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Coiling chirality? Wild eastern diamondback rattlesnakes (*Crotalus adamanteus*) do not exhibit clear lateralized coiling behaviour

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ABSTRACT
Behavioural lateralization has been recorded in various groups, from lower vertebrates to humans. Handedness, or the preferred use of one hand over the other, as observed in humans, is thought to be related to brain structure and function. Snakes have been recorded to potentially display such sided behaviours. The asymmetrical internal anatomy of snakes may provide a basis for coiling handedness in the form of clockwise versus anti-clockwise coiling to protect vital organs or provide an advantageous strike to capture prey. The few studies on behavioural lateralization in snakes have documented inconsistent evidence to accurately determine whether coiling direction biases exist. However, these studies either failed to include repeated individuals or were conducted in aseptic environments, producing results that may not reflect natural conditions. To determine whether coil position bias exists amongst wild individuals, we studied eastern diamondback rattlesnakes (*Crotalus adamanteus*) at two sampling sites. We found no clear bias for coiling direction across populations or individuals, though sex-biased differences in directionality were identified. We found that lateralized coiling is not found in all snakes, and the genetic and ecological significance of such polymorphism, if any, warrants further investigation.

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KEYWORDS *Crotalus adamanteus*; coiling directionality; lateralization bias

Introduction

Cerebral lateralization, referring to the specialization of the right and left hemispheres for various functions, remains an important aspect of evolutionary biology and has more recently received increased attention through studies of wide-ranging taxonomic groups (Miyashita & Palmer, 2014; Vallortigara et al., 2011). Traditionally, cerebral lateralization is explained by the

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ability to avoid unnecessary duplications of neural activity and functions between the two hemispheres, allowing for more efficient use of brain tissue to increase neural capacities (Ghirlanda & Vallortigara, 2004; Gonzalez et al., 2018; Güntürkün & Ocklenburg, 2017; Levy, 1977; Vallortigara & Rogers, 2005). This cost–benefit approach of hemispheric specialization is credited with the development of higher cognition and sensorimotor functionality (Gonzalez et al., 2018).

Generally, the study of lateralization has focused on human evolutionary biology and, most specifically, what is deemed "handedness" or our proclivity to prefer right- or left-handed use over the other. For humans, the preference for right-handedness is significantly greater than left-handedness (McManus, 2002), and this lateralization has been linked to a myriad of anatomical structuring, linguistic, and behavioural characteristics (Papadatou-Pastou et al., 2020; Prieur et al., 2018; Tzourio-Mazoyer et al., 2020). The strength of lateralization may vary across a spectrum amongst individuals (e.g., ambidexterity), and this individual-level lateralization may increase an individual's fitness. Some studies have shown that strongly lateralized individuals perform better in particular cognitive tests (Frasnelli & Vallortigara, 2018; Marcinowski et al., 2016). McGrew and Marchant (1999) illustrated that chimpanzees with stronger hand preferences were more efficient at foraging for termites ("termite fishing"), but the efficiency of the individual was not dependent on which hand was preferred. However, genetic studies suggest that individual-level lateralization does not necessarily correlate with the population level. Population-level lateralization may occur when the population's success and structure depend heavily on individual reactions (Ghirlanda & Vallortigara, 2004). For example, lateralization may affect predator detection rates (Lippolis et al., 2002), and synchronized turning direction may increase predator evasion success (Foster & Treherne, 1981; Cantelupo et al., 1995; Chivers et al., 2016). Despite these perceived benefits, specific lateralization alone, such as right-handedness, may not drive evolutionary forces within a population if the opposite preference is not detrimental (refer to McGrew & Marchant, 1999).

The study of the brain and behaviour lateralization in non-primates has recently emerged to better understand the evolutionary origins of brain asymmetries (Rogers et al., 2004; 2013; Stancher et al., 2018). Once considered only a phenomenon of humans and other primate neurobiology, cerebral lateralization is now documented in a variety of vertebrate taxa as well as invertebrates (refer to Frasnelli & Vallortigara, 2018). This may be the most well documented in avian taxa, particularly with domestic chickens and pigeons (Andrew, 1991; Güntürkün et al., 2000; Vallortigara et al., 2001). Handedness has been observed in some bird species that prefer a particular foot during feeding and object manipulation behaviours (Rogers & Workman, 1993; Tommasi & Vallortigara, 1999). Handedness preferences are also documented in anurans, showing lateralization for right-foot wiping during grooming behaviour in the South American cane toad, *Rhinella marina* (Bisazza et al., 1997), and left-forelimb bias in European green toads, *Bufo viridis*, during prey ingestion (Sovrano, 2007). Other research suggests that left-eye visual lateralization preference occurs in anuran tadpoles (Bisazza et al., 2002), hinting that differences may be found across closely related taxa as well as possibilities of ontogenetic shifts over time. Other taxa, like fishes, present unique discussions of cerebral lateralization indicating individual boldness in cichlids (Reddon & Hurd, 2009) and stress reactivity in sharks (Byrnes et al., 2016).

Snakes represent a novel look at lateralization and asymmetry (Davis, 1978). Despite lacking appendages, snakes may yet exhibit “handedness” through behaviours such as reproductive organ use or coiling directionality. However, limited and often anecdotal accounts have previously disagreed on the presence of handedness in snakes (Amaral, 1927; Davis, 1978; Klauber, 1997). Shine et al. (2000) found that male garter snakes (*Thamnophis sirtalus parietalis*) display a bias for asymmetrical hemipenis use in response to body temperature and prior successive mating events. Lateralized coiling behaviours may be more pronounced in ambush predators, such as vipers, that spend a significant portion of time in a coiled and anchored position in wait for prey. Amaral (1927) recounted anecdotal observations of rattlesnakes appearing to coil in a clockwise direction, hypothesizing that clockwise coiling behaviour could be incentivized to protect asymmetrical organs.

Roth (2003) was the first to systematically investigate coiling biases in a captive snake species (western cottonmouth, *Agkistrodon piscivorus leucostoma*). The study concluded coiling lateralization at the individual and population levels; however, only three individuals displayed a significant clockwise coil bias in a study of 30 snakes. Despite the conclusions presented in this paper, there was no clear evidence for coiling direction bias within individuals, between sexes, or among age groups. A similar study of captive copperheads (*Agkistrodon contortrix*) and cottonmouths (*Agkistrodon piscivorus*) found no evidence of behavioural laterality in coiling direction (Heatwole et al., 2007). While these studies provide important insight, captivity may greatly affect animal behaviour, particularly in cryptic species like snakes (Chiszar et al., 1993; Van Waeyenberge et al., 2018). A study utilizing citizen science platforms to monitor wild Southern Pacific Rattlesnakes (*Crotalus helleri*) also shows no particular coiling directional bias across age classes or microhabitats (Urquidi & Putman, 2021). While this study obtained an incredibly large dataset by utilizing social platforms like iNaturalist and HerpMapper to observe snakes *in situ*, it lacked repeated sampling of known individuals, which could have greatly enhanced these conclusions. To more accurately assess the presence of coiling lateralization behaviour in a species, it is important to study wild populations with repeated observations of individuals.

To determine coiling lateralization behaviour biases amongst wild snakes, we examined eastern diamondback rattlesnakes (*Crotalus adamanteus*) through repeated radio-telemetry of adult individuals at two sampling sites in Southwest Florida (refer to Metcalf et al., 2022). *Crotalus adamanteus* is a large pit viper endemic to the pine flatwoods and rocklands of the Southeastern United States (Enge et al., 2016; Klauber, 1997; Timmerman & Martin, 2003) and, as with most other viperids, *C. adamanteus* is a sit-and-wait predator that spends much of its life coiled in ambush (Means, 2017). The use of radio-telemetry allows us to track multiple individuals over an extended period while also allowing us to record the coiling behaviours of these snakes in natural conditions. Ultimately, we expect that coiling lateralization behaviour may be present in this species, possibly in part to protect asymmetrical internal organs, increase prey-striking success, and/or optimize thermoregulation for gravid females.

Methods

Study sites

We recorded coiling behaviour from congruent radio-telemetry projects of *C. adamanteus* from two distinct sampling locations in Southwest Florida: the campus of Florida Gulf Coast University in Fort Myers, Florida (FGCU; 26° 27′44″N, 81°46′14″W), and the Rookery Bay National Estuarine Research Reserve in Naples, Florida (RB; 25°58′11″N, 81°44′14″W). The study sites are approximately 46 km apart; both host populations of *C. adamanteus* in a similar mixture of peri-urban and natural landscapes, climate, and hydrology. For more details on the location specifics, refer to Metcalf et al. (2020, 2022) and Gunnels IV et al. (2021) for FGCU, and Barry et al. (2013) and Metcalf et al. (2021) for RB.

Study animals and radio-telemetry

We captured adult eastern diamondback rattlesnakes during visual encounter surveys and opportunistic captures, and fitted the snakes with SI-2T 13g internal transmitters (<5% of body weight, Holohil Systems Ltd., Ontario, Canada) as described by Reinart and Cundall (1982) and Bryant et al. (2010). We located each snake two to three times per week for at least one full year, using a handheld R-1000 receiver coupled with a Communication Specialist handheld Yagi antenna (Communications Specialists, Inc., Orange, California, USA). Once we visually confirmed the presence of the radio-tagged snake, we recorded GPS location, time of day, microhabitat,

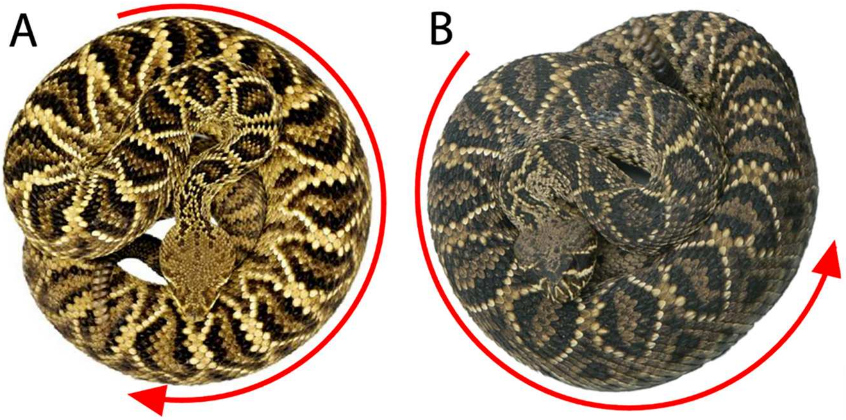

Figure 1. Examples of coiling directionality of Eastern Diamondback Rattlesnakes from this study: (A) clockwise coiling, illustrating the snake's right side of the body is exposed to the outer edge of the coil, and (B) anti-clockwise coiling, illustrating the snake's right side of the body is on the inside of the coil. Photo credit: M. Hogan & M. F. Metcalf.

ambient air temperature, coiling direction, and made additional behavioural observations (refer to Metcalf et al., 2022). We recorded the coiling direction (Figure 1) as described in Roth (2003) as either clockwise (CW), anti-clockwise (AC), random (R), or outstretched (O). Snakes in this study had unequal tracking events due to variances in the time an individual was included in the study, transmitter malfunctions, or the death of the study animal before the conclusion of the study. Although we attempted visual confirmations for every snake on every tracking event, the snakes were not always visible to the observers (e.g., underground or thick vegetation), and therefore no coiling direction could be determined for those tracking events. Observers attempted to limit their interactions with radio-tagged snakes to avoid disturbances and potentially alter the snakes' behaviour. Any perceived or apparent disturbance of the animal, such as fleeing upon approach or defensive rattling, was noted, and we removed those instances from further analyses.

Data analysis

Prior to analyses, observations of snakes that were either not coiled (i.e., random or outstretched) or not visible were discarded. We followed the analyses outlined in Roth (2003) and included additional analyses as described below. All analyses were completed in R (R Core Team, 2023). Laterality index (LI) was calculated for each snake by dividing the number of clockwise coils by the total number of coiled observations. Values close to 0 or 1 indicate bias, whereas intermediate values do not. To assess the coiling behaviour bias of individual snakes, we conducted a binomial test where clockwise coils were considered "successes"" ,following the LI conducted in Roth (2003). Significant LI was indicated by an alpha $\leq$ 0.05 in the binomial tests for each individual. To test for differences in mean laterality index (LI) between sexes, which could arise from anatomical differences (e.g., Shine et al., 2000), we performed a Welch's *t*-test. To evaluate whether either sex exhibited a significant directional bias in coiling, we conducted exact binomial tests within each sex to compare the proportion of clockwise versus counterclockwise coils against a random 50:50 expectation. To assess whether LI differed between FGCU and RB radio-tagged snakes, we conducted a permutated ANOVA due to unequal sample sizes. Additionally, we conducted binomial tests on snakes grouped by site to observe coiling behaviour biases within populations. Power for each individual's binomial test was calculated using the pwr.p.test function (Champely, 2020), which computes the power of a two-sided proportion test based on Cohen's *h*. Effect size was defined as Cohen's *h* using each snake's observed Laterality Index (p_1) compared to the null expectation of no bias ($p_0 = 0.5$), with sample size equal to the number of coil observations per snake. A chi-square test was used to determine coiling behaviour biases between the four seasons, categorized as in Roth (2003). All snakes in the study were adults; however, to assess whether coiling direction varied across life history, we used a regression to compare snout-vent length (SVL) to LI. Additionally, we conducted a repeated measures ANOVA to determine seasonal effects, temperature, and humidity separately on LI. Temperature and humidity observations were placed into groups using the cut_number function in R (temperature: 18.2–28.3, 28.3–31, 31–37.5; humidity: 36.8–67%, 67–78.7%, 78.7–99.9%). Interactions between temperature and humidity were also assessed using repeated measures ANOVA. Figures were created in the ggplot2 package (Wickham 2016).

Because LI can be inflated for snakes with few observations, in addition to Roth's (2003) analysis, we also used a generalized linear mixed-effects model (GLMM) using lme4 to test how environmental and biological factors influenced coiling direction (Bates et al., 2015). Each coiling observation was coded as either clockwise (1) or anticlockwise (0) and modelled as a binary response variable with a binomial error distribution and logit link function. Predictor variables included sex (female, male), site (FGCU, RB), seasonality (spring, summer, fall, winter), wet - or dry-seasonality classification (wet season defined as May 15–October 15), ambient temperature (°C), and relative humidity (%). Interaction terms among environmental predictors (humidity x temperature and humidity x season) were evaluated by incorporating interaction terms into the model and comparing model fit using likelihood ratio tests. To account for repeated behavioural observations from the same individuals, snake ID was included as a random intercept. Model coefficients were exponentiated to obtain odds ratios with 95% confidence intervals. Data used are available here: https://osf.io/juy2a/.

Ethical note

This study was conducted under FGCU-IACUC 1415-06, FWC LSSC-15-00037A, and VRC 1230. All precautions were taken in this study to reduce physical and psychological harm to the animals. The only disturbances inflicted were our physical presence during observational events. In instances where a visual could not be obtained, we did not attempt to alter the surrounding environment to obtain a visual in order to reduce our impact on the animal's well-being. We maintained an appropriate distance while recording data and made a strong effort to limit our time spent near the snakes throughout the study.

Results

During the 12-month study period, we tracked ten snakes (FGCU, $n = 6$; RB, $n = 4$) for a total of 416 observations. Of those observations, we visibly confirmed snakes in coiled positions, either clockwise or anti-clockwise, a total of 227 times (Table 1). During tracking events, snakes were visible and in a coiled position an average of 22 times per individual (range: 8–52, sd = 15.56). No individual showed a significant coiling bias (Figure 2a). However, these patterns showed moderate to low power across individuals (ranging from 0.05 to 0.35), indicating limited ability to detect moderate coiling biases and adequate power only for very strong biases.

The permutated ANOVA did not observe site-level biases between snakes at the two locations ($p = 0.62$). Within sites, binomial tests showed that snakes did not display LI differences (FGCU, $p = 0.36$; RB, $p = 0.78$). Snakes were coiled clockwise 46.3% of the time at FGCU and 47.2% at RB. Binomial tests to determine whether a bias occurred within each sex showed that neither sex

Table 1. Summary of Eastern Diamondback Rattlesnake coiling observations. AC = Anti-clockwise, CW = Clockwise, FGCU = Florida Gulf Coast University, RB = Rookery Bay.

	Individual	AC	CW	Total	LI	Bias
Females	FGCU 11	19	14	33	0.424	None
	FGCU 12	13	7	20	0.350	None
	FGCU 17	21	22	43	0.512	None
	RB 3	14	12	26	0.461	None
	RB 5	8	3	11	0.273	None
Males	FGCU 15	27	25	52	0.481	None
	FGCU 16	9	6	15	0.400	None
	FGCU 18	4	7	11	0.636	None
	RB 1	3	5	8	0.625	None
	RB 6	3	5	8	0.625	None

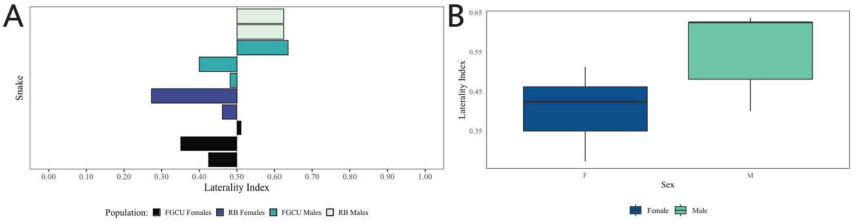

Figure 2. (a) Coil directionality, or laterality index (LI) of individual snakes categorized by location and sex. Values above 0.5 indicate a clockwise coil bias. Strong clockwise or counterclockwise bias would be indicated by values above 0.75 or below 0.25, respectively. No values are statistically significant. (b) There was a significant difference in LI between sexes, with males more likely to display clockwise coiling, though neither sex displayed significant directional preference. Abbreviations: AC = Anti-clockwise, CW = Clockwise, FGCU = Florida Gulf Coast University, RB = Rookery Bay, F = Female, M= Male. Colour palette from Garnier et al. (2024).

exhibited a statistically significant directional bias when considered independently (females: $p = 0.14$; males: $p = 0.91$). However, significant differences in mean laterality index (LI) were observed between males and females ($t = 2.34$, $df = 7.87$, $p = 0.048$), with males exhibiting a higher proportion of clockwise coiling when compared to females (Figure 2b; although not significantly independent as stated above). The regression revealed that the SVL of snakes did not have a significant relationship with LI ($p = 0.7357$, SVL range = 95-136 cm). We also did not find differences in coiling behaviour bias in relationship with seasonality ($p = 0.386$), temperature ($p = 0.556$), or humidity ($p = 0.556$) based on the repeated measures ANOVA. No interaction between humidity and temperature was present ($p = 0.613$).

Our GLMM yielded similar results. The random-effect variance for individual snake ID was estimated to be zero, indicating no consistent individual bias in coiling direction. Among predictors, only relative humidity significantly influenced coiling direction ($\beta = 0.03 \pm 0.013$, $p = 0.008$), with snakes more likely to coil clockwise under higher humidity conditions (Figure 3; odds ratio = 1.04, 95% CI: 1.01–1.06). No significant effects were detected for sex, site, temperature, season, or wet/dry seasonality ($p > 0.10$ for all; Table 2). Neither the temperature x humidity interaction nor the humidity x season interaction improved model fit (likelihood ratio tests, $p > 0.30$ for both), indicating that the effect of humidity on coiling direction was consistent across temperature and seasonal contexts; interaction terms were therefore not retained in the final model.

Discussion

We did not record clear coiling directionality within *Crotalus adamanteus*, suggesting that biased coiling in the clockwise or anti-clockwise direction

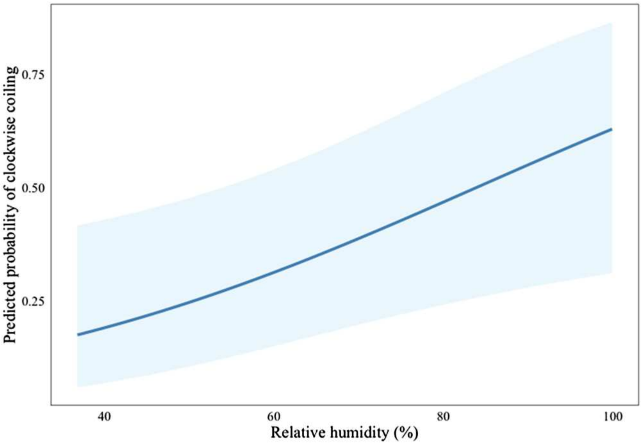

Figure 3. Positive relationship between relative humidity (%) and the probability of clockwise coiling. The curve shows predicted probabilities from the generalized linear model, with shaded areas representing 95% confidence intervals.

Table 2. Generalized linear mixed model results for effects on coiling direction. *β* estimate values, standard error (SE), *z* values, and *p*-values for each predictor variable are included.

Predictor	*β*	SE	*z*	*p*-value
Sex (M)	0.47	0.29	1.62	0.11
Site (RB)	0.30	0.34	0.88	0.38
Season (Summer)	−0.16	0.65	−0.24	0.81
Season (Autumn)	0.31	0.54	0.57	0.57
Season (Winter)	−0.17	0.51	−0.33	0.74
Temperature	−0.04	0.18	−0.21	0.83
Humidity	0.42	0.17	2.43	0.02
Seasonality (Wet)	−0.22	0.45	−0.49	0.62

may not be biologically or ecologically advantageous for wild snakes of this species. No patterns of coil directionality were observed between or within the two sampling sites, meaning population or site habitat differences likely played no role in body positioning. Although these sites vary in the degree of habitat fragmentation and human activity, these factors did not affect coiling directionality. Neither sex showed an independent significant directional bias, although males had higher average LI values than females. The difference likely reflects a slight shift in coiling direction rather than increased lateralization. Though age could not be properly assessed within our sample set, SVL of snakes had no relationship with coiling bias. Because of this, we do not have evidence to conclude that coiling behaviour is relevant in the context of population or size. Additionally, there was no trend for coil direction in any individual animal, suggesting it is not reflective of brain function or structure. The GLMM's results were concordant, with humidity as the only significant predictor variable, though this is unlikely to be reflective of biological significance.

More investigation is likely needed to determine the underlying factors that may influence a snake's coiling directionality. Rattlesnake species (*Crotalus* and *Sistrurus*) are ambush hunters, remaining coiled for prolonged periods of time in a particular area in wait of prey. This does, however, also expose these animals to potential predators. Coiled positioning allows these snakes to not only optimize their strike performance but also may increase their readiness to defensively counter a predatory attack (Kardong & Bels, 1998; Maag & Clark, 2022), despite the suggested reluctance of rattlesnakes to strike in defense (Gibert et al., 2022; Glaudas et al., 2005). Unfortunately, no studies to date have quantified the success or failure of lateralized coiling directionality in rattlesnakes during defensive striking, and our current study was unable to document such encounters. Yet, our study concludes that no individual or population-level lateralization appears to occur. This may suggest that coiling direction does not increase a snake's success and survival and is, therefore, not an evolutionary driver in these individuals or populations. The lack of biased directionality, or "ambidextrous" coiling, may allow *C. adamanteus* options when positioning around objects in the environment for prey ambush, predator avoidance, and/or mating. If *C. adamanteus* are able to utilize either directionality successfully, an ambidextrous coiling position would be advantageous.

The proposed biological functionality of biased coiling in a clockwise or anti-clockwise direction, such as protecting internal organs or thermoregulation, does not appear to influence the coil positioning of *C. adamanteus*. Thermoregulation may affect coiling bias in species that live in areas where the climate limits their seasonal activity. For example, timber rattlesnakes (*Crotalus horridus*) are a brumating species that moves slightly during brumation for thermoregulation (Nordberg & Cobb, 2017), and may non-randomly alter their positioning for temperature regulation to retain heat in cooler areas. While more northern populations of *C. adamanteus* survive in regions with more pronounced shifts in temperature and must remain inactive for extended periods during winter months (Means, 2017), southern populations of *Crotalus adamanteus*, such as those in this study, are more active year-round due to the warmer, sub-tropical climate of South Florida (Metcalf et al., 2022). Investigating the coiling positions of *C. adamanteus* and other snakes in cooler months and during brumation may be valuable to better understand thermoregulation as a factor in coiling behaviour.

Any evolutionary framework and significance of lateralized coiling behaviours for this species remains unknown, but similar studies across other Viperids (Heatwole et al., 2007; Roth, 2003; Urquidi & Putman, 2021) and early vertebrates like hagfish (Miyashita & Palmer, 2014) may serve as further evidence of the absence of convergent evolution in this species.

Other species that display lateralized coiling behaviour, like hagfish, salamanders, and lancets, likely developed this behaviour independently rather than from a common ancestor (Miyashita & Palmer, 2014). However, lateralized behaviour may still be represented in *C. adamanteus* through other mechanisms. Asymmetrical reproductive behaviours could be present in rattlesnakes, such as male hemipenis use, as seen in Shine et al. (2000), or basking positioning in gravid females. Defensive displays may also provide evidence for behavioural lateralization. For example, ring-neck snakes (*Diadophis punctatus*) will coil their tails to expose brightly coloured ventral scales in anti-predatory displays (Cox et al., 2021; McCallum et al., 2006), although no studies on the directionality of these coils have been conducted. Our study did observe a suite of reproductive behaviours (e.g., male-male combat, mating, and birth of young), including repeated observations of gravid females during gestation. However, our dataset remained too small to confidently measure these variables for detailed analyses. Occurrences of defensive posturing (i.e., tail rattling) were also limited in this study.

To our knowledge, this project is the first to test behavioural lateralization in the coiling directionality of eastern diamondback rattlesnakes. Our study emphasizes the importance of using wild populations and repeated individuals to complement behavioural research in aseptic environments. Several factors, including enclosure size, ambient environmental conditions, and human presence, can influence behavioural patterns in captivity (Doody, 2023; McPhee, 2004). The influences of these artificial environments can be partially eliminated by measuring animals in the proper ecological context. Moreover, repeated observations of multiple individuals ensure that unique trends in those individual biases across a myriad of external factors are captured. Despite no noticeable trends of lateralization at the individual nor population level in this study, this work provides a framework for future investigation into brain functionality and the mechanisms that drive neurobiological evolution in snakes.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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