



# Diel Cycles in Chemosensory Behaviors of Free-Ranging Rattlesnakes Lying in Wait for Prey

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## Abstract

The sensory ecology of foragers is fundamentally influenced by changes in environmental conditions such as ambient light. Changes in ambient light may hinder the effectiveness of particular senses (e.g., impaired vision at night), but many predators rely on multiple sensory systems and may continue to forage despite changes in light availability. Exactly how predator behaviors and sensory systems compensate under changes in light availability in the field is not well understood. We used radio telemetry and portable video surveillance cameras to quantify the sit-and-wait chemosensory foraging behavior of free-ranging red diamond (*Crotalus ruber*) and northern Pacific (*Crotalus oreganus oreganus*) rattlesnakes during day and night periods. The two most common behaviors we observed were chemosensory probes, a behavior we describe in detail for the first time, and mouth gapes. During chemosensory probes, rattlesnakes extend their head beyond their coil, explore the surrounding area while tongue-flicking, and subsequently return to a stationary position inside their coil. Foraging rattlesnakes probed at significantly higher rates during nocturnal vs. diurnal hours. Similarly, mouth gaping occurred during a higher percentage of nocturnal vs. diurnal hours for foraging snakes. Nearly half of all mouth gapes were followed immediately with a chemosensory probe, suggesting that mouth gaping also serves a chemosensory function in this context. Our results suggest that chemical cues play an increasingly important role in mediating rattlesnake foraging behavior at night. Examining how abiotic factors, such as light availability, influence the sensory ecology of free-ranging predators is essential for accurately characterizing their interactions with prey.

## Introduction

Understanding constraints on animal foraging has been a central research theme in behavioral ecology research for the past 40 yrs (Schoener 1971). An important first step toward this goal is to examine how organisms perceive and respond to their foraging environment (Barbosa & Castellanos 2005). This process may be relatively simple for foragers that rely primarily on one sensory system to both search for and capture prey (e.g., vision for terrestrial birds such as sparrows) (Getty & Pulliam 1993). Predators

that rely on a particular sensory system are constrained by changing environmental conditions (e.g., ambient light) that hinder sensory capabilities (Clarke 1983; Weissburg & Zimmer-Faust 1993). However, many organisms rely on multiple sensory systems during the foraging process and may be able to compensate for the deprivation of particular sensory systems (Barbosa & Castellanos 2005). For example, threespine sticklebacks (*Gasterosteus aculeatus*) rely on visual cues in clear water to capture prey, but switch to chemical cues under turbid conditions (Webster et al. 2007). This switch in sensory

systems may have important consequences on the dynamic of predator–prey interactions (Barbosa & Castellanos 2005; Weissburg & Browman 2005).

In this study, we quantified diel cycles in chemosensory foraging behaviors of free-ranging red diamond (*Crotalus ruber*) and northern Pacific (*Crotalus oreganus oreganus*) rattlesnakes. Analysis of rattlesnake diets suggests that they are cathemeral hunters (i.e., active during day and night) (Fitch 1949; Taylor 2001; Clark 2002; Glaudas et al. 2008) and consequently experience different sensory constraints depending on the time of day. We chose *C. ruber* and *C. o. oreganus* because, although they are cathemeral, their diets differ in composition of nocturnally and diurnally active prey. Specifically, *C. ruber*'s diet is composed primarily of nocturnally active small animals (76.8% of stomach contents) (E. A. Dugan & W. K. Hayes, pers. comm.), whereas *C. o. oreganus* feeds mostly on diurnally active California ground squirrels and lizards at our study site (own data). Therefore, we could examine whether both species respond similarly to sensory constraints imposed by time of day.

Rattlesnakes rely on multiple sensory systems while foraging. Like all the members of the snake subfamily Crotalinae (pit vipers), rattlesnakes have a pair of thermally sensitive, image-forming pits located at the front of their face (Hartline et al. 1978). Thermal cues from these pits are integrated with visual cues in the central nervous system to produce a single image of the environment (Goris 2011). These pits are particularly good at detecting warm images against cool backgrounds (Theodoratus et al. 1997) and therefore partially compensate for the low levels of ambient light during nocturnal hours. In addition to this unique thermo-visual sensory system, they also rely on a well-developed chemosensory system that is not restricted by the time of day (Schwenk 1995). Snakes obtain chemical cues in two ways: (1) a nasal olfactory system that detects volatile chemicals; and (2) a vomeronasal system which may obtain volatile and non-volatile chemical cues through tongue-flicking (reviewed in Schwenk 1995). The degree to which rattlesnakes rely on chemical and thermo-visual cues varies during the foraging process (Kardong & Smith 2002).

Rattlesnake foraging behavior can be partitioned into several phases. First, snakes search for a foraging site using both thermo-visual (Krochmal & Bakken 2003; Tsairi & Bouskila 2004; : non-crotaline Viperid) and chemical cues (Duvall et al. 1985; Chiszar et al. 1990; Roth et al. 1999; Theodoratus & Chiszar 2000). Upon selecting a foraging site, rattle-

snakes will wait for hours, or sometimes days, for prey to come within striking distance (Clark 2006a). In preparing for predatory strikes, rattlesnakes rely primarily on thermo-visual cues (Hayes & Duvall 1991; Kardong 1992). Upon striking their prey, pit vipers inject venom through hollow fangs and then release their envenomated prey to avoid injury (Kardong & Smith 2002). Predatory strikes induce elevated tongue-flicking rates and subsequent search for chemical cues of the struck prey item (Chiszar et al. 1977). Although ambush site selection, as well as pre- and post-strike behavior, has received considerable attention, the 'waiting' phase of their sit-and-wait foraging strategy has been largely overlooked in behavioral research (Kardong & Smith 2002). This period makes up the vast majority of time these predators spend foraging (Clark 2006a); yet, we know little about the sensory cues and behaviors that may be important during this period and how they may change over the course of the day.

To quantify snake behavior during their long waiting periods in the field, we used portable video surveillance cameras, a technique that has already revealed new insights into rattlesnake foraging behavior (Clark 2005, 2006a,b). The two most common behaviors we observed were chemosensory probing, a behavior we describe in detail for the first time, and mouth gaping (Graves & Duvall 1983; Cunningham & Burghardt 1999; Klauber 1972). Mouth gaping, which may range from a slight opening of the mouth to spreading of the jaws to an angle approaching 180 degrees (Graves & Duvall 1983), has been suggested to serve multiple functions in snakes, including realigning the jaw both after a strike and after swallowing their prey (Klauber 1972), warning potential predators of their willingness to strike defensively (Glaudas & Winne 2007), and facilitating vomerolfaction in general (Graves & Duvall 1983; Cooper & Burghardt 1990). Our study provides the first quantitative analysis of diel patterns in free-ranging rattlesnake behavior as they lie in wait for prey.

## Methods

### Study Sites and Animals

We used radio telemetry to monitor free-ranging *C. ruber* and *C. o. oreganus* for video recording. We opportunistically captured all adult snakes. Upon capture, we transported snakes to the field station to surgically implant miniature temperature sensitive radio transmitters (Holohil Systems Ltd., Ontario, Canada, models AI-2T and SI-2T) into their peritoneal cavities

under inhalation anesthesia (isoflurane) (Reinert & Cundall 1982). Implants weighed <5% of the snake's body mass. We kept snakes overnight and ensured that snakes were active (evidenced by frequent tongue-flicking upon inspection) before returning them to their point of capture. If radio transmitter signals had not failed prior to the expected date, we recaptured rattlesnakes and surgically removed their radio transmitters. Upon recovery, we released snakes back at their recapture site. Radio transmitter implantation methods were approved by the Institutional Animal Care and Use Committee (IACUC) at San Diego State University (APF 10-09-025C), and animals were collected under California Department of Fish and Game Permit SC-009704.

We radio-tracked six *C. ruber* (four females and two males) from April 2008 through Sept. 2008 at Santa Margarita Ecological Reserve in San Diego County, California. This study site is composed primarily of chaparral and coastal sage scrub vegetation communities. Of the six snakes, we were unable to collect sufficient behavioral data from one female that was gravid during our study period and spent most of her time underground. The five *C. ruber* used in this study ranged from 80 to 131 cm total length and 230–1450 g.

We radio-tracked 19 *C. o. oregonus* (five females and 14 males) from April 2009 through July 2009 at a site in Sunol Regional Wilderness in Alameda County, California. This study site is composed of mixed oak-savanna interspersed with non-native fruit and nut orchards owing to its location at a historic homestead. During our study period, snakes were usually hunting on the surface during the day and would retreat into ground squirrel burrows at night. However, individuals would occasionally remain in ambush coils on the surface at night, which allowed us to collect diurnal and nocturnal ambush foraging behavior from five individuals (two females and three males) that ranged in size from 79 to 94 cm total length and 410–565 g.

### Field Videography

We began field videography once radio-tagged snakes moved from their capture/release area and maintained coiled positions during the day. We opportunistically located snakes with radio telemetry and positioned portable video surveillance camera units 1–2 m from sedentary rattlesnakes to collect behavioral data. We maintained camera positions until snakes abandoned their site, after which we would relocate snakes and reposition cameras. Each camera

unit consisted of a security camera (Swann PNP-150) coupled to a mini-digital video recorder (SVAT CVP800 DVR) powered by a 12-V sealed lead-acid battery. Cameras recorded in color when ambient light was above 0.1 lux. Under low light conditions, cameras automatically switched to black and white recording with infrared light-emitting diodes. We used this change from color to black and white to categorize foraging data as diurnal or nocturnal. We set mini-DVRs to record continuously at 30 frames/s, with the date and time to the nearest second displayed on the recording. We then reviewed recordings to extract data on the occurrence of chemosensory probes and mouth gapes. Because condensation on camera lenses, obscuring vegetation, equipment failure, or other unanticipated events interfered with some of our video, we only quantified recordings where the image quality was sufficient to accurately document these behaviors.

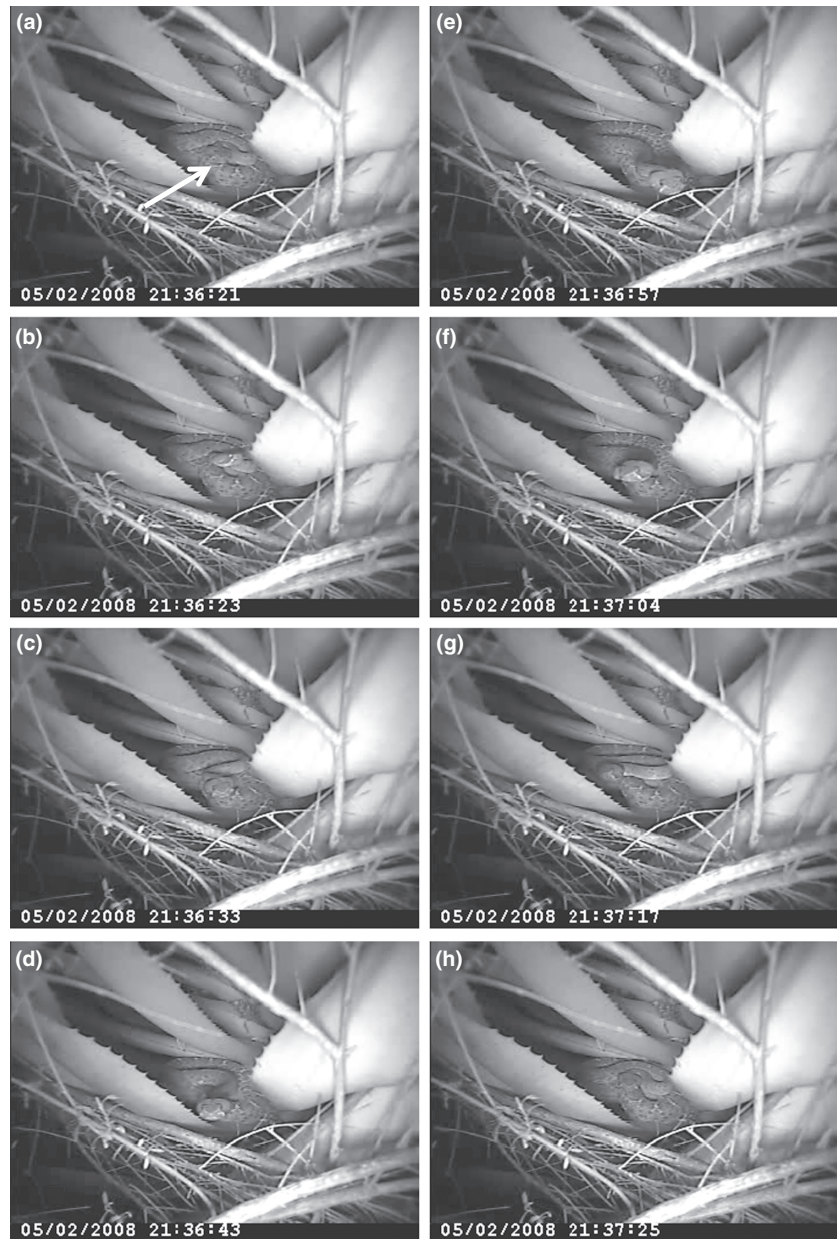
### Ethology

#### *Foraging*

Rattlesnakes typically hunt in stereotyped ambush postures and we classified them as foraging if they were in a tight coil, with their head and tip of nose pointed perpendicular to the arc of their coil (Beaupre 2008; Reinert et al. 2011).

#### *Chemosensory probing*

We defined a chemosensory probe as an extension of a snake's head beyond its coil, followed by a retraction of the head back into a stationary position inside the coil (Fig. 1A–H). This behavior is typically associated with elevated rates of tongue-flicking. This definition is consistent with Diller's (1990, p. 96) observation of a Great Basin rattlesnake (*Crotalus oregonus lutosus*) 'partially uncoil, probe back and forth along the trail [of a kangaroo rat], and resume its original position.' We recorded the time at which a snake probed to the nearest minute. We then quantified the number of probes occurring within the same hour at a site to determine the frequency for that observation hour (sample size = 5 *C. ruber* & 5 *C. o. oregonus*). To describe the structural components of this behavior, we subsampled probes from *C. ruber* (two females) to quantify the maximum distance of probes as well as their duration. Maximum probe distance was a measure of the distance from the anterior most point of the snake's head before a probe to the maximum distance the snake's nose extended during the probe. We



**Fig. 1:** Sequence of events during a typical chemosensory probe of *Crotalus ruber*. (A) Pre-probe: snake is stationary within its coil (white arrow points to the front of the snake's head). (B) Probe initiation: snake begins to extend its head beyond its coil. (C–G) Probe: snake is extending beyond its coil and is tongue-flicking the surrounding air and substrate. (H) Probe ends: snake returns to the same stationary position within its coil as in (A).

estimated these distances from the video by using 5 cm as a proxy for the head length of *C. ruber*. Klauber (1972) found that *C. ruber* ranging from 80 to 131 cm in total length had head lengths that varied between 4 and 6 cm. As these maximum probe distance estimates were imprecise, we categorized probe distances into short ( $\leq 10$  cm), medium ( $10 < \text{distance} \leq 20$  cm), and long ( $> 20$  cm) categories. We estimated probe duration to the nearest second and began at the initiation of a probe and ended once a snake returned to a stationary position inside its coil for at least 10 s. In a separate ethological

analysis, we quantified the tongue-flicking rate of *C. ruber* (two females and one male) while probing during nocturnal hours because only a few videos were of sufficient quality to accurately quantify tongue-flicks.

#### *Mouth gaping*

We defined a mouth gape as when a snake opened its mouth  $\geq 45^\circ$  angle. This behavior is often associated with the stretching of the upper jaw bones and protraction of both fangs. As with chemosensory

probes, we recorded the time at which a snake mouth gaped to the nearest minute (sample size = 5 *C. ruber* & 5 *C. o. oreganus*). Because mouth gaping occurred much more infrequently than probing, we calculated the percentage of hours that snakes mouth gaped one or more times during the day and night for each snake. We also noted whether a probe occurred within 1 min of a mouth gape or not and whether the probe preceded or followed the mouth gape.

### Data Analysis

To avoid pseudoreplication (Hurlbert 1984), we computed a single measure for each snake's chemosensory probe frequency by taking the median value across its observation hours. Median values are more robust measures of central tendency when data are not normally distributed (Zar 1999). We used general linear models to explore whether differences in nocturnal/diurnal probing or mouth gaping were influenced by species, sex, or an interaction between the two. We found no significant species, sex, or interaction effect for either probing (species:  $F = 2.24$ ,  $p = 0.19$ ; sex:  $F = 0.59$ ,  $p = 0.470$ ; species\*sex:  $F = 0.04$ ,  $p = 0.850$ ) or mouth gaping (species:  $F = 0.22$ ,  $p = 0.66$ ; sex:  $F = 0.89$ ,  $p = 0.380$ ; species\*sex:  $F = 0.17$ ,  $p = 0.690$ ); therefore, we pooled snakes for all analyses. Because differences in nocturnal/diurnal probing and mouth gaping measures were normally distributed (probing: Shapiro-Wilk Statistic = 0.96,  $p = 0.826$ ; mouth gaping: Shapiro-Wilk Statistic = 0.94,  $p = 0.600$ ), we analyzed these data using paired t-tests.

To examine whether mouth gapes and probes were associated temporally, we used a randomization test. We compared the observed percentage of mouth gapes occurring within 1 min of a probe to a distribution created under our highest average hourly probe rate. For example, a snake that probed five times per hour would have a 0.17 probability (10 of the 60 min) of a mouth gape occurring within 1 min of a probe by random chance. We then created a hypothetical data set that had a 17% chance of sampling a mouth gape occurring within 1 min of a chemosensory probe. We resampled, with replacement, these hypothetical data 10 000 times to examine the probability of obtaining our observed data by random chance alone (i.e.,  $p < 0.05$ ).

We also examined whether probes were more likely to precede or follow mouth gapes when they occurred within 1 min of each other. To do this, we performed a replicated  $G$ -test of goodness of fit with

snakes as replicates. We also performed a separate  $G$ -test with the pooled data. Using a heterogeneity  $G$ -test, which compares the replicated  $G$ -test to the pooled  $G$ -test, we examined whether we could justify pooling our data (McDonald 2009). There was no significant difference between our replicated  $G$ -test and pooled  $G$ -test ( $G = 0.82$ ,  $df = 8$ ,  $p = 0.999$ ); therefore, we used the pooled data to test whether probes were more likely to precede or follow mouth gapes.

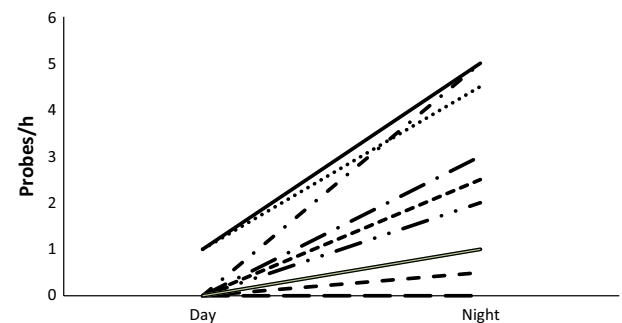
### Results

We collected 173 foraging observation hours for *C. ruber* (92 nocturnal and 81 diurnal) and 137 foraging observation hours for *C. o. oreganus* (50 nocturnal and 87 diurnal).

#### Chemosensory Probing

Our ethological analysis of chemosensory probes ( $n = 2$  snakes) showed that probes averaged 22 s (SE = 12) in duration. Most probes were less than 10 cm (61.6%) at full extension, with fewer between 10 and 20 cm (32.3%), and only a small percentage being over 20 cm (6.0%). During probes, rattlesnakes ( $n = 3$  snakes) tongue-flicked one to two times every 10 s ( $\bar{x} = 1.6/10$  s, SE = 0.4).

Foraging snakes probed at significantly higher rates during nocturnal vs. diurnal observation hours ( $\bar{x}$  difference = 2.25, 95% CI = 1.08–3.42,  $t = 4.35$ ,  $df = 9$ ,  $p = 0.002$ ) (Fig. 2). We further explored this dichotomy in diurnal/nocturnal probing behavior by examining the number of chemosensory probes per



**Fig. 2:** Change in median number of probes per hour between day and night observation hours of foraging snakes. Each line pattern represents a different individual's behavior. Two individuals exhibited the same change from day (0 probes/h) to night (1 probe/h) (compound line on graph), which is why only nine distinct lines are visible. For comparison, individuals in this figure have the same line patterns as Fig. 4.

hour at different time periods ( $n = 7\text{--}10$  snakes per time period). Mean probe frequency remains low throughout most of the day (05:00–16:00 h), begins to increase in the evening (17:00–19:00 h), reaches its peak in the early night (20:00–22:00 h), and then attenuates throughout the night (01:00–04:00 h) (Fig. 3).

### Mouth Gaping

Foraging snakes mouth gaped at least once during a significantly higher percentage of nocturnal vs. diurnal hours ( $\bar{x}$  difference = 17%, 95% CI = 5–29%,  $t = 3.19$ ,  $df = 9$ ,  $p = 0.011$ ) (Fig. 4). Nearly half of the mouth gapes of foraging snakes ( $n = 10$  snakes,  $\bar{x} = 48\%$ ,  $SE = 7$ ) occurred within 1 min of probing. This association is significantly non-random; even under the conservative assumption of our highest recorded average hourly probe frequency (4.3 probes/h rounded up to 5 probes/h; Fig. 3), the probability that 48% of mouth gapes would occur within

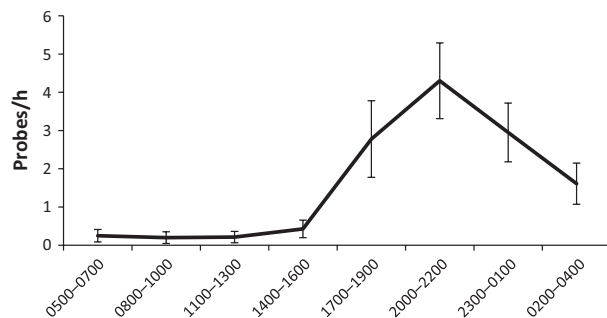
1 min of probes by random chance is less than 0.1% ( $\bar{x} = 16.9\%$ , 95th percentile interval = 9–25,  $p < 0.001$ ).

We further examined the temporal association of probes from foraging snakes that occurred within 1 min of mouth gapes to test whether mouth gapes were more likely to precede or follow chemosensory probes. Ninety-one percent (67/74) of these mouth gapes preceded chemosensory probes, an association that was statistically significant ( $G = 79.6$ ,  $df = 1$ ,  $p < 0.001$ ).

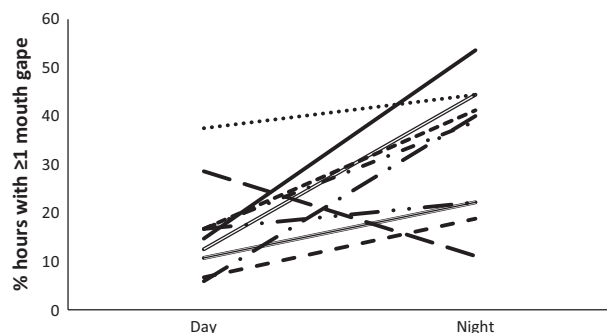
### Discussion

This paper provides the first quantitative analysis of rattlesnake foraging behavior as they lie in wait for prey and examines how these behaviors change with light availability. The two most common behaviors we observed were chemosensory probes and mouth gapes. During a chemosensory probe, rattlesnakes typically extended up to 20 cm from their coil for less than 30 s, while tongue-flicking one to two times every 10 s. Tongue-flicking captures both volatile and non-volatile chemical cues and deposits them in the vomeronasal organ (VNO) (Schwenk 1995), suggesting that probing serves a chemosensory function. Furthermore, nearly half of all mouth gapes immediately preceded chemosensory probes. Graves & Duvall (1983, 1985) also found that mouth gaping preceded tongue-flicking when rattlesnakes were exposed to conspecific chemical cues. In this context, mouth gaping may serve a chemosensory function by clearing the VNO to 'reset' the system for subsequent tongue-flicking (Schwenk 1995). A variety of other taxa also exhibit behaviors that facilitate vomerolfaction (e.g., flehmen response; reviewed in Døving & Trotier 1998). Taken together, our results suggest that rattlesnakes use probes and mouth gapes while they are lying in wait for prey to obtain chemical cues from their immediate surroundings. We know that rattlesnakes often experience long intervals between prey captures (Clark 2006a). Perhaps, probes and mouth gapes help rattlesnakes evaluate the potential profitability of staying at an ambush site, as some sit-and-wait spiders are known to do with visual cues (Persons & Uetz 1996, 1997).

Both probes and mouth gapes occurred more frequently during nocturnal vs. diurnal periods. This pattern suggests two possible mechanisms: (1) rattlesnakes may compensate for their impaired vision at night by probing and mouth gaping to obtain chemical information; and/or (2) high rates of probing and



**Fig. 3:** Mean ( $\pm$ SE) number of chemosensory probes per hour for different periods throughout the day for foraging rattlesnakes (all individuals combined).



**Fig. 4:** Change in percent hours with at least one mouth gape between day and night observation hours of foraging snakes. Each line pattern represents a different individual's behavior. For comparison, individuals in this figure have the same line patterns as Fig. 2.

mouth gaping during the day would increase the rattlesnake's probability of being detected by visually vigilant prey, such as California ground squirrels and diurnal lizards (Van Hooser & Nelson 2006; Pallus et al. 2010), or predators (e.g., raptors and mammalian carnivores). Indeed, Cooper (1998) suggested that ambush foraging snakes do not tongue-flick readily toward chemical cues presented in laboratory-based environments because doing so would compromise their crypsis. Either way, the primary sensory modality that rattlesnakes are using appears to change over the course of the day, which may alter the dynamic of predator–prey interactions at this stage of foraging.

In regard to probing, exploratory analysis revealed that probe frequency attenuates over the course of the night, even though low light conditions remain. One likely explanation for this decrease in probe frequency is a drop in snake body temperature after exposure to cooler air temperatures that typically occur later in the night. Many aspects of snake foraging behavior are influenced by body temperature (Beck 1996; Vincent & Mori 2008). Future work that examines whether nocturnal probing behavior is positively correlated with snake body temperature will shed light on the validity of this hypothesis.

## Conclusion

During the waiting period of their foraging strategy, rattlesnakes exhibit behaviors that extract chemical cues from their surroundings. In addition, we found that these chemosensory behaviors occur more frequently during nocturnal hours, suggesting that rattlesnakes (1) may compensate for their impaired vision by using chemosensory information and/or; (2) are no longer constrained to remain cryptic to successfully ambush prey or avoid predators. Future work should examine whether probing and mouth gaping have consequences on rattlesnake foraging efficiency. Understanding how predators alter their foraging behavior under changing environmental conditions is essential for developing an accurate understanding of their interactions with prey.

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## Literature Cited

- Barbosa, P. & Castellanos, I. 2005: Ecology of Predator-Prey Interactions. Oxford Univ. Press, New York, NY.
- Beaupre, S. J. 2008: Annual variation in time-energy allocation by timber rattlesnakes (*Crotalus horridus*) in relation to food acquisition. In: The Biology of Rattlesnakes (Hayes, W. K., Beaman, K. R., Cardwell, M. D. & Bush, S. P., eds). Loma Linda Univ. Press, Loma Linda, CA, pp. 111–122.
- Beck, D. D. 1996: Effects of feeding on body temperatures of rattlesnakes: a field experiment. *Physiol. Zool.* **69**, 1442–1445.
- Chiszar, D., Radcliffe, C. W. & Scudder, K. M. 1977: Analysis of the behavioral sequence emitted by rattlesnakes during feeding episodes. *Behav. Biol.* **21**, 418–425.
- Chiszar, D., Melcer, T., Lee, R., Radcliffe, C. W. & Duvall, D. 1990: Chemical cues used by prairie rattlesnakes *Crotalus viridis* to follow trails of rodent prey. *J. Chem. Ecol.* **16**, 79–86.
- Clark, R. W. 2002: Diet of the timber rattlesnake, *Crotalus horridus*. *J. Herpetol.* **36**, 494–499.
- Clark, R. W. 2005: Pursuit-deterrent communication between prey animals and timber rattlesnakes (*Crotalus horridus*): the response of snakes to harassment displays. *Behav. Ecol. Sociobiol.* **59**, 258–261.
- Clark, R. W. 2006a: Fixed videography to study predation behavior of an ambush foraging snake, *Crotalus horridus*. *Copeia* **2006**, 181–187.
- Clark, R. W. 2006b: Post-strike behavior of timber rattlesnakes (*Crotalus horridus*) during natural predation events. *Ethology* **112**, 1089–1094.
- Clarke, J. A. 1983: Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deer mice (*Peromyscus maniculatus*). *Behav. Ecol. Sociobiol.* **13**, 205–209.

- Cooper, W. E. Jr 1998: Evaluation of swab and related tests as a bioassay for assessing responses by squamate reptiles to chemical stimuli. *J. Chem. Ecol.* **24**, 841—866.
- Cooper, W. E. Jr & Burghardt, G. M. 1990: Vomero-faction and vomodor. *J. Chem. Ecol.* **16**, 103—105.
- Cunningham, D. S. & Burghardt, G. M. 1999: A comparative study of facial grooming after prey ingestion in colubrid snakes. *Ethology* **105**, 913—936.
- Diller, L. V. 1990: A field observation on the feeding behavior of *Crotalus viridis lutosus*. *J. Herpetol.* **24**, 95—97.
- Døving, K. B. & Trotier, D. 1998: Structure and function of the vomeronasal organ. *J. Exp. Biol.* **201**, 2913—2925.
- Duvall, D., King, M. B. & Gutzwiller, K. J. 1985: Behavioral ecology and ethology of the prairie rattlesnake. *Nat. Geo. Res.* **1985**, 80—111.
- Fitch, H. S. 1949: Study of snake populations in central California. *Am. Midl. Nat.* **41**, 513—579.
- Getty, T. & Pulliam, H. R. 1993: Search and prey detection by foraging sparrows. *Ecology* **74**, 734—742.
- Glaudias, X. & Winne, C. T. 2007: Do warning displays predict striking behavior in a viperid snake, the cottonmouth (*Agkistrodon piscivorus*)? *Can. J. Zool.* **85**, 574—578.
- Glaudias, X., Jezkova, T. & Rodríguez-Robles, J. A. 2008: Feeding ecology of the Great Basin rattlesnake (*Crotalus lutosus*, Viperidae). *Can. J. Zool.* **86**, 723—734.
- Goris, R. C. 2011: Infrared organs of snakes: an integral part of vision. *J. Herpetol.* **45**, 2—14.
- Graves, B. M. & Duvall, D. 1983: Occurrence and function of prairie rattlesnake mouth gaping in a non-feeding context. *J. Exp. Zool.* **227**, 471—474.
- Graves, B. M. & Duvall, D. 1985: Mouth gaping and head shaking by prairie rattlesnakes are associated with vomeronasal organ olfaction. *Copeia* **1985**, 496—497.
- Hartline, P. H., Kass, L. & Loop, M. S. 1978: Merging of modalities in the optic tectum: infrared and visual integration in rattlesnakes. *Science* **199**, 1225—1229.
- Hayes, W. K. & Duvall, D. 1991: A field study of prairie rattlesnake predatory strikes. *Herpetologica* **47**, 78—81.
- Hurlbert, S. H. 1984: Pseudoreplication and the design of ecological experiments. *Ecol. Monog.* **54**, 187—211.
- Kardong, K. V. 1992: Proximate factors affecting guidance of the rattlesnake strike. *Zool. Jb. Anat.* **122**, 233—244.
- Kardong, K. V. & Smith, T. 2002: Proximate factors involved in rattlesnake predatory behavior: a review. In: *Biology of the Vipers* (Schuett, G. W., Höggren, M., Douglas, M. E. & Greene, H. W., eds). Eagle Mountain Publishing, Eagle Mountain, UT, pp. 253—266.
- Klauber, L. M. 1972: Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind. Univ. of California Press, Berkeley, CA.
- Krochmal, A. R. & Bakken, G. S. 2003: Thermoregulation is the pits: use of thermal radiation for retreat site selection by rattlesnakes. *J. Exp. Biol.* **206**, 2539—2545.
- McDonald, J. H. 2009: Handbook of Biological Statistics, 2nd edn. Sparky House Publishing, Baltimore, MD, pp. 84—87.
- Pallus, A. C., Fleishman, L. J. & Castonguay, P. M. 2010: Modeling and measuring the visual detection of ecologically relevant motion by an Anolis lizard. *J. Comp. Physiol. A.* **196**, 1—13.
- Persons, M. H. & Uetz, G. W. 1996: The influence of sensory information on patch residence time in wolf spiders (Araneae: Lycosidae). *Anim. Behav.* **51**, 1285—1293.
- Persons, M. H. & Uetz, G. W. 1997: Foraging patch residence time decisions in wolf spiders: is perceiving prey as important as eating prey? *Ecoscience* **4**, 1—5.
- 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., Bushar, L. M. & Zappalorti, R. T. 2011: Foraging ecology of timber rattlesnakes, *Crotalus horridus*. *Copeia* **2011**, 430—442.
- Roth, E. D., May, P. G. & Farrell, T. M. 1999: Pigmy rattlesnakes use frog-derived chemical cues to select foraging sites. *Copeia* **1999**, 772—774.
- Schoener, T. W. 1971: Theory of feeding strategies. *Ann. Rev. Ecol. & Syst.* **2**, 369—404.
- Schwenk, K. 1995: Of tongues and noses: chemoreception in lizards and snakes. *Trends Ecol. Evol.* **10**, 7—12.
- Taylor, E. N. 2001: Diet of the Baja California rattlesnake, *Crotalus enyo* (Viperidae). *Copeia* **2001**, 553—555.
- Theodoratus, D. H. & Chiszar, D. 2000: Habitat selection and prey odor in the foraging behavior of western rattlesnakes (*Crotalus viridis*). *Behaviour* **137**, 119—135.
- Theodoratus, D. H., Chiszar, D. & Smith, H. M. 1997: Rattlesnake orientation to prey as a function of thermal backgrounds and edges. *Psychol. Rec.* **47**, 461—472.
- Tsairi, H. & Bouskila, A. 2004: Ambush site selection of a desert snake (*Echis coloratus*) at an oasis. *Herpetologica* **60**, 13—23.
- Van Hooser, S. D. & Nelson, S. B. 2006: The squirrel as a rodent model of the human visual system. *Vis. Neurosci.* **23**, 765—778.
- Vincent, S. E. & Mori, A. 2008: Determinants of feeding performance in free-ranging pit-vipers (Viperidae):



- Ovophis okinavensis*): key roles for head size and body temperature. *Biol. J. Linn. Soc.* **93**, 53—62.
- Webster, M. M., Atton, N., Ward, A. J. W. & Hart, P. J. B. 2007: Turbidity and foraging rate in threespine sticklebacks: the importance of visual and chemical prey cues. *Behaviour* **144**, 1347—1360.
- Weissburg, M. J. & Browman, H. I. 2005: Sensory biology: linking the internal and external ecologies of marine organisms. *Mar. Ecol. Prog. Ser.* **287**, 263—307.
- Weissburg, M. J. & Zimmer-Faust, R. K. 1993: Life and death in moving fluids: hydrodynamic effects on chemosensory-mediated predation. *Ecology* **74**, 1428—1443.
- Zar, J. H. 1999: *Biostatistical Analysis*, 4th edn. Prentice-Hall, Upper Saddle River, NJ.