TEXAS J. SCI. 52(2):83-92 MAY, 2000

FOOD HABITS OF THREE SPECIES OF STRIPED WHIPSNAKES, *MASTICOPHIS* (SERPENTES: COLUBRIDAE)

Jeffrey D. Camper* and James R. Dixon
Department of Wildlife & Fisheries Sciences, Texas A&M University
College Station, Texas 77843-2258
**Present Address:*
Department of Biology, Francis Marion University
Florence, South Carolina 29501-0547

Abstract.—The food habits of the striped whipsnake (*Masticophis taeniatus*), the Sonoran whipsnake (*Masticophis bilineatus*) and Schott's whipsnake (*Masticophis schotti*) were studied by examining the stomach contents of museum specimens. All three species ate lizards most frequently. Lizards of the genera *Cnemidophorus* and *Sceloporus* were the most abundant in the sample. Only larger whipsnakes ate mammals. Snakes, frogs and insects were found in low frequencies in the diet of striped whipsnakes. Geographic variation in the diet of *M. taeniatus* based upon a comparison of the two subspecies showed that the more northerly *M. taeniatus taeniatus* fed more frequently upon phrynosomatid lizards and less frequently upon *Cnemidophorus* and *Crotaphytus* than the southern populations assigned to *M. taeniatus girardi*. A positive relationship between prey mass and snake mass was found for the striped whipsnake.

Although the diet of *Masticophis taeniatus* has been well documented (Parker & Brown 1980; Brown & Parker 1982; Camper 1996c), little information exists concerning the diets of *Masticophis bilineatus* (cf. Camper 1996a) and *Masticophis schotti* (cf. Camper 1996b). Most reports concerning the food habits of *M. taeniatus* are based upon data from the northern subspecies, *M. taeniatus taeniatus*, which occurs in the Great Basin Desert of the western U.S.A.; however, there has been little reported on the diet of the southern form, *M. taeniatus girardi*, that inhabits the Chihuahuan Desert and Edwards Plateau of Texas and México (Camper 1996c). The objectives of this paper are to (1) report the diets of *M. bilineatus*, *M. schotti* and *M. taeniatus*, (2) examine geographic variation in the diet of *M. taeniatus* and (3) evaluate size relationships among *M. taeniatus* and its prey, based upon stomach contents removed from museum specimens.

Masticophis taeniatus, *M. schotti* and *M. bilineatus* are parapatrically distributed (Camper & Dixon 1994). *Masticophis taeniatus* is found in the Chihuahuan and Great Basin Deserts, the Edwards Plateau of central Texas, and western portions of the Mexican Plateau, whereas *M. schotti* is found south of the Edwards Plateau and along eastern portions of the Mexican Plateau east to the Gulf of Mexico. *Masticophis bilineatus*

occurs in the Sonoran Desert of southern Arizona, along the west coast of México south to the state of Colima, and east to the Continental Divide. Narrow zones of sympatry exist between *M. taeniatus* and *M. schotti* along the Balcones Escarpment in central Texas, between *M. bilineatus* and *M. taeniatus* in central Arizona and possibly all three in central México.

METHODS

A total of 1317 *M. taeniatus*, 316 *M. schotti* and 335 *M. bilineatus* museum specimens, that were collected from throughout the geographic ranges of each species, were examined for the presence of stomach contents (locality data from specimens examined is available from the author). Stomach contents were identified to species whenever possible. Age, mass and sex of each snake and each prey item were recorded. Juvenile and adult snakes were distinguished by ontogenetic color pattern differences (Camper & Dixon 1994). A P value of 0.05 or less was considered significant in all statistical tests.

RESULTS

Few whipsnakes examined contained prey. Only 9% of *M. taeniatus* and 5% of both *M. schotti* and *M. bilineatus* contained stomach contents. Thirty-five prey species for *M. taeniatus* and eight for both *M. bilineatus* and *M. schotti* were found. Unidentified lizards and snakes were not included (Table 1). Lizards were the most frequent category of prey and made up 88.9% of the diet of *M. taeniatus*, 91% of the *M. bilineatus* sample, and 78.3% of the *M. schotti* sample. Mammals and snakes made up only a small part of the diet by frequency. Intact insects were ingested by three adult *M. taeniatus* > 775 mm SVL. They were ingested intentionally because they were fairly large (two lepidopteran larvae and one cicada) and were the only stomach contents present in those specimens.

Most whipsnakes with stomach contents contained single prey items. However, 19 adult specimens, > 672 mm SVL, contained multiple prey. One *M. bilineatus* and one *M. schotti* each contained three different species of lizards. Eleven adult *M. taeniatus* contained two prey. Five contained conspecific lizards, one contained two mammals, and three *M. taeniatus* contained different prey species. Two *M. bilineatus* contained two lizards each. Four *M. schotti* had each eaten two prey. Two contained both lizards and mammals, whereas two had eaten lizards only, with one *M. schotti* harboring conspecific lizards.

Table 1. Frequency of occurrence of prey found in 118 *Masticophis taeniatus*, 18 *Masticophis bilineatus*, and 17 *Masticophis schotti* from throughout the species' geographic ranges. *N* is the number of prey items in the sample. Numbers in parentheses after prey taxa indicate the number of species from that taxon identified in the sample.

Prey category	Snake species		
	Masticophis taeniatus *n* (%)	*Masticophis bilineatus* *n* (%)	*Masticophis schotti* *n* (%)
Mammalia	7 (5.5)	2 (9)	5 (21.7)
Reptilia: Sqaumata			
Anguidae (1)	2 (1.6)	0	0
Crotaphytidae (1)	7 (5.5)	0	0
Phrynosomatidae			
Callisaurus	1 (0.8)	0	0
Cophosaurus (1)	5 (4)	1 (4.6)	0
Holbrookia	1 (0.8)	0	0
Phrynosoma (2)	2 (1.6)	0	0
Sceloporus (9)	49 (37.6)	3 (13.7)	8 (34.7)
Urosaurus (1)	2 (1.6)	2 (9)	0
Uta (1)	11 (8.4)	1 (4.6)	0
Polychridae (1)	1 (0.8)	0	1 (4.4)
Scincidae			
Eumeces	0	0	1 (4.4)
Scincella	0	0	1 (4.4)
Teiidae			
Cnemidophorus (12)	32 (24.5)	12 (54.5)	6 (26)
Unidentified lizards	1 (0.8)	1 (4.6)	1 (4.4)
Colubridae			
Bogertophis	1 (0.8)	0	0
Sonora (1)	2 (1.6)	0	0
Thamnophis	1 (0.8)	0	0
Unidentified snakes	1 (0.8)	0	0
Amphibia: Pelobatidae			
Scaphiopus	1 (0.8)	0	0
Insects	3 (2.4)	0	0
Total Prey	130	22	23

Direction of ingestion was inferred by examining the position of the prey in the stomachs of the snakes. Significantly more striped whipsnakes (88.5%) ingested their prey head-first ($\chi^2 = 64.7$, $df = 1$, $P < 0.05$) indicating that they may manipulate prey prior to ingesting it. Tail-first ingestion of prey by *M. taeniatus* were limited to smaller prey, less than 7% of the mass of the snake. *Masticophis bilineatus* consumed 86.7% of its prey head-first and *M. schotti* ate 85.7% of its prey head-first.

Table 2. Comparison of the frequency of mammals, lizards and snakes found in 65 *Masticophis taeniatus taeniatus* and 55 *Masticophis taeniatus girardi* museum specimens. *N* is number of prey items.

Prey category	Snake subspecies	
	Masticophis teaniatus taeniatus	*Masticophis teaniatus girardi*
	n (%)	*n* (%)
Mammalia	4 (6)	3 (5)
Reptilia: Squamata		
Crotaphytidae	1 (1.5)	6 (11)
Phrynosomatidae	45 (69)	24 (44)
Teiidae	14 (22)	18 (33)
Colubridae	1 (1.5)	4 (7)
Total prey	65	55
$\chi^2 = 11.6$, df = 4, $P < 0.05$		

Juvenile whipsnakes ate the same prey taxa as the adults. Juvenile *M. taeniatus* (N=19) ate *Sceloporus*, *Cnemidophorus*, *Uta*, *Anolis* and a neonatal *Thamnophis elegans*. Adults and juveniles consumed similar proportions of *Cnemidophorus*, phrynosomatids, and snakes ($\chi^2 = 0.15$, $df = 2$, $P > 0.05$). One juvenile male *M. taeniatus*, 286 mm SVL, consumed two juvenile *Sceloporus graciosus*. The *T. elegans* was 247 mm total length and was eaten by a 279 mm SVL *M. taeniatus*. The relative prey mass (RPM = prey mass/snake mass) was 0.45 for this specimen. The whipsnake may have been collected while ingesting the garter snake, or may have died during the ingestion attempt, because the posterior quarter of the *Thamnophis* protruded from the mouth of the whipsnake. One juvenile *M. bilineatus* contained a *Urosaurus ornatus*, and three juvenile *M. schotti* ate juvenile *Anolis carolinensis* and *Cnemidophorus gularis*, and an adult *Sceloporus grammicus*.

Geographic variation in the diet of *M. taeniatus* was examined by comparing the frequency of prey in the diets of both subspecies whose geographic ranges correspond to the Great Basin and Chihuahuan Deserts (Table 2). The desert striped whipsnake, *M. taeniatus taeniatus*, consumed phrynosomatid lizards more frequently and *Cnemidophorus* and *Crotaphytus* less frequently than the Central Texas whipsnake, *M. taeniatus girardi*. *Sceloporus graciosus* and *Uta stansburiana* occurred at frequencies of 27.5% and 14.5%, respectively, in the sample of *M. taeniatus taeniatus*. However, the most frequent taxon in the sample of *M. taeniatus girardi* was *Crotaphytus collaris*, which occurred at a frequency of only 10.2%. Data from stomach contents of museum

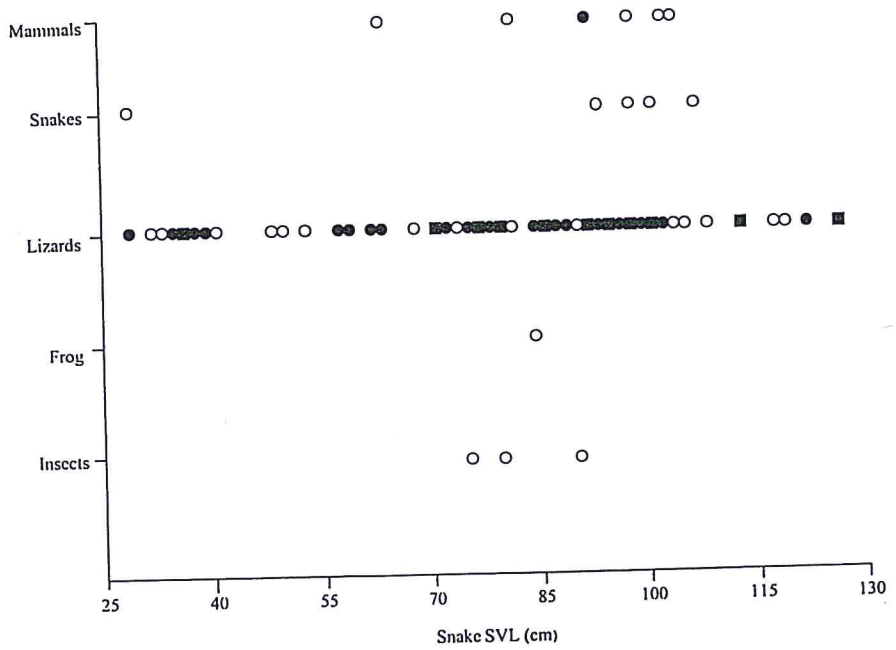

Figure 1. Relationship between prey category and snake body size (SVL) in *Masticophis taeniatus* ($N = 118$). Circles indicate one prey item, dots two prey and black squares three prey.

specimens may differ from data gathered in field studies from single localities. The relative frequencies of mammals, phrynosomatid lizards, teiid lizards and snakes in the diet of a population of *M. taeniatus* in northern Utah (Parker & Brown 1980) was compared with this sample. The Utah population ate mammals at a higher frequency and lizards less frequently than the sample from museum specimens ($\chi^2 = 13.6$, $df = 3$, $P < 0.05$).

Striped whipsnakes of all sizes ate lizards, whereas only large specimens, > 630 mm SVL, consumed mammals (Fig. 1). With the exception of one juvenile, only specimens > 950 mm SVL ate snakes. Even though large striped whipsnakes retain small prey in their diet, there was still a significant relationship between snake mass and prey mass (Fig. 2). Relative prey mass for adult *M. taeniatus* ranged from 0.011-0.313, $\bar{x} = 0.065 \pm 0.059$.

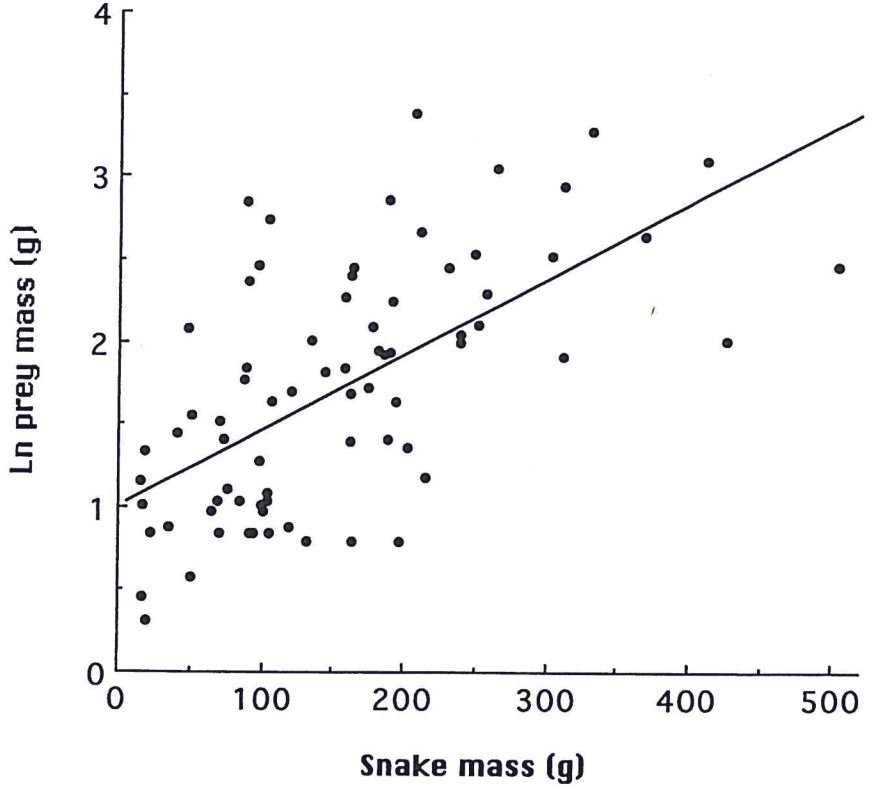

Figure 2. Ln-transformed prey mass as a function of snake mass in *Masticophis taeniatus* (adjusted $r^2 = .39$, $F = 48.09$, $df = 1, 74$, $N = 76$, $P < 0.05$).

DISCUSSION

Despite some discrepencies with the literature, this sample agrees fairly well with published reports of the diet of *M. taeniatus*. Lizards have been reported as occurring in the diet of *M. taeniatus* by Parker & Brown (1980), Brown & Parker (1982) and several anecdotal reports reviewed by Camper (1996c). Mammals have been reported in the diet of *M. taeniatus* by Parker & Brown (1980) and Reynolds & Scott (1982) and insects were reported by Fautin (1946). Predation upon birds and bats was reported for *M. taeniatus* by La Rivers (1944) and Herreid (1961), respectively. However, neither birds nor bats were found in this study. There is little agreement between published accounts of the diet of *M. bilineatus* and this sample. Birds and snakes have been reported as the prey of *M. bilineatus* (Stejneger 1902; Van Denburgh 1922; Ortenburger 1928); however, no birds or snakes were found in this sample. It is unclear if the large frequency of mammals eaten by *M.*

schotti is real or an artifact of a small sample size. The only literature report for this species lists rodents as well as birds, bird eggs, snakes and frogs fed to captive specimens (Gloyd & Conant 1934), however, only lizards and mammals were found in this sample.

Differences in the diet between the two subspecies of *M. taeniatus* probably reflect prey availability in the different geographic regions they inhabit. The lizard faunas of the Great Basin and Chihuahuan Deserts differ at the species level (Stebbins 1985; Conant & Collins 1991). The majority of the diet, by frequency, of both subspecies of *M. taeniatus* consisted of phrynosomatid lizards and *Chemidophorus*. However, there was little overlap of lizard species in the diets of the two *M. taeniatus* subspecies. Eleven species of *Chemidophorus* and 13 species of phrynosomatid lizards were found in this sample, with zero and three, respectively, being eaten by both subspecies of *M. taeniatus* (cf. Camper 1990). Geographic variation in diet resulting from prey availability has been reported in other snake species (Kephart 1982; Kephart & Arnold 1982; Greene 1984). Variation in diet between subspecies was found in the northern water snake (*Nerodia sipedon*) by King (1993) and the gopher snake (*Pituophis catenifer*) by Rodríguez- Robles (1998).

The relationships between snake size and prey size found in this study are similar to what has been found in other colubrid snakes. A positive relationship between snake mass and prey mass is probably common in snakes (Seib 1984; Jayne et al. 1988; King 1993; Rodríguez-Robles et al. 1999a; 1999b). Data from this study and from Parker & Brown (1980) show that only larger striped whipsnakes eat mammals. This pattern has been seen in other saurophagous racer-like snakes (Franz & Gicca 1982; Seib 1984; Rugiero & Luiselli 1995).

Mean RPM for *M. taeniatus* was lower than in many other colubrid snakes (Shine et al. 1996; Rodríguez-Robles et al. 1999a; 1999b). The low mean RPM for *M. taeniatus* occurs because the species does not drop small prey from its diet, a pattern that is relatively uncommon in snakes (Arnold 1993). Retention of small prey in the diet appears to occur more frequently in snakes that specialize on only one or two prey types, such as crayfish (*Regina*; Godley et al. 1984), fish (*Enhydrina*; Voris & Moffett 1981), lizards (*Uromacer*; Henderson et al. 1987) or frogs (*Notechis*; Shine 1977). Specializing on relatively small prey such as lizards and retaining small prey in the diet may explain the low mean RPM seen in this sample. The low mean RPM found in this study is

comparable to that reported for other attenuate colubrid snakes that feed mainly on lizards and frogs including neotropical racers *Drymobius chloroticus* (RPM: $\bar{x} = 0.041$) and *D. margaritiferus* (0.053; Seib 1984), a Hispaniolan vine snake (*Uromacer frenatus*; 0.125; Henderson et al. 1987), and a European racer (*Coluber viridiflavus*; 0.076; Rugiero & Luiselli 1995). It is hypothesized that other snakes that specialize on relatively small prey will retain small prey in their diets and exhibit low RPM values.

ACKNOWLEDGMENTS

G. Baumgardner helped identify stomach contents. We thank the following institutions (and curators) for loans of specimens and permission to examine their stomach contents: American Museum of Natural History (AMNH, C. Myers, R. Zweifel), Angelo State University (ASC, M. Engstrom), Arizona State University (ASU, M. Douglas), Baylor University-Strecker Museum (SM, D. Lintz), Brigham Young University (BYU, J. Sites), Chicago Academy of Sciences (CA, R. Vasile), California Academy of Sciences (CAS, R. Drewes, J. Vindum), Carnegie Museum of Natural History, Pittsburgh (CM, E. Censky, C. J. McCoy), Field Museum of Natural History, Chicago (FMNH, H. Marx), Illinois Natural History Survey (INHS, K. Cummings, L. Page, M. Retzer), University of Kansas Museum of Natural History (KU, J. Collins, W. Duellman), Los Angeles County Museum (LACM, R. Bezy, J. Wright), Harvard University-Museum of Comparative Zoology (MCZ, P. Alberch, J. Rosado), National Museum of Natural History (USNM, R. McDiarmid, R. Reynolds, G. Zug), New Mexico State University (NMSU, J. Lapointe), San Diego Natural History Museum (SDNHM, G. Pregill), Sul Ross State University (SRSU, J. Scudday), Texas A&I University (TAIC, A. Chaney, S. Smith), Texas A&M University-Texas Cooperative Wildlife Collections (TCWC, M. Retzer, R. K. Vaughan), University of Arizona (UAZ, G. Bradley, C. Lowe), University of California at Berkeley-Museum of Vertebrate Zoology (MVZ, D. Good, H. Greene), University of Illinois-Museum of Natural History (UIMNH, L. Maxson), University of Michigan Museum of Zoology (UMMZ, A. Kluge), University of New Mexico-Museum of Southwestern Biology (UNM, H. Snell), University of Southwestern Louisiana (USL, J. Jackson), University of Texas-Texas Memorial Museum (TNHC, R. Martin), University of Texas at Arlington (UTACV, J. Campbell, J. Darling), University of Texas at El Paso (UTEP, C. Leib), University of Utah (UU). This research was funded by the Texas Agricultural Experiment Station and

a Texas A&M University Faculty-Staff mini-grant and release time at Francis Marion University.

LITERATURE CITED

Arnold, S. J. 1993. Foraging theory and prey-size-predator-size relations in snakes. Pp. 87-115, *in* Snakes: Ecology and Behavior (R. A. Seigel and J. T. Collins, eds.), McGraw-Hill Inc. New York, xvi+414 pp.

Brown, W. S. & W. S. Parker. 1982. Niche dimensions and resource partitioning in a Great Basin Desert snake community. Pp. 59-81, *in* Herpetological Communities (N. J. Scott, Jr., ed.), US Dept. Int., Fish and Wildlife Service. Wildlife Res. Rep. 13. Washington D. C., iv+239 pp.

Camper, J. D. 1990. Systematics of the striped whipsnake, *Masticophis taeniatus* (Hallowell). Unpublished Ph.D. dissertation, Texas A&M Univ., College Station, 161 pp.

Camper, J. D. 1996a. *Masticophis bilineatus*. Catalogue of American Amphibians and Reptiles. Society for the Study of Amphibians and Reptiles. 637.1-637.4.

Camper, J. D. 1996b. *Masticophis schotti*. Catalogue of American Amphibians and Reptiles. Society for the Study of Amphibians and Reptiles. 638.1-638.4.

Camper, J. D. 1996c. *Masticophis taeniatus*. Catalogue of American Amphibians and Reptiles. Society for the Study of Amphibians and Reptiles. 639.1-639.6.

Camper, J. D. & J. R. Dixon. 1994. Geographic variation and systematics of the striped whipsnakes (*Masticophis taeniatus* complex; Reptilia: Serpentes: Colubridae). Ann. Carnegie Mus., 63(1):1-48.

Conant, R. & J. T. Collins. 1991. A field guide to the reptiles and amphibians of eastern and central North America. Houghton Mifflin Co., Boston, xviii+450 pp.

Fautin, R. W. 1946. Biotic communities of the northern shrub biome in western Utah. Ecol. Mono., 16(4):251-310.

Franz, R. & D. F. Gicca. 1982. Observations on the snake *Antillophis parvifrons alleni*. J. Herpetol., 16(4):419-421.

Gloyd, H. K. & R. Conant. 1934. The taxonomic status, range and natural history of Schott's racer. Occas. Pap. Mus. Zool., Univ. Michigan, 287:1-17.

Godley, J. S., R. W. McDiarmid & N. N. Rojas. 1984. Estimating prey size and number in crayfish-eating snakes, Genus *Regina*. Herpetologica, 40(1):82-87.

Greene, H. W. 1984. Feeding behavior and diet of the eastern coral snake, *Micrurus fulvius*. Pp. 147-162, *in* Vertebrate Ecology and Systematics-A Tribute to Henry S. Fitch (R. A. Seigel, L. E. Hunt, J. L. Knight, L. Malare, & N. L. Zuschlag, eds.) Univ. Kansas, Mus. Nat. Hist. Special Publ. No. 10. v+278 pp.

Henderson, R. W., A. Schwartz & T. A. Noeske-Hallin. 1987. Food habits of three colubrid tree snakes (Genus *Uromacer*) on Hispaniola. Herpetologica, 43(2):241-248.

Herreid, C. F. 1961. Snakes as predators of bats. Herpetologica, 17(4):271-272.

Jayne, B., H. K. Voris & K. B. Heang. 1988. Diet, feeding behavior, growth, and numbers of a population of *Cerberus rhynchops* (Serpentes: Homalopsinae) in Malaysia. Fieldiana Zool., 50: iii+15.

Kephart, D. G. 1982. Microgeographic variation in the diets of garter snakes. Oecologia, 52:287-291.

Kephart, D. G. & S. A. Arnold. 1982. Garter snake diets in a fluctuating environment: a seven-year study. Ecology, 63(5):1232-1236.

King, R. B. 1993. Microgeographic, historical and size-correlated variation in water snake diet composition. J. Herpetol., 27(1):90-94.

La Rivers, I. 1944. Observations on the nesting mortality of the Brewer Blackbird, *Euphagus cyanocephalus*. Am. Midl. Nat., 32(4):417-437.

Ortenburger, A. I. 1928. The whip snakes and racers, genera *Masticophis* and *Coluber*. Mem. Univ. Michigan Mus., 1:1-247.

Parker, W. S. & W. S. Brown. 1980. Comparative ecology of two colubrid snakes, *Masticophis t. taeniatus* and *Pituophis melanoleucus deserticola*, in northern Utah. Milwaukee Public Museum, Publications in Biology and Geology No. 7:1-104.

Reynolds, R. P. & N. J. Scott, Jr. 1982. Use of a mammalian resource by a Chihuahuan snake community. Pp. 99-118, *in* Herpetological Communities (N. J. Scott, Jr., ed.), US Dept. Int., Fish and Wildlife Service. Wildlife Res. Rep. 13. Washington D. C., iv+239 pp.

Rodríguez-Robles, J. A. 1998. Alternative perspectives on the diet of gopher snakes (*Pituophis catenifer*, Colubridae): Literature records versus stomach contents of wild and museum specimens. Copeia, 1998(2):463-466.

Rodríguez-Robles, J. A., D. G. Mulcahy & H. W. Greene. 1999a. Feeding ecology of the desert nightsnake, *Hypsiglena torquata* (Colubridae). Copeia 1999(1):93-100.

Rodríguez-Robles, J. A., C. J. Bell & H. W. Greene. 1999b. Food habits of the glossy snake, *Arizona* elegans, with comparisons to the diet of sympatric long-nosed snakes, *Rhinocheilus lecontei*. J. Herpetol., 33(1):87-92.

Rugiero, L. & L. Luiselli. 1995. Food habits of the snake *Coluber viridiflavus* in relation to prey availability. Amph.-Rept. 16:407-411.

Seib, R. L. 1984. Prey use in three syntopic neotropical racers. Journal of Herpetol., 18(4):412-420.

Shine, R. 1977. Habitats, diets, and sympatry in snakes: a study from Australia. Can. J. Zool., 55:1118-1128.

Shine, R., P. S. Harlow, W. R. Branch & J. K. Webb. 1996. Life on the lowest branch: sexual dimorphism, diet, and reproductive biology of an African twig snake, *Thelotornis capensis* (Serpentes, Colubridae). Copeia, 1996(2):290-299.

Stebbins, R. C. 1985. A field guide to western reptiles and amphibians. Houghton Mifflin Co., Boston, ix+332 pp.

Stejneger, L. 1902. The reptiles of the Huachuca Mountains, Arizona. Proc. U. S. Natl. Mus., 25:149-158.

Van Denburgh, J. 1922. The reptiles of western North America. Occas. Pap. California Acad. Sci., 2:617-1028.

Voris, H. K. & M. W. Moffett. 1981. Size and proportion relationship between the beaked sea snake and its prey. Biotrop., 13(1)15-19.

JDC at: jcamper@fmarion.edu