BRILL

Amphibia-Reptilia (2022) DOI:10.1163/15685381-bja10101

brill.com/amre

Short Note

Safety in coils: predation rates of ambush hunting rattlesnakes are extremely low

Dylan Maag*, Rulon Clark

Department of Biology, San Diego State University Biology Department, San Diego, CA 92182, USA
*Corresponding author; e-mail: dmaag3229@sdsu.edu
ORCID iD: Maag: 0000-0002-7255-7196

Received 20 May 2022; final revision received 31 August 2022; accepted 1 September 2022; published online 20 September 2022
Associate Editor: Fernando Martínez-Freiría

Abstract. Rattlesnakes are widespread mesopredators that are themselves killed and eaten by a host of other predators, including birds of prey and carnivorous mammals. Although anecdotal accounts of rattlesnake depredation are common, there are few quantitative data on encounter rates between rattlesnakes and their predators. Here we review a large database of encounters between rattlesnakes and their predators recorded from field videography of snakes in the sit-and-wait phase of their ambush hunting strategy. We found that, across 8300 hours of observation, adult rattlesnakes of six species and multiple populations exhibit low encounter rates with predators; furthermore, when predators were encountered, we never observed them to attack or kill coiled snakes. Thus, we propose that rattlesnakes are preyed upon while performing other, riskier behaviors associated with moving through the landscape. We also discuss why rattlesnakes are at low risk of predation while hunting on the surface.

Keywords: *Crotalus*, *Geococcyx californianus*, mesopredators, pitviper, predator-prey interactions, snake, videography.

Rattlesnakes (*Crotalus* and *Sistrurus*) are widespread, abundant mesopredators in ecosystems throughout North America. As such, they are not only important predators, but are preyed on by a variety of large animals (e.g., hawks, roadrunners, canids, badgers, and kingsnakes; Klauber, 1956). However, most published reports on encounters between rattlesnakes and their predators are anecdotal, and thus not well suited to developing a general understanding of predation risk. Studies on feeding ecology of animals that prey on rattlesnakes consistently indicate that rattlesnakes are only a minor part of the diet (Messick and Hornocker, 1981; Parmley, 1982; MacLaren, Anderson, and Runde, 1988; Kamler et al., 2007). This is even the case for species assumed to be rattlesnake specialists, such as kingsnakes (Greene and Rodríguez-robles, 2003; Wiseman et al., 2019). Additionally, several rattlesnake species are known to exhibit high annual survivorship as adults (Diller and Wallace, 2002; Brown, 2008; Jones et al., 2012), indicating that predation risk may be low, depending on the levels of anthropogenic fatalities (e.g., poaching, road kills).

Most rattlesnakes are sit-and-wait ambush hunters, and this strategy generally necessitates that they spend prolonged periods of time exposed to potential predators (i.e., not in shelters). This prolonged exposure could increase risk of predation. Rattlesnakes that are not actively foraging (e.g., snakes digesting meals or seeking thermal refuge) generally remain completely hidden in burrows, vegetation, or other microhabitat features that preclude attacks by their own predators (Cardwell, 2013; Gardiner et al., 2015; Maag, Maher and Greene, 2022). It is also possible, though, that ambush hunting snakes, even when exposed on the surface, do not often encounter their own predators because they are largely cryptic and remain undetected during the sit-and-wait phase of their feeding cycle. No quantitative study of predator encounter rates under natural conditions has been conducted so far. Therefore, we used a large database of field videography from our research program to assemble quantitative data on predator encounter rates of ambush foraging viperid snakes in nature.

Rattlesnakes of six species used in the included studies were collected via visual encounter surveys. Upon capture each snake was identified to species, sexed, weighed, and measured for various morphometrics. Very-high frequency (VHF) radio transmitters were implanted into the body cavity of snakes ($\leqslant 5\%$ of body mass) for telemetery. Anesthesia and surgical procedures followed a standard implantation procedure (Reinert and Cundall, 1982). Details of the tracking methods varied slightly across each respective study (Clark, 2006; Barbour and Clark, 2012; Clark et al., 2016; Putman, Barbour and Clark, 2016; Maag et al., unpubl. data; Hanscom et al., unpub. data), but generally snakes were tracked several times a week via a hand-held Yagi antenna and receiver. If the snake was found in a typical ambush coil (e.g., Reinert et al., 2011, Fig. 4) then a field videography device was placed to record the hunting behavior of the snake and encounters with predators and prey. Videography followed standardized procedures (reviewed in Clark, 2016), with minor differences between studies. Generally, the set-up was a near-infrared (IR) sensitive camera mounted 1 m from the snake approximately 45° to the left or right side in front of the snake's head along with separate IR lights positioned around 3 m away from the front of the snake to illuminate a 1 m^2 area around the snake.

A predator encounter was counted when the predator was seen moving on camera in front of the snake (i.e., in the 180° semicircle around the head of the snake which was positioned at the midpoint of the semicircle) or if the predator was behind the snake (while still in camera frame) and clearly stopped and changed the orientation of its head so that its eyes pointed toward the coiled snake. Predators were assumed to be the same individual if they encountered the snake repeatedly in a short time frame (within 10 min), even if they left the frame of the camera and returned, and all such repeated interactions with individual predators were classified as one encounter. To calculate predator encounter frequencies, the total numbers of predators encountered for every ambush position for every snake in each of the studied populations were divided by the total number of video hours that the snakes in that population were recorded coiled on the surface. Videos were scored *post-hoc* using event recording software (e.g., BORIS v. 7.4.11; Friard and Gamba, 2016).

Table 1 summarizes the predation rates from the included studies. Encounter rates were low (across populations average: 0.004 predators/hr [250 coiled hrs/predator encounter]), even for the populations with the highest rates of encounters with known snake predators (0.014 predators/hr [71 coiled hrs/predator encounter]; Maag et al., unpubl. data). No predator was observed attacking a snake and no snake was seen displaying apparent rattling or defensive posturing towards a predator. The only defensive behaviors observed were two defensive strikes by a *Crotalus scutulatus* x *viridis* toward a Greater Roadrunner, *Geococcyx californianus* (Maag et al., unpubl. data). Furthermore, potential predators almost always did not engage with the rattlesnakes beyond pausing and orienting towards the snake for a handful of seconds, after which they generally left the frame of the camera and did not return.

The only potential predator that was regularly observed to engage with coiled rattlesnakes was the Greater Roadrunner. During multiple

Table 1. Rates and outcomes of predator encounters from studies using fixed videography to document hunting behavior of rattlesnake species found in the United States of America.

Species	Locality	Predator encounter rate (predators/hours of ambush footage)	Encountered predator species	Snake defensive behaviors	Survival rate	Citations
C. cerastes	Mojave Desert, California	0.002 (2/998)	– Kit Fox (*Vulpes macrotis*)	none	100%	Clark et al., 2016
C. horridus	Southcentral New York	0.002 (3/1840)	– Striped Skunk (*Mephitis mephitis*) – Racoon (*Procyon lotor*) – Great Horned Owl (*Bubo virginianus*)	none	100%	Clark, 2006
C. o. oreganus	Central California	0 (0/173)	NA	NA	NA; no predators, no snakes killed	Barbour and Clark, 2012
C. o. oreganus	Blue Oak Ranch Reserve, Central California	NA; 3102	NA	NA	NA; no data on predator encounter rates, no snakes killed	Putman, Barbour and Clark, 2016
C. ruber	Santa Margarita Ecological Reserve, Southern California	0 (0/349.5)	NA	NA	NA; no predators, no snakes killed	Barbour and Clark, 2012; Barbour, unpubl. data
C. scutulatus	Mojave Desert, California	0.013 (1/76)	Unknown	none	100%	Barbour, unpubl. data
C. scutulatus	Cochise Filter Barrier, Southwest New Mexico	0 (0/229)	NA	NA	NA; no predators, no snake killed	Maag et al., unpubl. data
C. scutulatus × *viridis*	Cochise Filter Barrier, Southwest New Mexico	0.007 (4/555)	– Greater Roadrunner (*Geococcyx californianus*)	2 strikes	100%	Maag et al., unpubl. data
C. viridis	Cochise Filter Barrier, Southwest New Mexico	0.015 (6/410)	– Kit Fox (*Vulpes macrotis*) – Greater Roadrunner (*Geococcyx californianus*)	none	100%	Maag et al., unpubl. data
C. viridis	Marathon Grasslands, Southwest Texas	0 (0/596)	NA	NA	NA; no predators, no snake killed	Hanscom et al., unpubl. data

encounters, we recorded roadrunners orienting themselves towards and circling around rattlesnakes while performing a wing flashing/flipping behavior (detailed in Sherbrooke and Westphal, 2006). It was one of these encounters that led to the only defensive strikes elicited towards a potential predator, but the roadrunner in this instance did not further engage or attack the rattlesnake, and the rattlesnake resumed hunting for an additional 28 min after the roadrunner ceased engagement and left the frame of the camera (see supplementary video S1).

Our data show that snakes from multiple species and populations of *Crotalus* rarely encountered potential predators while in ambush coils, and when predators were encountered, escalation toward attack was rarer still, as it was not observed in over 8300 hours of observation of ambush hunting *Crotalus*. However, other studies indicate rattlesnakes are still killed and eaten by multiple types of predators (Klauber, 1956, pers. obs.), leading to the general conclusion that rattlesnakes are relatively safe from predation while in ambush coils, despite being exposed.

Studies of various pitvipers have shown that annual survival rates can be variable, ranging from very high for some populations (0.82–0.96),to relatively low, even within the same species, 0.35–0.70 (Diller and Wallace, 2002; Brown, 2008; Jones et al., 2012; Prival and Schroff, 2012). Considering that we never observed pitviper depredation over thousands of hours of recordings, and that mortality can be high in certain populations, we suggest that rattlesnakes are almost always killed by predators in compromised situations, such as when actively moving through the habitat or engaging in reproductive behaviors. However, it is possible our predator encounter rates might be underestimates if the presence of recording equipment deterred rattlesnake predators in some way. Although any method of recording data from free ranging animals also has the potential to impact their behavior to some degree, anecdotal observations of various mesopredators inspecting our recording devices in the field indicate to us that they are largely indifferent to the presence of the equipment (pers. obs.).

Low predation rates may be an underappreciated benefit of using an ambush foraging strategy with a very prolonged sit-and-wait phase, as the ambush hunter is generally cryptic while waiting for prey, and thus remains relatively safe from its own predators while hunting for extended periods. This crypsis stems from several factors. Snakes waiting in ambush are very still, moving only occasionally, and thus remain hidden from visually oriented predators. Also, many rattlesnakes often wait in ambush under the cover of low lying vegetation or other habitat structures (Cardwell, 2013; Gardiner et al., 2015; Maag, Maher and Greene, 2022), although there are notable exceptions (Schraft, Bakken and Clark, 2019). Lastly, although there is evidence that the background coloration can affect the predation rate and thus crypsis of snakes (Harmel et al., 2020), other studies have found dorsal patterning is primarily shaped by aposematism (Valkonen et al., 2011) or climatic variables (Santos et al., 2014) rather than crypsis.

Another factor impacting the behavior of rattlesnake predators could be the positioning of the snake during the sit-and-wait phase. While in an ambush coil, rattlesnakes are already optimally positioned for strike performance (Kardong and Bels, 1998), and could readily counterattack potential predators with defensive strikes. This scenario is largely in accordance with observations of how avian and mammalian predators dispatch rattlesnakes. Typically predators either pin down the head and bite quickly toward the head/back of the neck of the snake, or they harass the rattlesnake until the snake attempts to flee or strike, at which point they then quickly strike at the back of the head/neck region to kill the snake (Klauber, 1956; Sherbrooke and Westphal, 2006). Snakes are perhaps aware of the perils of elongating out of their coil to counterattack predators, as studies on the defensive behaviors of rattlesnakes have found a general reluctance to strike defensively (Glaudas, Farrell and May, 2005; Gibert et al., 2022).

One shortcoming of this study is the lack of survivorship estimates or predator surveys during the period that the snakes were monitored with fixed videography. Although the studies we reviewed spanned several different sites and habitat types, it may still be possible that predator density was low at all of them. However, fixed videography done with Puff Adders (*Bitis arietans*) in South Africa is in congruence with our data on North American rattlesnakes, with no predator encounters or predation events recorded after 4634 hours of monitoring (Glaudas and Alexander, 2017), even though adult survivorship of Puff Adders at this site is estimated to be only about 50%, with many individuals known to be lost to predation (Glaudas, pers. comm.). Thus, we find it likely that our results derive from an ambush foraging strategy being much less risky for snakes compared to other activities they must engage in to survive and reproduce.

Acknowledgements. For providing past video data we thank Barbour, M., Putman, B., and Hanscom, R. For additional help scoring videos, we thank Gibert, R., Dunlap, Z., Soni, A., Richardson, A., Weed, M., Shaw, N., Kollmorgen, L., Ramnani, A., Lundgren, J., and Quinn, M. We thank Glaudas, X. for providing information about his research and findings on Puff Adders. For supporting all the fieldwork required to collect the data we thank the Chiricahua Desert Museum, Blue Oak Ranch Reserve, Fingerlakes Land Trust, Desert Studies Center, and Santa Margarita Ecological Reserve. For funding we thank the National Science Foundation (IOS-1856404 & 0951010 to RWC), University of California, Riverside Department of Biology (to DWM), Society for the Study of Amphibians and Reptiles (Conant Grant in Herpetology awarded to DWM), American Society of Ichthyologists and Herpetologists (Gaige Grant awarded to DWM), Chiricahua Desert Museum (Painter Grant in Herpetology awarded to DWM), and Southwestern Center for Herpetological Research (Klauber Summer Research Grant awarded to DWM). The research associated with this article was approved by San Diego State University's IACUC APF, 19-08-009C. We are grateful to the two anonymous reviewers who provided comments that helped us improve this manuscript.

Supplementary material. Supplementary material is available online at:
https://doi.org/10.6084/m9.figshare.20765914

References

Barbour, M.A., Clark, R.W. (2012): Diel cycles in chemosensory behaviors of free-ranging rattlesnakes lying in wait for prey. Ethology **118**: 480-488.

Brown, W.S. (2008): Sampling Timber Rattlesnakes (*Crotalus horridus*): phenology, growth, intimidation, survival, and a syndrome of undetermined origin in a northern population. In: The Biology of Rattlesnakes, p. 235-256. Hayes, W.K., Beaman, K.R., Cardwell, M.D., Bush, S.P., Eds, Loma Linda University Press, Loma Linda, CA, USA.

Cardwell, M.D. (2013): Behavioral Changes by Mohave Rattlesnakes (*Crotalus scutulatus*) in Response to Drought. California State University, Sacramento.

Clark, R.W. (2006): Fixed videography to study predation behavior of an ambush foraging snake, *Crotalus horridus*. Copeia **2006**: 181-187.

Clark, R.W. (2016): The hunting and feeding behavior of wild rattlesnakes. In: Rattlesnakes of Arizona, p. 91-118. Schuett, G.W., Feldner, M.J., Smith, C.F., Reiserer, R.S., Eds, Eco Publishing, Rodeo, NM.

Clark, R.W., Dorr, S.W., Whitford, M.D., Freymiller, G.A., Putman, B.J. (2016): Activity cycles and foraging behaviors of free-ranging sidewinder rattlesnakes (*Crotalus cerastes*): the ontogeny of hunting in a precocial vertebrate. Zoology **119**: 196-206.

Diller, L.V., Wallace, R.L. (2002): Growth, reproduction, and survival in a population of *Crotalus viridis* oreganus in north central Idaho. Herpetol. Monogr. **16**: 26-45.

Friard, O., Gamba, M. (2016): BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol. Evol. **7**: 1325-1330.

Gardiner, L.E., Somers, C.M., Parker, D.L., Poulin, R.G. (2015): Microhabitat selection by Prairie Rattlesnakes (*Crotalus viridis*) at the northern extreme of their geographic range. J. Herpetol. **49**: 131-137.

Gibert, R.G., Maag, D.W., Sanders, L.N., Clark, R.W. (2022): Investigating personality in vipers: individual rattlesnakes exhibit consistent behavioral responses in defensive and exploratory contexts. Behav. Ecol. Sociobiol. **76**: 132.

Glaudas, X., Alexander, G.J. (2017): A lure at both ends: aggressive visual mimicry signals and prey-specific luring behaviour in an ambush-foraging snake. Behav. Ecol. Sociobiol. **71**: 1-7.

Glaudas, X., Farrell, T.M., May, P.G. (2005): Defensive behavior of free-ranging Pygmy Rattlesnakes (*Sistrurus miliarius*). Copeia **2005**: 196-200.

Greene, H.W., Rodríguez-robles, J.A. (2003): Feeding ecology of the California Mountain Kingsnake, *Lampropeltis zonata* (Colubridae). Copeia **2003**: 308-314.

Harmel, M.V., Crowell, H.L., Whelan, J.M., Taylor, E.N. (2020): Rattlesnake colouration affects detection by predators. J. Zool. **311**: 260-268.

Jones, P.C., King, R.B., Bailey, R.L., Bieser, N.D., Bissell, K., Campa III, H., Crabill, T., Cross, M.D., Degregorio, B.A., Dreslik, M.J., Burbian, F.E., Harvey, D.S., Hecht, S.E., Jellen, B.C., Johnson, G., Kingsbury, B.A., Kowalski, M.J., Lee, J., Manning, J.V., Moore, J.A., Oakes, J., Phillips, C.A., Prior, K.A., Refsnider, J.M., Rouse, J.D., Sage, J.R., Seigel, R.A., Shepard, D.B., Smith, C.S., Vandewalle, T.J., Weatherhead, P.J., Yagi, A. (2012): Range-wide analysis of eastern Massasauga survivorship. J. Wildl. Manage. **76**: 1576-1586.

Kamler, J.F., Ballard, W.B., Wallace, M.C., Gilliland, R.L., Gipson, P.S. (2007): Dietary overlap of Swift Foxes and Coyotes in northwestern Texas. Am. Midl. Nat. **158**: 139-146.

Kardong, K.V., Bels, V.L. (1998): Rattlesnake strike behavior: kinematics. J. Exp. Biol. **201**: 837-850.

Klauber, L.M. (1956): Enemies of rattlesnakes. In: Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind, p. 1064-1115. University of California Press, Ltd., Berkley, CA, USA.

Maag, D.W., Maher, S.P., Greene, B.D. (2022): Spatial ecology and microhabitat selection of the Pygmy Rattlesnake (*Sistrurus miliarius*) in southwestern Missouri. Herpetol. Conserv. Biol. **17**: 316-330.

MacLaren, P.A., Anderson, S.H., Runde, D.E. (1988): Food habits and nest characteristics of breeding raptors in southwestern Wyoming. Gt. Basin Nat. **48**: 548-553.

Messick, J.P., Hornocker, M.G. (1981): Ecology of the badger in southwestern Idaho. Wildl. Monogr. **1981**: 3-53.

Parmley, D. (1982): Food items of roadrunners from Palo Pinto County, north central Texas. Texas J. Sci. **34**: 94-95.

Prival, D.B., Schroff, M.J. (2012): A 13-year study of a northern population of Twin-Spotted Rattlesnakes (*Crotalus pricei*): growth, reproduction, survival, and conservation. Herpetol. Monogr. **26**: 1-18.

Putman, B.J., Barbour, M.A., Clark, R.W. (2016): The foraging rehavior of free-ranging rattlesnakes (*Crotalus oreganus*) in California Ground Squirrel (*Otospermophilus beecheyi*) colonies. Herpetologica **72**: 55-63.

Reinert, H.K., Cundall, D. (1982): An improved surgical implantation method for radio-tracking snakes. Copeia **1982**: 702-705.

Reinert, H.K., Macgregor, G.A., Esch, M., Bushar, L.M., Zappalorti, R.T. (2011): Foraging ecology of Timber Rattlesnakes, *Crotalus horridus*. Copeia **2011**: 430-442.

Santos, X., Vidal-García, M., Brito, J.C., Fahd, S., Llorente, G.A., Martínez-Freiría, F., Parellada, X., Pleguezuelos, J.M., Sillero, N. (2014): Phylogeographic and environmental correlates support the cryptic function of the zigzag pattern in a European viper. Evol. Ecol. **28**: 611-626.

Schraft, H.A., Bakken, G.S., Clark, R.W. (2019): Infrared-sensing snakes select ambush orientation based on thermal backgrounds. Sci. Rep. **9**: 3950.

Sherbrooke, W.C., Westphal, M.F. (2006): Responses of Greater Roadrunners during attacks on sympatric venomous and nonvenomous snakes. Southwest. Nat. **51**: 41-47.

Valkonen, J., Niskanen, M., Björklund, M., Mappes, J. (2011): Disruption or aposematism? Significance of dorsal zigzag pattern of European vipers. Evol. Ecol. **25**: 1047-1063.

Wiseman, K.D., Greene, H.W., Koo, M.S., Long, D.J. (2019): Feeding ecology of a generalist predator, the California Kingsnake (*Lampropeltis californiae*): why rare prey matter. Herpetol. Conserv. Biol. **14**: 1-30.