

RESEARCH ARTICLE

Aerial maneuvering by plethodontid salamanders spanning an arboreality gradient

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ABSTRACT

Wandering salamanders (*Aneides vagrans*) inhabit the crowns of the world's tallest trees, taking refuge in epiphytic fern mats within these complex arboreal environments. These salamanders readily jump from the canopy when disturbed and maintain stable postures while falling via fine adjustments of the limbs and tail in lieu of dedicated aerodynamic control surfaces, thus reliably carrying out non-vertical descent. Here, we examined the aerial behavior and performance of *A. vagrans* and three other species of plethodontid salamander across a habitat gradient of arboreality by recording salamanders falling from short heights and moving within the jet of a vertical wind tunnel. Kinematic performance of aerial behavior in plethodontid salamanders was correlated with a gradient of arboreal habitats; moreover, salamanders from arboreal niches were more effective in slowing and redirecting descent compared with other salamanders. *Aneides vagrans* and the closely related *Aneides lugubris* consistently engaged in parachuting and gliding when falling; their trajectories were very steep, but were sufficiently angled to enable contact with either the home trunk or nearby branches during falls or jumps from great heights. Aerial maneuvering in arboreal salamanders is similar to that seen in other vertebrates capable of non-vertical and controlled descent, suggesting that the long limbs and active tail of these arboreal plethodontids (often cited as adaptations for climbing) may also contribute to parachuting and gliding when falling from trees. These aerial behaviors within the redwood canopy warrant further investigations into other canopy residents that lack conspicuous surfaces for aerodynamic control.

KEY WORDS: Aerial righting, Biomechanics, Canopy, Gliding, Parachuting, Redwood

INTRODUCTION

Wandering salamanders, *Aneides vagrans*, live in the crowns of old-growth coast redwood trees (*Sequoia sempervirens*) and other sympatric conifers, taking refuge in complex arrays of epiphytic fern and humus mats. The crowns of *S. sempervirens* are spatially complex with much vertical and lateral branching. Crotches at the bases of vertical trunk reiterations, as well as large horizontal branches, provide platforms for debris accumulation, thereby promoting humus development and facilitating colonization by vascular epiphytes that contribute to the formation and structure of

large fern mats (Sillett, 1999). Fern mats soak up moisture during the wet season and then retain it throughout the year, providing refuge for arboreal but also desiccation-sensitive organisms (Sillett, 1999). *Aneides vagrans* occupies these epiphytic fern mats year-round, making use of tunnels and cavities deriving from decay of roots and rhizomes (Spickler et al., 2006). Permanent canopy residency of *A. vagrans*, together with its prehensile tail, square toe-tips and aptitude for climbing, suggests that it is among the most arboreal of salamanders.

Several plethodontid salamanders, including *A. vagrans*, jump to avoid predation (Ryerson et al., 2016; Brown and Deban, 2020). Canopy-dwelling *A. vagrans* have been observed jumping from coast redwood crowns in response to human observers (Lanchester, 2017; C. Brown, personal observation). Interestingly, jumping in arboreal salamanders of the genus *Aneides* differs biomechanically and kinematically relative to other plethodontids. *Aneides* take off at a relatively low horizontal velocity; however, they achieve skydiving-like postures more quickly after a jump, likely via toeing off from vertical surfaces with two feet and limiting lateral bending of the body (Brown and Deban, 2020). Furthermore, horizontal velocity of an escape jump may be irrelevant in the context of selection if the desired outcome of the jump is to effect vertical escape. While falling, *A. vagrans* is able to maintain dorsoventrally stable postures, slow descent and effect gliding at non-vertical angles (Brown et al., 2022), perhaps mitigating the likely risks of uncontrolled falls from a canopy niche (see Cartmill, 1985; Dudley et al., 2007; Jusufi et al., 2011, Humphreys and Ruxton, 2019).

Many organisms known to direct their aerial descent (*sensu* Yanoviak et al., 2005) possess conspicuous morphological features that facilitate this behavior [e.g. patagia of gliding lizards (*Draco*) and flying squirrels (*Glaucomys*); body fringes of flying geckos (*Ptychozoon*)]. These examples are well characterized because of their prominence; however, recent studies have revealed that even taxa with modest aerodynamic features are capable of directing aerial descent through postural control and movements of appendages (Stewart, 1985; Yanoviak et al., 2005, 2010; Jusufi et al., 2008; Vanhooydonck et al., 2009). Various small terrestrial animal taxa, including ants (e.g. *Cephalotes* spp.), spiders (e.g. *Selenops* spp.) and anoles (*Anolis* spp.), possess no obvious aerodynamic control surfaces but can regulate their falls from trees with varying degrees of force and moment control. These behaviors involve either parachuting or gliding (*sensu* Dudley and Yanoviak, 2011) to slow or to direct descent, respectively, back towards the home trunk (Yanoviak et al., 2005, 2015; Jusufi et al., 2011). Gliding can be defined as any controlled descent by an organism that converts gravitational potential energy into useful aerodynamic work effecting horizontal translation (Dudley and Yanoviak, 2011).

For aerial taxa, there is often a trade-off between maneuverability and stability (Maynard Smith, 1952; McCay, 2001). Intrinsic

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instability requires continuous correction in pitch, yaw and roll, but also facilitates rapid maneuvers. The generally thin cylindrical body of salamanders is clearly not conducive to stability, and the absence of dedicated control surfaces suggests the need for active postural and appendicular motions to maintain an oriented posture in the air. Here, we compared aerial performance of plethodontid salamanders to assess how they might control descent without dedicated control surfaces such as skin flaps or winglike structures. We also examined whether aerial maneuvering by *A. vagrans* (particularly as indicated by their minimum descent angle) is sufficient to allow them to remain within coast redwood crowns after a jump or fall. To address these issues, we first dropped and coaxed *A. vagrans* to jump from heights of 3 m. Then, we simulated aerial descent in live individuals of four species of plethodontid salamander representing a gradient of arboreality in a vertical wind tunnel, and reconstructed their aerial postures, movements and maneuvers. For *A. vagrans*, these kinematic data were then used to extrapolate possible descent trajectories within empirically characterized three-dimensional geometries for coast redwood crowns, based on known salamander capture sites within the canopy.

MATERIALS AND METHODS

We captured five adult *Aneides vagrans* Wake & Jackman 1998 from Humboldt and Del Norte Counties, CA, USA, in December 2018 (Table S1). For comparison, we captured five adults each of three additional species: *Aneides lugubris* (Hallowell 1849), *Aneides flavipunctatus* (Strauch 1870) and *Ensatina eschscholtzii* Gray 1850. *Aneides vagrans* inhabits the canopy of old-growth redwood forests year-round and has been found as high as 88 m in a tree crown (Spickler et al., 2006). *Aneides lugubris* is morphologically specialized for climbing and has often been found in trees (Ritter and Miller, 1899; Ritter, 1903; Stebbins, 2003). *Aneides flavipunctatus* does have a prehensile tail (Van Denburgh, 1895) and is able to climb when coaxed (C. Brown, personal observation), but unlike its more arboreal congeners, this species is primarily ground-dwelling throughout lowland forests and meadows (Myers and Maslin, 1948). *Ensatina eschscholtzii* is not specialized for climbing and is associated with forest floor and leaf litter microhabitats (Stebbins, 2003). Together, these four species represent a gradient of arboreality: the highly arboreal *A. vagrans*, the moderately arboreal *A. lugubris*, the marginally arboreal *A. flavipunctatus* and the non-arboreal *E. eschscholtzii*. Among the four species tested, *E. eschscholtzii* represents the outgroup as it is more distantly related relative to the other three species, which are all in the genus *Aneides* (see Shen et al., 2016).

We measured the relative limb and tail lengths ($N=3$ per species) of all four species tested in the vertical wind tunnel divided by snout–vent length (SVL) to account for slight variations in salamander size (Table 1) and used these basic morphometric data to contextualize aerial performance. We used total length of salamanders to calculate Reynolds numbers for each individual (Table S1) and calculated an average for each species (Table 1). We transported salamanders on moist, unbleached paper towels in individual deli cups with fitted, aerated lids (at air temperatures no higher than 15°C) to the University of California, Berkeley. We housed salamanders in individual containers at 15±2°C with a 12 h:12 h light:dark cycle and fed them live house crickets (*Acheta domesticus*). Experimental trials were conducted at an average room temperature of approximately 25°C. The Animal Care and Use Committee at the University of California, Berkeley approved all experimental procedures described for this research.

Table 1. Morphometrics including average body mass and relative forelimb, hindlimb and tail lengths as well as approximate Reynolds number for four plethodontid salamander species used in vertical wind tunnel trials

Species (N)	Mass (g)	FL	HL	Tail	Reynolds number
<i>Aneides vagrans</i> ($N=3$)	3.3	0.30	0.38	0.85	~6.1×10 ⁴
<i>Aneides lugubris</i> ($N=3$)	5.4	0.25	0.30	0.86	~7.8×10 ⁴
<i>Aneides flavipunctatus</i> ($N=3$)	3.5	0.22	0.25	0.88	~7.1×10 ⁴
<i>Ensatina eschscholtzii</i> ($N=3$)	2.6	0.24	0.28	0.82	~5.4×10 ⁴

FL, relative forelimb length; HL, relative hindlimb length; Tail, relative tail length. Relative FL, HL and tail lengths were calculated by dividing appendage length by the snout–vent length.

Aerial behavior

Drops

We qualitatively examined features of aerial behavior in *A. vagrans* by dropping salamanders safely and consistently from a height of 3 m onto an ultralight down feather quilt (Alpine Ridge Outfitters, Dallas, TX, USA). We dropped all individuals ($N=5$) 40 times for a total of 200 drops over 16 days. In order to drop the salamanders, we held them by the tip of the tail and then dropped them directly next to a downward-facing camera (V-Raptor, Red Digital Cinema, Irvine, CA, USA) to image at 50 Hz a vertical view of the descent. We used the fixed position of the camera to ensure consistent drop points and initial heading as well as consistent imaging across trials. Image sequences were used to confirm observations of falling posture to determine whether a salamander ever turned upside down and to characterize landing position. Similarly, we used tactile stimulation to coax salamanders ($N=5$) to jump (60 total jumps) from a plank of wood (30×10×1 cm) strapped to the top of the same camera, and recorded the take-off, descent and landing.

Wind tunnel

Dropping salamanders from heights greater than 3 m resulted in unreliable observations and blurry, undecipherable image sequences of descent owing to rapid movement and a limited depth of focus. Therefore, for all four aforementioned species, we used a custom vertical wind tunnel (Wind Generator 01-10, Aerolab, Laurel, MD, USA) with a working section width of 30.4 cm, length of 30.4 cm and height of 25.7 cm to simulate conditions of aerial descent in lieu of dropping salamanders from natural heights to reduce risk to the animals and to facilitate imaging (Movies 1–3; see also McCay, 2001). In a vertical wind tunnel, suspension under such conditions is reached by salamanders when the vertical aerodynamic drag and lift forces balance the force of gravity. Depending on individual surface area and mass, salamanders achieved stable vertical positions in the airstream at vertical airspeeds between 8.6 and 10.6 m s⁻¹. We verified airspeed using a hand-held anemometer (VelociCalc model 8346, TSI Inc., Shoreview, MN, USA) held in the center of the test section for all wind tunnel settings at which salamanders performed. We positioned the anemometer 10 cm from the floor of the wind tunnel and recorded the wind speed once every 10 s for three such consecutive recordings, and then averaged these values for subsequent analyses. We also assessed spatial variation of the test section of the wind tunnel. Briefly, we partitioned the cross-section into 144 equally sized squares and recorded the average speed within each square using the technique described above. We then calculated the mean and standard deviation of these values.

The variation was always within 10% or less of the overall mean, which is comparable to spatial variation across meter- to decimeter-scale vertical gradients within forest canopies (Parker, 1995; McCay, 2003). Airspeeds as measured at the center of the wind tunnel exceeded the averaged cross-sectional speed by approximately 7%, but this deviation was also within the range of spatial variation.

Mounted transparent acrylic sidewalls around the opening of the wind tunnel (Fig. 1) prevented salamanders from maneuvering out of frame, and enabled high-speed imaging at 400 Hz from one dorsal and two lateral perspectives from axes elevated 20 deg above horizontal (HiSpec cameras, Fastec Imaging, San Diego, CA, USA). Safety nets and mesh prevented animals from entering the lower contraction chamber of the wind tunnel. Wind tunnel trials were conducted over several days to minimize animal stress; for all four species, we conducted nine wind tunnel trials for each individual salamander ($N=5$) for a total of 45 trials per species. Circular (6 mm) white paper markers were attached to salamanders immediately prior to being placed in the wind tunnel; markers were positioned on the dorsal surface of the head and on the vertebral column midway between the head and the cloaca at the visually estimated center of mass. Markers were constructed from hole-punched paper disks that were soaked in spring water and then attached to the skin of salamanders by wet adhesion. We placed the salamanders directly within airflow at constant vertical wind speeds adjusted to the mass of each individual to elicit longer periods of stable gliding behavior. Salamanders were imaged within the vertical airstream for 5 s per trial, and any periods of the trial involving external force application (e.g. contact with the wall, working section floor, netting or observers) were omitted from analyses. Consequently, a single 5 s trial could potentially contain either one or multiple aerial behaviors or maneuvers (e.g. aerial righting, parachuting, gliding, etc.).

We analyzed the kinematics of aerial maneuvers recorded in the wind tunnel using ImageJ software (version 1.53a, National

Institutes of Health, Bethesda, MD, USA). We then noted the frames over which these aerial behaviors occurred, as well as any movements or postural changes made by the salamander immediately prior to a maneuver. We counted the number of frames (with 2.5 ms interframe interval) between movements or postural changes and aerial maneuvers to estimate times between biomechanical action and aerodynamic reaction in salamanders.

To assess the biomechanics of maneuvers in salamanders, we analyzed all instances of correction in pitch, yaw and roll. Correction was defined as any movement in the direction of restoring an upright posture that did not result in a salamander over-correcting and tumbling out of control. We characterized parachuting as any trial for which a salamander held an uninterrupted skydiving posture (defined as a parasagittal extension of the vertebral column and extension of all four limbs laterally perpendicular to the trunk; Brown et al., 2022) and experienced a change in its vertical velocity without tumbling out of control; changes in vertical velocity were calculated after point-tracking, but also appeared in the wind tunnel videos as salamanders were observed slowing in vertical descent, coming to a full midair stop after descending, ascending vertically after descent or a full stop, or even increasing the rate of descent (suggesting that parachuting was being employed before descent, followed by speeding up). We quantitatively confirmed all instances of parachuting by calculating vertical velocities and measuring their change in response to adoption of the skydiving posture. To ensure that vertical velocity was not influenced by external forces, we only analyzed trials for which the salamander began descent and parachuting from a stationary position (i.e. with no initial horizontal movement), and without contact with chamber walls.

Parachuting and gliding kinematics

We defined a successful gliding trial as one in which a salamander (i) adopted an uninterrupted skydiving posture, (ii) then remained

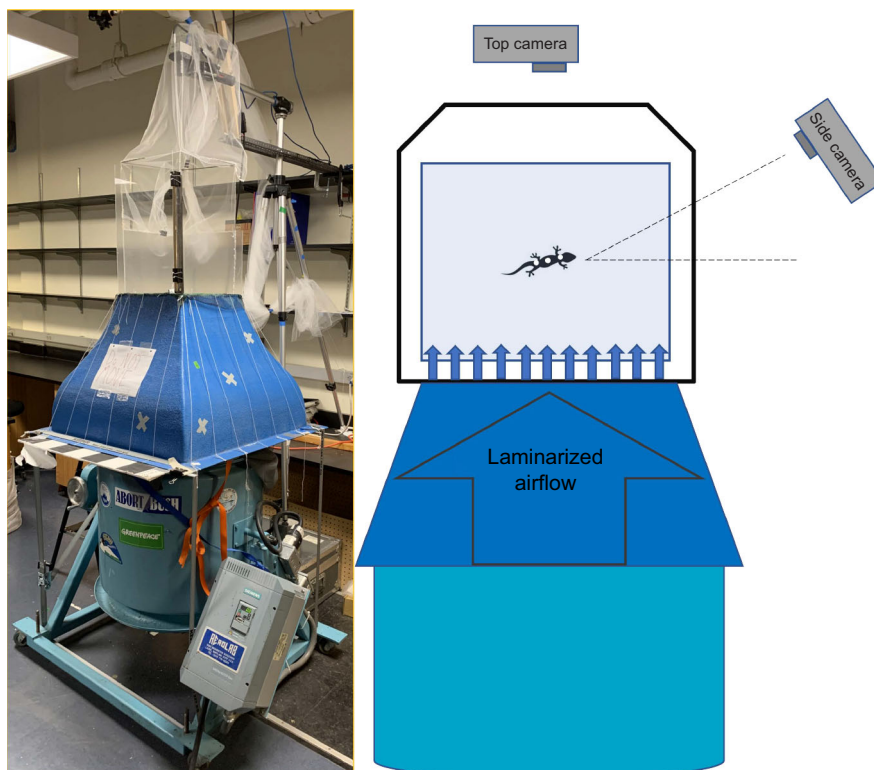


Fig. 1. A photo (left) and polygon schematic (right) showing the vertical wind tunnel setup for lungless salamanders from the frontal view. Airflow from a large fan was laminarized (large arrow) using honeycomb ducting, funneled through the viewing chamber (smaller blue arrows), and used to induce salamander support (silhouette) within the 30.4×30.4×25.7 cm working area of the chamber (inner blue rectangle). All trials were recorded from dorsal (top camera), lateral (side camera) and frontal (reader's point of view) perspectives for analysis.

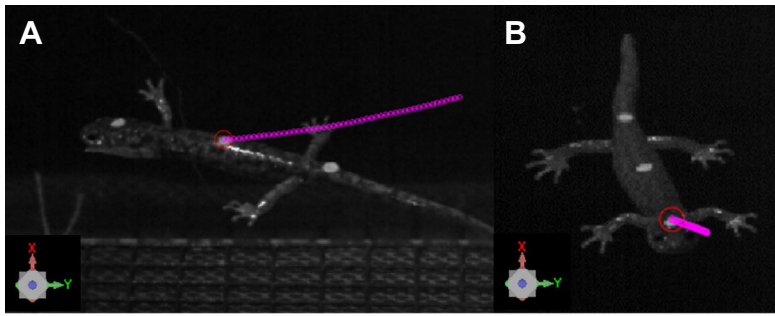


Fig. 2. Lateral views of *Aneides vagrans* gliding in a vertical wind tunnel at an airspeed approximately corresponding to the animal's terminal velocity. White paper markers (6 mm) at (A) the approximate center of mass and (B) the head were tracked using DLTdv software; the chain of purple circles shows the salamander's trajectory in the wind tunnel frame of reference and was used to calculate glide kinematics. The red circle represents the point-tracking tool in the DLTdv software. Axes are shown at the bottom left of each image.

relatively stable in the airflow and (iii) translated horizontally without lateral bending or flipping out of control (see Brown et al., 2022) (Movie 2). We quantitatively confirmed all instances of gliding by calculating horizontal velocity and the glide angle (see below); salamanders that achieved glide angles below 89 deg were considered to have glided. To ensure that such horizontal movements did not derive from non-aerodynamic forces, we evaluated only those trials in which the salamander began gliding from a near-stationary point in the vertical axis of the tunnel, with no initial horizontal component of velocity. Glide duration was limited by the size of the working section of the wind tunnel, and animals often collided with the walls of the wind tunnel while gliding; therefore, we may not report the lowest possible glide angle for the species here. Regardless, all species were given the same opportunity to exhibit gliding, thus the species comparison is valid.

For each glide and parachuting event, we tracked markers near the center of body mass (i.e. mid-trunk; Fig. 2) and on the head of the salamander across all three camera views using DLTdv point-tracking software in MATLAB (Hedrick, 2008). Cameras were calibrated in pairs by detecting and digitizing checkerboard points in stereo image pairs. We held a 10 square \times 7 square checkerboard (square length of 16 mm) such that it was visible in all three camera views, and then slowly shifted its orientation and position within the test section. The checkerboard occupied approximately 25% of the frame. We also recorded a polystyrene sphere falling vertically through the test arena to generate a gravity vector that was then used to align axes of reconstructed data with global coordinates. We estimated extrinsic and intrinsic parameters as well as distortion coefficients for each camera using these image stacks. Extrinsic parameters include rotation and translation of the three-dimensional lab coordinate system to match that of the camera's, whereas intrinsic parameters include focal length, optical center and skew coefficient of the camera that are used to transform its three-dimensional coordinate system into the recorded two-dimensional images. Using custom MATLAB code, we then reconstructed marker positions in three dimensions from each possible pair of the three camera views (i.e. front and side, front and top, side and top),

and used camera calibration information for each specific pair. Data from the two camera views that provided the best images of the markers (as quantified by smallest mean reprojection error) were selected for analysis. We used a quintic spline algorithm with tolerance values custom fitted to each tracked point and camera view to smooth positional data, interpolate points for frames in which markers were obscured, and estimate the instantaneous velocity and acceleration from the first and second derivatives of the positional data spline function, respectively. All splines were generated using the splintool function in MATLAB at a default tolerance of 0.1, which we assessed and adjusted according to the fit for each dataset. We did not filter the raw position data from any trials; the smoothing spline with custom fitted tolerance values sufficiently corrected for any noise in the data. We then used these smoothed data to calculate instantaneous vertical and horizontal velocity, vertical and horizontal acceleration, and glide angle through the recorded parachute and glide sequences (Table 2). We used the Pythagorean theorem to calculate horizontal velocity and horizontal acceleration for the approximate center of mass as the hypotenuses between the x - and y -components of total velocity and acceleration, respectively. Glide angle is considered to be the angle between the animal's trajectory and the horizontal, as calculated with Pythagorean theorem using the horizontal and vertical components of velocity. We also used the smoothed positional data to digitally reconstruct the body axis of the salamander as the line between the head and center of mass, which we then used to calculate body angle and crab angle. We considered body angle to be the angle between the salamander's body axis and the horizontal. Crab angle is defined as the absolute angle between the horizontal velocity and the projection of the salamander's body axis on the (x,y) plane, without distinguishing between the left or right direction of travel. Glide ratios were calculated by dividing the horizontal distance the salamander traveled in 1 s by the effective vertical distance traveled in that same second, and were used to calculate instantaneous glide angles through the recorded sequence (Table S2). We used RStudio (<https://www.rstudio.com/>) to run ANOVAs comparing kinematic performance between all four species and regression analyses

Table 2. Aerial performance metrics for four plethodontid salamander species used in vertical wind tunnel trials

Species (N)	Vertical velocity (m s^{-1})	Vertical acceleration (m s^{-2})	Horizontal velocity (m s^{-1})	Horizontal acceleration (m s^{-2})	Glide angle (deg)	Body angle (deg) (Avg, Δ)	Crab angle (deg) (Avg, Δ)
<i>A. vagrans</i> ($N=45$)	9.4 \pm 0.1	-0.1 \pm 0.3	0.71 \pm 0.1	2.64 \pm 0.3	85.6	0.6, 39.4	56.0, 58.1
<i>A. lugubris</i> ($N=40$)	9.9 \pm 0.3	0.2 \pm 0.2	0.35 \pm 0.1	1.90 \pm 0.1	87.3	3.6, 33.7	81.8, 97.2
<i>A. flavipunctatus</i> ($N=20$)	10.9 \pm 0.2	0.8 \pm 0.4	0.22 \pm 0.1	1.25 \pm 0.3	88.7	10.0, 21.5	128.4, 90.4
<i>E. eschscholtzii</i> ($N=3$)	9.4 \pm 0.1	0.4 \pm 0.3	0.13 \pm 0.1	1.40 \pm 0.2	89.3	5.1, 18.8	74.2, 95.9

Performance metrics include average instantaneous vertical velocity and acceleration (± 1 s.e.m.), horizontal velocity and acceleration (± 1 s.e.m.), glide angle, body angle, crab angle and average magnitude of change (Δ) in these latter two angles over behaviors of varying time intervals lasting up to 5 s.

examining the relationship between maximum amplitude of oscillations in body angle and glide performance metrics, such as glide angle and horizontal velocity and acceleration.

Finally, we qualitatively predicted the utility of gliding *in situ* for *A. vagrans* using kinematic results from the wind tunnel and trigonometry to calculate a range of hypothetically possible glide trajectories. We overlaid the range of hypothetical salamander trajectories onto existing maps of old-growth redwood crowns featuring known salamander capture locations (Spickler et al., 2006). We caution that, because duration and magnitude of parachutes and glides were functionally limited by the finite space inside the wind tunnel chamber, these predictions are likely conservative estimates of *in situ* performance for this species. The change in aerodynamics resulting from increases in horizontal speed during descent, for example, cannot be measured in the vertical wind tunnel because there is not enough space to allow salamanders to build up maximum lateral velocity before collision with the walls.

RESULTS

Aerial behavior

Drops

When jumping or dropped from a height of 3 m, *A. vagrans* exhibited control in pitch, roll and yaw that allowed maintenance of a dorsoventrally stable body orientation in the skydiving posture. Of the 200 drop trials, *A. vagrans* maintained skydiving postures 92.5% of the time (i.e. 185 ‘skydiving’ trials), and landed in prone positions 192 times (96%). In the 185 trials for which *A. vagrans* consistently maintained skydiving postures, salamanders never assumed an inverted posture. In the other 15 trials, salamanders instead bent their trunks laterally and formed a C-shape just before being dropped, then either maintained this posture throughout the descent or switched to a skydiving posture. Salamanders rotated their tails when switching from the C-shape to a skydiving posture in mid-air, resulting in aerial righting as also observed in wind tunnel trials. Salamanders that were dropped in a C-shape posture rolled into inverted positions 15 times (8.1% of skydiving trials), landed in non-prone positions eight times (4.3% of skydiving trials), and often yawed continuously in the direction of body bending. Jumping salamanders exhibited clean take-offs without foot slips or tail dragging (see Brown and Deban, 2020) in 50 jumps (83.3%), and maintained skydiving postures with prone landings 49 times (81.7%). In the other 10 trials, take-off by salamanders was hindered by either a foot slipping or a tail dragging against the substrate, resulting in either inverted body positions (9 times) or non-prone landings (5 times).

While working in the canopy, two additional observations of aerial behavior in *A. vagrans* were made *in situ*: two individuals jumped from the same coast redwood crown branch at a height of ~60 m in response to cameras moving overhead. One of these 60 m jumps was not captured on camera for closer analysis, but the salamander was observed to maintain a skydiving posture during descent. The other jump, which featured both a foot slip and a tail drag, was captured on camera and shows the salamander tumbling out of control before disappearing into the lower crown ~20 m below (C. Brown, personal observation). No salamander was subsequently located or seen falling by observers at the base of the tree.

Wind tunnel

Aneides vagrans, *A. lugubris* and *A. flavipunctatus* in free fall within a vertical airstream exhibited control in pitch, roll and yaw

that allowed maintenance of an upright skydiving posture. *Ensatina eschscholtzii* is extremely limited in control and ability to maintain a skydiving posture, occasionally assuming inverted postures; the only salamanders of genus *Aneides* to assume inverted postures did so following disturbance from external forces, such as bumping a wall inside the wind tunnel, or if dropped into the wind tunnel upside down. All species were capable of aerial righting once inverted postures were achieved, but *E. eschscholtzii* was sometimes incapable of controlling the maneuver and immediately resumed an inverted posture (Movie 3). *Aneides vagrans* and *A. lugubris* frequently held uninterrupted skydiving postures and affected vertical velocity, thus functionally parachuting; the occasional

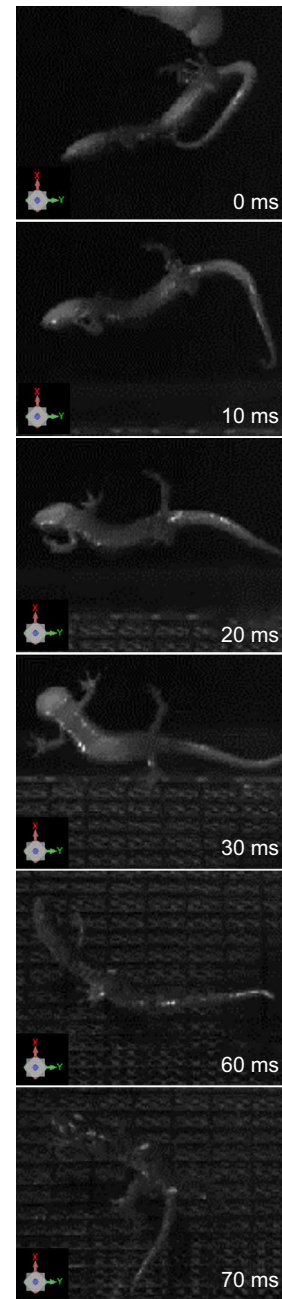


Fig. 3. An *Aneides vagrans* rapidly rotates the tail to execute an aerial righting maneuver after being dropped upside-down in a vertical wind tunnel. Time (0–70 ms) since the beginning of the aerial righting maneuver is noted in each panel. Axes are shown at the bottom left of each frame.

(*A. flavipunctatus*) to rare (*E. eschscholtzii*) skydiving postures seen in the other species were brief, often surrounded by even longer bouts of ineffective undulating, and had relatively small effects on vertical velocity and no effects on horizontal velocity or acceleration. The key feature that distinguished parachuting and gliding from uncontrolled behaviors, such as inert falling and ineffective undulating, was a lack of lateral bending and the extension of all four limbs perpendicular to the trunk.

Unless actively maneuvering, a skydiving posture was the default for *A. vagrans*, *A. lugubris* and, to a lesser extent, *A. flavipunctatus* in vertical descent. Wind tunnel recordings revealed that, in addition to extending the limbs laterally, *A. vagrans* and *A. lugubris* retract the limbs (especially the forelimbs) dorsally, placing much of the limb area above the center of mass. From this stable posture, all three studied *Aneides* species then used movements of the tail and limbs to alter body roll, pitch and yaw; importantly, *Aneides* spp. returned to a skydiving posture after correcting for roll, pitch or yaw and did not spin out of control from inertial forces as did *E. eschscholtzii*. Swinging the tail upward through the sagittal plane pitched salamanders head-down; contrariwise, tail motion downward pitched salamanders head-up (Movie 2). Body yaw was similarly elicited, but with the tail swinging left through the coronal plane to yaw right and swinging right through the coronal plane to yaw left. The limbs moved as coordinated ipsilateral pairs to correct for changes in roll. A coordinated adduction of the right forelimbs and hindlimbs resulted in rolling right; simultaneous abduction of the right forelimbs and hindlimbs resulted in a left roll, with vice versa outcomes for comparable motion of the left-side limbs. In *A. vagrans* and *A. lugubris*, body roll occasionally resulted in a banked turn rather than as a stabilizing maneuver. Banked turns in descending *A. vagrans* and *A. lugubris* correlated with asymmetric movements of the hindlimbs. Adducting a single hindlimb while in the skydiving posture resulted in banking turns and changes in the crab angle during descent (Movie 1). Once hindlimbs were asymmetrically positioned, the salamander banked in the direction of the adducted limb. Total duration of the banked turn depended on the amount of time a single limb was held adducted; the maneuver ended shortly after the salamander returned to a skydiving posture

with all limbs extended. Visible changes in pitch, yaw and roll began an average of 42 ± 13 ms after the onset of the appendage movement, but these maneuvers could take up to 100 ms to initiate. Occasionally, these controls failed when the salamander contacted the acrylic walls of the flight chamber, resulting in an inverted position. Individuals in this condition then exhibited a rapid rotation of the tail to rapidly effect righting and to assume a skydiving posture, a maneuver that took an average of 116 ± 56 ms to complete (Fig. 3).

A skydiving posture was often deployed by *A. vagrans* and *A. lugubris* immediately upon being dropped into the wind tunnel. Parasagittal extension of the vertebral column resulted in an overall ventral-convex body shape, with the head and the tail of the salamander positioned above the center of body mass. Salamanders that held uninterrupted skydiving postures could slow their descent, come to a near standstill in the vertical airflow, and even ascend, all of which correspond to a reduction in descent velocity and thus indicate functional parachuting.

Gliding in *A. vagrans* and *A. lugubris* was associated with repeated parasagittal undulations of the tail and torso coupled with absence of lateral bending, an abduction of all four limbs laterally perpendicular to the trunk, and a slight dorsal retraction of all four limbs. In one trial, gliding was accomplished via a repeated circumduction of all four limbs that resembled flapping. Several observed instances of gliding began with a mid-air directional change of trajectory in the horizontal plane. Kinematic data from these glides showed that horizontal velocity increased through the glide. The horizontal acceleration was slightly higher at the beginning of glides, coinciding with the beginning of the tail-pumping, and leveled out after initiation.

Parachuting and gliding kinematics

Aneides vagrans parachuted longer than the other species before breaking the skydiving posture, moving out of frame, or hitting a wall ($F_{3,58}=7.821$, $P<0.001$; Fig. 4). These skydiving postures corresponded to changes in vertical velocity and deceleration in the vertical plane. While parachuting and gliding, *A. vagrans* and *A. lugubris* had average instantaneous vertical velocities of 9.40 and

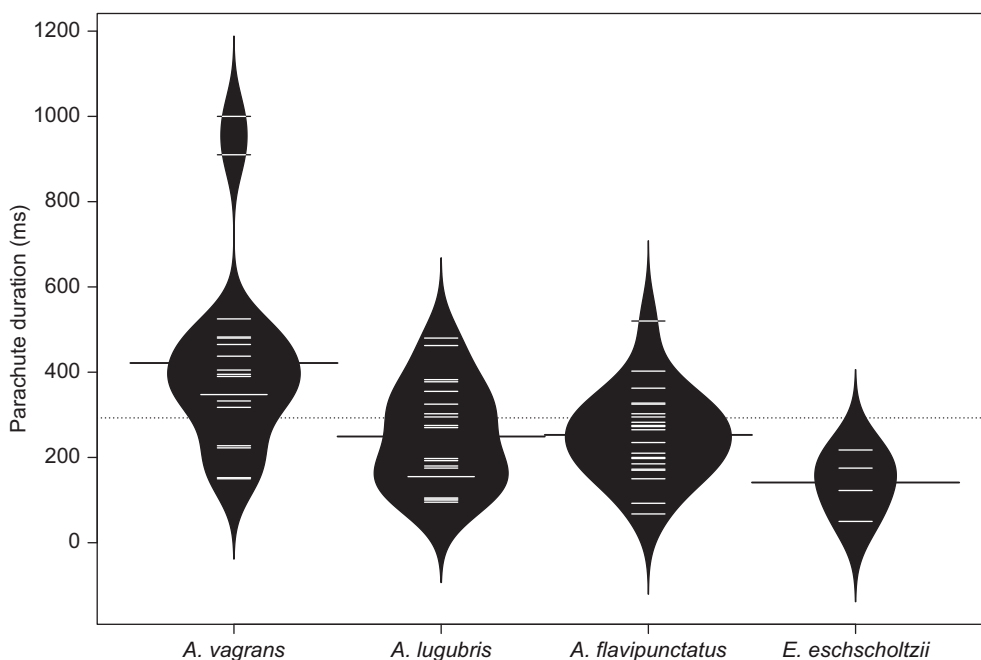


Fig. 4. Bean plots of parachuting duration (ms) in *Aneides vagrans*, *Aneides lugubris*, *Aneides flavipunctatus* and *Ensatina eschscholtzii*. Bean shape is given by a normal density trace and its mirrored equivalent. Black lines represent the mean parachuting duration; white lines represent actual durations, with wider white lines indicating multiple parachuting events of roughly the same duration. The horizontal dashed line represents the overall average parachuting duration for all species. Bean height represents ± 3 standard deviations from the mean.

9.90 m s⁻¹ and accelerations of -0.10 and 0.20 m s⁻², respectively (Table 2). Average instantaneous horizontal velocity was 0.71 and 0.35 m s⁻¹ and acceleration was 2.64 and 1.90 m s⁻² for *A. vagrans* and *A. lugubris*, respectively. Instantaneous glide angles averaged 85.6 deg for *A. vagrans* and 87.3 deg for *A. lugubris*, though the minimum glide angle achieved was lower compared with the species averages for nearly all individuals tested (Table S2). Brief bouts of parachuting by *A. flavipunctatus* and *E. eschscholtzii* were less effective and never resulted in instantaneous glide angles below ~88 and ~89 deg, respectively (Table S2).

For *A. vagrans*, body angle oscillated around 0.6 deg while parachuting and gliding; maximum amplitude of oscillations in body angle as low as 3 deg and as high as 88 deg were observed but did not correlate with horizontal velocity ($F_{1,9}=2.317$, $P=0.144$), horizontal acceleration ($F_{1,9}=0.055$, $P=0.817$) or glide angle ($F_{1,9}=1.686$, $P=0.209$). Average crab angle while gliding was 56±30 deg (Table 2) (with 0 deg representing a head-first glide and 90 deg representing a lateral or sideways glide). Crab angles during glides often varied through time; the average minimum crab angle

relative to the glide direction was 27 deg, and the average maximum crab angle was 81 deg. On average, crab angle changed 58±27 deg during a single glide (Table 2). *Aneides lugubris* also oscillated between positive and negative body angles, pivoting around an average body angle of ~3.6 deg. Oscillations between positive and negative body angles did not significantly correlate with horizontal velocity, horizontal acceleration or glide angle, as with *A. vagrans*. The average minimum crab angle for *A. lugubris* was 42 deg, and the average maximum crab angle was 103 deg. On average, crab angle changed 97±29 deg during a single glide (Table 2).

At an equilibrium glide angle of 85 deg and a horizontal velocity of roughly 0.7 m s⁻¹ (Brown et al., 2022), *A. vagrans* can hypothetically intercept the home trunk of old-growth *S. sempervirens* (with over 60 vertical branches via reiterated trunks; Sillett, 1999) from numerous starting locations in a given crown (Fig. 5).

DISCUSSION

Arboreal plethodontid salamanders (genus *Aneides*), especially the highly arboreal *A. vagrans*, exhibit considerable aerial control

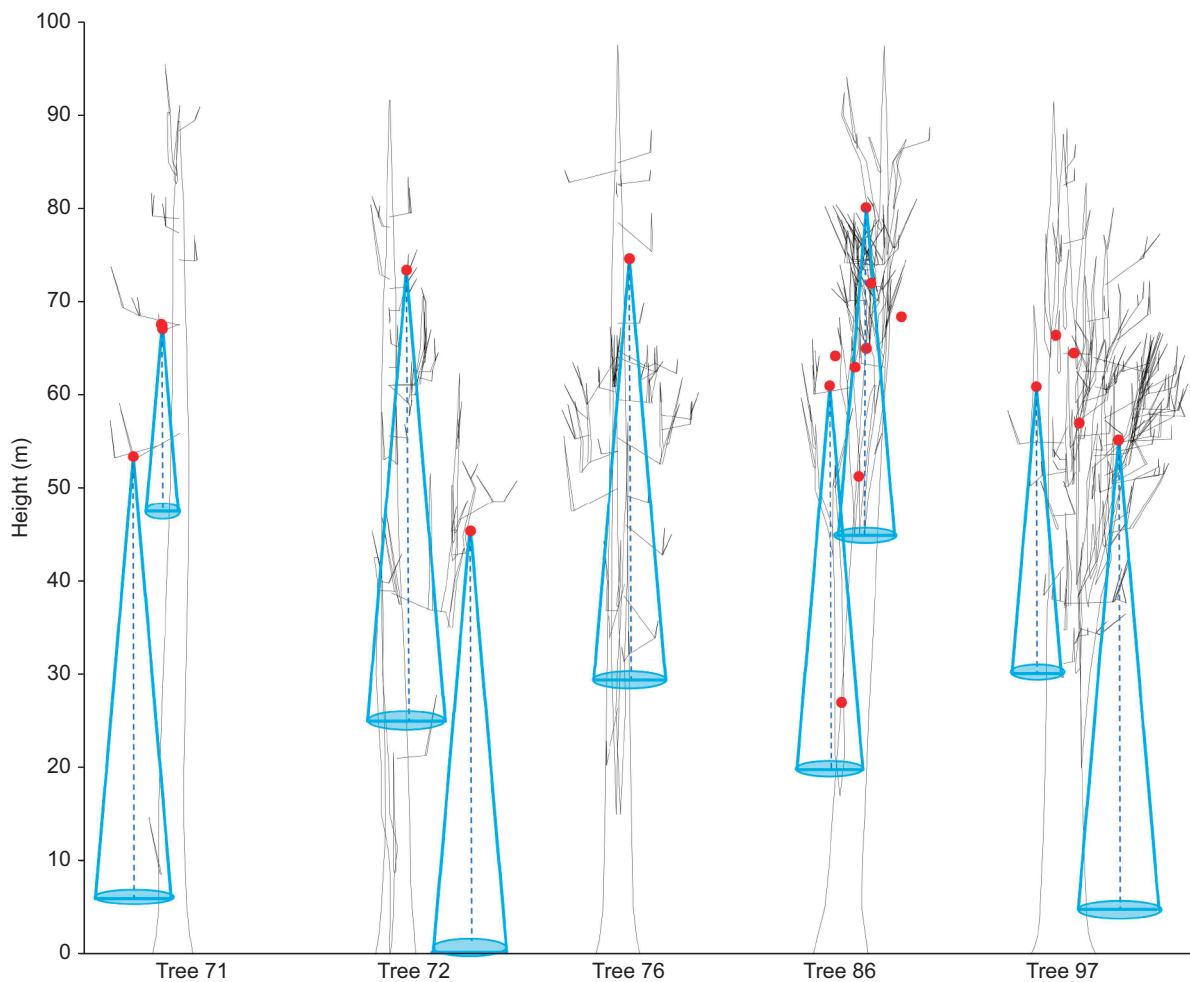


Fig. 5. Two-dimensional projected spatial geometries for five coast redwoods (*Sequoia sempervirens*; trees 71, 72, 76, 86 and 97) showing hypothetical parachute and glide trajectories of wandering salamanders (*Aneides vagrans*). Parachute (dashed blue lines) and glide trajectories (solid blue lines) were calculated using a glide angle of 90 and 85 deg, respectively, and begin from known salamander capture locations (red circles) in these five redwood crowns (tree-shaped black lines). The triangles above, which *in situ* and in three dimensions would take the form of cones, terminate once they have made sufficient contact with the home trunk; salamanders are likely capable of landing within the radius created by such cones (blue ellipses). Identification numbers for trees are located below each tree and height is marked in meters. Note that the trajectories shown are likely insufficient for delivering a gliding salamander from one tree to another, but sufficient in delivering a gliding salamander to another location within a given crown (except for one salamander in the lower crown of tree 72).

during descent, both when dropped from heights and when falling within the jet of a vertical wind tunnel. Aerial behavior in *A. vagrans* and *A. lugubris* is comparable to that of small arboreal squamates, some of which glide via appendicular and axial movements (e.g. repeated parasagittal undulations of the tail), and parachute via specific skydiving postures that maximize projected area and thus drag during falling (Jusufi et al., 2008; Wassersug et al., 2005). From a stable dorsoventral posture within an airstream, *Aneides* can alter its rate of vertical descent, and *A. vagrans* and *A. lugubris* can utilize appendage movements to initiate horizontal movement. However, much like other animals in freefall, these salamanders can execute actions to reorient and slow the rate of descent, but cannot necessarily optimize these actions simultaneously (Wassersug et al., 2005). Jumping salamanders that exhibited foot slipping or tail dragging during take-off also frequently assumed inverted body positions with reduced aerial control. Jumping *Aneides* otherwise tend to limit lateral body bending, push off with two feet, and display lower horizontal take-off speeds compared with other plethodontids (Brown and Deban, 2020). When falling upside-down, salamanders sometimes employ rapid tail rotation similar to the aerial righting reflex seen in other tetrapods of comparable size, such as house geckos (Jusufi et al., 2011).

Behavior frequencies (Brown et al., 2022) and kinematics suggest that *A. vagrans* has the most and *E. eschscholtzii* the least aerial control of all species tested. That only three of five individual *E. eschscholtzii* tested ever achieved an effective skydiving posture begs questions about variability of responses to falling; within individuals, qualitative observations suggested that no individuals of any species improved aerial performance as trials progressed. Very steep glide angles (~84 deg) were observed here for *A. vagrans* (Table 2). These angles are nonetheless comparable to that derived from a resolved-flow analysis for a simple cylinder (see Ellington, 1991). The body morphology of salamanders is not conducive to simple geometric modeling (and inclusion of the narrow tail results in length:diameter estimates exceeding 25), but descent angles are nonetheless not vertical. Although seemingly very steep, associated trajectories would be sufficient to contact the home trunk or nearby branches during falls from tall home trees (Fig. 5). These calculations assume instantaneous acquisition of a near-equilibrium glide (as is effectively attained when salamanders are dropped into the vertical wind tunnel), whereas in nature, animals must fall and accelerate to reach a terminal velocity. Nonetheless, free fall under gravity requires only 1 s to attain a speed of ~10 m s⁻¹, with an associated vertical displacement of ~5 m. This distance is small relative to the heights of coast redwood trees (see Fig. 5), suggesting that gliding and associated maneuvering can convey substantial benefits once the appropriate aerial posture has been achieved.

At an equilibrium glide angle of 85 deg and a horizontal velocity of roughly 0.7 m s⁻¹, *A. vagrans* would likely not be able to glide from one tree to another; however, salamanders can potentially intercept the home trunk from numerous starting locations in the crowns of old-growth *S. sempervirens* (Fig. 5). Such trees can harbor over 60 vertical branches (i.e. reiterated trunks) within a single crown complex (Sillett, 1999), so if the home trunk were not in range, *A. vagrans* could instead parachute or glide into a number of reiterated trunks. However, reaching a vertical trunk does not necessarily imply an end to descent, especially at high translational velocities. Considering the abundance of relatively soft, horizontally oriented fern mats in the crowns of *S. sempervirens*, it is plausible that *A. vagrans* employs repetitive glides while

dropping from one fern mat to another, which might facilitate escape from predators such as owls and omnivorous mammals. That *A. vagrans* readily jumps from great heights (~60 m) in the redwood canopy suggests that this may be a common behavioral response to as yet uncharacterized stimuli.

Gliding could also potentially facilitate foraging efficiency in these salamanders. Invertebrates inhabiting fern mats of coast redwoods experience population explosions during the wet season, resulting in much higher invertebrate biomass density compared with other parts of the tree (Jones, 2005). Also, the upper canopy during the dry season receives more light and wind as compared with the lower canopy, and the air is less humid (Parker, 1995; Sillett and Van Pelt, 2007). Fern mats in the upper canopy, regardless of size, are thus subject to more frequent and severe periods of desiccation than those in the lower canopy. Salamanders that disperse in search of food and mates during the wet season may use gliding into the lower canopy for these purposes during the dry season; mummification in the upper canopy might otherwise be the outcome (see Spickler et al., 2006). The only alternative, walking down redwood trunks, only prolongs exposure to desiccation and predation and would hypothetically require greater expenditure of energy (Full, 1986; Feder, 1987). Additionally, walking from the upper to lower crown would likely require non-linear translation along the trunk and an increase in the total distance traveled, as *A. vagrans* is reluctant to walk straight down and does so less efficiently than walking upward or horizontally (Aretz et al., 2022).

Stable body postures in the air, alteration of descent speed and frequent controlled gliding in the vertical wind tunnel suggest that *A. vagrans* routinely undergoes aerial descent, but the natural ecological occurrence of this behavior remains to be established. Previously overlooked morphological features underpinning such flight also warrant closer inspection. Although similar to other climbing plethodontids, *A. vagrans* and *A. lugubris* also possess relatively long limbs (Table 1) and digits as well as large feet relative to body size, features traditionally attributed to a highly arboreal lifestyle (Stebbins, 2003). The large feet and long toes of *A. vagrans* and *A. lugubris* do seem to form ventrally concave surfaces while parachuting (Fig. 2), and may serve to produce useful lift and drag (Holden et al., 2014). The relatively long limbs position the feet uncommonly far from and above the center of mass in *A. vagrans* and *A. lugubris*, suggesting the possibility for enhanced stability and aerodynamic torque as well as adaptation for aerial maneuvering compared with species with shorter limbs (see Table 1; see also Wang et al., 2013). Perhaps the larger feet and longer limbs of *A. vagrans* and *A. lugubris* relative to other plethodontid salamanders known to climb associate with the additional selective pressure of occasional extended descents. The selection pressures imposed on controlled falling from heights are substantial, and have resulted in the evolution of diverse aerial behaviors among arboreal invertebrates and vertebrates alike. Nonetheless, their presence in arboreal salamanders is surprising, and calls for further work on the natural occurrence of falling, gliding and aerial behaviors in other inconspicuous canopy-dwelling tetrapods.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: C.E.B., R.D., S.M.D.; Methodology: C.E.B., E.S., R.D., S.M.D.; Software: E.S.; Validation: C.E.B., R.D., S.M.D.; Formal analysis: C.E.B., E.S.; Investigation: C.E.B., E.S.; Resources: C.E.B., R.D.; Data curation: C.E.B., E.S.; Writing - original draft: C.E.B.; Writing - review & editing: C.E.B., E.S., R.D., S.M.D.; Visualization: C.E.B.; Supervision: R.D., S.M.D.; Project administration: C.E.B., S.M.D.; Funding acquisition: C.E.B., R.D.

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Data availability

Data and code needed to replicate these results, including metadata and explanatory documents, are available at Zenodo: 10.5281/zenodo.6724451. All data are also available upon request to the corresponding author.

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