Title: Snake Herders: Novel cultural adaptation in response to prairie rattlesnakes in a local population of Black-tailed prairie dogs.

Authors: Verdolin, J.L.[1,2], Peterson, Elizabeth K.[3-5], Bledsoe, Ellen K.[1]

Affiliations:
[1]School of Natural Resources and the Environment, University of Arizona, Tucson AZ, USA
[2]Department of Biology, Duke University, Durham, NC, USA
[3]Department of Biology, Colorado State University-Pueblo, Pueblo CO, USA
[4]Communities to Build Active STEM Engagement Program, Colorado State University-Pueblo, Pueblo CO, USA
[5]Project CUATRO, Colorado State University-Pueblo, Pueblo CO, USA

Corresponding author: Verdolin, J.L. verdolin@email.arizona.edu
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Abstract

Local cultural adaptation through social transmission can act as a selective force that can influence behavior. We describe a case of a unique antipredator behavior sequence in response to rattlesnakes observed in a population of black-tailed prairie dogs in Fort Collins, Colorado. An analysis of 5 independent opportunistic video recordings of 6 identifiable individuals revealed individuals across multiple social groups within the population engaged in the unique sequence. We describe the behavioral sequence, compare the behaviors with previously published accounts, and propose a pathway whereby novel behavioral traits can be transmitted across social groups. Our findings also provide a preliminary assessment as to whether prairie dogs in this population are manipulating snakes by utilizing behaviors that capitalize on their sensory modalities.

Keywords: Predator harassment, antipredator behavior, cultural adaptation, cultural transmission, prairie dog

Introduction

Local cultural adaptation through social transmission is recognized as a powerful selective force that can shape behavior and contribute to the resiliency of populations (Smolla and Akçay 2019). Social species are predicted to have the greatest potential for cultural complexity and previous research suggests a positive relationship between social connectedness and breadth of cultural traits (Muthukrishna et al. 2013). There is growing evidence from non-human primates that, in the face of anthropogenic change, there are both losses and gains of cultural traits (Gruber et al. 2019). Loss of cultural behaviors has been documented in Japanese long-tailed macaques who reduced stone tool use in response to an increased presence of dogs at important foraging sites (Gumert et al. 2013). Novel behaviors can also emerge, as seen in a chimpanzee community that adopted the use of leaf tools to consume Raphia palm wine, a novel food item (Hockings 2015). For bottlenose dolphins of Shark Bay, Australia, dolphins that use sponges for feeding, a behavior transmitted across generations, were better able to survive a catastrophic heatwave in 2011 (Wild et al. 2019).

Like foraging behavior, antipredator strategies also have a significant impact on survival. Socially learned antipredator behavior has been demonstrated in both conspecifics and heterospecifics (Avarguès-Weber et al. 2013; Keen et al. 2020). Acoustic signals, such as alarm calls, have provided the best evidence for social transmission of novel responses to predation threat. For example, in blue and great tits, conspecifics learned with direct experience, while heterospecifics acquired responses to predators through indirect acoustic transmission (Keen et al. 2020).

Black-tailed prairie dogs (*Cynomys ludovicianus*) are known to exhibit specific alarm calls in response to different predators and juveniles learn through exposure to adults in the

community (Shier and Owing 2007; Frederikson and Slobodchikoff 2010). More recently, Dennis et al. (2020) reported that black-tailed prairie dog colonies more than 30 km from each other exhibit distinct dialects in alarm calls. Furthermore, differences between populations were positively correlated with distance, such that the farther colonies were from each other, the greater the difference in acoustic properties (Dennis et al. 2020). This suggests cultural differences in acoustic properties of alarm calls that are learned and transmitted locally.

Another anti-predator behavioral strategy observed to vary in prairie dogs is predator harassment and mobbing (Haplin 1983; Owings and Owings 1979). Rattlesnakes (*Crotalus spp.*) are a common predator of prairie dogs, and colonies represent an important resource for them (Chiszar et al. 2014). Black-tailed prairie dogs have been observed engaging in harassment of rattlesnakes under both natural and experimental conditions (Loughry 1987a; Loughry 1987b; Loughry 1988; Loughry 1989). Loughry (1987a,b) reported that adult males in a Texas population were more likely to participate in confrontations with rattlesnakes. However, this behavior varies by geographic location, as Loughry (1988) reported no difference between adult males and females in a South Dakota population.

Despite this early research, it remains unclear if there are differences in snake-directed behaviors across populations and whether there is a socially learned component to snake antipredatory behavior in prairie dogs. Given the complexity, variability, and flexibility of prairie dog behavior, they are an ideal species to examine how local cultural adaptations may shape responses to predators.

On July 9th, 2012, we witnessed a black-tailed prairie dog exhibiting unique predator harassment behaviors toward a prairie rattlesnake (*Crotalus viridis*) in Fort Collins, Colorado. As we continued to observe the population for several more days, additional individuals engaged in

similar behaviors in response to the presence of rattlesnakes. Here, we describe the unique antipredator behavior sequences opportunistically observed in this population. More specifically, we ask if there was a non-random, stereotyped sequence of behaviors exhibited by these prairie dogs in response to the rattlesnake and, if so, which behavior transitions contribute to the non-random nature of the behavior sequence.

Methods

Study Species

Black-tailed prairie dogs are a gregarious colonial sciurid occupying the Great Plains from Chihuahua in northern Mexico to Saskatchewan in Canada (Slobodchikoff et al. 2009). Within colonies, the population lives in social groups that vary in size, composition, and social connectivity influenced by ecological conditions (Kusch and Lane 2020, 2021).

Study Area

All observations occurred at Coyote Ridge Natural Area, northwest of the city of Fort Collins, Colorado, USA. Coyote Ridge is in a region of the Great Plains categorized as montane shrublands, a transition zone between shortgrass prairie and the montane forests of the Rocky Mountains (Davis and Thompson 2020). It's maintained as 840 ha of open space for recreational use and wildlife viewing of several species, including black-tailed prairie dogs (Davis and Thompson 2020; Graeme et al. 2020).

The main trail at Coyote Ridge Natural Area, Coyote Ridge Trail, is frequented by the public, utilizing the space for recreational use. The colony at Coyote Ridge is adjacent to the main trail and is regularly exposed to human presence. Therefore, the prairie dogs at Coyote Ridge are acclimated to the presence of humans.

Data Collection

Direct opportunistic observations were made by JLV from July 9, 2021 to July 13, 2021, sitting in the open alongside the Coyote Ridge Trail at Coyote Ridge Natural Area. All observations were recorded by JLV with a Canon PowerShot SX70 HS Digital Camera. Six different individual prairie dogs were recorded interacting with and responding to prairie rattlesnakes in the colony. Individual prairie dogs were identified unique marks, such as scars, bald spots, and other distinguishing features.

Ethograms were created using a combination of observed behaviors and the previous literature. To describe new behaviors we conducted a preliminary review of the videos and recorded a description of the behaviors seen in each video. We then used the published literature to describe previously observed behaviors in both rattlesnakes and prairie dogs. These behaviors are provided in the supplementary materials (Suppl Table 1 and Suppl Table 2).

For each video, JLV and EKP recorded the date, time stamp, bout, and video sequence to distinguish between different prairie dogs. In addition, we recorded the sex (male or female) and age (adult or juvenile) of each individual and recorded any physical identifiers that distinguished individuals from each other. Then we recorded the name of the specific behavior using the ethograms (see Suppl Table 1 and Suppl Table 2). Data were recorded only when individuals were in the frame of view. For snakes, we did not record tail behavior because the tail was not visible in most videos.

Data Analysis

All statistical analyses were conducted in R 4.1.2 (R Core Team, 2020). The data and R scripts for all analyses can be found on GitHub (https://github.com/bleds22e/SnakeHerders). We created a behavior transition matrix for prairie dogs, tabulating all the instances in which one behavior led to another. We did not include all behaviors recorded in the analysis because either

1) the behavior was not related to the prairie dog-snake interaction (e.g., greet-kiss or foraging), and/or 2) the behavior only occurred one time (e.g., fake-foraging). This left 12 behaviors for analysis (see Suppl Table 1). We used single-order Markov chains to test whether the behavioral transitions were non-random using the `verifyMarkovProperty` function from the package `markovchain` (Spedicato, 2017).

We were also interested in evaluating whether certain transitions were more likely to occur than others. To do this, we ran chi-squared tests on the transition matrices to determine overall significance and calculate "expected" values of each transition. Using the `FTres` function from the `kequate` package (Andersson et al. 2013), we used the values from the transition matrix and expected values to calculate the Freeman-Tukey residuals for each transition. From there, we calculated correlation values and significance values for each transition using the Freeman-Tukey residual values (`Hmisc` package; Harrell 2022).

Results and Discussion

Prairie Dog Anti-snake Behavior

We observed a total of 6 interactions between prairie dogs and snakes. In our preliminary review of the video recordings, we noted several novel behaviors not previously reported in the literature. Specifically, we observed prairie dogs engaged in foreleg drumming, back leg scratching, and simultaneously rocking and sniffing (Suppl Table 1). Most often these behaviors appeared to occur in a sequence after a prairie dog initially approached the snake. Occasionally the prairie dog would walk alongside the rattlesnake for some period of time, what we describe as "escorting" (Suppl Table 1) and then repeated the behavioral sequence. For example, an individual approached the rattlesnake and patted the ground with her front feet (foreleg drumming), then she rocked and sniffed simultaneously, and then scratched herself with her back

right leg (Figure 1A-C). There were two instances where a prairie dog struck the tail of the rattlesnake (Figure 1D).

We did not observe any instances of multiple prairie dogs interacting with rattlesnakes simultaneously. In addition to these novel behaviors, we also observed behaviors that have been previously described. For example, we observed prairie dogs sniffing and head-bobbing. Prairie dogs surrounding the focal prairie dog that was engaged with the snake did not alarm call or assist the individual in confronting the snake. In three instances, a second prairie dog was in close proximity (<0.5 meter) and was either observing, posting, or foraging. On two other occasions an adult female had juveniles in close proximity that were observing the adult female. Subsequently, they engaged in the rocking and sniffing behavior. Given the close proximity of other adults and occasionally juveniles, there is an opportunity for learning through observation and exposure. This is similar to reports by Owings and Loughry (1985) and Hennessy et al. (1981) that prairie dogs nearby monitor the snake-directed behavior of others.

The Markov chain analysis of prairie dog behavioral transitions indicated a nonrandom pattern of behavioral sequences (χ^2 = 75.27, df = 36, p = 0.00014). A Pearson's Chi-squared test was also significant (χ^2 = 353.6, df = 121, p<0.0001).

Subsequent pairwise comparisons using Spearman's rank correlation revealed the specific transitions that were contributing to these results (Figure 2; Table 1). Notably, there were four significant behavioral transitions, including escorting → retreat (r_s = 0.64, p = 0.024), jump-yip → retreat (r_s = -0.65, p = 0.022), and rocking →>rocking + sniffing (r_s = 0.71, p=0.010), foreleg drumming → jump back. Two additional behavioral transitions–rocking + sniffing → scratching (r_s = -0.54, p = 0.071) and foreleg drumming → escorting (r_s = 0.51, p = 0.090) were borderline significant.

When we looked at the Freeman-Tukey residuals for each significant transition pair all except jump-yip → retreat occurred more frequently than expected. These behavioral transitions are driving the nonrandom pattern detected by the Markov-Chain analysis but in different ways. For example, escorting transitions to retreating more frequently than expected, while retreating happens less frequently than expected after jumps-yipping (Figure 2). The reason for this may be because while a prairie dog is escorting, the snake is moving out of the area making it safe to retreat. However, when jump-yipping, the prairie dog is still engaged in a display toward the rattlesnake, thus is less likely to retreat if the rattlesnake is still present.

Although the prairie dogs are engaged in nonrandom behaviors in response to rattlesnakes, and we have identified specific behavioral transitions that occur more or less often than expected, we recognize we have a small sample size involving six individual prairie dogs and 189 total behavioral transitions.

Prairie Dog Snake Detection

In several instances it was clear the prairie dogs were trying to determine the exact location of the snake. This was done by sniffing, rocking and sniffing, or head bobbing. Although prairie dogs are known to have color vision, it is difficult for them to discriminate in the yellow and green spectrum (Cain and Carlson 1968; Slobodchikoff et al. 2009b). Prairie rattlesnakes are well camouflaged and, when present in green grass, may be especially difficult for prairie dogs to see until they are very close to the snake.

We suspect that prairie dogs may be using olfaction to identify the specific location of a rattlesnake before engaging in additional snake-directed behaviors. We observed prairie dogs rocking and sniffing, cautiously approaching the snake, and then quickly jumping back as soon as they were in close proximity (approximately <15 cm), after which they approached the snake

more confidently. Once the snake's location was determined, prairie dogs remained in this range of proximity during the majority of the interaction.

On one occasion there was a clear flehmen response by a focal prairie dog, further pointing to chemosensory information being used to locate the snake. Most organisms, including snakes, have a natural scent and there is evidence that other species can detect the odor of rattlesnakes. For example, California ground squirrels (*Spermophilus beecheyi*) have been observed actively applying rattlesnake scent from shed snakeskin to their fur (Clucas et al. 2008), a behavior not observed in this or other populations of prairie dogs. It is likely that prairie dogs were cueing in on the natural scent of the rattlesnake as part of their antipredator strategy.

Prairie Dog Manipulation of Prairie Rattlesnake

We discovered that when a focal prairie dog engaged in foreleg drumming, scratching, or jump yipping the snake responded by moving its body, orienting its head, or raising its head in the direction of the prairie dog. For example, in one interaction, the snake was coiled, with its head down, and rattle unmoving. A prairie dog approached the snake and was positioned directly in front of the snake (<15cm). After the prairie dog rocked and sniffed, drummed its forelegs, and scratched, the snake lifted its head and oriented toward the prairie dog. After jump yipping and additional rocking and sniffing, the snake began moving toward the prairie dog. In another sequence, a snake was moving and a prairie dog approached its head. The focal prairie dog rocked, scratched, jump-yipped, and positioned itself parallel to the snake. She proceeded to walk alongside the snake for a few seconds before moving in front of the snake, scratching and jump-yipping. This sequence continued until the snake left the immediate area, and presumably, the territory of the focal prairie dog.

Rattlesnakes use scent, vibrations, and infared radiation to detect prey (Schraft et al. 2019; Teshera and Clark 2021). At the same time, prairie rattlesnakes are cryptic ambush hunters relying on being undetected. By displaying toward the snake by foreleg drumming, back leg scratching, and jump yipping, prairie dogs were advertising to the snake that it was seen. In response to being detected, snakes may remain still or leave the area (ref xx). Given that prairie dogs continued displaying until the snake left, it provides further evidence that the display is designed to communicate with the snake. Lastly, prairie dogs interacting with the snake did not alarm call. This may be because rattlesnakes can't hear, rendering an auditory signal useless if the behaviors were directed at the snake and not for the benefit of other prairie dogs.

Unfortunately, there were not enough behavioral transitions to analyze the prairie dog-snake interaction data quantitatively. However, it appears that whether the snake was at rest or on the move, the behavior of the prairie dogs elicited a response from the snake. That response was to orient and begin moving toward the prairie dog. Once the snake was moving, the prairie dogs shifted position walking alongside the snake (escorting), then returned toward the head of the snake, or, on two occasions, struck the tail of the snake as it passed.

What is interesting to note is that individuals on this colony were in close proximity (<15 cm) to the rattlesnake during the majority of the interaction. This distance is clearly within striking distance. Unlike other species of ground squirrels (e.g., rock squirrels and California ground squirrels; Owings et al. 2001), adult prairie dogs have not evolved resistance to rattlesnake venom. This makes proximity to and direct interaction with rattlesnakes potentially deadly. Indeed, on July 9th the first observation made was that of a swollen, bluish colored deceased prairie dog on the outside of a burrow and another prairie dog rocking and sniffing at the lip of the burrow (Fig 3A-B). This is consistent with a prairie dog being exposed to

239 rattlesnake venom. Several hours later a rattlesnake was observed attempting to consume the
240 deceased prairie dog (Figure 3C). The proximity may again reflect that the display is to the snake
241 not toward conspecifics.

242 There is evidence for variation in snake-directed behaviors in black-tailed prairie dogs
243 depending on the species of snake. In some populations prairie dogs attacked nonvenomous bull
244 snakes more frequently than rattlesnakes and spent more time in snake-directed behaviors toward
245 rattlesnakes, while in another population prairie dogs behave similarly toward bull snakes and
246 rattlesnakes (Owings and Loughry 1985; Loughry 1989). Loughry (1989) concludes that the
247 degree of exposure and experience a colony has with snakes contributes to this difference.

248 The prairie dogs at Coyote Ridge are not naive to prairie rattlesnakes. JLV observed
249 prairie rattlesnakes at Coyote Ridge in 2015 and in 2017. Despite exposing themselves to
250 considerable risk, adult prairie dogs on this colony appear to use a set of deliberate and
251 structured behaviors to deal with a prairie rattlesnake in their territory. We further suggest that
252 this behavior is likely learned and opens the door for a closer examination of socially mediated
253 cultural complexity in this species.

254 **Conclusions**

255 We found that black-tailed prairie dogs on this colony engaged in anti-predator behavior in
256 response to prairie rattlesnakes that included a combination of novel and previously documented
257 behaviors. Specifically, we found that these prairie dogs exhibited novel nonrandom behavioral
258 sequences that included foreleg drumming, scratching, and rocking and sniffing.

259 Previous reports on interactions between black-tailed prairie dogs and rattlesnakes
260 describe mobbing, attacks, and killing of snakes by prairie dogs (Tang and Haplin 1983),
261 something not observed in this population. Given the structured nature of the behavioral

sequences exhibited by the prairie dogs we do not classify their behavior as harassment, mobbing, or attacking. Most of the interactions were deliberate and appeared aimed at signaling to the snake and encouraging and escorting it out of the focal prairie dog's territory.

The response of the prairie rattlesnakes included orienting the head toward the prairie dog and moving the body in the direction of the prairie dog. Although we were unable to quantitatively analyze the prairie dog-snake behavioral transitions, we strongly suspect that prairie dogs in this population are altering snake behavior through these nonrandom behavior sequences.

We propose that black-tailed prairie dogs in this population have evolved a strategy that exploits the heat and vibration sensory systems of the rattlesnake. The presence of juveniles and other prairie dogs near an individual that is interacting with the prairie rattlesnake provides the opportunity for learning and social transmission through observation and exposure.

Figure 1A-D.

Figure 1. Behavioral sequence of an interaction between a prairie dog and a rattlesnake. In this sequence, a female engaged in foreleg drumming (A), rocking and sniffing (B), and then back leg scratching (C). Finally, she struck the tail of the rattlesnake (D).

Figure 2.

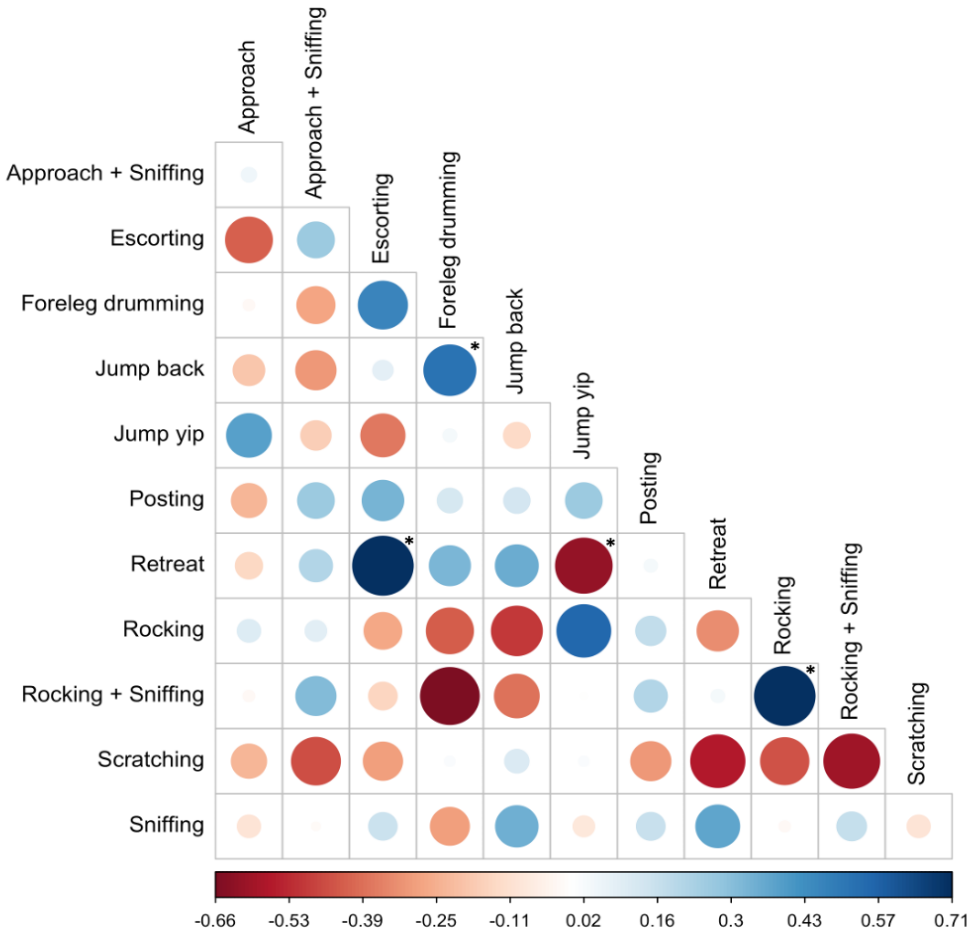

Figure 2. Freeman-Tukey residuals for each behavioral transition pair. Transitions are from the behavior on the x-axis to the behavior on the y-axis; for example, the transition state of the box in the upper left-hand corner is an "approach" to "approach and sniff." Color of dots indicates the value of the Freeman-Tukey residuals for each transition pair, calculated from the observed and expected values of the transition matrix. Positive (blue) values indicate that the transition occurred more frequently than would be expected, while negative (red) values indicate the transition occurred less frequently than expected. Size of dots corresponds to the absolute values of the Freeman-Turkey residuals. Asterisks indicate significant transition pairs.

Figure 3A-C.

Figure 3. Panel A shows a deceased prairie dog on the edge of a burrow. Panel B is a second prairie dog investigating, sniffing and rocking at the lip of the same burrow. Panel C shows the rattlesnake attempting to consume the deceased prairie dog.

346 **Supplement 1.**

347 **Suppl1A. Table 1.** Ethogram of Black-tailed Prairie Dog (*Cynomys ludovicianus*) Behavioral
348 Elements Toward Prairie Rattlesnakes (*Crotalus viridis*). Italicized behaviors were used in the
349 analysis.
350

Behavior	**Description**
Alarm call	Defined as "repetitious barks" by Waring (1970)
Approach	Apprehensive movement toward the vicinity of the snake
Escorting	Walking in variable orientation to the snake
Fake foraging	Appearing to consume food but not actually consuming food
Flehmen response	Mouth open
Foraging	Actively searching and consuming food
Foreleg drumming	Both forelegs alternatively moving up and down in repetitive manner against the substrate
Greet-kiss	Defined as "two prairie dogs come toward one another, open their mouths, and press their tongues together" by Slobodchikoff et al. (2009)
Investigating	Moving towards an area where the individual appears to think something is
Jump back	Defined as "a variable amplitude leap away from the snake that could be elicited by snake movement but also occurred frequently in the absence of snake movement" by Owings & Owings (1979)
Jump-yip	Defined as "throws its forequarters into the air and drops to the ground again while emitting a two-syllable vocalization" by Owings and Owings (1979)
Moving toward	Direct, purposeful movement toward the snake's head or body
Observing	Watching snake move past
Orientation (3 types)	Oriented body either: 1) head-to-head with snake, 2) perpendicular to snake, or 3) parallel to snake
Posting	Bipedal posture of vigilance
Pushing dirt	Using forelegs to move dirt
Retreat	Turning away from and/or walking away from snake

Rocking	Elongating body and moving head forward and backwards with feet stationary
Running	Fast quadrupel movement (faster than walking) towards something
Scanning	Quadrupedal posture of vigilance with head raised
Scratching	Scratching the side of the body with the rear leg
Sniffing	Directed smelling of the air
Startled	A quick upward movement, or jump, in response to a startling stimulus or threat
Strike	Make contact with snake body, such as poking the snake
Tail posture (4 types)	Tail is either: 1) upright, 2) upright but close to back, 3) down parallel to ground, and 4) piloerect
Touching face	Uses its front foreleg to touch its face
Two-step	A step forward or in reverse followed by another step in opposing direction
Vocalization	Unidentified vocalization, not including alarm call or jump-yip calls

Suppl 1B. Table 2. Ethogram of Behavioral Elements of Prairie Rattlesnakes (*Crotalus viridis*) in response to Black-tailed Prairie Dog (*Cynomys ludovicianus*) *Known behaviors in snakes that were not observed in this study

Behavior	**Description**
*Body flattening	Defined as "adult flattens its head and trunk against the substrate and elevates its tail without rattling" by Carbajal-Márquez et al. (2018)
Body orientation	Oriented body toward the prairie dog
Coiled (2 types)	Snake coiled in two ways: 1) "Coiled resting": coiled while resting (fully coiled and head is resting on top of body), and 2) "Coiled strike": coiled in strike pose
*Dorsal-ventral flattening	While gliding, "the snake becomes airborne, the body flattens sequentially from head to vent,forming a cross-sectional shape that is roughly triangular, with a flat surface and lateral 'lips' that protrude ventrally on each side of the body" as defined by Socha (2011)
Half-coil	Approximately ⅓ of the head and body elevated off the ground

Head concealment	Hiding the head in the coiled body
Head orientation	Oriented head toward the prairie dog
Head raise	Head is raised off the ground or body
Moving	Snake moves elongated along the substrate (e.g., surface such as rock, grass or dirt)
*Neck flattening	Defined as "the neck (immediately posterior to the head) spreads laterally and the cervical spine is straight and aligned with the head" by Carbajal-Márquez et al. (2018)
Rattling	Fast waving movements of the tail usually accompanied by sound
Striking	Quick movement of the head to make contact with the prairie dog with the mouth, including both a strike where the snake does or does not bite the prairie dog
Tail posture (two types)	Tail is either: 1) "Tail elevated": elevated off the substrate (e.g., surface such as rock, grass or dirt), or 2) "Tail resting": Parallel and resting on body or substrate (e.g., surface such as rock, grass or dirt)
Tongue flicking	Investigative behavior to collect information via scent or taste by extending tongue outside the mouth and moving it in the air

References

Andersson, B., Branberg, K., and Wiberg, M. 2013. Performing the kernel method of test Equating with the package kequate. Journal of Statistical Software. 55:1-25. https://doi.org/10.18637/jss.v055.i06

Avarguès-Weber, A., Dawson, E.H. and Chittka, L., 2013. Mechanisms of social learning across species boundaries. Journal of Zoology. 290: 1-11.

Carbajal-Márquez, R.A., Rogelio Cedeño-Vázquez J., García-Balderas C.M., Ramírez-Valverde T., Quintero-Díaz G.E. 2018. The defensive behaviour of Tzabcan Rattlesnake, *Crotalus tzabcan* Herpetology Notes. 11:429-431.

Cain, R.E. and Carlson, R.H., 1968. Evidence for color vision in the prairie dog (Cynomys ludovicianus). Psychonomic Science. 13:185-186.

Davis, S.K. and J.L. Thompson. 2020. Investigating the impact of interpretive signs at neighborhood natural areas. Journal of Interpretative Research 16:55-66.

Dennis, P., S.M. Shuster, and C.N. Slobodchikoff. 2020. Dialects in the alarm calls of black-tailed prairie dogs (*Cynomys ludovicianus*): A case of cultural diffusion? Behavioural Processes. 181:104243.

Graeme, S., M.F. McKenna, G. Wilson-Henjum, L. Angeloni, K. Crooks, G. Wittemyer. 2020. Vocal characteristics of prairie dog alarm calls across an urban noise gradient. Behavioral Ecology. 31: 393–400.

Graves, B.M. and D. Duvall. 1988. Evidence of an alarm pheromone from the cloacal sacs of prairie rattlesnakes. The Southwestern Naturalist. 33:339-345.

Gruber, T., L. Luncz, J. Mörchen, C. Schuppli, R.L. Kendal, and K. Hockings. 2019. Cultural change in animals: a flexible behavioural adaptation to human disturbance. Palgrave Communications. *5*:1-9.

Gumert, M.D., Y. Hamada, and S. Malaivijitnond. 2013. Human activity negatively affects stone tool-using Burmese long-tailed macaques Macaca fascicularis aurea in Laem Son National Park, Thailand. Oryx. 47: 535-543.

Halpin, Z.T., 1983. Naturally occurring encounters between black-tailed prairie dogs (Cynomys ludovicianus) and snakes. American Midland Naturalist. 109:50-54.

Harrell, Jr., F. 2022. Hmisc: Harrell Miscellaneous. R package version 4.7.0, <https://CRAN.R-project.org/package=Hmisc>.

Hockings, K.J., N. Bryson-Morrison, S. Carvalho, M. Fujisawa, T. Humle, W.C. McGrew, M. Nakamura, G. Ohashi, Y. Yamanashi, G. Yamakoshi, and T. Matsuzawa. 2015. Tools to tipple: ethanol ingestion by wild chimpanzees using leaf-sponges. Royal Society Open Science, *2*(6):150.

Jordán, F., B. Kovács, J.L. Verdolin. 2021. Resource availability influences global social network properties in Gunnison's prairie dogs (*Cynomys gunnisoni*). Behaviour. 159:321-338.

Kusch, J.M. and J.E. Lane. 2020. Variation of social strategies within and between individual black-tailed prairie dogs (*Cynomys ludovicianus*) during the reproductive season. Behavioural Ecology and Sociobiology. 75:10.

Kusch, J.M. and J.E. Lane. 2021. Determinants of social structure in a northern population of black-tailed prairie dogs, *Cynomys ludovicianus*. Animal Behaviour. 178:1-10.

Loughry, W.J. 1987a. Differences in experimental and natural encounters of black-tailed prairie dogs with snakes. Animal Behaviour. 35(5):1568-1570.

Loughry, W.J. 1987b. The dynamics of snake harassment by Black-tailed prairie dogs. Behaviour. 103:27-48.

Loughry, W.J. 1988. Population differences in how black-tailed prairie dogs deal with snakes. Behavioral Ecology and Sociobiology. 22:61-67.

Loughry, W.J. 1989. Discrimination of snakes by two populations of BTPDs. Journal of Mammology. 70(3):627-630.

Muthukrishna M., B.W. Shulman, V. Vasilesc, J. Henrich. 2013. Sociality influences cultural complexity. Proceedings Biological Science. 281(1774):20132511. doi: 10.1098/rspb.2013.2511. PMID: 24225461; PMCID: PMC3843838.

Owings, D.H. and W.J. Loughry. 1985. Variation in snake-elicited jump-yipping by black-tailed prairie dogs: Ontogeny and snake-specificity. Zeitschrift für Tierpsychologie. 70:177-200.

Owings, D.H. and S.C. Owings. 1978. Snake-directed behavior by Black-tailed prairie dogs (*Cynomys ludovicianus*). Zeitschrift für Tierpsychologie. 49:35-54.

Owings, D.H. and S.C. Owings. 1979. Snake-directed behavior by black-tailed dogs (*Cynomys ludovicianus*). Zeitschrift für Tierpsychologie 49:35-54.

Owings, D.H., R.G. Coss, D. McKernon, M.P. Rowe, and P.C. Arrowood. 2001. Snake-directed antipredator behavior of rock squirrels (Spermophilus variegatus): population differences and snake-species discrimination. Behaviour. 138:575-595.

Schraft, H.A., G.S. Bakken, and R.W. Clark. 2019. Infrared-sensing snakes select ambush orientation based on thermal backgrounds. Science Reports. 9:3950. https://doi.org/10.1038/s41598-019-40466-0

Shier, D.M. and D.H. Owings. 2007. Effects of social learning on predator training and postrelease survival in juvenile black-tailed prairie dogs, Cynomys ludovicianus. Animal Behaviour. 73:567-577.

Slobodchikoff, B.N., B.S. Perla, and J.L. Verdolin. 2009a. Prairie Dogs: Communication and Community in an Animal Society. Harvard University Press, Cambridge, MA.

Slobodchikoff, C.N., A. Paseka, and J.L. Verdolin. 2009b. Prairie dog alarm calls encode labels about predator colors. Animal Cognition. 12(3):435-439.

Smolla, M. and E. Akçay, E. 2019. Cultural selection shapes network structure. Science Advance., *5*(8):eaaw0609.

Socha J.J. 2011. Gliding Flight in *Chrysopelea*: Turning a Snake into a Wing. Integrative and Comparative Biology. 51(6):969–982.

Spedicato, G. A. 2017. Discrete Time Markov Chains with R. The R Journal. 9(2): 84-104.

Teshera, M.S. and R.W. Clark. 2021. Strike-induced chemosensory searching in reptiles: a review. Herpetological Monographs. *35*(1):28-52.

Waring, G.H. 1970. Sound communications of Black-tailed, white-tailed, and Gunnison's prairie dogs. The American Midland Naturalist 83(1):167-185.

Wild, S., M. Krützen, R.W. Rankin, W.J. Hoppitt, L. Gerber, and S. J Allen. 2019. Long-term decline in survival and reproduction of dolphins following a marine heatwave. Current Biology. 29(7): R239-R240.