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ACTIVITY PATTERNS OF THE DESERT NIGHTSNAKE (*HYP SIGLENA CHLOROPHAEA*)

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ABSTRACT—Data on activity patterns of the desert nightsnake (*Hypsiglena chlorophaea*) were obtained from 121 specimens. *Hypsiglena chlorophaea* was active on roads in central Washington during April–October. Specimens were collected at temperatures of 9.1–40.8°C. Males were collected more frequently than females during May, but in equal numbers during June and July, while more females were found in August–September. Hatchling snakes were collected in July–September. *Hypsiglena chlorophaea* was active 2100–0500 h. Snakes were collected more often during periods of low moon-light (e.g., new moon) than high moon-light (e.g., full moon).

RESUMEN—Se colectaron datos sobre patrones de actividad para 121 especímenes de la culebra nocturna (*Hypsiglena chlorophaea*). *Hypsiglena chlorophaea* estuvo activa en los caminos en el centro del estado de Washington durante abril–octubre. Especímenes fueron recolectados entre temperaturas de 9.1–40.8°C. En mayo se capturaron más machos que hembras, pero en proporciones equivalentes durante junio y julio, y más hembras en agosto y septiembre. Recién nacidos fueron recolectados desde julio hasta septiembre. *Hypsiglena chlorophaea* estuvo activa entre las 2100–0500 h. Las culebras se capturaron más frecuentemente durante periodos de baja iluminación lunar (por ejemplo, luna nueva) que durante alta iluminación lunar (por ejemplo, luna llena).

What is known about activity patterns of snakes is based primarily upon studies of diurnal, medium-to-large bodied colubrids (Gregory, 1984; Gregory and Nelson, 2002; Krysko, 2002; Bell et al., 2007) or viperids (Gannon and Secoy, 1985; Beverlander et al., 2006; Marshall et al., 2006), and recently on tropical and sub-tropical species of snakes (Marques et al., 2001; Brown and Shine, 2002). Those studies describing activity of small, cryptic species have been conducted in a small portion of the southeastern United States (Willson and Dorcas, 2004; Todd et al., 2008a, 2008b). This has resulted in large gaps in knowledge of activity patterns and levels of activity in many other species of snakes. This is especially true for the many small-bodied and secretive species of snakes broadly distributed in the western United States (Stebbins, 2003).

The desert nightsnake (*Hypsiglena chlorophaea*) is a small (usually <60 cm in total length), secretive, nocturnal, and little-studied snake that is distributed from the desert Southwest and intermountain western United States northward into the Okanagan Valley of south-central British

Columbia (Mulcahy, 2008). *Hypsiglena chlorophaea* is a relatively common species in many parts of the Southwest (Wright and Wright, 1957; Williamson et al., 1994; Werler and Dixon, 2000). However, the secretive nature of *H. chlorophaea* usually means it is not encountered often, leading to just one field-based ecological study (Diller and Wallace, 1986); consequently, little is known about many aspects of the ecology of this species.

The northern one-half of the range of *H. chlorophaea* encompasses southern Idaho, eastern Oregon, and central Washington (Nussbaum et al., 1983), where it occurs in a variety of habitats, including shrub-steppe dominated by big sagebrush (*Artemisia tridentata*), Oregon white oak (*Quercus garryana*) savannah, and Douglas-fir (*Pseudotsuga meinziesii*) and ponderosa pine (*Pinus ponderosa*) forests (Diller, 1995; St. John, 2002). *Hypsiglena chlorophaea* feeds primarily on sceloporine lizards and squamate eggs (Rodríguez-Robles et al., 1999). *Hypsiglena chlorophaea* possesses a small Duvernoy's gland (Taub, 1967) and slightly enlarged rear maxillary teeth that do

not possess grooves (Young and Kardong, 1996). Anecdotal evidence (Cowles, 1941; Lewis, 1942), has suggested that secretions of the Duvernoy's gland are effective against small lizards, such as common side-blotched lizards (*Uta stansburiana*). Biochemical analysis of secretions of the Duvernoy's gland has shown it to have enzymatic properties that result in edema and hemorrhaging in prey (Vest, 1988; Hill and Mackessey, 2000). While largely nocturnal, limited observations suggest *H. chlorophaea* may occasionally forage during the day (Woodbury, 1931; Rodriguez-Robles et al., 1999; Grimser, 2002).

Objectives of my study were to elucidate monthly and diel activity patterns of *H. chlorophaea*. I sought to describe activity patterns with regard to sex, lunar phase, and temperature. Data gathered on activity patterns of *H. chlorophaea* are of importance because of potential application to management techniques that involve surveying for small, secretive species of snakes similar to *H. chlorophaea*.

MATERIALS AND METHODS—Searches were conducted March–November 2004 and 2005 by driving (30–35 km/h) equal amounts each hour and month along selected paved roads at 2000–0600 h in eight counties in central Washington. These roads were selected because they passed through appropriate habitat and traffic levels generally were low (50–100 vehicles/day; Weaver, 2008). Roads were driven every 2 days with an average of 232 km (range = 85–305 km) driven each night. Total distance driven each month was divided into 100-km transects.

Snout–vent length to the nearest 1 mm, mass to the nearest 0.1 g, and sex of each snake were recorded. Using published data (Diller and Wallace, 1986; Goldberg, 2001), snakes were categorized as adult males or females, juveniles (captured in spring, <20-cm snout–vent length), and hatchlings (captured in late-summer and autumn with visible yolk-sac scar). Upon capture, cloacal temperatures were recorded with a Schulteis quick-reading thermometer (Model T-4000, Miller and Weber, Queens, New York). All snakes that were dead on the road were collected, fixed in 10% buffered formalin and stored in 70% ethanol.

Month, day, and time for each observation of live snakes on roads were recorded. Using a digital thermocouple (Atkins Electronics, Newark, New Jersey), ground and air temperatures (1 m above the ground) were recorded to the nearest 0.1°C. Collection locations were recorded with a hand-held global positioning system unit (Garmin, Garmin International Inc., Olathe, Kansas). In addition, phases of the moon (when it was above the horizon) for each night of surveying were recorded. Phases of the moon were grouped into low or no moonlight (≤ 0.05 lux) or bright (≥ 2.10 lux). Intensity of moonlight was measured (to the nearest 0.01 lux) in the field using a

hand-held light meter (Gossen Luna-Pro, Numberg, Germany).

Chi-square tests of independence were used to compare monthly frequency of snakes, activity during lunar phases, diel activity, and sex ratio. A non-parametric Kruskal-Wallis test was used to compare mean cloacal, ground, and air temperatures. For all statistical tests, $\alpha = 0.05$.

RESULTS—While driving ca. 24,800 km in 180 days, I observed 121 *H. chlorophaea* (74 alive on the road and 47 dead on the road). There was a significant difference across months in number of specimens ($\chi^2 = 74.56$, $df = 4$, $P < 0.05$), with most snakes observed during late-May–September. Surface activity peaked during June ($n = 24$, 19% of specimens), July ($n = 34$, 28% of specimens), and August ($n = 30$, 24% of specimens). Numbers of specimens were lower in September ($n = 14$, 11.5% of specimens) and May ($n = 17$, 14% of specimens). Number of snakes/100-km transect was lowest during May, September (0.80 specimens each), and June (1.00 specimens). Highest numbers were 1.2 and 1.4 specimens in August and July. Only one snake was observed during April and October. No snake was observed during March or November (Fig. 1).

Hypsiglena chlorophaea was on the surface during 2100–0500 h. There was a significant difference in number of snakes across these 1-h blocks ($\chi^2 = 34.52$, $df = 3$, $P < 0.05$). Highest numbers within a given 1-h block were 0100–0200 h ($n = 32$, 0.64 specimens/100 km) and 0200–0300 h ($n = 20$, 0.51 specimens/100 km). Only 10 specimens were observed before 2300 h (0.09 specimens/100 km) and 4 specimens after 0300 h (0.09 specimens/100 km). No snake was observed before 2100 h or after 0500 h (Fig. 2).

During June–August, *H. chlorophaea* was active at a mean air temperature of 22.9°C (range = 9.1–40.8°C, ± 5.16 SD). Substrate temperatures recorded at these air temperatures had similar values, with a mean of 24.9°C (range = 15.5–36.4°C, ± 4.69 SD). Mean cloacal temperature of 62 specimens was 33.2°C (range = 23.5–38.6°C, ± 1.98 SD). Variation in monthly cloacal temperature increased steadily from June (mean = 28.6°C, range = 23.5–32.3°C, ± 3.71 SD) to July (mean = 30.8°C, range = 25.7–36.2°C, ± 3.54 SD) and August (mean = 32.4°C, range = 28.6–38.6°C, ± 2.78 SD). There was a significant difference between mean cloacal temperatures of snakes and both air and substrate tempera-

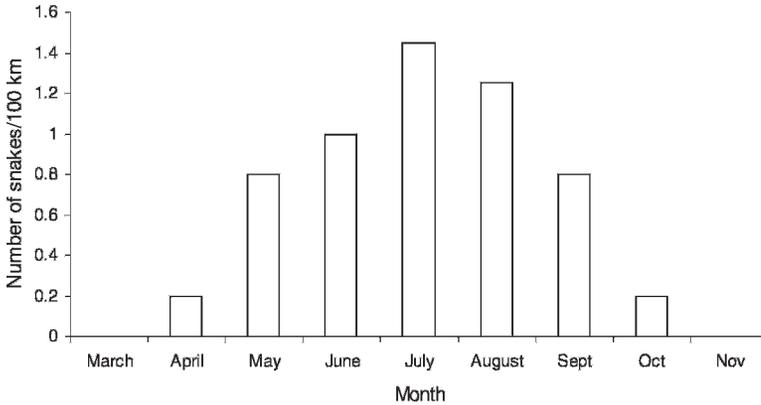


FIG. 1.—Monthly activity patterns of the desert nightsnake (*Hypsiglena chlorophaea*) in central Washington, May–October 2004 and 2005 ($n = 121$).

tures (Kruskal-Wallis, $H = 21.34$, $df = 2$, $P < 0.05$). While 31 specimens were collected May–September, data on temperature for this period were not available.

There was no significant difference between monthly observations of adult males or females ($\chi^2 = 3.02$, $df = 5$, $P > 0.05$). Adult males were observed more often than adult females during April and May, with females observed more often during August and September. Sexes were found in equal numbers during June and July. From late July ($n = 4$), through August ($n = 8$), and into early September ($n = 2$, Fig. 3), 17 hatchlings were observed.

Lunar phase was recorded upon capture of 105 *H. chlorophaea*. There was a significant difference between number of snakes observed during periods of low or bright moonlight ($\chi^2 = 112.23$, $df = 1$, $P < 0.05$). Between the last one-

quarter and first one-quarter lunar phase (low moonlight), 71 specimens (67%, 1.4 specimens/100 km driven) were observed. Between a first one-quarter and last one-quarter lunar phase (bright moonlight), 34 specimens (33%, 0.30 specimens/100 km driven) were observed.

DISCUSSION—*Monthly Activity*—Throughout its range, *H. chlorophaea* is most active April–October (Klauber, 1931; Woodbury, 1931; Anderson, 1940; Lewis, 1942). It has been collected in November in the Mojave Desert (Pickwell, 1947) and year-round in southern California (Klauber, 1939). In southwestern Idaho, desert nightsnakes were collected from late April into early September, with a peak in occurrence during June (Diller and Wallace, 1986). In Washington, *H. chlorophaea* appears to differ little from these overall trends, with desert

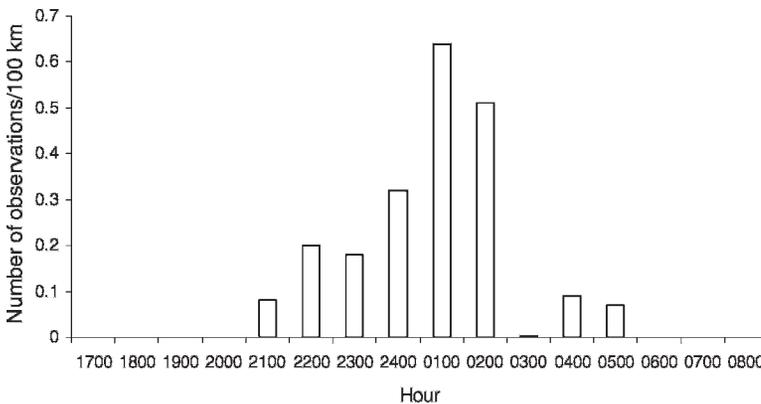


FIG. 2.—Diel activity patterns for alive-on-road desert nightsnakes (*Hypsiglena chlorophaea*) in central Washington, May–October 2004 and 2005 ($n = 66$).

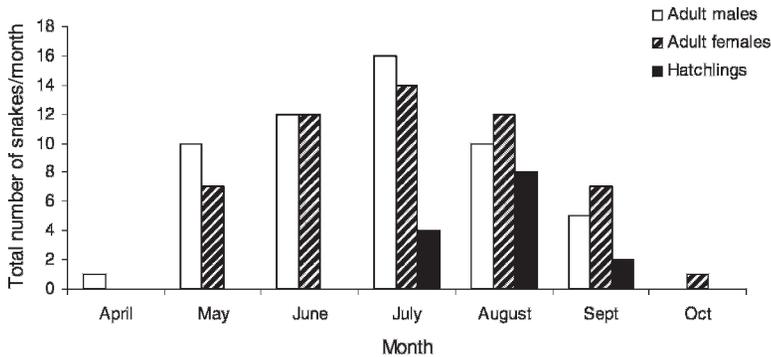


FIG. 3—Monthly activity for three classes of the desert nightsnake (*Hypsiglena chlorophaea*) in central Washington, May–October 2004 and 2005 (adult males, $n = 58$, adult females, $n = 45$, and juveniles, $n = 14$).

nightsnakes observed late April–early October. This strong unimodal pattern of occurrence (a peak during June and July) observed during my study makes *H. chlorophaea* different from the more typical bimodal (high number of observations in spring and autumn) recorded for larger-bodied, temperate species of colubrid snakes (Oliver, 1955), such as racers (*Coluber constrictor*), hognose snakes (*Heterodon*), and ratsnakes (*Pantherophis*). However, monthly activity patterns of *H. torquata* are similar to some small-bodied snakes, such as southeastern crowned snakes (*Tantilla coronata*; Todd et al., 2008b). Data from other studies indicate that activity of *H. torquata* differs from species such as earth snakes (*Virginia striatula* and *V. valeriae*), eastern worm snakes (*Carphophis amoenus*), ring-necked snakes (*Diadophis punctatus*), and red-bellied snakes (*Storeria occipitomaculata*), with such species observed more frequently during autumn (Willson and Dorcas, 2004; Todd et al., 2008a).

Diel Activity—Little is known with regard to diel activity patterns in *H. chlorophaea*. What has been recorded is anecdotal or based on the work of Klauber (1939). Klauber recorded *H. chlorophaea* active on the surface in southern California during 1900–2400 h. Other recorded times of activity for *H. chlorophaea* include 1600 h (Utah; Woodbury, 1931), 1845 h (Arizona; Brennan, 2004), 1410 h (Baja California Sur; Rodriguez-Robles et al., 1999), and 1500 h (California; Rodriguez-Robles et al., 1999).

In Washington, *H. chlorophaea* appears to have a broad range of diel activity with records during 2100–0500 h. Because little is known about daily activity patterns in *H. chlorophaea* in the Southwest and throughout its range, it is difficult to

make comparisons to other populations. However, in Washington, *H. chlorophaea* primarily is nocturnal with 120 of 121 (99%) individuals observed at night. The rare occurrence of diurnal activity appears to coincide with foraging behavior, as all but one of the cases reported in the literature involved snakes capturing or consuming prey. It has been hypothesized (Rodriguez-Robles et al., 1999) that diurnal foraging behavior in *H. chlorophaea* is a derived trait, and that this behavior allowed it to expand its range into much of western North America. Rodriguez-Robles et al. (1999) also suggested that in the northern extent of its range, temperatures at night may be too low to allow for nocturnal foraging behavior; however, my study indicates otherwise.

Current research has shown *H. chlorophaea* to be entirely nocturnal with regards to activity patterns. Activity is correlated strongly with foraging behavior. Desert nightsnakes selected shelters near odors of prey, such as western fence lizards (*Sceloporus occidentalis*) and terrestrial gartersnakes (*Thamnophis elegans*), and actively forage for potential prey near such shelters. Additional observations have shown that snakes capture both diurnally and nocturnally active prey at such shelter sites (R. E. Weaver and K. V. Kardong, unpublished data).

Relationship of Temperature to Activity Patterns—Detailed studies on thermal ecology of snakes have dealt almost entirely with diurnal snakes such as *Thamnophis* (Scott, 1978; Peterson, 1982; Stevenson, 1983; Gregory, 1990), *Coluber*, and *Masticophis* (Hammerson, 1979), or are based on studies of colubrid or viperid taxa (Jacob and Painter, 1980; Sanders and Jacob, 1981; Graves

and Duvall, 1987; Goode and Duvall, 1989). Other than research on elapids in southeastern Australia (Webb and Shine, 1998; Webb et al., 2004), research on thermal ecology of small, primarily nocturnal snakes is limited.

Recorded body temperatures of individual *H. chlorophaea* are known from only four specimens (prior to my study). Temperatures of one snake in a refugium during February was 5.4°C (Cunningham, 1966), while recorded body temperatures for three snakes collected in May were 30.2, 31.2, and 27.0°C (Brattstrom, 1965). Mean body temperature of 33.2°C for *H. chlorophaea* ($n = 62$) in Washington is within the range of what is considered normal for snakes and squamate reptiles as a group (Porter, 1967; Huey and Bennett, 1987; Peterson et al., 1993; Beck, 2004). However, such values are based upon studies that dealt with entirely diurnal squamates, such as various genera of desert lizards, or are from snakes that mostly are diurnal.

What is known about the typical thermoregulatory pattern of largely diurnal snakes such as *Thamnophis* may not apply to *H. chlorophaea*. The behavioral pattern of diurnal snakes involves emergence on a warm spring morning from cold refugia to begin thermoregulation until an optimal body temperature is reached (Peterson, 1982). *Hyspilgena chlorophaeta* is a snake that hides by day and emerges on many occasions on cool nights to forage. In terms of its behavioral thermoregulation, *H. chlorophaea* is the opposite of a diurnal snake. Several *H. chlorophaea* were captured on cool nights (<15°C) with cloacal temperatures 10–15°C higher than air temperature. These body temperatures indicate that such snakes had emerged recently from warm refugia and had likely just begun moving across the surface.

Reverse thermoregulatory patterns in nocturnal snakes have been recorded in a small temperate boid, the rubber boa (*Charina bottae*), and in a nocturnal elapid from southeastern Australia, the broad-headed snake (*Hoplocephalus bungaroides*). Radiotelemetry conducted on *C. bottae* in southeastern Idaho showed that it sought warm refugia by day and emerged with high body temperatures on cool nights to forage for prey. These snakes returned in the morning to bask secluded in a refugium that was warmer than ambient air temperature (Peterson et al., 2002). In Australia, radiotelemetry revealed that

H. bungaroides actively seeks rocks that retain heat in a manner that allows snakes to reach optimal body temperatures just before onset of activity (Webb and Shine, 1998). There is a lack of radiotelemetry data for *H. chlorophaea*, but data on body temperature gathered during my study are suggestive of similar behavioral patterns.

Other predominantly nocturnal colubrid snakes, such as glossy snakes (*Arizona elegans*), long-nosed snakes (*Rhinocelchus lecontei*), and lyresnakes (*Trimorphodon*) have been observed actively moving on the surface under cold, windy conditions. Research conducted by Klauber (1928, 1931, 1939, 1941) in southern California showed these species commonly were encountered crossing roads at night (after 2400 h) at air temperatures of 15–20°C. However, it is not known if these snakes behave in a manner similar to that I propose for *H. chlorophaea*.

Lunar Phase—The common conjecture that nocturnal snakes such as *H. chlorophaea* are less active during periods of bright moonlight was first proposed by Klauber (1939). However, few quantitative data exist to support this hypothesis. In a study conducted on captive prairie rattlesnakes (*Crotalus viridis*), Mackessey et al. (1996) reported that adult snakes were less active during one-half, three-quarter (waxing gibbous), and full moon, while juveniles showed no behavior to avoid moonlight. At Lake Tanganyika in Africa, a higher percentage of fish-eating snakes (*Lycodon-tomorphus bicolor*) contained prey during periods of low-to-no moonlight (last one-quarter and new moon), indicating increased activity during this time (Madsen and Osterkamp, 1982). Experiments with the brown tree snake (*Boiga irregularis*) demonstrated avoidance of open areas and increased use of refugia during periods of a simulated full moon (Campbell et al., 2008).

During my study, *H. chlorophaea* was observed more often during periods of dim-to-no moonlight than bright moonlight. This is suggestive of an avoidance of open spaces (e.g., paved roads) during bright conditions similar to the pattern shown by *B. irregularis* and adult *C. viridis*. This pattern may suggest predator-avoidance behavior.

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