



SYMPOSIUM

Gliding Flight in *Chrysopelea*: Turning a Snake into a Wing

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Synopsis Although many cylindrical animals swim through water, flying snakes of the genus *Chrysopelea* are the only limbless animals that glide through air. Despite a lack of limbs, these snakes can actively launch by jumping, maintain a stable glide path without obvious control surfaces, maneuver, and safely land without injury. Jumping takeoffs employ vertically looped kinematics that seem to be different than any other behavior in limbless vertebrates, and their presence in a closely related genus suggests that gap-crossing may have been a behavioral precursor to the evolution of gliding in snakes. Change in shape of the body by dorsoventral flattening and high-amplitude aerial undulation comprise two key features of snakes' gliding behavior. As the snake becomes airborne, the body flattens sequentially from head to vent, forming a cross-sectional shape that is roughly triangular, with a flat surface and lateral “lips” that protrude ventrally on each side of the body; these may diminish toward the vent. This shape likely provides the snake with lift coefficients that peak at high angles of attack and gentle stall characteristics. A glide trajectory is initiated with the snake falling at a steep angle. As the snake rotates in the pitch axis, it forms a wide “S” shape and begins undulating in a complex three-dimensional pattern, with the body angled upward relative to the glide path. The head moves side-to-side, sending traveling waves posteriorly toward the tail, while the body (most prominently, the posterior end) oscillates in the vertical axis. These active movements while gliding are substantially different and more dynamic than those used by any other animal glider. As the snake gains forward speed, the glide path becomes less steep, reaching minimally recorded glide angles of 13°. In general, smaller snakes appear to be more proficient gliders. *Chrysopelea paradisi* can also maneuver and land either on the ground or on vegetation, but these locomotor behaviors have not been studied in detail. Future work aims to understand the mechanisms of production and control of force in takeoff, gliding, and landing, and to identify the musculoskeletal adaptations that enable this unique form of locomotion.

Introduction

Flying and gliding vertebrates have evolved bilaterally symmetrical “wings” from limbs, ribs, and feet, but the snake body plan presents particular functional challenges for successful aerial locomotion. To be a glider, a cylindrical, limbless snake must produce forces that propel it into the air, maintain stability and forward velocity while airborne, and land without injury. One small genus of colubrid snakes, the *Chrysopelea* flying snakes, evolved the ability to glide under control in an arboreal environment. Although known for over 100 years (Daly 1899; Flower 1899), gliding by snakes has only recently received concerted attention (Socha 2002; Socha and LaBarbera 2005; Socha and Sidor 2005; Socha et al. 2005; Socha

2006; Miklasz et al. 2010; Socha et al. 2010), and these few studies provide only a basic understanding. Here I summarize current knowledge of gliding flight in snakes, discussing issues of takeoff, glide trajectory, and landing.

Overview

Chrysopelea constitutes a group of five species of lowland tropical tree snakes found in southern and southeastern Asia. They are not particularly large, with lengths on the order of 0.6–1.2 m and body mass ranging from tens to a few hundred grams. I have observed gliding in three species *Chrysopelea ornata*, *C. paradisi*, and *C. pelias*) under experimental conditions, but little is known about how snakes

actually use gliding in the wild. All three species display the same general behavioral repertoire: a jumping J-loop takeoff, undulation while gliding, and the ability to land on ground or vegetation. *Chrysopelea rhodopleuron*, which occurs in Sulawesi and the Molucca islands of Indonesia, has also been observed to glide (J. McGuire, personal observation). The gliding abilities of the Sri Lankan endemic *C. taprobatica* are unknown.

Although its gliding performance of *Chrysopelea* is surprising for its body plan, the snake itself does not appear in any way morphologically exceptional or unique. It is a typical snake, with no appendages, skin flaps, or other features that other animals employ in flying. Instead, the snake undergoes aerial locomotion by using its entire body as a flattened, moving wing, constantly reconfiguring throughout flight. In this review, I focus largely on the kinematics of gliding from takeoff to landing, and present new information on the shape of the body, which appears to play a prominent role in creating favorable aerodynamics in the snake's gliding flight.

Takeoff

Takeoff behaviors

All terrestrial gliders begin a glide by becoming airborne from a high perch, usually a tree, either by jumping or falling (Dudley et al. 2007). Quadrupedal gliders jump from the substrate impulsively by extending bent limbs and leaping forward from a horizontal position (Essner 2002), or pushing off from a vertical position on a tree trunk (Byrnes et al. 2008). Snakes can only produce takeoff forces by straightening lateral body bends.

Our understanding of snake takeoff derives solely from studies in which the snake becomes airborne from a horizontal branch, of diameter similar to the snake's body (Socha 2002; Socha et al. 2005; Socha 2006). Effects of substrate on takeoff behavior and performance are unexplored, and parameters such as perch size, orientation, texture, branching patterns, and leaf cover should be relevant for understanding arboreal takeoff.

Three general takeoff behaviors have been identified: snakes either jump, dive, or fall from the branch. A fall is the least kinematically complex behavior; the snake hangs by the tail and simply releases its grip. Jumps are more complex and are the most commonly observed behaviors. In more than a thousand locomotor trials of *C. paradisi*, *C. ornata*, and *C. pelias*, the most prevalent

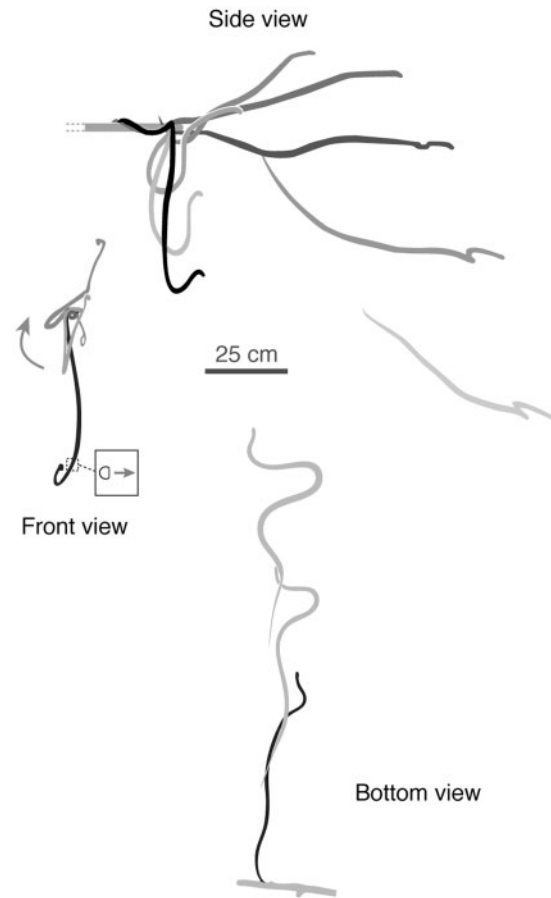


Fig. 1 Takeoff from a branch by *C. paradisi*. The side and front views depict a J-loop jumping takeoff at intervals of 133 ms, starting from a hanging position. The front view shows an outward bowing of the body in the bottom of the loop, where the ventral surface faces to the side (shown in the inset box). As the snake accelerates upward, the loop travels posteriorly and rotates from a vertical to a horizontal orientation, shown in two tracings corresponding to $t = 267$ and $t = 400$ ms. The bottom view depicts a takeoff in which the snake jumped laterally from the branch. This sequence starts as the snake becomes fully airborne at the end of takeoff, with the body fully extended and a lateral curve beginning to form just behind the head. As the snake falls in the initial phase of the trajectory, it coils along the anterior–posterior axis, and the curve behind the head moves posteriorly as a traveling wave. The time interval is 200 ms. Adapted from (Socha et al. 2005; Socha 2006).

mechanism observed is the J-loop takeoff (Fig. 1), representing 74% of trials in one study (Socha 2006).

In an anchored J-loop takeoff, the snake drops its anterior body from the branch and forms a body bend near the head, while the posterior body anchors the snake to the branch by gripping with one or more small loops. The anterior loop consists of a single lateral body bend, with the ventral belly facing to the side (rather than downward). Anterior to the loop, the body has a twist, positioning the head in a forward-facing orientation with the ventral

side downward. After dropping the forebody from the branch, the snake either jumps immediately, or can hold station in the hanging position. Hanging snakes may turn the head using short, fast movements, appearing to search visually. These searching scans can include lateral wagging-type movements of the head, which suggests that the snake increases parallax to better judge distance to potential landing sites. *Chrysopelea paradisi* and *C. ornata* have also been observed to track flyers moving overhead (Socha and Sidor 2005), but in general their visual system is largely unstudied.

From the hanging loop, the snake initiates a jump by accelerating the forebody up and forward, creating an arched path that usually rises above the initial vertical height of the branch. As the head moves up, the anterior loop travels posteriorly, suggesting that a wave of lateral bending propels the snake through the jump. Early in the acceleration, the posterior body remains gripped to the branch, providing friction for ground reaction forces against the substrate. As the snake arcs away from the branch, the grip is released, and the snake becomes fully airborne. At this point, the snake is relatively straight in plain view, and the anterior body has been rotated laterally roughly 90° so that the ventral surface returns to facing downward. The snake begins the glide trajectory from this extended posture. In some cases, the anterior body has already begun forming multiple lateral coils by the time it becomes fully airborne.

Other takeoff behaviors include a dive, in which the snake laterally undulates off the branch leading downward with the head, and intermediate modes such as a sliding J-loop takeoff. This mode is kinematically similar to the anchored version, but with the snake forming a smaller anterior loop and continuously moving throughout the takeoff, without forming a static grip. Both such behaviors are quicker than the anchored J-loop takeoff, suggesting that they are employed when escaping predators.

What is the advantage of a jumping takeoff versus a dive or fall—why not just slip off the branch to enter the air? Jumping takeoffs effectively increase the starting height of the trajectory, but in *C. paradisi* only marginally so—an increase of height of 15 cm adds <0.1 J to the initial potential energy of the glide. Perhaps more importantly, jumping takeoffs push the animal away from the substrate, relevant for avoiding surrounding obstacles, and also for imparting a nonzero initial velocity at the start of the trajectory. Because lift scales with velocity squared, greater initial speeds mean that a glider begins producing significant aerodynamic forces earlier in the

trajectory. When comparing the effect of takeoff type on trajectory performance based on a starting a height of 7 m, *C. paradisi* traveled almost twice as far when using jumping takeoffs versus nonjumping takeoffs. Furthermore, a simple theoretical model (Socha et al. 2010) showed that increasing the takeoff velocity served to damp the initial oscillations in acceleration that were predicted to occur early in the trajectory. If true, a jumping snake may experience attenuated (or reduced) forces that could lead to rotational instabilities. In general, the consideration of the snake's changing body posture throughout takeoff as a series of rigid body rotations has not been rigorously analyzed, and such dynamics likely play a large role in determining the specific takeoff kinematics used by the snake.

Vertically looped takeoffs may be an evolutionary novelty in snakes, as they are different than any other locomotor or strike behavior in snakes or other limbless vertebrates. In particular, the anchored J-loop takeoff may represent a behavioral precursor to gliding in *Chrysopelea*. At maximum, the snake's head reaches 0.25 body lengths (snout-vent length; SVL) vertically and 1.0 SVL horizontally away from the branch (Socha 2006). Rather than serving to initiate a glide trajectory *per se*, this behavior may have evolved as a mechanism to cross small gaps in the canopy (Jayne and Riley 2007) or as a means of evading a predator. I have observed a similar jumping behavior in one species of the bronzeback, *Dendrelaphis* (Fig. 2), an arboreal colubrid genus that represents the sister taxon to *Chrysopelea* (Pyron et al. 2010). Although its behavioral capabilities have not been studied, *Dendrelaphis* is not known as a glider, and despite some ability to jump, it may lack other specializations required for ophidian gliding flight. Studies that explore the aerial, jumping, and gap-bridging behaviors of *Chrysopelea*, *Dendrelaphis*, and other related taxa, such as the whipsnake *Ahaetulla*, would lend insight into the behavioral acquisition of specific glide-related traits in snakes.

Cross-sectional shape reconfiguration

A prominent characteristic of gliding in *Chrysopelea* is the dorsoventrally flattened body. The snake reconfigures from a round to a flattened cross-section while airborne, a transformation that was first identified by Shelford (1906), who noted that the snake “hollowed out the ventral surface as it moved.” For any flyer, the cross-sectional shape of the wing is a critical determinant of overall flight performance. A snake's resting cross-sectional



Fig. 2 Jumping in a nonflying snake, the bronzeback *Dendrelaphis pictus*. This sequence (duration, 587 ms; interval, 147 ms) shows the snake crossing a gap between vegetation by jumping in an experimental trial near ground level. As in *Chrysopelea*, the snake forms a vertically oriented loop near the head, and accelerates up and away from the branch to become airborne; the loop moves posteriorly as the jump progresses. This sequence represents preliminary data from a single specimen, used to demonstrate the presence of a similar locomotor behavior to that used in jumping by *Chrysopelea*; the kinematic details of jumping in *Dendrelaphis* remain unexplored. *Dendrelaphis* is an arboreal colubrid genus closely related to *Chrysopelea*, and this sequence suggests that acquisition of gap-crossing behavior may have been a first step in the evolution of gliding in snakes.

shape—nearly circular and symmetrical—is unfavorable for producing aerodynamic forces at intermediate Reynolds numbers, and it is unlikely (though untested) that an unflattened snake could glide. Understanding change in shape by *Chrysopelea* is therefore key to explaining its unique capabilities for gliding. Below, I discuss some general features of body shape based largely on preliminary observations using high-speed video and stereophotography

of *C. paradisi*. More rigorous studies are required to understand their details and the morphological mechanism of producing a change in shape, as well as the potential differences among species. *Chrysopelea paradisi* flattens dorsoventrally throughout the entire body, from just posterior to the head to the vent, a widening of the body that can be seen in images of the airborne snake. The tail remains rounded. The flattening process proceeds from anterior to posterior, with a duration on the order of 100–350 ms. In a J-loop takeoff, flattening begins during the upward acceleration phase with the posterior body still gripping the branch, and is complete shortly after the snake becomes fully airborne (Fig. 3).

Change in cross-sectional shape is greatest near mid-body (Fig. 4), where the snake's width is doubled relative to the resting configuration. Here, the cross-sectional shape is roughly triangular, with a semi-triangular dorsal surface, flat ventral surface, and a pair of ventrally-oriented lips on each lateral edge. Although mostly flat, the ventral surface may display some three-dimensional features. Most noticeably, the heart protrudes along the ventral midline, and at times irregular bumps can be seen in the posterior body (Fig. 4F), likely formed by remnants of digesting food. On the ventral surface, there are also a pair of slight ridges formed by the “keel” in the ventral scute, located on either side of the midline. When the snake is not gliding, these two keels form the bottom corners of the cross-section, and appear to be used in gaining purchase when climbing on bark or other rough surfaces.

The ventrally-oriented lateral lips give the bottom of the cross-section a concave shape. These lips become less prominent (or may be not present) more posteriorly along the body toward the vent. Precise three-dimensional measurements are needed to determine the exact details of the snake's aerial body shape and how it changes with time. Although it appears that the snake maintains a constant cross-sectional shape throughout a glide, it is not known if small modulations in shape are used to locally alter aerodynamic forces as a mechanism of control or enhancement of force.

Based on these patterns of change in shape, it is evident that movements of the ribs are involved in dorsoventral flattening in *Chrysopelea*, an idea first hypothesized by Mertens (1960). The exact morphological mechanism has not been investigated, but preliminary manipulation of a dissected trunk of the body suggests that the ribs move as a four-bar linkage system (Westneat 1990), in which the ribs rotate anteriorly and dorsally to flatten the body

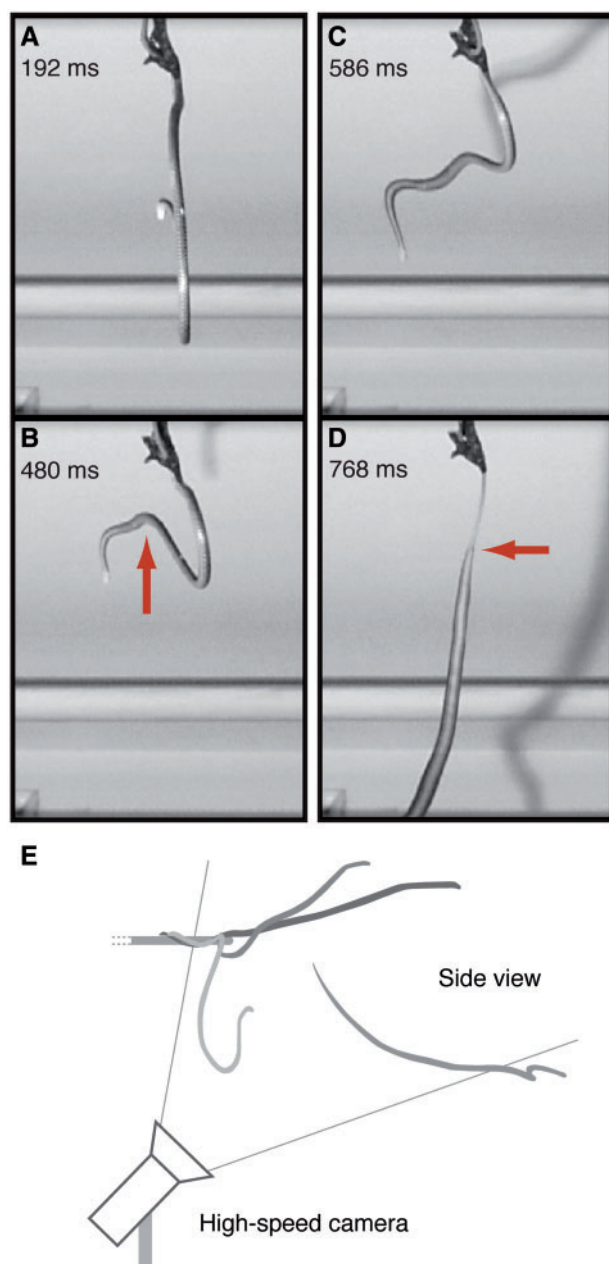


Fig. 3 Reconfiguration of body shape by dorsoventral flattening occurs as a wave of anterior-to-posterior flattening during J-loop takeoffs in *Chrysopelea paradisi*. Images (A–D) are high-speed video stills recorded at 125 Hz from an orientation below and behind the snake, which jumps away from the camera. The setup is shown in side view in (E), with the silhouettes of the snake roughly corresponding to A–D. Time zero is marked by the start of the upward acceleration, as depicted in Fig. 1. The red arrow in (B) depicts the extent of flattening (roughly 25% SVL) early in the process. In (C), the snake is simultaneously flattened anteriorly and rounded posteriorly. In (D), the dorsoventral flattening is complete, with the arrow indicating the full extent of flattening at the vent. See Supplementary Movie 1 for corresponding video. In this snake ($m = 63$ g, $SVL = 83$ cm), the average flattening time was 270 ± 50 ms (avg \pm SD, $n = 4$). Across seven snakes, the duration of flattening was 200 ± 30 s, with a range of 100–350 ms.

(Fig. 5). The whole-body flattening of *Chrysopelea* may share similar features to hooding in cobras (*Naja*), who form the hood via action of the ribs to laterally widen and dorsoventrally compress the body. Young and Kardong (2010) have shown recently that in cobras, the mechanism consists of the following elements: (1) rib-erector muscles that run caudo-laterally from vertebrae to the ribs, (2) intercostal muscles that transmit forces between ribs, and (3) costocutaneous muscles that keep the skin taut. Dorsoventral flattening occurs in other major snake taxa as well, such as in defensive displays of the elapid death adder (*Acanthophis*) and the cylindrophiid red-tailed pipe snake (*Cylindrophis rufus*) (Greene 1997) and in thermoregulatory flattening and tilting of the body by the Australian red-bellied black snake during basking (Heatwole and Johnson 1979, 1987), suggesting that body flattening may require little specialization from the basal musculoskeletal morphology of snakes. Active flattening in the lateral axis is also known, for example, in the defensive displays that expand the anterior body in bronzebacks (*Dendrelaphis*). However, *Chrysopelea* are the only known snakes that locomote while dorsoventrally flattened, suggesting that specific musculoskeletal adaptations are required for gliding. Furthermore, the involvement of the ribs in creating the snake's airfoil shape suggests that the ribs are not available for normal ventilatory movements; most likely, flying snakes cannot breathe while gliding. If so, glide performance may be limited physiologically by anaerobic factors.

Gliding

Kinematics of gliding and the dynamics of snake trajectories

The kinematics of snakes' movements while gliding have been investigated only within the past decade (Socha 2002; Socha and LaBarbera 2005; Socha et al. 2005, 2010). Historically, gliding by snakes has been described from a few visual observations in the wild, with varying degrees of accuracy. Pendlebury (1931) described a glide in Malaysia in which he thought that the snake held its body rigid in a "double S" posture, and moved the tail vigorously. Vaughn-Arbuckle (1959) was the first to identify that the snake moved its entire body in the air, with the body held horizontally. Heyer and Pongsapipatana (1970) provided the first experimental report, providing data on the range of trajectories in two *C. ornata* specimens dropped by hand from a 41-m high tower in Thailand. In addition to estimating glide speeds and angles of descent, they described

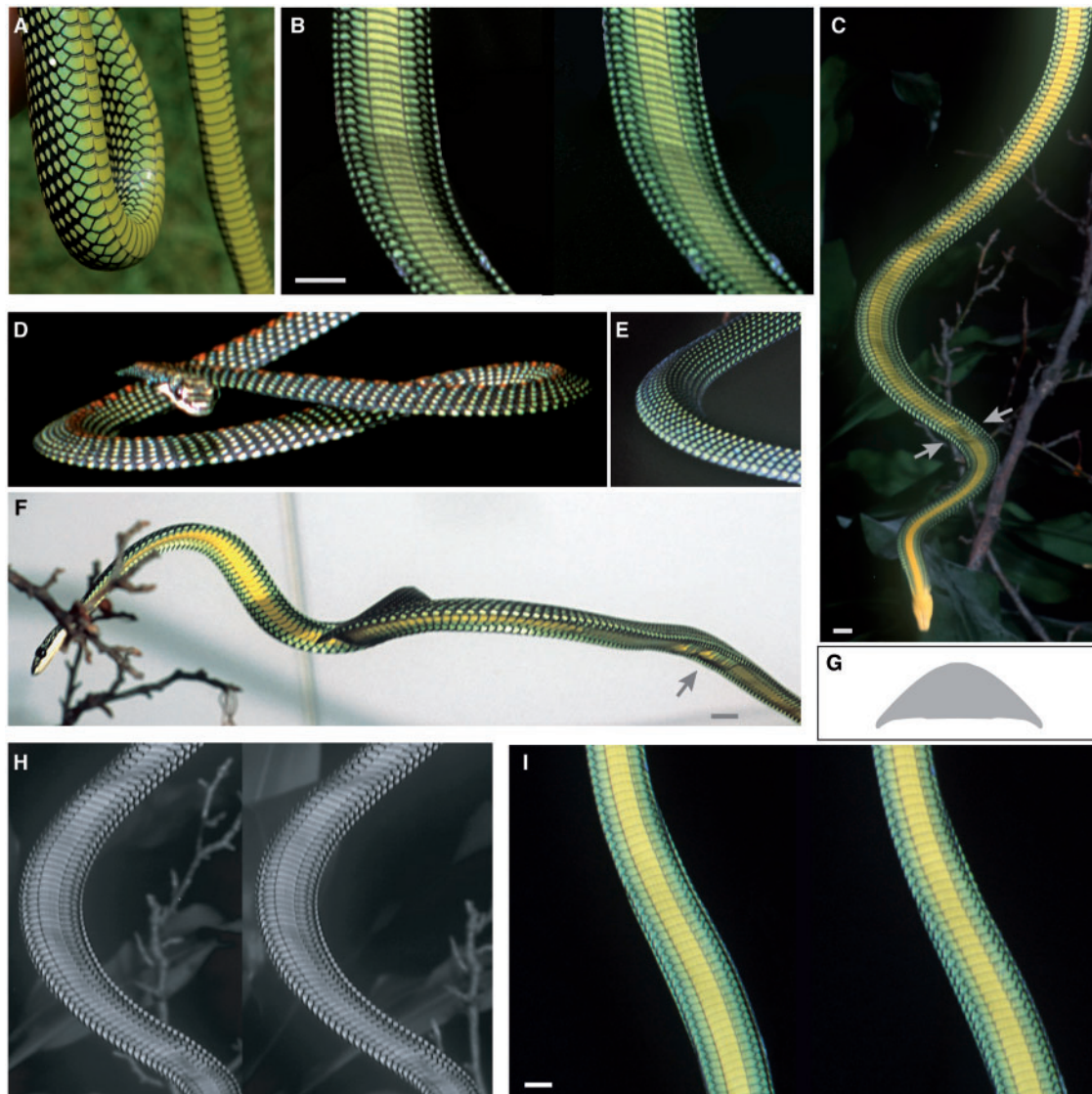


Fig. 4 The body shape of *Chrysopelea paradisi* at rest (**A**) and in the air (**B–H**). At rest, the snake displays a typical cylindrical shape. The white dot indicates the scale row that becomes the lateral-most edge of the flattened body in ventral view, which can be seen in (**B**). In the air, the snake takes a roughly triangular cross-sectional shape with a concave ventral surface, defined by two “lips” at each lateral edge. Images in (**B–H**) are photographs of the aerial snake showing ventral (**B**, **C**, **H** and **I**), dorsal (**D** and **E**), and lateral (**F**) aspects. The pair of arrows in (**C**) indicates the location of the heart; this was verified in separate high-speed video trials by manually palpating the heart and marking its location with nontoxic paint. The arrow in (**F**) indicates irregular bumps in the posterior body, which appear to be digesta. Stereophotos (**B**, **H** and **I**) were taken with a coupled pair of Nikon F5 and F100 film cameras, lit by strobed flash triggered when the snake crossed an infrared beam. The scale bars (**B**, **C**, **F** and **I**) represent 1 cm. (**G**) Hypothesized cross-sectional shape of an airborne *C. paradisi* at midbody.

the snake’s aerial behavior as “swimming through the air.”

Studies using video photogrammetry and high-speed imaging have revealed more detailed features of snakes’ gliding, which has been studied most extensively in *C. paradisi* (Fig. 6). Here, I describe general patterns in an average glide of *C. paradisi* commenced by a J-loop takeoff, which provides an initial velocity of 1.7 m/s. Upon becoming airborne

and after the jump’s apex, the snake falls along a ballistic trajectory angled downward 57° from horizontal. As it falls, the airborne snake begins to form lateral body-curves of large amplitude, providing a wide “S” shape in plan view, and the snake begins laterally undulating. In side view, the snake first rotates nose-down in the pitch axis; this rotation is then arrested as the posterior body moves downward. The snake gains speed, and after a vertical

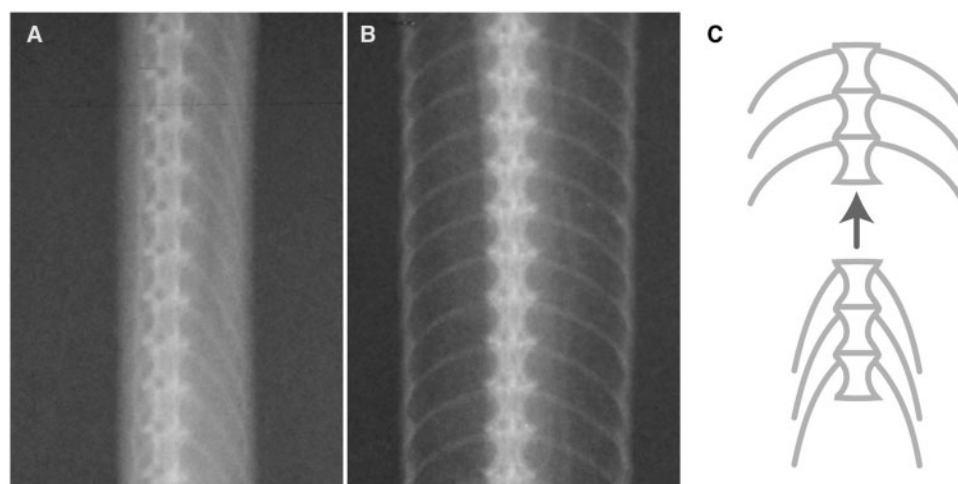


Fig. 5 Rotation of the ribs in one form of dorsoventral flattening in *Chrysopelea paradisi*. In handling *C. paradisi*, I found that certain specimens would dorsoventrally flatten using apparent deep ventilatory movements, forming a body shape that is similar, although not as pronounced, to those seen in Fig. 4. This specimen was radiographed using medical X-rays at the University of Chicago Medical Center in normal (A) and dorsoventrally flattened (B) conditions, with the dorsum apposed to the plate. In (A), the snake's body was rotated slightly along the axis, resulting in a radiograph in which the vertebral column was not symmetrically aligned, as in (B). The net effect of the dorsoventral flattening shown in this projection is an anterior rotation of the ribs of about 25° , as depicted in (C). The actual three-dimensional rotation of the ribs during gliding is unknown.

drop of 2.3 m in 0.7 s, the trajectory begins to become less steep, with glide angle decreasing. This deviation from a ballistic trajectory indicates production of aerodynamic forces providing upward and horizontal components of force, although actual forces on the snake's body have not been measured. In most recorded trajectories, the glide path continues to become horizontal, with the snake reaching a glide speed of 10 m/s and glide angle of 28° when launched from a height of 10 m.

The most striking feature of snakes' gliding behavior is aerial undulation. This is a form of lateral undulation in which oscillations of lateral bending of the body (1–2 Hz) create traveling waves that move posteriorly at an average speed of 0.24 m/s (0.35 SVL/s). The amplitude of lateral movement is least at the head ($\sim 10\%$ SVL) and greatest at the vent ($\sim 17\%$ SVL). This undulation creates an S-like shape comprising 3–4 major curves connected by straighter sections. When considering spans of body in the cross-wise direction (i.e., perpendicular to the direction of forward motion), the coiled snake has an aspect ratio on the order of 11–13 including the curves, or 8–10 including only the straight sections. In addition to movement in the lateral plane, the body also moves vertically, with the greatest excursions occurring at the vent. The tail whips around, subtending an even greater volume than the vent, but movements of the tail have not been quantified, and its role in gliding is unknown. Overall, the head moves the least, and the anterior

body is the most stable relative to the rest of the snake. In the gravitational reference frame, the anterior body is oriented roughly in the horizontal plane, whereas the posterior part of the body (and tail) move up and down. In the trajectory's frame of reference, the snake's body is oriented upward at an angle of roughly 25° , which changes as the snake undulates. The orientation of the local body segments relative to the whole body have not been determined, so it is not possible to accurately describe the angle of attack either spatially (along the length of the snake) or temporally (throughout the trajectory). Angle of attack is a critical aerodynamic variable (Bertin 2001), and the current lack of data on this aspect significantly limits our understanding of the snake's aerodynamics.

Nonequilibrium gliding

Theoretically, given sufficient space, a glider should reach an equilibrium state with steady speed and glide angle, at values determined by coefficients of lift and drag and by weight. However, equilibrium gliding has not yet been identified unequivocally in *Chrysopelea*. The bulk of data on trajectories derive from glides from a launch height of 10 m, but even at a height of 15 m, equilibrium was not observed in two specimens of *C. paradisi* (Socha et al. 2010). A first-order theoretical model of gliding suggests that snakes should require 3.3–6.6 s to reach equilibrium, but glides from 15 m took roughly 3 s, suggesting that greater launch heights are required to reach

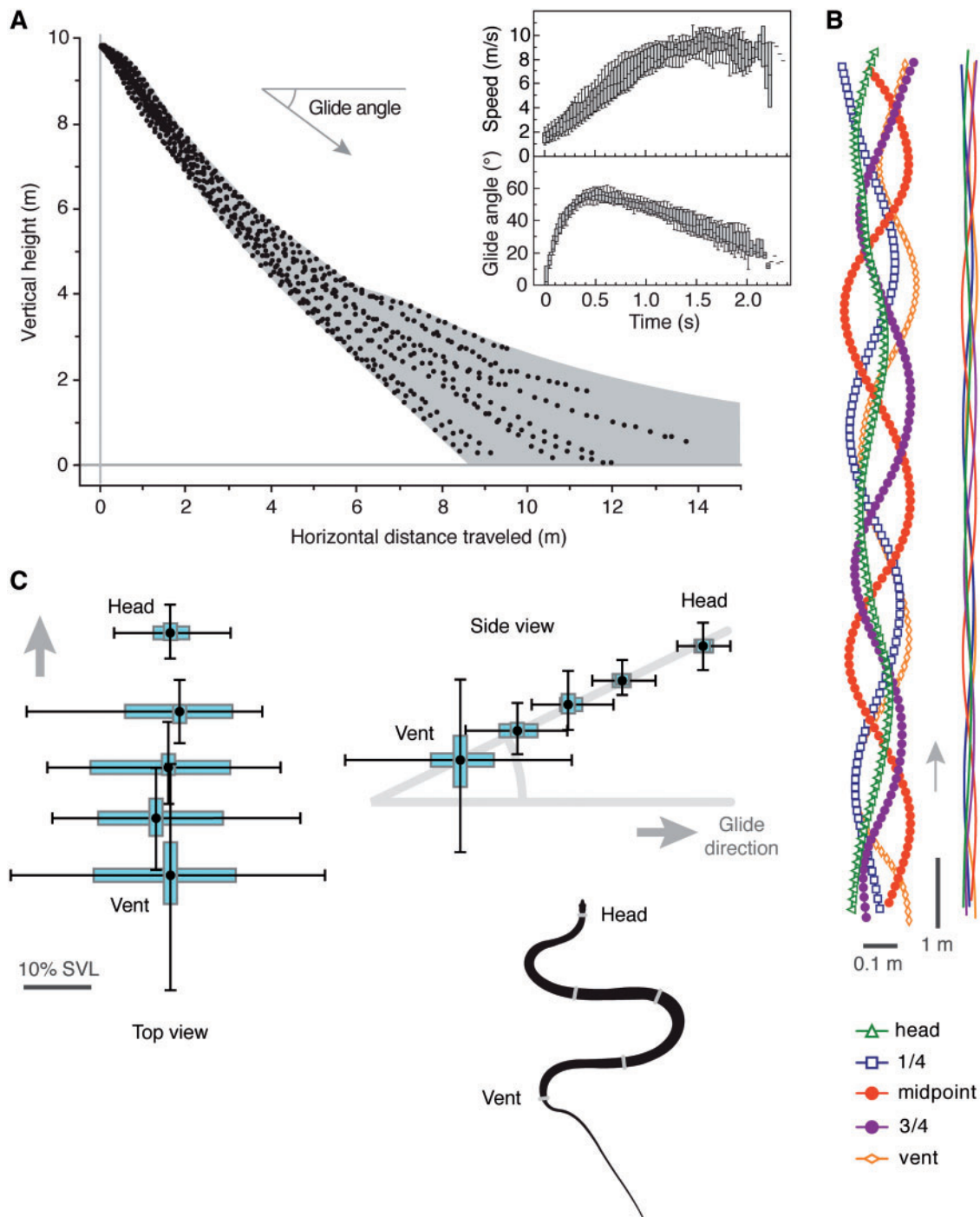


Fig. 6 Kinematics of gliding flight in *Chrysopelea paradisi*. **(A)** Characteristics of the trajectories of 14 snakes, showing a side view of trajectories and the corresponding glide angle and glide speed through time. The points in each trajectory represent the snake's midpoint (between head and vent) sampled at 30 Hz. Glide angle is the angle between the glide velocity and the horizontal plane in the gravitational frame of reference (e.g., glide angle = 90° is straight down). **(B)** The pattern of aerial undulation in the late phase of a glide (initiated from a height of 15 m), seen in top view. The five points represent evenly spaced landmarks on the snake's body. In the left sequence, the lateral axis has been exaggerated so that the patterns of lateral movement can be seen; the sequence on the right depicts the same trial with proper spatial scaling. **(C)** Limits of body posture in a fully developed glide. These two figures represent the relative travel of the five landmark points through one undulation cycle, averaged across two snakes and eight glides. The top view shows that the head moves least, the excursions of the middle points are roughly similar, and the vent subtends the greatest side-to-side and fore-aft movement. In side view, these points have been rotated so that the glide path lies in the horizontal axis; this is equivalent to freestream air moving from right to left. This figure shows that on average, the snake assumes a head-up, tail-down posture relative to the glide path. Adapted from (Socha et al. 2005, 2010).

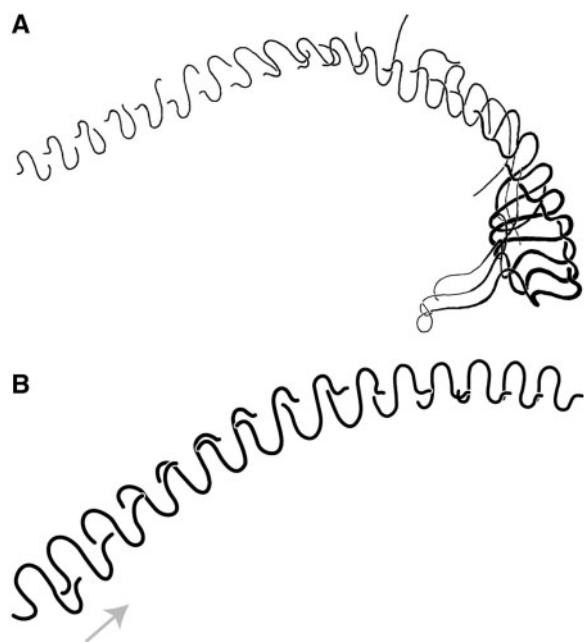


Fig. 7 Turning in *C. paradisi*. This kinematic series represents tracings from deinterlaced standard videos (60 Hz) of snakes launched from a height of 11.4 m, recorded from above. In (A), the snake turns left early in the trajectory, during the ballistic dive. The relative size of the snake decreases as it moves away from the camera. In (B), the snake turns right during the shallowing phase of trajectory, closer to landing.

equilibrium, if indeed snakes glide in this fashion. This analysis of equilibrium gliding assumes passive dynamics, but gliders can actively modulate forces during flight (Bishop 2006, 2007), and the use and relevance of equilibrium in gliders in the wild is still an open question (Byrnes et al. 2008).

Maneuvering

Perhaps the most surprising feature of aerial locomotion in snakes is the ability to maneuver (Fig. 7). *Chrysopelea paradisi* can turn laterally, both in the late glide phase when the snake is near full speed, and in the ballistic dive shortly after takeoff, when forward speed is lower and presumably the ability to create aerodynamic forces is diminished. Turning is relatively common in experimental trials of *C. paradisi*, particularly in snakes that jumped without pausing; in such cases, the snakes seemed to turn in response to sighting an off-axis visual target that came into view as the glide path progressed. In contrast, I have never observed turning behavior in *C. ornata* (Socha and LaBarbera 2005) or *C. pelias* (J. Socha, unpublished data). These species may turn less often, or may be less capable of turning (i.e., using greater turning radii) and require far greater launch heights to observe. In fact, Heyer and

Pongsapipatana (1970) reported a single trial in which a *C. ornata* specimen turned 180° and landed back on the 41-m launch tower. Overall, little is known about how snakes turn, and an understanding of their underlying mechanics may be of particular interest for engineering use in bio-inspired applications to flight, such as in robotic flyers.

To veer laterally from the direction of forward travel along the glide path, a glider must impart momentum to one side. Although turning has not been well studied in animal gliders, there are known mechanisms of producing asymmetrical forces on the body using available behavioral and morphological control surfaces. For example, gliding frogs can change the position of a webbed foot and thus create a rotational moment (McCay 2001). Sugar gliders can alter limb position to increase or decrease the tension in the patagium, altering the camber and changing the characteristics of lift and drag (Bishop 2007). Snakes have no such obvious mechanisms of control. One possibility is that the snake uses differential rib movements to change locally the cross-sectional shape of a body segment, thus altering the local airflow. This might involve a difference between left and right members of a pair of ribs, producing a fore-aft asymmetry, or more simply, the snake could return locally to a more rounded configuration and lower the lift coefficient. Another possibility is that the snake initiates a rotational torque inertially by altering the relative positioning of body segments. Alternatively, the tail may act as a rudder and direct turns by asymmetrically shedding vortices.

Turning is just one manifestation of maneuverability, which includes the ability to adjust speed (Dudley 2002). Although turning has been commonly observed in *C. paradisi*, it is not known whether *Chrysopelea* can volitionally alter speed. This might be most useful in landing, as lower speeds would reduce impact forces, but limited data suggest that *Chrysopelea* do not appreciably decelerate prior to landing.

How snakes glide

What determines glide performance in *Chrysopelea*? The relevant aerodynamic parameters include orientation of the body and its changes during aerial undulation, cross-sectional shape, skin texture, and body size. Two general approaches have provided complementary means to address this issue. The first examines correlates of glide performance within an individual and within a species, and compares differences among species (Socha and LaBarbera 2005). The second uses physical and

computational models to isolate physical effects of individual features (Miklasz et al. 2010). The latter approach is a more precise way to control individual variables and provides greater physical insight, but is limited both by difficulty of making accurate models (e.g., replicating the snake's complex three-dimensional undulation) and by our incomplete understanding of the actual features of gliding snakes. A third approach would be to test performance on manipulated snakes, for example by temporarily paralyzing the tail or by adding weights to the body to examine the effects of distribution of mass, but such studies have not yet been undertaken.

Inferences from differences in performance

Analyses of the results of behavior and performance within and among species have produced somewhat conflicting results (Socha and LaBarbera 2005). Within individuals, only two specimens of *C. paradisi* have been analyzed using full trajectory data, with a small number of glides for each individual. For both individuals, the amplitude subtended by the vent was positively correlated with speed of the glide; one individual also showed a correlation between the frequency of undulation and the distance traveled.

Within *C. paradisi*, amplitudes normalized by body length were also positively correlated with glide speeds; it appears that the wider the sweep of the body, the faster the snake travels. However, frequency of undulation was unrelated to any parameter tested. Although this lack of effect suggests that aerial undulation may be behaviorally neutral, it is likely that undulation plays a critical role in the stability of the glide, a hypothesis that remains untested. Body size showed strong effects. Smaller snakes demonstrated greater proficiency in gliding, traveling farther and achieving lower glide angles with higher shallowing rates. The largest snakes also had the deepest ballistic dives and created trajectories that moved more steeply toward the ground. The smallest snake used was not the best glider, but it was the only young juvenile tested (compared to adults or subadults), suggesting developmental effects on performance. Additionally, fluid dynamic effects of lower Reynolds number regimes ($Re \sim 2500\text{--}3500$ versus $5000\text{--}15,000$ for all others) may have contributed to this snake's sub-maximal performance. Smaller snakes also appear to be more maneuverable (capable of shorter turning radii), consistent with their overall greater capabilities for gliding, but this has not been rigorously examined.

Chrysopelea paradisi are superior gliders compared to *C. ornata*; performance in other species has not

been quantified. Comparing trajectories at a common vertical drop of 7 m, *C. paradisi* traveled over twice as far on average, displaying higher shallowing rates and lower glide angles. These results are consistent with glides from a much greater vertical height. Heyer and Pongsapipatana (1970) indicated a maximum horizontal travel for *C. ornata* of only 30 m (from a 41 m drop), a glide ratio (horizontal: vertical travel) of <1 . In comparison, *C. paradisi* can maximally achieve a glide ratio of 4.2. Currently, we have little explanation for inter-specific differences in ability to glide; for example, undulation frequencies were not significantly different. However, the kinematic data for *C. ornata* are relatively poor in quality and in number, so caution is warranted in describing the two species as behaviorally similar, and improved kinematic studies are needed. One known difference is that the body of *C. ornata* is more robust than that of *C. paradisi*; at any body length, *C. ornata* are more massive. Additionally, body mass scales with positive allometry in *C. ornata*, but appears to scale isometrically in *C. paradisi*. These differences imply higher wing loadings in *C. ornata*, but this has not been measured directly. Finally, *C. ornata* begin the trajectory with steeper ballistic dives, which suggests differences in their jumping kinematics, another issue that demands further study.

Aerodynamics of snakes' cross-sectional shape

Given their trajectories, it is clear that *Chrysopelea* produce significant aerodynamic forces, but we are only beginning to understand the role of specific features of their glides. The snake's cross-sectional shape is unusual for an airfoil, but its fore-aft symmetry may be beneficial for producing relatively uniform forces. During aerial undulation, the snake continuously reconfigures its body during a glide; it is a true morphing wing. As the traveling wave moves posteriorly down the body, a local body segment effectively reverses orientation. This means that the leading edge becomes a trailing edge roughly every 400 ms. The snake's fore-aft symmetrical cross-sectional shape may be ideally suited for producing sufficient force independent of orientation.

One study has examined the aerodynamics of cross-sectional shape using a semi-circular model as a rough approximation (Miklasz et al. 2010). The snake was experimentally treated as a straight, concave section with varying degrees of filler to simulate different cross-sectional areas, and tested across angles of attack (α) at one Reynolds number (15,000). The most snake-like model produced a maximum lift coefficient of 1.5 at $\alpha = 30^\circ$, and displayed gentle stall characteristics, with lift being

produced even at high angles of attack. The highest lift-to-drag ratios occurred over a broad range, between $\alpha = 10\text{--}30^\circ$. Force coefficients were nearly identical for the empty and half-full models, but values of lift significantly decreased when the model was filled. These results demonstrate that the fore and aft “lips” of the ventral cross-section must significantly alter the pattern of airflow over the snake’s body and contribute positively to the snake’s production of force. This also implies that different segments of the snake’s body may experience differential loading via differences in shape alone, particularly if the ventral lips are not present in the posterior part of the snake (as suggested by Fig. 3).

The snake’s particular cross-sectional shape may also contribute aerodynamically by the wake it produces interacting with the body itself. Relative to the oncoming airflow, the snake’s body has upstream and downstream segments, akin to staggered airfoils (Fig. 6C). *Chrysopelea paradisi* glides with an angled orientation of the body, with body segments moving up and down and fore and aft, so it is likely that downstream segments encounter the wake produced by upstream segments. In general, such wake interactions can change the pattern of force on both the upstream and downstream airfoils. Therefore in addition to examining the aerodynamics of a single model, we also conducted preliminary trials of tandem models to simulate the effects of staggered configurations of the body. When the downstream model was positioned one chord-length below and multiple chord-lengths behind the upstream model, the downstream model experienced increased lift-to-drag ratios, indicating a beneficial interaction with the upstream wake. However, it is unclear if, and how, the snake uses this mechanism, which is well known from staggered airfoils, including those tested in intermediate Reynolds-number regimes (Scharpf and Mueller 1992).

These results suggest that the snakes employ strategies that improve their otherwise detrimental aerodynamic characteristics, but this single study is merely a starting point, and the underlying fluid mechanics of gliding snakes remain obscure. In collaboration with Pavlos Vlachos (Mechanical Engineering, Virginia Tech), we are currently conducting more sophisticated studies, including particle image velocimetry measurements using more anatomically accurate shapes, and computational studies that will incorporate aspects of the snakes’ movements. Ultimately we aim to measure forces and visualize flows over real snakes in mid-glide, but these experiments will be logistically challenging.

Landing

The functional challenges of landing with a cylindrical body plan may be as demanding as those involved in gliding, but landing in flying snakes has not been studied rigorously. Impact forces of landing are governed by the relationship between momentum and impulse (I),

$$I = F\Delta t \quad (1)$$

where F is impact force and t is time. Specifically, the animal’s change in momentum is equal to its impulse:

$$m\Delta v = F\Delta t \quad (2)$$

where m is mass and v is velocity. Thus, a knowledge of the animal’s speed prior to impact and the duration of impact allow one to estimate the average force of landing. Prior to landing from a full glide, mammalian gliders are known to reduce speed and therefore reduce momentum, producing peak forces in the range of 3–10 BW (body weight) for northern flying squirrels (Paskins et al. 2007) and 2.4–17.0 BW for colugos (Byrnes et al. 2008). In addition, these gliders produce rotational torques, which pitch the animal in a nose-upward direction, reorienting the body so that the legs are in position to contact a vertical substrate. Not only does this distribute the landing loads across the legs, but it also helps to avoid a head-on collision with the substrate. Preventing head injury is likely an important consideration for all vertebrate gliders.

Preliminary analyses of landings recorded with high-speed video suggest mechanisms that *Chrysopelea* may use to successfully land on the ground and in vegetation (Fig. 8). Prior to landing on the ground, *C. paradisi* appear to rotate the tail and posterior body downward, such that the tail strikes first. Contact then progresses anteriorly, with the head contacting the ground last. This “rolling” landing should serve to increase the total contact time and reduce peak impact forces, and potentially the body may absorb energy to further protect the head. Using impact times estimated from high-speed video to be 50–80 ms, snakes moving at 6–10 m/s should land on the ground with impulses of 0.1–0.8 J and forces of 12–20 BW. Unlike other arboreal gliders, snakes do not appear to slow down prior to landing, but better data on trajectories are needed to address this issue.

Landing on vegetation should be more kinematically challenging. Based on short trajectory trials, *C. paradisi* appear to land on horizontally-oriented branches by approaching with an angled body

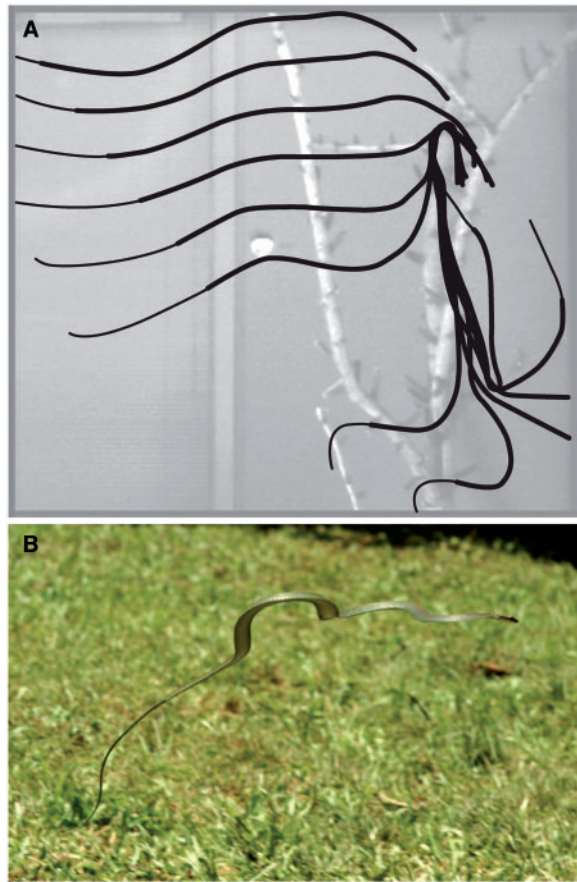


Fig. 8 Landing in *C. paradisi*. **(A)** Side view of a landing on a tree branch with multiple branches. The tracings are taken from high-speed video stills recorded at 125 Hz, shown here at intervals of 24 ms. In this landing, the snake first makes contact with the branch at the ventral surface of the anterior part of the body. The posterior part of the body and the tail then rotate in a counterclockwise direction about the contact point. Because the snake transfers the kinetic energy of the glide into both impact energy and rotational energy, the force of impact must be reduced by this additional movement. This rotation is partially arrested by contact with a second branch, about which the posterior body rotates again. See Supplementary Movie 2 for corresponding video. **(B)** Landing on the ground. This video still shows the snake in a tail-down posture just prior to contact, which begins with the tip of the tail (image courtesy of National Geographic Television).

posture. After contact, the momentum of the anterior and posterior parts of the snake induces a wrapping motion around the branch. Pendlebury (1931) also observed a glide in which the snake dropped the tail prior to landing on a bush. For a snake, landing on a horizontal branch should entail a smaller total contact area on the body relative to ground-based landings, meaning that local stresses may be much higher than in ground landings; limb compliance should mitigate this effect, as should the body

wrapping kinematics seen in Fig. 8A. Frictional forces and the material properties of the skin are therefore relevant parameters for future consideration. Finally, it is not known whether snakes can land on relatively flat, vertical surfaces such as a rock face or a tree trunk of large diameter. If indeed they are incapable of whole-body pitch-up rotations (such as those used by gliding mammals), then a successful tree trunk landing may entail an off-axis approach so that the lateral part of the body, rather than the head, strikes first. Landing experiments involving force plates, strain-gage instrumented “trees,” and body accelerometers are currently being developed to address these questions.

Future directions

Our studies have focused on the locomotor kinematics and aerodynamics of gliding, but the question of how a cylindrical animal can produce a stable glide remains unanswered. Future work must consider the snake’s complex three-dimensional undulatory movements; unsteady aerodynamic effects and fluid–structure interactions likely play a major role in both forward gliding and turning. Overall, understanding how a snake controls gliding, from the viewpoints of aerodynamics and inertial body positioning to neuromuscular design, is a major goal.

In addition to addressing purely functional questions, the ever-increasing miniaturization and sophistication of on-board instrumentation (Byrnes et al. 2008) suggest the possibility of examining gliding behaviors of snakes in an ecological context. Studies that track snake movements in the wild would help establish a behavioral baseline including frequency, timing, and motivation for gliding, along with information on habitat utilization. Such data would enable the testing of evolutionary hypotheses of gliding, as demonstrated in a recent study of colugos in the wild (Byrnes et al. 2011). Data loggers that recorded acceleration were used to infer that these mammals do not gain an energetic benefit from gliding; it is cheaper to travel horizontally by crawling through the canopy than to climb and glide. Instead, gliding in colugos may have evolved as a means of quick travel. Alternatively, it has also been suggested that the motivation to jump and escape predators may have been an important selective force in the evolution of flight (Dudley and Yanoviak 2011). Given the new data on *Dendrelaphis* shown here, it is indeed likely that the ability to jump preceded

other aerial behaviors in the evolution of gliding flight in snakes. Overall, the biomechanical and evolutionary challenges of turning a limbless vertebrate into a highly capable glider provide an intriguing area of study.

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Supplementary material

Supplementary material is available at *ICB* online.

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