Fig. 9, large gap silhouettes).

These U- and J-shaped movements have only been observed in flying snakes. Brown tree snakes have not been observed creating below-branch loops for horizontal crosses, and the primary bending mechanism they use for lunging is dorsiflexion (Byrnes and Jayne, 2012; Jayne and Riley, 2007). Overall, only a few of the looped movements used by flying snakes during gap crossing matched the

body positioning of J-loop launches, and typically these movements were used for the very largest gap size crossed by a given individual. Nevertheless, many of the looped behaviors that did not quantitatively match the J-loop launches still appeared quite similar, involving a roughly J-shaped loop, a posterior body anchor and a similar launch trajectory (Fig. 9, 116% SVL column).

Additional studies should investigate more deeply the differences between looped behaviors in the glide launch and gap-crossing contexts. The sample sizes here are too small to make strong conclusions, but do provide ideas for future directions. Although we were not able to observe the degree of axial twisting from the motion-capture data, observations of the video taken for exhibition

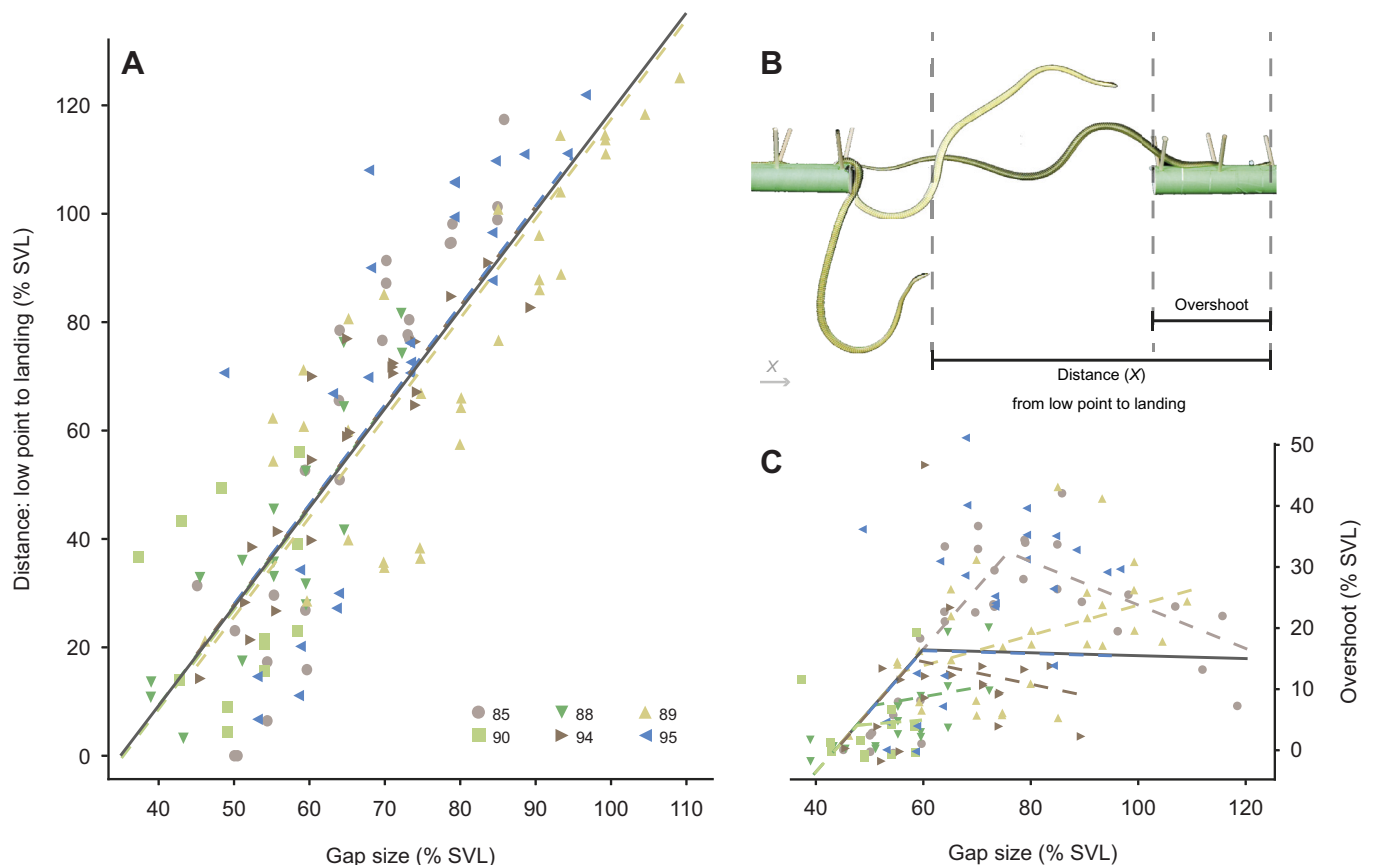


Fig. 8. Distance traveled and overshoot versus gap size. (A) The distance a snake's head traveled horizontally from the low point to landing increased linearly with gap size (slope: 1.83; 95% CI: 1.62, 2.03), showing that snakes did not simply travel their maximum distance each time. (B) Three time points from a looped jumping behavior, illustrating the appearance of the body at the low point, high point and landing. Overshoot is the horizontal distance from the end of the target to the position of the head at landing. Distance traveled from the low point to landing is the horizontal distance traveled by the head from the low point to the position at landing. (C) Snakes exhibited varied relationships between overshoot and gap size (dashed lines). The fixed-effects estimate supported a breakpoint at 61.2% SVL (95% CI: 50.9%, 71.5%), although there was variation between snakes. For larger gaps, some snakes showed decreased overshoot and others showed stable or increased overshoot for gap sizes past the breakpoint, leading to a fixed-effect estimate (solid line) of slope that was near 0 after the breakpoint. Note that not all snakes crossed the largest gaps, so it is unclear what would have occurred for each individual.

purposes (Movie 2) suggest that J-shaped gap crosses involved the same axial twisting and lateral bending described in the anchored J-loop launch. However, the snakes only sometimes formed the ribbon-like flattening of the body during gap crossing, which is always utilized in gliding (Socha, 2011). The presence of a target to aim for may be an important factor, as snakes appeared to have greater arc heights during gap crossing, perhaps to keep their head more in line with the target. Looking at all trials in which snakes used non-cantilever behaviors with larger loop depth than arc height, low loop depth and low arc height were $33 \pm 13\%$ SVL and $17 \pm 8\%$ SVL (mean \pm s.d.), respectively, compared with $55 \pm 8\%$ SVL and $5 \pm 5\%$ SVL for J-loop launches.

Overall, the data presented here support an understanding of gap-crossing behaviors in snakes as follows: most, if not all, snakes can cantilever across gaps, with arboreal species in particular exhibiting the greatest cantilevering ability. A few colubrid species can also use arching lunges – in addition to the brown tree snake and paradise tree snake discussed here, it appears that at least one species of *Dendrelaphis* (the sister taxon to *Chrysopelea*) may also be able to perform such lunges or perhaps even J-loop jumps (Socha, 2011). And, finally, the flying snakes in particular are able to use large dynamic movements, involving below-branch loops, to significantly extend their performance. While many species

have been examined in terms of their cantilevering performance, developing a better understanding of how widespread the ability to perform arching lunges might be, comparing the kinematics between these different lunging snakes, and identifying what other gap-crossing behaviors may exist in snakes, are important issues for future study.

Lastly, although arching lunges and U- and J-shaped movements are distinct, examination of the deviation of the body from a straight line (Fig. 4C) shows a wide transition zone between relatively straight and highly curved movements. There may not, therefore, be a discrete shift between the straight-bodied cantilevers and curved non-cantilevers. Instead, flying snakes appear to gradually increase the size of their body bends, first increasing the arc height and then the loop depth (Fig. 7i) as gap size increases.

Is the use of dynamic behaviors advantageous for gap crossing?

The use of dynamic non-cantilever behaviors appears to confer a significant advantage in distance capability for *C. paradisi*, with all individuals studied here being able to cross gaps larger than 90% SVL, and one individual crossing a gap of 118% SVL. This result contrasts strongly with all other previous reports of maximum gap crossing in a horizontal configuration for snakes: 65% body length

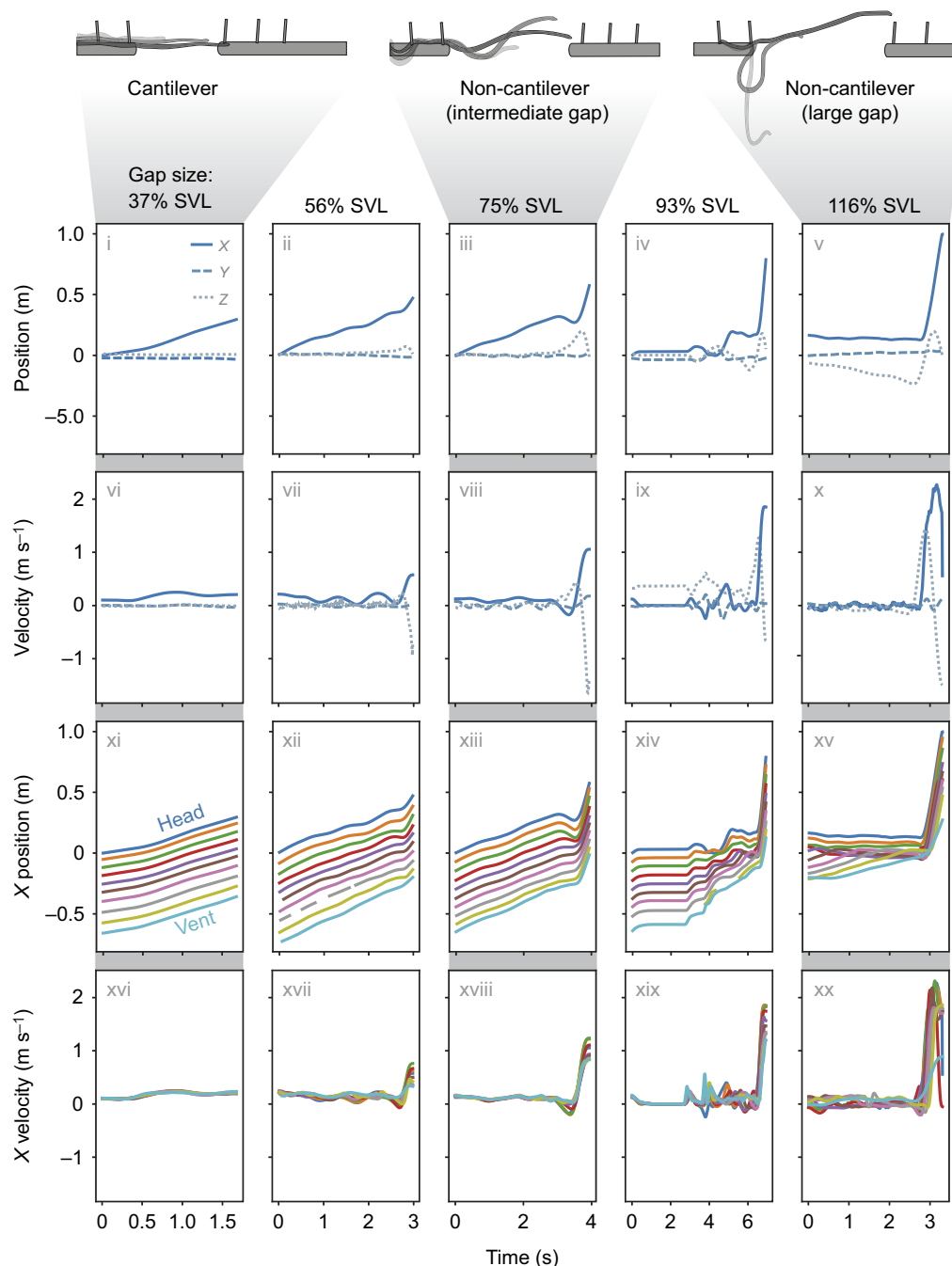


Fig. 9. Representative kinematic plots of the position (i–v, xi–xv) and velocity (vi–x, xvi–xx) of various body points at different gap sizes. The top two rows show data for the position and velocity of the head, in all three dimensions. The bottom two rows display position and velocity data along the X-axis for all markers. Each column corresponds to the same trial, and the relative gap size is listed in the first row. These correspond to absolute gap sizes of 27.4, 47.3, 53.4, 66.8 and 83.9 cm, respectively. Pop-outs (top) show silhouettes of what the corresponding movements look like.

for cantilevering (*Sibon argus*; Ray, 2012) and 64% SVL for lunging (brown tree snake; Jayne and Riley, 2007).

Interestingly, *C. paradisi* are just as likely to use non-cantilevers as cantilevers at a gap size of 47.5% SVL, which is about the same maximum cantilever ability seen in many other species, particularly arboreal ones (Hoefer and Jayne, 2013; Lillywhite et al., 2000; Ray, 2012). Additionally, the maximal torques experienced by flying snakes occurred at intermediate gap sizes, and are similar to those experienced by the brown tree snake at the initiation of lunging (mean \pm s.d., flying snakes: 0.06 ± 0.03 N m, $N=6$ individuals; brown tree snakes: 0.069 ± 0.014 N m, $N=9$ individuals; Byrnes and Jayne, 2012). However, examining all non-cantilever crosses in this study shows that the average torque experienced at the initiation of a dynamic movement in flying snakes is much lower: 0.024 ± 0.02 N m. Thus, the cantilever and intermediate lunging ability of *C. paradisi* is

unremarkable for an arboreal snake, but its gap-crossing ability is exceptional, owing entirely to the use of more dynamic gap-crossing movements. The data presented here therefore support the hypothesis that the use of dynamic movements enables flying snakes to cross gaps of at least one full body length (100% SVL), a substantial difference compared with similar non-gliding species.

The advantages conferred by the dynamic movements appear to relate strongly to torque limitations associated with cantilevering. In general, when an animal is reaching across a gap, it will face increasingly large torques as the gap size increases. These torques can be separated into whole-body pitching torques and buckling torques. For snakes, as an individual extends outward into a gap, the force of gravity acts on the suspended portion of its body, which is counteracted by the force of gravity acting on the supported body and any gripping force exerted by the snake. Once the torque due to

the suspended body becomes high enough, the snake will have to grip to avoid pitching forward, and when the suspended body torque becomes too high, buckling or pitching occurs, an instability requiring a control response.

A theoretical analysis of cantilevering in snakes demonstrates how morphology determines the onset of buckling (Astley, 2020). A gap-crossing snake will buckle specifically when the force acting on the suspended portion of its body exceeds the maximum strength of the muscle acting at the most posterior suspended portion. This distance depends on multiple morphological factors, including the ratio of tendon length to muscle length, the span and cross-sectional area of the relevant muscles (most significantly, the spinalis–semispinalis), vertebral length, and mass (Astley, 2020).

We lack sufficient morphological data for *C. paradisi* to be able to identify the theoretical buckling point, but data from one snake may be instructive: its observed transitions may have occurred very close to its buckling torque limits, further supporting the idea that dynamic movements allow flying snakes to avoid a torque limitation. The seven instances of a recovery movement involving a crossing failure from this individual all occurred at intermediate gap values, around where other specimens transitioned from cantilevering to non-cantilevering. Although we cannot be certain that the snake's initial failed attempts were due to the individual reaching the limit of its ability to hold the suspended body up, observation of the video does not suggest other obvious causes of the initial failure (e.g. mis-aim); rather, the snake simply started to buckle before enough of its head was over the target to secure purchase. Our analysis of the torques experienced by all snakes in this study while in a cantilevered body position (Fig. 6) further supports this conclusion: in the three trials in which the snake (#89) attempted a cantilever but failed, the torque experienced at failure was greater than the torque experienced during any of its successful cantilevers.

Does torque act as a trigger for the transition to lunging?

For both the brown tree snake (Byrnes and Jayne, 2012) and the flying snakes studied here, the use of dynamic movements results in a decrease in the maximum static torque the snake experiences, comparing the moment just before lunge initiation with what the snake would have experienced had it cantilevered across a gap of the same size. However, in contrast to brown tree snakes, which typically extend through their maximum cantilever ability before initiating a lunge, flying snakes sometimes initiate dynamic movements shortly after entering the gap. In particular, for gaps above 70% SVL, most snakes were crossing only 20–40% of the total gap distance before initiating a dynamic movement. Therefore, our data do not support the hypothesis that flying snakes extend to their maximum cantilever distance before initiating dynamic movements.

In correspondence with short extension into the gap at transition for larger gap sizes, flying snakes experience decreasing pre-launch torques during non-cantilever crosses as gap size increases. This pattern suggests that torque does not act as a trigger for the initiation of lunging. If torque were acting as a trigger, we would expect to see a consistent transition torque value across all gaps for a given individual. Instead, transition torque decreased with gap size. Flying snakes must therefore use other cues (likely visual, discussed later) to determine whether to employ non-cantilever behaviors.

Why do flying snakes avoid non-cantilever behaviors for small gaps?

Each *C. paradisi* primarily used non-cantilever behaviors for larger gaps. However, the smallest gap size at which any individual used a non-cantilever behavior was 35% SVL, demonstrating that flying

snakes are physically capable of using non-cantilevers for small gaps. As such, the clear behavioral pattern with gap size demands explanation: what advantages or disadvantages might guide behavioral choice?

Flying snakes may prefer to select slower cantilever movements when possible to reduce the risk of missing the target. The non-cantilever behaviors are characterized in part by greater landing and maximum head speeds, which may result in a decrease in landing accuracy. Thus, dynamic crossing modes might be faster, but they could be riskier, resulting in more complete failures of missing the target and falling. Such speed–accuracy trade-offs are common in reaching and gap crossing, and have been observed in the brown tree snake (Jayne and Riley, 2007). Alternatively, perhaps fast movements are more noticeable, so using the slower cantilever can help the snake avoid detection by predators and prey alike.

When launching long glides, flying snakes use both anchored and ‘sliding’ jumps, the latter of which involves significantly less preparation time (Socha, 2006). In this study, we observed many anchored movements, as well as several movements that, similar to the sliding jumps, involved the formation of a small loop that the snake ‘fed’ its body through to accelerate away from the origin. During gap crosses, however, *C. paradisi* typically extended a much larger amount of body off the edge of the branch before forming the loop, increasing the preparatory time. So, while flying snakes are capable of launching jumps that require less preparatory time, they do not appear to use such movements when crossing gaps, perhaps because they are aiming towards a narrow target.

The increased preparatory time during non-cantilever behaviors may help explain why, despite high maximum speeds, average speeds were comparatively low when crossing large gaps. Most snakes displayed only moderate increases in average speed with increasing gap size, with high variance among trials, such that trials with dynamic non-cantilevers were not always faster than those with cantilevers. Thus, when performing a non-cantilever behavior with a long preparatory period, flying snakes potentially experience the accuracy disadvantages of high speeds without the benefit of getting to their destination more quickly.

Finally, flying snakes might avoid using non-cantilever behaviors at small distances for energetic reasons. Our data are not sufficient to assess energy use, but theoretical considerations may provide some insight. For cantilevering, the metabolic cost is proportional to the number of extended vertebral units cubed, and therefore distance cubed (Astley, 2020). During non-cantilever behaviors, dynamic movements should be governed by projectile mechanics (Biewener and Patek, 2018), and so the work required to cross a given distance should be proportional to that distance (assuming constant acceleration in the takeoff phase). As such, cantilevering likely requires less effort for very small gaps, and there may be some distance at which the two behavior types are equally taxing (beyond which lunges are less taxing than cantilevers). Future work should examine the role of energetic considerations in governing gap-crossing behavior choice.

Overall, there are multiple indications that flying snakes tailor their movements to gap size. In addition to selecting between cantilever and non-cantilever behaviors, there are several suggestions that particular non-cantilever postures are used for particular gap sizes. First, flying snakes did not merely travel the maximum distance each time they used a dynamic movement. Instead, flying snakes increased the distance they traveled as gap size increased, although the overshoot data show that they did not perfectly match their lunge distance to the gap size. Second, we found that snakes generally used very similar movements when

presented with the same gap size on different days. Future studies should explore behavioral consistency in gap-crossing locomotion.

Jumping in elongate animals

We have so far refrained from using the term ‘jumping’ to describe the non-cantilever behaviors of flying snakes. In general, jumping is a term reserved for behaviors in which the animal departs the substrate and becomes airborne. This is most familiar with legged jumpers, but also seen in legless taxa such as gall midge larvae (Farley et al., 2019) and bony fishes (Ashley-Ross et al., 2014). Unfortunately, the motion-capture data collected in this study did not enable precise analysis of the posterior body relative to the origin support, leading to two unaddressed questions: (1) how often do the flying snakes become airborne during gap crossing?; and (2) what is the role of the rear body during non-cantilever behaviors?

For both questions, our study provides some preliminary data. In terms of the role of the rear body, the incidental partial lack of tail in the snake that exhibited the recovery response is indicative of the use of the rear body to grip, as during failure instances the snake was not capable of wrapping the tail. Gripping considerations reveal another constraint to cantilevering or other behaviors in which the snake extends a significant portion of the body into the gap: as the gap gets longer, the snake runs out of body to use for gripping. Future studies should investigate the role of the rear body, and how much gripping it exerts, across different gap-crossing behaviors.

In the case of distinguishing between lunges and jumps, a large number of the non-cantilever behaviors are likely most correctly described as lunges. However, one video taken for exhibition purposes (Movie 2) shows that flying snakes using the J-shaped movements do sometimes become airborne. As described above, these movements did not appear visually distinct from anchored J-loop launches, which always become airborne (by dint of initiating a glide), and are thus considered to be jumps. It is interesting to note, therefore, that there may in fact be no difference in muscle activation between J-shaped movements that are aimed toward a target and J-shaped movements that are glide-initiating jumps, and mere target positioning can influence whether a particular non-cantilever behavior is a lunge or a jump. Future work should investigate muscle activation during these movements to probe this distinction.

Future work: sensory modalities used during gap crossing

Several characteristics of flying snakes’ response to changing gap size suggest that they decide whether to use a non-cantilever behavior partly by assessing gap size. At intermediate distances, flying snakes proceeded through a substantial portion of the gap in a cantilever before initiating the arch or loop that precedes a dynamic movement. In contrast, with large gaps, *C. paradisi* extended only a small distance before initiating a loop to begin the dynamic portion of their movement (Fig. 6B). This behavior strongly suggests that *C. paradisi* use visual input to judge gaps that are large. Several other anecdotal observations suggest that vision plays a significant role. In some trials, the snakes proceeded slowly along the origin, stopping regularly to lift their heads up, and appeared to look at the target. Often, they would also exhibit small lateral oscillations (‘head wagging’) during this period. This behavior might be used to visually assess depth, increasing parallax and augmenting the possible region of stereo vision at the center of their visual field (Zamore et al., 2020).

Conclusions

To cross horizontal gaps, flying snakes use multiple behaviors that vary with distance, some of which are similar to known snake locomotor behaviors. At the smallest gap sizes, *C. paradisi* uses the

cantilever cross, identical to that of all other recorded snake species. At intermediate gap sizes, flying snakes sometimes use movements that appear similar to lunges used by the brown tree snake, but also use looped behaviors that appear novel. Finally, for the largest gap sizes, flying snakes use a looped movement that is kinematically similar to the anchored J-loop used to launch glides. The variations in body posture, speed and overshoot with gap size indicate that flying snakes can finely tune their behavior to gap size. Overall, this study demonstrates that, similar to limbed species (Graham and Socha, 2020), limbless animals use less dynamic reaching behaviors for small gap sizes and reserve more dynamic behaviors for large gap sizes, providing strong support for the generality of this pattern among animals of broadly varying morphology.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: J.J.S.; Methodology: M.G., J.J.S.; Software: M.G.; Formal analysis: M.G.; Investigation: M.G., J.J.S.; Resources: J.J.S.; Data curation: M.G.; Writing - original draft: M.G.; Writing - review & editing: J.J.S.; Visualization: M.G.; Supervision: J.J.S.; Project administration: M.G.; Funding acquisition: J.J.S.

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Data availability

All datasets, processing code and R scripts are available on GitHub: <https://github.com/TheSochaLab/FlyingSnakeGaps>

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Supplementary Information

Supplementary Materials and Methods

Infrared marker placement

The spacings between the markers were measured as they were placed, to facilitate later analysis. The markers were affixed using adhesive dots (Removable Dots, Glue Dots ® Adhesive, Germantown, WI, USA) attached to stickers (Color Coding Labels, Jot ™, Greenbrier Intl Inc., Chesapeake, VA, USA), which were then placed on the snake to increase visual contrast. We also marked a dot of white paint (Basics Acrylic, Liquitex ®, Cincinnati, OH, USA) caudally to each of the markers, to enable replacement of the marker at the same location if it fell off.

Gap size calculations

The size of the gap in each trial was calculated using the locations of the origin and target markers, using the averages of their values throughout a trial. These positions were then adjusted by the relative offset from the true branch end, defined as the center point of the top surface at the end of the PVC. The absolute gap size was calculated as the Euclidean distance from the target end to the origin end.

In eight trials, the position of one of the branch markers was not properly recorded, either because the marker fell off or was occluded. In these cases, the gap size was inferred to be the size of the gap in the other replicate trials conducted at that gap distance that day; if a replicate was not available, the size of the gap was set to that measured using a measuring tape on the day of the experiment.

Across all trials, the average error between the intended gap size (compared to that calculated using the 3D data) was 1.6% (min: 0.02, max: 14). The average error between the binned gap size (the gap size rounded to the nearest 5% SVL) used for statistical analysis and the gap size calculated using the 3D data was 1.3% (min: 0.01, max: 4.8). In absolute terms these values corresponded to 0.68 cm (min: 0.01cm, max: 3.7 cm) and 0.73 cm (min: 5.5e-3 cm and 2.2 cm), respectively.

Distinguishing between cantilevers and non-cantilevers

For most trials, the distinction between cantilever and non-cantilever behaviors was obvious. Ambiguous cases were adjudicated as follows:

- Trials in which the snake deviated from a straight line path (e.g., formed a loop or an arch) but then did not initiate any sort of lunging, jumping, or arching movement, and instead returned to a roughly straight body posture before continuing steadily across the gap, were classified as cantilever.
- Trials in which the snake moved in a relatively straight line path until its head was vertically above the target, and then seemed to release tension in order to “drop” onto the target, were classified as cantilever.
- Trials in which the snake moved in a relatively straight line path until nearing the target branch, and then initiated a very small upward and outward (lunge-like) movement toward the target to land, were classified as non-cantilever.

Calculation of moving and landing velocities

In some trials, the snake paused for long periods before continuing across the gap, artificially depressing the total average speed. Therefore, we defined an average head speed using only frames in which the snake was moving toward the target branch. To determine this average speed, the data were filtered to exclude frames where the X velocity component of the head was less than 0.025 m/s. This criterion was selected by comparing the 3D motion capture data to the corresponding video for three sections of data: one in which the snake was moving very slowly, and two in which the snake was entirely still (Fig. S3).

Random effects structure

The random effects structure was determined for each model by comparing a random slopes and intercepts vs. a random intercept-only model with the same fixed effects structure, fit by REML. The Akaike information criteria (AIC) was calculated for each model, and for the model set under consideration, $\Delta_i = AIC_i - AIC_{\min}$ was determined for each model i in the set. Following Burnham and Anderson (Burnham and Anderson, 2004), $\Delta_i < 2$ is considered to provide strong support for the less complex model i , $4 < \Delta_i < 7$ provides moderate support for the less complex model i , and if $\Delta_i > 10$, there is no support for the less complex model i over the minimal AIC model. If the random slopes model was singular, we used the intercept-only model without comparing the AIC.

Missing and excluded data

Overall, we recorded 289 gap-crossing events from seven snakes. 64 of these events were not included in the analyzed data because they were used to establish methods, familiarize the snakes with the setup, or encourage the snake to cross a larger gap by presenting smaller gaps. However, in three cases (snake #94, gap = 30% SVL; snake 90, gap = 35% and 40%), measurement error led to unintended gap sizes being presented.

Data from an additional 15 trials from one snake were removed because the snake was later found to have been gravid. In 23 other trials, the snake did not complete a crossing event. In these cases, generally the snake either jumped off-target or repeatedly turned back to the origin (a refusal) (Fig. S4). Finally, five trials had to be excluded because the quality of the motion capture data was too poor to analyze or the file was corrupted. In total, 182 trials from six snakes were used for analysis.

For three trials, loop depth could not be calculated because the origin marker was not recorded properly by the motion-capture system. Additionally, in seven trials, as part of attempting to coax the snake across the branch, the snake was held near the target until it began to initiate a loop, and then moved back to the origin. Because the snake was being held during the transition frame for these trials, they are excluded from the torque and postural analyses. The torque analysis and head position at transition analysis also exclude the three trials where the origin marker was missing, and one trial in which the head position was missing from the transition frame. Finally, the overshoot analysis excludes five trials in which the target marker was not recorded.

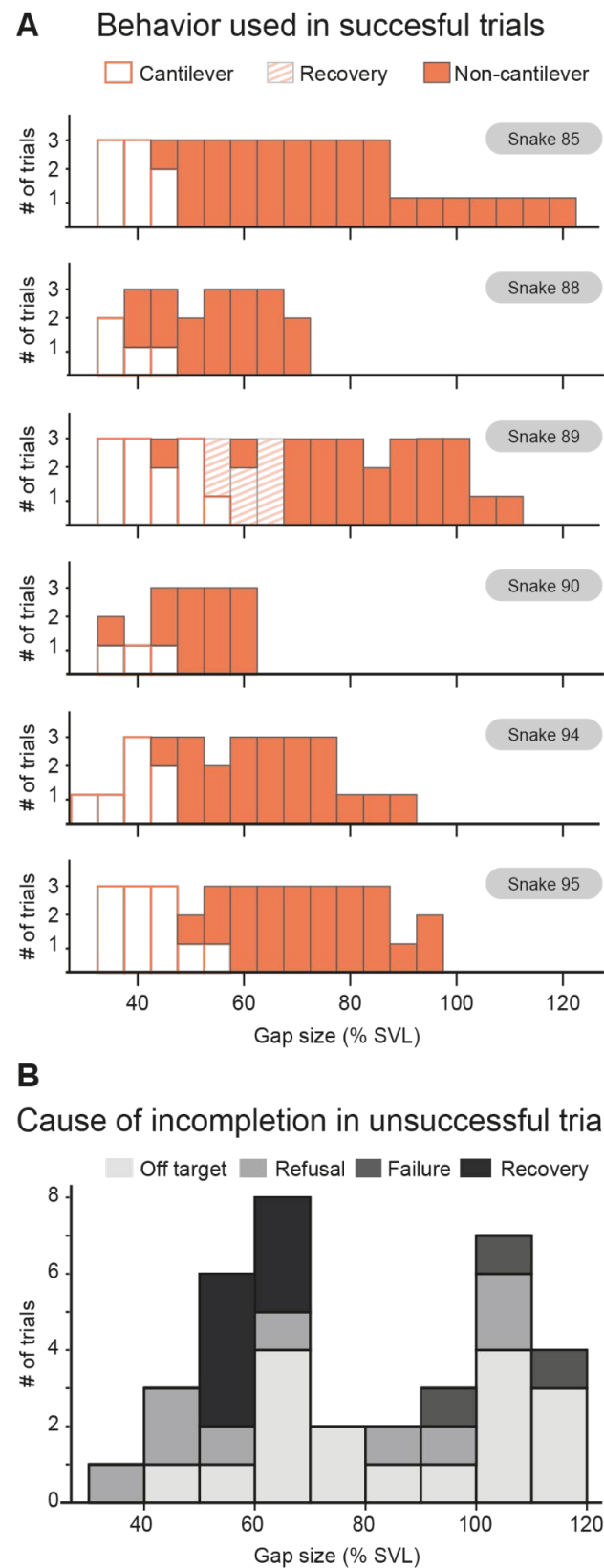


Fig. S1. Behavior and gap size. Top: Each subplot contains a plot of the number of instances of each behavior used by gap size for a given individual. Fewer total crosses are present for the largest gap sizes due to the snake's unwillingness to cross large gaps. Bottom: A summary of each trial, by gap size (% SVL), in which the snake did not successfully reach the target. Off-target trials were those in which the snake's movements appeared to be directed toward a non-target destination, as judged by where the snake was looking at the time of departure. Refusals are those in which the snake did not depart the origin. Failures are those in which the snake did not reach the target despite seemingly attempting to reach it. Recovery trials are those where the snake failed a first attempt, but succeeded on a subsequent attempt within the same crossing bout.

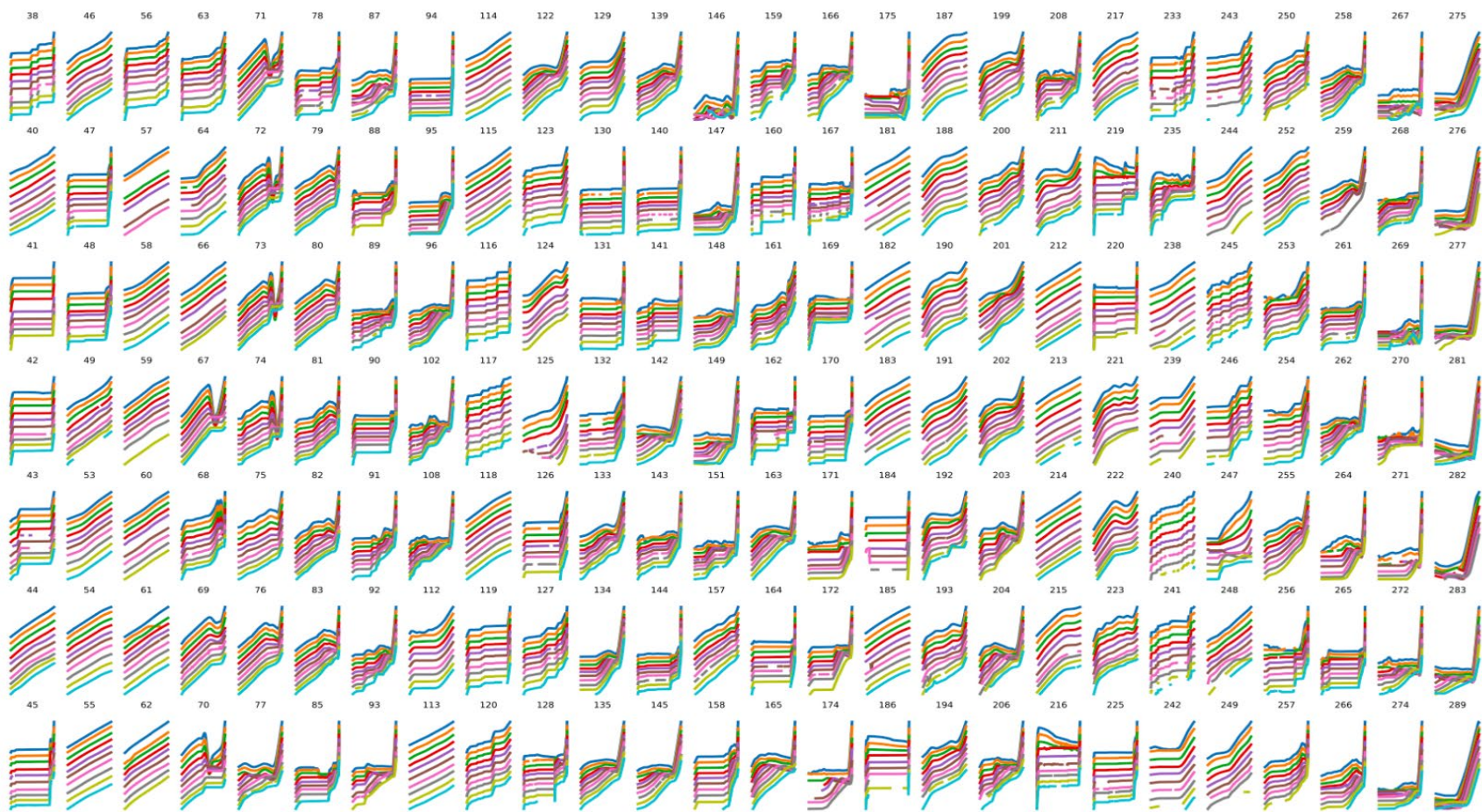


Fig. S2. Interpolated position data. Each subplot in this figure contains the X position trajectories (vertical axis) against time (horizontal axis) for all markers on the snake in that trial after interpolation of small sections of missing data. Trials in which a marker was missing for all or part of the trial can be noted by white space in the line; gaps of greater than 0.2 seconds were not interpolated. Subplot titles reflect trial numbers.

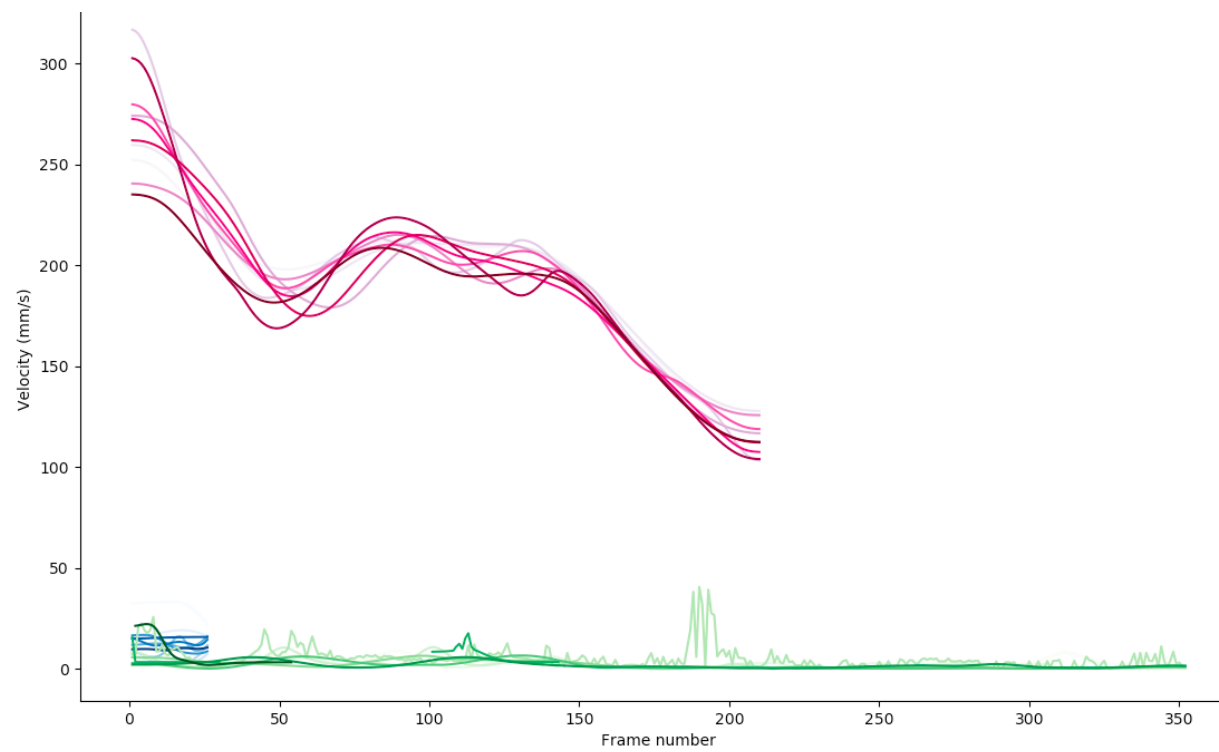


Fig. S3. Establishing threshold for moving velocities. Pink lines show raw speed data for all 10 markers during a trial period in which the snake was consistently moving, according to video data. Green and blue lines show 10 markers of data during which the snake appeared to be still, according to the video data. In each case, the darkest line represents the head. The comparisons presented here were used to set the cut-off speeds for determining sections of data where the snake was still: 0.025 m/s was used as the cutoff.

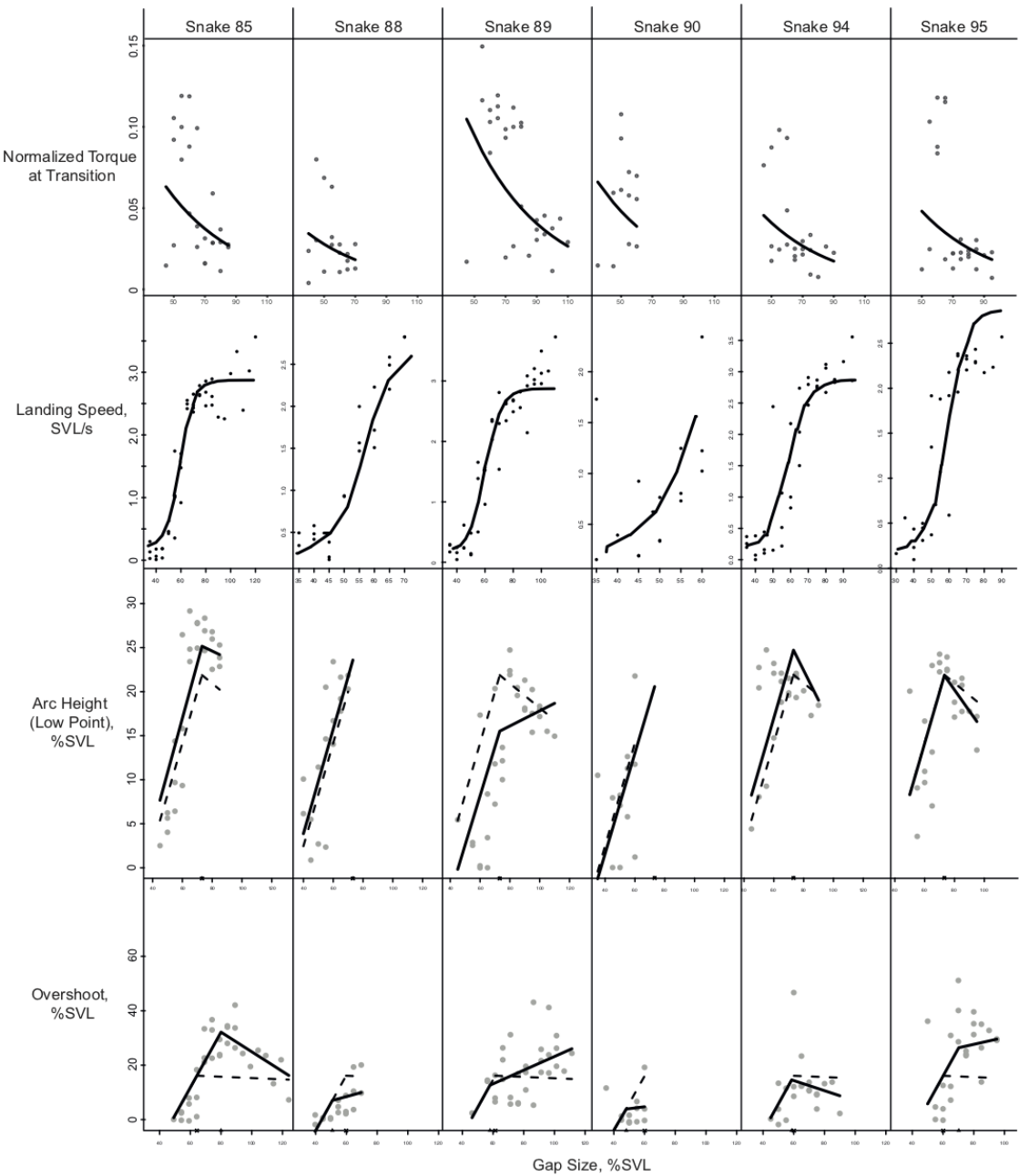


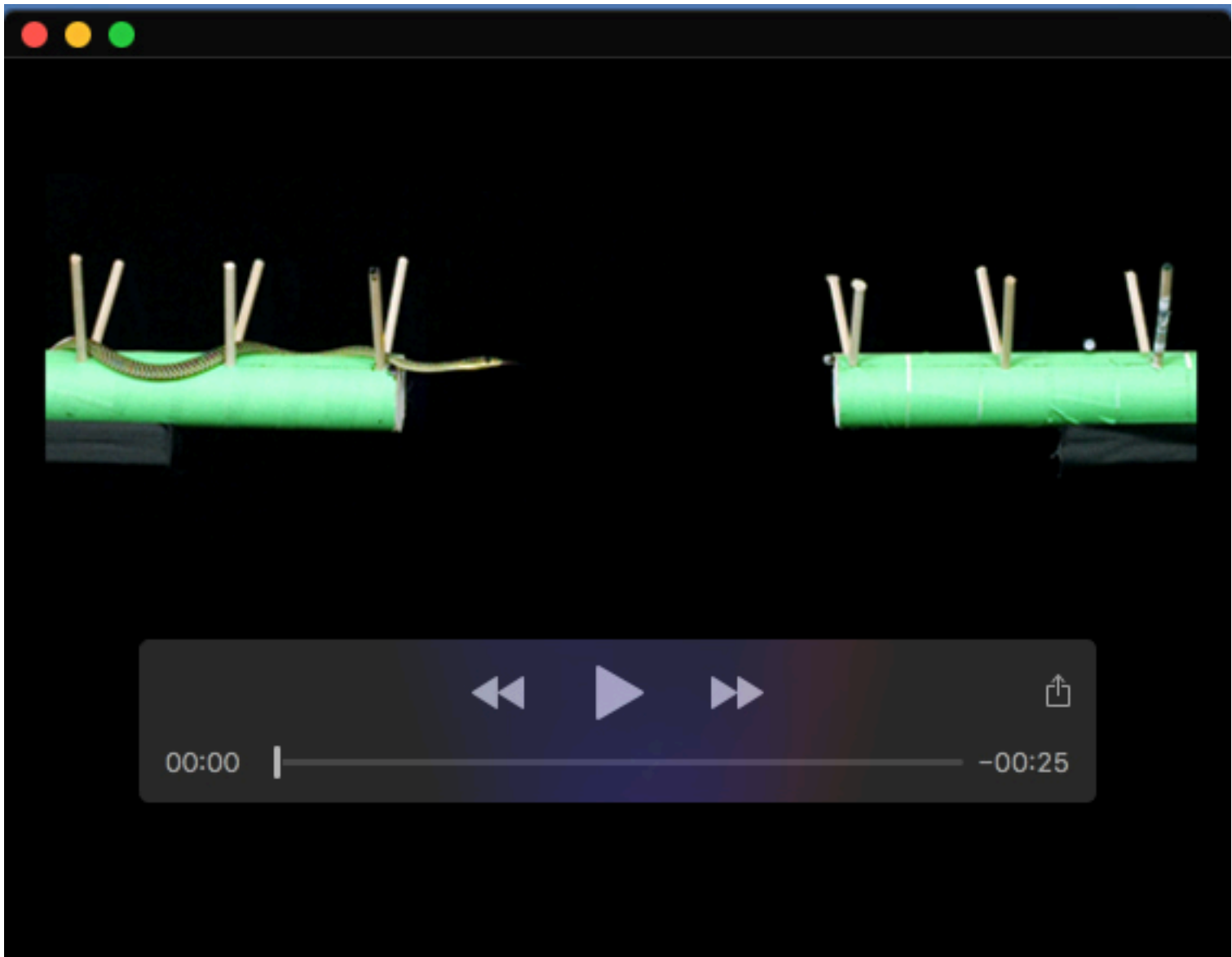
Fig. S4. Variation in specific kinematic metrics between individuals. Results of a mixed effects model for four analyses (normalized torque measured at the transition point, landing head speed, arc height at the low point, and overshoot) against gap size are presented, showing variation between individual snakes. For breakpoint analyses (bottom two rows), the dotted lines represent the population estimate, while the solid line represents the estimate for the given individual.

Table S1: Maximum torques recorded for each snake during cantilever and non-cantilever movements

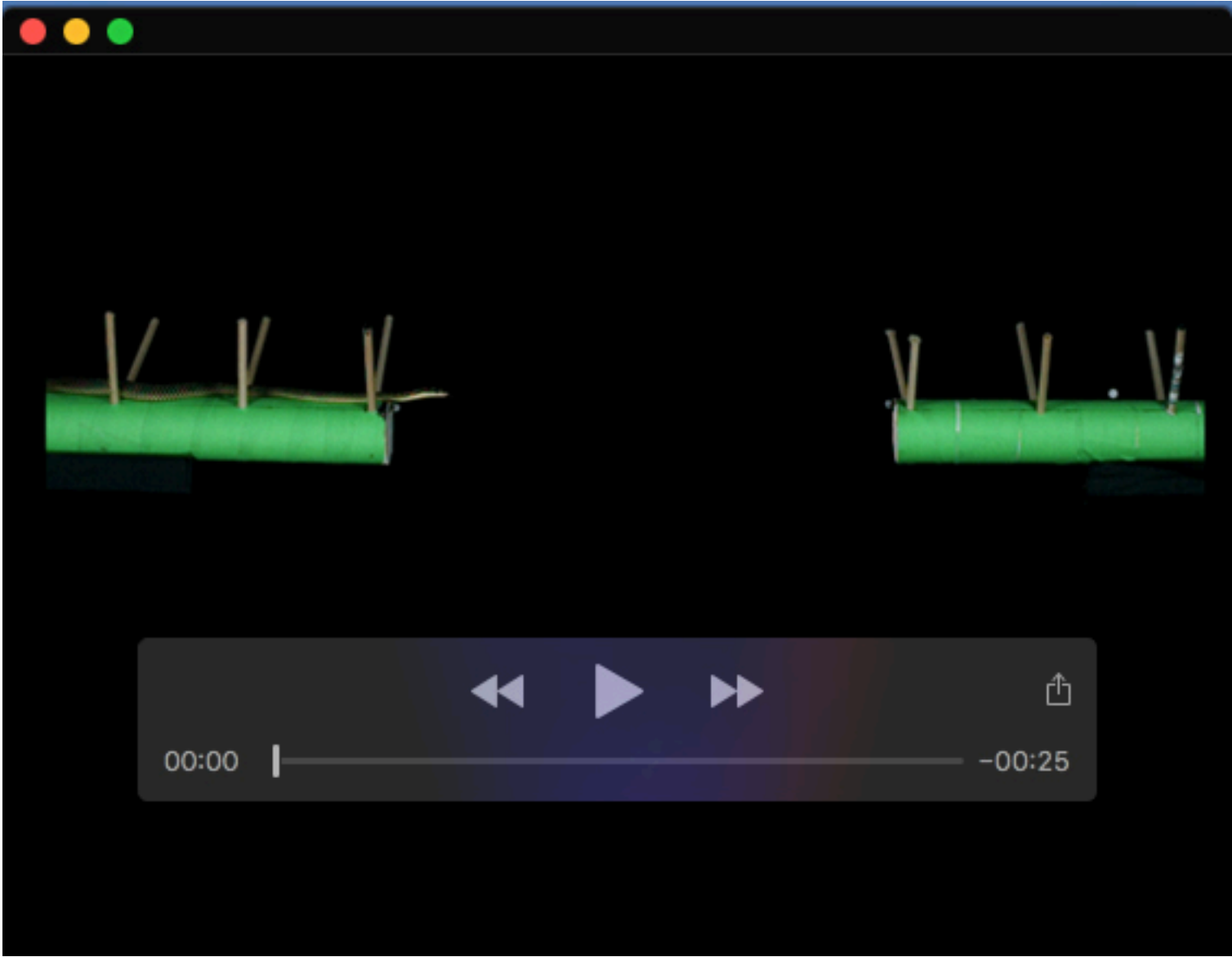
ID	Behavioral category	Gap size at which largest transition torque value recorded (%SVL)	Largest transition torque (Nm)	Largest gap size for which a transition torque was recorded (%SVL)	Corresponding transition torque (Nm)
85	Cantilever	45.0	0.04	-	-
	Non-cantilever	54.4	0.04	85.8	0.01
88	Cantilever	45.4	0.09	-	-
	Non-cantilever	43.3	0.08	72.3	0.01
89	Cantilever	55.1	0.07	-	-
	Non-cantilever	55.1	0.07	109.1	0.01
90	Cantilever	42.7	0.04	-	-
	Non-cantilever	49.1	0.04	58.7	0.02
94	Cantilever	45.5	0.11	-	-
	Non-cantilever	55.6	0.10	89.4	0.02
95	Cantilever	53.2	0.03		
	Non-cantilever	58.6	0.03	96.6	1.6e-3

Table S2. Comparisons between J-loop crosses and J-loop launches. “Prep” and “Vert” refer to the preparation time (from snake entering the gap to beginning of first downward movement) and vertical acceleration time (from start of upward acceleration until movement becomes more horizontal than vertical, respectively. “Max” and “L” refer, respectively, to maximum and landing speeds in both Z (vertical) and X (horizontal) directions. “Dist” refers to the distance traveled horizontally by the head from the origin to the position at landing, and “Height” refers to the maximum vertical height of the head above the origin. Data were compared using a Mann Whitney U test, and the only significant difference between J-loop launches and crosses was in the distance traveled.

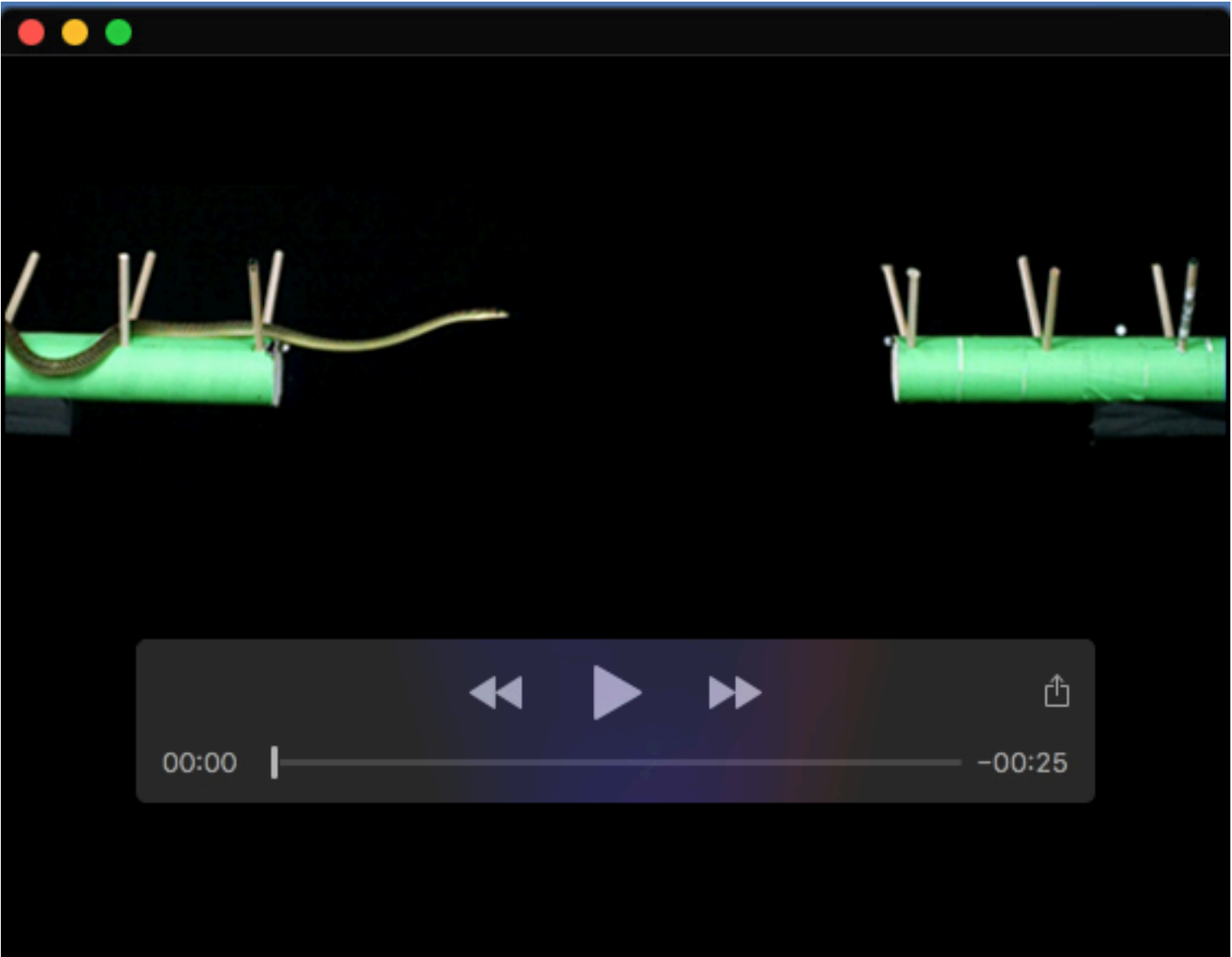
			SVL/s				SVL	
	Prep (s)	Vert (s)	Max Z	Max X	LZ	LX	Dist	Height
J loop launches (Socha, 2006)								
Media n	1.82	0.32	2.64	2.92	-2.64	2.01	0.97	0.25
N	10	11	11	11	11	11	11	11
Data from this study								
Media n	2.82	0.36	2.09	2.66	-1.99	2.40	1.27	0.33
N	3	3	3	3	3	3	3	3
Statistical comparison - Mann Whitney U Test								
Ua	21	23	3	11	25	19	33	24
Ub	9	10	30	22	8	14	0	9
f	0.7	0.70	0.09	0.33	0.75	0.58	1	0.73
0.05 crit value	3	3	3	3	3	3	3	3
Is U < Crit?	Fail to Reject	Fail to Reject	Fail to Reject	Fail to Reject	Fail to Reject	Fail to Reject	Reject Null	Fail to Reject
Null hypothesis: for randomly selected values X and Y from two populations, the probability of X being greater than Y is equal to the probability of Y being greater than X.								



Movie 1.



Movie 2.



Movie 3.