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Diet and Reproductive Ecology of the Desert Nightsnake (*Hypsiglena chlorophaea*) in Central Washington State

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ABSTRACT.—Little is known about many aspects of the ecology of the Desert Nightsnake (*Hypsiglena chlorophaea*). I studied the ecology of *H. chlorophaea* from 121 specimens collected May to October 2004 and 2005 in central Washington State. In this region, males ranged in size from 184–382 mm SVL (283.7 ± 5.8 mm, $N = 49$), whereas females were 158–532 mm SVL (335.5 ± 69.4 mm, $N = 58$). Body mass of males was 2.6–22.1 g (10.2 ± 5.04 mm) and females 2.3–53.9 g (15.1 ± 9.49 mm). In Washington, *H. chlorophaea* feeds on a wide variety of prey such as scincid and anguid lizards, thamnophiine snakes, anurans, and the eggs of other squamate reptiles. In addition, I report the first mammalian prey item taken by *H. chlorophaea*. The reproductive ecology differs little from other parts of the range of *H. chlorophaea*. Males ($N = 22$) with enlarged testes were found from mid-May through late August. Females ($N = 17$) with enlarged follicles and ova were found from May through June, with recent hatchlings collected during mid-August. Based upon these data, in Washington, *H. chlorophaea* has a more varied diet compared to southern populations but shows a similar preference for lizards. With regard to reproductive patterns, Washington populations of *H. chlorophaea* differ very little from other populations.

Much of what is known about the ecology of snakes is based upon studies on medium- to large-bodied species of snakes (Greene, 1997). These species are primarily temperate (Gregory, 1978, 1983; Kephart, 1982; Kephart and Arnold, 1982) and subtropical or tropical species (Luiselli and Angelici, 2000; Luiselli et al., 2000; Madsen and Shine, 2000). In many studies, such species are easily collected in large numbers, either at a given locality or during spring and fall movements from hibernacula (Diller and Wallace, 1984).

Bias in sampling large snake species for ecological studies occurs despite the fact that in some areas, small, cryptic species can be found in abundance. In areas of the Midwestern United States, Ring-Necked Snakes (*Diadophis punctatus*) are extremely abundant (Fitch, 1999). In the southeastern United States small aquatic species, such as Striped Crayfish Snakes (*Regina alleni*) and Black Swampsnakes (*Seminatrix pygaea*), may be collected in large numbers (Godley, 1980; Willson et al., 2008). Other small nocturnal species, such as the Southeastern Crowned Snakes (*Tantilla coronata*) and Eastern Wormsnakes (*Carphophis amoenus*), are broadly distributed and abundant (Willson and Dorcas, 2004; Todd et al., 2008). Alternatively, species like the Rough Greensnake (*Ophedryx aestivus*) are small, diurnal, and readily collected in large numbers (Plummer, 1981, 1985, 1997). These abundant species have formed the basis for extensive ecological studies. However, such examples may be considered the exception, and few studies have been conducted on other similar-sized snakes.

The Desert Nightsnake (*Hypsiglena chlorophaea*) is a small (usually <60 cm TL), secretive little-studied snake. *Hypsiglena chlorophaea* is found from the desert southwest, throughout the intermountain western

United States, and north into the Okanogan Valley of south-central British Columbia (Mulcahy, 2008). Within this 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).

Previous work has considered *H. chlorophaea* a dietary specialist, feeding on primarily sceloporine lizards and squamate eggs (Rodriguez-Robles et al., 1999). *Hypsiglena chlorophaea* possess a Duvernoy's gland (Taub, 1967) and slightly enlarged rear maxillary teeth without grooves (Young and Kardong, 1996). Limited observations suggest that the Duvernoy's secretion of *H. chlorophaea* is effective against small lizards, such as Common Side-Blotched Lizards (*Uta stansburiana*). Captive specimens that have been observed feeding display a slight chewing action after biting prey items (Cowles, 1941; Lewis, 1942), with most small prey dying within 10–15 min.

Reported clutch sizes for *Hypsiglena* spp. range from 2–6, with a mean of 3.2 (Hibbard, 1937; Clark and Lieb, 1973; Diller and Wallace, 1986; Goldberg, 2001). Males undergo spermiogenesis from April to September (Goldberg, 2001). Recorded dates of oviposition are 25 April (Texas), 7 July (Oklahoma), 15 July (Santa Cruz County, Arizona), 28 August (Sonora, Mexico), and 1 September (Maricopa County, Arizona; Fitch, 1970; Clark and Lieb, 1973; Vitt, 1975; Tanner and Otley, 1981).

The purpose of this study was to elucidate variation in diet and patterns of reproduction in *H. chlorophaea*. I compare these data to what is known about the ecology of *H. chlorophaea* from previous studies. Additionally, I compare the ecology of *H. chlorophaea* with what is known about snake ecology in a broader sense.

MATERIALS AND METHODS

Sampling Techniques.—I searched for snakes throughout central Washington State (eight counties: Benton, Chelan, Douglas, Grant, Kittitas, Klickitat,

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Lincoln, and Yakima) from May to October 2004 and 2005. Snakes were collected by slowly driving roads during the early to late evening (1930–2200 h) from May through June (and again in October) and beginning at 2200–2300 h during July through September, usually stopping just before sunrise. Roads were driven every one to two days with an average of 232 km driven each night.

Specimen Data.—I recorded the snout–vent length (SVL), mass, and sex of each snake collected. Using a quick-reading cloacal thermometer, I recorded cloacal temperature readings to nearest 1.0°C for all live snakes. Live specimens were gently palpated for any recently ingested meals, and fecal samples were collected (Fitch, 1987). For some females I was able to palpate their oviducts for follicles or eggs.

Dead-on-road males were examined to assess the extent of testicular development. Males were considered mature if they had enlarged, turgid testes or thickened opaque efferent ducts (Shine, 1977). I calculated individual testis volume using the formula for the volume of an ellipsoid ($V = 4 / 3\pi a^2 b$), where a is one-half the shortest diameter and b is one-half the longest diameter (Ramirez-Bautista and Gutierrez-Mayen, 2003). Dead-on-road females were examined in the lab to assess development of follicles or ova. I counted and measured all follicles that were present in each oviduct to the nearest 1.0 mm. No live females or males were sacrificed to examine for reproductive condition.

Collected snakes were brought into the lab, fixed in 10% buffered formalin, and stored in 70% ethanol. Prey items, whether whole or partially digested, were collected, weighed, measured, and identified to the lowest taxonomic level possible. These were then fixed and stored in the same manner as the snakes. Fecal samples were examined for the remains of bones, osteoderms, scales, or sections of shed skin. These were identified using light microscopy and, when feasible, stored permanently in 10% buffered formalin. Statistics were performed with StatMost 3.0 (StatMost Data Corp., Sandy, UT). Sample sizes (N) are reported as the number of snakes. For all statistical tests (Kruskal-Wallis and Tukey Test), $\alpha = 0.05$, and I report means ± 1 SD.

RESULTS

Population Dynamics.—A total of 121 specimens was collected at 53 localities from eight counties in eastern Washington. Of these 121 specimens, 54 were males and 67 were females. Males were 184–382 mm SVL (283.7 ± 5.8 mm, $N = 54$) and females 158–532 mm SVL (335.5 ± 69.4 mm, $N = 67$). Body mass of males was 2.6–22.1 g (10.2 ± 5.04 mm) and females 2.3–53.9 g (15.1 ± 9.49 mm).

Diet.—Of the 121 specimens of *H. chlorophaea*, 48 (39.6%) contained 48 identifiable prey types or remains thereof. Lizards were the most common prey type found ($N = 31$, 64.5% of the 48 specimens with prey), followed by squamate eggs ($N = 7$, 14.5%), snakes ($N = 6$, 12.5%), anurans ($N = 3$, 6.25%), and mammals ($N = 1$, 2.0%). With regard to specific prey species or items, the Western Skink (*Plestiodon skiltonianus*) was the most abundant species in the diet of *H. chlorophaea* ($N = 21$).

A total of 25 squamate eggs was found in seven snakes (1, 1, 2, 2, 3, 4, and 12 eggs, respectively). All eggs found in one stomach were considered a single prey item consumed during a single feeding event (following Rodriguez-Robles et al., 1999). However, one specimen contained 12 eggs, which may represent more than one clutch of eggs.

Small, fragmented sections of shed skin (each approximately 2.0–3.5 cm in length) from *Thamnophis* spp. were obtained from six different snakes. The distinctive dorsal stripe and heavily keeled scales were evident in all pieces of shed skin. *Elgaria* spp. were identified from partially digested remains in three specimens and by undigested osteoderms collected from two fecal samples. Partially digested remains of the sceloporine lizards, *U. stansburiana*, were found in two specimens and the Western Fence Lizard (*Sceloporus occidentalis*) in three specimens. Northern Pacific Treefrogs (*Pseudacris regilla*) were identified in two specimens.

Additional dietary data are available for two specimens. A female specimen (470 mm SVL, 38.6 g) was collected 7 June 2006 whose fecal sample contained the remains (clumped fur) of an unidentified small mammal. A hatchling specimen (185 mm SVL, 2.1 g) was collected on 28 September 2006 that was in the process of consuming a recently metamorphosed Western Toad (*Anaxyrus boreas*).

There was a significant difference in mean SVL of snakes consuming each prey type (Kruskal-Wallis, $H_6 = 28.3$, $P < 0.01$). The largest specimens of *H. chlorophaea* consumed anurans (422 ± 16.1 mm, range 185–512, $N = 3$), snakes (375 ± 14.2 mm, range 301–482, $N = 6$), and mammals (SVL = 470 mm). Skinks (327 ± 10.2 mm, range 185–462, $N = 21$), anguid lizards (320 ± 12.2 mm, range 242–402, $N = 5$), squamate eggs (304 ± 7.4 mm, range, $N = 7$), and sceloporine lizards (303 ± 8.2 mm, range 212–401, $N = 5$) were taken by smaller snakes. A multiple comparison test (Tukey Test) revealed significant differences in the SVL of *H. chlorophaea* consuming frogs, mammals, and snakes ($Q_6 = 6.34$, $P < 0.01$). There was no difference between those that consumed either lizards or eggs ($Q_6 = 1.03$, $P = 0.23$).

Reproductive Patterns.—Mean clutch size (all follicles > 10 mm) for 17 Washington *H. chlorophaea* was 4.1 ± 1.15 follicles (range 2–6). There was a significant difference observed in follicular size among all months ($H_4 = 18.5$, $P < 0.01$). Follicular size was greatest during May (16.1 ± 3.91 mm, range 12–21, $N = 16$), followed by June (mean = 12.8 ± 4.45 mm, range = 8–20, $N = 6$), July (5.1 ± 5.35 mm, range 1–18, $N = 18$), September (3.07 ± 1.49 mm, range 1–6, $N = 14$), and August ($1.6 \pm .0744$ mm, range 1–3, $N = 8$). Two specimens collected 21 May and 23 May (450 mm and 410 mm SVL, respectively) contained the largest ova of all specimens examined (21.5 and 19.8 mm). Post hoc analysis showed these differences were greatest for the months of May, June, and August ($Q_4 = 7.04$, 6.81, and 5.88, $P < 0.05$) and all other months. There was no difference between July and September ($Q_4 = 1.02$, $P = 0.66$).

Twenty-two dead males were examined for testicular development. Males with enlarged, turgid testes were collected from May to August. Testis volume did not vary significantly throughout the season, from

May through August ($H_3 = 2.3$, $P = 0.24$). Testis volume showed a slight increase from May ($12.7 \pm 1.4 \text{ mm}^3$, range 11.6–14.3, $N = 40$ to June ($13.2 \pm 4.9 \text{ mm}^3$, range 6.3–18.6, $N = 4$) and then decreased during July ($12.7 \pm 6.1 \text{ mm}^3$, range 2.5–19.7, $N = 6$) and August ($11.9 \pm 7.9 \text{ mm}^3$, range 3.83–19.7, $N = 8$).

DISCUSSION

Diet.—In general, these data support prior studies that showed *H. chlorophaea* to feed primarily on lizards and the eggs of squamate reptiles (Cowles, 1941; Diller and Wallace, 1986; Rodriguez-Robles et al., 1999). The occurrence of *A. boreas*, *Thamnophis* spp., and an unidentified small mammal in the diet of Washington *H. chlorophaea* represent the first report of such prey items consumed by *Hypsiglena* spp. Skinks were the sole prey item consumed by *H. chlorophaea* at one locality, which implies that *H. chlorophaea* may specialize on particular prey taxa within parts of its distribution. The likelihood of *P. skiltonianus* contributing to the diet of *H. chlorophaea* was first hypothesized by Lacey et al. (1996) and the lack of skinks in the diet of *H. chlorophaea* elsewhere in its range is puzzling. Skinks are very abundant in habitats occupied by *H. chlorophaea* and are certainly a suitable prey item. Of all the prey items reported here, anguid lizards seem the most unlikely prey. As adults such lizards are generally bulky, aggressive, and have unique antipredator behaviors (e.g., preventing ingestion by grasping their tail). I was unable estimate the size of the Alligator Lizards consumed.

Anurans are suitable prey for *H. chlorophaea*, and the consumption of *Pseudacris* and *Anaxyrus* is not surprising and represents the more ancestral and predominantly anuran diet preferred within the clade of snakes to which *H. chlorophaea* belongs (Mulcahy, 2007). Given the high relative abundance throughout the region where this study was conducted, *P. regilla* may be more common in the diet of *H. chlorophaea* than reported here. The techniques of collecting fecal remains or examining stomach contents may insufficiently sample amphibian remains. Anuran prey items lack diagnosable osteoderms or scales that may be easily recovered from such samples. This problem of documenting soft-bodied prey through collection of fecal samples has been reported in other studies on squamates (Pincheira-Donoso, 2008).

Considering the wide habitat preference, and multiple prey taken across those habitats, this study has shown that *H. chlorophaea* is a generalist in terms of diet. Other species of snakes, such as Terrestrial Gartersnakes (*Thamnophis elegans*) and Gophersnakes (*Pituophis catenifer*), are considered dietary generalists, whereas in some parts of these species' wide geographic distributions, they feed on a limited number of prey species (Kephart, 1982; Kephart and Arnold, 1982; Rodriguez-Robles, 2002). Thus, it is not surprising that species such as *H. chlorophaea* with wide distribution follows a similar pattern.

Reproductive Patterns.—Mean clutch size for Washington *H. chlorophaea* fall within the range previously reported for *Hypsiglena* spp. (Clark and Lieb, 1973; Vitt, 1975; Diller and Wallace, 1986; Goldberg, 2001). Female *H. chlorophaea* exhibit a prenuptial or type I secondary vitellogenic pattern (Aldridge, 1979) characterized by immediate follicular development fol-

lowing emergence from hibernation. However, because two females collected in September contained somewhat enlarged previtellogenic follicles, a postnuptial, or type II breeding pattern cannot be ruled out. Such a pattern is characterized by fall enlargement of follicles and winter atresia, with spring completion of follicular development. Given the possible appearance of both patterns of reproduction in some female *H. chlorophaea*, factors other than season may be responsible for triggering reproductive development in females. Similar to many other species of snakes, coelomic fat reserves (Blem, 1982; Plummer, 1983; Aldridge et al., 2003), precipitation patterns (Vitt and Vangilder, 1983), food availability (Aldridge, 1979; Blem, 1982), and temperature regimes may all play important roles in the reproductive ecology of *H. chlorophaea*. The overall low frequency of reproductive females ($N = 17$, 37.7% of all females) may indicate a triennial breeding cycle for *H. chlorophaea*. Other genera of similar-sized temperate snakes show higher overall rates of gravid females ranging from 70–100% (Clark, 1970, 1974; Semlitsch and Moran, 1984).

The time period for egg laying for female *H. chlorophaea* observed within the temporal framework of this study is from mid-June to early July. During a study in southwestern Idaho, a gravid female weighing 48 g was captured on 10 June. This specimen weighed 41 g when recaptured on 6 July and was presumed to have oviposited between captures (Diller and Wallace, 1986), indicating a gestation period close to 30 days. These dates suggest that two female specimens (488 and 463 mm SVL) captured on 21 and 23 May 2004 and a smaller female (380 mm) captured on 15 June were likely three to four weeks away from ovipositing (middle to end of June and early July). Incubation times for *Hypsiglena* spp. are known from clutches laid by one Oklahoma specimen and two Texas specimens (Werler, 1951). These clutches of three, three, and four eggs had an average incubation time of 58.3 days (54, 59, and 62 days, respectively). If *H. chlorophaea* in Washington oviposit from mid-June into July, hatching specimens could be collected as early as mid-August, and indeed this appears to be the case. Five hatchling specimens with average SVL of 176.4 mm were collected at different locations from 13 August through 19 August 2004. Each of these specimens retained a yolk-sac scar, indicating recent hatching.

There appears to be no peak in testicular development in *H. chlorophaea* collected during this study. However, a lack of samples from April and September may obscure noticeable trends. In Idaho, male *H. chlorophaea* did show peak testes development during June and July (Diller and Wallace, 1986), which corresponded to an increase in the size of the proximal sexual segment of the kidney (not measured in this study). Similar to this study, Arizona males were found to be undergoing spermiogenesis throughout the active season from April through September (Goldberg, 2001).

If male *H. chlorophaea* in Washington are undergoing spermiogenesis throughout the active season it may not be possible to classify them as either prenuptial/spring breeders (Shine, 1977; Saint-Girons, 1982) or postnuptial/fall breeders (Saint Girons, 1982). It appears the cycle is closer to aseasonal cycles displayed by several species of tropical colubrid

snakes (Fitch, 1970; Vitt and Vangilder, 1983), where males are ready to breed year-round.

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