Microhabitat and Prey Odor Selection in *Hypsiglena chlorophaea*

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We studied the effects of various shelter and prey odor combinations on selection of microhabitat characters by the Desert Nightsnake, *Hypsiglena chlorophaea*, a dipsadine snake. We also examined the activity patterns of these snakes over a 23-h period. Three prey odors were tested, based on field work documenting natural prey in its diet: lizard, snake, mouse (plus water as control). In the first experiment, each odor was tested separately in various shelter and odor combinations. We found that snakes preferred shelter to no shelter quadrants, and most often selected a quadrant if it also had prey odor in the form of lizard or snake scent. However, snakes avoided all quadrants containing mouse (adult) odor. In the second experiment, all three odors plus water were presented simultaneously. We found that snakes showed a preference for lizard odor over the others, but again showed an aversion to mouse odor, even compared to water. The circadian rhythms in both experiments showed generally the same pattern, namely an initial peak in activity, falling off as they entered shelters, but then again increasing even more prominently from lights off until about midnight. Thereafter, activity tapered off so that several hours before lights on in the morning, snakes had generally taken up residence in a shelter. Prey preference correlates with field studies of dietary frequency of lizards, while activity exhibits strong endogenous nocturnal movement patterns.

SEVERAL factors may influence habitat preference and circadian patterns of activity. Among squamates, microhabitat (e.g., shelter sites) use varies across size and age class (Langkilde and Shine, 2004; Webb and Whiting, 2006). It may also change within or between seasons (Martin and Lopez, 1998; Beck and Jennings, 2003; Heard et al., 2004), habitats (Beck and Lowe, 1991), or sexes (Brito, 2003; Whitaker and Shine, 2003). Shelters play many important roles, with individuals utilizing sites for thermoregulation (Slip and Shine, 1988), predator avoidance (Downes, 2001; Diaz et al., 2006), or when ambushing prey. This is especially true for some snakes that are often ambush predators (Slip and Shine, 1988; Beck, 1995; Theodoratus and Chiszar, 2000; Bevelander et al., 2006).

Much of the research on shelter selection in squamates has been conducted on primarily diurnal species, such as various species of iguanid (Hertz et al., 1994), agamid (Melville and Schulte, 2001), or scincid lizards (Klingenböck et al., 2000; Quirt et al., 2006). Such species use visual cues typically not available to nocturnal species (Heatwole, 1977). What is known about shelter use by small, nocturnal squamates is limited to studies on gekkonid lizards (Kearney and Predavec, 2000; Kearney, 2002) or Australian elapids (Schlesinger and Shine, 1994; Webb and Shine, 1997, 1998; Downes, 1999; Webb and Whiting, 2006).

In terms of their behavior, dipsadinae snakes are some of the least known of snakes. This is despite being a very species-rich group, found throughout the Western Hemisphere (Zug et al., 2001). While most species of dipsadine snakes are confined to the Neotropics of Central and South America, some species have distributions that extend into Mexico and north into the United States and southern Canada.

One nearctic species of dipsadine snake is the Desert Nightsnake (*Hypsiglena chlorophaea*). *Hypsiglena chlorophaea* is a small (usually <60 cm TL), secretive, nocturnal, and little studied snake found from the desert southwest, throughout the intermountain western United States, and north into the Okanagan Valley of south-central British Columbia (Mulcahy, 2008). Throughout its range, *H. chlorophaea* is most often found in dry, rocky habitat (Stebbins, 2003), with an abundance of lizards, on which they commonly feed (Diller and Wallace, 1986; Rodriguez-Robles et al., 1999).

In the Pacific Northwest, *H. chlorophaea* ranges from southern Idaho, into eastern Oregon and Washington (Nussbaum et al., 1983). *Hypsiglena chlorophaea* is a habitat generalist, being found in shrub–steppe dominated by Big Sagebrush (*Artemisia tridentata*), to disturbed range land, and agricultural fields, as well as Oregon White Oak (*Quercus garryana*) savannah, and Douglas Fir (*Pseudostuga meinziesii*) and Ponderosa Pine (*Pinus ponderosa*) forests (Storm et al., 1995; St. John, 2002; Weaver, 2006).

Hypsiglena chlorophaea is considered a dietary specialist, feeding primarily on sceloporine lizards and squamate eggs. However, the diet in the Pacific Northwest is quite varied. Lizards, *Sceloporus* spp., *Uta stansburiana*, *Plestiodon skiltonianus*, and *Elgaria* spp., juvenile snakes, *Thamnophis* spp., and *Crotalus oreganus*, anurans, *Pseudacris regilla*, *Anaryxus boreas*, and small mammals (Weaver, unpubl.) have all been recorded as prey taken by *H. chlorophaea* of all sizes (Diller and Wallace, 1986; Rodriguez-Robles et al., 1999; Weaver, 2006).

Historically, *H. chlorophaea* has been considered a species of concern in Washington State, and was known from very few specimens (McAllister, 1995). However, recent field work (Weaver, 2006) has shown that *H. chlorophaea* is a somewhat more abundant snake that can be found in sufficient numbers allowing for specimens to be collected, brought into captivity, and utilized for behavioral studies. Our experiments focused on microhabitat (shelter) selection in *H. chlorophaea* as it relates to the presence or absence of potential prey. To conduct our experiments, we used shelters in combination with three potential prey items (lizard, snake, mouse), plus a control (water). In Experiment one, an individual odor was presented in four combinations with or without shelters. In Experiment two, we presented snakes simultaneously with all three odors, plus the control, and shelters in all. Additionally, we recorded the circadian activity patterns of snakes during both experiments. Our purposes were to identify the effects of shelter and prey odor on microhabitat choice, the relative preference for different

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prey odors, and the basic circadian activity pattern of *H. chlorophaea*.

MATERIALS AND METHODS

We conducted our experiments with nine adult (five male and four female) *H. chlorophaea* (225–502 mm snout–vent length). All were collected during 2006 from three counties (Kittitas, Klickitat, and Yakima) in central Washington State. Snakes were housed individually in 26 × 51 cm glass aquaria, and maintained on a 12:12 light cycle year around (lights on at 0830 h and off at 2030 h). Temperatures in both the rooms housing the snakes and where experiments were performed were held at 25–30°C. Snakes were provided with water *ad libitum*, and each snake was alternately fed a variety of prey items (various species of lizards, snakes, and nestling mice) on an irregular basis. This was done to control for bias that may arise from feeding snakes exclusively one prey species.

Prey items used during the trials included the Western Fence Lizard (*Sceloporus occidentalis*) and Terrestrial Garter-snake (*Thamnophis elegans*), both of which are known prey items of *H. chlorophaea* (Weaver, 2006). Bedding from adult Swiss-Webster mice (*Mus musculus*) was also used as potential mammalian prey. All prey items (except *M. musculus*) were collected from the same localities as *H. chlorophaea*. Snakes were maintained under these conditions for at least six months before experimental trials were begun.

Experiments were conducted using square testing arenas (1.25 m wide × 0.5 m high) constructed out of compressed fiberglass panels, resting on a metal platform 20 cm above the floor. Overhead lighting provided 12 h of simulated daylight, while 20-watt red, incandescent bulbs were used during 12 h of darkness. The floor of the testing arena was covered with plain white butcher paper and divided into four equal quadrants using black tape (Fig. 1). Before each trial a fresh piece of butcher paper covered the arena floor that allowed each marked quadrant to show through. Individual prey odors were presented in covered plastic Petri dishes (diameter = 15 cm), with seven evenly spaced holes (diameter = 1.2 cm) drilled through the top of the dish.

Prey odors were collected by placing one to two specimens each of either a lizard or snake into 400 cc of distilled water (Bevelander et al., 2006). Prey items were swirled gently for about 10 min and then removed. This water was poured into the dish, the bottom of which was lined with filter paper. Soiled bedding from cages containing adult mice was used and enough was added to the dish to cover the bottom (Melchiors and Leslie, 1985; Lee and Waldman, 2002; Ślusarczyk and Rygielska, 2004; Robert and Thompson, 2007). Controls during each trial consisted of placing a similar amount of distilled water into a dish, again lined with filter paper. During the trials, shelters were provided that consisted of opaque plastic hide-boxes (10 × 6 × 5 cm). Shelters were provided with or without each odor during Experiment one (Fig. 1). During Experiment two, shelters were present with each of the three odors, plus the control.

Trials were run for 23 h with one hour for change over (between 1700 and 1800 h). Snakes were placed into the center of an arena and kept under a small plastic cup. This was then lifted at the start of a trial, recording commenced, and all personnel left the room. Behaviors were filmed with Panasonic cameras suspended over each arena and recorded with a Panasonic time-lapse VCR.

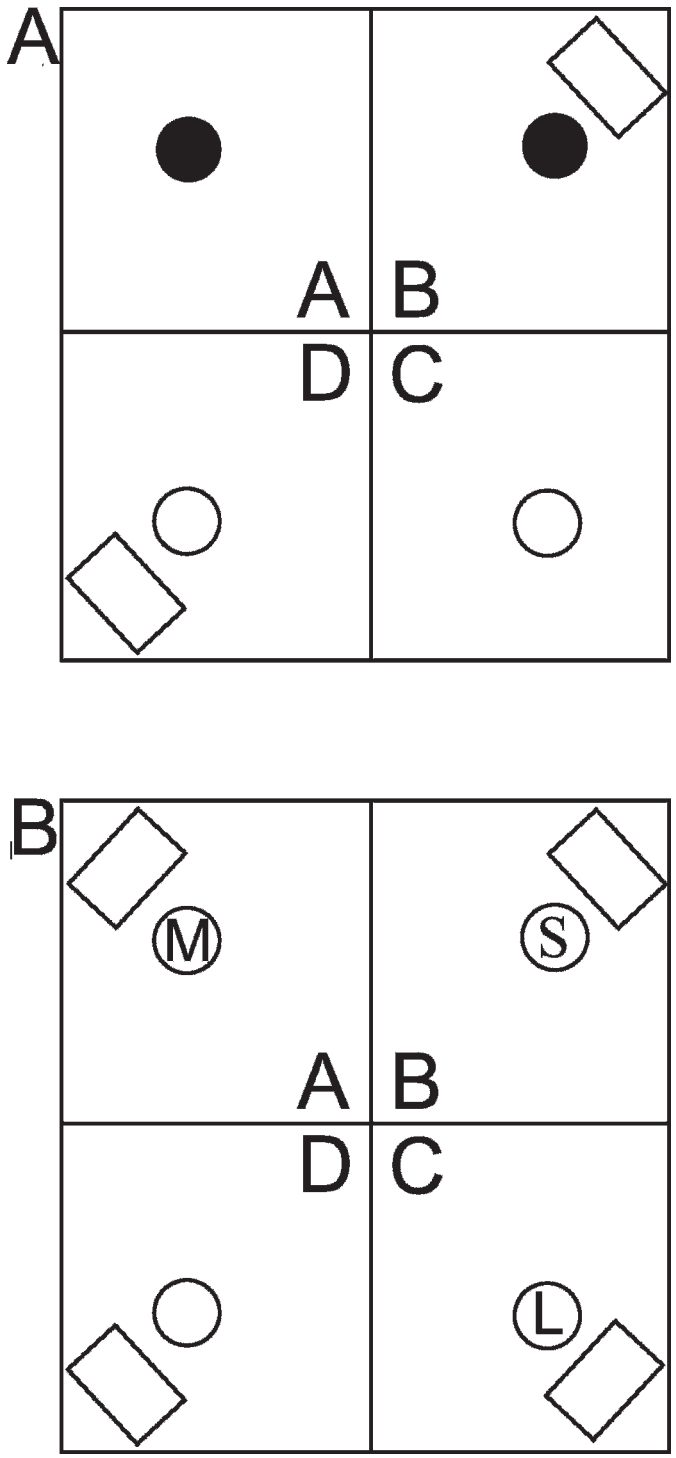

Fig. 1. Test Arena. (A) Experiment one. For each of the four quadrants A–D, a choice was provided—A: no shelter, prey odor; B: shelter, prey odor; C: no shelter, no prey odor; D: shelter, no prey. (B) Experiment two. An odor was provided in each of the four quadrants A–D—A: Mouse (M), B: Snake (S), C: Lizard (L), D: water, plus a shelter in each quadrant. The four odor/shelter combinations were changed and positioned at random during each of the trials. Circles, petri dishes with prey odor (closed circles) or water (open circles); rectangles, shelters.

Several variables were recorded during playback of tapes. We recorded the amount of time spent in each quadrant in minutes. This was recorded once a snake's head entered a quadrant and until its head left a quadrant. These times were recorded and totaled for each quadrant during each hour.

Table 1. Shelter-Site and Prey Odor Selection during 23-h Trials. A: No shelter/Odor; B: Shelter/Odor; C: No Shelter/No Odor; D: Shelter/No Odor. *Significant at $\alpha = 0.05$. NS (not significant). Results of pair-wise multiple comparisons (Tukey test) in parentheses.

	Lizard				Snake				Mouse			
	A	B	C	D	A	B	C	D	A	B	C	D
A	—	0.050* (5.822)	NS (0.506)	NS (3.227)	—	0.050* (5.347)	NS (0.158)	NS (2.531)	—	0.050* (3.702)	0.050* (3.923)	0.050* (7.625)
B	—	—	0.050* (5.315)	NS (2.594)	—	—	0.50* (5.189)	NS (2.816)	—	—	NS (0.721)	0.050* (3.923)
C	—	—	—	NS (2.721)	—	—	—	NS (2.373)	—	—	—	0.050* (3.702)

Experiment one: shelter-site and prey odor selection.—During this experiment each snake was provided with a combination of a single prey odor (lizard, snake, mouse) and control (demineralized water), with the presence or absence of a shelter. Four combinations were used, one for each of the four quadrants: A: no shelter/prey odor, B: shelter/prey odor, C: no shelter/ no prey odor (water), D: shelter/no prey odor (water; Fig. 1A). The position of the choices was randomly changed at the beginning of each experimental trial. The order of prey item tested was also randomized for each snake.

Experiment two: prey odor preference.—In this experiment the same three odors were tested simultaneously (lizard, snake, mouse), plus a control (water, Fig. 1B). To control for shelter effects, a hide-box was placed into each of the four quadrants with the door facing the Petri dish holding the odor. Again, similar to Experiment one, the position of the choices was randomly changed at the beginning of each experimental trial, with the order of prey item tested also random.

During both experiments, shelters and Petri dishes were washed between trials with 70% ethanol, rinsed with demineralized water, and allowed to dry overnight. During the set-up of experiments gloved hands (Microflex, non-sterile, latex) were used when handling dishes, shelters, and when changing the paper that covered the bottom of the arena floor. When placing the dishes into the arena we were careful not to cross-contaminate quadrants. One week was allowed to pass between trials of the same snake. Snakes were fed after each trial, confirming hunger.

Statistical analysis.—Each snake was run twice, its score averaged, and these means examined with a non-parametric test (Kruskal-Wallis, *H*-test). When this test produced statistical significance, we performed a Tukey Test (*Q*-score) test of multiple pair-wise comparisons to discover which were significantly different from one another.

RESULTS

Experiment one: shelter-site and prey odor selection.—After placement into the arena at about 1800 h, Nightsnakes spent the first few minutes in the center of the arena before moving toward the edges. Snakes made several movements around the arena, moving along the walls, and making quick movements across the arena. While making these movements, snakes would crawl into and around shelters. Snakes would crawl toward the dishes, usually pausing if a dish contained a prey odor. These behaviors usually lasted for 30 minutes to an hour. All snakes settled into a shelter after one hour and remained in that shelter until lights off. During this time, no part of a snake's body was out of the shelter.

Just after lights off (2030 h), snakes emerged. Often just a head would initially be visible from the shelter opening. After a few minutes, snakes would leave the shelter and begin to move around the arena. During these movements snakes would move through quadrants containing shelters, moving into and out of that shelter. Snakes ignored (crawling past, not pausing) dishes that contained no prey odor (water). When a snake crawled near a dish that contained either a lizard or snake odor they would pause while moving their heads from side to side across the top of the dish.

The darkened room did not allow us to confidently count tongue flicks or record the rate of flicks, but tongue flicks were evident. We observed snakes moving their heads back and forth while making circuitous routes around the dish. This behavior would continue for several hours, until eventually settling into a shelter near a dish usually containing prey odor. Snakes would coil inside the shelter with just their heads visible in the opening of the shelter, pointing toward the dish. They remained in this position for the rest of the night and into the following day. During trials most snakes behaved in this manner. However, in two trials snakes selected a shelter almost immediately and remained in that shelter for the total duration of the 23-h trial.

During the 23-h trials (54 total) there was a significant quadrant effect for snake (Kruskal-Wallis, $H = 18.876$, $P < 0.001$), lizard ($H = 22.778$, $P < 0.001$), and mouse ($H = 29.098$, $P < 0.001$). During the lizard and snake trials, *post-hoc*, pair-wise multiple comparisons (Tukey test) revealed a significant preference for quadrants containing a shelter–odor combination (B) over quadrants with odor only (A), or no odor/no shelter (C). However, there was no preference for quadrant D (no odor/shelter) over quadrant B (shelter/odor; $Q = 2.816$, $P > 0.05$) or A (odor/no shelter; $Q = 2.531$, $P > 0.05$) during the snake or lizard trials (Table 1).

During trials when snakes were presented with the mouse odor, most snakes spent significantly less time in a quadrant containing a mouse odor only (A) and significantly more time in a quadrant without mouse odor (C and D). There was, however, no significant difference between quadrant C (no odor/no shelter) and B (odor/shelter, $Q = 0.221$, $P > 0.05$) during the mouse odor trial (Fig. 2).

When comparing the presence or absence of a shelter, there was a significant effect of shelter for all trials, snake ($H = 14.899$, $P < 0.001$), lizard ($H = 18.243$, $P < 0.001$), and mouse ($H = 13.704$, $P < 0.001$). This was not true for odor. During both the snake and lizard odor trials there was no

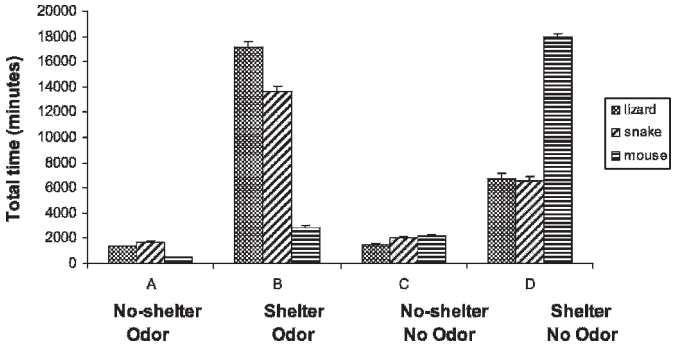

Fig. 2. Total amount of time (minutes) spent in quadrants for all snakes during each 23-h trial for Experiment one (shelter and odor choices). Standard deviations are at the top of each bar.

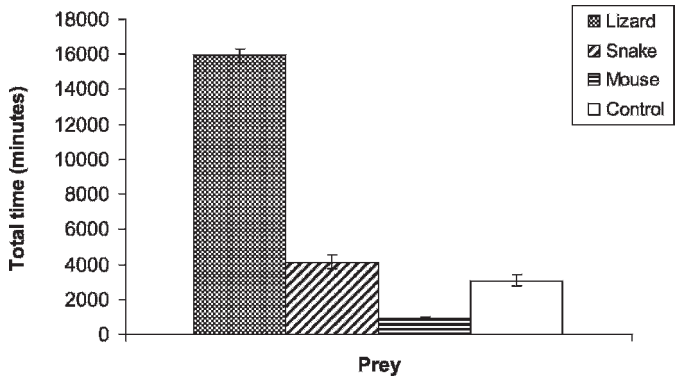

Fig. 3. Total amount of time (minutes) spent in quadrants for all snakes during each 23-h trial for Experiment two (prey odor preferences). Standard deviations are at the top of each bar.

difference in selection for quadrants with an odor, or without ($H = 1.766$, $P = 0.184$ and $H = 1.090$, $P = 0.296$, respectively). However, during the mouse trial, there was a significant difference between quadrants with and without odor, the snakes preferring quadrants without mouse odor ($H = 15.393$, $P < 0.001$).

Experiment two: prey odor preference.—As in Experiment one, upon placement into the arena, snakes remained motionless for a few minutes and then moved about the arena, making several circuits, investigating both shelters and dishes. Unlike Experiment one, some snakes continued these movements up to lights out. However, most snakes moved into a shelter and remained there until just after lights out. In only one trial out of 18 did a snake enter a shelter immediately and not emerge for the remainder of the 23-h trial.

When presented with all three odors simultaneously (lizard, snake, mouse) and control (water), each accompanied by a shelter, *H. chlorophaea* showed a preference for the quadrant containing the lizard odor, spending a significant amount of time in that quadrant, over either mouse ($Q = 6.106$, $P < 0.05$) or control ($Q = 3.797$, $P < 0.05$, Fig. 3). *Post-hoc* comparisons showed no difference between quadrants containing either snake or mouse odor ($Q = 3.322$, $P > 0.05$), and snake or lizard ($Q = 2.784$, $P > 0.05$, Table 2).

Experiment one and two: activity patterns.—For each prey type, the trials for *H. chlorophaea* were combined, with the average number of movements for each hour plotted to show activity patterns. Overall, there was no significant difference ($H = 0.2815$, $P = 0.963$) in the average number of movements made during trials for either experiment one or two. Average movements during trials for each prey odor during experiment one were: lizard (mean = 3.25 ± 4.11 SD), snake (3.13 ± 4.43 SD), and mouse (mean = 2.77 ± 4.64 SD). During experiment two when all odors were present, snakes moved an average of 3.44 ± 4.64 SD.

During two trials (lizard and snake), *H. chlorophaea* showed similar bi-modal activity patterns, making several movements during the first few hours, before settling into a shelter before lights out (Fig. 4A, B). Then, after lights out (2030 h), renewed activity characterized by a steady increase in activity peaking around midnight. Activity continued until 0100 or 0200 h, which dropped off thereafter, with only a few individuals making brief movements just before lights on (0830 h).

After being placed into the arena, snakes were initially more active for the first few hours (1800–1900), making 8.15 and 9.36 moves, respectively (Fig. 4C), during the mouse odor trials. For either the lizard or snake odor trials, snakes made fewer movements during that two-hour span, (4.52 and 4.63 times, and 4.35 and 3.68 times during each hour; Fig. 4A, B). Activity decreased just before lights out (2030) and did not increase again until 2200 h, about one hour after activity during the lizard or mouse trials, with a peak at 2300 h. Thereafter, activity levels dropped, with snakes making few movements between 0100 and 0300 h. Unlike both the lizard and snake trials, activity during the mouse trials stopped at 0600 h, with no snakes making any movements just before lights on at 0830 h (Fig. 4C).

During Experiment two, again we combined both trials of all snakes which were averaged per each hour, and then plotted to show activity patterns. Similar to Experiment one, snakes made several movements during initial introduction. However, some snakes did not settle into a shelter before lights out. Movements plateaued between 1900 and 2100 h, with an increase in activity from 2200 to 2300 h. Starting at about midnight, activity declined steadily into the morning hours, with all activity stopping at about 0600 h (Fig. 4D).

Table 2. Prey Odor Preference during 23-h Trials. *Significant at $\alpha = 0.05$. NS (not significant). Results of pair-wise multiple comparisons (Tukey test) in parentheses.

	Lizard	Snake	Mouse	Control
Lizard	—	NS (3.332)	0.050* (6.106)	0.050* (3.797)
Snake		—	NS (2.784)	NS (0.475)
Mouse	—	—	—	NS (2.310)

DISCUSSION

Experiment one: shelter and prey odor selection.—During Experiment one, *H. chlorophaea* (except the two individuals that remained in a shelter the entire time) showed a preference for quadrants with lizard or snake odors that included a shelter over other combinations without a shelter. Time spent in quadrants with such odors and shelter was significantly greater than those with odor alone.

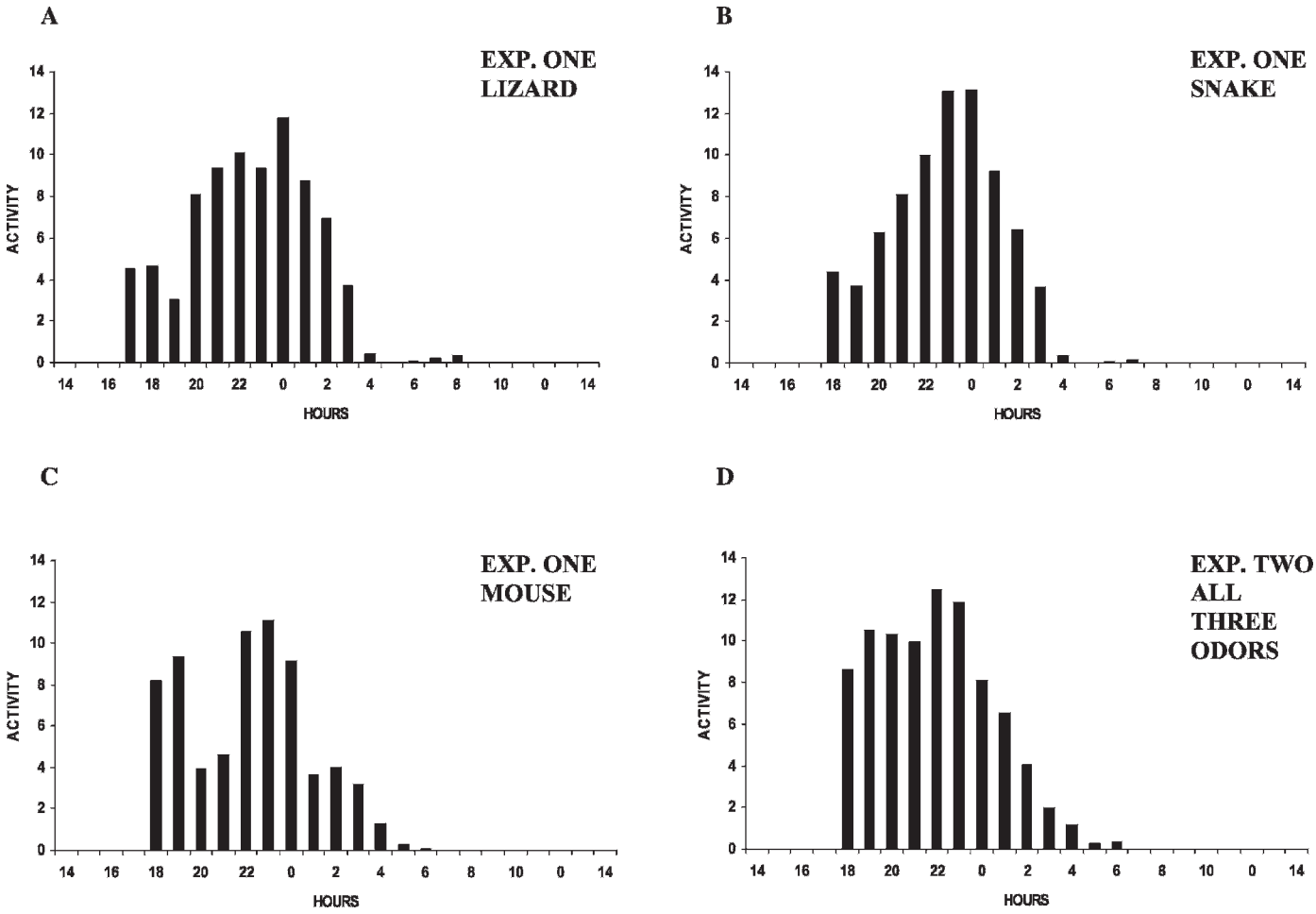

Fig. 4. Activity patterns. Average number of movements for all snakes per hour during the 23-h period. (A–C) Activity patterns for Experiment one for each of the three prey odors—lizard, snake, mouse. (D) Activity patterns for Experiment two, where all three prey odors and water were presented simultaneously.

With mouse odors, there was a shelter and odor effect, but in a complicated way. Nightsnakes exhibited significantly less interest in a shelter quadrant if mouse odor was present than if mouse odor was absent (Fig. 2). Some *H. chlorophaea* did initially investigate the quadrant with mouse odor, slowly approaching the dish, but then usually quickly turned away from the dish and moved away in a rapid manner. We interpret these responses to mouse odor, relative to water, as representing a negative preference, even active avoidance of adult mouse odors. Our general observations, reported above, are also consistent with this interpretation.

A strong selection for quadrants with lizard or snake odor (plus shelter) is not surprising. Prior work examining museum specimens (Rodriguez-Robles et al., 1999) and field work in both southwestern Idaho (Diller and Wallace, 1986) and Washington State (Weaver, 2006) revealed *H. chlorophaea* to feed primarily on lizards. However, Weaver (2006) also showed that *H. chlorophaea* take snake prey (*Thamnophis* spp.).

Experiment two: prey odor preference.—Overall, snakes behaved in much the same way during Experiment two (all three prey odors plus control presented simultaneously). Nearly all individuals (83%) made just a few movements after introduction and then settled into a selected shelter until lights off. Evaluation of choice of snake odor is complicated. There was no significant difference between lizard and snake odor preferences, but there was also no significant difference between snake odor and all other choices either (Table 2). This may reflect natural prey preference or result from the large variation in choices for snake odor in our study. However, a preference for lizard odor quadrants is significant, with snakes spending a greater amount of time in those quadrants containing lizard odor (plus shelter) than mouse or control (water). Similar to Experiment one, snakes in Experiment two displayed avoidance behavior when encountering the mouse odor (with or without shelter).

Overall results from both experiments suggest that snakes are not making random movements. The statistical results show a strong selection for the combinations of odors and shelter, especially lizard odor. Little or no time was spent in quadrants lacking a shelter, with or without odor. Snakes avoided quadrants with mouse odor, and qualitative observations indicate such behavior was extreme and may be in response to the odor of an adult mouse as a threat rather than as a food item.

Experiment one and two: activity patterns.—While we observed no significant difference in the activity patterns of *H. chlorophaea* during either Experiment one or two, there were distinctive movements and behaviors displayed by *H. chlorophaea* during trials. When first placed into the arena, most snakes moved in a slow irregular manner, making

several movements around the arena. A few snakes made quick, erratic movements, and two snakes moved immediately into a shelter and remained there during the entire 23-h period. In those two trials, the immediate seeking of cover may have been the result of introduction into the arena in spite of our taking great care to introduce the snakes into the arena in a gentle and stress free manner. In nearly all trials (96%) snakes settled into a shelter after a few minutes of initial orientation within the center of the arena.

During both Experiments one and two, there were two peaks in activity patterns. The first occurred following introduction into the arena, while the second bout of activity started with lights out (2030 h) and peaked about midnight. Thereafter, snakes tended to settle into a shelter as morning approached and activity waned, and all snakes were in a shelter before lights on (0830 h).

There were only slight differences in activity patterns between the two experimental conditions. During Experiment one activity peaked during 2300 and 0000 h, with three snakes making brief movements during the time just before lights on at 0830 h. Activity levels showed a slow steady decline until 0500 and 0600 h. The snakes that made crepuscular movements did so quickly, moving between shelters. During Experiment two, activity peaked an hour earlier at 2200 h, but again showed a slow steady decline, with all activity ceasing at 0600 h.

We interpret the first peak in activity related to introduction effects, and the second peak in activity related to intrinsic circadian rhythms. As interpreted by others (Bevelander et al., 2006), we too suggest that the first activity peak may represent investigation of a novel microhabitat and/or be related to the introduction procedure itself. Other than movements made after introducing an individual snake into the arena, the movements made by *H. chlorophaea* were strictly nocturnal. *Hypsiglena chlorophaea* has been anecdotally reported as being occasionally encountered during the day (Woodbury, 1931; Grimser, 2002), but most encounters in the field are nocturnal. Activity times from the field reported for 74 individual *H. chlorophaea* from May to October ranged from 2100–0600 h, with peaks between 2300 and 0100 h (Weaver, 2006), very similar to our laboratory activity results reported here. As the common name suggests for this snake, *H. chlorophaea* is nocturnal in habit, sometimes engaged in low levels of crepuscular, predawn movements.

Period of or conditions in captivity could conceivably affect basic prey choice, but this seems unlikely. Pilot studies of snakes collected in the field and run within a few days of capture showed similar shelter–odor choices (Experiment one), odor choices/aversions (Experiment two), and circadian rhythms to snakes in this controlled study. Further, correlation between experimental and field data is also evident in prey preferences. In this study, *H. chlorophaea* showed a statistically significant preference for lizard and snake odors (with shelter) over controls and over mouse odors. These choices are similar to documented prey choices in the field (Weaver, 2006).

While the avoidance of adult mice odor by *H. chlorophaea* is also probably an intrinsic behavior, it is interesting to note that using similar protocols, other laboratory studies (Theodoratus and Chiszar, 2000; Bevelander et al., 2006) of shelter–odor choices showed preferences for, not aversion to, mouse odors. The possible reasons for this avoidance by Nightsnakes of adult mouse odors is likely related to its limited defense ability and the resulting vulnerability to rodent retaliation from protective adult mice. In contrast, the larger (50–60 cm SVL) Western Rattlesnake (*Crotalus oreganus*) feeds on adult rodents and is equipped with the venom apparatus to quickly kill (Kardong, 1986) and the strike and release behavior to protect itself from retaliation (Chiszar et al., 1992). These rattlesnakes show a preference for environmental mouse odors when moving in microhabitats (Theodoratus and Chiszar, 2000). The Pygmy Rattlesnake (*Sistrurus miliarius*) is smaller (38–51 cm SVL), about the same size as large *H. chlorophaea*. But, similar to *C. oreganus*, *S. miliarius* exhibits a preference for mouse odors (and shelter), although the more natural frog prey is slightly preferred (Bevelander et al., 2006). Although small, *S. miliarius* has a venom apparatus capable of injecting a painful defensive bite (Klauber, 1956), and thereby is able to meet a challenge even from an adult mouse. However, *H. chlorophaea* possesses no such specialized venom apparatus to rapidly kill its prey or to effectively inflict immediately painful defensive bites. Nesting adult mice may inflict damage (incisor teeth) while protecting their young. The behavior displayed during the mouse trials indicates that *H. chlorophaea* may avoid large adult mice as they would any other possible threat.

The idea that *H. chlorophaea* is ''venomous'' is an old idea (Cowles, 1941), often repeated in field guides today. This unqualified claim is unwarranted for several reasons. *Hypsiglena chlorophaea* does not possess a venom gland but instead a Duvernoy's gland (Taub, 1967) associated with a tooth that is neither hollow nor grooved (Young and Kardong, 1996). Although such systems are sometimes termed ''venom systems'' (Jackson, 2007), this is a premature conclusion until experimental studies verify directly that it is actually deployed in rapid killing of prey and/or in successful defense (Kardong, 1996). The oral glands and associated teeth of *H. chlorophaea* are unlike the hollow fangs and true venom system of rattlesnakes, and therefore the biological role of the jaw apparatus of *H. chlorophaea* is not as a venom system, or if a ''venom system'' it is much less capable of quickly dispatching prey (Kardong, 2002). These differences help account for why rattlesnakes equipped with a true venom apparatus (*C. oreganus* and *S. miliarius*) show a preference for mouse odors, and *H. chlorophaea* without a comparable venom system actually shows an aversion to mouse odor. Rattlesnakes have the venom system to exploit rodent prey or defend against them; *H. chlorophaea* do not.

While our study focused on three factors (shelter, prey, and temporal variables) affecting activity patterns in *H. chlorophaea*, such activity patterns in snakes may vary in response to several other factors as well. For instance, activity in small, nocturnal snakes such as *H. chlorophaea* could also be influenced by factors such as moonlight. However, most work conducted on snakes addressing any such factors has been on larger species, primarily viperid snakes (Yamagishi, 1974; Clarke et al., 1996; Theodoratus and Chiszar, 2000). Our laboratory study extends our knowledge to small colubroids by showing an endogenous rhythm in *H. chlorophaea* with shelter and time of day being important correlates with activity patterns and use of microhabitat.

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