Effects of size and behavior on aerial performance of two species of flying snakes (*Chrysopelea*)

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Summary

Aerial locomotion in snakes (genus *Chrysopelea*) is kinematically distinct from any other type of gliding or powered flight, with prominent, high amplitude body undulations visually dominating the behavior. Because it is not known how flying snakes produce aerodynamic forces in flight, the factors that determine snake flight performance are not clear. In this study, the effects of size and behavior on aerial performance were examined both within a species (*C. paradisi*) and between two species (*C. paradisi* and *C. ornata*), using stepwise multiple regressions to identify relevant variables. Smaller *C. paradisi* traveled farther than larger snakes at lower sinking speeds, with trajectories that shallowed more quickly and reached lower minimum glide angles. Although wing loading increased faster than expected for isometric size increase, wing loading *per se* was not responsible for performance differences between large and small snakes. Snakes with higher interactions between relative undulation amplitude and body size transitioned out of the initial acceleration phase at higher airspeeds and sinking speeds, and attained higher maximum airspeeds and horizontal speeds; snakes that used higher average relative amplitudes transitioned out of the initial acceleration phase at higher horizontal speeds. Undulation frequency was not significantly related to any performance variable within *C. paradisi* and was not significantly different between the two species, suggesting that this variable (in contrast to relative undulation amplitude) may have a minor influence on the aerodynamic mechanism of force production in snake flight. *C. paradisi* and *C. ornata* differed significantly in most performance comparisons. *C. ornata* were more massive than *C. paradisi* at any given body length and in general exhibited poorer gliding performance than *C. paradisi*. This study contributes towards understanding how an unconventional body form and kinematics can produce a novel mode of aerial locomotion in a vertebrate glider.

Introduction

Gliding flight in snakes is kinematically distinct from gliding and powered flight in other animals and man-made aircraft (Socha, 2002b; Socha et al., 2005). Generally, most gliders use a fixed wing or wings to generate lift. Powered flyers generate aerodynamic forces either through wing oscillation (flapping), jetting or rotating. In stark contrast, when flying snakes (*Chrysopelea*) move through the air, they pass lateral traveling waves posteriorly along a long, dorsoventrally flattened body. When a flying snake takes to the air, it becomes a 'wing' that constantly reconfigures throughout flight, moving in a complex motion in three dimensions. Thus, not only do flying snakes possess a unique body shape among flying and gliding animals, but their aerial behavior is the most dynamic of any vertebrate glider. Given this combination of morphology and behavior, it is unclear to what extent predictions of flight performance based on simple aerodynamic expectations conform to actual snake gliding performance.

Basic aspects of aerial locomotion have been described for adult individuals of the paradise tree snake, *Chrysopelea paradisi* (Socha, 2002b; Socha et al., 2005). *C. paradisi* usually begin aerial locomotion with a jumping takeoff. A short jump up and away from the branch is followed by a 1–5 m ballistic dive in which the snake travels at an angle of 52–62° relative to the horizon. During this dive, the snake's body rotates from a nose-up to a nose-down position, and it begins to undulate, with the waves originating at or near the head. The snake takes on a wide 'S' shape (in plan view) in fully developed aerial undulation, with low frequency (1–2 Hz), high-amplitude (wave heights, 20–34% SVL) traveling waves that differ in shape from undulations used during terrestrial and aquatic locomotion in this species. As the snake falls, its speed increases linearly with time until it either transitions to a steady speed, or the rate of increase falls dramatically. Concurrently, the snake's trajectory shallows; the

glide angle (defined relative to the horizon) decreases and the glide path becomes more horizontal. During this shallowing phase of the glide, the snake undulates in a plane tilted upward towards the head at approximately 20–40° to the direction of forward movement; the posterior body translates substantially in the vertical axis. These data indicate that several aspects of flight behavior show moderate to substantial variability. However, because of the unusual morphology and flight dynamics of *C. paradisi*, it is unclear if and how variation in these parameters affects gliding performance.

The aerial snake's constantly changing body orientation should have profound consequences for its aerodynamic force production and stability. The snake's aerodynamic force production is a function of the geometry of its individual segments. Each segment's cross sectional shape, angle of attack, and position relative to the other segments will influence the net aerodynamic force vector. It is therefore likely that the magnitude, direction and location of this force changes as the snake's body constantly reconfigures while gliding. Similarly, stability is determined by the relative locations of the net aerodynamic force vector and the weight vector. The center of gravity is a function of the spatial distribution of mass; because the snake's body continuously reconfigures in three dimensions, its center of gravity also must shift continuously.

Consequently, the shifting of the center of gravity and center of pressure (the location of the net aerodynamic force vector) should influence the snake's kinematics. For example, when the tail swings downward in the undulatory cycle, the angle of attack of the posterior segment may differ from that of the anterior. With the anterior segment in a more horizontal posture, the difference in magnitude and direction of the forces acting on the anterior and posterior segments of the snake may create a moment that rotates the snake about the pitching axis. If this posture results in less lift on the snake as a whole, the glide angle may momentarily increase or the shallowing rate may decrease, with velocity changing in kind.

In addition to variability in flight behavior, flying snakes also exhibit variation in body size and shape among different species and through ontogeny. In addition to becoming less flattened during flight than *C. paradisi* (Socha, 2002a), *C. ornata* reaches larger body size in both length and mass (Mertens, 1968). Body size has pervasive effects on organismal function (Schmidt-Nielson, 1984), and scaling effects on flight performance have been shown in gliding lizards, one of the few gliders in which flight trajectories have received detailed study (McGuire, 1998). Therefore, in addition to effects of flight behavior, the potential effects of size and shape on flight performance also deserve attention in *Chrysopelea*.

For gliders that operate at moderate Reynolds numbers (which encompasses most animal gliders), *a priori* predictions can be made regarding the scaling of some glide performance parameters. At glide equilibrium, by definition the net aerodynamic force (the vector sum of the lift and drag) is equal to the glider's weight. Lift and drag, in turn, are both proportional to some characteristic area multiplied by the square of speed. Therefore,

$$M\boldsymbol{g} \alpha S U^2 , \qquad (1)$$

where M is mass, $\boldsymbol{g}$ is acceleration due to gravity, S is area and U is speed. Rearranging and recognizing that weight divided by area defines wing loading (WL), gives the following:

$$U \alpha \sqrt{WL} . \qquad (2)$$

Dimensional analysis of this expression predicts that gliding speed should vary as a function of body length or mass:

$$U \alpha \sqrt{l} , \qquad (3)$$

$$U \alpha M^{1/6} , \qquad (4)$$

where l is body length and M is mass. Therefore a glider with greater length, mass, or wing loading is predicted to require a higher speed at glide equilibrium. Because lift and drag both increase proportionally with speed squared, the lift-to-drag ratio should remain constant. The lift-to-drag ratio determines glide angle and, therefore, gliders of the same geometry but different size are theoretically capable of traveling at equal glide angles (Vogel, 1994). Thus, glide speed might be expected to increase, and glide angle remain constant, if body size increases isometrically in flying snakes.

A complicating factor in such analyses is that much (and sometimes all) of a glider's trajectory may not be at equilibrium. The ballistic dive and shallowing glide phases (Fig. 1) of a trajectory are by definition non-equilibrium; it is unclear how size should affect performance during these portions of a snake's glide trajectory, given the snake's complex postural changes. It is also possible that the snake may actively choose to employ non-equilibrium gliding, even given sufficient takeoff height to reach equilibrium. For example, a snake might maximize takeoff speed for escape, with overall horizontal distance traveled unimportant, or it might maximize maneuverability to avoid collisions with obstructions. Such variation is possible only if the snake is able to modulate behavior to control performance.

Thus, active behavioral modulation is a second major consideration in the analysis of gliding flight performance. Animal gliders have been traditionally viewed as 'static' or 'passive' flyers, implying rigidly held postures similar to those of man-made gliding craft (from paper airplanes to sailplanes). However, animal gliders can manipulate the size, shape and orientation of their body and wings, and these behavioral adjustments can alter simple size dependencies of flight parameters. For example, flying squirrels pitch nose-up prior to landing by increasing the camber of the patagium to effect stall (Scholey, 1986); flying lizards may use similar fine adjustments of their rib-reinforced 'wings' (McGuire, 1998). Active and continuous movement stands out as a hallmark of aerial locomotion in *Chrysopelea*, suggesting that behavior features prominently in determining performance. However,

unlike other gliders that can effectively change the size and shape of their 'wings', flying snakes have no obvious morphological control surfaces. Instead, whole body movements – frequency, amplitude and orientation of body waves – may be used by the snake to control flight speed, direction or orientation. In most other animals that locomote using undulation, posteriorly directed waves propel the animal forwards (Gray, 1968). Alternatively, these behaviors may simply be a performance-neutral vestige of lateral undulation (the most prominent locomotor mode in snakes; Pough et al., 2001), in the context of movement through a different medium (air).

In this study, we empirically test the effects of size and behavior on gliding performance in flying snakes. We examine size effects by measuring flight performance in different ontogenetic stages of *C. paradisi*, and by comparing the performance of *C. paradisi* to that of *C. ornata*, which reaches larger adult sizes than *C. paradisi*. Using data from these snakes, we also test two hypotheses of behavioral effects of undulation on the gliding performance in snakes. (1) The rate of undulation affects aerodynamic forces. Specifically, we test the prediction that snakes that use higher undulation frequencies generate more lift and glide farther than those with lower undulation frequencies. (2) The amplitude of undulation affects aerodynamic forces. Specifically, we test whether snakes that use greater amplitudes of undulation (a wider 'S', in effect) generate more lift and hence travel farther than do snakes with smaller amplitudes. Together, these comparisons will contribute substantially to the understanding of how a highly non-standard body form can be used for aerial locomotion.

Materials and methods

Animals

Gliding performance data were collected from a series of 20 *C. paradisi* Boie caught wild in Singapore, and eight *C. ornata* Shaw, including two caught wild in Thailand and six captive. The captive *C. ornata* were purchased from a commercial supplier (Glades Herp, Inc., Bushnell, FL, USA); although of unknown origin, *Chrysopelea* species are rarely bred in captivity and, therefore, these animals were likely also wild-caught. Individuals from the two species overlapped in size; *C. paradisi* and *C. ornata*, respectively, ranged from 3.0–82.7 g and 43.0–158.3 g in mass, and from 31.0–86.5 cm and 62.0–92.0 cm in snout–vent length (SVL). These sizes represent a series from young juvenile to adult for *C. paradisi*. Larger individuals were available for *C. ornata* because it reaches the largest adult size of the five species of *Chrysopelea* (Mertens, 1968). Animal care and experimental procedures were approved by the University of Chicago Animal Care and Use Committee (IACUC #70963), Singapore Zoological Gardens and the Thailand National Research Council.

Performance trials

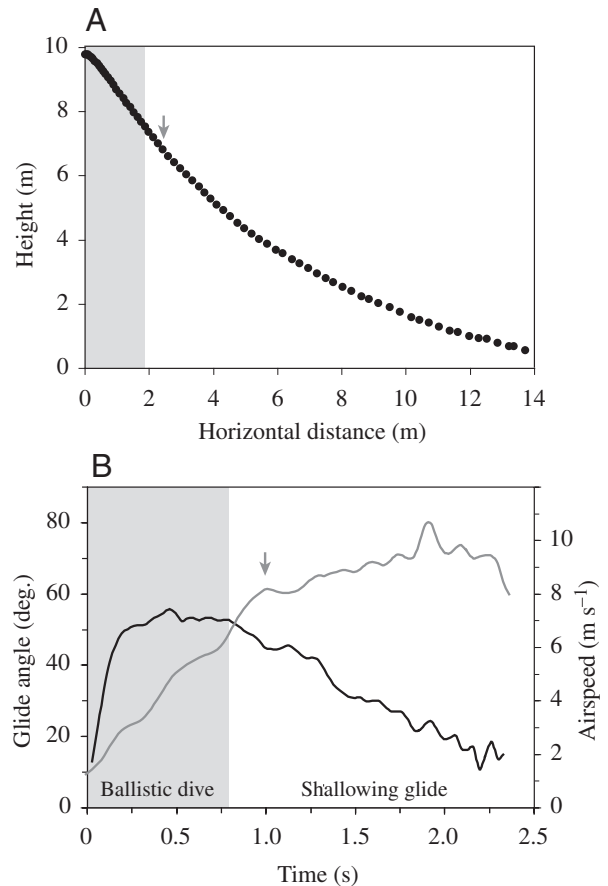Snakes were manually placed on a horizontal branch at the

Fig. 1. Definitions of trajectory variables. Data from a single snake (*C. paradisi*, mass=27 g, SVL=63 cm) are shown to illustrate features of a snake glide trajectory. Filled circles represent the snake's midpoint throughout its trajectory, as seen in lateral projection (A). The black and grey lines (B) represent the snake's glide angle and airspeed, respectively, through time. By definition, the ballistic dive (grey background) ends and the shallowing glide (white background) begins at the point when glide angle begins to decline. The grey arrow represents the transition in airspeed from initial acceleration to a steady speed or lower rate of acceleration. (Adapted from Socha et al., 2005.)

top of a scaffolding tower and were allowed to aerially descend to a grassy field below (see Movies 1–4 in supplementary material). Digital videocameras and 35 mm SLR cameras were used to record various aspects of the aerial locomotion. Snakes were marked on the dorsal surface with 1 cm bands of non-toxic white paint (Wite-Out, Bic Corporation, Milford, CT, USA) at the head-body junction, midpoint and vent. All trials were conducted under similar ambient conditions (temperatures from 25–32°C, humidity 50–70%). Wind speed was measured with a Kestrel 2000 digital anemometer (Nielsen-Kellerman, PA, USA) at the top of the tower. For most trials there was no noticeable wind; the maximum recorded wind speed was less than 0.5 m s⁻¹.

Two different methods were used to record performance in the two species. *C. ornata* trials were conducted first, in two different locales – on the Prince of Songklha University

campus in Hat Yai, Thailand from a height of 8.87 m, and in an open field in Lockport, Illinois from heights of 7.3–8.3 m. One videocamera (Sony DCR-TRV900, Tokyo, Japan) was placed to the side to record a lateral view of the snake's trajectory, and a second videocamera was placed at the top of the tower to record an overhead view. Video records from the overhead camera were used to determine frequency of undulation and to observe the orientation of the trajectory; only trials in which the snake moved perpendicularly to the lateral view camera were used for analysis. The lateral view video records were used to reconstruct the path of the snake in two dimensions. Video records were transferred at highest quality to a Macintosh G4 computer *via* Firewire (IEEE 1394) using Adobe Premiere (version 6.0) software, with a raw image size of 720×480 pixels. Video sequences were deinterlaced using NIH Image software (version 1.62, National Institutes of Health, Bethesda, Maryland), yielding a sampling frequency of 60 Hz. In each sequence, the position of the snake was digitized using QuickImage (Walker, 2001), a modified version of NIH Image. Because the snake was small relative to the size of the frame, the three landmarks could not be seen consistently from frame to frame. Instead, the midpoint was digitized by either directly digitizing the midpoint landmark (where visible) or by visually estimating the location of the middle of the snake. The two-dimensional midpoint coordinates were smoothed with a Lanczos five-point moving regression using QuickSAND software (Walker, 1997).

Instantaneous glide angle was calculated as the angle between the horizon and a least-squares fit line of three temporally consecutive midpoint coordinates. Speeds were calculated by taking the first derivative of the position data in QuickSAND. Error due to visual estimation of the midpoint of the snake led to apparent fluctuations of about 5° in glide angle and about 1 m s^{-1} in gliding speed. Trends in glide angle and speed were identified by visually fitting a curve to coincide with the midpoint of these fluctuations. Over 200 trials were recorded from *C. ornata*; data from eight trials (representing eight snakes) were selected for analysis based on the quality and completeness of the video records.

A more precise data collection method, stereo photogrammetry using videocameras, was used to obtain 3-D trajectory coordinates from *C. paradisi* trials (Socha et al., 2005). Snakes were launched from a height of 9.62 m in an open field at the Singapore Zoological Gardens in Singapore. Two digital videocameras (Sony DCR-TRV900) recorded the trajectories in stereo from the top of the tower. Videocameras were synchronized by matching short-duration, high-amplitude peaks in the audio signals. Better resolution (relative to the *C. ornata* footage) permitted direct digitization of the marked bands on the snake. The 3-D coordinates of the head, midpoint and vent landmarks were reconstructed at 30 Hz using ERDAS Imagine with Orthobase software (version 8.4; Leica Geosystems GIS and Mapping, LLC, Atlanta, USA). The mean RMS coordinate error ranged from 1–14 cm, with error increasing as the trajectory progressed. A total of 237 trials was recorded; data from 20 trials (representing 20 snakes) were used for inter-individual comparisons, and nine trials (representing two snakes) were used for preliminary intra-individual analyses. See Socha et al. (2005) for details of this protocol and analysis.

Variables

The size and behavior variables quantified for analysis are given in Table 1. Snout–vent length, mass, projected area, wing loading and the square-root of wing loading were used as metrics of size. The projected area of the entire snake, measured from photographs of the snake's ventral silhouette in mid-trajectory, was used to calculate wing loading. Mid-flight photographs were needed for these calculations because airborne *Chrysopelea* have a different cross-sectional shape relative to their non-flight configuration.

Two aspects of aerial behavior were quantified – the frequency and the lateral amplitude of the snake's aerial undulation. Undulation frequency was calculated as the inverse of the period of one undulatory cycle, either calculated from the reconstructed 3-D data of the head's side-to-side movement (*C. paradisi*) or estimated directly from the video records by visually identifying the lateral-most extent of the midpoint throughout its cycle (*C. ornata*). The two methods were tested for consistency using the *C. paradisi* records and found to produce indistinguishable results. Because no single amplitude metric was obviously superior, three measures of amplitude were used – the undulation wave heights of the head, the vent and their average. Undulation wave height was measured as the maximum lateral separation (based on the direction of forward travel) between the landmark and the midpoint, and represents a proxy for the width of the snake's traveling waves (see Socha et al., 2005). (For the reader's benefit, hereafter the term 'amplitude' will be used in place of 'wave height'. Strictly, amplitude values are one-half of wave height values.)

Table 1. *Size and behavior variables*

Size
Mass (g)
Snout–vent length (cm)
Projected area (cm^2)
Wing loading (N m^{-2})
Square root of wing loading (N$^{0.5}$ m^{-1})
Behavior
Undulation frequency (Hz)
Amplitude, head (cm or %)
Amplitude, vent (cm or %)
Amplitude, average (cm or %)
Freq. (Hz) × Amplitude, head (cm or %)
Freq. (Hz) × Amplitude, vent (cm or %)
Freq. (Hz) × Amplitude, average (cm or %)
Behavior by size
Freq × SVL
Amplitude, head (%) × SVL (cm)
Amplitude, vent (%) × SVL (cm)
Amplitude, average (%) × SVL (cm)

Amplitude data were also normalized by snout–vent length to create dimensionless measures of amplitude. Amplitude data for *C. ornata* are not available because only 2-D trajectory data were recorded for this species, and it was not possible to measure side-to-side excursion of the snake from the single overhead view with sufficient accuracy. For *C. paradisi*, the possibility of an interactive effect of frequency and amplitude was explored by defining six interaction effect variables – the amplitudes (absolute and relative) of the head and vent separately, and the average amplitude (absolute and relative) of the head and vent, each multiplied by the undulation frequency. Furthermore, to test for effects of interactions between size and behavior, each relative amplitude variable and frequency were separately multiplied by snout–vent length to create four behavior by size interaction variables.

Because it is not known how *Chrysopelea* uses aerial locomotion in the wild (e.g. to traverse short gaps or to travel long distances), multiple measures of performance were analyzed. Seven variables associated with the beginning of the trajectory were considered – the airspeed at takeoff, the ballistic dive angle (the maximum glide angle during the dive; the larger the angle, the more vertical the dive), the ballistic dive depth (the vertical travel of the dive), the ballistic dive time, and the acceleration in the initial (pre-transition; see Fig. 1) phase of the trajectory. Assuming equal performance in the shallowing phase, snakes that use a smaller ballistic dive angle or a smaller ballistic dive depth should travel farther horizontally. Twelve variables associated with the shallowing glide phase of the trajectory were considered. These include the speed and time at transition; the shallowing rate (the rate of change of glide angle

during the shallowing phase of the trajectory); the maximum speed and minimum glide angle achieved; and total horizontal distance traveled. Because the snakes' trajectories were still shallowing when they exited the view of the cameras or landed (Socha et al., 2005), the minimum observed glide angle was not an equilibrium glide angle (which defines the absolute minimum glide angle obtainable in still air at a given speed). To compare minimum glide angle in trajectories of different length and video recording coverage, the minimum glide angle was defined at the lowest common vertical height for all snakes, 7 m below the starting height. Detailed definitions of these performance variables can be found in Socha et al. (2005).

Data selection criteria

Because this study is concerned with the upper limits of performance, only data from the 'best' trajectories were used, where 'best' is defined as the trial with adequate video records in which the snake traveled the greatest horizontal distance. We attempted to minimize the effect of motivation on performance by recording as many trials as possible and by using the same stimulus protocol for each snake. Because the path of the snake in its 'best' trial did not always coincide with the region of overlap in the views of the two videocameras, some variables in certain trials were undetermined. For the two intra-individual analyses, all digitizable trials (regardless of horizontal distance traveled) were examined.

Statistical analyses

To separate the effects of size and behavior on *C. paradisi* flight performance, a multiple regression was performed on each

Table 2. *Results of stepwise multiple regressions on performance variables in* C. paradisi

Performance variable	Predictor	d.f.	r^2	'F-ratio'	'Prob>F'
Airspeed at takeoff[†]	None	–	–	–	–
Ballistic dive angle[†]	None	–	–	–	–
Ballistic dive time[†]	None	–	–	–	–
Ballistic dive depth[†]	None	–	–	–	–
Forward acceleration, initial	None	–	–	–	–
Sinking acceleration, initial	None	–	–	–	–
Horizontal acceleration, initial	None	–	–	–	–
Time at airspeed transition	None	–	–	–	–
Time at sinking speed transition	None	–	–	–	–
Time at horizontal speed transition	None	–	–	–	–
Airspeed at transition	Vent amp. (%) × SVL	7	0.794	26.90	0.001
Sinking speed at transition	Average amp. (%) × SVL	7	0.843	37.49	0.001
Horizontal speed at transition	Average amp. (%)	4	0.811	14.95	0.018
Airspeed, maximum	Vent amp. (%) × SVL	8	0.757	24.86	0.001
Sinking speed, maximum	SVL	8	0.815	35.30	0.000
Horizontal speed, maximum	Vent amp. (%) × SVL	8	0.675	16.64	0.004
Shallowing rate	SVL	7	0.795	27.18	0.001
Glide angle, mininum	Mass	8	0.697	18.42	0.003
Horizontal distance traveled	SVL	14	0.797	16.03	0.001

Each size, behavior and interaction variable was included in the analysis, except for variables indicated with [†]. 'Amp.' refers to amplitude. For each significant regression, only one predictor variable was retained in the final model. The F-ratio and significance levels are in quotation marks because they are not true F-statistics; no F-distribution was used.

performance variable using all size, behavior and interaction variables as possible predictors. The goal of this exploratory analysis was to eliminate spurious correlations and only include variables that significantly contribute to the overall performance variation. Because there were no *a priori* reasons to exclude any size, behavior, or interaction variable prior to analysis, a stepwise regression technique was employed (Sokal and Rohlf, 1995). Variables entered the model at a probability of 0.25 ('*P*-to-enter') and were removed at a probability of 0.10 ('*P*-to-remove'). For regressions on airspeed at takeoff and ballistic dive performance variables, behavioral variables were not included because, within this early stage of the trajectory, aerial undulation was not fully developed. After the winnowing of variables *via* multiple regression, each significant predictor was regressed on its associated performance variable to determine the direction and strength of trends. All statistical analyses were conducted using JMP statistical software (version 5.0, SAS Institute, Cary, NC, USA).

To test the effects of behavior on performance independent of size, we conducted the same multiple regression tests on multiple trials within an individual. Because sufficient data were only available from two snakes (four and five trials each), results from these tests should be regarded as preliminary.

To evaluate the hypotheses of performance variable scaling among individuals, airspeed and minimum glide angle were regressed on wing loading, snout–vent length, and body mass using reduced major-axis (RMA) regressions (LaBarbera, 1989; Rayner, 1985). Ninety-five percent confidence intervals of the slopes were estimated using bootstrap standard errors (10,000 bootstrap replicates; analyses performed using a custom Hi-Q program written by M.L.). To evaluate the scaling of basic morphological features, a permutation test with was used to compare the RMA slopes and intercepts of the snout–vent length/mass regressions for each species (2000 replicates; analyses performed using a custom Hi-Q program written by M.L.). All data were log-transformed prior to analysis.

Student's *t*-tests were used to compare behavior and performance between *C. paradisi* and *C. ornata*. To accommodate different launch heights for the two species, horizontal distance traveled was measured after the snake reached at a common vertical drop 7.5 m below the takeoff branch. Note that this is a different standard than that used to determine a common point for glide angle within *C. paradisi*. Some performance variables were not compared between species due to lack of sufficient data for *C. ornata*.

Results

Intraspecific comparisons

For nine performance variables, each stepwise multiple regression reduced to a single predictor variable in *C. paradisi* (Table 2). A size variable was the best predictor for four performance variables: snout–vent length for shallowing rate, maximum sinking speed, and horizontal distance traveled, and mass for minimum glide angle. A behavior variable was the best predictor for one performance variable: average relative

amplitude for horizontal speed at transition. The remaining four performance variables were related to a behavior by size interaction variable: vent relative amplitude by snout–vent length for airspeed at transition, airspeed maximum and horizontal speed maximum, and average relative amplitude by snout–vent length for sinking speed at transition. No undulation frequency by amplitude or by size interaction variable was significantly associated with any performance variable. Projected area, wing loading, and square root of wing loading also were not significantly associated with any performance variable. For 10 of the 19 performance variables examined (all associated with the early portion of the trajectory), the stepwise regression did not produce a significant model.

Each significant size and behavior predictor was regressed on its associated performance variable. Maximum sinking speed and minimum glide angle were directly proportional to snout–vent length and mass, respectively; shallowing rate and horizontal distance traveled were indirectly proportional to snout–vent length (Fig. 2). Thus smaller snakes traveled farther than larger snakes (Fig. 2A), with trajectories that shallowed more quickly (Fig. 2B), and reached lower minimum glide angles (Fig. 2C) and lower maximum sinking speeds (Fig. 2D). Airspeed at transition, maximum airspeed and maximum horizontal speed were directly proportional to the interaction of vent relative amplitude by snout–vent length; sinking speed at transition was directly proportional to the interaction of average relative amplitude by snout–vent length, and horizontal speed at transition was directly proportional to average relative amplitude (Fig. 3). Thus snakes with higher interactions between relative amplitude and body size transitioned out of the initial acceleration at higher airspeeds (Fig. 3A) and sinking speeds (Fig. 3B), and attained higher maximum airspeeds (Fig. 3C) and horizontal speeds (Fig. 3D). Snakes that used higher average relative amplitudes transitioned out of the initial acceleration at higher horizontal speeds (Fig. 3E).

Within individuals, there were few consistent trends (Table 3). For the most part, performance variables that yielded significant predictors were not congruent either between the two individuals or in comparison with the inter-individual data. However, both maximum airspeed and horizontal speed included vent relative amplitude (either alone or interacting with another variable) as a consistent predictor between the individual and inter-individual data. In contrast to the inter-individual analysis, undulation frequency figured prominently as a predictor for five of nine performance variables. For one individual, using lower undulation frequencies yielded longer trajectories.

In scaling of performance comparisons, RMA slopes for snout–vent length *vs* airspeed (equation 3) and mass *vs* airspeed (equation 4) were not significantly different from those expected under isometry, whereas the slope of wing loading *vs* airspeed (equation 2) was significantly different (Table 4). The RMA regressions for each size variable on minimum glide angle were significantly different from zero,
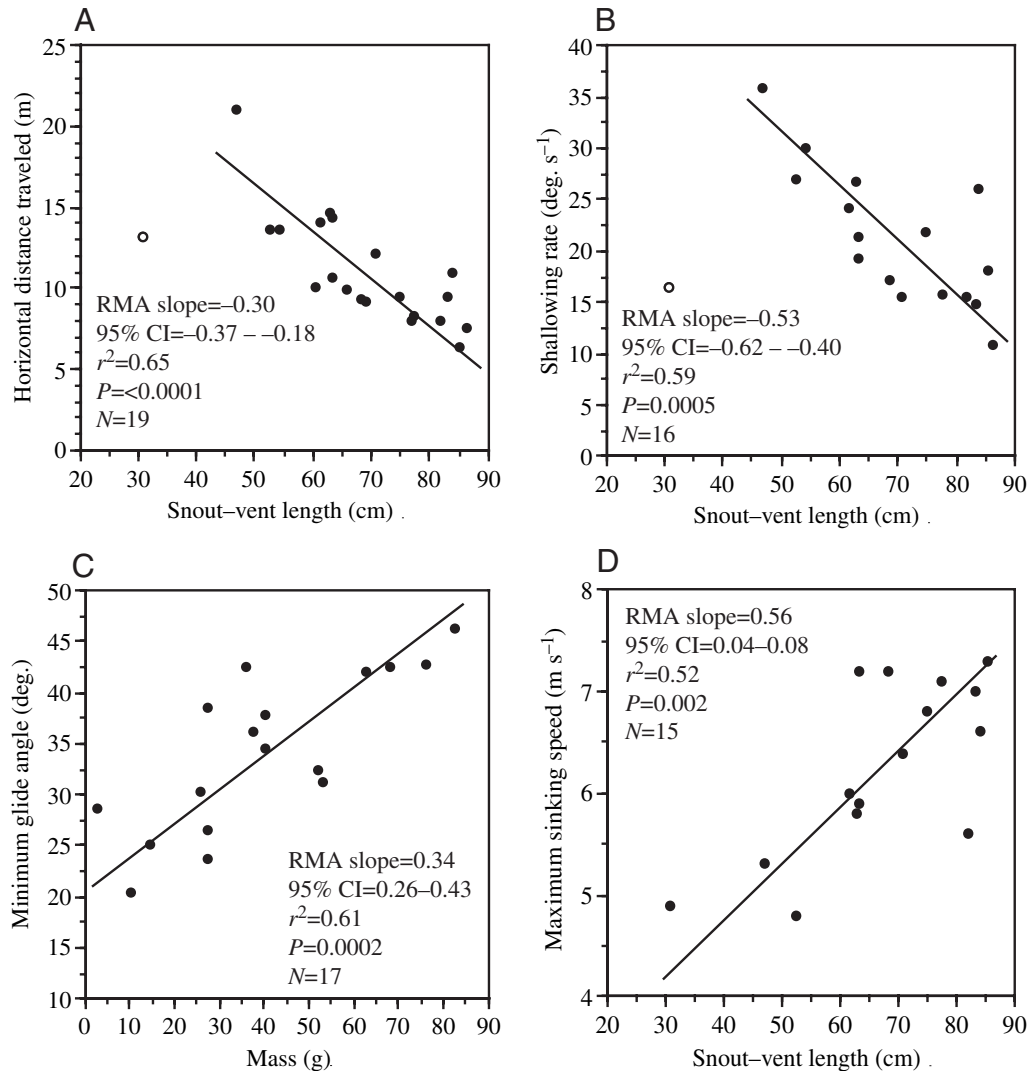
Fig. 2. Significant correlations between performance and size variables in *C. paradisi*. RMA regression lines and associated statistics are shown for each relationship. Horizontal distance traveled (A) and shallowing rate (B) were indirectly proportional to snout–vent length, and minimum glide angle (C) and maximum sinking speed (D) were directly proportional to mass and snout–vent length, respectively. In A and B, the young juvenile snake (open circle) was deemed an outlier and was therefore excluded from the regressions.

meaning that size significantly affected glide angle at a given point in the trajectory (namely after 7 m of vertical drop).

Because size was found to influence most aspects of performance, the relationships among size variables within *C. paradisi* were examined further. Projected area, mass and wing loading were regressed on snout–vent length using RMA regressions as described above. The RMA slopes for mass and area relative to snout–vent length were not significantly different from those expected under isometry (Table 4). Wing loading exhibited positive allometry with snout–vent length – larger snakes had relatively higher wing loadings than smaller snakes. To explore the effect of the smallest snake (a young juvenile) on these relationships, the RMA regressions and bootstrap algorithms were rerun with this individual removed; no effect was found on mass or area, and the positive allometry with wing loading was further strengthened.

Interspecific comparisons

C. paradisi and *C. ornata* differed significantly in most performance comparisons (Fig. 4). *C. paradisi* traveled a greater horizontal distance (7.9±1.3 m *vs* 3.6±0.9 m, mean ± s.D., d.f.=21, *P*<0.0001), with trajectories that started with a lower ballistic dive angle (57±4° *vs* 74±3°, d.f.=24, *P*<0.0001), shallowed at a higher rate (21±7° s⁻¹ *vs* 11±8° s⁻¹, d.f.=24, *P*=0.002), and achieved a lower minimum glide angle (34±8° *vs* 65±6°, d.f.=24, *P*<0.0001) and higher maximum horizontal speed (8.0±0.9 m s⁻¹ *vs* 3.3±0.6 m s⁻¹, d.f.=18, *P*<0.0001). Mean undulation frequency (1.3±0.3 Hz *vs* 1.1±0.2 Hz), sinking speed at transition (6.0±0.7 *vs* 6.6±1.3 m s⁻¹), and maximum sinking speed (6.3±0.9 *vs* 6.9±1.0 m s⁻¹) were not significantly different between the two species.

To evaluate factors that might contribute to the performance differences between *C. paradisi* and *C. ornata*, we compared

basic morphological features between these species. *C. ornata* were generally more massive than *C. paradisi* at any given snout–vent length (Fig. 5). Permutation tests revealed that the intercepts of the RMA regression lines of mass on snout–vent length are significantly different (–4.26 *vs* –5.23 for *C. paradisi* and *C. ornata*, respectively; *P*=0.01, one-sided test), with marginally different slopes (3.16 *vs* 3.79, *P*=0.07, one-sided test). Furthermore, unlike *C. paradisi*, *C. ornata* shows strong positive allometry, with longer snakes having relatively higher masses than expected under isometric scaling. Projected area could not be measured for *C. ornata*, but it is likely that wing loading is also higher than in *C. paradisi* (at equal snout–vent
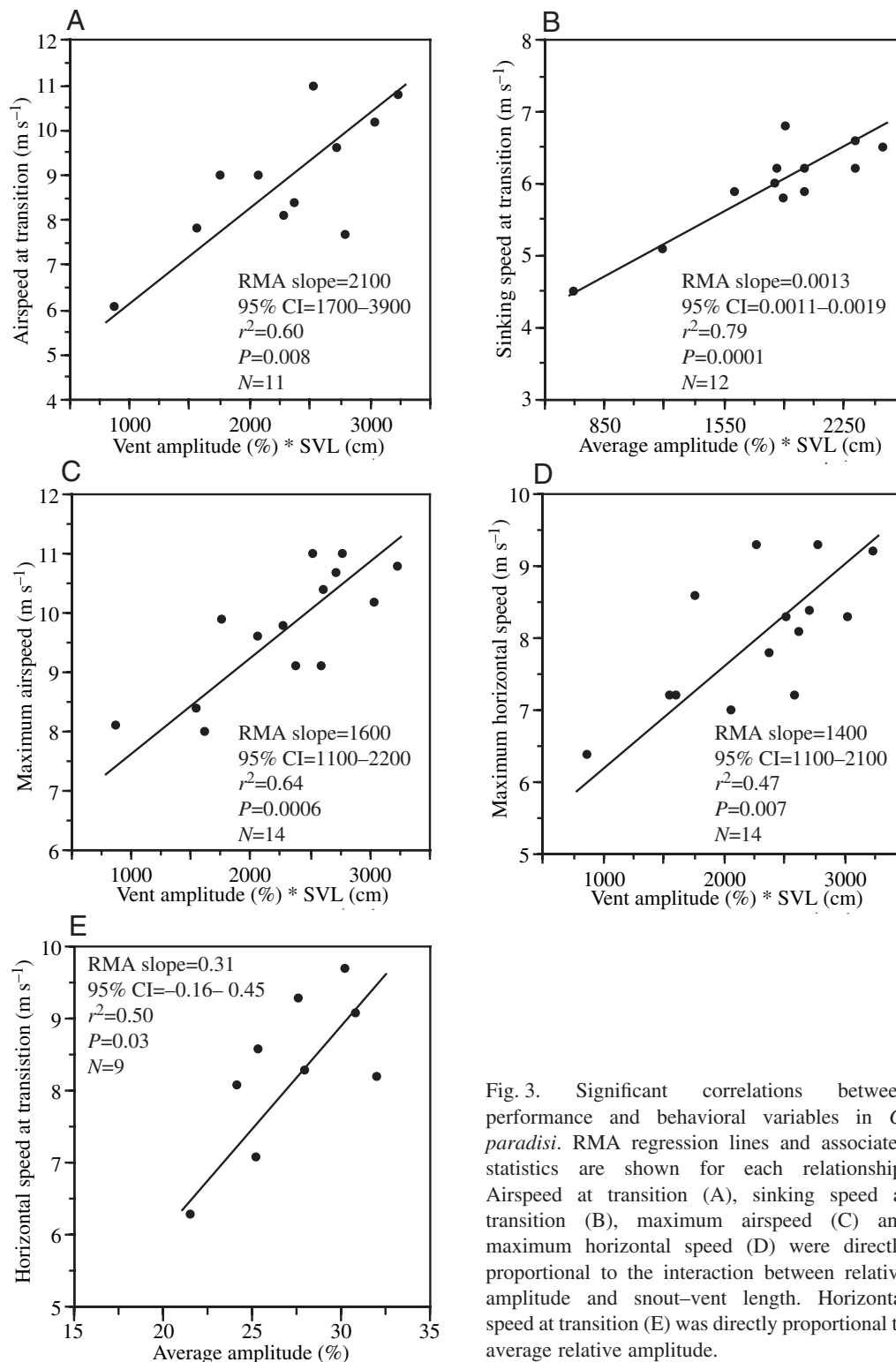

Fig. 3. Significant correlations between performance and behavioral variables in *C. paradisi*. RMA regression lines and associated statistics are shown for each relationship. Airspeed at transition (A), sinking speed at transition (B), maximum airspeed (C) and maximum horizontal speed (D) were directly proportional to the interaction between relative amplitude and snout–vent length. Horizontal speed at transition (E) was directly proportional to average relative amplitude.

lengths) because *C. ornata* are more massive and do not flatten to the same extent (a smaller change in relative body width; Socha, 2002a).

Discussion

Multiple regression predictors

In this study, stepwise multiple regression was the primary tool used to identify possible predictors for snake flight performance; therefore, it is important to understand the limitations of this approach. Stepwise multiple regression was chosen because there was no *a priori* physical/aerodynamic reason to include or exclude any variable, given the lack of a theoretical framework specific to the unique characteristics of snake flight. Other techniques such as path analysis, which explicitly test relationships in a pre-determined model, were deemed less appropriate. The stepwise regression technique establishes functional relationships among variables by excluding variables that do not significantly contribute to the overall variation (Sokal and Rohlf, 1995). However, this method, which produces the smallest set of predictor variables 'adequate' to explain the variation, should only be viewed as exploratory. As described by Sokal and Rohlf (1995), the addition or subtraction of a single variable can cause

radical changes in the composition of the final predictor set (although this effect was not apparent here). In addition, in a stepwise regression the '*P*-to-enter' and '*P*-to-leave' values (corresponding to the significance values to include or remove a regressor term from the model, respectively) are arbitrarily chosen and can similarly produce differences in predictor sets. (However, the results here were generally robust to small changes in *P*-value.) Lastly, the predictor variables chosen by the stepwise regression should not be viewed as the most important or sole set of variables. Some variables may be functionally important but can be excluded due to correlation with variables in the predictor set. Therefore, the results presented here should not be viewed as a 'solution', but rather as a starting point for further investigation, particularly by informing attempts to experimentally examine questions about the aerodynamics of snake flight.

Given these caveats, it can be broadly stated that size had a strong influence on gliding flight performance in *C. paradisi*. Of the nine significant relationships determined by multiple regression analysis, eight were influenced by size alone or by size interacting with behavior. Furthermore, the trends for performance variables with size predictors all pointed in the same direction. Within a 7 m vertical drop, smaller snakes were more capable of long-distance travel – they used higher

Table 3. *Results of stepwise multiple regressions on performance variables within two* C. paradisi *individuals*

Performance variable	Predictor	d.f.	r^2	'F-ratio'	'Prob>F'
Individual 1 (M = 27 g, SVL = 63 cm)					
Time at sinking speed transition	Frequency	1	0.996	231.15	0.042
Airspeed, maximum	Vent amp. (%)	2	0.928	25.67	0.037
Horizontal speed, maximum	Freq. × Vent amp. (%)	2	0.994	351.25	0.003
Individual 2 (M = 63 g, SVL = 83 cm)					
Horizontal distance traveled	Frequency	2	0.879	14.48	0.063
Glide angle minimum	Frequency	2	0.982	111.00	0.009
Airspeed, maximum	Freq. × Vent amp. (%)	2	0.994	303.44	0.003
Horizontal speed, maximum	Vent amp. (%)	2	0.991	207.78	0.005

Five and four trials were analyzed for individuals 1 and 2, respectively. 'Amp.' and 'Freq.' refer to amplitude and frequency, respectively. Each performance variable is directly proportional to its predictor, except for horizontal distance traveled in individual 2, which shows an indirect proportionality with frequency. The F-ratio and significance levels are in quotation marks because they are not true F-statistics; no F-distribution was used.

Table 4. *Scaling relationships in* C. paradisi *evaluated using RMA regressions*

Regressor	Dependent variable	Expected slope	Slope	95% CI	r^2	P	N
Snout–vent length	Glide angle minimum*	0	0.91	0.42–1.47	0.405	0.006	17
Mass	Glide angle minimum*	0	0.29	0.14–0.46	0.448	0.003	17
Wing loading	Glide angle minimum*	0	0.7	0.38–1.06	0.583	0.002	14
Snout–vent length	Airspeed	0.5	0.40	0.26–0.62	0.531	0.002	15
Mass	Airspeed	0.167	0.13	0.08–0.20	0.48	0.004	15
Wing loading	Airspeed*	0.5	0.31	0.19–0.48	0.464	0.01	12
Snout–vent length	Projected area	2	2.01	1.89–2.17	0.982	<0.0001	17
Snout–vent length	Mass	3	3.16	2.99–3.35	0.989	<0.0001	20
Snout–vent length	Wing loading*	1	1.25	1.05–1.54	0.912	<0.001	17

Expected slopes assume isometric scaling and glide equilibrium. Slopes and corresponding 95% confidence intervals that do not include the predicted value are indicated by *.
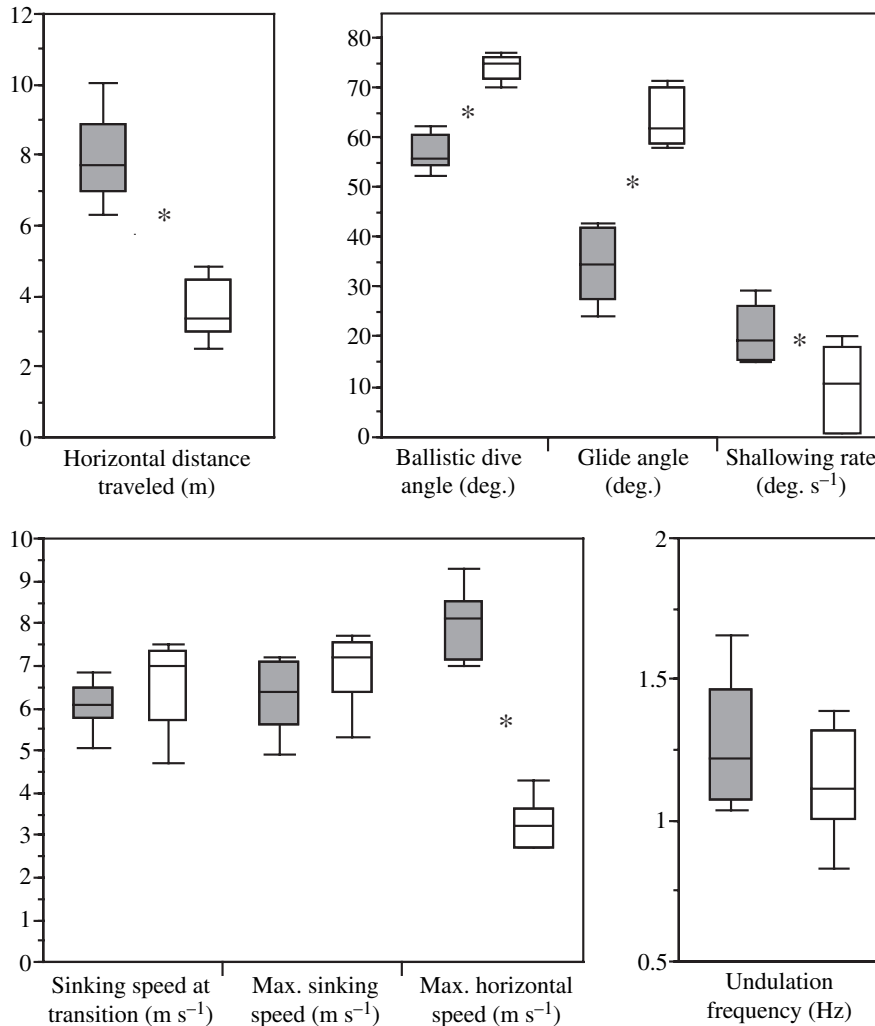
Fig. 4. Box plots comparisons of performance and behavior between *C. ornata* and *C. paradisi*. Values for *C. paradisi* are represented in gray. Significantly different comparisons, as determined by *t*-tests, are indicated with an asterisk (*).

shallowing rates, lower minimum glide angles and achieved greater horizontal distances. Although these variables appear to be correlated, their relationship is not physically constrained – it is possible for snakes to use different shallowing rates for different amounts of time to reach the same minimum glide angle. Furthermore, smaller snakes reached lower maximum sinking rates. Therefore, smaller snakes must generate relatively more lift and/or create less drag than do larger snakes. How they do so is unclear, but it is evident that within *C. paradisi*, smaller snakes are better gliders. Although there were insufficient data for rigorous testing, this trend appears to be true for *C. ornata* as well.

Only one performance variable, horizontal speed at transition, was related to a behaviorial variable alone. All but one other speed variable were related to the interaction between amplitude and size. Within individuals (and thus independent of size), vent amplitude was related to multiple performance variables, strengthening the conclusion that the larger the lateral sweep of the vent during undulation (relative to body size), the faster the

snake traveled, from the start of the shallowing phase onward. Functionally, it is unclear if it is the movement, posture, or size of the posterior end of the snake that drives this relationship. One possibility is that the greater the relative vent amplitude, the greater the length of snake body that lies perpendicular to the oncoming airflow, with relatively more lift produced in this region. If this were the case, the lift vector would have to be angled in a direction that favors increasing the flight speed. However, the limited number and position of landmarks preclude the precise determination of how vent amplitude relates to snake posture and shape in the air. Another possibility is that the lengths of the snake's body that are perpendicular to the flow may be physically closer together, making them act increasingly like one larger airfoil with a bigger chord length, rather than as two separate airfoils with smaller chord lengths. As the two body sections move closer together at higher undulation amplitudes, the aerodynamic effects on the two body sections may become coupled, with the emergent property of higher aerodynamic force. Future studies that provide a greater number of landmarks on the snake during flight would more precisely resolve these issues.

The fact that undulation frequency was not related to any performance variable strongly suggests that frequency has a relatively minor role, if any, in aerodynamic force production during snake flight. Additionally, no significant differences in frequency were found between the species, even though there were large differences in performance. This means that the traveling wave motion of aerial undulation is probably not involved in generating aerodynamic forces. If true, then standard fixed-airfoil theory should be sufficient to explain snake flight aerodynamics. By contrast, frequency had an effect on five of eight performance variables within individuals. However, these results should be viewed with caution because there was no replication of frequency effects between the two individuals. This lack of consistency may be a consequence of small sample size, both in number of trials analyzed per individual (four and five), and in total number of individuals (two). To resolve this issue, it is necessary for future studies to analyze trials from multiple individuals, with trials encompassing the full range of performance for each individual.

Although it would appear surprising that the most prominent feature of snake flight (undulation) plays little role in force generation, this does not preclude the possibility of second-
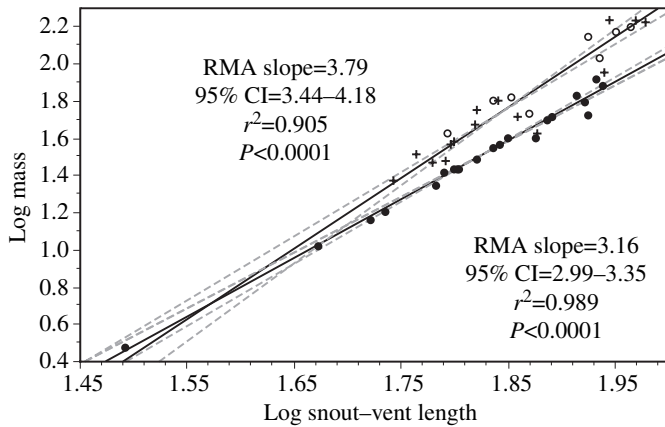
Fig. 5. RMA comparison of snout–vent length and mass differences in *C. ornata* and *C. paradisi*. As determined using a permutations test, the slopes and the intercepts between the species are marginally significantly different and significantly different, respectively. Filled circles represent *C. paradisi*, unfilled circles represent *C. ornata*, and crosses represent *C. ornata* whose trajectories were not analyzed in this study. RMA slopes and 95% confidence intervals are shown.

order effects of undulation on glide angle (see Socha et al., 2005). Aerial undulation may serve other roles, such as maintenance of stability, in which undulation would prevent rolling or pitching by moving the centers of gravity and pressure so that their average locations coincide (Thomas and Taylor, 2001). Alternatively, aerial undulation may be a functionless behavioral vestige. However, given the considerable sophistication of gliding in *C. paradisi* (e.g. control of flight direction, morphological specialization; Socha et al., 2005), it seems plausible that undulation plays a functional role in snake flight, related to stability or control.

It is possible that the behavioral correlations with flight performance reflect an underlying relationship to size. In fact, both absolute undulation amplitude and frequency are size-dependent – larger snakes produce larger amplitudes and lower undulation frequencies (Fig. 6). Flapping frequencies decrease with increasing size in insects and birds (Greenwalt, 1975), a similar effect of body size. However, only relative amplitude variables, not absolute, affected performance in *C. paradisi*, and relative undulation amplitude is not correlated with body size. Vent relative amplitude in particular was a prominent predictor of performance, both in combination with size among *C. paradisi*, and in combination with frequency within individuals. Although the preliminary intra-individual results suggest that vent amplitude may be a size-independent predictor of performance for certain features of the glide trajectory, performance variables may respond differently in comparisons of intra- and inter-individual relationships.

No combination of size, behavior, or interaction variables significantly explained the variation in over half of the performance variables for *C. paradisi*. All of these performance variables were related to the initial phases of the trajectory, which suggests that performance in the initial phase is determined by unexamined variables, or that it is uncoupled
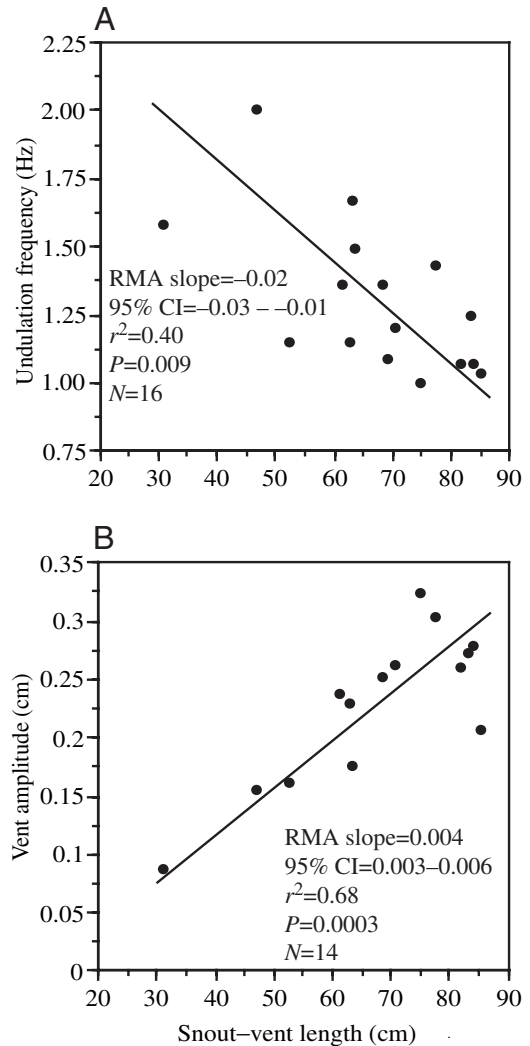

Fig. 6. Size dependence of two behavioral variables in *C. paradisi*. RMA regression lines and associated statistics are shown for each relationship. Undulation frequency (A) was indirectly proportional to snout–vent length, whereas vent amplitude (B) was directly proportional to snout–vent length.

from late-glide performance. Whatever the proximate cause, it is clear that performance differences among individuals developed in the shallowing phase of the trajectory, and not during the ballistic dive. This conclusion is somewhat surprising, as it would be expected that the steeper the ballistic dive, the shorter the horizontal distance traveled. However, this is indeed the case when the data are compared at sufficiently shallow points in the trajectory.

Predicted scaling of performance

Following basic aerodynamic theory, flight speed was predicted to be positively correlated with length, mass and wing loading. Indeed, airspeed scaled isometrically with snout–vent length and mass; however, it increased at a marginally slower rate than expected with respect to wing loading. These results suggest that as size increases, some other control features partially compensate for increased wing

loading, presumably by generating extra lift and/or drag and thus slowing descent.

Minimum glide angle was predicted to be size-independent, but here was found to be positively correlated with all size variables. The prediction was based on the assumption that minimum glide angle was measured at equilibrium, a condition not met by the snakes in this study. Reasons that equilibrium gliding flight was not observed include experimental design (see Socha et al., 2005), but it is also possible that snake gliding flight is inherently unsteady. This possibility is seldom discussed in the gliding literature – equilibrium gliding is generally assumed as the norm. Given complex 3-D environments and multiple reasons for gliding, it is possible that equilibrium gliding in many gliders is the exception rather than the rule. To address this hypothesis, it is most relevant to measure the kinematics of gliding flight in animals that are locomoting in the wild, rather than in controlled settings such as in this study.

Clearly, size plays a major role in driving performance differences within *C. paradisi*. Larger snakes should be equally good gliders (traveling equal distances, but at higher speeds) as smaller snakes if equilibrium theory is a reliable guide; instead, smaller snakes are much better gliders. That this result was not predicted may simply reflect that this study did not model the non-equilibrium aspects of a glider's trajectory. Future studies comparing full trajectories that reach equilibrium with theoretical models that consider how drag and lift change from takeoff will help further clarify if and how gliders modify their performance through behavior. In addition, unexamined variables, such as cross-sectional shape and angle of attack, may have strong effects on performance. Angle of attack was not addressed due to lack of precise data; similarly, there are no data available on if and how cross-sectional shape differs within a trajectory or among snakes.

In the few other gliders that have been examined in detail, performance also generally decreases as size increases. McGuire (1998) found similar patterns of size and performance among flying lizard species (*Draco*) – interspecifically, smaller lizards achieved lower glide angles and were generally more flexible in performance. In parachuting geckos (*Ptychozoon lionatum*), horizontal distance traveled decreases with wing loading (Marcellini and Keefer, 1976). By contrast, larger birds achieve lower glide angles (e.g. pigeon, 9.5°; falcon, 5.5°; albatross, 3°; Vogel, 1994), but body size is only one of many differences among these flyers; wing shape (particularly wing aspect ratio) may strongly drive these differences.

Interspecific differences in performance

Differences in performance between the two snake species were striking. In all aspects, *C. paradisi* outperformed *C. ornata*, traveling more than twice as far using a shallower ballistic dive and higher shallowing rate, and achieving a lower minimum glide angle and lower maximum sinking speed. Although this study identifies these differences, their causes remain unclear. There are no significant differences in undulation frequency between the two species, although

individual *C. paradisi* reach higher maximum frequency and *C. ornata* lower minimum frequency. At least three other possibilities remain untested. First, the species may differ in undulation amplitude. Amplitude could not be measured from the footage we were able to collect from *C. ornata* but, as shown, undulation amplitude can affect multiple aspects of glide performance in *C. paradisi*. Second, there may be differences in body orientation throughout flight, which was unexamined for both species. Differences in orientation should cause differences in wakeflow patterns, and therefore the resulting aerodynamic forces, which in turn may affect performance. Comparisons of both amplitude and orientation could be accomplished through further work to document the 3-D kinematics of *C. ornata*. Third, differences in flight morphology between the species have only been partially examined here. *C. ornata* are more robust (greater mass per length) than *C. paradisi* and likely have higher wing loadings. Furthermore, *C. ornata*'s cross-sectional shape is more rounded on the ventral surface than that of *C. paradisi* (Socha, 2002a). Modeling studies of the effects of cross-sectional shape on aerodynamic force generation are required to relate these morphological differences to performance differences.

The performance differences between the two species are likely to be even more pronounced when snakes take off from greater heights. Heyer and Pongsapipatana (1970) launched *C. ornata* from a 41 m tower, a height that should have provided sufficient vertical distance for the snakes to reach equilibrium. Even from this great height, the maximum distance traveled by *C. ornata* was only 30 m. In marked contrast, the 'best' *C. paradisi* specimen in this study would travel an estimated 142 m if launched from the same height (assuming a linear scaling of performance with launch height). Given such differences, *C. paradisi* should be classified as 'gliders' and *C. ornata* as 'parachuters' (*sensu* Oliver, 1951) although the value of this terminology has been questioned (Moffett, 2000; Vogel, 2003). Furthermore, this study confirms the prediction of Mertens (1970), who suggested that such differences in flight ability would exist based on his observation that *C. paradisi* dorsoventrally flattened when sunning in captivity, whereas *C. ornata* did not.

Ecological implications

Differences in morphology and locomotor performance can drive differences in ecology (e.g. Losos, 1990; Garland and Losos, 1994; Norberg 1994; and references therein). Intra- and inter-specific differences in performance ability in flying snakes can be used to generate hypotheses of ecological differences in their usage of flight, which in turn should be tested with field data. Within *C. paradisi*, smaller snakes are better gliders and therefore might glide more often and/or travel greater distances between trees. Larger snakes cannot glide as far from a given height and therefore might use aerial locomotion primarily to traverse small gaps between trees or branches. Furthermore, these differences in performance may influence microhabit utilization in the trees. For example, smaller snakes need less vertical height to travel a given distance in the air, so they may

spend more time at lower levels of the tree or take off from lower average heights. Between *C. paradisi* and *C. ornata*, *C. paradisi* are better gliders, which suggests that *C. paradisi* use flight more often and travel greater distances than *C. ornata*. Unlike *C. paradisi*, *C. ornata* appear to be unable to maneuver in the air (Socha, 2002a); therefore, flight may pose a greater risk from potential aerial predators.

Because size is related to age in reptiles (at least until growth asymptotes; see Andrews, 1982), size-related performance differences found in this study should also reflect ontogenetic differences in performance. The *C. paradisi* used in this study approximately span the full size range of the species and, thus, the full ontogenetic range was nearly represented. Although on the whole smaller snakes were better gliders, the smallest snake (a young juvenile, mass = 3 g) did not have the highest scores for any performance variable. This suggests that performance ability peaks at an intermediate point in ontogeny. This peak seems to occur at a fairly small body size – the 'best' snake was about four times greater in mass than the young juvenile, but about eight times less massive than the largest snake. This ontogenetic pattern contrasts with locomotor performance in terrestrial snakes. For example, larger (and thus older) garter snakes have higher absolute burst speeds and endurances than smaller snakes (Jayne and Bennett, 1990), a difference that reflects effects of size rather than experience. That the young juvenile could glide well suggests that little to no learning period exists in ontogeny – *C. paradisi* are likely functional gliders upon emerging from the egg.

In conclusion, it is clear that size and behavior strongly affect gliding flight performance in the flying snake, *C. paradisi*. Smaller snakes travel farther, using higher shallowing rates and lower speeds. These results can be used to inform future studies in which these features are isolated to determine their physical affect on aerodynamic force generation. *C. paradisi* are significantly better gliders than *C. ornata*, which are more robust but use the same undulation frequency. The differences in cross-sectional shape between the two species may be largely responsible for their performance differences; modeling studies should therefore highlight the effects of variation of body shape on aerodynamics. This study is a first step to understanding which factors most significantly affect flight performance in snakes, a novel form of gliding locomotion in animals.

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