Feeding Ecology of the Desert Nightsnake,
Hypsiglena torquata (Colubridae)

JAVIER A. RODRÍGUEZ-ROBLES, DANIEL G. MULCAHY, AND HARRY W. GREENE

We studied the diet of the North American desert nightsnake, *Hypsiglena torquata*, based on the stomach contents of 397 museum specimens, field observations, and published dietary records. Based on 92 prey from throughout much of its distribution, *H. torquata*, feeds mainly on sceloporine lizards and squamate eggs and occasionally eats frogs, snakes, insects, and amphisbaenians. Lizards are typically swallowed head- first, whereas frogs are swallowed from the rump. Prey mass increases with snake mass and prey/predator mass ratios range from 0.03 to at least 0.50. Three genera of abundant lizards (*Cnemidophorus*, *Coleonyx*, *Xantusia*) are infrequently eaten, which suggests that these lizards chemosensorily avoid desert nightsnakes. *Hypsiglena* arose within a Neotropical clade of predominantly nocturnal, frog-eating snakes, and its occupancy of arid western North America correlates with two derived feeding traits: at least occasional ambush predation on diurnal lizards, and inclusion of squamate eggs in its diet.

D IET and foraging tactics are among the central concerns of modern behavioral ecology (Krebs and Davies, 1997) and are relevant to an understanding of habitat use (Reinert et al., 1984; Chandler and Tolson, 1990; Henderson, 1993), movement and activity patterns (Secor, 1995; Madsen and Shine, 1996), life-history evolution (Shine and Slip, 1990; Shine, 1996), and patterns of community structure (Vitt, 1983; Cadle and Greene, 1993; Rodríguez-Robles and Greene, 1996). Moreover, with information on the phylogenetic relationships of a species and its close relatives, feeding biology can be placed in a historical framework and thereby help us to elucidate evolutionary divergence within a lineage (Brooks and McLennan, 1991; Larson and Losos, 1996).

Hypsiglena torquata, the desert nightsnake, belongs to a predominantly Central American clade of dipsadine colubrids (Cadle, 1984; Dowling and Jenner, 1987). Desert nightsnakes are found from southwestern Canada through much of the western United States to Baja California and the Mexican state of Guerrero (Tanner, 1944; Dixon and Dean, 1986; for taxonomic comments, see Results), occur in a wide variety of habitats, including grassland, chaparral, sagebrush flats, deserts, woodland, and mountain meadows, and are found from sea level to approximately 2700 m (Bogert and Oliver, 1945; Hardy and McDiarmid, 1969; Degenhardt et al., 1996). Although commonly mentioned as predators on lizards, small snakes, and frogs (e.g., Collins, 1993; Degenhardt et al., 1996), the diet of desert nightsnakes has been previously studied in any detail only in southwestern Idaho (Diller and Wallace, 1986). Thus, as part of our

ongoing analyses of the feeding ecology of several snake species in western North America, we herein describe the food habits of *H. torquata*. Our study is based on stomach contents of museum specimens from throughout much of the geographic range of the species, fortuitous field observations, and judicious use of literature records. Our goals are to evaluate variation in taxonomic composition of the diet, predator/prey size relationships, foraging tactics, and the evolutionary significance of feeding biology in *H. torquata*.

MATERIALS AND METHODS

We examined 178 and 219 specimens of *H. torquata* in the California Academy of Sciences, San Francisco (CAS) and the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), respectively. We checked for stomach contents by making a midventral incision in all specimens, avoiding only type specimens and fragile individuals. Whenever possible, for each snake with prey, we recorded locality data, snout–vent length (SVL ± 1 cm), body mass (± 0.1 g), and minimum number of items in the stomach. All squamate eggs in a single stomach were counted as one item because they may represent a feeding event at the same site and because sometimes their exact number was impossible to determine. Direction of ingestion (inferred from orientation in the stomach) was recorded to the extent possible. We weighed snakes and their intact or slightly digested prey after blotting and draining them briefly on paper towels to remove excess fluid. Weights and linear measurements of partially digested items

were estimated by comparison with complete preserved specimens in the MVZ of conspecifics of similar size from the nearest locality available. We excluded specimens that we suspected were fed in captivity before being preserved (e.g., MVZ 94798). Our dataset also incorporates published and unpublished dietary records of *H. torquata* (Appendix). We took care to account for redundancy among literature records (e.g., Tanner, 1929 with Tanner, 1944), and between museum specimens and literature records (e.g., CAS 150090 with Papenfuss, 1982). Values given are means ± 1 SD, and *P*-values are two-tailed. Significance level for all tests was determined at alpha ≤ 0.05.

RESULTS

Forty-eight *H. torquata* (SVL = 27.3 ± 5.5 cm, range = 15.2–39.4 cm, n = 47; body mass = 9.4 ± 4.6 g, range = 1.8–19.7 g, n = 48), 12.1% of all specimens examined, contained at least partly identifiable prey items. Including 39 literature records (from 37 snakes), three unpublished observations (R. Bello, B. Dial, and R. Reiserer, pers. comm.), and one witnessed predatory event in the field, 48 (52.2%) of 92 prey eaten by *H. torquata* were "lizards" (i.e., squamate reptiles other than snakes or amphisbaenians), 21 (22.8%) were squamate eggs, 11 (12.0%) were frogs, six (6.5%) were snakes, three (3.3%) were insects, one (1.1%) was an amphisbaenian, and two (2.2%) were unidentified animals (Appendix; the high number of unidentified lizards is the result of stomach contents that consisted exclusively of a few scales). Published dietary records for which we could not determine their frequency of consumption by *H. torquata* included scorpions (Cowles, 1941), *Batrachoseps* sp. (slender salamanders), *Bufo* sp. (true toads), *Elgaria multicarinata* (southern alligator lizard), *Coleonyx variegatus* (western banded gecko), *Dipsosaurus dorsalis* (desert iguana), and *Uta stansburiana* (side-blotched lizard; Stebbins, 1954; Tanner, 1981). How many species *Hypsiglena* comprises has long been controversial (e.g., Tanner, 1944; Bogert and Oliver, 1945), but the genus includes at least *H. tanzeri* and *H. torquata* (Dixon and Lieb, 1972; Dixon and Dean, 1986). Should further studies confirm the existence of a third species (*H. ochrorhyncha*) within the range of what is presently considered *H. torquata*, most of our dietary records (81 of 83, 97.6%) would belong to *H. ochrorhyncha*. In any case, we discovered no evidence of geographic variation in the diet of *H. torquata* [our records are from British Columbia, Canada (1); Arizona (4), Cal-
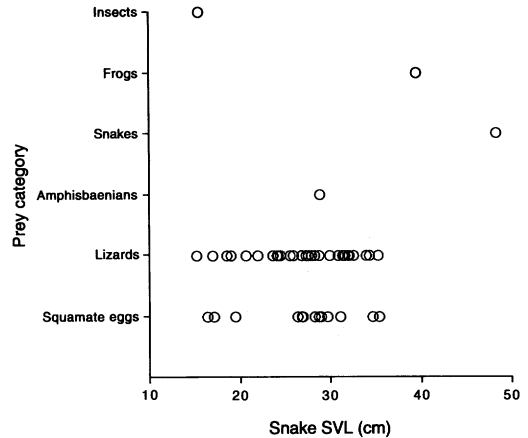

Fig. 1. Relationship between prey category (i.e., insects, frogs, amphisbaenians, snakes, lizards, and squamate eggs) and snake body size (SVL) in *Hypsiglena torquata* (n = 50).

ifornia (21), Colorado (2), Idaho (13), Nevada (4), New Mexico (1), Oklahoma (1), Texas (7), and Utah (5) in the United States; and from Baja California (18) and elsewhere in Mexico (8)].

Excluding the 21 snakes that had ingested squamate eggs as their only prey, 63 of 66 (95.5%) *H. torquata* with food contained a single prey, whereas one snake ingested two *Bufo alvarius* (Sonoran desert toads; Bogert and Oliver, 1945), another ate two *Spea hammondii* (western spadefoots; Woodin, 1953), and a third (CAS 198450) ate three *Pseudacris* sp. (chorus frogs). Assuming that the three *Pseudacris* represent three independent observations of direction of ingestion of prey, desert nightsnakes swallow squamates head-first with a higher frequency than they do frogs (23 vs three, zero vs three, respectively; Fisher's exact test, *P* = 0.005).

Hypsiglena torquata of all sizes feed on lizards and squamate eggs, whereas it seems that smaller snakes rarely also take insects, and larger ones occasionally eat amphisbaenians, frogs, and snakes (Fig. 1). Additional records of insects, amphisbaenians, frogs, and snakes in the diet of *H. torquata* are needed to assess the generality of these findings. There were no significant differences in body size between snakes that fed on squamate eggs (SVL = 26.2 ± 5.7 cm, range = 16.3–35.3 cm, n = 12) and those that ate lizards (SVL = 27.4 ± 5.4 cm, range = 15.2–35.2 cm, n = 34; ANOVA, F = 0.43, df = 1,44, *P* = 0.52).

We have reliable estimates of prey mass for nine items: one coleopteran larva, three *Pseudacris* sp. (combined), two *Xantusia vigilis* (de-
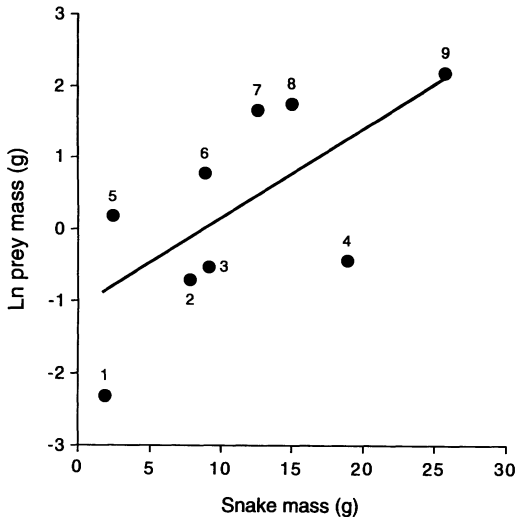
Fig. 2. (Ln-transformed) prey mass as a function of snake mass in *Hypsiglena torquata* (adjusted r^2 = 0.35, F = 5.34, df = 1,7, P = 0.05). Numbers next to the data points identify the prey: 1 = coleopteran larva, 2,5 = *Xantusia vigilis*, 3 = *Uta stansburiana*, 4 = three *Pseudacris* sp. (combined), 6 = *Bipes biporus*, 7 = *Sceloporus graciosus*, 8 = *Cnemidophorus tigris*, 9 = *Crotalus viridis*.

sert night lizard), and one each *Bipes biporus* (mole lizard), *Sceloporus graciosus* (sagebrush lizard), *Uta stansburiana*, *Cnemidophorus tigris* (western whip-tailed lizard), and *Crotalus viridis* (western rattlesnake). Larger desert nightsnakes fed on larger prey (Fig. 2), and relative prey mass (prey mass/snake mass) ranged from 0.03–0.50, with a mean = 0.24 ± 0.19. The relatively largest item was a 1.2 g *X. vigilis* in a 2.4 g *H. torquata*, although a juvenile *C. viridis* was estimated to amount to 0.35–0.54 of the mass of the *H. torquata* that contained it (Lacey et al., 1996).

Two incidental field observations document diurnal feeding by desert nightsnakes. On 10 January 1997, at 1410 h on a sunny, warm day on the outskirts of La Paz, Baja California Sur, Mexico, one of us (HWG) found a small *H. torquata* (total length approximately 15 cm) ingesting a juvenile *Cnemidophorus hyperythrus* (orange-throated whip-tailed lizard, SVL approximately 6 cm) under a small board. No burrows were evident, suggesting that the snake was under the board when the active lizard sought shelter and was ambushed. Upon discovery, the *C. hyperythrus* was inert and swallowing had proceeded (head-first) to the base of its forelimbs; approximately 20 min later ingestion had proceeded to the tail (the board was gently replaced after discovery to avoid exposing the snake to bright sunlight; color slides of the in-

cident are on file in the MVZ). On 26 May 1998, at approximately 1500 h on a sunny day at San Onofre State Beach, San Diego County, California, T. J. Papenfuss saw an adult female *Uta stansburiana* run into a burrow (diameter approximately 6 cm), and after about 30 sec, the lizard struggled to emerge. When he pulled the *U. stansburiana* from the burrow, a small *H. torquata* was biting one of the lizard's hind legs.

DISCUSSION

Our study confirms the often stated generality that *H. torquata* eats mainly lizards and demonstrates that it also frequently takes squamate eggs, as well as occasionally anurans, snakes, insects, and amphisbaenians. Desert nightsnakes also eat carrion at least rarely, as demonstrated by a wild specimen from Arizona that ate a *Scaphiopus couchii* (Couch's spadefoot toad) that had been crushed by a car (Kauffeld, 1943). Although at least 16 species of squamate reptiles were eaten throughout *H. torquata*'s geographic range, 27 of 35 (77.1%) lizards taken are diurnally active iguanians that seek shelter in crevices, burrows, and under cover at night.

Certain prey species are surprisingly infrequent or even absent in the diet of *H. torquata*. Although xantusiid lizards are abundant, readily available, and seemingly appropriate prey for *H. torquata* in parts of its range (Zweifel and Lowe, 1966:42), we found only three *Xantusia vigilis* among 17 prey items in snakes from within the range of *X. vigilis*. Eublepharid lizards (*Coleonyx* spp.) are also common and sympatric with desert nightsnakes over most of southwestern North America, but we found only one *C. variegatus* among 44 prey from within the range of that species; perhaps the nearly complete absence of *C. variegatus* in the diet of desert nightsnakes reflects chemosensory detection of and avoidance of *H. torquata* by these geckos (see Dial and Schwenk, 1996). Whip-tailed lizards (*Cnemidophorus*) are abundant over most of the range of desert nightsnakes, but we encountered only four individuals among 82 prey items from within the range of that genus, so perhaps whip-tailed lizards also chemosensorily avoid *H. torquata*.

Mean relative prey mass for *H. torquata* (0.24) is not especially large relative to other snakes [e.g., *Crotalus viridis oreganus* (northern Pacific rattlesnake, 0.40); *Anilius scytale* (red pipesnake, 0.32); *Micrurus fulvius* (harlequin coralsnake, 0.42); Fitch and Twining, 1946; Greene, 1983, 1984], as is the case for some other colubrids [e.g., *Psammodynastes pulverulentus* (Asian mock viper, 0.13); *Boiga irregularis* (brown treesnake,

0.11); *Thelotornis capensis* (savanna twigsnake, 0.19); Greene, 1989a, 1989b; Shine et al., 1996]. *Hypsiglena torquata* swallows squamate reptiles primarily head-first [as do *M. fulvius* and *Ophiophagus hannah* (king cobra); Greene, 1976], whereas frogs are ingested from the rump [as is the case in *Alsophis portoricensis* (Puerto Rican racer); Rodríguez-Robles and Leal, 1993]. Perhaps this behavioral difference reflects the fact that reptile scales provide directional cues for prey ingestion (Greene, 1976), and in their absence desert nightsnakes either ingest their prey from the rear or else by that portion of the body initially grasped (see Cooper, 1981).

The widely used English name for *H. torquata*, desert nightsnake, reflects its vertical pupils and the fact that these snakes often are found crawling in the open at night and under cover by day (e.g., Wright and Wright, 1957; Diller and Wallace, 1986). *Hypsiglena torquata* presumably locates buried squamate eggs by using chemosensory cues while widely foraging (Diller and Wallace, 1986), and desert nightsnakes may also locate inactive diurnal iguanians at night by the same foraging tactic. Diller and Wallace (1986), however, reported four dead *H. torquata* in the nests of diurnally foraging hawks, and our field observation of predation by *H. torquata* (see also Goodman, 1953) demonstrates that desert nightsnakes may ambush active lizards before dusk or even at midday.

Hypsiglena torquata belongs to the "*Leptodeira* clade," a group of predominantly Neotropical dipsadine colubrids that includes *Eridiphas slevini* (the Baja California nightsnake), *Pseudoleptodeira latifasciata* (the banded nightsnake), *Cryophis hallbergi* (the cloud forest snake), six species of *Imantodes* (blunt-headed vinesnakes), and eight species of *Leptodeira* (cat-eyed snakes; Bogert and Duellman, 1963; Tanner, 1966; Cadle, 1984; Fig. 3). Desert nightsnakes belong to the "*Hypsiglena* clade" with *E. slevini* and *P. latifasciata* from western Mexico (Leviton and Tanner, 1960; Cadle, 1984; Dowling and Jenner, 1987), but they are smaller in body size and inhabit more arid regions than the latter (Bogert and Oliver, 1945; Hardy and McDiarmid, 1969; Diller and Wallace, 1986). Other species in the *Leptodeira* clade are at least partially arboreal, strictly nocturnal, wide-searching predators that feed mainly on frogs and their eggs (Cadle and Greene, 1993; H. Greene and W. Roberts, unpubl. data). Our findings thus suggest that *H. torquata* (or perhaps the entire *Hypsiglena* clade) has two derived feeding traits: at least occasional reliance on diurnal ambush foraging tactics, and a diet that includes squamate eggs. Perhaps these ecological shifts occurred as the ancestors
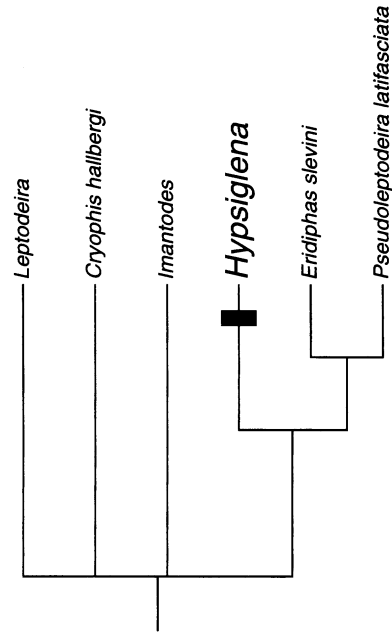

Fig. 3. Phylogenetic relationships among snakes of the genera *Cryophis, Eridiphas, Hypsiglena, Imantodes,* and *Leptodeira* (after Cadle, 1984). The black bar indicates the putative origin of preference for relatively arid habitats, a diurnal ambushing foraging strategy, and a diet that includes squamate eggs.

of *Hypsiglena* occupied arid temperate parts of western North America, since that region is characterized by a relatively high diversity and abundance of diurnal, terrestrial, oviparous iguanian lizards (Pianka, 1986). A shift from strict nocturnality also might have allowed *H. torquata* to range far north to where most nights, even during the summer, may be too cold for substantial activity. Additional studies of the feeding ecology of *H. torquata* in other parts of its range, of the extremely rare *H. tanzeri,* and of the closely related *E. slevini* and *P. latifasciata* should provide further insights into the evolutionary ecology of these species.

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MUSEUM OF VERTEBRATE ZOOLOGY AND DEPARTMENT OF INTEGRATIVE BIOLOGY, UNIVERSITY OF CALIFORNIA, BERKELEY, CALIFORNIA 94720-3160. PRESENT ADDRESSES: (DGM) DEPARTMENT OF BIOLOGY, UTAH STATE UNIVERSITY, 5305 UNIVERSITY BOULEVARD, LOGAN, UTAH 84322-5305; AND (HWG) SECTION OF ECOLOGY AND SYSTEMATICS, CORNELL UNIVERSITY, ITHACA, NEW YORK 14853-2701. E-mail (JAR) javier@socrates.berkeley.edu. Send reprint requests to JAR. Submitted: 21 Sept. 1997. Accepted: 6 July 1998. Section editor: S. T. Ross.

APPENDIX.   PREY EATEN BY *Hypsiglena torquata*. "Sceloporine lizard" refers to species of *Uta, Urosaurus,* or *Sceloporus*. "Frequency" refers to the number of times each prey taxon was found in the entire sample; numbers in parentheses indicate the number of snakes that had eaten a particular prey.

Prey taxon	Frequency	% of total number of prey	Source
INSECTA			
Coleoptera			
Larva	1 (1)	1.1	this study
Orthoptera			
Grasshopper	1 (1)	1.1	Diller and Wallace, 1986
Homoptera			
Cicada	1 (1)	1.1	Diller and Wallace, 1986
AMPHIBIA			
Anura			
Bufonidae			
Bufo alarius	2 (1)	2.2	Bogert and Oliver, 1945
Bufo mazatlanensis	1 (1)	1.1	Bogert and Oliver, 1945
Hylidae			
Hyla arenicolor	1 (1)	1.1	Tanner, 1929
Pseudacris sp.	3 (1)	3.3	this study
Pelobatidae			
Spea hammondii	2 (1)	2.2	Woodin, 1953
Spea intermontana	1 (1)	1.1	Diller and Wallace, 1986
Unidentified anuran	1 (1)	1.1	Tanner, 1944
REPTILIA			
Squamata			
Anguidae			
Anniella pulchra	1 (1)	1.1	Kuhns, 1961
Elgaria multicarinata	1 (1)	1.1	this study
Bipedidae			
Bipes biporus	1 (1)	1.1	Papenfuss, 1982
Crotaphytidae			
Crotaphytus collaris	1 (1)	1.1	Hammerson, 1982; Hammerson and Livo, in litt.
Gambelia wislizenii	1 (1)	1.1	this study
Eublepharidae			
Coleonyx variegatus	1 (1)	1.1	this study
Phrynosomatidae			
Holbrookia maculata	1 (1)	1.1	this study
Sceloporus graciosus	3 (3)	3.3	Barry, 1933; Goodman, 1953; this study
Sceloporus sp.	3 (3)	3.3	this study; Ditmars, 1936
Uta stansburiana	7 (7)	7.6	this study; Schmidt and Owens, 1944; Minton, 1958; Diller and Wallace, 1986
Sceloporine lizard	9 (9)	9.8	this study
Teiidae			
Cnemidophorus tigris	2 (2)	2.2	this study; Diller and Wallace, 1986
Cnemidophorus hyperythrus	1 (1)	1.1	this study
Cnemidophorus sp.	1 (1)	1.1	McCallion, 1945
Xantusiidae			
Xantusia vigilis	3 (3)	3.3	this study; R. Bello, pers. comm.
Unidentified lizard	13 (13)	14.1	this study; Klauber, 1932
Serpentes			
Colubridae			
Sonora semiannulata	1 (1)	1.1	McCallion, 1945

APPENDIX. CONTINUED

Prey taxon	Frequency	% of total number of prey	Source
Leptotyphlopidae			
Leptotyphlops dulcis	2 (2)	2.2	Webb, 1970; Degenhardt et al., 1996
Leptotyphlops humilis	2 (2)	2.2	Greene, 1976; Tennant, 1984
Viperidae			
Crotalus viridis	1 (1)	1.1	Lacey et al., 1996
Squamate eggs			
1	4 (4)	4.3	this study; Diller and Wallace, 1986
2	4 (4)	4.3	this study; Diller and Wallace, 1986
3	3 (3)	3.3	this study; Diller and Wallace, 1986
4	2 (2)	2.2	this study
5	2 (2)	2.2	B. Dial and R. Reiserer, unpubl. data
9	1 (1)	1.1	this study
11	1 (1)	1.1	this study
12	1 (1)	1.1	this study
Unknown number	3 (3)	3.3	Ditmars, 1936; Perkins, 1949; Minton, 1958
Unidentified animal	2 (2)	2.2	this study
Total	92		