

Rain-harvesting behavior in free-ranging prairie rattlesnakes (*Crotalus viridis*)

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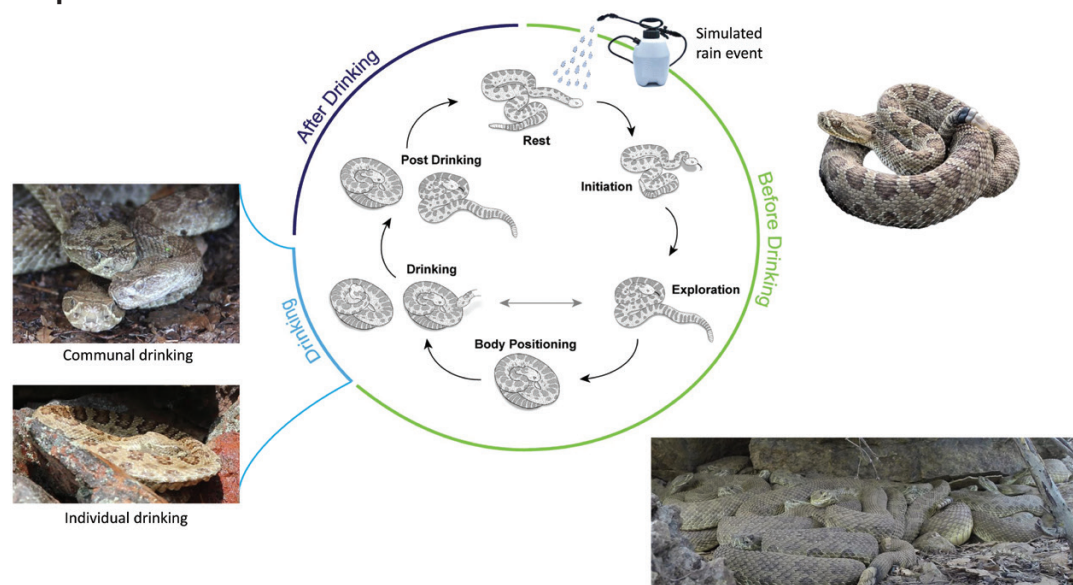
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Abstract

Organisms inhabiting arid environments face challenges to obtain dietary water. To prevent desiccation, some organisms possess unique adaptations to harvest water from infrequent and unpredictable rainfall, including several squamates (snakes and lizards). While most squamates consume precipitation as it pools in the environment, a small number engage in behaviors to enhance water collection by capturing precipitation from their own skin, referred to as rain-harvesting behavior (RHB). Details of this behavior remain unclear, particularly the sequence of behaviors associated with RHB. We developed a method to simulate rainfall to observe RHB in prairie rattlesnakes (*Crotalus viridis*) in situ and recorded 72 events in 94 snakes, the most robust sampling of RHB to date. Using video analysis, we describe the postures and kinematics of RHB and develop the first illustrated ethogram of this behavior for any vertebrate. Our results demonstrate that RHB contains fixed and variable patterns useful in cross-species comparisons and in exploring proximate causes of the behavior. In addition, we describe novel features of RHB including suspended head drinking, body levering, and drinking from neighboring snakes. Our results reveal RHB to be an intricate suite of movements and actions, some of which allude to acute sensory abilities of these animals that warrant further study. Furthermore, observations of RHB at dens and rookeries suggest a potential, novel benefit of snake aggregation is the formation of large, communal surfaces for rain harvesting. We suggest that the extremely elongated body plan of snakes may be well-suited for a rapidly deployed, modular rain-harvesting system effective at capitalizing on fleeting rainstorms characteristic of arid ecosystems of the world.

Key words: climate, drinking, ethogram, rainfall, reptile, squamate.

Graphical Abstract



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Organisms inhabiting xeric environments face formidable challenges obtaining water due to unpredictable and infrequent precipitation (Sharon 1972; Whitford and Duval 2019). Increasingly volatile weather patterns (Williams et al. 2022) could exacerbate such challenges, and hydoregulation will become more urgent. Understanding the ways in which organisms obtain water in the face of these extreme conditions is of basic (Seely and Hamilton 1976; Gurera and Bhushan 2020) and applied interest (Comanns 2018).

Terrestrial ectotherms are good models for understanding survival in arid ecosystems because they are low-energy specialists that must behaviorally thermoregulate while avoiding dehydration (Huey and Slatkin 1976; Angilletta 2009). Ectotherms control heat gain and loss by exploiting thermal variation within their environment, yet thermoregulation presents several costs including increased predation risk (Webb and Whiting 2005; Herczeg et al. 2006), reduced time for other activities (Grant and Dunham 1988; Bradshaw 1997), and dehydration (Ladyman and Bradshaw 2003). As body temperature increases, evaporative water loss also increases, resulting in a behavioral trade-off between thermoregulation and hydoregulation (Angilletta 2009; Dupoue et al. 2015; Dezetter et al. 2023). This trade-off becomes more complex during metabolically demanding life-history events such as pregnancy and/or digestion (Peterson et al. 1993; Angilletta 2009; Dupoue et al. 2015; Black et al. 2019). Thus, understanding the details of how, when, and why xeric-adapted ectotherms drink can help reveal the evolutionary drivers of adaptations used to balance thermal and hydric constraints (Porter et al. 1973; Nagy 1988; Rozen-Rechels et al. 2019).

Several taxonomic groups inhabiting arid environments have evolved striking adaptations to obtain environmental water. Approximately 40 species have been documented to passively collect and/or transport water using various anatomical structures and distinctive behaviors: beetles (Seely and Hamilton 1976), tortoises (Auffenberg 1963), birds (Cade and Maclean 1967), mammals (Lillywhite and Stein 1987), and squamate reptiles (snakes and lizards; Bentley and Blumer 1962; Schwenk and Greene 1987; Sherbrooke 1990). Within squamates, the thorny devil (*Moloch horridus*) and the Texas horned lizard (*Phrynosoma cornutum*) have been extensively studied and found to use a unique system of inter-scalar channels and body postures to direct water accumulated on the skin toward the mouth for ingestion via capillary action or gravity (Sherbrooke 1990; Comanns et al. 2011; Yenmis et al. 2023). In fact, thorny devils can transport water via capillary action from their feet to their mouths simply by standing in moist sand (Withers 1993).

To facilitate the collection of moisture, the exterior surface of many rain-harvesting animals has adapted to collect and aggregate precipitation. For instance, the Namib desert beetle (*Stenocara* sp.) uses both hydrophilic and hydrophobic microstructures on its exoskeleton to capture and condense water from fog (Parker and Lawrence 2001). Male sandgrouse (*Pterocles namaqua*) possess a unique feather structure that readily absorbs water from desert pools to be transported to chicks more than 20 km away (Mueller and Gibson 2023). Some snakes also possess unique morphology to collect and drink rainwater that accumulates on their skin (Phadnis et al. 2019). For instance, the scales of western diamond-backed rattlesnakes (*Crotalus atrox*) have a microporous nanostructure that facilitates pinning (i.e., securing) and pooling of rain droplets; this is absent in the scales of sympatric species that

do not drink rainwater from their skin (Phadnis et al. 2019). Hence, these snakes possess unique morphological features in their integument that facilitate harvesting of precipitation, but little is known about the behavioral mechanisms used to successfully collect and drink rainwater.

Several species of snakes show behavioral responses to precipitation that enable drinking including members of the Colubridae, Viperidae, and Elapidae (Ashton and Johnson 1998; Bonnet and Brischoux 2008; Cardwell 2006; Glaudas 2009; Lillywhite et al. 2015; Lillywhite et al. 2019; Mata-Silva et al. 2014; Repp and Schuett 2008; Sasaki and Duval 2003; Table 1). These behaviors are highly variable among snake groups and not limited to terrestrial species. For instance, some species of sea snakes will drink rainwater from freshwater lenses that form on the ocean surface after heavy rainfall (Lillywhite 1996; Lillywhite et al. 2008, 2012, 2015, 2019). Other snakes position the anterior portion of their bodies below the posterior body during rainstorms and then drink the water that runs down their necks and head (Miller 1985; Guinea 1991; Sasaki and Duval 2003). However, stereotyped behaviors that enhance rainwater capture (i.e., alterations to body surface area, changes in body posture) have been specifically referred to as rain-harvesting behavior in desert-dwelling squamates (lizards, Sherbrooke 1990; rattlesnakes, Cardwell 2006; hereafter “RHB”) and, to our knowledge across snakes, only occur in the Viperidae (Table 1). It is plausible that behaviors that facilitate collection of precipitation exist on a continuum across the rich diversity of snake taxa, therefore we also acknowledge that RHB may not be exclusive to Viperidae.

Cardwell (2006) described a “stereotypical” body posture of viperids during RHB in which the trunk was coiled, spiraling outward with the tail located in the center. During RHB, body loops were dorsoventrally flattened and placed adjacent to one another, forming shallow troughs between each (Cardwell 2006; Glaudas 2009). Flattening was most pronounced in the posterior region of the body and presumably functions to increase the surface area to intercept and capture raindrops (Cardwell 2006). However, dorsoventral flattening of the body does not appear ubiquitous among rain-harvesting viperids (Table 1). In addition, Cardwell (2006) only observed Mojave rattlesnakes (*Crotalus scutulatus*) drinking from their own skin, which he argued was more energy efficient (and perhaps safer via maintenance of crypsis) than moving around to locate a suitable drinking surface. Hence, features of RHB vary, and it is currently unclear whether these differences are adaptations to local conditions or reflect plastic responses to environmental variation. It is therefore prudent to characterize this behavior in detail to facilitate species comparisons and expose conserved features, advancing our understanding of the evolution of RHB. Unfortunately, comprehensive descriptions of RHB in free-ranging snakes have been hampered by challenges in observing these cryptic animals long enough to capture drinking behaviors during infrequent rainfall events that, in some arid habitats, can total only minutes out of each year (Zhang et al. 2016; Bohm et al. 2021). To conduct investigations of RHB in the field, we developed a methodology to release the behavior without the need to rely on temporally and spatially unpredictable rainfall in arid ecosystems. We investigated RHB in free-ranging prairie rattlesnakes (*Crotalus viridis*) using simulated rainfall (e.g., Shine et al. 2005) generated from a standard garden sprayer. In preliminary tests, simulated rain elicited behaviors that superficially matched those reported in the literature (e.g., coiling of body, dorsoventral flattening, Cardwell

Table 1 Summary of all reports of rain (and moisture) harvesting in snakes.

	Lab/ Field	Location	Drinking surface		Body coiling	Dorsoventral flattening	References
			Snake	Non-snake			
Colubridae							
	<i>Pantherophis (Elaphe) bairdi</i>	L	Unknown	Y	N	N	Somma 1989
	<i>Nerodia clarkii (fasciata) compressicauda</i>	F	Florida, USA	Y	Y	N	Miller 1985
	"	L	Florida, USA	N	Y	N	Miller 1985
Elapidae							
	Laticaudinae						
	<i>Laticauda saintgironsi</i>	F	New Caledonia	N	Y	N	Bonnet and Brischoux 2008
	<i>Laticauda laticaudata</i>	F	New Caledonia	N	Y	N	Bonnet and Brischoux 2008
	<i>Laticauda colubrina</i>	F	Fiji	Y	Y	N	Guinea 1991
	Hydrophiinae						
	<i>Hydrophis curtus</i>	L	Western Australia	N	Y	N	Lillywhite et al. 2015
	<i>Hydrophis elegans</i>	L	Western Australia	N	Y	N	Lillywhite et al. 2015
	<i>Hydrophis platurus</i>	L	Costa Rica	N	Y	N	Lillywhite et al. 2019
	<i>Hydrophis zweifeli</i>	L	Western Australia	N	Y	N	Lillywhite et al. 2015
Viperidae							
	Viperinae						
	<i>Bitis caudalis</i>	F	Namibia, Africa	Y	N	N	Murray and Irish 2015
	<i>Bitis peringueyi</i>	L	Namibia, Africa	Y	N	Y	Louw 1972
	"	L	Namibia, Africa	Y	N	N	Robinson and Hughes 1978
	"	F	Namibia, Africa	Y	N	N	Robinson and Hughes 1978
	Crotalinae						
	<i>Bothrops asper</i>	F	Costa Rica	Y	N	Y	Greene 1986
	<i>Bothrops moojeni</i>	L	Sao Paulo, Brazil	Y	N	Y	Andrade and Abe 2000
	<i>Crotalus atrox</i>	F	Arizona, USA	Y	Y	Y	Repp and Schuett 2008
	<i>Crotalus lepidus</i>	F	Texas, USA	Y	Y	Y	Mata-Silva et al. 2014
	<i>Crotalus mitchellii pyrrhus</i>	F	Nevada, USA	Y	Y	Y	Glaudas 2009
	<i>Crotalus molossus</i>	F	Arizona, USA	N	Y	N	Greene 1990
	"	F	Texas, USA	Y	N	Y	Mata-Silva et al. 2012
	<i>Crotalus oreganus</i>	L	California, USA	Y	Y	N	Bogert 1927
	<i>Crotalus scutulatus scutulatus</i>	F	California, USA	Y	N	Y	Cardwell 2006
	<i>Crotalus viridis lutosus</i>	L	Utah, USA	Y	N	Y	Arid and Arid 1990
	<i>Crotalus viridis concolor</i>	F	Wyoming, USA	Y	Y	Y	Ashton and Johnson 1998
	<i>Gloydius blomhoffii</i>	F	Hokkaido, Japan	N	Y	N	Sasaki and Duvall 2003

Table 1 additional references not included in the main text:

Aird and Aird 1990; Bogert 1927; Greene 1986; Louw 1972; Murray and Irish 2015; Robinson and Hughes 1978; Somma 1989.

2006) and validated the methodology. Based on previous work (Cardwell 2006; Glaudas 2009), we hypothesized that snakes would preferentially drink from their own body surfaces, possibly as an adaptation to reduce movement and/or maintain crypsis (Greene 1988). We predicted that snakes would first drink off themselves and only secondarily from other surfaces like rocks or vegetation that required more movement. Likewise, we hypothesized that drinking duration would vary with drinking surface. Because rattlesnake skin structure facilitates beading of water on its surface, we predicted that snakes would drink from their own bodies for a greater duration than from other surfaces where water may not remain as long. RHB includes postural changes that may help water to pool on the skin, and we predicted that snakes would drink pooled water on their skin first and for the longest duration. Lastly, we suspected that head position relative to the ground (head angle)

could reflect differences in drinking mechanics (Cundall et al. 2012) and hypothesized that the position of the head would vary based on the type of drinking surface. We developed the first illustrated ethogram to describe RHB quantitatively and qualitatively in a snake. Videography of animals in situ allowed us to characterize specific kinematic movements useful in delineating ethogram phases. Lastly, we detailed several previously undescribed/or insufficiently described features of RHB that should be fruitful areas for continued study.

Materials and Methods

Study site

The study site was located on a private ranch 15 km northwest of Steamboat Springs, Colorado, USA (Moniz et al. 2024). The habitat at the site is a mixture of montane forest (high

elevation), montane shrubland (mid-elevation), and semidesert shrubland (low elevation) ecosystems (Armstrong et al. 2010). A major feature of the site is Rattlesnake Butte, an igneous sill that harbors a large snake hibernaculum on the south facing slope that contains nearly 1,000 individuals (Goetz et al., in preparation). While precipitation in montane shrubland averages 38 cm/year (Armstrong et al. 2010), precipitation during the snake's active season is much lower (average of less than 2 mm of rain per month; April to October NOAA data 2017–2021). Most of our field experimentation occurred on the butte which consists of loose, porous soil, and some large rocks. Overhanging rock slabs and Gambel Oak (*Quercus gambelii*) thickets above den openings presumably help protect snakes from aerial and other predators. These same features permitted covert observations of snake behavior.

All work involving live vertebrates was approved by the IACUC of Dickinson College (Protocol # 895) and by Colorado Parks and Wildlife.

Field experiments and videography

To elicit RHB in the field, we simulated rainfall by atomizing water with a 3.78-L pressurized sprayer (Chapin International Inc. Batavia, NY), similar to a previous study that simulated precipitation in the field to test thermoregulatory behavior of free-ranging red-sided gartersnakes (*Thamnophis sirtalis parietalis*; Shine et al. 2005). We performed a pilot study to test the efficacy of our atomizing method. Prairie rattlesnakes ($N = 24$) were captured in the field, placed in locked containers, and transported to the laboratory. The following day, containers were taken outside, the snakes were removed with tongs, placed on the ground, and exposed to atomized water. Duration of water disbursement, nozzle aperture, distance from subject, and the snake's behavior were recorded. The pilot study allowed us to refine the method and predict the extent of spray disbursement (i.e., size of the rain shadow) depending on our distance from a targeted snake.

Between 25 May 2021 and 5 June 2021, we recorded 72 videos of 94 snakes (24 snakes recorded during the pilot study followed by 70 free-ranging snakes recorded in situ) for a total of 5.26 h of video footage. Hence, some videos contained multiple snakes. Trials were conducted primarily in the afternoon (average time of day = $15:55 \pm 0.11$) when snakes were frequently found basking. Age classes (based on size) were estimable for 95% (89 of 94) of snakes: 43 adults, 21 subadults, and 25 yearlings (e.g., snakes that were born the previous summer). On 1 to 3 August 2021 and 19 to 24 August 2022, we recorded additional drinking behavior ($n = 13$ recordings) of females aggregated at birthing sites (aka rookeries; Klauber 1956; Moniz et al. 2024). Due to the large number of snakes in each of these recordings (up to 24 individuals), some aspects of individual behavior could not be easily documented. Therefore, we focused our analysis on head angles and the order in which snakes drank from different surfaces while in these large aggregations (≥ 5 individuals) to understand if and how these parameters might differ from when snakes are in smaller aggregations (≤ 4 individuals).

To create simulated rainfall events in the field (hereafter referred to as “SREs”), 2 researchers (one spraying, the other filming) were positioned 2–9 m away from field-active snakes. Before approaching a snake and staging an SRE, the sprayer was pressurized from a sufficient distance (~ 6 m) to avoid disturbing the snakes visually and by vibration. The absence of tongue-flicking and/or head movement were used to affirm we

had not disturbed snakes in early trials. The nozzle aperture was positioned to dispense water droplets approximately the same size as an average rain droplet (~ 2 mm diameter). Plumes of water were directed ~ 2 m above a given snake such that the droplets collected on the snake slowly. During some SREs, snakes were beneath vegetation (e.g., Gambel oaks) and water droplets were filtered through these short canopies before contacting the snake. Upon approach, SREs were initiated for 20–30 seconds (~ 48 pulses in rapid succession) to deliver enough water to sufficiently wet the snake (determined by visual pooling of water on multiple sections of the snake). A Canon EOS 80D Digital SLR camera with a variable (28–300 mm) zoom lens allowed us to record snake behavior before, during, and after the SRE.

Video recordings were continued for ~ 4 min once RHB ceased. Occasionally, snakes initiated RHB but then abruptly stopped (head up in an alert posture). When this occurred, a second SRE was delivered (set of ~ 12 pulses). Snakes that exhibited no RHB in response to two or more SREs were counted as zeroes. To confirm these zeroes, the trial recording continued for 3 min or until the snake moved out of view of the researchers. For each SRE, we recorded environmental data (cloud coverage, percentage of sun exposure, windspeed; via local weather data), body position (outstretched, loosely coiled, tightly coiled), age (adult, subadult, or yearling), sex, and location (via handheld Garmin Oregon 650 GPS, resolution ± 5 m). Of the 94 snakes tested, 32 had been previously marked/captured and were identified via PIT tag and a unique rattle color coding system as part of a mark-recapture study (Goetz et al., in preparation). On a few occasions, a snake's body was partially obscured by an object (e.g., a rock) when subjected to an SRE. When calculating proportions, we omitted individuals in which we could not confirm presence/absence of a behavioral response (e.g., dorsoventral flattening).

Definitions of behavioral characters

Video recordings were separated into 2 categories: those that captured snakes exhibiting swallowing kinematics suggestive of drinking (Cundall et al. 2012; hereafter referred to as “drinking”) and those that did not. We quantified movement kinematics and other behavioral characters using software for video (Tracker v6.0.0; <https://physlets.org/tracker/>) and still image analysis (Image J v1.53; <https://imagej.net/ij/>).

Tongue-flicking

The presence and rate of tongue-flicking in snakes indicates interest in a stimulus (Gove and Burghardt 1983). We thus assumed that an increase in tongue-flicking indicated an increase in interest in an SRE or at least an increase in exploratory behavior. Presence of tongue flicks was compared between snakes that drank and those that did not.

Head elevation

A positive change in head or neck angle upon introduction of the stimulus (herein: head elevation) is associated with exploratory and chemosensory searching behavior (Gove and Burghardt 1983). The presence/absence of head elevation was documented in all snakes regardless of participation in drinking.

Coiling

Coiling of concentric body loops plays an important role in RHB (Cardwell 2006). Coiling in response to SREs was

marked as either present or absent during the observation. These data were analyzed for frequency of coiling between snakes that drank and snakes that did not drink.

Dorsoventral flattening

We documented the presence or absence of dorsoventral flattening in both snakes that drank and those that did not. When a snake's body was clearly visible and perpendicular to the camera, we estimated the magnitude of dorsoventral flattening by calculating the percent increase in body width during RHB relative to body width at rest using the line tool in ImageJ. The magnitude of flattening was determined at 2 arbitrary points along the body: one more anterior and one more posterior. It was not possible to choose exact spots to use across all snakes because these field-active snakes were variably postured and visible to researchers.

Drinking surfaces

Snakes that participated in drinking were capable of drinking from 3 different surfaces: their own skin, the skin of a neighboring snake, or any proximate, non-snake surface (i.e., rocks, leaves, sticks, soil). Hereafter, these 3 surfaces are referred to as self, neighbor, and substrate, respectively. The frequency with which snakes drank from a specific surface was recorded and reported as percentages. For the snakes that drank from more than one surface ($N = 21$), we noted the order in which this occurred and recorded the duration of drinking per surface to analyze snakes' preference among surfaces. The distance that a snake traveled to drink from each surface was estimated using the line tool in ImageJ with number of head lengths as the measure of distance. Head lengths were converted to distance assuming the size of an adult male prairie rattlesnake head was 5.2 cm (Klauber 1956).

Head angle while drinking

During most observations of RHB, snakes positioned their snouts against a surface and initiated swallowing movements. The angle of the head (relative to horizontal plane) during drinking facilitates ingestion and may influence total water volume consumed (Cundall et al. 2012). We calculated head angles for snakes drinking from self, neighbor, and substrate using the protractor tool in Tracker software. We anchored the protractor to easily visible anatomical points on the snake's head (vertex = noticeable bulge of the posterior mandibular joint, arm one = nares) and a reference point in the environment (arm 2 = substrate feature that resulted in a line perpendicular to the horizon; Supplementary Figure 1). We calculated average head angle from measurements taken from 35 video frames. Angles from 0 to 180 °C were possible, with 90 °C being parallel to the horizontal plane.

Ethogram phases

Using these characters, we categorized RHB in prairie rattlesnakes into 5 unique phases (Figure 1). Phases encompassed the stereotypical postures and movements of snakes as they harvested simulated rainfall in natural, undisturbed environments (Supplementary Video 1: <https://vimeo.com/942991483/de0cb4cfa?share=copy>).

Initiation

All snakes started in a resting position, commonly found during basking/ambush behavior (Cardwell 2006). We

characterized rest by a low rate (or absence) of tongue-flicking, a coiled body, and the head resting on the ground or on a body loop. Initiation occurs at the onset of the SRE and is defined by head elevation and increased tongue-flicking. During this phase, snakes often exhibited increased ventilation rates as could be seen by rhythmic expansion of the body wall.

Exploration

The Exploration Phase was defined by increased head and neck movement beyond elevation and continued increased TFRs. Snakes in this phase explored various drinking surfaces for water. Once the SRE began, some snakes were startled by the stimulus and moved their head and neck rapidly. The snake's head occasionally exhibited a bobbing motion with the tip of the snout brushing against surfaces. When this occurred, we observed short, rapid tongue flicks as the snake moved its head along these surfaces. This tongue-flicking pattern is characteristic of chemosensory sampling in snakes (Gove and Burghardt 1983). Snakes that did not drink entered the Initiation Phase but failed to move to Exploration.

Body positioning

The Body Positioning Phase was defined by re-positioning of the body into concentric loops with each loop adjacent to the one below it. For most observations, the posterior end of the body was in the center (and on the bottom) with the anterior end of the body spiraling outward. This created a teacup-like posture (flat, semi-ellipsoid), allowing water droplets that collect on body loops to pool in troughs between adjacent coils (Figure 2). However, several snakes (16 of 33) went from Exploration to Drinking, skipping the Body Positioning Phase. Further, snakes occasionally proceeded to the next phase (Drinking) while their bodies were loosely coiled and still moving. Thus, Body Positioning and Drinking often overlapped. In addition to coiling, during Body Positioning, snakes would flatten their bodies dorsoventrally. Snakes were typically in a tightly coiled posture at the start of the SRE with body loops overlapping one another. At the start of the SRE, snakes could either adjust their bodies so that concentric loops were adjacent to one other, proceed to dorsoventral flattening, or do both.

Drinking

The Drinking Phase is defined by the presence of mandibular movements suggestive of drinking behavior (Cundall et al. 2012) and a tipping of the head toward the drinking surface. Drinking could occur from 3 surfaces (self, neighbor, substrate), and snakes often drank from more than one of these surfaces during an SRE. While drinking, tongue flicks were typically absent unless snakes changed drinking surfaces, then TFR would increase. Hence, tongue-flicking during Drinking was contextual and infrequent.

Post-drinking

The terminal phase of RHB is the Post-Drinking Phase. The Post-Drinking Phase was defined by behaviors and body positions similar to Rest or Exploration. TFR increases relative to the previous phase (Drinking), and the snake loosens its body coils while also relaxing dorsoventral flattening. Occasionally snakes entered the Post-Drinking phase for a short duration only to then re-enter Exploration, often, seeking out a water source other than its own body (neighbor or substrate).

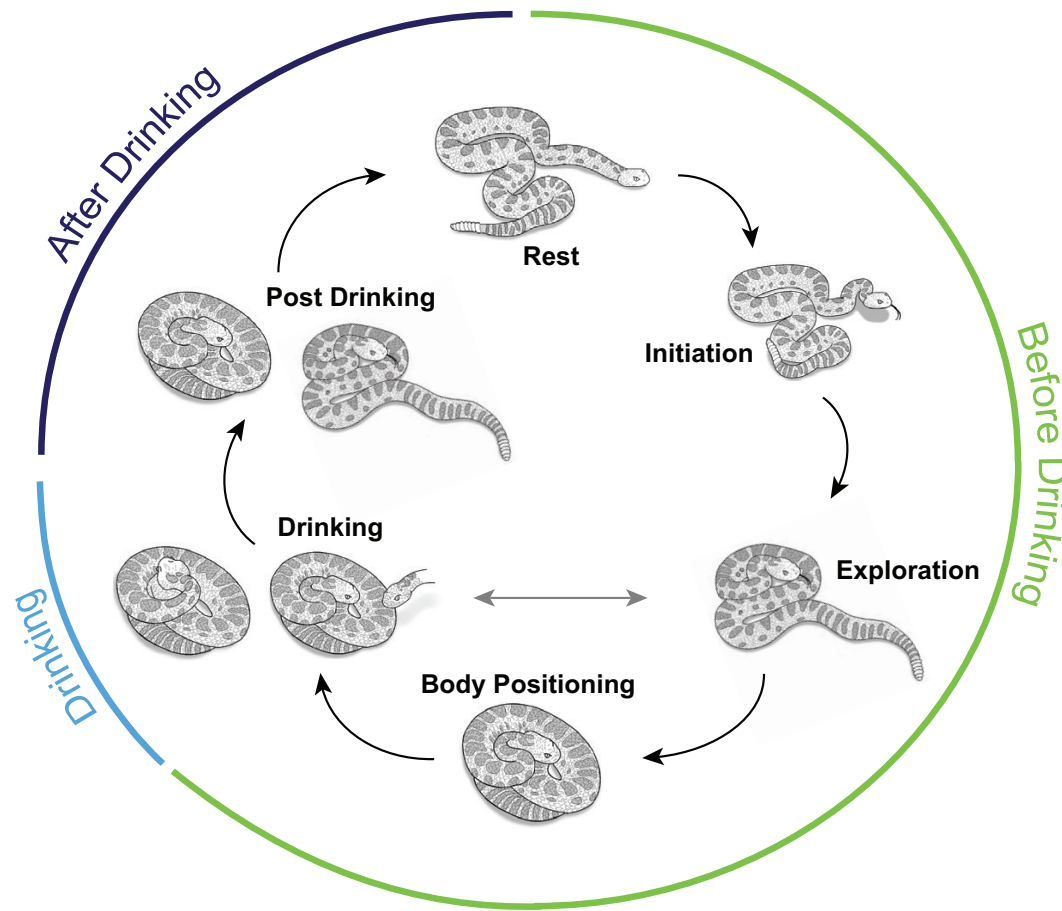


Figure 1. An ethogram of rain-harvesting behavior (RHB) in prairie rattlesnakes (*Crotalus viridis*). The outer green line encompasses behaviors before drinking occurred, the light blue line encompasses drinking behavior, and the purple line encompasses behaviors after drinking ceases. Typical progression through the behavior is indicated with black arrows. Gray arrows indicate how snakes can bypass the Body Positioning phase and/or briefly re-enter the Exploration phase from the Drinking phase. Phases are defined by several characteristics highlighted in the results. The relative lengths of each phase do not reflect the amount of time snakes spend in each (see text). **Rest:** Prior to the onset of the simulated rain event (SRE) with little to no tongue-flicking, **Initiation:** Occurs immediately after the start of the SRE. Tongue flicking and head elevation occurs, **Exploration:** Increased tongue-flicking continues with greater head movement as the snake probes the surrounding environment for suitable drinking surfaces, **Body Positioning:** The snake moves its body appropriately to capture and pool water including coiling and dorsoventral flattening its body, **Drinking:** The snake drinks and adjusts its head angle based on drinking surface, **Post-Drinking:** Relaxation of body flattening and mimics behaviors in rest or exploration.

Analysis

All data were analyzed using the R programming environment (v4.1.2). Ethogram illustrations were generated with Procreate (v5.2). Measures of central tendency are reported as means \pm one standard deviation unless otherwise noted. Due to small sample sizes, Fisher-exact tests were used to analyze count data for the presence of coiling, dorsoventral flattening, head elevation, tongue-flicking, and types of drinking surfaces used. Upon a significant Fisher-exact test, we performed post-hoc pairwise comparisons. When there were more than 2 groups (e.g., when comparing frequency of drinking off self, neighbor, and substrate), we adjusted our alpha level by applying a Bonferroni adjustment for multiple comparisons ($\alpha = 0.05/3$ groups = 0.0167). A one-way ANOVA was used to analyze duration of drinking from the various surfaces (self, neighbor, substrate). Significant ANOVA results were followed with Tukey post-hoc tests. Using the R package *rstatix*, repeated measures ANOVAs were used to analyze tongue flick rates (time [before, during, after SRE] was the within-subjects factor) and head angles while drinking (drinking surface [self, neighbor, substrate] was the within-subjects factor).

Results

Of the 94 snakes subjected to SREs, 41 snakes drank and 53 did not. Of the snakes that drank, 18 were adults, 13 were subadults, and 10 were yearlings. Of the snakes that did not drink, about a third of them (17/53) were subjected to an SRE after being captured in the pilot study.

Ethogram phases

Rain-harvesting behavior in prairie rattlesnakes was categorized into 5 unique phases of varying durations (Initiation: 16.3 ± 28.4 s; Exploration: 10.5 ± 15.8 s; Body Positioning: 6.3 ± 16.4 s; Drinking: 114.4 ± 176.7 s; and Post-Drinking: 16.0 ± 31.9 s; Figure 1). Generally, snakes progressed through phases in order. However, some snakes skipped and/or cycled back to previous phases. Some individuals exhibited unique modifications of RHB to acquire water. These modifications will be described in depth, but their general body postures and movements followed the illustrations in Figure 1.

During the Initiation phase, snakes typically exhibited tongue-flicking. The presence of tongue-flicking differed between snakes that drank and those that did not (Fisher Exact test: $P < 0.001$). Post-hoc pairwise comparisons revealed that



Figure 2. Example of a prairie rattlesnake (*Crotalus viridis*) before (A) and after (B) a simulated rain event (SRE). Note in (B) the snake is dorsoventral flattening its body and is drinking from a trough created by the junction of one body coil (foreground) with another (beneath snake's head).

snakes that drank were more likely to exhibit tongue-flicking than those that did not drink during and after, but not before, the SRE ($P_{\text{before}} = 0.10$, $P_{\text{during}} = 0.0002$, $P_{\text{after}} = 0.006$; Figure 3).

During the Body positioning phase, the magnitude of dorsoventral flattening was qualitatively greater in the posterior body (an increase of $38.5 \pm 7.2\%$) compared to the anterior body (an increase of $20.9 \pm 2.6\%$), but this difference was non-significant ($T = 2.306$, $df = 8$, $P = 0.103$). Snakes that drank differed from those that did not drink in the frequency of coiling (Fisher-exact test: $P < 0.001$). Snakes that did not drink never coiled (0 of 52; the body of one individual could not be seen and was omitted) whereas those that did drink coiled 39% of the time (16 of 41). In addition, snakes that drank differed from those that did not drink in the frequency of flattening (Fisher-exact test: $P < 0.001$). Snakes that did not drink exhibited dorsoventral flattening only 2% of the time (1 of 52) whereas those that did drink exhibited dorsoventral flattening 49% of the time (20 of 41). When snakes drank during an SRE, they frequently exhibited coiling and dorsoventral flattening together. Snakes rarely dorsoventrally flattened their bodies without being coiled (6 of 20) and rarely exhibited coiling without dorsoventral flattening (2 of 16; Table 2).

Frequency of drinking surfaces

We observed 41 free-ranging snakes that drank from themselves, a neighbor, the substrate, or some combination of these during the SRE. When we compared among snakes that only drank off one surface ($N = 20$), we found 8 (40%) drank from themselves, 3 (15%) drank from a neighbor, and 9 (45%) drank from the substrate. When we compared among snakes that drank off multiple surfaces ($N = 21$), we found 10 (47%)

drank from themselves and the substrate, 6 (28%) drank from themselves and a neighbor, 0 drank from a neighbor and the substrate, and 5 (23%) drank from all 3 surfaces (Figure 4). When comparing snakes in small versus large aggregations, the frequency of drinking from different surfaces (self, neighbor, substrate) varied (Fisher's exact test: $P = 0.002$; Table 3). Snakes in large aggregations drank from a neighbor more frequently (52% vs. 31%, respectively) and the substrate less frequently (15% vs. 33%) than those in small aggregations. However, after adjusting for multiple comparisons, post-hoc pairwise comparisons revealed these differences were not significant ($P_{\text{self}} = 0.84$, $P_{\text{neighbor}} = 0.05$, $P_{\text{substrate}} = 0.03$).

Order of drinking surface

In 11 of 21 (52%) cases where snakes drank from multiple surfaces, they first drank from themselves. The first drinking surface differed between snakes in large and small aggregations (Fisher-exact test: $P < 0.001$). Post-hoc tests with Bonferroni correction showed that snakes in large aggregations drank more frequently from a neighbor (59%, 16 of 27 instances; $P < 0.001$) and less frequently from themselves (22%, 6 of 27 instances; $P < 0.001$) compared to snakes in small aggregations (23%, 3 of 13 instances drank from a neighbor; 46%, 6 of 13 instances drank from self). Because this choice could be influenced by proximity to a particular drinking surface (their own body being closer than that of a neighbors), we measured the distance (cm) from the focal snake to neighboring snakes. The maximum distance a snake traveled to drink off a neighbor was 28 cm (average 6.2 ± 10.6 cm). However, proximity did not guarantee drinking from a neighbor. When a snake did not drink off a neighbor within the rain shadow, the maximum distance to that neighbor was 10 cm (average = 2.8 ± 4.1 cm), suggesting proximity is not the only factor affecting a snake's selection of drinking surface.

Head angles while drinking

Snakes that drank off their neighbor tended to have greater head angles (e.g., head pointed slightly up; $X = 93.8 \pm 28.4$) compared with those drinking off themselves ($X = 81.7 \pm 13.3$) or the substrate ($X = 88.8 \pm 20.0$). However, these differences were not significant ($F_{2,26} = 1.02$, $P = 0.38$) and the distribution of these values largely overlapped (Figure 5A). We found a significant effect of surface (self, neighbor, substrate) on drinking duration ($F_{2,105} = 5.53$, $P = 0.005$). A Tukey post-hoc test indicated that snakes drank from themselves for a greater duration than when they drank from a neighbor ($P = 0.04$) or the substrate ($P = 0.007$). There was no significant difference in duration when snakes drank from a neighbor and the substrate ($P = 0.87$; Figure 5B).

During the Post-Drinking Phase, TFRs tended to increase. Average TFRs were greater after an SRE (mean = 1.18 ± 0.54 /second) relative to during an SRE (mean 0.96 ± 0.47 /second) but this difference was not significant ($F_{1,11} = 1.04$, $P = 0.33$).

Additional behaviors

During these experiments, we occasionally observed other behaviors that warrant their own description but these were not used to define phases of the ethogram. Prior to SREs, most snakes were encountered while resting on relatively flat ground. When snakes were resting on non-flat surfaces (e.g., rocks and talus) they positioned their bodies horizontally in response to SREs despite irregularity of the substrate. In addition, some snakes exhibiting RHB on uneven surfaces drank

off the superior body coil first then, as rainfall ceased, moved their heads to a coil located further down slope. During one SRE, a snake encountered resting on a talus slope coiled and dorsoventrally flattened its body in response to the SRE. This effectively caused one half of its body to cantilever out from the rocks supporting the rest of its body forming a teacup shape (Figure 6). After 5 min of drinking, the snake paused, levered its body away from the horizontal plane, and continued to drink off the downslope body region (Supplementary Video 2).

During some SREs, snakes were partially hidden underneath a structure, typically rock ledges. When these snakes received a large amount of water on their heads, some retreated further into the refugia ($N = 14$), while others ($N = 10$) elevated their heads horizontally and began swallowing motions without moving any other part of their bodies. During these episodes, no part of the snake's head contacted any surface that could be a source of water (Supplementary Video 3). Snakes that exhibited this behavior (hereafter referred to as “suspended head drinking”) entered Initiation briefly, Exploration was minimal or absent, Body Positioning was absent, and Drinking occurred as normal. Therefore, snakes in these SREs bypassed the typical RHB ethogram and began to drink immediately after Initiation. Some of these snakes occasionally levered their heads forwards, allowing water droplets to accumulate on and around their supralabial and infralabial scales that disappeared during swallowing movements (Supplementary Video 4).

Discussion

Using simulated rain events, we have described rain-harvesting behavior (RHB) in prairie rattlesnakes and created the first

detailed ethogram of this behavior in any vertebrate in situ. Phases of the ethogram were delineated by the presence of kinematic movements (e.g., head elevation, drinking, dorsoventral flattening) and tongue-flicking. During these experiments, we observed novel and nuanced behaviors associated with rain harvesting that have not been previously reported in the literature. These included suspended head drinking, body levering, and drinking off neighboring snakes. In the discussion below, we position our ethogram observations within the context of previous reports of RHB and identify aspects of this behavior that warrant additional investigation.

Snakes in this study generally progressed through ethogram phases in the order presented (Figure 1). Most of the early phases of RHB (Initiation, Exploration, Body Positioning) were brief, averaging less than 16 sec each, while Drinking was the longest phase (~4 min). Many snakes (16 of 33) went from Exploration to Drinking, skipping Body Positioning. However, of these, some (6/16) were under a rock ledge, thus body positioning would not have enhanced rain collection. When SREs were delivered in front of den openings, additional snakes often emerged and immediately entered the Drinking Phase by drinking off one of the coiled snakes and/or the substrate. Future experiments could be performed to determine the stimulus or stimuli that snakes use to release RHB (e.g., chemosensation, tactile stimulation, barometric pressure, thunder, ground-borne vibrations, etc.).

During the Body Positioning phase, snakes coiled, dorsoventrally flattened, or did both. Snakes are well documented to control local (e.g., defensive hooding displays: Young and Kardong 2010; ventilation: Capano et al. 2022) and whole-body flattening (e.g., gliding: Holden et al. 2014) for a variety

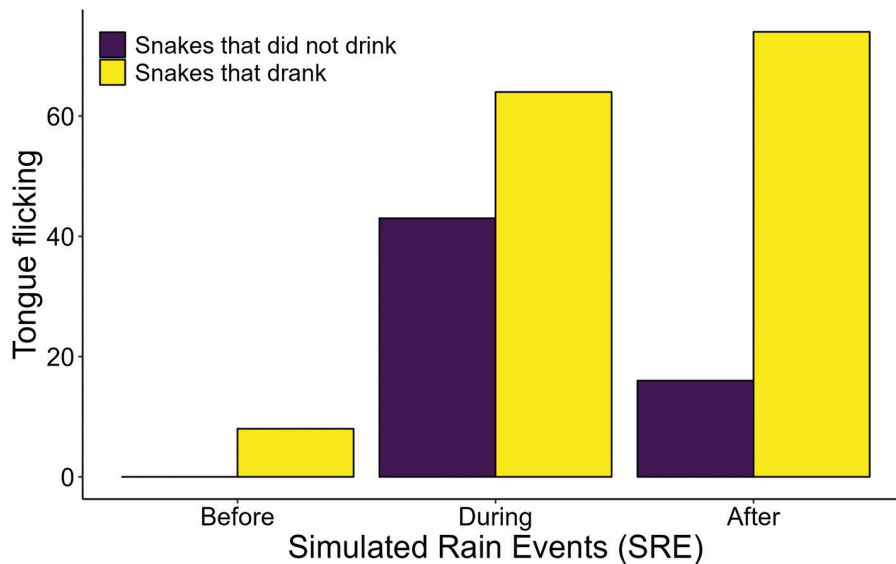


Figure 3. A barplot representing the number of prairie rattlesnakes (*Crotalus viridis*) that exhibited tongue flicking behavior before, during, and after simulated rain events (SREs) that ultimately drank (yellow bars) or did not drink water (purple bars).

Table 2 Number of prairie rattlesnakes (*Crotalus viridis*) that drank or did not drink after exposure to simulated rain events (SREs) that coiled, dorsoventrally flattened or both. Values in parentheses represent proportions.

	<i>n</i>	# coiled	# flattened	# coiled and flattened	# flattened without coiling	# coiled without flattening
Snakes that drank	41	16 (39)	20 (49)	14 (34)	6 (15)	2 (5)
Snakes that did not drink	52	0 (0)	1 (2)	0 (0)	1 (2)	0 (0)

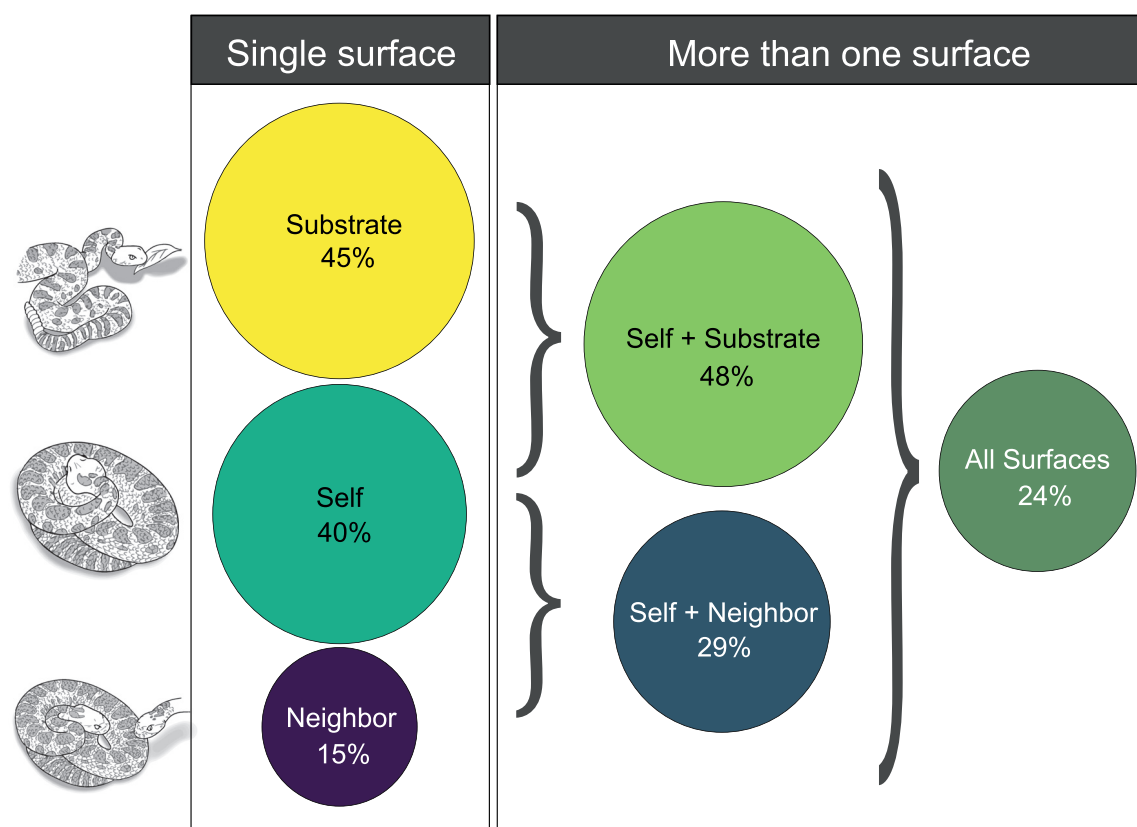


Figure 4. Proportional area plot showing the relative proportion of snakes that drank water off different surfaces during simulated rain events (SREs) when drinking off a single surface (left side, $N = 20$) or more than one surface (right side, $N = 21$). Circle colors on the right side are blended from those on the left (e.g., Substrate = yellow, Self = teal, thus Self + Substrate = light green).

Table 3 Total number of instances in which prairie rattlesnakes (*Crotalus viridis*) drank off different surfaces when they were part of a small aggregation (≤ 4 individuals) or a large aggregation (≥ 5 individuals). Data were pooled from all observed instances of drinking whether it was the first, second, third, etc. Values in parentheses represent proportions.

Aggregation size	Self	Neighbor	Substrate
Small (≤ 4)	15 (36)	13 (31)	14 (33)
Large (5 or more)	22 (33)	34 (52)	10 (15)

of functions. We demonstrate that dorsoventral flattening has a potentially broad utility across snakes in RHB. In our experiments, 34% of the snakes that drank both coiled and dorsoventrally flattened. Thus, many snakes in our study failed to exhibit “stereotypical” rain-harvesting posture before drinking (Andrade and Abe 2000; Cardwell 2006). Most published reports of RHB in snakes describe individuals drinking water off their bodies, but less than half of these (7/17) mention dorsoventrally flattening (Table 1).

We see at least 3 reasons why snakes may bypass the Body Positioning Phase. First, dorsoventral flattening is likely most important during extremely brief rain events. If sufficient water rapidly accumulates on their bodies or elsewhere (e.g., Mata-Silva et al. 2012), dorsoventral flattening may not be necessary. Second, we performed SREs on non-rainy days, and snakes may have had insufficient natural stimuli to release flattening behavior. However, we observed snakes coiling and dorsoventrally flattening their bodies on the same days when other snakes completely bypassed the Body Positioning Phase.

Lastly, this may be due to the microhabitat where the snake was located when the SRE began. For instance, rattlesnakes frequently use burrows, rock ledges, and dense vegetation for refuge (Reinert 1993; Seigel and Collins 1993). To maximize their exposure to precipitation, it may be necessary for snakes to relocate from such refugia, and they may not have sufficient time to do so during brief precipitation events.

Several studies have demonstrated links between precipitation-associated environmental cues and snake behavior. Researchers have observed other rattlesnake species concealed in heavy brush or rocks before a rain event and then found them in rain-harvesting postures in more exposed areas after it began to rain (Cardwell 2006; Glaudas 2009; Mata-Silva et al. 2014). Also, another desert-dwelling rattlesnake species, *Crotalus atrox*, synchronizes parturition (birth) with major rainfall periods (Schuett et al. 2013). In marine environments, snake species show responses to precipitation-associated cues. For instance, sea kraits (*Laticauda* spp.) take shelter prior to the arrival of typhoons and may anticipate storms (Liu et al. 2010), and activity in sea kraits and “true” sea snakes (spine-bellied sea snakes [*Hydrophis curtus*]) is influenced by rainfall (Bonnet and Brischoux 2008; Udyawer et al. 2015). Whether rattlesnakes anticipate rainstorms and release RHB remains unexplored.

In observing RHB in Mojave rattlesnakes (*Crotalus scutulatus*), Cardwell (2006) suggested dorsoventral flattening both increased surface area and slowed water runoff. He also noted that dorsoventral flattening was most obvious in the posterior body (i.e., abdominal region). We found a similar trend for a greater increase in the width of the posterior

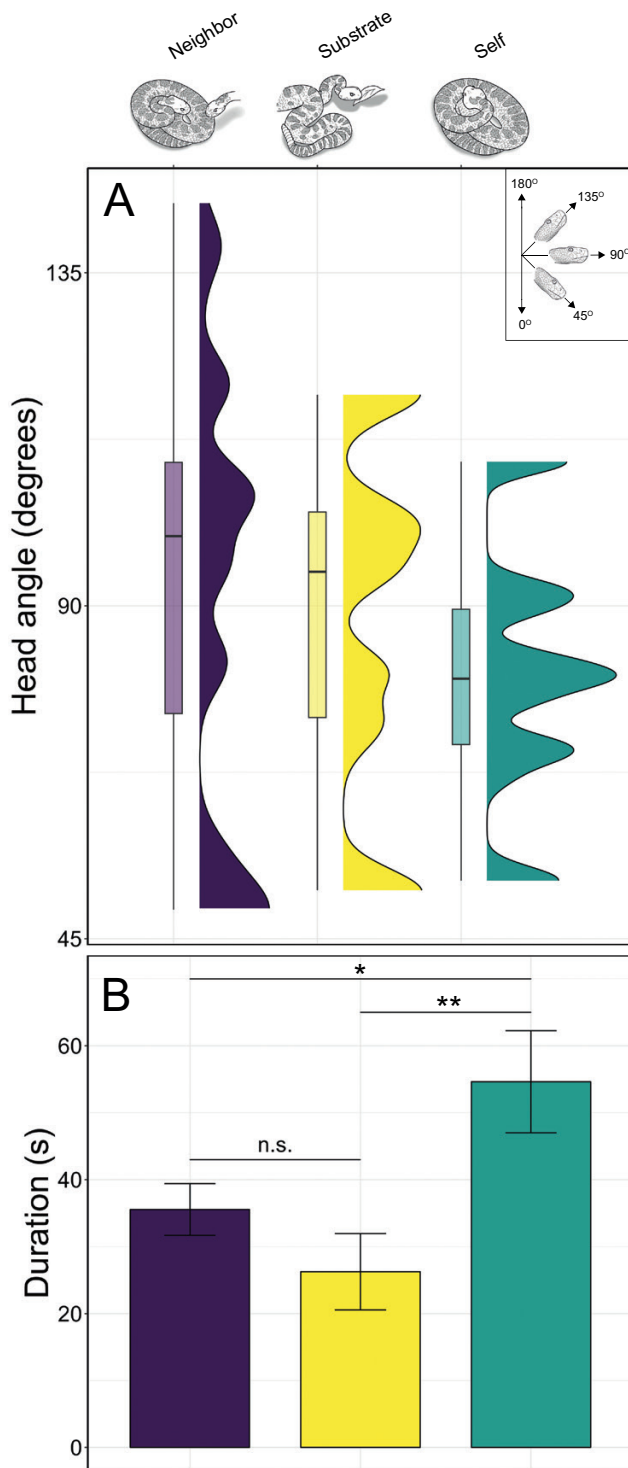


Figure 5. Raincloud plots of head angles (A) and drinking durations (B) when prairie rattlesnakes (*Crotalus viridis*) drank off different surfaces: neighboring snake (purple), non-snake surfaces like rocks and leaves (yellow), and self (teal). Head angles varied based on the surface that the snake was drinking from, but these differences were not significant. Head angles varied between 0 degrees through 180 degrees, with 90 degrees being horizontal to the ground (see Supplementary Figure 1).

versus anterior trunk during dorsoventral flattening. Annual life-history events (e.g., prey ingestion, gestation) could compromise dorsoventral flattening as they do during ventilation (Capano et al. 2022). Furthermore, we found a non-significant

trend for snakes in large aggregations to drink from a neighbor more frequently than those in small aggregations. Because these observations of large aggregations occurred at rookeries in early August, all (or nearly all) of these snakes were pregnant females. Therefore, it would be valuable to further explore whether pregnant or digesting snakes dorsoventrally flatten less and/or drink off neighbors more than males and non-pregnant females.

We observed snakes that drank off themselves, their neighbors, and non-snake surfaces like rocks and leaves. Drinking off non-snake surfaces is consistent with reports from other rattlesnake species living in habitats where such features are common (Greene 1990; Repp and Schuett 2008; Glaudas 2009). In contrast, drinking off neighboring snakes has not been reported in the literature. We suspect other species exhibit neighbor drinking, but this has gone unreported because observations of aggregating snakes during rainstorms are infrequent. Further, we observed some instances where snakes simultaneously drank off each other (Video 5). A growing body of literature suggests snakes exhibit cryptic sociality mediated by chemosensory cues (Schuett et al. 2016; Doody et al. 2021; Skinner et al. 2023). In snake species that aggregate, both kin-based (Clark et al. 2012; Schuett et al. 2016) and personality-based aggregations (Skinner and Miller 2020) imply sociality. Hence, it may be useful to test whether interactions observed in snake aggregations, such as neighbor-drinking, could be cooperative (Schuett et al. 2016; Doody et al. 2021). Our study suggests a potential, previously unrecognized benefit of snake aggregations at dens and rookeries: the spontaneous formation of communal surfaces for rain harvesting (Video 6: <https://vimeo.com/893089244/fe8fe8e398?share=copy>). Additionally, pregnant snakes maintain higher nighttime body temperatures and thermoregulated more accurately than non-pregnant females (Moniz et al. 2024), which could intensify the trade-off between thermoregulation and hydration. With heightened physiological demands, pregnant females may especially benefit from the large amount of surface area for collecting rain available in these aggregations.

During SREs performed on snakes partially hidden under rock ledges, several snakes exhibited suspended head drinking in which the head was not in contact with any surface that could be a source of water. The ability to capture and drink rain by exposing only their heads would allow snakes to remain mostly concealed from predators and potentially within a preferred microclimate. This would be extremely beneficial for snakes living in arid ecosystems attempting to minimize dehydration by reducing the amount of environmentally exposed body surface area (Dupoue et al. 2015; Dezetter et al. 2023). During a few observations of suspended head drinking, individuals levered their heads forward and water droplets accumulated on the snout would disappear during swallowing motions. Levering the head and the anterior trunk is similar to what has been described for mangrove saltmarsh watersnakes (*Nerodia [fasciata] clarkii compressicauda*), mamushi snakes (*Gloydius blomhoffii*), and yellow-lipped sea snakes (*Laticauda colubrina*) (Miller 1985; Guinea 1991; Sasaki and Duval 2003). Although we do not know if any or how much water was consumed during suspended head drinking, snakes exhibited jaw movements consistent with those described as snake swallowing kinematics (e.g., cottonmouths, *Agkistrodon piscivorus*; Cundall et al. 2012). Many squamates possess interscalar channels (Allam



Figure 6. A still image obtained from a video of a prairie rattlesnake (*Crotalus viridis*) subjected to a simulated rain event (SRE) on a talus slope. Note the snake is exhibiting coiling and dorsoventral flattening despite the uneven surfaces where it is positioned. A body loop (coil) can be seen projecting horizontally (right side of snake) and above the rocks supporting the rest of the snake.

et al. 2016), and rain-harvesting lizards utilize these channels to direct accumulated rain toward their mouths (Sherbrooke et al. 2007; Comanns 2018; Yenmis et al. 2023). Prairie rattlesnakes may do the same, but functional and mechanistic experimentation will be necessary to confirm how water might be directed to the snake's mouth (e.g., Comanns 2018) and subsequently how much water is ingested (e.g., Kardong and Haverly 1993; Bels et al. 2020).

Our recordings revealed nuanced components of RHB that connote subtle functions of this behavior. When water volume was sufficiently large, it accumulated within troughs formed at the junction of the snake's apposed body loops. Snakes then placed the tips of their snouts into these troughs and moved their heads within and along them as they drank (Figure 2), consistent with descriptions of other rattlesnake species (Cardwell 2006; Glaudas 2009). However, we found trough drinking to be rare. When less water accumulated, snakes pressed their snouts into the middle of a body loop and occasionally tipped the distal end of their bodies upwards relative to where they were drinking. Such body levering could be akin to tilting a bowl of soup to gather up the last spoonful and may function similarly to postures exhibited by rain-harvesting lizards: individuals will bend their head down and lift their hindquarters up to facilitate water movement toward the mouth (Schwenk and Greene 1987; Sherbrooke 1990).

Many snakes subjected to SREs neither exhibited RHB nor drank. Individual variation in hydration level likely influences the probability of the occurrence of RHB. Dehydrated Brazilian lanceheads (*Bothrops moojeni*) were more likely to exhibit RHB than well-hydrated individuals (Andrade and Abe 2000), and in the laboratory, marine snakes are much more likely to drink freshwater when dehydrated (Lillywhite et al. 2008, 2012, 2014, 2015). The influence of human observers and/or aversive effects of the SREs are also complicating factors. During the pilot phase of this project, snakes

were captured in the field, transported 1 km, and maintained in the lab overnight. The following day snakes were brought outside, placed on the ground, and immediately subjected to an SRE. The effect of this series of disturbances was not enough to prevent RHB, as 7 of 24 of these snakes exhibited RHB. These observations suggest water is limited within arid environments and that thirsty snakes are willing to drink despite being disturbed.

The postures and movements we observed mimicked those reported both in the literature and from remote videostreams during natural rainstorms (<https://rattlecam.org/>), collectively suggesting that using SREs to elicit RHB is a repeatable technique that releases a behavior pattern in wild reptiles. We further purport that this technique will be useful to biologists in both field and laboratory settings. The kinematic aspects of RHB were variable in prairie rattlesnakes, particularly with respect to whether snakes coiled and dorsoventrally flattened their bodies. Snakes drank accumulated water off their own skin, the skin of neighboring snakes, and non-snake surfaces, and we suggest this functions to maximize water intake. Some of our observations hint at the possibility that prairie rattlesnakes possess physical (e.g., interscalar channel morphology) and kinematic (e.g., head and body levering) adaptations to direct accumulated water toward their mouths, like those described in other rain-harvesting animals. Nevertheless, our observations indicate this adaptive behavior pattern is more complex and flexible than previously realized and could represent a widespread homoplasy among arid-adapted vertebrates. We suggest the elongate, hyperflexible body of snakes may be ideal for forming a mobile, modular, rain accumulation device within the variable landscapes of desert ecosystems.

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Ethics Statement

The Dickinson College Animal Care and Use Committee approved the study (Protocol # 895) that was carried out under Colorado Parks and Wildlife scientific collection licenses (1880291759, 2520788611).

Conflict of Interest

The authors declare that they have no conflict of interest.

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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