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Arthropod Diets In Chihuahuan Desert Snakes

Victor Manuel Parga
University of Texas at El Paso, jokerparga4@yahoo.com

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VICTOR MANUEL PARGA, JR.

Master's Program in Environmental Science

APPROVED:

Carl S. Lieb, Ph.D., Chair

Vanessa Lougheed, Ph.D.

Richard Langford, Ph.D.

Charles Ambler, Ph.D.
Dean of the Graduate School

ARTHROPOD DIETS IN CHIHUAHUAN DESERT SNAKES

by

VICTOR MANUEL PARGA, JR., A.S., B.S.

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Abstract

Over the past century, studies in herpetology regarding snake diets have been commonly focused on those species that feed or specialize in vertebrate prey items. For those that feed primarily on invertebrates however, little work has been done in determining diet specializations and comparing diets within a community of species. This thesis focuses on small species of snakes that feed primarily on arthropods in a Chihuahuan Desert community, and will investigate if these are diet generalists or specialists. To this end, stomach contents were examined from preserved specimens of the following species: *Rena humilis* and *Rena dissecta* (Leptotyphlopidae), *Gyalopion canum* (Colubridae), *Sonora semiannulata* (Colubridae), *Tantilla hobartsmithii* (Colubridae), *Tantilla nigriceps* (Colubridae), *Diadophis punctatus* (Dipsadidae), *Sistrurus tergeminus* (Viperidae). These specimens were drawn from northern Chihuahuan Desert populations in Trans-Pecos Texas and southern New Mexico, and represent a total of 280 individuals across the seven species. Using similar statistical methods as Hamilton et al. (2011), I found a common dietary emphasis on ground-dwelling spiders. Thus the data show signs of diet preference, and suggest that these snakes are dietary opportunists that seem to feed primarily on spiders as well as other arthropods of appropriate size that are abundant during the periods of feeding activity.

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Introduction

Snakes are by their nature secretive animals, and it was not until the late 20th century that an understanding of the behavioral ecology of individual species began to be revealed (e.g., Seigel and Collins, 1993; Greene, 1997). Such studies have continued, enhanced by new methods and technologies into the 21st century. Scarcely a decade ago, Mullin and Seigel (2009) claimed that snake ecology "provides a seemingly inexhaustible source of research topics to pursue." But, despite the tremendous increase in knowledge of snake biology, there have still been topics that have received little to no attention. One such area includes diet studies in regards to arthropod-eating snakes. Although there have been several studies regarding the topic of dietary behavior, most of them have involved individual snake species that feed primarily on vertebrate prey (e.g., Beavers, 1976; Best, 1977; Cundall and Greene 2000; Hamilton et al., 2012). There are also diet comparison studies between multiple snake species inhabiting the same community (Reynolds and Scott, 1982; Diller and Johnson, 1988; Rodriguez-Robles *et al.,* 1999), but these also focus on vertebrate predators. Published studies involving insectivorous snakes in the past fifty years are few, and include the reports of Goldsmith (1986) on *Opheodrys aestivus* (Rough Green Snake), Rosen et al., (1990) on Chionactis (Shovel-nosed Snakes), Stafford (2005) on *Symphimus mayae* (Yucatán Cricket-eating Snake), and Solórzano, and Greene (2012) on *Stenorrhina freminvilli* (Freminvill's Spider-eating Snake). The only comparative works on diets of sympatric arthropod-eating species (e.g., Conant and Collins, 1998; Stebbins, 2003; Punzo, 1974) on the two Threadsnakes *Rena humilis and R. dulcis*) [Now *R. dissecta*].

The present study seeks to describe and compare the diets of multiple species of northern Chihuahuan Desert snakes that are known or have been reported to feed on arthropods as adults. This study will also address food specialist versus generalist designations for each species. Svanback, et al., (2004) has proposed that when a species is a diet specialist, it has a much more restricted niche breath due to an adaptation to selective prey, while generalists are more flexible as they are opportunists. The latter would allow generalists to potentially occupy multiple niches, rather than be restricted to just one. This project may also provide insight into the prey selection behavior of the species. For example, Punzo's (1974) diet study on the two species Threadsnakes (*Rena*) unexpectedly found that one of his species was feeding exclusively on beetles rather than the widely assumed leptotyphlopid diet of eggs and pupae of ants (Stebbins, 1966, Conant 1975). My working hypothesis, derived from the literature on diet, was that at least one species of arthropod-eating snake that would show signs of diet specialization, specifically a preference for particular category of prey.

Diet specialization versus diet generalization in snakes are descriptive terms widely used in herpetological literature, and these terms seem to be largely interchangeable with "stenophagy" and "euryphagy." A review of this literature shows none of these terms have been rigorously defined in terms of proportions of prey items taken by a species, the frequency of occurrence per snake n a series of gastrointestinal tract samples, or the frequency of occurrence of a prey-item per individual GI tract. Moreover, the level of prey identification (LPI) varies greatly from study to study (Greene and Jaksić, 1983). Brischoux et al. (2009) indicate specialists show no dietary shifts, taking larger individuals of the same or similar food types as the snake grows in size with age. However, this approach does not fit the manner in which most herpetologists, would approach narrow versus broad diets in snakes: smaller individuals might continue very broad diets into adulthood. Rodriguez-Robles and Greene (1999) point out that evolutionary biologists would see dietary specialists having a derived feeding morphology, one of "modified design for prey consumption." They contrasted this view with the more general biologists' view that specialization is indicated by "one or a few prey types are predominate in diet." In this study, I am using the latter the definition.

Materials and Methods

The following eight snake species were targeted for analysis of diet (species nomenclature follows Powell et al., 2016). A few juvenile individuals of larger snake species that feed primarily on rodents were also examined. All specimens dissected are listed in Appendix I.

Rena humilis – Western Threadsnake (Leptotyphlopidae)

Rena dissecta – New Mexico Threadsnake (Leptotyphlopidae)

Gyalopion canum – Chihuahuan Hook-nosed Snake (Colubridae)

Sonora semiannulata – Western Groundsnake (Colubridae)

Tantilla hobartsmithii – Smith's Black-headed Snake (Colubridae)

Tantilla nigriceps – Plains Black-headed Snake (Colubridae)

Diadophis punctatus- Ring-necked Snake (Dipsadidae)

Sistrurus tergeminus - Massasauga (Viperidae)

These species, all of which occur in Chihuahuan Desert habitats, were selected based on the summaries of food habits in various field guides and regional publications (e.g., Conant and Collins, 1991; Degenhardt et al., 1996; Werler and Dixon, 2000; Stebbins, 2003).

This study utilized preserved specimens of snakes in the herpetological collections of the Museum of Southwestern Biology (MSB) at the University of New Mexico, the Texas Natural History Collection (TNHC) at the University of Texas at Austin, and UTEP Biodiversity Collections at the University of Texas at El Paso (see Appendix I). The specimens selected for examination were from desert and desert grassland regions in the Trans-Pecos region of Texas, and from similar regions in southern New Mexico. Care was taken to exclude snake specimens from montane woodland areas over this portion of the Chihuahuan Desert ecoregion, and specimens that had been maintained alive in captivity for any length to time. Salvaged, preserved road-killed individuals were particularly well-suited for sampling. I also investigated the gut contents a few specimens of juvenile *Heterodon kennerlyi* and rattlesnakes (*Crotalus*) for study, although these did not provide any digestive tract contents.

Snakes were dissected by a mid-ventral incision, and the stomach and intestine slit for assay of presence or absence of potentially identifiable remains of ingested/partially digested prey. These procedures are fairly standard for snake dietary studies (e.g., Hamilton, 1951; Rodriguez-Robles et al., 1999a, 1999b; Hamilton et al., 2012). Identifiable remains were manually evacuated from the stomach and intestines, and then individually placed in vials with alcohol (70 % ethanol for TNHC and UTEP, 50% isopropanol for MSB). These remains were later removed from the vials and identified. In many cases, there were no identifiable contents in either the stomach or intestine, and occasionally an individual specimen had already been dissected for removal of GI tract contents (and was entirely removed) from the specimen. The vials were labeled with the museum number of the specimen, so that the contents could be returned to the originating museum and associated with the original specimen. The contents of each vial were examined using a dissecting microscope, and the remains of arthropods (and rarely, vertebrates) were identified to the taxonomic level possible given their condition.

Chi-square (χ^2) analyses were used to test the differences in frequency of prey items in the digestive tract and prey categories, a procedure similar to that of Hamilton et al. (2011) using MINITAB (Minitab Inc., 2010). For these analyses, prey items were sorted into the following categories: spider, insect, scorpion, larva, centipede, snake, solifugae, and mammal. I will also use the chi-square to separate by each species. My null hypothesis is that all taxonomic prey groups are being selected at equal frequency.

Results

A total of 280 individual specimens were dissected, almost half of which had prey remains within their gastrointestinal tracts. The species that most frequently had prey items present were *Sonora semiannulata and Gyalopion canum*, whereas no items at all were found in either species of *Rena* (sample sizes, however, for these genera were low). Over all prey items found in the target species, almost 95% were invertebrates with the remaining 5% consisting of vertebrates. I found that the most frequent prey that was found in the specimens were spiders, typically ground-dwelling families such as *Dipluridae, Ctenizidae, Theraphosidae, Homalonycidae* and *Lycosidae*. Most of the few vertebrates that were found came from the digestive tracts of the juvenile *Crotalus* snakes. There was only one specimen that contained an unidentifiable prey item, likely to have been parts of a spider.

Table 1. Chi-square table of prey items identified and put into their own categories. Note that last category was reserved for prey item too altered by digestive acid and enzymes to be properly identified.

Category	OBS	EXP	RES	RES^2	Component
Spiders	62	17.125	44.875	2013.766	117.592
Insects	29	17.125	11.875	141.016	8.234
Scorpions	21	17.125	3.875	15.016	.877
Insect Larvae	10	17.125	-7.125	50.766	2.964
Centipedes	5	17.125	-12.125	147.016	8.585
Snakes	4	17.125	-13.125	172.266	10.059
Solifugae	3	17.125	-14.125	199.516	11.650
Mammals	3	17.125	-14.125	199.516	11.650

In my Chihuahuan Desert specimen samples, the most common arthropods found were spiders, scorpions and various insects. For the most part, these represent small prey with weak defenses for small snakes with inefficient or absent venom delivery systems. More durable and dangerous prey, such as centipedes, solfugids, and scorpions appear in lower numbers. Kassing (1961) relates an anecdotal observation of a Ground Snake (*Sonora*) seizing a scorpion by the tail such that the snake was not stung, but the story lacks an accompanying narrative as to how the prey item was subsequently oriented to a swallowing position (Werler and Dixon, 2000). Moreover, large individuals of the genus *Scolopendra* could variously serve as both predator or prey in different snake-to-centipede size relationships

For insects, I could identify no families that occurred more frequently. The most common scorpions that I was able to identify were in the Family *Vejovidae*, and that the centipedes were primarily assignable to the genus *Scolopendra*. Remains of vertebrates found among the samples included the remains of three mammals and four snakes, but only one of these, a *Tantilla nigriceps* in the stomach of a *Diadophis punctatus,* was identifiable (identification by C. Lieb, University of Texas at El Paso). With the DF equaling to 7, the Chi-square statistic equaling to 171.611 and the p-value being less than 0.0001, my null hypothesis is rejected.

Below are Tables 2-5, each of them are chi-square analyses of four species that had reasonable sample sizes and had enough positive turnouts for testing. As in Table 1, the highest component values came from spiders. Prey categories that were not found in this study, but reported in literature to occur in diets of these species were added to minimize bias in the final results. For *Sonora semiannulata,* the DF equaled to 5 as was the same for the following tables, with a Chi-square stat of 48.59 and the p-value was less than 0.001. In *Tantilla nigriceps*, the Chi-square stat equaled to 14.001 and the p-value was at 0.015. The results for *Tantilla hobartsmithi* were 13.525 for the Chi-square stat and a p-value equaling 0.015. Lastly, for *Gyalopion canum*, the p-value was less than 0.0001 with a Chi-square stat of 51.055.

Table 2: Chi-square table on prey items found in *Sonora semiannulata*.

Category	OBS	EXP	RES	RES^2	Component
Insects	12	8.167	3.83	14.694	1.799
Spiders	23	8.167	14.83	220.028	26.941
Scorpions	11	8.167	2.83	8.028	0.983
Centipedes	1	8.167	-7.767	51.361	6.289
Snakes	1	8.167	-7.767	51.361	6.289
Solifugae	1	8.167	-7.767	51.361	6.289

Table 3: Chi-square table on prey items found in *Tantilla nigriceps*.

Category	OBS	EXP	RES	RES^2	Component
Spiders	11	4	7	49	8.167
Insects	2	4	-2	4	.667
Centipedes	1	4	-3	9	1.5
Larvae	7	4	3	9	1.5
Snakes	1	4	-3	9	1.5
Scorpions	2	4	-2	4	.667

Table 4: Chi-square table on prey items found in *Tantilla hobartsmithi*.

Category	OBS	EXP	RES	RES^2	Component
Insects	5	3.167	1.833	3.360	1.061
Centipedes	2	3.167	-1.167	1.362	.430
Snakes	0	3.167	-3.167	10.030	3.167
Larvae	5	3.167	1.833	3.360	1.061
Spiders	7	3.167	3.833	14.692	4.639
Scorpions	0	3.167	-3.167	10.030	3.167

Table 5: Chi-square table on prey items found in *Gyalopion canum*.

Category	OBS	EXP	RES	RES^2	Component
Spiders	20	5.667	14.333	205.435	36.251
Scorpions	8	5.667	2.333	5.443	.960
Solifugae	3	5.667	-2.667	7.113	1.255
Insects	3	5.667	-2.667	7.113	1.255
Centipedes	0	5.667	-5.667	32.115	5.667
Snakes	0	5.667	-5.667	32.115	5.667

A very limited number of snakes of the families Leptotyphlopidae and Viperidae were assayed, and the resultant findings were zero in the former and slight in the latter. These data were insufficient to contribute to the above analyses.

Species Accounts

The following accounts summarize the observations on a per species basis. The term "positive" will refer to individual specimens of a snake species in which recognizable prey items were present in the digestive tract, and "negative" will refer to those specimens whose dissected stomachs and colons were either empty or contained no recognizable items.

***Sonora semiannulata* (Colubridae) – Western Groundsnake**

A total of 70 specimens were examined, with 31 individuals (44.3%) having prey items in their digestive tracts. Of these specimens, six were found to have either multiple or different prey items fragments, often a combination of spider and scorpion or insect and scorpion. The most numerous prey items were spiders (present in 71% of the positives, including those with other types of prey items). Insects and scorpions were present in 35% and 32% of the positives, respectively. One specimen contained fragments of a centipede, and another had remains of an unidentified snake. The latter is a novel observation for this species, although an anecdote of a Ground Snake in Big Bend National Park attempting to swallow road-killed Banded Gecko (*Coleonyx brevis*) appears in Degenhardt, *et al.* (1996). This gecko, however, is probably not a normal food item for this snake, as shown by the prey scent trial experiments of Dial and Schwenk (1996).

Sonora semiannulata has a large distribution in western North America exclusive of the Chihuahuan Desert, extending to the west into the Sonoran, Mohave, and Great Basin Deserts, and into the southern Great Plains in the east (Stebbins, 2003). The most comprehensive dietary study of the species (using a former name *Sonora episcopa*) was by Kassing (1961), who examined the stomach contents of 81 specimens from the vicinity of Tulsa, Oklahoma. She found identifiable remains in 39 individuals, the most "frequently and abundantly" represented being wolf spiders of the family Lycosidae, and after that, in decreasing order, stone centipedes, buthid scorpions, beetles, hymenopterans, and orthopterans. The insects were of types associated with "moist habitats under rocks."

The last edition of the Conant *et al*., Eastern North America reptile/amphibian field guide to contain dietary summaries (3rd edition, 1991) follows Kassing's findings in listing the diet of this species to include "small centipedes, scorpions, spiders, and insects"; whereas the current Western North America field guide (Stebbins, 2003) has an expanded list of dietary items, specifically "spiders, scorpions, centipedes, crickets, solifugids, grasshoppers, and insect larvae including ant brood." Cox *et al.* (2014) stated that these snakes prey upon arthropods in arid regions, and Degenhardt *et al.* (1996) for New Mexico specifically mention scorpions, centipedes and spiders in the diet, and single out black widow spider remains as being "common in stomach contents and fecal samples". These authors also mention an individual from the Chihuahuan Desert area of Texas feeding in captivity on "a wolf spider, a small solifugid, and unidentified black spider, and baby crickets," while turning down thysanurans. With exception of finding snake remains in the stomach of one of the specimens of this species, my findings are concordant with the dietary items observed by others to date.

***Tantilla nigriceps* (Colubridae) – Plains Black-headed Snake**

The digestive tracts of 38 museum specimens of this species were examined, with over half of them providing positive results. Twenty-one specimens were found to have multiple prey items present, with spider fragments were the most numerous and occurring in almost 60% of the diet item positive specimens. Six specimens had beetle larva part in the digestive tract. A juvenile centipede was also found in one of the specimens, concordant with the suggestions in the herpetological literature that this type of arthropod is part of the diet of this species (e.g.., Werler and Dixon, 2000; Stebbins, 2003), and also supported with anecdotal observation of this species eating centipedes in captivity (Degenhardt *et al.* , 1996). It has been suggested that venomous salivary secretions of Duvernoy's gland may be important in subduing of this "dangerous" type prey by this opistoglyphous genus of snakes (Rodríguez-Robles, J.A., 1994; Hill and Mackessy, 2000). Holm (2008) indicated that members of the genus fed on centipedes, and Wilson and Mata-Silva (2014) specifically mention centipedes in the diet of *Tantilla nigriceps.* However*,* millipedes and caterpillars were also indicated by these authors as dietary items. Insect adults, larvae, and pupae have also been included as well (Degenhardt *et al*., 1996; Werler and Dixon, 2000; Stebbins, 2003), but whereas coleopteran larvae were found in the present study, no caterpillar or millipede remains were identified. *Tantilla nigriceps* is widespread in the Great Plains of the United States as well as the adjoining parts of the Chihuahuan Desert in the U.S. and Mexico. It is not clear how much of the wide variety of prey items assigned to this species are utilized range-wide, are different in grassland versus desert grassland parts of the species distribution, or are actually only generalizations about what is known or surmised about members of the speciose genus *Tantilla* (e.g., Holm, 2008).

***Tantilla hobartsmithi* (Colubridae) – Smith's Black-headed Snake**

In comparison to the previous species in this genus, although more specimens were examined (44) for this study, there were fewer positive results for identifiable food items (19, or 43%). The majority of the prey items in *Tantilla hobartsmithi* consisted of spiders, with beetle larvae as their second most common prey. As was the case for the *Tantilla nigriceps* sampling, a single centipede was found as a prey item in this species as well. Also, as for *Tantilla nigriceps*, Wilson and Mata-Silva (2014) indicate a much wider variety of prey in *Tantilla hobartsmithi* than was found here, including "beetle larvae, centipedes, millipedes, spiders and caterpillars." However, *Tantilla hobartsmithi* also has a large distribution, being found in this case across the warm deserts of the Southwestern U.S. and northern Mexico. Therefore, there may well be regional differences in diet within this species' range. For example, one diet study of thirty-one Arizona individuals of this species (using the older name, *Tantilla atriceps*) by Lindner (1962, described in Werler and Dixon, 2000) suggests a Sonoran Desert narrow diet of beetle and lepidopteran larvae. On the other hand, Degenhardt *et al.* (1996), in addition to citing mealworms as being eaten by captive individuals, reported a list of stomach contents of New Mexico specimens that is almost identical to those of Wilson and Mata-Silva (2014), but do not include spiders.

***Gyalopion canum* (Colubridae) – Chihuahuan Hook-nosed Snake**

Of all the species of Chihuahuan Desert snakes reported to specialize on arthropod prey, *Gyalopion canum* showed most positive individuals for identifiable digestive tract contents (24 out of 32, 75%). Over 80% of the specimens contained spiders, with the second most frequent prey being scorpions. Additionally, 5 of the 24 individuals had multiple prey items in the stomachs. Many of the spiders were Lycosids (wolf spiders), which is concordant with an observation by Bogert *et al*., 1945) for a Sonoran Desert snake. The general diet according to herpetological literature is usually described as mostly consisting of spiders, with other arthropods, principally centipedes and scorpions, also taken (*e.g.,* Conant and Collins, 1991; Dial *et al.*, 1996; Degenhardt *et al*., 1996; Werler and Dixon, 2000; Stebbins, 2003). Stebbins also cites "small snakes" as part of the diet, seemingly supported by anecdotes involving attempted two separate predation attempts on or by *Diadophis punctatus* (Degenhardt *et al*., 1996, Werler and Dixon, 2000) in the wild, and a captive *Gyalopion canum* from Texas eating a dead *Diadophis punctatus* from Oklahoma (Vaeth, 1980). On the other hand, Kauffeld (1948), reporting on attempts to offer various food items to a captive individual at the Staten Island Zoo (received from El Paso, Texas), cite it accepting spiders and centipedes as food, but refused the repeatedly offered millipedes, frogs, lizards, small snakes, and neonate mice. Degenhardt *et al*. (1996) provide anecdotes from Texas herpetologist Ernest Tanzer of a large specimen of this species eating newborn laboratory mice, and a second specimen that would eat legs of lizards and pieces of rat and bovine meat; these authors make a point that they consider such diets in captivity as "unnatural."

Diadophis punctatus **(Dipsadidae) – Ring-necked Snake**

Although 31 individuals were inspected, only five of these were positive. Moreover, two of the positives contained the remains of ingested snakes and no arthropods. The arthropod remains included one individual having spider fragments in the gastrointestinal tract, and the remainder having insect fragments. Unfortunately, the contents of the fifth stomach were misplaced or mislabeled, and therefore not available for the analysis.

The nominal species *Diadophis punctatus* has a very large distribution across temperate North America, with numerous subspecies having been described in the early literature of the genus. In the Chihuahuan Desert region, the currently recognized subspecies is *Diadophis punctatus regalis*. This subspecies, and those located further west, attain considerably larger body sizes than the subspecies from the adjacent Great Plains and those from deciduous woodlands in the eastern United States (Degenhardt *et al*., 1996, Werler and Dixon, 2000). The Great Plains subspecies, *Diadophis punctatus arnyi,* seems to feed almost on exclusively on earthworms (Fitch, 1975; Greenwald and Kanter, 1979; Upton and Oppert, 1991), the eastern woodland ring-necked snakes subspecies feed extensively on earthworms and salamanders, with a variety of insects and other small invertebrate and invertebrate prey supplementing this diet. In the more arid areas where *D. p. regalis* occurs, however, snakes and lizards apparently substitute for earthworms and lizards (Gelhbach, 1974, Degenhardt *et al*., 1996, Werler and Dixon, 2000).

It is clear that an understanding of the diet of this species in southwestern North America will only be attained by much larger sample sizes taken over the diversity of habitats utilized by the species. In the Chihuahuan Desert region, ring-necked snakes occur both in desert scrubland as well as montane woodland habitats. I was careful to exclude from my survey of specimens those taken from woodland habitats and included only those collected in desert environments (which also lowered my own sample size). Moreover, it has been indicated to me (C. S. Lieb, University of Texas at El Paso, personal communication) that revisiting of the genetic lineages in the American Southwest might reveal species-level divergence between the Great Plains and Chihuahuan Desert populations of ring-neck snakes not detected by the evolutionary genetics study performed by Fontanella *et al.* (1988).

Rena dissecta **(Leptotyphlopidae) New Mexico Threadsnake**

For this species, I examined fourteen specimens, all of which were negative (Appendix I). In contrast to my lack of success in sampling, Punzo (1974), utilizing only 17 specimens collected in a single field season (1971) in southeastern Arizona (cited as *Leptoyphlops dulcis dulcis*, but populations now allocated to *Rena dissecta*) found at least some of a wide variety of arthropod remains in every stomach!

Rena humilis **(Leptotyphlopidae) Western Threadsnake**

For this secretive species, I was only able to dissect eleven individuals, and only one was positive. The prey item found seemed to be a termite, reportedly a common prey for this species in the family Leptotyphlopidae. Nevertheless, according to Punzo (1974), *Rena humilis* in southeastern Arizona feeds on a variety of small arthropods in addition to ants and termites. There are other reports indicating that termites are much more important food items in *Rena humilis* (Webb and Shine, 1992; Parpinelli and Marquees, 2015).

Miscellaneous Other Species Examined

For this In addition to the above focal snake species above for which there was prior literature indicating the adults fed on arthropod prey, I was also interested in juveniles of a few other species that possibly were feeding on arthropods as juveniles, and then transitioned to feeding on vertebrate prey. Such dietary shifts occur in many reptile species, and are associated with age-related increase in body size (Vitt and Caldwell, 2009). The species in this study were represented by a few individuals of *Heterodon kennerlyi, Sistrurus tergiminus*, and a few individuals of young-of-year species of *Crotalus*. The vertebrate (especially mammalian) diet of rattlesnakes in the latter genus has been reasonably well-reported in herpetological literature (e.g., Beavers, 1976; Reynolds and Scott, 1982; Andrade and Abe, 1999; Taylor and Denardo, 2005). Athropod or other invertebrate ingestion events in the young-of-year and in juvenile rattlesnakes are mostly to be found as images or anecdotes on the Internet.

***Heterodon kennerlyi* (Dipsadidae) New Mexico Threadsnake**

I examined 16 juvenile specimens of this species, only one of which had identifiable remains in the digestive tract. That individual (specimen number 10451) did have insect fragments present. Adults are known to feed on a variety of vertebrate prey, especially toads and small mammals, but also is known to feed on lizards and amphibians, as well as small turtles and birds (Werler and Dixon, 2000; Durso, 2011; Walley and Eckerman 1999). There is no mention in the literature of this species or its close relatives that the diet of juveniles differs from the adults, or that insects may be eaten by young hog nosed snakes.

***Crotalus atrox* (Viperidae) – Western Diamond-backed Rattlesnake**

The two juveniles of this rattlesnake examined, and both had food items in the digestive tract (UTEP 21590 and 12079). One specimen had two different sets of insect fragments, from a beetle and ant drone. The second had mammalian fur present, most likely from a rodent.

***Crotalus lepidus* (Viperidae) Rock Rattlesnake**

Four juveniles were dissected for gut contents, and two had identifiable remains present. The two positives (UTEP 10787, 10788) were for spider fragments and centipede segments, respectively. The other two specimens had no identifiable remains, although one of these did have debris that could have been from some type of invertebrate. The adults of this rattlesnake species have been known to primarily feed on lizards, but their second most common prey found in large diet study of the subspecies *Crotalus lepidus klauberi* (Holycross, et al., 2002) was centipedes. In another study resulted in discarded arthropod fangs and chitinous exoskeleton fragments were found in the fecal matter of wild caught specimens (Beaupre, 1995).

***Crotalus scutulatus* (Viperidae) Mohave Rattlesnake**

Only one specimen was dissected (UTEP 21582), and its digestive tract was found to contain rodent fur.

***Sisturus tergeminus* (Viperidae) Western Massasagua**

When originally planning this study, I wanted to include this small species of rattlesnake in the survey for arthropod prey items, even though its spotty distribution in the Chihuahuan Desert would likely make obtaining very many positive individuals unlikely. That scarcity proved to be the case, as only six specimens were available for dissection (and half of them had food items). Of the three positives, one had mammalian prey debris, the second had spider fragments and the third had insect fragments. The insect fragments were subsequently identified by C. M. Wilson (University of Texas at El Paso) as representing a bee of the Family Halictidae.

The Chihuahuan Desert populations of massasagua are currently allocated to the subspecies *Sistrurus tergeminus edwardsii*, the Desert Massasagua (Powell, et al., 2016). A large study of this subspecies (under its former taxonomic allocation of *Sistrurus catenatus edwardsii*) over its range in Arizona, Colorado, and New Mexico was conducted by Holycross and MacKessy (2002). Of a total of 165 prey items identified, these authors found only centipedes to be the arthropods in the diet (9.1%), with vertebrate prey making up the balance (lizards 58.8 %, mammals 30.9%, snake and spadefoot toad, less than 1% each). The Eastern Massasagua (*Sistrurus catenatus* in the strict sense) is known to include spiders and insects in its diet (Hallock, 1992; Holycross and Mackessy, 2002; Gibbs and Rossiter, 2008; Weatherhead et al., 2009), but these prey types in the Desert Massasagua are apparently the first for *S. tergeminus*.

Discussion

The results of this study affirm that arthropods are important prey items for the snake species studied in the Family Colubridae (the genera *Gyalopion, Sonora, and Tantilla,* for which I had reasonable sample sizes). The most common prey items were spiders, insects and scorpions. In my observations, it became clear that these snakes feed primarily on spiders because they are probably the most frequently occurring prey items in their environment. Spiders are also relatively fragile and easily disabled by a snake's dentition. However, there were a few specimens that had multiple different prey items in their digestive tracts, suggesting to me that despite spiders being the most commonly encountered prey, these snakes are highly likely to feed on any arthropod of appropriate size they encounter while foraging. For example, I found one *Gyalopion canum* specimen that had ingested such diverse fare as a solifugid and a vejovid scorpion in addition to a spider. The other species had specimens which had different prey items in their stomachs, even though the most common were spiders.

Does this group of species represent dietary specialists, that is, are they stenophagous species? Seib (1985) pointed out that broad diets versus narrow diets are on a "continuum of possible feeding strategies." As mentioned earlier, there is little indication in the snake diet literature as to decide at what threshold frequency a prey item or prey category must be reach before a species could be placed on the "specialist" end of the continuum. Henderson and Schwartz (1986), after reviewing the available stenophagous versus euryphagous snake diet literature, pointed out a general pattern where snakes apparently feeding on only a single prey group will usually feed on several genera in that group. Moreover, in the literature surveyed for this thesis, the most common prey categories are usually in the 30-75% frequency range. Snakes whose diets are composed of 95% or more of one prey type are apparently quite rare in nature (e.g., Kofron, 1978; Henderson and Schwartz, 1986). The best that can be said from the present study is that in the colubrid species examined for this study, spider remains were the most numerous.

Although more data on the two species of *Rena*, and on *Diadophis punctatus*, would be needed before any generalizations about these snakes in Chihuahuan Desert habitats could be made. Many species of snakes are opportunistic foragers and/or sit-and-wait predators, and will eat anything that provides a feeding behavior stimulus. Thus, despite small sample sizes, I suggest that in Chihuahuan Desert communities, the species *Gyalopion canum, Sonora semiannulata, Tantilla nigriceps* and *T. hobartsmithi* are selecting spiders as their primary prey items.

For the future direction of this research, the employment of greater discrimination of prey species identification from the fragments present in the digestive tract and larger sample sizes would be required. Requirements for the former involve microscope canvassing of species-specific exoskeletal diagnostic features for an entire desert arthropod fauna. Also, biomechanical aspects of gape limitations of the various species and genera on possible prey selection of hard-bodied (beetles) versus relatively soft-bodied (spider) prey would also be worthy of study (Cobb, 2004). Lastly, the entire "dietary shift" phenomena in snakes that feed on mammalian and avian prey as adults, but are presumed to take mostly invertebrates as neonates and juveniles, could be more thoroughly investigated across a larger community assemblage of snake species. Another subject in regards to biomechanics and prey shifting, include species in such genera as *Thamnophis, Rhinocheilis,* and *Hypsiglena*. These species could potentially have dietary shifts from invertebrates to vertebrates, such as *Thamnophis* as juveniles feeding on invertebrates like worms and or tadpoles, then shifting to vertebrates as adults like small lizards or toads (Hamilton, 1951). Another candidate is *Hypsiglena*, night snakes. According to a study in 1999 (Rodríguez-Robles, Mulcahy, and Greene, 1999) on members of this genus, there seemed to be evidence of such a shift in that the smaller individuals fed on insects, small snakes and squamate eggs, but the larger ones went on to small lizards and frogs. I recommend these dietary shift phenomena be looked into in the future.

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Appendix: Museum Specimens Examined

Crotalus atrox (Juveniles)
(positive)
UTEP 12079
(negative)
UTEP 21580

Crotalus lepidus (Juveniles)
(positive)
UTEP 10787
UTEP 10788

Crotalus viridis (Juveniles.)
(negative)
UTEP 21519
(negative)
UTEP 101643
UTEP 12334

Diadophis punctatus
(positive)
MSB 60604
TNHC 49888
TNHC 99115
UTEP 15815
UTEP 10642
(negative)
MSB 19751
MSB 51994
MSB 61817
MSB 61839
MSB 74293
TNHC 4150
TNHC 81129
TNHC 89595
TNHC 89596
TNHC 98140
UTEP 195
UTEP 1983
UTEP 3734
UEP 10019
UTEP 10716
UTEP 11109
UTEP 11164

Diadophis punctatus, continued:
UTEP 11209
UTEP 11929
UTEP 12061
UTEP 12106
UTEP 15956
UTEP 17440
UTEP 18504
UTEP 21747

Gyalopion canum
(positive)
MSB 53327
MSB 56803
TNHC 60235
TNHC 65334
TNHC 80862
TNHC 80863
TNHC 80864
TNHC 85307
TNHC 89597
TNHC 90429
TNHC 97406
TNHC 99417
UTEP 8812
UTEP 12000
UTEP 12327
UTEP 12328
UTEP 12329
UTEP 12335
UTEP 15895
UTEP 16302
UTEP 17167
UTEP 17490
UTEP 19830
(negative)
MSB 11576
MSB 56802
MSB 71614
TNHC 16265
TNHC 80856
TNHC 89759
TNHC 97049
UTEP 2036

Heterodon kennerlyi (Juveniles)
(positive)
UTEP 10451
(negative)
MSB 48010
MSB 49548
MSB 50224
TNHC 84304
UTEP 9991
UTEP 10450
UTEP 11348
UTEP 14145
UTEP 15467
UTEP 15810
UTEP 16127
UTEP 17672
UTEP 18532
UTEP 18947

Heterodon nasicus (Juveniles)
(all negative)
MSB 60730
MSB 74802
TNHC 11622
UTEP 11005

Pituophis catenifer (Juveniles.)
(all negative)
UTEP 21512]
UTEP 21513]
UTEP 21572]
UTEP 21573]
UTEP 21574]

Rena dissecta
(all negative)
MSB 59515
MSB 61819
TNHC 66447
TNHC 66486
TNHC 60639
TNHC 62346
TNHC 85322
UTEP 1200
UTEP 1525
UTEP 1529
UTEP 1530

Rena dissecta,, continued:
UTEP 1721
UTEP 1862
UTEP 17787

Rena humilis
(positive)
TNHC 68780
(negative)
MSB 20869
MSB 33646
MSB 60588
TNHC 3922
UTEP 85
UTEP 792
UTEP 793
UTEP 2488
UTEP 2775
UTEP 2776

Sistrurus tergeminus (arthropod prey)
(positive)
MSB 72088
UTEP 16268
(negative)
UTEP 16104
UTEP 16220
UTEP 18639
UTEP 21683

Sonora semiannulata
(positive)
MSB 9898
MSB 9904
MSB 9905
MSB 9907
MSB 20806
MSB 20815
MSB 66855
MSB 71622
MSB 71646
MSB 86560
MSB 86563
TNHC 11623
TNHC 12606
TNHC 12683

Sonora semiannulata, continued:
TNHC 32538
TNHC 66592
TNHC 85544
TNHC 85545
TNHC 88125
TNHC 99317
UTEP 570
UTEP 11012
UTEP 11094
UTEP 11526
UTEP 10651
UTEP 10652
UTEP 10655
UTEP 13625
UTEP 16106
UTEP 17724
(negative)
MSB 9901
MSB 9906
MSB 19758
MSB 20757
MSB 59516
MSB 66861
MSB 86561
MSB 86562
TNHC 240
TNHC 3080
TNHC 12273
TNHC 14137
TNHC 14990
TNHC 19228
TNHC 19230
TNHC 29229
TNHC 32536
TNHC 32537
TNHC 32609
TNHC 42217
TNHC 61465
TNHC 61466
TNHC 61467
TNHC 66593
TNHC 66594
TNHC 85547
UTEP 10027
UTEP 11222

Sonora semiannulata, continued:
UTEP 16000
UTEP 10653
UTEP 10654
UTEP 10998
UTEP 12103
UTEP 15718
UTEP 16312
UTEP 17729
UTEP 19294

Tantilla hobartsmithi
(positives)
MSB 18416
TNHC 12716
TNHC 66740
TNHC 66741
TNHC 68780
TNHC 86072
TNHC 86075
TNHC 86077
UTEP 571
UTEP 789
UTEP 2461
UTEP 2804
UTEP 9060
UTEP 10028
UTEP 10038
UTEP 12000
UTEP 15957
UTEP 18380
UTEP 19232
(negative)
MSB 18350
MSB 18371
MSB 18417
MSB 18418
MSB 18420
TNHC 3922
TNHC 4174
TNHC 12548
TNHC 28408
TNHC 66742
TNHC 66743
UTEP 235
UTEP 791

UTEP 1722
UTEP 2460
UTEP 2467
UTEP 9415
UTEP 11413
UTEP 11864
UTEP 13895
UTEP 14165
UTEP 15335
UTEP 15448
UTEP 16070
UTEP 17555
UTEP 17556
UTEP 20467

Tantilla nigriceps
(positive)
MSB 38461
MSB 38525
MSB 43647
MSB 43674
MSB 60372
MSB 60374
MSB 72798
TNHC 12730
TNHC 86095
TNHC 86146
TNHC 86147
TNCH 89881
UTEP 1981
UTEP 11120
UTEP 12347
UTEP 14133
UTEP 14791
UTEP 16357
(negative)
MSB 15135
MSB 26030
MSB 38494
MSB 60373
MSB 60377
MSB 60379
MSB 72148
TNHC 11734
TNHC 12637
TNHC 12762

Tantila nigriceps (continued):
TNHC 60279
TNHC 66173
TNHC 86119
TNHC 89679
TNHC 89694
UTEP 6098
UTEP 11126
UTEP 11172

Vita

Victor Manuel Parga, Jr. was born in El Paso, Texas. He graduated from Del Valle High School in El Paso in May 2010, and attended El Paso Community College (EPCC) starting in the fall of 2010. While at EPCC, he volunteered as a research assistant to Dominic Lannutti, a faculty member involved in snake research. He received an Associate's Degree in Biological Sciences (Pre-Veterinary Option) from EPCC in winter of 2012.

Still very much interested in reptile biology, he enrolled in the spring of 2013 at the University of Texas at El Paso (UTEP) to pursue a B.S. degree in Biological Sciences (Ecology and Evolutionary Biology Option). This degree was completed in the Spring of 2015. In the Fall of 2015 he was accepted and entered into the M.S. program in the Environmental Science, housed in the Department of Geological Sciences. While an M.S. student, he was a graduate teaching assistant for the laboratory courses in Introductory Biology and Organismal Biology (Fall 2015, Spring 2016, and Spring-Fall 2017). His research for this thesis was performed under the direction of Dr. Carl Lieb of the Biological Sciences Department.

He hopes to continue investigations in herpetology after completing the M.S. degree. This thesis was typed by Victor Manuel Parga Jr.

Contact information: vmparga2@miners.utep.edu