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Prey Chemical Discrimination by the Desert Nightsnake (*Hypsiglena chlorophaea*): A Comparison of Invertebrate and Vertebrate Prey

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ABSTRACT.—We investigated responses of adult and juvenile Desert Nightsnakes (*Hypsiglena chlorophaea*) to odor extracts of potential invertebrate and vertebrate prey. Snakes were collected during 2009 from three localities in Washington state. We obtained odor from three potential invertebrate prey—spider (*Tegenaria* spp.), scorpion (*Paruroctonus boreus*), and field cricket (*Gryllus* spp.)—and compared responses with a vertebrate prey item, a Western Terrestrial Gartersnake (*Thamnophis elegans*). All potential prey items were collected at the same site as *H. chlorophaea*. We presented odors on 15-cm cotton swabs held 2.5 cm in front of the snake's snout. For each trial we recorded the number of tongue flicks in 60 sec, the latency to first tongue flick, and whether the stimulus elicited an attack. We observed no significant difference in latency of responses between spider, scorpion, cricket, or snake odors. However, both adult and juvenile *H. chlorophaea* responded with higher tongue-flick rates to snake odor. Juveniles showed an increase in tongue-flick rate toward crickets. Attacks were made against snake odor with no difference between adult and juvenile responses. Our results indicate that adults and juveniles of *H. chlorophaea* do not feed on invertebrates, and in some cases invertebrates may pose a threat to small snakes such as *H. chlorophaea*. However, the diet of *H. chlorophaea* may vary geographically, and populations of *H. chlorophaea* with a more southerly distribution may feed on invertebrates. Whether such differences in diet exist between populations will remain unresolved until additional studies of the diet of southern populations of *H. chlorophaea* are compared with those of northern populations.

The chemical ecology of squamates has been well studied. Most research has been conducted on prey chemical discrimination (PCD) in scleroglossan lizard taxa such as gekkonids (Cooper, 1998), scincids (Cooper and Hartdegen, 1999), varanoids (Cooper and Arnett, 1995; Garrett et al., 1997), and pygopodids (Wall and Shine, 2009). Generally, nonscleroglossan lizards such as agamids and iguanids do not discriminate among prey using chemical cues (Cooper, 2003).

The foraging ecology of a species plays an important role as to whether PCD abilities are present, especially for snakes. Species that are active foragers such as natricine (Burghardt, 1993) and colubrine snakes (Cooper et al., 1990, 2000) exhibit PCD. Ambush foragers such as viperids, however, may not respond directly to prey odor cues prestrike (Lavin-Murcio and Kardong, 1995; Smith and Kardong, 2005); these snakes instead use a variety of chemical cues poststrike (Smith et al., 2005). The relative ease of collecting and maintaining some snakes, especially natricines and viperids, has led to a disproportionate amount of research on and more complete understanding of the chemosensory abilities of these taxa. Chemosensory abilities of less common species, such as dipsadines, are poorly understood. Because of this, we investigated the presence of PCD in a temperate dipsadine snake, the Desert Nightsnake (*Hypsiglena chlorophaea*).

The Desert Nightsnake is a small (usually <66 cm snout-vent length [SVL]) cryptic snake (Stebbins, 2003) found throughout intermountain North America, from Arizona (and northern Mexico) north to British Columbia (Mulcahy, 2008). Although strongly saurophagous (Rodriguez-Robles et al., 1999), *H. chlorophaea* occasionally feeds on insects (Diller and Wallace, 1986; Werler and Dixon, 2000) and scorpions (Cowles, 1941).

Recent work on the ecology of *H. chlorophaea* in the northern half of its distribution (Weaver, 2010) has shown that both juveniles and adults consume a wide range of vertebrate taxa (e.g., snakes, lizards, frogs, and small mammals). This work also showed *H. chlorophaea* does not consume invertebrates. Because

previous studies have reported that *H. chlorophaea* preys upon invertebrates, we investigated the behavioral responses of adults and juveniles of *H. chlorophaea* to three potential invertebrate prey species against a known vertebrate prey species.

MATERIALS AND METHODS

Collection and Maintenance of Snakes.—Adults and juveniles of *H. chlorophaea* were collected from May through September 2009 from two counties in central Washington state. Twenty-one adults (SVL, mean \pm SD = 364 \pm 14.3 mm) and 17 juvenile (SVL, 164 \pm 4.2 mm) were housed individually in glass aquaria (26 \times 31 \times 51 cm) lined with paper. Age classes of *H. chlorophaea* were established using data from current fieldwork on this species (Weaver, 2010). The room in which snakes were kept was maintained on a 12:12 light:dark cycle, at a relatively constant temperature of 28°C, with water available ad libitum. Snakes were maintained in this manner for 3 weeks before testing.

Behavioral Experiments.—The cage in which each snake was maintained was used as the testing arena. We recorded the responses of individual snakes to chemical stimuli by presenting odors on 15-cm wooden, cotton-tipped swabs. We recorded latency period (time before first tongue flick) and the number of tongue flicks exhibited by a snake in response to stimulus odors for 60 sec after the first recorded tongue flick (Cooper and Burghardt, 1990). We measured the above responses by snakes to six odors. One was a control odor that consisted of dipping a cotton swab into demineralized water. The second odor was a pungency control in which a cotton swab was dipped into 3:1 mixture of water and commercial cologne (Aqua Velva brand). The third odor was obtained from a cricket (*Gryllus* spp.). The fourth was an odor obtained from a spider (*Tegenaria* spp.), and the fifth odor was obtained from a scorpion (*Paruroctonus boreus*). The sixth odor was collected from a known vertebrate prey item (Weaver, 2010), a juvenile Western Terrestrial Gartersnake (*Thamnophis elegans*). Following the methodology of Cooper

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TABLE 1. ANOVA table showing response of Box-Cox-transformed latency period of snakes partitioned into an age factor (adult and juvenile), odor factor (water, cologne, cricket, scorpion, spider, and snake), and the interaction between age and odor. The random blocking factor is associated with the repeated measure on individual test snakes.

	df	SSE	MSE	F	P
Between-subject error					
Age	1	0.08	0.08	0.49	0.487
Residual	35	5.92	0.17		
Within-subject error					
Odor	5	13.39	2.68	17.12	<0.001
Age × odor	5	0.59	0.12	0.75	0.585
Residual	187	29.25	0.16		

(1998), invertebrate odors were collected by running a premoistened swab along the dorsal surface of possible invertebrate prey. Similarly, the snake odor was obtained by running a swab along the anterior dorsal surface of the snake.

Trials started after lifting the top of the cage housing the snake to be tested. If any snake reacted in adverse manner, we allowed it to resume normal movements (or posture) before continuing with a trial. We then presented snakes with one of the six odors on a cotton swab. We held the swab 10–15 mm in front of the snake's snout and then moved the swab as the snake moved so the swab remained 10–15 mm in front of the snake's snout even if the snake approached the swab, or backed away. All trials were conducted during peak activity periods (2230–0130 h) (Weaver and Kardong, 2009). Observations were made under a dim 20-Watt red light. One odor trial was tested for each snake on a given night, with additional single odor trials conducted on separate nights, with a minimum of 24 h between trials. For each trial, both fresh swabs and fresh odors from potential prey were used for all snakes.

Statistical Analysis.—Two separate split-plot analyses of variance (ANOVA) were used to test snake responses to odor. One test was used to assess the response in latency time, and the other test was used to assess tongue-flick rate. The split-plot design used individual snakes as blocks with odor as a subplot, replicated within block, and age as the whole plot. Before the analysis the Levene test for equal variance was applied among blocks (i.e., individual snakes), age (i.e., adult, juvenile), and odor groups separately. Unequal variance between some groups made it necessary to transform data to meet ANOVA model assumptions, and we did so using the Box-Cox power transformation method (Box and Cox, 1964). Responses were retested after the transformation to ensure variance was equalized. Residuals from the ANOVA were tested for normality using Lilliefors (Kolmogorov-Smirnov) normality test, and in no case was there evidence for non-normality after the transformations. If ANOVA effects were statistically significant, we performed a multiple pairwise comparison test (Tukey's honestly significant difference) post hoc by significant factors to show which individual odor or odor-age combinations elicited a significantly different response. We also tested the odds for an attack on an odor presentation by using a logistic regression model with multiplicative effects for odor and age. For all analyses, α was set at 0.05. Unless otherwise noted, results are reported for back-transformed means and standard errors. All statistical procedures accomplished using R 2.12 (R Core Development Team, 2010). Data are reported as mean \pm SE.

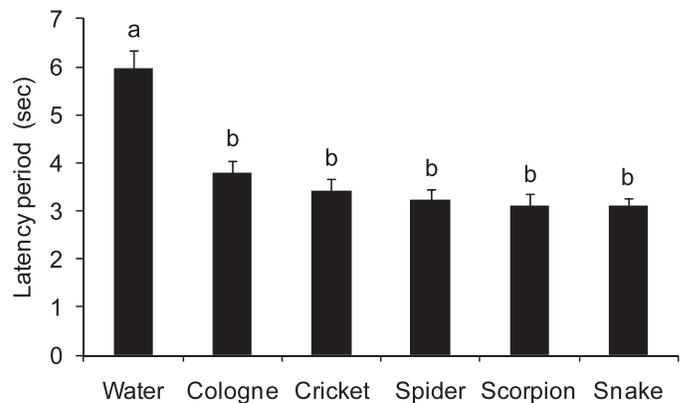


FIG. 1. Latencies (time to first tongue flick; mean \pm SE, $N = 38$) for *Hypsiglena chlorophaea* in response to odors of one vertebrate prey (a snake), two control odors (water and cologne), and three potential invertebrate prey odors (cricket, spider, and scorpion). Letters represent distinct groups determined by Tukey's honestly significant difference post hoc multiple pairs comparisons.

RESULTS

There was a significant effect for odor type on the latency period ($F_{5,187} = 17.12$, $P < 0.001$), but no interaction between age and odor (Table 1). A post hoc analysis showed latency period to water was longer than to all other odors tested (cologne, snake, cricket, spider, and scorpion), with no differences between any of the other odors (Fig. 1). The mean latency for water was 5.97 ± 0.37 sec, and for all other odors combined was 3.33 ± 0.23 sec.

There was a statistically significant interaction between age class and odor for the mean tongue-flick rate of adults ($F_{5,187} = 3.17$, $P < 0.01$; Table 2). The age-related difference was manifest only for faster tongue-flick rates with crickets presented to juveniles (3.42 ± 0.27 sec) compared with how adults responded to spiders (1.96 ± 0.27 sec) and scorpions (2.05 ± 0.44 sec). Both adults and juveniles displayed the highest tongue-flick rate toward snake odor compared with all other odors (Fig. 2). The next highest tongue-flick rate was for water, against which all adults and juveniles showed a depressed rate with the exception of cricket odor, toward which juveniles showed a similar response as toward water. Adults (55%) and juveniles (76%) attacked cotton swabs with snake odor. However, the logistic regression revealed that there was not sufficient evidence to reject the null hypothesis of similar odds for attack between the two age classes ($Z = 1.40$, $P = 0.163$).

DISCUSSION

Hypsiglena chlorophaea tongue flicked during each trial and responded more toward the vertebrate odor (small snake). In some trials, both adult and juvenile *H. chlorophaea* approached the swab with a spider or scorpion odor, briefly tongue flicked, and then quickly crawled away. This behavior was especially true when presented with scorpion odor. The reaction to these arachnids is not surprising. There are recorded predation events by such terrestrial arthropods on snakes similar in size to *H. chlorophaea* (Greene, 1994, 1997). This is also true for other types of arthropods. Crayfish (Weaver, 2004) and marine crabs (Voris and Jefferies, 1995) have been reported to kill and consume snakes typically much larger than *H. chlorophaea*, such as *Thamnophis elegans*, *Cerberus rynchops*, and *Oxybelis aeneus*. Maitland (2003) reported that terrestrial crabs preyed upon

TABLE 2. ANOVA table showing response of Box-Cox-transformed tongue flicks of snakes partitioned into an age factor (adult and juvenile), odor factor (water, cologne, cricket, scorpion, spider, and snake), and the interaction between age and odor. The random blocking factor is associated with the repeated measure on individual test snakes.

	df	SSE	MSE	F	P
Between-subject error					
Age	1	0.03	0.03	0.11	0.745
Residual	35	8.29	0.24		
Within-subject error					
Odor	5	337.71	67.54	534.96	<0.001
Age × odor	5	2.00	0.40	3.17	<0.01
Residual	187	23.61	0.13		

juvenile snakes similar in size to *H. chlorophaea*, including *Sibon nebulata* and *Atractus trilineatus*.

The spiders used were small and likely pose little threat to even the smallest individuals (e.g., hatchlings) of *H. chlorophaea*. However, the species of scorpion used reaches an adult size that may enable it to capture and consume juveniles of *H. chlorophaea*. During our experiments, individuals of *H. chlorophaea* (both adult and juvenile) reacted in a more overtly defensive or aversive manner toward scorpion odors. Snakes would rapidly recoil, hiding their heads within coils or making rapid side movements of their heads. In other geographic regions of the Pacific Northwest, larger scorpions such as *Hadrurus spadix* could conceivably kill small adult *H. chlorophaea*. Although such predation events are rarely documented, there is a report of a similar-sized species of scorpion killing (but not consuming) a snake (*Leptotyphlops humilis*), albeit a species smaller than *H. chlorophaea* (Anderson, 1956). In the southwestern United States, with its abundance of larger arachnids, such predation events on *H. chlorophaea* may be more likely (McCormick and Polis, 1982). When presented with cricket odors, snakes approached, tongue flicked for just a few seconds, and then ignored the odor. Individuals of *H. chlorophaea* of all sizes consume vertebrate prey, including small snakes (Weaver, 2010); hence, the lower latency and substantially higher tongue flicks of both adult and juveniles toward this odor are not surprising.

Snake species with wide geographic distributions generally have broad dietary preference. This has been documented for natricines (Burghardt, 1993), colubrids (Cooper et al., 1990, 2000; Shewchuk and Austin, 2001), and viperids (Greenbaum, 2004). In some cases where populations are separated by short distances (<100 km), the separated populations may have very different diets (Aubret et al., 2006; Weatherhead et al., 2009). *Hypsiglena chlorophaea* is found from northern Sonora and Baja California, Mexico, north into British Columbia (Mulcahy, 2008). Hence, its diet may vary geographically, and populations of *H. chlorophaea* with a more southerly distribution may feed on invertebrates.

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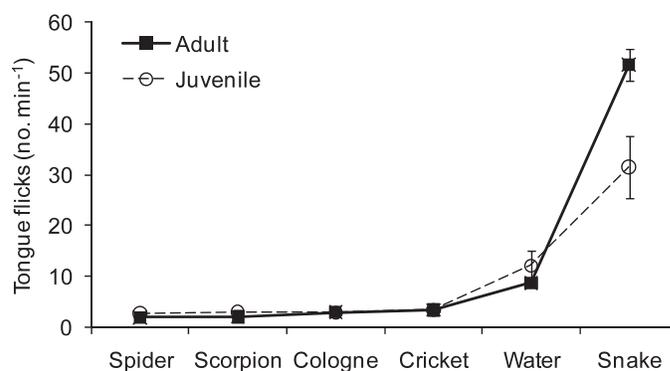


FIG. 2. Rate of tongue flicks/60 sec (mean ± SE) for adult ($N = 21$) and juvenile ($N = 17$) *Hypsiglena chlorophaea* in response to odors of one vertebrate prey (a snake), two control odors (water and cologne), and three potential invertebrate prey odors (cricket, spider, and scorpion).

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