

MICROHABITAT AND PREY ODOR SELECTION IN THE FORAGING PIGMY RATTLESNAKE

GIDEON BEVELANDER^{1,4}, TAMARA L. SMITH^{2,5}, AND KENNETH V. KARDONG^{3,6}

¹*Universiteit Leiden, Institute for Evolutionary and Ecological Sciences, Section of Evolutionary Morphology, P.O. Box 9516, NL-2300RA Leiden, The Netherlands*

²*Center for Teaching, Learning, and Technology, Washington State University, Pullman, WA 99164, USA*

³*School of Biological Sciences, Washington State University, Pullman, WA 99164-4236, USA*

ABSTRACT: We tested the roles of shelter and prey odor cues on the prestrike movement patterns of the dusky pigmy rattlesnake, *Sistrurus miliarius barbouri*. In the first experiment, prey odors—mouse, frog, lizard, plus control—were presented in various combinations with and without shelters. The pigmy rattlesnake initially preferred sites with both frog odor and shelter. However, this changed over a 23-h period so that shelter alone became the most preferred feature of the microhabitat choices. The initial 2 h pigmy response was similar to that reported for the western rattlesnake (*Crotalus viridis*), in that they responded differently to the four choice combinations of shelter and prey odor. This initial pigmy response differed in that only frog odor (but not mouse or lizard odor) affected their initial choices. Our work also indicates that when foraging, novel prey odors (frog) initially attracted their attention, but preference for this odor soon declined. In the second experiment, we examined the preference for prey odors by simultaneously presenting all three prey odors plus control (water). The snakes exhibited no prey odor preference during the first 2-h or during the total 23-h of the trials. In both experiments, the pattern of circadian activity was the same. Circadian activity showed two peaks, one shortly before onset of the nocturnal phase and the second just before midnight; thereafter, activity gradually declined so that most snakes were in, and remained in, a shelter by morning when the diurnal phase began. In these experiments, active movement in pigmy rattlesnakes occurred nocturnally and by day they remain in settled locations. While in such settled positions, the pigmy rattlesnakes coiled into stereotypic ambush postures facing the opening in their shelter where prey would most likely pass.

Key words: Foraging behavior; Microhabitat selection; Pigmy rattlesnake; Snake ecology

RATTLESNAKE predatory behavior includes three major phases of unequal duration—prestrike, strike, poststrike (Cock Buning, 1983). Each phase involves or emphasizes different proximate sensory inputs (Chiszar et al., 1992; Cock Buning, 1983; Kardong and Berkhoudt, 1999). Field studies of the western and prairie rattlesnakes (Duvall and Chiszar, 1990; Duvall et al., 1985) and timber rattlesnake (Clark, 2004a,b), genus *Crotalus*, indicate that they place themselves in ambush close to microhabitats rich in rodent odor. Laboratory studies, using simulated microhabitats and controlled prey odors, documented that their use of microhabitats interacts in complex ways with prey odors (Theodoratus and Chiszar, 2000). In particular, western rattlesnakes methodically investigated edges and crevices within rocks containing prey odor (Theodoratus and Chiszar, 2000). They

exhibited stereotypical search patterns and ambush postures, preferring habitat that included cover. Consequently, both prey odor and habitat shelter affected prestrike predatory behavior in western rattlesnakes (Theodoratus and Chiszar, 2000).

To extend such studies of prestrike behaviors within rattlesnakes, we examined interacting effects of microhabitat and prey odor in the pigmy rattlesnake (*Sistrurus miliarius barbouri*). We picked *Sistrurus* because they are characterized by a different foraging strategy and ecological pattern than *Crotalus* species so far studied. The adult pigmy rattlesnake is smaller and occupies a different microhabitat than *Crotalus* (Klauber, 1956). Its prey items include rodents and lizards, but also amphibians (frogs) in higher proportion than *Crotalus* species. Field experiments suggest that pigmy rattlesnakes respond prestrike to prey odor (Roth et al., 1999) and they may add caudal luring to their predatory repertoire (Rabatsky and Farrell, 1996).

The prestrike behavior of pigmy rattlesnakes was examined using the experimental

⁴ PRESENT ADDRESS: Department of Animal Physiology, University of Nijmegen, Nijmegen, The Netherlands.

⁵ PRESENT ADDRESS: Department of Biology, University of Nebraska, Kearney, NE 68849, USA.

⁶ CORRESPONDENCE: e-mail, kcardong@wsu.edu

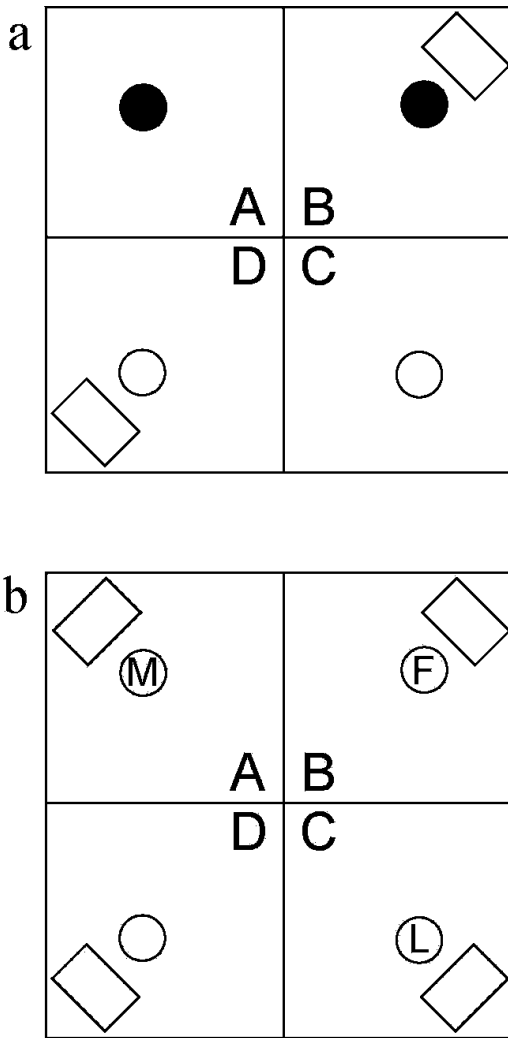


FIG. 1.—Test arena. (a) Experiment 1. In each of the four, equal quadrants A–D, a choice was provided—A: no shelter, prey odor; B: shelter, prey odor; C: shelter, no prey odor; D: no shelter, no prey odor. (b) Experiment 2. In each of the four, equal quadrants A–D, an odor was placed—A: mouse (M), B: frog (F), C: Lizard (L), and D: water, plus a shelter in each quadrant. In both experiments, nocturnal activity was viewed with special cameras sensitive to a red, darkroom bulb; the four odor/shelter choices were changed and randomly positioned in the quadrants on each trial. Circles, petri dishes with prey odor or control (water); Rectangles, shelters.

protocol that Theodoratus and Chiszar (2000) employed for their study of the western rattlesnake, *Crotalus viridis*, except we extended observations from two hours (used by Theodoratus and Chiszar) to 23 hours of total scored behavior. We used combinations of

shelter with four different odors—mouse, frog, lizard, control (water). In our first experiment, we examined the interacting effects of each prey odor and shelter on prestrike behavior. In our second experiment, we examined the relative effects of the three prey odors themselves, separate from shelter effects on pigmy rattlesnake activity.

MATERIAL AND METHODS

Two experiments were performed using 11 dusky pigmy rattlesnakes, *Sistrurus miliarius barbouri*, (SVL: 38–51 cm), caught in the wild, but purchased from licensed Florida herpetological dealers, and individually housed as part of a permanent long-term snake colony. All snakes, except for four purchased three weeks before trials began, were in captivity for one year prior to the experiments. During captivity, they were fed live white laboratory mice (Swiss Webster) twice a month and provided water *ad libitum*. Safety procedures for snakes generally followed those of Gans and Taub (1964). Temperature in the experimental room was kept at 25–30 C, on a 12:12 light:dark cycle matched approximately to Florida summer day length schedule—lights on at 8:40 h; off at 20:40 h. Two of the prey used herein (frogs, lizards) were similarly collected in pigmy rattlesnake habitat.

Both experiments were conducted in square test arenas (1.25 m side \times 0.5 m high) made of compressed fiberglass panels resting 20 cm above the floor on metal supports. During the 12 h of light, the areas were illuminated by overhead fluorescent room lights; during 12 h of “dark” these lights switched off leaving a red (25 watt), darkroom safety light as the sole light source (Fig. 1). The arena floor was divided into four equal quadrants with black tape. Over this, and before each trial, a square piece of fresh, semi-transparent butcher paper (1.25 m/side) was placed which allowed the outlines of the four quadrants to show through. Odors were presented in covered petri dishes (diameter: 15 cm) with seven evenly placed holes (1.3 cm diameter) drilled in the plastic lids. Three prey odors plus control were used—mouse (Swiss Webster), frog (*Acris* spp), lizard (*Anolis* spp), and water (control). Soiled bedding from mouse cages was sprinkled into and just covered the bottom of a petri

dish; three to six frogs were kept in 400 cc of distilled water for several hours, and this water then poured into and just covered the bottom of a petri dish; similarly, three to six anoles were placed in 400 cc of distilled water, gently swirled for about 10 min, and then this water was poured into the bottom of a petri dish, just covering it. A "no odor" control was used by similarly filling the bottom of a petri dish with only demineralized water. Opaque plastic hide-boxes (10 × 6 × 5 cm) with a single door were used as shelters. In Experiment 1, each prey odor was presented separately, in various combinations with shelters. In Experiment 2, all three prey odors plus control were presented simultaneously.

All trials were run for 23 h, with one hour for change over, beginning at the same time of the day (15:00). At the beginning of a trial, the snake was removed from its home cage with a hook and gently placed in the center of the test arena. All experimenters then left the area, and ensuing behaviors were videotaped over the next 23 h with low-light sensitive Panasonic VHS cameras suspended above the arena (2 m from arena floor to camera) and recorded on a VCR video recorder (Panasonic). Protocols approved by the Institutional Animal Care and Use Committee.

For all experiments several variables were scored during playback of the recorded trial: **Time spent**, the time (in seconds) a snake spent in each quadrant was recorded. A snake's time in a quadrant was timed from the moment its head entered until its head left that quadrant. As a snake may enter and leave multiple times during a 23-h trial, these separate scores were totaled each hour for each quadrant. **Activity**, the number of times a snake changed quadrants per hour. We used this scoring method to capture the amount of activity (movement) or inactivity (stationary). Other scoring methods (e.g., measuring distance moved per hour) of activity were considered, but this simple and unambiguous method of quadrant change correlated very directly with persistent episodes of movement around the arena or with extended episodes of motionless behavior. Quadrant change was correlated with activity because activity patterns of the snakes were distinctive—either they were settled and motionless for extended periods of time or they were moving from

quadrant to quadrant for extended periods of time. The dim nocturnal lights and small image of the small snakes precluded accurate counts of tongue flicks during the trials. But, we recorded qualitative observations of specific postures and behaviors. Two experiments were conducted.

Experiment 1: Shelter and Prey Choice

In Experiment 1, we examined the separate and collective effects on snake behavior of shelter (hide-box) and prey odor. Each snake was presented with four combinations of mouse, frog, or lizard related odors with shelter. No odor (water) and no shelter were controls. The four different combinations, one per quadrant, were as follows: A: NS-prey odor (no shelter, prey odor); B: S-prey odor (shelter, prey odor); C: NS-water (no shelter; water); D: S-water (shelter; water) (Fig. 1a). The position of the four choices was randomly (coin toss) changed for each trial.

Experiment 2: Prey Odor Choice

In Experiment 2, the same four choices were used again—mouse, frog, lizard, water—placed respectively in quadrants A–D, but, in this experiment all four odors were presented simultaneously, allowing a test of prey odor preference, if any. To make shelter effects equal, a hide-box was placed next to each of the four petri dishes, with its single door facing the petri dish (Fig. 1b). The position of the four choices was randomly (coin toss) changed for each trial.

Notice that in Experiment 1 the choices included controls of prey odor without shelter (A) and shelter without prey odor (C), and in Experiment 2, the choices included a control for no prey odor (water). In both experiments, the petri dishes were thoroughly washed after each trial, the location of each lettered quadrant randomly changed (coin toss), and the previous butcher paper replaced with fresh butcher paper before each trial. Gloved hands (Microflex, nonsterile, latex) were used when handling all arena dishes and hide boxes, with care taken not to cross contaminate prepared quadrants. At least one week separated trials of the same individual. Immediately following a trial, the snake was fed a small mouse to confirm hunger (Chiszar et al., 1981; Hayes, 1993). All fed.

Data Summary and Statistical Analyses

We looked at the actual time (minutes) spent in each of the quadrants for a 23-h period. Our treatments recorded activity for 23 h, whereas the similar laboratory study of *Crotalus* examined just the first two hours after placing snakes in the test arena (Theodoratus and Chiszar, 2000). To compare our results more directly to theirs, we additionally compiled the choices and activity scores of the pigmy rattlesnakes during just the first two hours of each 23-h trial. Each of the 11 snakes were run twice in each experiment, but they did not significantly differ between their own two runs, $F(10, 150) = 3.36^E - 7$, $P = >0.9999$. This gave us a randomized complete block design ($n = 11$) with four treatments (A, B, C, D). The two runs of each snake were averaged, and nonparametric statistical tests performed on the averages (Statview, SAS Institute). Kruskal-Wallis (H) was used initially to examine overall response to the four choices. When this test was significant, we applied Wilcoxon signed-rank tests (Z) to pairwise comparisons of the choices to see which particular treatments were significantly different from the others (Zar, 1999). In all tests, $\alpha = 0.05$.

Snake activity, the number of times a snake changed quadrants in each hour of the 23-h period, was also scored. These scores were then averaged across all trials, hour by hour, and the averages plotted to show the pattern of activity throughout 23-h.

RESULTS

Experiment 1: Odor and Shelter Choices

General behavior.—When first placed in the center of the arena, the snakes usually assumed a coiled posture. After 1–5 minutes, they then entered a quadrant, usually a quadrant with a shelter. The snakes often reinvestigated a quadrant before proceeding to another quadrant. When moving through the arena from quadrant to quadrant snakes commonly used the edges of the arena walls. They also traveled over, and presumably investigated, the shelters and petri dishes, passing over the holes of the petri dish lids, the surroundings, and through the insides of the shelters.

Some rattlesnakes coiled up in front of an odor petri dish facing it or behind a shelter.

The snakes that were so coiled stayed in that position ranging from 2 min up to 23 h. Some of the coiled snakes held their anterior bodies in a sigmoidal curve, believed to be a typical ambush posture for viperids (Klauber, 1956). However, in most trials the snakes entered and spent most of their time in a shelter (see below).

At night, snakes commonly switched from one shelter to another, but eventually took up residence in a shelter with which they remained into the day. In 18 of the 66 trials snakes resided almost from the beginning of the trial in the shelter first selected until the end of the 23-h trial. Positioned within a shelter, they often would peer out just showing their head and hold that same position until moving to a new shelter.

Time spent in the quadrants.—During the first 2 h of the trials, there was a significant quadrant effect for each prey type—mouse, frog, lizard ($[H = 23.851, P \ll 0.0001$ [mouse]; $= 24.415, P \ll 0.0001$ [frog]; $= 17.998, P = 0.0004$ [lizard]). In particular, shelter had a significant overall effect with snakes spending most of the first 2 h in quadrants with shelter (B, D) and significantly less time in quadrants without shelters (A, C), Fig. 2. Post-hoc comparison (Wilcoxon, $\alpha = 0.05$) within each of the three experiments, summarized in Table 1, revealed a significant preference for quadrants with shelters whether they included prey odor (A) or not (D). Further response to these two quadrants were statistically equivalent, except when frogs were the prey odor wherein the quadrant (B) with both shelter and frog odor were preferred over the quadrant (D) with just shelter ($Z = 1.956, P = 0.05$, Table 1). No such preference for one of these two quadrants emerged if mouse and lizard odors were used.

During the full 23 h of the trials, there was also a quadrant effect ($H = 26.120, P \ll 0.0001$ [mouse]; $= 23.829, P \ll 0.0001$ [frog]; $= 28.128, P \ll 0.0001$ [lizard]). As in the first two hours, shelter had a significant overall effect with snakes spending most of the 23 h in quadrants with shelter (B, D) and significantly less time in quadrants without shelters (A, C), Fig. 2. Notice that for all three prey odors, the snakes most commonly frequented quadrants with shelters, B and D (Fig. 2), although there was no longer a preference for B (shelter/odor) over D (shelter/no odor) (Table 2).

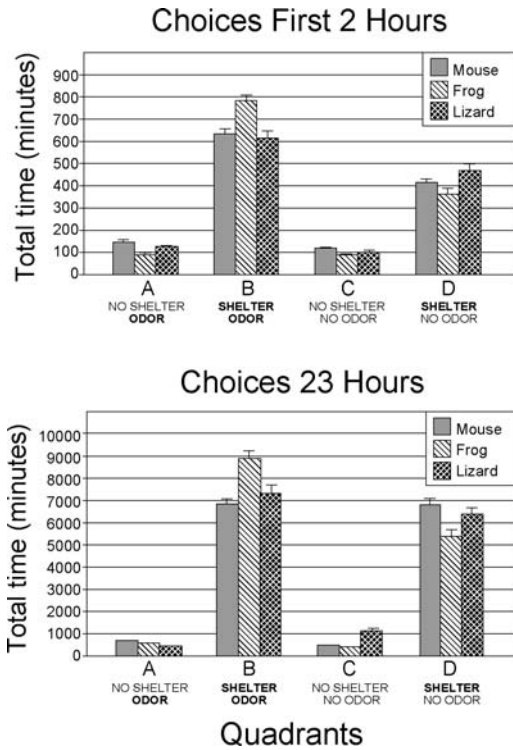


FIG. 2.—Experiment 1—shelter and odor choices. Shown are the total times the eleven snakes spent in each quadrant during the first 2 (top) and 23 (bottom) h. Standard deviation at the top of each bar.

Experiment 2: Prey Odor Choice

General behavior.—The snakes did not differ in their general behavior from Experiment 1. The rattlesnakes would travel through the arena just after they were introduced, investigating shelters and petri dishes, and soon thereafter took up residence in one of the shelters; only in three trials did snakes enter a shelter immediately after being placed in the arena.

Time spent in the quadrant.—During the first 2 h of the trials, the snakes showed no preference for any of the four choices—mouse, frog, lizard, water [$H = 2.172, P = 0.537$] (Fig. 3a). Similarly, no significant quadrant preference emerged during the full 23-h trial [$H = 1.196, P = 0.753$] (Fig. 3b).

23-h activity.—From Experiment 1, we combined the two runs for each prey type of the data, then plotted the hourly activity pattern of the pigmy rattlesnakes for each prey type (Fig. 4 A–C). From Experiment 2, we similarly combined the two runs of the three prey odors simultaneously, and then plotted the hourly activity pattern, which revealed a bimodal pattern (Fig. 4D). Variation between snakes occurred but generally each snake, on each prey type, exhibited two peaks during the 23-h period. Or stated the other way around, no single snake accounted for the overall bimodal pattern.

Thus, two peaks in activity occur—one soon after introducing the snakes, and a second nocturnal peak reaching highest activity around midnight. This daily activity pattern was similar regardless of the prey type. Snakes were active for the first two to three hours at the beginning of the trial. This dropped until lights out (20:40) after which activity again rose. After midnight activity fell gradually and stayed low into and during the day. In general the snakes were active between midnight and about 05:00, thereafter settling into a shelter for the rest of the morning and afternoon until the trial ended (Fig. 4A–D).

DISCUSSION

Experiment 1: Odor and Shelter Choice

During the first 2 h of entry into the arena, frog odor along with shelter was a significant factor in affecting snake choice. However,

TABLE 1.—Shelter and prey odor choices over 2 h. A: No Shelter/Odor; B: Shelter/Odor; C: No Shelter/No Odor; D: Shelter/No Odor. *Significant at $\alpha = 0.05$. P and (Z -score) Wilcoxon sign-rank.

	Mouse				Frog				Lizard			
	A	B	C	D	A	B	C	D	A	B	C	D
A	—	0.008* (2.667)	0.533 (0.622)	0.016* (2.400)	—	0.003* (2.934)	0.423 (0.800)	0.012* (2.497)	—	0.004* (2.845)	0.423 (0.800)	0.008* (2.667)
B	—	—	0.003* (2.934)	0.328 (0.978)	—	—	0.004* (2.845)	0.050* (1.956)	—	—	0.007* (2.667)	0.373 (0.889)
C	—	—	—	0.013* (2.489)	—	—	—	0.016* (2.400)	—	—	—	0.005* (2.803)

TABLE 2.—Shelter and prey odor choices over 23 h. A: No Shelter/Odor; B: Shelter/Odor; C: No Shelter/No Odor; D: Shelter/No Odor. *Significant at $\alpha = 0.05$. P and (Z-score) Wilcoxon sign-rank.

	Mouse				Frog				Lizard			
	A	B	C	D	A	B	C	D	A	B	C	D
A	—	0.003* (2.934)	0.789 (0.622)	0.003* (2.934)	—	0.004* (2.845)	0.286 (1.066)	0.010* (2.578)	—	0.003* (2.934)	0.182 (1.333)	0.004* (2.845)
B	—	—	0.003* (2.934)	0.593 (0.533)	—	—	0.003* (2.934)	0.286 (1.066)	—	—	0.003* (2.934)	0.423 (0.800)
C	—	—	—	0.004* (2.845)	—	—	—	0.006* (2.756)	—	—	—	0.012* (2.489)

during 23-h trials, the snakes' lost their preference for frog odor, and shelter had the most significant effect on quadrat choice.

2-h.—Although care was taken to gently place the snake in the arena and retreat quickly from view, we cannot rule out the possibility

that transfer provoked an initial threat response to the presence of a human. However, such an effect, if present, was momentary. This initial peak in activity lasted for several hours, well after humans had left the experimental area, and not just for the brief time of introduction. All odors received snake interest suggesting that the statistical significance of odor represents a normal behavior of the snake early in its entry into the arena, and not a handling effect. To the newly introduced snake, it is in a novel habitat with novel odors, and it responds by investigating. This response is also consistent with field studies wherein addition of novel odors to habitats containing pigmy rattlesnakes was followed by interest in these odors by resident snakes (Roth et al., 1999).

Our results over 2 h are generally comparable to choices of the western rattlesnake, *Crotalus viridis viridis* (Theodoratus and Chiszar, 2000), in that, like western rattlesnakes, the pigmy rattlesnakes spent an unequal amount of time in the four quadrants. Generally, the snakes favored a shelter over the other treatments without shelter. However, when frog odor was used, pigmy rattlesnakes preferred shelter and odor (frog) to the other three combinations. The western rattlesnake preferred, during the first 2 h, quadrants with mouse and shelter. This particular difference, western rattlesnake for mouse plus shelter and pigmy for frog plus shelter, probably represents differences in basic ecology. But, for the pigmy (similar data are not available for the western rattlesnake), beyond this 2-h period, this preference and activity pattern changed.

23-h.—Frog odor became less of a factor throughout the remainder of the day so that overall shelter alone was the single factor accounting for snake choice. This drop in level of interest in odor might be due to a decay of prey odor levels during the day. However, this

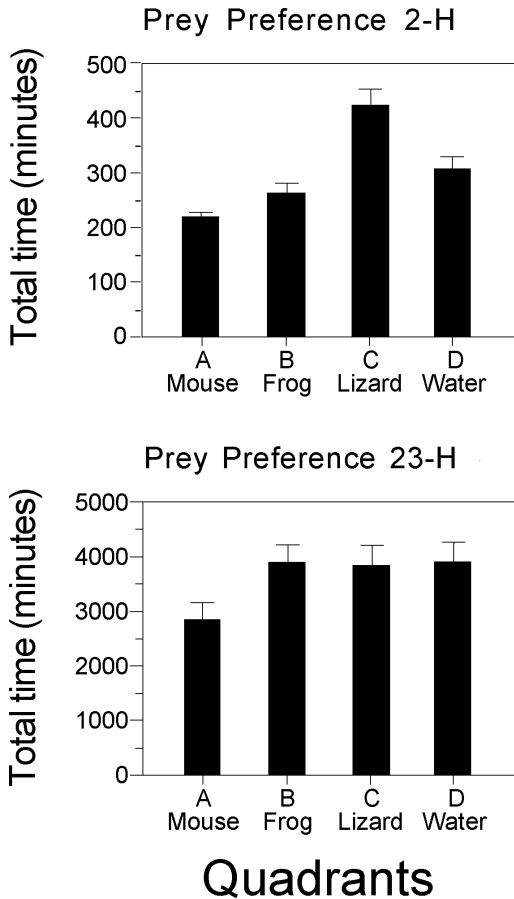


FIG. 3.—Experiment 2—prey odor choices. Shown are the total times the eleven snakes spent in each quadrant during the first 2 (top) and 23 (bottom) h. Standard deviation at the top of each bar.

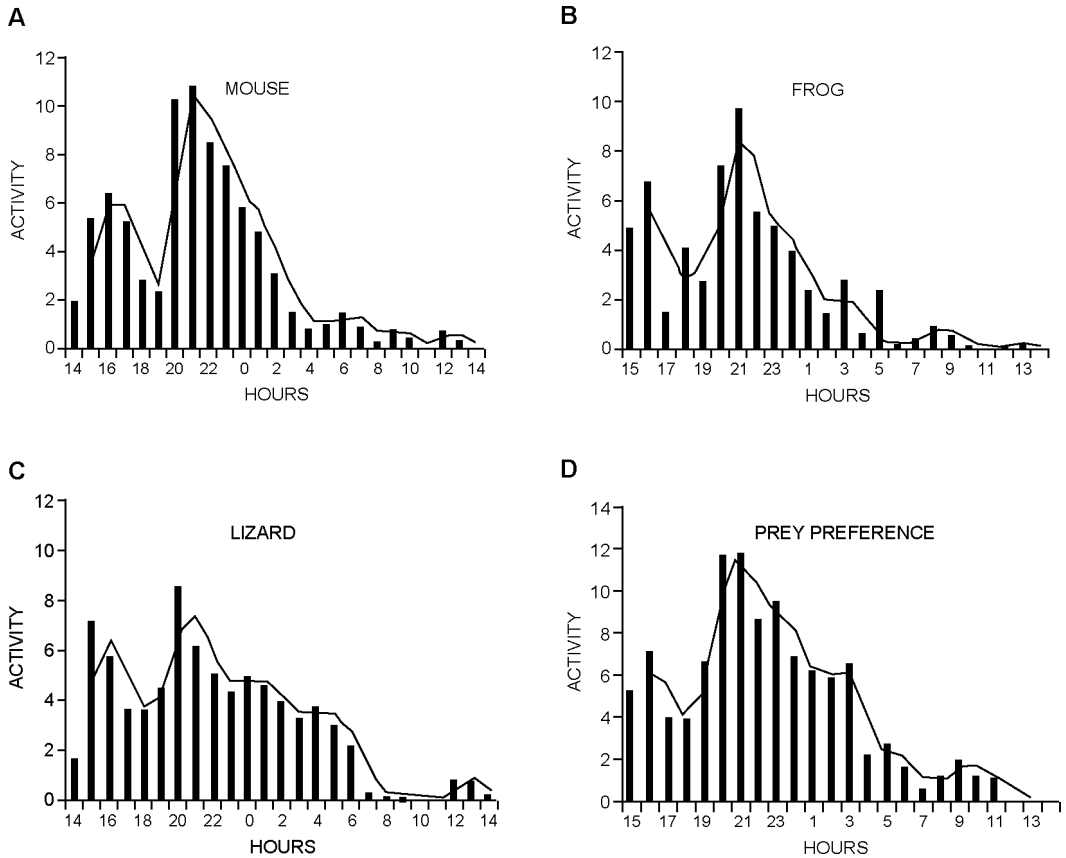


FIG. 4.—Circadian activity. Average total movements (for all snakes) per hour during 23 h. A–C, show activity results from Experiment 1 for each of the three prey odors—mouse, frog, and lizard. D, shows activity results from Experiment 2 wherein all three prey odors plus water were presented simultaneously.

seems unlikely. In field tests of frog extract, pigmy rattlesnakes showed a statistically significant response to frog odor up to 72 h after placement (Roth et al., 1999). Thus more likely than decay of frog odor, we are observing an endogenous change in actual pigmy foraging behavior during the day in the arena, wherein the frog odor became a familiar and less important chemosensory cue.

Experiment 2: Prey Odor Choice

In our second experiment, pigmy rattlesnakes were presented simultaneously with all three prey odors (mouse, frog, lizard) plus a control (water). A shelter was placed at each location thereby eliminating its selective effects on choice, leaving only differences in prey odor. The snakes exhibited no prey pre-

ference during the first 2-h or during the total 23-h period in the arena. Preferential behavior for frog odor presented in the wild has been reported (Roth et al., 1999). Even though our snakes and frogs and lizards were captured in the wild (Florida, USA), the snakes exhibited no such preference. The pigmy rattlesnake includes a wide variety of prey items in its diet (Ernst, 1992) which may account for why no prey odor in particular is preferred among the three prey choices—mouse, frog, lizard.

Arena size or period of captivity conceivable could have an effect on prey choice, but this too seems unlikely. These same arenas have been used to successfully test chemosensory abilities of larger individuals of *Crotalus oreganus* with no evidence of arena size affecting natural behavior (e.g., Kardong and Smith, 2002; Smith et al., 2005). Separately, these

Sistrurus were run in chemosensory trailing trials similar to those done on *Crotalus* (e.g., Smith and Kardong, 2005). As with *Crotalus*, the pigmy rattlesnakes did trail mouse, frog, and lizard scents, albeit at lower average frequencies (*Crotalus* vs. *Sistrurus*, ~93% vs. ~63%) (T. L. Smith and G. Bevelander, unpublished data). From Experiment 1, the pigmy rattlesnakes are clearly, in this arena, making statistically significant choices and not just engaged in random movements; at least with frog odors, they even adjust choices during the first 2 h. Finally, like those in captivity longer, the pigmy rattlesnakes recently wild caught showed no prey preference suggesting further that captivity conditions did not affect behaviors.

23-h activity.—Our experiments were begun to test odor and shelter effects on pigmy rattlesnake activity, placing us in a position to compare them to other snakes (e.g., Theodoratus and Chiszar, 2000) tested under similar conditions. However, because of our extended protocol, we can additionally report general activity patterns over a day.

Two peaks in activity occurred. Pigmy rattlesnakes were placed in the arena about 4 h before the end of the diurnal light period, and immediately showed a high level of activity, remaining active for several hours before a decline occurred. A second increase in activity began at about the onset of the nocturnal period. This second activity period increased, almost doubling its previous level, until about midnight, when it starting a slow decline that lasted throughout the remainder of the night and into the diurnal period.

The first peak in pigmy rattlesnake activity that followed introduction we provisionally interpret as an initial response to a novel environment. This would account for the exhibited interest in at least frog prey odor initially, but interest declined later as the snake failed to encounter prey and accommodated to the arena environment.

The second peak in activity we interpret as part of the snakes' general nocturnal behavior. As such, our interpretation is in agreement with studies of free-ranging snakes. In the wild during summer months, pigmy rattlesnakes become mainly crepuscular or nocturnal and are less frequently found exposed during midday (May et al., 1996). Similarly, our

laboratory studies found pigmy rattlesnakes to be crepuscular/nocturnal in activity. This activity declined late in the nocturnal phase as the snakes took up residence in shelters and remained there throughout most of the day.

Diel activity patterns might vary as snakes attempt to take advantage of thermal resources. In turn, thermoregulation of body temperature is a function of season, feeding condition, body size, and reproductive condition (Gibbons and Semlitsch, 1987; May et al., 1996). Nocturnal activity also varies with moonlight (Clarke et al., 1996; Yamagishi, 1974) in other pit vipers, implying that exposure to predator detection may also affect activity pattern. And still other factors too may affect predatory patterns (Chiszar et al., 1981; Hayes, 1993).

What our study demonstrates is the presence of a strong endogenous rhythm in pigmy rattlesnakes with shelter and time of day being important correlations with activity pattern. We certainly agree with others (May et al., 1996) that activity in snakes incurs energetic costs, mortality risks, and reproductive opportunities. Future, research designed to investigate these additional separate factors upon activity patterns of pigmy rattlesnakes would be helpful in understanding additional proximate influences on activity patterns and contribute to comparative studies of adaptive activity strategies.

Acknowledgments.—We thank J. Jacobson, E. K. Johnson, C. Wallner, and G.D.E. Povel for thoughtful advise and input. Dr. Povel also was instrumental in securing funds to make the study of GB feasible. We thank M. Evans who consulted on the statistical treatments.

LITERATURE CITED

- CHISZAR, D., R. K. K. LEE, C. W. RADCLIFFE, AND H. M. SMITH. 1992. Searching behaviors by rattlesnakes following predatory strikes. Pp. 369–382. In J. A. Campbell and E. D. Brodie (Eds.), *Biology of the Pit Vipers*. Selva, Tyler, Texas, U.S.A.
- CHISZAR, D., C. W. RADCLIFFE, H. SMITH, AND H. BASHINSKI. 1981. Effect of prolonged food deprivation on response to prey odors by rattlesnakes. *Herpetologica* 37:237–243.
- CLARK, R. W. 2004a. Feeding experience modifies the assessment of ambush sites by the timber rattlesnake, a sit-and-wait predator. *Ethology* 110:471–483.
- . 2004b. Timber rattlesnakes (*Crotalus horridus*) use chemical cues to select ambush sites. *Journal of Chemical Ecology* 30:607–617.

- CLARKE, J. A., J. T. CHOPKO, AND S. P. MACKESSY. 1996. The effect of moonlight on activity patterns of adult and juvenile prairie rattlesnakes *Crotalus viridis viridis*. *Journal of Herpetology* 30:192–197.
- COCK BUNING, T. D. 1983. Thermal sensitivity as a specialization for prey capture and feeding in snakes. *American Zoologist* 23:363–375.
- DUVALL, D., AND D. CHISZAR. 1990. Behavioural and chemical ecology of vernal migration and pre- and post-strike predatory activity in prairie rattlesnakes: field and laboratory experiments. Pp. 539–554. In D. W. Macdonald, D. Müller Schwarze, and S. E. Natynczuk (Eds.), *Chemical Signals in Vertebrates*. Oxford University Press, Oxford, U.K.
- DUVALL, D., M. B. KING, AND K. J. GUTZWILLER. 1985. Behavioral ecology and ethology of the prairie rattlesnake. *National Geographic Research* 1:80–111.
- ERNST, C. H. 1992. *Venomous Reptiles of North America*. Smithsonian Institution Press, Washington, D.C., U.S.A.
- GANS, C., AND A. TAUB. 1964. Precautions for keeping poisonous snakes in captivity. *Curator* 7:196–205.
- GIBBONS, J. W., AND R. D. SEMLITSCH. 1987. Activity patterns. Pp. 396–421. In R. A. Seigel, J. T. Collins, and S. S. Novak (Eds.), *Snakes: Ecology and Evolutionary Biology*. Macmillan Publishing Co., New York.
- HAYES, W. K. 1993. Effects of hunger on striking, prey-handling, and venom expenditure of prairie rattlesnakes (*Crotalus viridis viridis*). *Herpetologica* 49:305–310.
- KARDONG, K. V., AND H. BERKHOUDT. 1999. Rattlesnake hunting behavior: correlations between plasticity of predatory performance and neuroanatomy. *Brain Behavior and Evolution* 53:20–28.
- KARDONG, K. V., AND T. L. SMITH. 2002. Proximate factors involved in rattlesnake predatory behavior: a review. Pp. 254–266. In G. W. Schuett, M. Höggren, M. E. Douglas, and H. W. Greene (Eds.), *Biology of the Vipers*. Eagle Mountain Publishing, Eagle Mountain, Utah, U.S.A.
- KLAUBER, L. M. 1956. *Rattlesnakes, their Habits, Life Histories, and Influence on Mankind*. University of California Press, Berkeley, California, U.S.A.
- MAY, P. G., T. M. FARRELL, S. T. HEULETT, M. A. PILGRIM, L. A. BISHOP, D. J. SPENCE, A. M. RABATSKY, M. G. CAMPBELL, A. D. AYCRIFF, AND W. E. RICHARDSON, II. 1996. Seasonal abundance and activity of a rattlesnake (*Sistrurus miliarius barbouri*) in central Florida. *Copeia* 1996:389–401.
- RABATSKY, A. M., AND T. M. FARRELL. 1996. The effects of age and light level on foraging posture and frequency of caudal luring in the rattlesnake, *Sistrurus miliarius barbouri*. *Journal of Herpetology* 30:558–561.
- ROTH, E. D., P. G. MAY, AND T. M. FARRELL. 1999. Pigmy rattlesnakes use frog-derived chemical cues to select foraging sites. *Copeia* 1999:772–774.
- SMITH, T. L., G. S. BEVELANDER, AND K. V. KARDONG. 2005. Influence of prey odor concentration on the poststrike trailing behavior of the northern Pacific rattlesnake. *Herpetologica* 61:111–115.
- SMITH, T. L., AND K. V. KARDONG. 2005. Blood as not a cue for poststrike trailing in rattlesnakes (*Crotalus viridis oreganus*). Pp. 389–396. In R. T. Mason, M. P. LeMaster, and D. Müller-Schwarze (Eds.), *Chemical Signals in Vertebrates*, 10. Springer Press, Berlin, Germany.
- THEODORATUS, D. H., AND D. CHISZAR. 2000. Habitat selection and prey odor in the foraging behavior of Western rattlesnakes (*Crotalus viridis*). *Behaviour* 137:119–135.
- YAMAGISHI, M. 1974. Observations on the nocturnal activity of the habu with special reference to the intensity of illumination. *Snake* 6:37–43.
- ZAR, J. H. 1999. *Biostatistical Analysis*. Prentice-Hall, Upper Saddle River, New Jersey, U.S.A.

Accepted: 4 October 2005
Associate Editor: Nathan Mills