

Becoming airborne without legs: the kinematics of take-off in a flying snake, *Chrysopelea paradisi*

John J. Socha

Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL 60637, USA

Address correspondence to: Argonne National Laboratory, Building 438, Sector 32, 9700 Cass Avenue, Argonne, IL 60439, USA
(e-mail: jjsocha@uchicago.edu)

Accepted 12 June 2006

Summary

Among terrestrial vertebrate gliders, take-off presents a unique problem to flying snakes (*Chrysopelea*). Without legs, snakes must use fundamentally different kinematics to begin their aerial trajectories. To determine the effectiveness of different modes of take-off in a gliding snake (*C. paradisi*), I videotaped multiple views of take-off from a horizontal branch and quantified the two- and three-dimensional coordinates of three points on the snake's body. Performance values derived from these coordinates were used to describe take-off in *C. paradisi*, compare modes of take-off, and make predictions about the ecological use of take-off in the wild. Four types of take-off were identified. In most observed take-offs, snakes used a vertically looped take-off (termed 'anchored J-loop' and 'sliding J-loop'), which represent the only true jumping in snakes. In an anchored J-loop take-off, the snake formed an anterior hanging loop and then jumped by holding the posterior body static on the branch and accelerating up and away from the branch. This was the most commonly used take-off mode. A sliding J-loop take-off was similar but occurred with the entire body in motion. Snakes using such take-offs lowered less of their

body below the branch than in an anchored J-loop take-off, resulting in shorter preparation and vertical acceleration durations and producing a lower maximum vertical velocity. However, these differences did not produce significant differences after the snakes were fully airborne and had started their aerial trajectories. The non-looped take-offs (termed 'dive' and 'fall') were the least kinematically complex. Compared to the non-looped take-offs, looped take-offs allowed snakes to reach higher, range farther, and attain greater speeds. Furthermore, snakes that launched with looped take-offs traveled farther over the course of a full glide trajectory when starting from a 10 m high perch. Take-off in *C. paradisi* is qualitatively similar to that in other species of *Chrysopelea* and may represent a suite of behaviors that preceded the evolution of gliding flight in snakes.

Supplementary material available online at
<http://jeb.biologists.org/cgi/content/full/209/17/3358/DC1>

Key words: *Chrysopelea paradisi*, take-off, kinematics, snake, glider, performance, behavior, locomotion, jumping.

Introduction

Multiple lineages of terrestrial vertebrates, including frogs, snakes, lizards and mammals (Nowak, 1999; Tweedie, 1960), use controlled descents to locomote through the air. Aside from accidental falls, animals generally initiate these descents with a powered take-off. Although take-off has not been well studied in most gliders (but see Essner, 2002; Keith et al., 2000), take-off for most vertebrates can broadly be described as a rapid straightening of bent limbs that produces an acceleratory jump (Emerson, 1985). Even birds, which could employ rapid wingbeats to produce take-off thrust, use their legs as the primary means of accelerating to flight velocity (Bonser and Rayner, 1996; Earls, 2000; Heppner and Anderson, 1985; Tobalske et al., 2004). In contrast, snakes have no obvious means of producing a jumping take-off. As in many other

aspects of their biology, being cylindrical and lacking legs presents locomotor challenges to snakes, especially gliding snakes, which need to move both in a complex 3D arboreal environment as well as through the air. The study explores the question, how does a limbless animal initiate aerial locomotion from a high perch?

Because launch represents the initiation of an aerial trajectory, understanding variation in take-off behavior and performance may be a key component to understanding a glider's aerial locomotion and evolution. Different aspects of take-off performance may be targets of evolutionary selection, depending upon the reason for becoming airborne. For example, an animal attempting to escape a predator should maximize its acceleration and minimize its total take-off duration, whereas an animal crossing a large gap between trees

should maximize its net displacement and velocity. Does variation in take-off behavior produce differences in take-off performance? If so, are such differences ecologically relevant? It is intuitive how such differences could matter on a scale local to the take-off; for example if an animal is attempting to jump to a nearby branch, a 1 cm reduction in range may result in a miss and inadvertent fall. However, it is unclear if and how variation in take-off performance translates to performance over the course of a much longer glide. Gliders may make mid-air postural adjustments [e.g. angle of attack (Bishop, 2006)], dramatically altering the course of their trajectories.

A previous study of take-off in leaping, parachuting and gliding squirrels demonstrated that squirrels use a highly stereotyped behavior to become airborne during horizontal launching despite large differences in aerial performance (Essner, 2002). Take-off in squirrels involves using changes in hindlimb joint angle and body axis bending to propel themselves from a horizontal perch. In contrast, snakes are constrained to using body axis bending if they are to produce acceleration for take-off. For example, the rapid straightening of body curves involved in a predatory or defensive strike could be used to spring off the perch. Alternatively, snakes may employ lateral undulation to locomote off the branch or, more simply, they could enter the air by releasing their grip from the substrate. These statements represent null hypotheses of take-off behavior in snakes.

The aerial phase of locomotion in snakes has been described in multiple species of *Chrysopelea*, the South and Southeast Asian genus of so-called 'flying' snakes. Upon becoming airborne, flying snakes flatten the body from head to vent, send high-amplitude lateral traveling waves posteriorly down the body, and move the posterior body up and down in the vertical plane, with the tail whipping back and forth (Socha, 2002a; Socha et al., 2005). Smaller snakes are generally better gliders, and on all counts the paradise tree snake (*Chrysopelea paradisi*) seems to be the most adept performer, able to glide significantly farther than other taxa (Socha and LaBarbera, 2005); this species can even maneuver in the air (Socha, 2002a). However, although anecdotal reports exist (e.g. Flower, 1899; Greene, 1997; Shelford, 1906; Tweedie, 1960; Vaughn-Arbuckle, 1959), there has been no formal description of take-off in flying snakes, and quantitative data are lacking.

The purpose of this paper is twofold. First, to describe the kinematics of take-off in the paradise tree snake, *C. paradisi*, in order to understand how a limbless vertebrate can overcome an apparent biomechanical constraint. Second, to determine the effect of different take-offs on overall performance. From observations it was noted that snakes use multiple behaviors to take off from a horizontal branch. Do such behaviors result in performance differences local to the region of the branch, and if so, do these initial differences matter when considering the full course of a long glide trajectory? In particular, take-offs are compared in duration, range, velocity and acceleration, and these comparisons are used to make inferences about the ecological use of take-off in *C. paradisi*. Because successful take-off of any kind, including a fall, must logically precede a

successful aerial trajectory, the results presented here may inform studies that examine the evolution of gliding flight.

Materials and methods

This study reports take-off data recorded concurrently with aerial trajectory data reported previously (for details, see Socha et al., 2005).

Animals

I observed a total of 21 wild-caught *Chrysopelea paradisi* Boie in Singapore. Snakes ranged from 3.0 to 82.7 g in mass and from 31.0 to 86.5 cm in snout-vent length (SVL). The smallest snake was a young juvenile, with an estimated age of 2–4 months (Mundkur, 1978); the largest snakes were fully developed adults. Both males and females were used.

Snakes were housed in a non-public animal room in the Reptiles Division of the Singapore Zoological Gardens, following standard approved zoo protocol. Snakes were kept in 38-liter aquaria with copious branches and water and were fed wild-caught geckos once per week. Because the animal room was open-air, temperature (25–32°C) and relative humidity (50–70%) were similar to ambient conditions of the snakes' natural habitat. Animal care and experimental procedures were approved by the University of Chicago Animal Care and Use Protocol Committee (IACUC #70963).

Take-off protocol and recording

Snakes were launched from a horizontal branch at the top of a scaffolding tower located in an open field at the Singapore Zoological Gardens. The branch was approximately straight, tapering in diameter from 4 cm at the base to 2 cm at the tip, and protruded from the edge of the tower's platform by about 1 m. This branch (of unknown origin) was chosen for its sufficient roughness to prevent slipping, and for its thickness to minimize branch compliance (Alexander, 1991), reducing the vibration created as the snake loaded and unloaded the branch during take-off. The height of the branch was 9.62 m above the ground. A second scaffolding tower approximately 10 m to the side of the launch tower was used to record a lateral view of the take-off. A fabric sheet was hung adjacent to the branch to serve as a visual backdrop for a lateral view videocamera.

Prior to launch, snakes were marked on their dorsal surface at the head-body junction (hereafter referred to as 'head'), body midpoint and vent, with a 1 cm band of non-toxic white paint (Wite-Out, Waterman-Bic, Milford, CT, USA). Individual snakes were sampled multiple times per day, with at least 15 min of recovery between trials. Observational days were usually followed by a day of rest. No trials were conducted during the 2 days following feeding.

Snakes were placed onto the proximal end of the branch by hand, with the snake's head facing away from the tower. The snake usually moved toward the end of the branch and either stopped or began take-off immediately. In trials in which the snake hesitated, it was gently prodded on the posterior body

and tail to provoke an escape response. As much as possible, this protocol was intended to elicit the snake's 'natural' take-off behavior. Snakes that didn't respond within 10 min were removed from the branch.

Trials were recorded with two Sony DCR-TRV900 digital videocameras, synchronized *post-hoc* with an audio calibration signal using Adobe Premiere software (Adobe, San Jose, CA, USA). Two recording configurations were used. In the first, a videocamera was stationed above the take-off platform to record the dorsal view, and another was stationed on the second tower at the same height as the launch branch to record a lateral view. Only trials in which the snake moved primarily in the plane perpendicular to the lateral view videocamera were used from this configuration.

In the second configuration, both videocameras were stationed at the top of the launch tower, approximately 12 m above the ground and 2 m apart, to record dorsal views in stereo. This configuration was used for the 3D reconstruction of the head, midpoint and vent throughout the take-off. A grid of points (located on the ground, spaced 1–2 m apart) in view of both cameras was used as a photogrammetric reference system. The mean RMS error was about 2 cm (Socha et al., 2005).

Video was recorded at 30 frames s^{-1} and deinterlaced *post-hoc* with NIH Image software (National Institutes of Health, Bethesda, Maryland, USA) to yield 60 Hz data. Effective shutter speeds were typically between 1/1000–1/2000 s. The smallest effective focal length was used to obtain the largest field of view for the dorsal videocameras; a larger focal length was used for a more detailed view in the lateral view videocamera.

A total of 239 take-offs were recorded, all classified on the basis of take-off behavior. A total of 24 trials were digitized and analyzed in detail, representing 13 individual snakes. Within different behavior categories, each trial represented a different snake.

Performance variables

Both 2D and 3D coordinates of the head, midpoint and vent were used to analyze performance during take-off. The 3D coordinates were reconstructed from the stereo dorsal video records using ERDAS Imagine with Orthobase software (version 8.4; ERDAS, Atlanta, GA, USA) [for details of this photogrammetric method see (Socha et al., 2005)]. Two-dimensional coordinates were digitized from the lateral video records using QuickImage (Walker, 2001).

Although three landmarks were digitized, most of the results presented here are from the head data, because only the head landmark was in view throughout the entire take-off in each sequence. Velocity and acceleration were calculated using QuickSand software (Walker, 1997). Prior to calculations, the digitized coordinates were smoothed with a Lanczos five-point moving regression, which takes a weighted average of the two smoothed values immediately prior to and following the point of interest (Walker, 1998). This algorithm was chosen because it most accurately reproduced the original values.

The following performance variables were analyzed: take-off duration, vertical height gained, horizontal range, velocity and acceleration. The beginning of take-off was defined as the video field preceding the first identifiable vertical movement of head away from the branch (usually downward), and the end was defined as the last video field before all parts of the snake became fully airborne. 'Take-off duration' is the total time encompassing this sequence. Two variables quantify the net displacement of take-off relative to the snake's initial position on the branch: 'height gained' is the maximum vertical excursion of the snake's head above the branch, and 'range 0' is the maximum distance of the snake's head away from the branch in the horizontal plane, measured at the height of the branch. Because two of the observed modes of take-off had no initial vertical component upward, a second metric of horizontal distance, 'range -1', was defined at an arbitrary depth of 1 m below the branch. 'Total range' is the horizontal distance of the trajectory over the entire 9.62 m descent. 'Horizontal' and 'vertical velocity', and the corresponding 'resultant velocity', were also identified at a height of 1 m below the branch. The vertical plane encompassing the snake's forward motion throughout take-off was used to define the horizontal and vertical axes. 'Accelerations' represented the maximum positive values (upward in the case of vertical acceleration) produced during take-off. For purposes of comparison, the beginning of the horizontal acceleration phase was defined as the video field in which the path of the snake's head became more horizontal than vertical.

These performance metrics are meant to quantify the effects of take-off, rather than to simply describe events that occur during take-off (strictly, with the snake contacting the branch). As such, for some variables in some trials the snake was entirely airborne at the point of measurement.

Statistical analyses

To test whether looped take-offs differed in performance from non-looped take-offs, one-way ANOVAs were performed among all measured performance variables. Within each take-off type, each trial represented a different snake. Because an *f*-max test showed unequal variances among average take-off times, time was log-transformed prior to analysis. To account for body size differences among snakes, metrics using distances were normalized by snout-vent length (*SVL*) to yield non-dimensional body length (*BL*). To identify differences within looped and non-looped take-off types, one-way ANOVAs were performed using take-off modes as effects. Significant tests were followed by a Tukey-Kramer Honestly Significant Difference (HSD) test to determine which groups were different from each other ($P < 0.05$). Statistical analyses were conducted using JMP software (version 5.0).

Results

Two distinct modes of take-off were distinguished—looped and non-looped take-offs. Looped take-offs (Fig. 1 and Fig. 2A,B) were characterized by the formation of a single loop

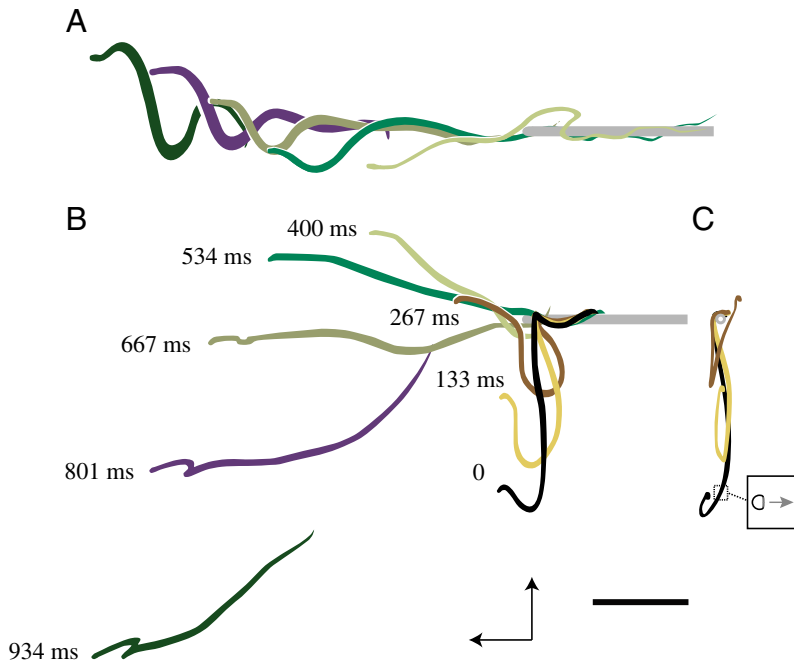


Fig. 1. Representative anchored J-loop take-off sequence in *C. paradisi*. Overhead (A), side (B) and front (C) views, traced from video records. Sequence starts just prior to the first upward movement. The preparation phase, in which the snake drops down from the branch, is not shown. In side view, arrows refer to horizontal and vertical axes. Scale bar, 25 cm. Mass=83 g, SVL=83 cm.

in the anterior body, usually oriented vertically, followed by an active jumping movement. Snakes predominantly used such take-offs (78%, 187 of 239 trials), with the majority being the anchored J-loop type (74%, 177 trials). Non-looped take-offs include a 'dive' (Fig. 2C) and a 'fall', both of which were observed less often (18%, 43 trials). In a few other take-offs, the snake used different behaviors, none of which were included within these categories as defined. The kinematic details of these modes of take-off are summarized in Table 1 and are described in detail below.

Anchored J-loop take-off

The most commonly observed take-off was the anchored J-loop take-off (Fig. 1), a jumping take-off that began with the snake hanging from the branch, with the posterior body and tail gripping the branch (Fig. 3) and the anterior body forming a J-shaped loop (hereafter termed 'J-loop'). An anchored J-loop take-off can be broken down into two phases: a preparatory phase in which the J-loop is formed, and a acceleratory phase in which the snake jumps upward and away from the branch. In some trials, take-off included an intermediate phase in which the snake paused before jumping.

Take-off began with the snake lowering approximately 60–70% of the anterior body from the branch and forming the J-loop. Contrary to first appearances, the bottom curve of the 'J' was not composed of a dorsoventral bend, but of a lateral bend in the body, such that the snake's ventral side faced to the left and dorsal to the right (or *vice versa*) (Fig. 1C). Anterior to the loop, the body was twisted such that the head was oriented in a 'normal' posture with the ventral side facing down. The bottom of the J-loop was $55 \pm 8\%$ SVL from the branch, with the anteriormost portion of the snake rising up vertically $5 \pm 5\%$ SVL. The topmost portion of the 'J' was swept back from the branch at angle between 6 and 28° . From a frontal view of the take-off, the J-loop appeared slightly bowed in shape, with the loop extending out of the vertical plane by about 10% SVL (see Fig. 1C).

Once the snake formed the J-loop, it either paused or immediately began the jumping phase of the take-off. During a pause, the snake sometimes

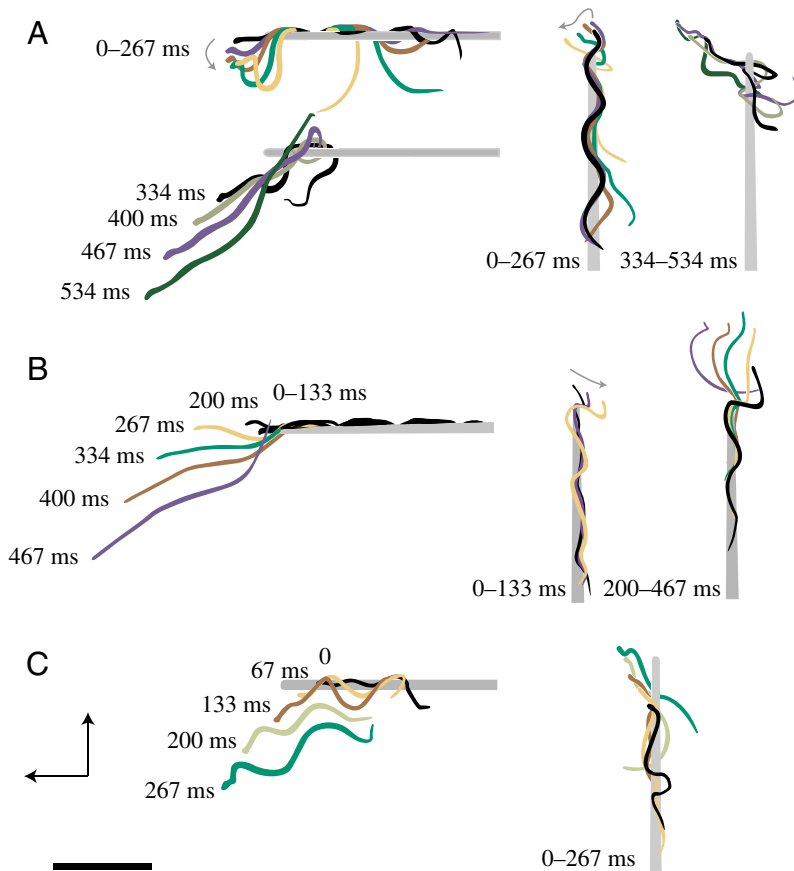


Fig. 2. Representative traces of other modes of take-off in *C. paradisi*. Side (left) and overhead (right) views of sliding J-loop, side-loop and dive take-offs. In side view, arrows refer to horizontal and vertical axes. Scale bar, 25 cm. (A) Sliding J-loop take-off sequence. Mass=26 g, SVL=62 cm. (B) Side-loop take-off sequence. Mass=16 g, SVL=54 cm. (C) Dive take-off sequence. Mass=11 g, SVL=47 cm.

Table 1. Summary data for *C. paradisi* take-off performance, separated by take-off mode

	Anchored J-loop	Sliding J-loop	Dive	Fall
<i>N</i>	11	4	4	5
Duration				
Take-off total (s)	2.52±1.10	0.70±0.22	0.19±0.04	3.26±3.47
Preparation (s)	2.04±1.04	0.38±0.15	N/A	N/A
Acceleration total (s)	0.49±0.09	0.33±0.07	N/A	N/A
Vertical acceleration (s)	0.30±0.09	0.17±0.05	N/A	N/A
Horizontal acceleration (s)	0.19±0.05	0.16±0.04	N/A	N/A
Distance				
Height gained (cm)	0.17±0.12	0.10±0.08	0.00±0.00	0.00±0.00
Range 0 (cm)	0.69±0.18	0.55±0.11	0.00±0.00	0.00±0.00
Range -1 (cm)	1.19±0.13	1.27±0.28	0.25±0.10	0.09±0.05
Total range (m)	8.64±2.56	12.16±2.76	6.66±4.11	3.83±2.73
Velocity				
Horizontal, max (m s ⁻¹)	2.1±0.2	2.1±0.2	0.6±0.3	N/A
Horizontal, 0 m (m s ⁻¹)	1.6±0.5	1.8±0.6	0.5±0.1	N/A
Horizontal, -1 m (m s ⁻¹)	2.0±0.7	2.5±1.0	0.2±0.1	0.2±0.3
Vertical, max (m s ⁻¹)	1.8±0.4	0.9±0.3	N/A	N/A
Vertical, 0 m (m s ⁻¹)	-1.8±0.9	-1.0±0.8	-0.3±0.1	N/A
Vertical, -1 m (m s ⁻¹)	-4.1±0.3	-3.6±0.1	-2.7±0.3	-2.4±0.1
Resultant, max (m s ⁻¹)	2.3±0.2	2.0±0.2	N/A	N/A
Resultant, 0 m (m s ⁻¹)	2.5±0.7	2.1±0.6	0.6±0.1	N/A
Resultant, -1 m (m s ⁻¹)	4.6±0.5	4.4±0.6	2.7±0.3	2.5±0.2
Acceleration				
Horizontal, max (m s ⁻²)	14±4	20±2	4±2	N/A
Vertical, max (m s ⁻²)	16±7	10±3	0±0	N/A
Resultant, max (m s ⁻²)	20±4	20±7	4±2	N/A

Values are means ± s.d. N/A, not applicable.

Note that maximum horizontal and vertical velocities and accelerations occur at different times; thus each snake's resultant maximal values do not represent combinations of those values.

'wagged' its head, moving a few centimeters from side-to-side at a frequency of about 2 Hz. Less frequently, the snake wagged its head while lowering its body from the branch. This behavior is likely a form of motion parallax, a mechanism used to judge distance in diverse taxa including insects, birds, rodents and humans (Kral, 1998); other gliders have been

observed to sway from side to side prior to jumping as well [e.g. flying squirrels (Nowak, 1999)].

In the acceleratory phase of the take-off, snakes became airborne by jumping upward and away from the branch. In the first phase of the jump, the anterior body accelerated upward, and the point of maximum curvature in the J-loop moved posteriorly along the body. During this upward acceleration, there was usually a slight backward component to the head's movement (Fig. 4A; also see horizontal velocity in Fig. 5A). During the second phase, the body straightened out and moved outward away from the branch, staying horizontal relative to

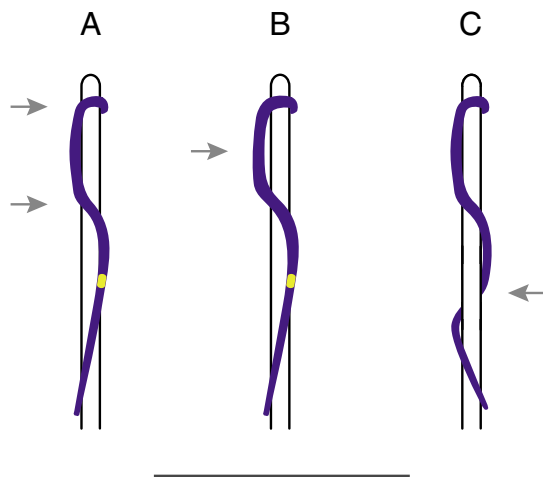


Fig. 3. Types of branch 'grips'. Overhead view of the snake on the branch, with the anterior body of the snake hanging off the right side and below the branch (into the page). The location of the snake's vent is represented by a yellow dot. (A) Most common grip configuration. Grips generally comprised at least one loop with two points of orthogonal contact (gray arrows). (B) Grip with the first loop hanging from the branch, with the middle of the loop (gray arrow) not contacting the branch. (C) Grip with posterior body and tail wrapping under the branch in a spiral (gray arrow), used less frequently than A or B. In some trials, the snake threw multiple wraps around the branch in a more circular fashion.

the ground. In some trials in which the snake took off at an angle to the branch (as viewed from above), the last part of the snake to straighten was a small posterior loop near the branch, suggesting that snakes may alter their kinematics when able to push off from a vertical substrate. As the head accelerated outward, the snake released its grip on the branch, and the body began to markedly flatten from head to vent. Body width approximately doubled, with the ventral surface taking a slightly concave shape (Socha, 2002b). The snake's midbody then rotated approximately 90° from the vertical to the

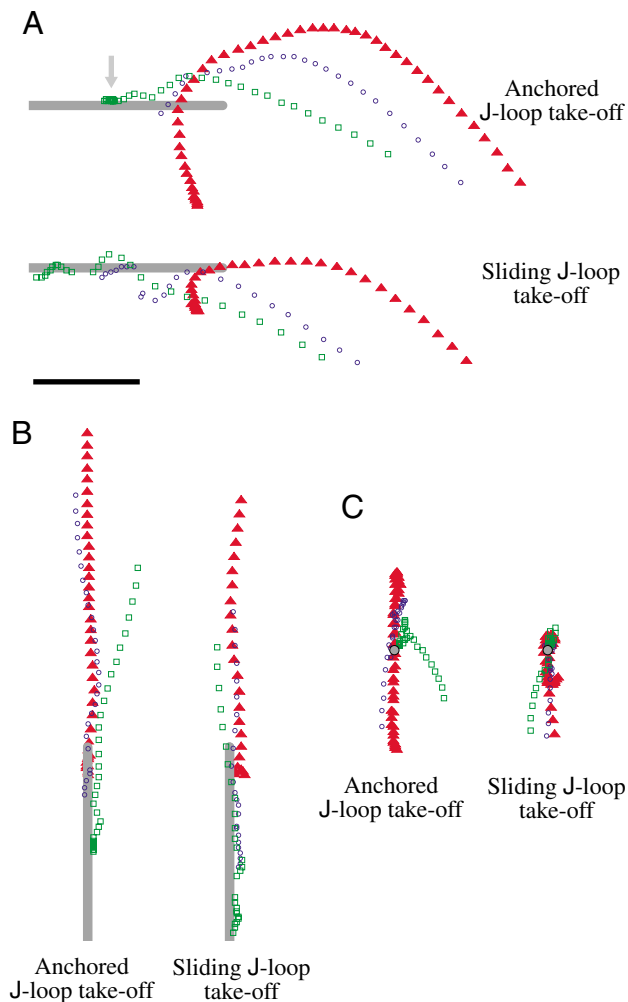


Fig. 4. Three-dimensional positions of the head, midpoint, and vent in representative anchored and sliding J-loop take-offs. Head, midpoint and vent points are represented with triangles, circles and squares, respectively. Scale bar, 25 cm. Side (A), overhead (B) and rear (C) views of unsmoothed data sampled at 60 Hz. In both take-offs, the head traces approximately the same path, moving upward, outward, and then down. In the anchored J-loop take-off, the snake's head has a slight rearward component during the first upward movement. The upward movement during the initial acceleration has almost no lateral component. Note the relative lack of movement of the vent (gray arrow, A) early in the anchored J-loop take-off. Anchored J-loop take-off: mass=27 g, SVL=63 cm; sliding J-loop take-off: mass=26 g, SVL=62 cm.

horizontal plane, untwisting the snake and returning the dorsal and ventral surfaces to their 'normal' upright positions.

As the body underwent this series of contortions, the head maintained a relatively constant orientation, with the head angled downward relative to the horizon. In one sequence (Fig. 6), the snake's head angle relative to the horizon (in the vertical plane) began at about 20° at the end of the J-loop formation phase and decreased slightly as the snake accelerated upward. Near the end of take-off and during the initial part of the aerial trajectory, the head rotated downward, increasing the head angle to about 40°. At this point in its trajectory, the snake was following a path of about 50° from the horizon, meaning that the head was oriented almost straight ahead relative to the snake's forward motion.

Although the posterior body and tail were in motion throughout most of the take-off, during the upward acceleration they remained stationary on the branch, forming a static 'grip' that formed a posterior anchor (Fig. 3). The grip consisted of one or more loops on the branch. In some take-offs, the body forming the loops maintained contact with the branch, and in others the loops hung freely, making contact only where the body intersected the branch. Generally, snakes kept a minimum of two points of contact orthogonal with the branch during take-off, although a few trials occurred with a single point of contact. After the upward acceleration phase, the posterior body either lifted off the branch or slid across or down the branch, depending on the vertical excursion during take-off. Occasionally part of the snake's body and/or tail completely wrapped around the branch. In these situations, the snake simply released the branch by unwrapping itself during upward acceleration of the jump.

Upon becoming airborne, the straightened snake began to form an initial undulatory wave approximately one-eighth the way down the body, posterior to the head (Fig. 1A). As this lateral wave traveled posteriorly down the body, a second wave formed posterior to the first; in some trials, both waves were formed simultaneously. In trials with a single initial wave, the side of this wave was the same side that the ventral surface faced while the snake was hanging in the J-loop posture for 86% of the trials. A χ^2 test ($\chi^2=7.47$, d.f.=1, $P<0.05$) showed that for most trials the J-loop becomes the initial wave as the snake's anterior body rotates from vertical to horizontal.

Sliding J-loop take-off

The other type of vertically looped take-off observed is termed a 'sliding J-loop' take-off (Fig. 2A). Though similar to an anchored J-loop take-off, sliding loop take-offs were distinguished by the snake's continuous motion of the entire body throughout take-off. In particular, snakes did not use a posterior static anchor during upward acceleration.

A sliding J-loop take-off began with the snake lowering the anterior body from the branch to form a small loop. Immediately upon forming the loop, the snake began to accelerate upward and away from the branch without pausing at the bottom of the loop, analogous to a running jump in mammals. In some trials, the direction of the motion was

diagonally downward. Besides the lack of a static anchor, sliding J-loop take-offs differed from anchored ones in two regards: (1) the vertical loop was smaller, resulting from a greater percentage of the posterior body remaining on the branch, and (2) the total duration of the take-off was shorter.

The sliding J-loop take-off was less commonly observed in both absolute terms (10 of 239 trials) and in number of specimens that employed it (4 of 21).

Other looped take-offs

A few types of take-off were observed once each, and are briefly noted here to document the full repertoire of *C. paradisi*'s take-off behavior. In one trial (Fig. 2B), the snake accelerated using a lateral loop in the horizontal plane, formed by moving the head back and to the side. The snake then accelerated forward by feeding the body through this loop, akin to a 'tractor-tread' rattlesnake strike described by Kardong and Bels (Kardong and Bels, 1998). In another trial, the snake formed the J-loop but then accelerated diagonally downward instead of upward, which appeared to be a combination of dive and J-loop take-offs. Lastly, one snake performed a sliding J-loop take-off above the branch by raising its head up and forming the bottom of the loop on the branch. Such trials demonstrate that intermediate take-off behaviors are possible.

Dive and fall take-offs

Snakes using non-looped take-offs became airborne without using an anterior body curve to accelerate from the branch. Two such modes were identified, distinguished by the degree of motion prior to release of the branch. In a dive, the snake initiated take-off with movement of the anterior body, starting either from a static position or in motion as a continuation of lateral undulation along the branch. In a fall, there was no preliminary movement of the head or anterior body; the snake simply released its grip from the branch. For some falls, the snake was hanging from the branch when it released, and in others, the fall began with snake's entire body on the branch. In both dive and fall take-offs, there was no upward component of the movement.

Differences in performance among take-off types

For every performance variable in which comparisons were possible, ANOVAs showed significant differences between looped and non-looped take-offs (Table 2). Looped take-offs were longer in duration (Fig. 7A), but were superior for

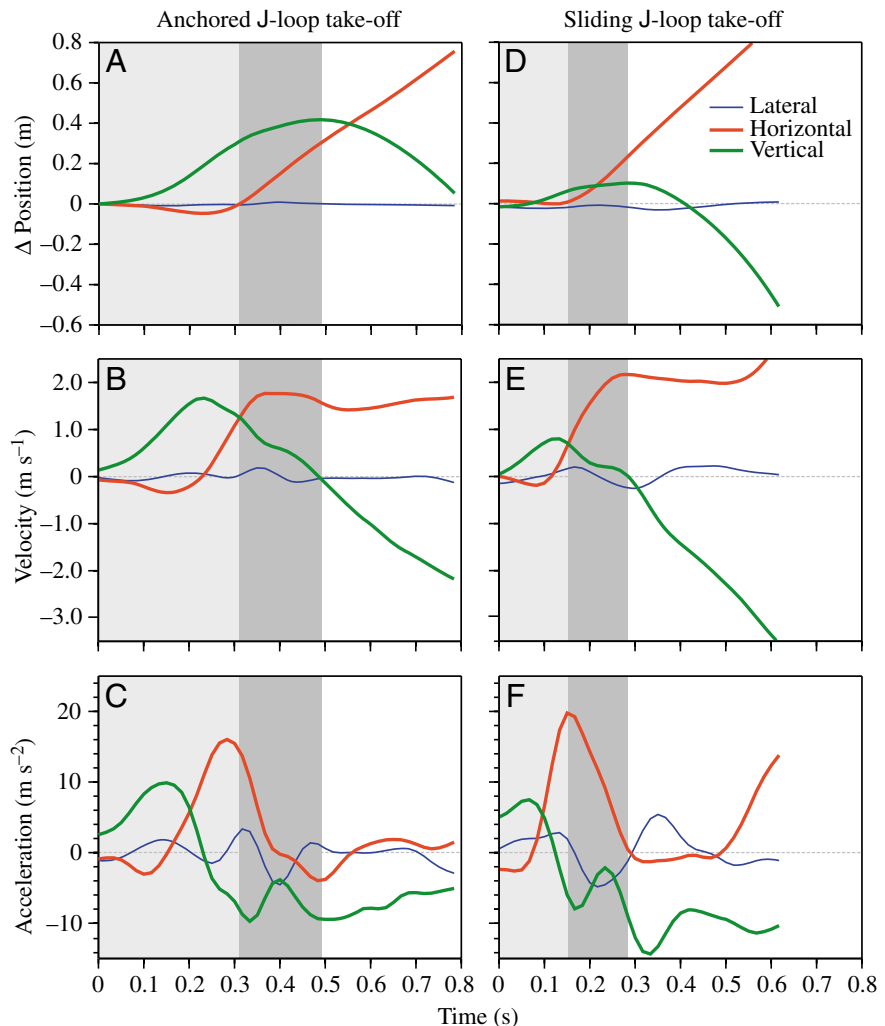


Fig. 5. Representative traces of position, velocity and acceleration in looped take-off modes. Data are from 3D coordinates of the head. The lateral, horizontal and vertical components are represented by a thin blue line, thick red line and thick green line, respectively. Gray banding represents the vertical (light gray) and horizontal (dark gray) acceleration phases. (A–C) Anchored J-loop take-off. (D–F) Sliding J-loop take-off.

producing distance (Fig. 7B), acceleration (Fig. 7C) and velocity (Fig. 7D). Snakes using looped take-offs traveled farther in height, in range at both criteria (level with the branch and 1 m below), and in total range over the course of a full trajectory from a 10 m high perch. Looped take-offs produced higher starting speeds resulting from higher initial accelerations.

Within looped and non-looped take-off types, *post-hoc* tests revealed the following differences (Table 2). Among non-looped take-offs, snakes using dives started with small positive horizontal velocities in contrast to zero horizontal velocity for falls (Table 1), though this comparison was not statistically significant. Among looped take-offs, the primary difference was in the duration of take-off phases (Fig. 7E). Sliding J-loop take-offs were faster as a result of shorter preparation and vertical acceleration phases; the duration of the horizontal

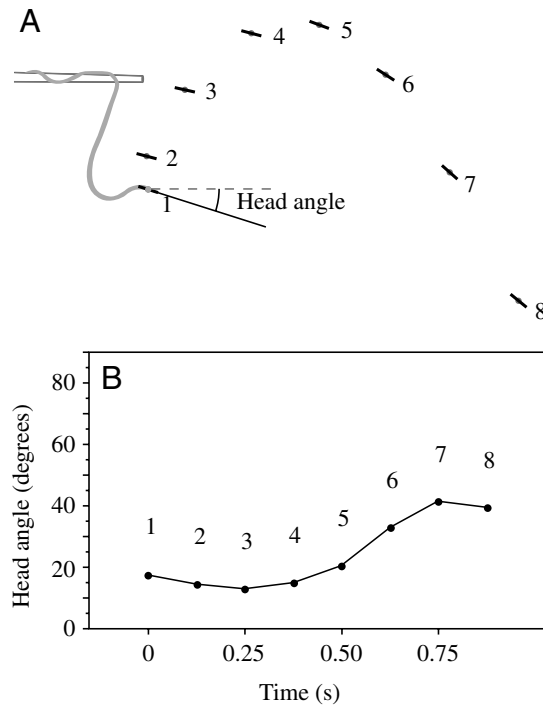


Fig. 6. Head angle changes in an anchored J-loop take-off. Head angle is the angle between the head axis and the horizon in lateral view. Intervals are 125 ms. (A) Head angle vs position. Head angles are represented by the angle of the black bars drawn at successive head positions, labeled '1' through '8'. Position 1 represents the snake just prior to the first upward movement. (B) Head angle vs time. The head angle starts at 18° and begins to increase at about position 4, when the snake reaches the apex of the jump. At position 8, the head angle is 40°, aligned approximately 10–20° above the trajectory path in the post-take-off ballistic dive. Mass=53 g, SVL=75 cm.

acceleration phase was not significantly different. The longer vertical acceleration phase resulted in higher vertical maximum velocities in anchored J-loop take-offs (Fig. 7F). The maximum horizontal acceleration was higher in sliding J-loop take-offs (Fig. 7G), but this result may be a consequence of small sample size.

Discussion

Kinematics

Two general types of take-off behavior were observed in *Chrysopelea paradisi*: looped take-offs in which the snake formed a single vertical loop and jumped from the branch, and non-looped take-offs in which the snake simply released the branch, either with or without a preceding movement of the anterior body or entire body. Vertically looped take-offs are different from other types of movements described in snakes and may represent an evolutionary locomotor novelty. *C. ornata* and *C. pelias* also use J-loop take-offs (Socha, 2002b) with no general differences in behavior; it seems likely that if other *Chrysopelea* species are aerial locomotors, that they use this type of take-off as well.

The dominant mode of locomotor behavior was the anchored J-loop take-off. In the J-loop posture, the snake hangs on its side. Forces generated during the upward acceleration are therefore likely to be produced by the lateral musculature, starting with a unilateral contraction of muscles on the upper portion of the loop. If the loop were formed by dorsiflexion, the amount of hypaxial musculature available to effect straightening is likely to be much lower than the corresponding lateral musculature, lending further weight to a lateral flexor hypothesis. As the snake straightens, the midbody rotates upward from the vertical to the horizontal plane, bringing the ventral surface from a side-facing posture back to a normal downward-facing posture. This torsional movement may require complex neuromuscular control or simply result from the passive mechanical properties of the backbone. Future studies of the timing and pattern of muscle activation would yield insight into the control of body movements during take-off.

A defining feature of the anchored J-loop take-off is that the posterior body contacting the branch remains static during the vertical acceleration phase. One question is why most snakes used at least two points of orthogonal contact and not one. These two points of contact may serve different functions, with one used primarily to transmit jumping forces to the branch and the other to provide stability or prevent slipping.

The non-looped take-offs, the dive and the fall, are the least kinematically complex. Other arboreal snakes are known to occasionally fall from the trees [especially when hanging over a body of water (e.g. Shelford, 1906)], and it is likely that they use similar behaviors to drop from a perch. These take-offs seem to require no specialization; as such, the dive and fall likely represent phylogenetically primitive behaviors in *Chrysopelea*.

Comparisons to take-off in other gliders and active flyers

The repertoire of take-off behaviors observed in snakes contrasts dramatically with that of mammalian gliders. Essner compared take-off in three species of squirrel representing taxa that leap, parachute, and glide (Essner, 2002). Although the abilities of these taxa in the aerial phase of trajectory differ dramatically, the observed take-offs were surprisingly similar, with only 6 of 23 kinematic variables differing, and these were ultimately attributable to morphological variation. Hindlimb kinematics did not differ among the three species, indicating a conserved mechanism of propulsion for species with wide variation in aerial locomotion. In contrast, the present study shows a wide degree of kinematic and performance differences in take-off within a single species of gliding snake. Furthermore, take-off in *C. paradisi* is not limited to a single behavior, whereas all three squirrels used the same stereotyped behavior during horizontal take-off. However, the observed stereotypy in squirrels may be related to the relatively low launching height used in the study; squirrels may use other behaviors when launching from a high perch or from vertical substrates (Jackson, 1999).

Although their morphologies are extremely different, the

kinematics and performance of squirrels and snakes can be compared in broad strokes. Squirrels and snakes both employ preparatory and propulsive phases. Squirrels hop into a crouched posture to prepare for propulsion by extension of the hindlimbs, and snakes form a loop to prepare for propulsion by rapid straightening of the loop. Squirrels add an additional step in between, a countermovement in which the center of mass rocks backward. In some looped take-offs there was a rearward component of the head during the J-loop formation, but it is unclear if this is a countermovement that pre-loads tissue in tension. Given the relatively small masses of the snakes, this seems unlikely. The hanging loop likely increases the distance over which the center of mass accelerates, improving performance.

Comparisons of overall performance show further congruences. Despite the vast differences in body plan and size between squirrels and snakes, take-off velocities are similar ($2.2 \pm 0.3 \text{ m s}^{-1}$ for looped take-offs in snakes and 2.3–3.0 for squirrels). It is not clear if squirrels ranged farther than snakes, because range was not reported at similar points in the trajectory.

Velocity and acceleration in relation to other snake behaviors

Looped take-offs in *Chrysopelea* are kinematically different than any other known rapid movement in snakes, particularly in comparison with predatory and defensive strikes. The general mechanism of striking [documented in colubrids, elapids and viperids (e.g. Alfaro, 2002; Alfaro, 2003; Kardong and Bels, 1998; Whitaker et al., 2000)] is to coil the anterior body into a series of lateral loops and then to accelerate by straightening the body while keeping the posterior body static; the head moves along a central axis orthogonal to these loops. In an anchored J-loop take-off, the posterior body is also static, but the straightening of the body from the single anterior loop produces a dramatic displacement along a non-central axis. Snake take-offs also differ from aquatic strikes in which the entire body is submerged. Two types of aquatic strikes have been observed: a fast forward strike, in which the head accelerates by simultaneous vertebral angle change throughout the anterior body (Alfaro, 2002; Alfaro, 2003), and a lateral head sweeping strike, in which the

snake swings the anterior body laterally toward the prey (Drummond, 1983; Halloy and Burghardt, 1990; Jayne et al., 1988; Savitzky, 1992; Voris et al., 1978). This lateral head sweep strike similarly involves unilateral bending of the anterior body, but in the J-loop take-off, there are two additional twists to the body: one anterior to the site of bending where the head is returned to a normal orientation, and one posterior to the bending where the snake twists to contact the branch. However, kinematic differences between strikes and snake jumping take-offs may simply reflect a conserved motor program enacted in a different behavioral context; future EMG studies that examine muscle usage are necessary to address this issue.

The only take-off mode with a clear analogue to striking or terrestrial locomotion was the singly observed side-loop take-off, in which the snake formed a lateral loop to the side of the

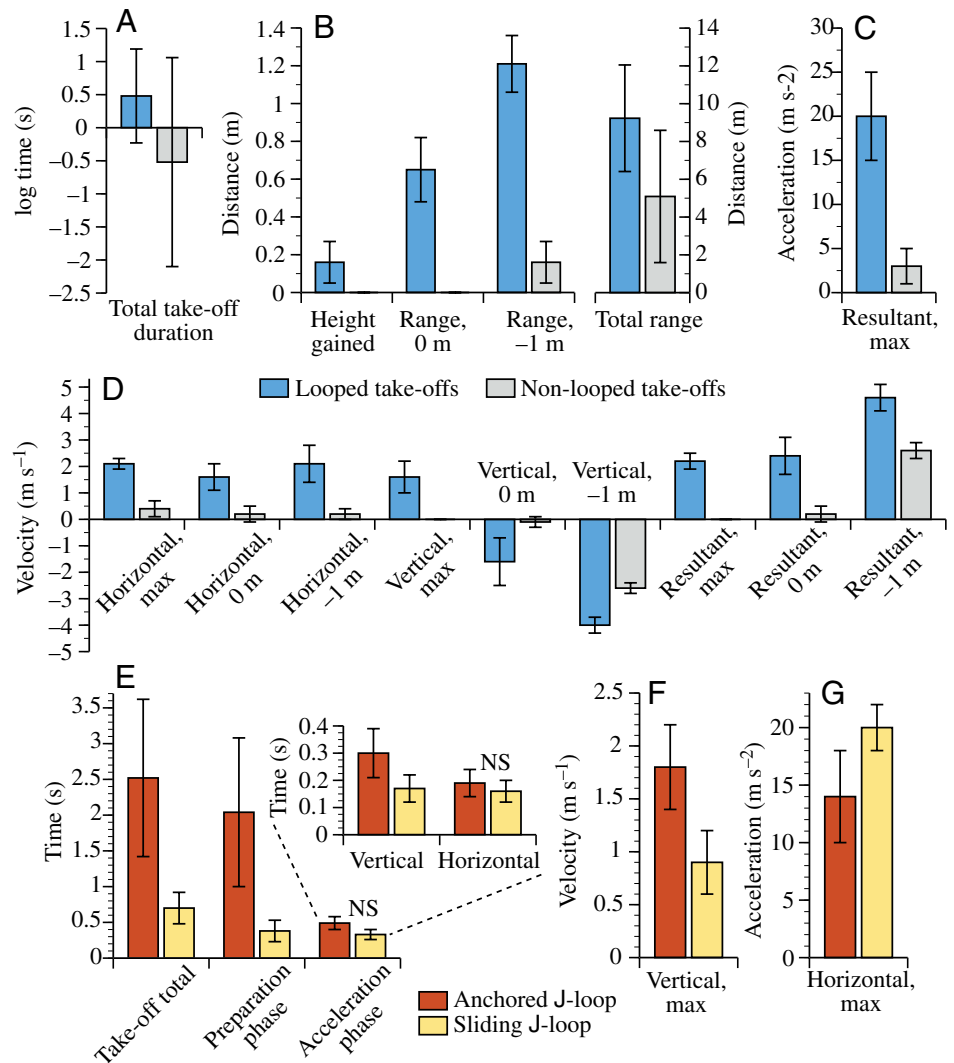


Fig. 7. Summary of performance comparisons. (A–D) Differences in looped take-offs (blue; $N=15$) vs non-looped take-offs (gray; $N=9$). (E–G) Differences in anchored J-loop take-offs (red; $N=11$) vs sliding J-loop take-offs (yellow; $N=4$). All comparisons are statistically significant except where noted by 'NS'.

Table 2. Summary statistics of comparisons among take-off types using one-way ANOVAs

	Looped vs non-looped take-offs			Anchored vs sliding loop take-offs			
	d.f.	F	P	d.f.	F	P	q*
Duration							
Take-off total (s)	22	4.4	0.05	13	10.3	0.008	2.18
Preparation (s)		N/A		13	25.8	0.0003	2.18
Acceleration total (s)		N/A		14	12.4	0.004	2.16
Vertical acceleration (s)		N/A		14	9.3	0.009	2.16
Horizontal acceleration (s)		N/A				NS	
Distance							
Height gained (BL)	23	17.9	0.0003			NS	
Range 0 (BL)	23	225.5	<0.0001			NS	
Range -1 (BL)	19	195.0	<0.0001			NS	
Total range (m)	20	9.8	0.0073			NS	
Velocity							
Horizontal, max (BL s ⁻¹)	23	83.2	<0.0001			NS	
Horizontal, 0 m (BL s ⁻¹)	22	36.3	<0.0001			NS	
Horizontal, -1 m (BL s ⁻¹)	17	40.1	<0.0001			NS	
Vertical, max (BL s ⁻¹)		N/A		14	14.3	0.002	2.16
Vertical, 0 m (BL s ⁻¹)	22	23.6	<0.0001			NS	
Vertical, -1 m (BL s ⁻¹)	17	15.9	0.001			NS	
Resultant, max (BL s ⁻¹)		N/A				NS	
Resultant, 0 m (BL s ⁻¹)	22	81.3	<0.0001			NS	
Resultant, -1 m (BL s ⁻¹)	17	26.0	0.0001			NS	
Acceleration							
Horizontal, max (BL s ⁻²)	23	41.8	<0.0001	23	25	<0.0001	2.80
Vertical, max (BL s ⁻²)		N/A				NS	
Resultant, max (BL s ⁻²)	23	65.0	<0.0001			NS	

N/A = Comparisons that were not valid; NS = not significant. Duration values were log transformed prior to testing.

branch and accelerated forward through the loop. Kardong and Bels observed this type of behavior in striking by the northern Pacific rattlesnake (*Crotalus viridis oregonus*) (Kardong and Bels, 1998). They noted that this strike is similar to lateral undulation on the ground in that the snake 'flows' through the loop, but differs in that the kinematically active region of the snake is not in contact with the substrate in a strike. In the side-loop take-off in *C. paradisi*, the active region was similarly not in contact with the substrate.

Although the kinematics of the looped take-off are different, the velocities and accelerations are similar to those of strikes in terrestrial snakes. Peak velocities (measured at the head) for a number of species have been reported: 1.5–3.5 m s⁻¹ for *Crotalus viridis* (Van Riper, 1954), 1.22–2.85 m s⁻¹ for *Pituophis* (Greenwald, 1974), 2.2 m s⁻¹ for *Vipera ammodytes* (Janoo and Gasc, 1992), 0.6–2.1 m s⁻¹ for *Elaphe obsoleta* (Alfaro, 2002; Alfaro, 2003) and 1.73 m s⁻¹ for *Thamnophis couchii* (Alfaro, 2002). The peak velocities obtained by *C. paradisi* in looped take-offs (1.8–2.6 m s⁻¹) fall within this range. Estimates of acceleration can be made from plots of velocity vs time (Janoo and Gasc, 1992), suggesting peak accelerations of 8, 34 and 73 m s⁻² for *Bitis nasicornis*, *Bitis gabonica* and *Vipera ammodytes*, respectively. The peak accelerations of *C. paradisi* ranged from 11 to 31 m s⁻², falling

within the range of strike performance (but maximum values are less than half of that in *Vipera ammodytes*). Body size should have strong effects on acceleration values, but this issue was not examined in the present study.

One other obvious comparison among snake locomotor movements is to the alleged jumping of the so-called 'jumping' snakes (e.g. *Atropoides nummifer*). Although the kinematics of these snakes are not well known, Campbell and Lamar (Campbell and Lamar, 1989) suggest that reports of jumping in these snakes is exaggerated, with 'jumping' likely a form of a strike in which the head travels only slightly more than one-half body length. Horned adders (*Bitis caudalis*) are also reported to use saltation during strikes and escape efforts (Greene, 1997), but their locomotion is similarly unstudied.

Ecological predictions of take-off usage in the wild

Although snakes in this study demonstrate a range of behaviors in an experimental setting, little is known about how snakes actually use take-off in the wild. The limits of performance amongst the four modes of take-off in *C. paradisi* reported here can be used to make inferences about the ecological usage of take-off in snakes. To assess which take-off would be most appropriate in various ecological scenarios,

differences in performance of each mode of take-off were used to form the following hypotheses.

To travel short distance between branches or trees, flying snakes use a looped take-off

For arboreal animals crossing small gaps between trees or branches, in cases where the gap is small it is likely to be temporally and energetically advantageous for the animal to cross the gap without first traveling to the ground (Caple et al., 1983). Based on values of height gained and range, looped take-offs are far more effective for crossing gaps than are non-looped take-offs. Only looped take-offs produced positive values for height gained and range level with the branch, and at 1 m below the branch, looped take-offs were eight times greater in range on average.

To travel long distances in the horizontal direction, flying snakes use a looped take-off

In order to maximize horizontal travel, a glider must do two things: it must minimize its glide angle (the angle between the glide path and the horizontal plane), and it must minimize the time spent in achieving that angle. Because lift is proportional to the square of the speed (Vogel, 1994), it is advantageous for a glider to reach its maximum speed as quickly as possible.

Based on values of velocity at a height of 1 m below the branch, looped take-offs were more effective than non-looped take-offs. Snakes using looped take-offs were moving about twice as fast vertically as snakes using non-looped take-offs, resulting from their greater effective take-off height in the jump. This difference is even more pronounced in the horizontal axis, with looped take-offs resulting in horizontal speeds 10 times greater than in non-looped take-offs on average. All else being equal, snakes using looped take-offs should generate lift quicker within the trajectory and should travel farther in the horizontal direction. This pattern was indeed observed; for each snake, the longest glides started with looped take-offs and the shortest trajectories started with non-looped take-offs.

To drop to a lower height, flying snakes use a non-looped take-off

When simply dropping (for example, to escape predation), slower falling results in lower impact forces upon landing, and therefore should reduce the chance of injury. In addition, an animal falling more slowly will have more time to make adjustments toward a more favorable landing orientation and location, if possible.

Unlike traveling short or long horizontal distances, in this case the non-looped take-offs are better; because they effectively have lower starting heights than the looped take-offs, they result in lower vertical speeds. But this difference is slight; vertical speeds are 1.5 times slower than in the looped take-offs 1 m below the branch. Furthermore, these differences only apply within the vertical space where the snake is

accelerating. Given sufficient height, snakes should reach terminal velocity, rendering irrelevant any differences in take-off behavior.

To escape predators or chase prey, flying snakes do not use an anchored J-loop take-off

When predators or potential prey are considered, arguments for 'best' are more complex. If the snake is being chased by a predator that cannot fly, then the quickest take-off may be best. If the predator can actively fly or if the snake is chasing a gliding prey, a take-off with some combination of short duration and high speed may be best. To catch a prey item that can actively fly, the snake's acceleration, height gained and range should matter.

Although the quickest take-off is the dive, the sliding J-loop take-off, with its combination of short duration, high acceleration, and positive height gained and range, is probably the most effective for escape or chase. Lack of head wagging during this take-off further suggests a role as a quick getaway. In comparison, the anchored J-loop take-off, with its long preparatory phase, is too slow to be considered effective for escape.

Conclusion

This study provides baseline knowledge of how flying snakes are able to become airborne from a horizontal perch. Evolutionarily, they have overcome the apparent limitations imposed by a lack of limbs to be able to jump into the air. Vertically looped take-offs in *Chrysopelea* are locomotor novelties, with no behavioral analogues among snakes. Many questions remain unanswered. For example, how do these snakes actually take off in the wild, and under what motivational contexts? Do kinematics differ between take-offs from horizontal and vertical substrates? To what extent do the physical characteristics of the branch (e.g. branch length, diameter, shape and stiffness) affect take-off performance? Take-off behaviors in *Chrysopelea* are well defined, and this system could provide a model system for testing hypotheses of form, function and ecology in relation to the evolution of aerial locomotion in gliding animals.

I thank the Zoological Gardens of Singapore staff for support, in particular W. H. Cheng, S. Chandran, S. Herbert, F. Lim and P. Martelli. T. O'Dempsey contributed greatly to the experimental setup that enabled this analysis. T. Chong, C. C. Kong, D. Lau, D. Lauw, K. Lim, N. Lim, W. Lim, Y. Lin, K. Su, K. Y. Tan, S. K. Tng, W. Toh, J. Wong, Y. Yatiman, T. K. Yen, J. Yeo, L. YeQiang, and F. Yuwono provided help with snake handling and equipment operation. I thank K. Lim, N. Sivasothi, T. H. Hui, S. Rashid and members of the P. Ng lab for logistical support. I thank R. Dudley, M. LaBarbera, J. McGuire, H. Voris, M. Westneat, and the University of Chicago Biomechanics Group for discussion and advice. C. Abraczinskas provided generous illustration advice. C. Diteresi provided help with digitization. R. Blob, R. Essner, A. Rice, B. Jayne and an anonymous reviewer provided

comments and critical reading of the manuscript. This work was supported by grants from the National Geographic Society, the Journal of Experimental Biology, the Explorers Club, Sigma Xi, the Hinds Fund and the Chicago Herpetological Society.

References

- Alexander, R. M.** (1991). Elastic mechanisms in primate locomotion. *Z. Morphol. Anthropol.* **78**, 315-320.
- Alfaro, M. E.** (2002). Forward attack modes of aquatic feeding garter snakes. *Funct. Ecol.* **16**, 204-215.
- Alfaro, M. E.** (2003). Sweeping and striking: a kinematic study of the trunk during prey capture in three thamnophiine snakes. *J. Exp. Biol.* **206**, 2381-2392.
- Bishop, K. L.** (2006). The relationship between 3-D kinematics and gliding performance in the southern flying squirrel, *Glaucomys volans*. *J. Exp. Biol.* **209**, 689-701.
- Bonser, R. and Rayner, J.** (1996). Measuring leg thrust forces in the common starling. *J. Exp. Biol.* **199**, 435-439.
- Campbell, J. A. and Lamar, W. W.** (1989). *The Venomous Reptiles of Latin America*. Ithaca: Cornell University Press.
- Caple, G., Balda, R. P. and Willis, W. R.** (1983). The physics of leaping animals and the evolution of preflight. *Am. Nat.* **121**, 455-476.
- Drummond, H.** (1983). Aquatic foraging in garter snakes: a comparison of specialists and generalists. *Behaviour* **86**, 1-30.
- Earls, K. D.** (2000). Kinematics and mechanics of ground take-off in the starling *Sturnis vulgaris* and the quail *Coturnix coturnix*. *J. Exp. Biol.* **203**, 725-739.
- Emerson, S. B.** (1985). Jumping and leaping. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem and D. B. Wake), pp. 58-72. London: Belknap Press.
- Essner, R. L.** (2002). Three-dimensional launch kinematics in leaping, parachuting and gliding squirrels. *J. Exp. Biol.* **205**, 2469-2477.
- Flower, S. S.** (1899). Notes on a second collection of reptiles made in the Malay Peninsula and Siam, from November 1896 to September 1898, with a list of the species recorded from those countries. *Proc. Zool. Soc. Lond.* **16**, 682-685.
- Greene, H. W.** (1997). *Snakes: The Evolution of Mystery in Nature*. Berkeley: University of California Press.
- Greenwald, O. E.** (1974). Thermal dependence of striking and prey capture by gopher snakes. *Copeia* **1974**, 141-148.
- Halloy, M. and Burghardt, G. M.** (1990). Ontogeny of fish capture and ingestion in four species of garter snakes (*Thamnophis*). *Behaviour* **112**, 299-318.
- Heppner, F. H. and Anderson, J. G. T.** (1985). Leg thrust important in flight take-off in the pigeon. *J. Exp. Biol.* **114**, 285-288.
- Jackson, S. M.** (1999). Glide angle in the genus *Petaurus* and a review of gliding in mammals. *Mamm. Rev.* **30**, 9-30.
- Janoo, A. and Gasc, J.-P.** (1992). High speed motion analysis of the predatory strike and fluorographic study of oesophageal deglutition in *Vipera ammodytes*: more than meets the eye. *Amphib-Reptil.* **13**, 315-325.
- Jayne, B. C., Voris, H. K. and Kiew, B. H.** (1988). Diet, feeding behavior, growth, and numbers of a population of *Cerberus rynchops* (Serpentes: Homalopsinae) in Malaysia. *Fieldiana Zool. New Ser.* **50**, 1-15.
- Kardong, K. V. and Bels, V. L.** (1998). Rattlesnake strike behavior: kinematics. *J. Exp. Biol.* **201**, 837-850.
- Keith, M. M., Scheibe, J. S. and Hendershott, A. J.** (2000). Launch dynamics in *Glaucomys volans*. In *Biology of Gliding Mammals* (ed. R. L. Goldingay and J. S. Scheibe), pp. 185-198. Furth: Filander Verlag.
- Kral, K.** (1998). Side-to-side head movements to obtain motion depth cues: a short review of research on the praying mantis. *Behav. Proc.* **43**, 71-77.
- Mundkur, T.** (1978). A note on reproduction in the flying snake *Chrysopelea ornata* (Shaw). *J. Bombay Nat. Hist. Soc.* **75**, 854-859.
- Nowak, R. M.** (1999). *Walker's Mammals of the World*. Baltimore: Johns Hopkins University Press.
- Savitzky, B. A. C.** (1992). Laboratory studies on piscivory in an opportunistic predator. In *Biology of the Pitvipers* (ed. J. A. Campbell and E. D. J. Brodie), pp. 347-368. Tyler, TX: Selva.
- Shelford, M. A.** (1906). A note on 'flying' snakes. *Proc. Zool. Soc. Lond.* **1**, 227-230.
- Socha, J. J.** (2002a). Gliding flight in the paradise tree snake. *Nature* **418**, 603-604.
- Socha, J. J.** (2002b). The biomechanics of flight in snakes. PhD thesis, University of Chicago, IL, USA.
- Socha, J. J. and LaBarbera, M.** (2005). Effects of size and behavior on aerial performance of two species of flying snakes (*Chrysopelea*). *J. Exp. Biol.* **208**, 1835-1847.
- Socha, J. J., O'Dempsey, T. and LaBarbera, M.** (2005). A 3-D kinematic analysis of gliding in a flying snake, *Chrysopelea paradisi*. *J. Exp. Biol.* **208**, 1817-1833.
- Tobalske, B. W., Altshuler, D. L. and Powers, D. R.** (2004). Take-off mechanics in hummingbirds (Trochilidae). *J. Exp. Biol.* **207**, 1345-1352.
- Tweedie, M. W. F.** (1960). The Malayan gliding reptiles. *Proc. South London Entomol. Nat. Hist. Soc.* **1959**, 97-103.
- Van Riper, W.** (1954). Measuring the speed of a rattlesnake's strike. *Animal Kingdom* **57**, 50-53.
- Vaughn-Arbuckle, K. H.** (1959). Flying snakes. *J. Bombay Nat. Hist. Soc.* **56**, 640-642.
- Vogel, S.** (1994). *Life in Moving Fluids*. Princeton: Princeton University Press.
- Voris, H. K., Voris, H. H. and Liat, L. B.** (1978). The food and feeding behavior of a marine snake, *Enhydrina schistosa* (Hydrophiidae). *Copeia* **1978**, 134-146.
- Walker, J. A.** (1997). *QuickSAND. Quick Smoothing and Numerical Differentiation for the Power Macintosh*.
- Walker, J. A.** (1998). Estimating velocities and accelerations of animal locomotion: a simulation experiment comparing numerical differentiation algorithms. *J. Exp. Biol.* **201**, 981-995.
- Walker, J. A.** (2001). *QuickImage. A modification of NIH Image with Enhanced Digitizing Tools*.
- Whitaker, P. B., Ellis, K. and Shine, R.** (2000). The defensive strike of the Eastern Brownsnake, *Pseudonaja textilis* (Elapidae). *Funct. Ecol.* **14**, 25-31.