Herpetology Notes 19: 209–214, published on 10 April 2026

Backing out: dead-end tunnels reveal capacity for reverse concertina movement in Cornsnakes, *Pantherophis guttatus* (Linnaeus, 1766)

Bizaya Gurung[1], Christine Vega[2,3], and Henry Astley[3,*]

Snakes' limbless, elongated bodies allow them to fit through tight spaces and conform to geometrically complex substrates, allowing them to excel in complex, cluttered, and confined spaces (Mosauer, 1932; Jayne, 2020; Astley, 2022; Tingle et al., 2024). This versatility relies upon diverse locomotor strategies (e.g., slithering, tunnel concertina, sidewinding, rectilinear), which are matched to the mechanical demands of particular environments (Jayne, 2020). Concertina is especially useful in tight tunnels and on cylindrical branches — snakes anchor sections of their body against tunnel walls, extend the anterior part of their body, contract, then repeat this locomotion (Jayne, 1986, 2020; Astley and Jayne, 2007; Astley, 2018). Despite the higher cost of transport and slower progress compared to slithering (Jayne, 1986; Walton et al., 1990; Jayne and Davis, 1991), concertina locomotion allows snakes to move in tight, smooth, and narrow spaces, which lack suitable surfaces for slithering propulsion, such as moving through a rodent burrow (Mosauer, 1932; Gray, 1946; Jayne, 1986).

Dead ends are a common problem in real-world tunnels, but how snakes respond to this challenge is unknown. This problem is particularly acute due to the uncertainty surrounding whether snakes are capable of "reverse" locomotion. During all of the modes of snake locomotion, motions propagate in an anterior-to-posterior fashion, whether this is the vertebral bending of slithering or sidewinding, the ventral scale motions of rectilinear, or establishment of anchor points during concertina (Mosauer, 1932; Gray, 1946; Jayne, 1985, 1986, 2020; Jayne and Davis, 1991; Astley and Jayne, 2007; Astley, 2018; Newman and Jayne, 2018); posterior-to-anterior propagation has only been observed in Hydrophiinae (Heatwole, 1999) and Acrochordidae (Jayne, 2020), in both cases only during swimming. However, the absence of observed instances cannot prove that posterior-to-anterior motions are impossible, only that they are likely rare, mechanically disadvantageous, difficult to elicit, or some combination thereof. Amphisbaenian lizards provide a striking counter-example, being capable of rectilinear locomotion both forwards and backwards (Gans, 1969; Hohl et al., 2014). Conversely, the neural control of snake locomotion remains poorly studied, and it remains possible that some longitudinal asymmetry in the nervous system may indeed preclude posterior-to-anterior propagation, only being overcome in a few highly aquatic lineages (Jayne, 2020).

To test whether snakes are capable of "reverse" (posterior-to-anterior) locomotion in an ecologically relevant manner, we recorded the motions of cornsnakes moving through an extremely narrow, dead-end tunnel. By categorising the locomotion observed once the snakes became aware of the dead end, we could document the range of strategies employed and whether any such strategies included posterior-to-anterior motions.

Materials and Methods

Study Species. Twelve wild-caught adult Cornsnakes, *Pantherophis guttatus* (Linnaeus, 1766), were originally purchased from a commercial vendor (Glades Reptiles, Bushnell, FL, USA); all animals have been in captivity for over five years. The average snout-vent length and weight of the individuals used in this study were 113 ± 8 cm (range: 99–128 cm) and 552 ± 60 grams (range: 445–675 g), respectively. There were no perceptible differences in behaviour across snake sizes. Snakes were

---

[1] Akron STEM High School, Akron, Ohio, 44306, USA.

[2] Department of Biology, Wesleyan College, Macon, Georgia, 31210, USA.

[3] Department of Biology, University of Akron, Akron, Ohio, 44325, USA.

[*] Corresponding author. E-mail: hastley@uakron.edu

housed individually in 61 x 122 x 38 cm PVC cages with aspen substrate and kept on a 12h:12h light:dark cycle. They were fed pre-killed adult mice bi-weekly. All experiments were approved by the University of Akron IACUC (22-06-08-ASD).

Setup. A dead-end narrow tunnel 243.8 cm long, with inner dimensions of 5.1 cm wide and 3.7 cm tall was constructed using expanded PVC (Home Depot, Veranda HP Cellular White PVC Trim Model # H190HWS4 and 827000002). These dimensions were used because the tunnel was only about two snake body widths, which would limit the physical space snakes had to turn around once they reached the dead-end, allowing for the possibility of a turn but making it difficult enough to potentially induce reverse concertina locomotion. An acrylic infrared (IR) transparent sheet (ePlastics.com, SKU ACRY31430.080PM24X48) was placed over the top of the tunnel and secured with tape. This film had near-zero transmission below 750 nm, rendering it opaque to visible light, while being nearly transparent at 850 nm, the frequency of the camera's sensor, thereby simulated a tunnel environment for the snake while allowing the snake's behaviours within the tunnel to be filmed using a night-vision camera (Minolta MN80NV). All trials were filmed in dorsal view with the camera mounted on a tripod. As the snake progressed through the tunnel, we moved the camera to keep the snake in view.

Experiments. Each individual snake was filmed for three, 20-minute trials. Temperature during behavioural trials was maintained at 28–31°C. The snake was placed head-first into the tunnel entrance and allowed to either move freely or habituate to the tunnel. We gently nudged the snake with a meter stick or stiff wire to encourage movement as needed, either touching the tail during the initial progression towards the dead-end, or the portion closest to the dead-end once the snake had reached the end and was turning around or performing reverse concertina. Gentle taps and scraping motions on the outside of the tunnel were also found to prompt movement from still snakes. Trials where the snake reached the dead-end and turned more than 50% of their total body length around were considered a success. Trials where the snake either did not reach the dead-end or did not turn at least 50% of their total body length around within the 20-minute window were considered a failure. Trials were terminated for individuals that resisted entering the tunnel at all.

Trials videos were reviewed and the frequency of consistent behaviours within and across trials were determined. Detailed descriptions of each observed behaviour and the per-trial frequency of these behaviours are reported in the results.

Results

Observed behaviour categories. Snakes moved through the tunnel in most trials, with only one trial in which a snake refused to enter the tunnel at all. The behaviours exhibited fall into the following categories, some of which co-occur.

Forward concertina.—In all 35 trials, the snake initially performs tunnel concertina as described in numerous prior papers, broadly consisting of a cycle in which the posterior body anchors by statically pressing against the tunnels walls while the anterior body straightens, pushing the head forward, followed by lateral flexion of the anterior-most body for the establishment of an anchor. New anchor bends are formed in an anterior-to-posterior propagating manner, while the posterior bends are straightened in a similar manner, resulting in posteriorly propagating regions of movement and stasis.

Hairpin (sharp) turns.—In 21 of 35 trials, the snake forms a tight bend in its anterior body, and begins to propagate the body through this bend in an anterior-to-posterior manner, either by continuous motion (indicating slithering, possibly with contributions from rectilinear) or cyclic start-and-stop motion (indicating concertina) (Fig. 1). All motions proceed in an anterior-to-posterior manner, resulting in the snake's head and anterior body now being oriented in the opposite direction, towards the open end of the tunnel rather than the dead-end. There are two variants of this, but snakes could switch from one to the other sequentially during a hairpin turn behaviour:

- ○ Parallel alignment: The anterior portion of the body is positioned lateral to the posterior portion of the body as they move past each other (Fig. 1A). This occurred in 20 of 21 hairpin turn trials.
- ○ Crossing over: The anterior portion of the body is superior to the posterior portion of the body as they move past each other (Fig. 1B). This occurred in four of 21 hairpin turn trials.

Reverse concertina.—Identical to forward concertina, but the direction of propagation of moving and static regions is reversed, as is the overall motion. The posterior body straightens and moves posteriorly while the anterior regions use lateral bends to anchor against the walls, then the posterior-most region of the body laterally bends to form a new anchor region, with new anchor bends forming in an anteriorly-propagating

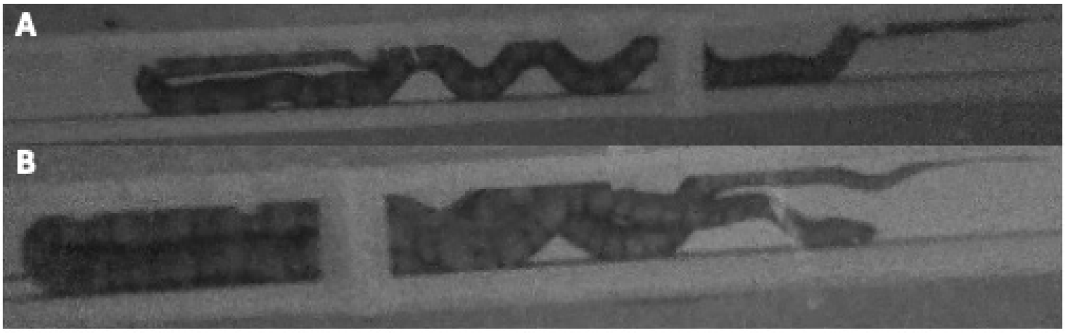

Figure 1. Two types of hairpin turns are used by Cornsnakes in extremely narrow tunnels to turn around. Snakes can use a combination of these different types to successfully turn around. (A) Parallel hairpin turn where the anterior portion of the body is positioned lateral to the posterior body as they move past each other. (B) The anterior portion of the body is superior to the posterior portion of the body as they move past each other. Photos by Bizaya Gurung and Henry Astley.

fashion along the body, with a similarly anteriorly-propagating pattern of straightening in the anterior body (Fig. 2). This was the rarest behaviour, occurring in only three of 35 trials, for a total of eight cycles.

Trial Behavioural Pattern. In each trial, snakes exhibited similar patterns of movement: the snake was introduced into the tunnel and, once completely within the tunnel, proceeded forward using forward concertina locomotion, motivated by occasional prodding. Upon reaching the dead-end, either making contact with their snout or tongue, they would explore the area briefly, then select one of the strategies listed below; snakes would sometimes use only a single behaviour, but other times would transition from one to another. As noted, once the snake had reoriented sufficiently to easily move through the remainder of the tunnel, the trial was ended (Tab. 1).

Detailed description of the reverse concertina. Reverse concertina, although rare, was observed in a few snakes when manoeuvring within tight, narrow, and confined environments—especially when encountering a dead-end. In forward concertina movement, a snake alternately anchors portions of its body against the tunnel walls, extends its anterior section forward, forms new anchor points, and then pulls the rest of its body forward. This movement is then repeated over and over for forward progression. In reverse concertina locomotion, the process is executed in the opposite direction. The snake anchors sections of its body against the tunnel wall, but then extends the posterior part of its body backward, instead of the anterior half. The snake then re-anchors its body rearwards, allowing itself to pull itself backward instead of forward. A video of this behaviour is available on-line (Astley et al., 2025).

Discussion

When faced with a dead-end tunnel, *Pantherophis guttatus* employ multiple strategies (e.g., hairpin turns, parallel alignment, body overlap manoeuvres) to turn around in tight, confined spaces. Most interestingly, they are capable of "reverse" concertina, which requires propagation of body motion from posterior-to-anterior. Axial bending is common across several vertebrate groups (e.g., fish, salamanders, snakes, and lizards), but propagation of whole-body bending motion in terrestrial environments has currently only been documented from anterior-to-posterior direction or in standing waves (Gray, 1953; Hildebrand, 1985; Alexander, 1992; Biewener, 2003). A few rare examples of posterior to anterior propagation exist, including the aforementioned swimming snakes and rectilinear locomotion in amphisbaenians (Gans, 1969; Heatwole, 1999; Hohl et al., 2014; Jayne, 2020). There is also an observation of a South American Small-eyed Coralsnake (*Micrurus lemniscatus*) generating a large lateral bend caudally, which was propagated anteriorly to regurgitate a Brown-banded Watersnake (*Helicops angulatus*) (Mortensen et al., 2025). However, the propagation of this lateral bend did not involve the whole body and was not used for locomotion (Mortensen et al., 2025). Nevertheless, alongside previous publications, our results show that snakes are indeed capable of generating "reverse" propagation under different conditions. The implications for neural control remain uncertain, particularly given the minimal knowledge of the neural control of snake locomotion (Tingle et al., 2024), but would require any such system to be capable of anterior flow of information. As a counter-example, a network of central

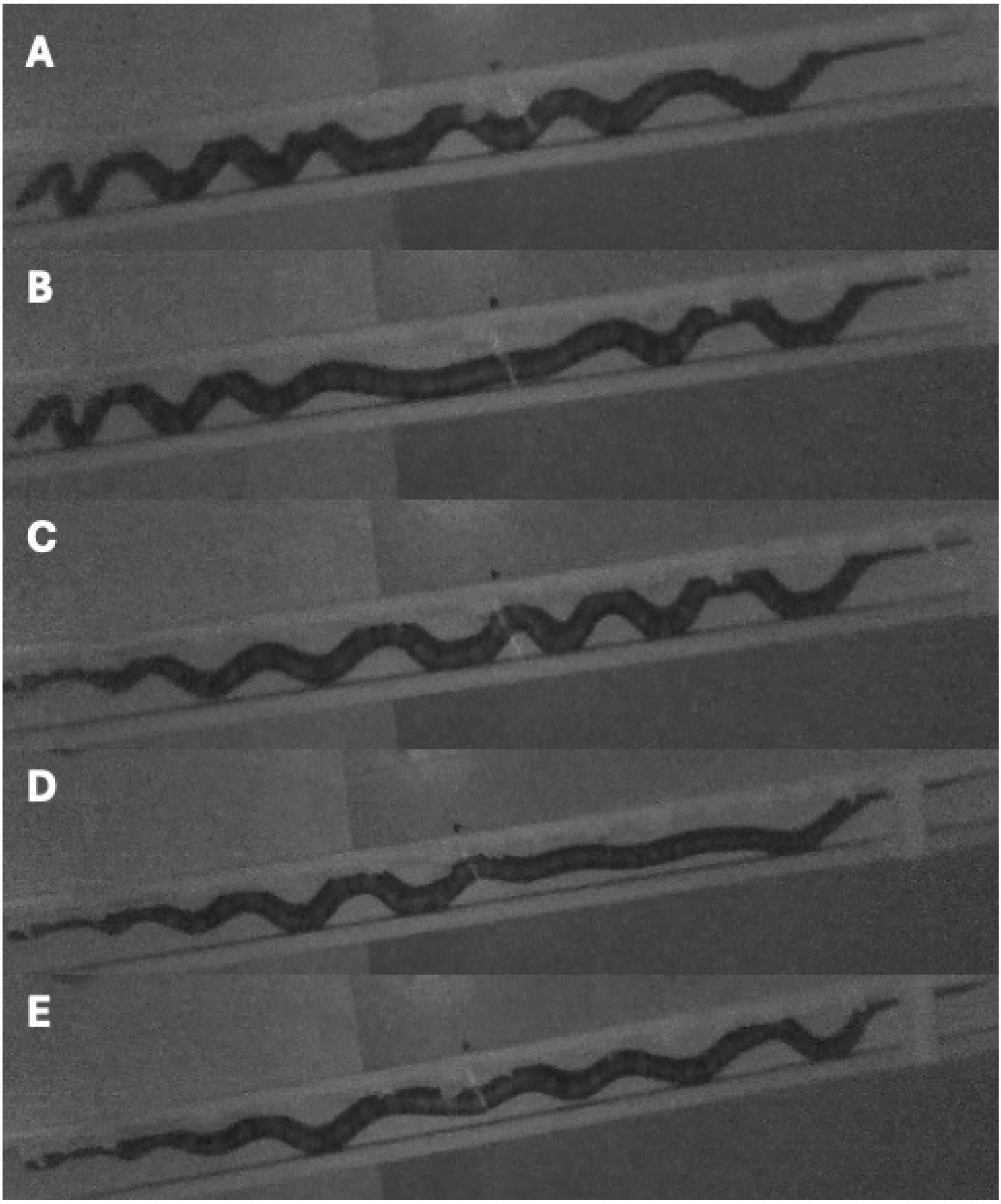

Figure 2. Cornsnake performing reverse concertina in an extremely narrow tunnel. (A) The Cornsnake initiated reverse concertina by posteriorly propagating bends toward the tail which it will use to pull its body backward. (B) A relatively straight extension region forms approximately halfway down the snake's body length. (C) and (D) show this cycle of anchoring and propagating repeating to move the snake backwards. Photos by Bizaya Gurung and Henry Astley.

pattern generators (CPGs) in which neural connections are only in the anterior-to-posterior direction is capable of generating typical anterior-to-posterior motions (Lu et al., 2006), but would be incapable of producing posterior-to-anterior motions observed here, thus can be ruled out unless supplemented with additional paths for anterior information flow.

Snakes frequently utilise burrows and tunnels

Table 1. Frequency of behavioural strategies used by individual snakes during each trial. Individual 11 only completed 2 trials because of shedding.

Individual	Trial number	Response type (# of cycles)				Outcome
		Concertina	Hairpin turns		Reverse concertina	
			Crossing over	Parallel		
1	1	6	0	0	0	success
1	2	4	0	0	0	success
1	3	3	0	1	0	success
2	1	3	0	0	0	fail
2	2	2	0	0	0	success
2	3	2	0	1	1	success
4	1	0	0	0	0	fail
4	1	3	0	0	0	fail
4	2	3	0	0	0	fail
5	1	3	2	1	0	success
5	2	1	1	0	0	success
5	3	3	0	0	0	success
6	1	2	0	1	0	fail
6	2	2	0	0	0	fail
6	3	4	0	1	0	fail
7	1	1	0	1	0	fail
7	2	3	0	0	0	success
7	3	3	0	1	0	success
9	1	1	0	0	0	success
9	2	3	0	1	5	fail
9	4	4	1	1	0	success
10	1	5	0	0	0	fail
10	2	2	0	1	0	success
10	3	4	0	1	0	success
11	1	4	0	3	2	fail
11	2	2	0	1	0	success
12	1	4	1	1	0	success
12	2	4	0	1	0	success
12	3	3	0	1	0	success
13	1	3	0	1	0	ends
13	2	4	0	0	0	success
13	3	4	0	2	0	success
14	1	2	0	1	0	fail
14	2	1	0	2	0	success
14	3	1	0	0	0	success

constructed by other animals, for foraging or shelter (Himes, 2001; Whitaker and Shine, 2003; Rudolph et al., 2007; Bruton et al., 2014; Johnson et al., 2022; Bolt et al., 2023). Some tunnels may expand near the end, which allows both the original inhabitants and the snakes to easily turn around and exit the tunnel, but tunnel architecture is unpredictable and snakes may encounter tunnels that narrow and come to a dead end, either by design as an anti-predator measure or due to structural failures (Coss and Owings, 1978). These results show not only that snakes are capable of navigating the most difficult aspects of confined environments, but also that they are capable of novel and previously undescribed strategies which give deeper insights into the neural control of snake locomotion. However, future work is needed to determine the ratio of responses in freely-moving animals which are not provided additional stimuli or prompting.

Acknowledgments. Funded by NSF BIO Award #2045581 to HCA and NSF DRL Award #2342578 to Drs. Rollmann, Layne, DeJarnette, and Vanderelst of the University of Cincinnati. The authors also thank Jenna Griffith for snake length measurements.

References

Alexander, R.M. (1992): Exploring Biomechanics: Animals in Motion. New York, USA, W H Freeman.

Astley, H.C. (2018): Traversing Tight Tunnels—Implementing an Adaptive Concertina Gait in a Biomimetic Snake Robot. In: Earth and Space 2018, Proceedings of the 16th Biennial International Conference on Engineering, Science, Construction, and Operations in Challenging Environments. p. 158–168. Malla, R.B., Goldberg, R.K., Roberts, A.D. (Eds.), Reston, VA, USA, American Society of Civil Engineers.

Astley, H.C. (2022): Slithering Across Worlds – Snake-Inspired Robots for Extraterrestrial Exploration. In: Biomimicry for Aerospace: Technologies and Applications. p. 261–290. Eggermont, M., Shyam, V., Hepp, A. (Eds.), Cambridge, MA, US, Elsevier Science.

Astley, H.C., Jayne, B.C. (2007): Effects of perch diameter and incline on the kinematics, performance and modes of arboreal locomotion of corn snakes (*Elaphe guttata*). Journal of Experimental Biology **210**(21): 3862–3872.

Astley, H., Vega, C., Gurung, B. (2025): Reverse Concertina Locomotion Video. figshare. Media. https://doi.org/10.6084/m9.figshare.30913673.v1

Biewener, A.A. (2003): Animal Locomotion. New York, USA, Oxford University Press.

Bolt, M.R., Bauder, J.M., Legare, M.L., Jenkins, C.L., Rothermel, B.B., Breininger, D.R. (2023): Eastern Indigo snake (*Drymarchon couperi*) shelter site use in peninsular Florida, USA, and implications for habitat conservation. Herpetological Conservation and Biology **18**(2): 362–373.

Bruton, M.J., McAlpine, C.A., Smith, A.G., Franklin, C.E. (2014): The importance of underground shelter resources for reptiles in dryland landscapes: A woma python case study. Austral Ecology **39**(7): 819–829.

Coss, R.G., Owings, D.H. (1978): Snake-directed Behavior by Snake Naive and Experienced California Ground Squirrels in a Simulated Burrow. Zeitschrift für Tierpsychologie **48**(4): 421–435.

Gans, C. (1969): Amphisbaenians, reptiles specialized for a burrowing existence. Endeavour 28(105): 146–151.

Gray, J. (1946): The mechanism of locomotion in snakes. Journal of Experimental Biology **23**: 101–120.

Gray, J. (1953): The locomotion of fishes. In: Essays in Marine Biology. p. 1–16. Marshall, S.M., Orr, A.P. (Eds.), London, UK, Oliver and Boyd.

Heatwole, H. (1999): Sea Snakes. Malabar, Florida, USA, Krieger Publishing Company.

Hildebrand, M., Bramble, D.M., Liem, K.F., Wake, D.B. (Eds.) (1985): Functional Vertebrate Morphology. Cambridge, Mass, USA, Harvard University Press.

Himes, J. (2001): Burrowing ecology of the rare and elusive Louisiana pine snake, *Pituophis ruthveni* (Serpentes: Colubridae). Amphibia-Reptilia **22**(1): 91–101.

Hohl, L.S.L., Loguercio, M.F.C., Buendía, R.A., Almeida-Santos, M., Viana, L.A., Barros-Filho, J.D., Rocha-Barbosa, O. (2014): Fossorial gaits of a shovel-headed amphisbaenian. Journal of Zoology **294**(4): 234–240.

Jayne, B.C. (1985): Swimming in constricting (*Elaphe g. guttata*) and nonconstricting (*Nerodia fasciata pictiventris*) colubrid snakes. Copeia **1985**: 195–208.

Jayne, B.C. (1986): Kinematics of terrestrial snake locomotion. Copeia **1986**: 195–208.

Jayne, B.C. (2020): What Defines Different Modes of Snake Locomotion? Integrative and Comparative Biology **60**(1): 156–170.

Jayne, B.C., Davis, J.D. (1991): Kinematics and performance capacity for the concertina locomotion of a snake (*Coluber constrictor*). Journal of Experimental Biology **156**: 539–556.

Johnson, N.B., Poulin, R.G., Somers, C.M. (2022): Thermoregulation by Bullsnakes (*Pituophis catenifer sayi*): do burrows make life easier on the prairies? Canadian Journal of Zoology **100**(5): 303–314.

Lu, Z., Ma, S., Li, B., Wang, Y. (2006): Design of a cyclic inhibitory CPG controller for the locomotion of a snakelike robot. Frontiers of Mechanical Engineering in China **1**(4): 396–402.

Mortensen, T.L., Marsh, A., Anderson, Jr J., Moore, I.T., Socha, B.Z., Moore, A.E., Pacaya, E.T., et al. (2025): Two steps forward, one back: kinematic observations of a South American Small-eyed Coralsnake, *Micrurus lemniscatus* (Linnaeus, 1758), regurgitating a Brown-banded Watersnake, *Helicops angulatus* (Linnaeus, 1758). Herpetology Notes **18**: 293–298.

Mosauer, W. (1932): On the locomotion of snakes. Science **76**: 583–585.

Newman, S.J., Jayne, B.C. (2018): Crawling without wiggling: muscular mechanisms and kinematics of rectilinear locomotion in boa constrictors. The Journal of Experimental Biology **221**(4): jeb.166199.

Rudolph, D.C., Schaefer, R.R., Burgdorf, S.J., Duran, M., Conner, R.N. (2007): Pine Snake (*Pituophis ruthveni* and *Pituophis melanoleucus lodingi*) Hibernacula. Journal of Herpetology **41**(4): 560–565.

Tingle, J.L., Garner, K.L., Astley, H.C. (2024): Functional diversity of snake locomotor behaviors: A review of the biological literature for bioinspiration. Annals of the New York Academy of Sciences **1533**: 16–37.

Walton, M., Jayne, B.C., Bennett, A.F. (1990): The energetic cost of limbless locomotion. Science **249**: 524–527.

Whitaker, P.B., Shine, R. (2003): A Radiotelemetric Study of Movements and Shelter-Site Selection by Free-Ranging Brownsnakes (*Pseudonaja textilis*, Elapidae). Herpetological Monographs **17**(1): 130–144.

Accepted by Julie M. Ray