

DIET OF A POPULATION OF PRAIRIE RATTLESNAKES (*CROTALUS VIRIDIS*) IN KANSAS

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ABSTRACT: This study examined prey items consumed and seasonal feeding events within a Prairie Rattlesnake (*Crotalus viridis*) population near Ulysses, Kansas, USA. A total of 183 specimens were collected over a period of three consecutive years (2012–2015) during the active season from April to October. Most prey items consumed by this population were taken in spring between emergence from hibernacula and mating in early summer. Gravid females continued to take prey, likely opportunistically, while gestating. The only ontogenetic shift in diet composition was related directly to prey size. Larger snakes exhibited a preference for larger prey items. The two most abundant taxa in the diet of this population were *Peromyscus* spp. (29.8%) and *Sylvilagus* spp. (17.0%). Only one juvenile had consumed any prey within a week of capture.

Key Words: *Crotalus viridis*, diet, Prairie Rattlesnake, prey, rodent

INTRODUCTION

Rattlesnakes are unique to the Americas and inhabit a variety of ecosystems, including deserts, wetlands, forests, and open grasslands. Several species have seen dramatic contractions in range due to habitat loss/fragmentation (Wittenberg and Beaupre 2014) and persecution by humans (Martin et al. 2008). Four species of rattlesnakes can be found in Kansas, USA. One, the Prairie Rattlesnake (*Crotalus viridis*), ranges across the western half of the state (Collins et al. 2010). The Prairie Rattlesnake's range overlaps with those of several rodent species often regarded as pests and/or disease vectors by humans (Reid 2006, Kays and Wilson 2009).

Many snake species, including rattlesnakes, exert a measure of population control over pest species such as rats, mice and rabbits, as well as limit the quantity and scope of diseases spread by these prey species (Bouskila 1995). Deer mice (*Peromyscus* spp.) are reservoirs for a number of diseases that affect humans such as Hantavirus (Centers for Disease Control 2021), Ehrlichiosis and Babesiosis (Cronin 2014). *Peromyscus* species are a major part of the diet of many *Crotalus* species, including the Prairie Rattlesnake (Fitch 1998). Control of these pest species can in part be assisted by their known predators (Collins et al. 2010, Fogell 2010).

Several studies and field guides have identified diet composition in populations of Prairie Rattlesnakes and other crotalid species (Conant and Collins 1998; Clark 2002; Collins et al. 2010; Fogell 2010). Diet items reported mostly include small mammals and birds with some geographic variation in composition (Conant and Collins 1998, Fitch 1998). Prairie Rattlesnakes have been identified as generalist predators that tend to utilize the most abundant prey species within the area (Holycross 1993). Diet composition within and between populations of Prairie Rattlesnakes can provide researchers with information on prey presence in a study area, as well as identify shifts associated with growth and development of individual predators (ontogenetic shifts).

Prairie Rattlesnake diet varies across time and space, as well as across life stages. As individuals grow, they are able to consume larger prey, while younger, smaller individuals are limited by gape size to correspondingly smaller prey items. The goal of this study was to identify what and when this population of Prairie Rattlesnakes was eating and to compare those data with those previously reported.

While data for adult Prairie Rattlesnakes are readily available, no other published study has examined such a large portion of a single population (183 individuals) from

a single area (approx. 129.5 hectares) collected over three consecutive short active periods. There are records of many large individuals collected from single populations, as in rattlesnake round-ups (Fitch 1998, Schmidt 2002), but there are no collections currently available for study that are as comprehensive as that upon which this paper is based. This unique collection is particularly valuable from an ecological standpoint in that it represents all age classes of a single population and may be used to identify ontogenetic changes in prey consumption.

MATERIALS AND METHODS

A preserved collection of 183 Prairie Rattlesnake specimens housed in the Sternberg Museum of Natural History at Fort Hays State University, Hays, Kansas, USA was used to collect data for this study. These specimens were collected by a group of environmental consultants contracted to facilitate a safe working environment, free of venomous snakes, for workers removing structures and materials from a decommissioned natural gas processing facility on privately owned property near Ulysses, Kansas. In compliance with contractual agreements specified by clients, all removed snakes were humanely euthanized. Specimens were deposited and catalogued in the Sternberg Museum of Natural History in Hays, Kansas to be used for future ecological studies (Dan Fogell, pers. comm. 2015).

Standard dissection techniques (Smith and Schenk 2014) were used to determine the presence/absence of prey items. Liver samples were removed and preserved in 95% ethanol for use in future genetic analysis studies. The stomach and intestines of each individual were dissected and examined for intact prey, partially digested prey, and indigestible mammalian guard hairs. Prey items were visually identified to lowest taxonomic level possible.

Whole or partial prey items were fixed in 10% neutral buffered formalin and stored in 70% isopropanol until they could be identified using body measurements, skull and bone characteristics, and hair samples. If only guard hairs were found, they were allowed to air dry and were stored for later identification in petri dishes marked with an alpha-numeric code associated with the individual from which the sample was removed.

Using a timeline for digestion based on methods adapted from Wallace and Diller (1990), we estimated the time elapsed between feeding and capture of individuals by documenting the location of prey remains within the digestive system of the snake. This method was used to estimate discrete numbers of prey items ingested by individual snakes. If a prey item was in the stomach, feeding was estimated to have occurred within one day of capture. If a prey item was in the small intestine, the snake was estimated to have fed three days prior to capture. If a prey item was in the large intestine, the snake was estimated to have fed four days prior. If scat was able to be palpated out, the snake was estimated to have fed seven days prior to capture. If prey and guard hairs were found in separate locations in the digestive tract (e.g. a hair sample in the stomach and another hair sample in scat from the cloaca), they were assumed to be two different prey items and identified accordingly. Prey items were recorded and prey species composition was analyzed. Feeding frequency and abundance of prey consumed were compared with results from other population diet studies.

Intact prey items were identified using field guides (Reid 2006, Kays and Wilson 2009, Collins et al. 2010). Partially digested prey was identified using skull and oth-

er skeletal features (Reid 2006, Kays and Wilson 2009). Often, skull characteristics could not be used for prey identification because the snake had ingested the prey head first and the head was the first part of the body dissolved by digestive fluids. In these cases, the hind feet and tail were examined and identified when possible using guidebooks on North American mammals (Reid 2006, Kays and Wilson 2009). Any remaining prey items that were not clearly identifiable were identified from guard hairs using techniques adapted from Moore et al. (1974). In mammals, dorsal guard hairs are unique to species Moore et al. 1974). They are largely indigestible by snakes and can be used to help identify prey (Clark 2002). Several characteristics are useful in identifying dorsal guard hairs, including basal configuration, hair color, band color and location, cortex, medullary configurations, shield configurations, scale patterns and margins, and hair strictures (Moore et al. 1974, Holycross 1993).

Hairs were isolated from digestive tract and cloacal samples and cleared of natural oils and debris in xylene for approximately one hour. Hairs were then placed on a glass slide marked with a number-letter combination unique to each individual and examined at 40x, 100x, and 400x magnification using a light microscope (Leica™). Characteristics visible at 40x magnification were hair strictures and length of hairs. At 100x magnification, color bands and basal configuration could be identified. Medullary configurations and scale patterns were not evident until they were examined under 400x magnification.

If a scale pattern could not be seen clearly and if identification relied solely on the scale pattern, a scale cast was made using techniques modified from the forensics website Identification of Human and Animal Hair ([Accessed 3/18/2016](https://www.fda.gov/oc/ohrt/identification-of-human-and-animal-hair)). Scale casts were created by brushing a thin layer of clear nail polish (Sally Hansen – Hard as Nails™) onto a clean glass slide and placing a hair sample onto the polish. Once the polish was almost dry (tacky), the hair was pulled quickly off the polish, leaving an imprint of the scale pattern which could then be examined using light microscopy.

Table 1. Identification, frequency and percent occurrence of prey items found during dissection of a population of *Crotalus viridis*.

Prey item	Frequency	
	(count)	(%)
Aves	4	7.8
Reptilia		
<i>Plestiodon obsoletus</i>	1	1.9
Mammalia		
Rodentia		
<i>Microtus</i>	6	11.8
Muridae	3	5.9
<i>Onchomys</i>	1	1.9
<i>Perognathus</i>	3	5.9
<i>Peromyscus</i>	14	27.5
<i>Chaetodipus</i>	1	1.9
<i>Spermophilus</i>	1	1.9
Lagomorpha		
<i>Sylvilagus</i>	9	17.6
Insectivora		
Soricidae*	4	7.8

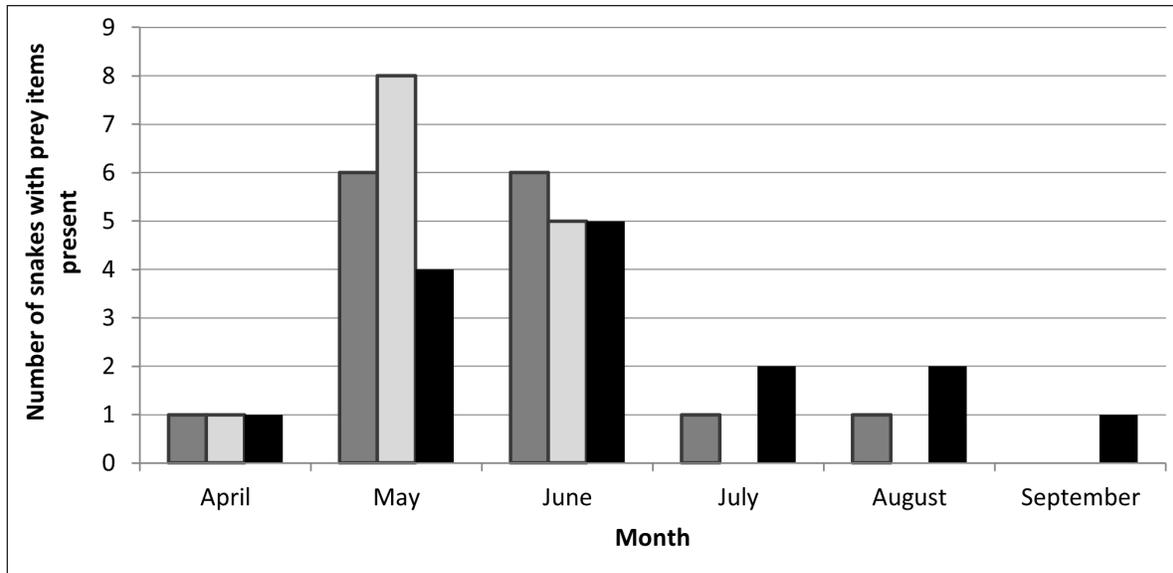


Figure 1. Frequency of prey items consumed by month for gravid females, non-gravid females and males in a population of Prairie Rattlesnakes (*Crotalus viridis*) near Ulysses, Kansas. Prey items were most often consumed in May and June each year. Dark gray: gravid females; light gray: non-gravid females; black: males.

Table 2. Adapted from Fitch (1998). Geographic variation in *Crotalus viridis* prey composition

Study	Origin of Sample	Main prey
Present study	SW Kansas	<i>Peromyscus</i> , <i>Sylvilagus</i>
Fitch (1998)	W Kansas	Ground squirrel, wood-rat
Wallace and Diller (1990)	Nez Perce Co. and Latah Co., N Idaho	Ad: vole, deer mouse Yg: shrew
McCartney (1989)	Okanagan Valley, S British Columbia	Ad: vole, gopher, mouse Yg: vole, shrew
McCartney and Gregory (1988)	Okanagan Valley, S British Columbia	Ad: vole, gopher, mouse Yg: vole, shrew
Duvall, King, and Gutzwiller (1985)	Carbon Co., S-central Wyoming, 6900'	Deer mouse
Gannon and Secoy (1984)	Leader, SW Saskatchewan	Ground squirrel, cottontail
Diller and Wallace (1985);	Nez Perce Co. and Latah Co., N Idaho	Ad: vole, deer mouse Yg: shrew
Klauber (1936)	Platteville, Boulder Co., N central Colorado	Ad: deer mouse Yg: lizard (<i>Holbrookia</i>)
Klauber (1936)	South Coronados Is., Baja California	Lizards: <i>Uta</i> , <i>Eumeces</i> , <i>Elgaria</i>
Heyrend and Call (1951) Glissmeyer (1951)	Grantville, Tooele Co., NW Utah	Ad: small mammals Yg: lizards
Fitch (1949)	Madera Co., central California	Ad: ground squirrel Yg: pocket mouse, spadefoot toad
Klauber (1956)	Pierre, Hughes Co., central South Dakota	Vole, lark bunting, deer mouse

RESULTS

Of the 183 snakes examined, 47 had prey items in the stomach or intestines. Sixteen of the 47 had identifiable animals in the stomach. Four had feathers in stomach and intestines. The remaining 27 individuals had only hairs and bone fragments in the intestines. (Appendix A). The majority (90.2%) of prey items consumed were small mammals; 7.8% were birds and one lizard accounted for 1.9% of the prey items consumed (Table 1).

Sixteen males, 15 gravid females and 16 non-gravid females had consumed prey items. There were three individuals that were notably successful at prey acquisition prior to capture. One male and one gravid female

each had two different prey items in different locations within the digestive tract. One non-gravid female had three individual murids in her stomach, suggesting she found a nest and consumed its occupants. In summary, seventeen snakes fed within 24 hours of capture. Seven snakes had eaten within 2-3 days of capture, suggested by the presence of hair and no identifiable bones or intact body parts (e.g., tails, feet) in the stomach. Twenty-three snakes contained only hairs in the small and large intestines, indicating they had eaten within 4-6 days prior to capture.

Many prey items, especially small mammals, were consumed in spring between emergence from hibernac-

ula and mating in early summer (Figure 1). Four snakes (8.9%) had eaten in April; 34 snakes (75.5%) had eaten in May and June; three snakes (6.7%) had eaten in July; three snakes (6.7%) had eaten in August; and one snake (2.2%) had eaten in September. Of the 47 snakes with prey items, gravid females (33.3%), non-gravid females (33.3%) and males (33.3%) were equally represented. Two snakes with prey items – one non-gravid female and one male – had no capture date associated with them and were subsequently removed from the timeline statistics.

DISCUSSION

In this study population, a diverse composition of prey species was consumed. The majority of prey consisted of small mammals, though a small percentage consisted of birds and a single lizard species. The more frequent appearance of *Sylvilagus* spp. prey in larger adults is consistent with an expected ontogenetic shift towards larger prey. There was little overall difference in the diet composition of this population compared to other populations of Prairie Rattlesnakes and closely related species along similar latitudes (Table 2). However, the data comparison from other latitudes indicates geographic shifts in prey composition, supporting the suggestion that Prairie Rattlesnakes are generalist and opportunistic predators.

Wallace and Diller (1990) examined 106 prey remains from Northern Pacific Rattlesnakes over the course of nine years in northern Idaho. They found that first-year juveniles consumed shrews (Soricidae) exclusively and immature snakes fed exclusively on small mammals, including shrews, deer mice (Cricetidae), and voles (Cricetidae). Adult diets consisted of mice, voles, rabbits (Leporidae), and more rarely a bird or lizard. Several shrew species occur in Kansas that do not occur in Wyoming. Therefore, hairs from Kansas shrews are not part of the guard hair key published by Moore et al. (1974). While there are some species of Soricidae included in Moore et al. (1974), the medullary configurations and scale patterns were different enough from those present in the Kansas Prairie Rattlesnake diet samples that they could not be identified as any species included in the Wyoming key. Shrews are sympatric with Prairie Rattlesnakes in Kansas (Kays and Wilson 2009, Reid 2009) and there is no reason to believe they would not be part of the snake's prey base; thus, we feel confident that our samples were identifiable as shrews.

In more southerly populations, lizards and amphibians tend to be more inclusive in Prairie Rattlesnake diets (Fitch and Twining 1946, Fitch 1949, Glissmeyer 1951, Klauber 1956, Sparks et al. 2015), especially in young individuals (summarized in Fitch 1998, Sparks 2015). Diet composition in populations of Northern Pacific Rattlesnakes (*Crotalus oregonus oregonus*, previously *C. viridis oregonus*) in British Columbia were similar to that of populations in California (Macartney 1989, Sparks et al. 2015) except that in California, lizards were present in the diet (Sparks et al. 2015). Lizard populations sympatric with Prairie Rattlesnakes are not as common at more northern latitudes than in more southern portions of their range (Powell et al. 2016, McGinnis and Stebbins 2018), though Wallace and Diller (1990) did find that a Western Skink (*Plestiodon skiltonianus*) was consumed by a gravid female in Idaho. In Kansas, skinks (*Plestiodon* spp.), Prairie Lizards (*Sceloporus consobrinus*), Lesser Earless Lizards (*Holbrookia maculata*), Six-lined Racerunners (*Aspidoscelis sexlineatus*) and Texas Horned Lizards (*Phrynosoma cornutum*) all are sympatric with Prairie Rattlesnakes throughout their range (Collins et al. 2010). Therefore, we would expect lizards to be

prevalent as part of the diet in the Kansas population. However, only one lizard, a Great Plains Skink (*P. obsoletus*), was identified among the prey remains. The specific lizard assemblage at the site of this study population is unknown, therefore we cannot predict which species to expect in the diet, nor can we predict how prevalent they should be. Given that only one immature (< 500 mm) specimen was identified to have prey contents during this study, it is still possible that lizards are consumed more frequently by smaller and younger size classes.

Prey items from each population of Timber Rattlesnakes (*Crotalus horridus*) studied by Clark (2002) varied significantly. As expected, adults ate prey larger than sub-adults and juveniles. Large snakes did not eliminate small prey from their diets as they grew; they included them along with larger prey items, as the data we collected here also demonstrate. These observations also support the idea that Prairie Rattlesnakes are generalist and opportunistic predators and consume any suitable prey that is readily available in their locale.

Graves and Duvall (1993) discussed prey selection and stated that reproductive female Prairie Rattlesnakes did not cease eating while gravid. Instead, they captured prey items as opportunities presented themselves, rather than actively foraging. Gravid females in this study population from Kansas also did not cease eating, supporting the suggestion of opportunistic feeding and consistent with the findings of Graves and Duvall (1993). The number of gravid females with prey items was surprising, given previous assumptions that food intake notably decreases or ceases altogether during gestation (Lourdais et al. 2002). Nearly 45% of all gravid females had prey items present in their digestive systems. Of these, 20% had *Sylvilagus* spp. prey in their systems. These results suggest that gravid females may select gestation areas based on microhabitat preferences that align with those of an abundance of small and large prey species, thereby maximizing the number of interactions with prey items while minimizing energy consumed in typical foraging behavior.

CONCLUSIONS

In conclusion, the prey most frequently consumed by individuals in this population was *Peromyscus* spp., followed mainly by other rodents and *Sylvilagus* spp., with only a few non-mammalian prey items selected. This is supportive of the conclusions of other studies that noted small mammals are the principal prey selected across populations (Diller and Johnson 1988, Clark 2002, Glaudus et al. 2008, Dugan and Hayes 2012). Snakes in this study consumed prey throughout the season with peak occurrences in May and June, and gravid females did not cease eating.

By comparing diet data from the population studied here with those of other populations, we can observe the species feeding ecology across populations in a more comprehensive context. The data can then be used to assess feeding variations, including ontogenetic and/or geographic shifts in prey selection, prey availability in a region, and seasonal changes in predation between or within populations.

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SPECIAL DEDICATION

In loving memory of an amazing herpetologist and prodigious teacher, Dr. James D. Fawcett.

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Appendix A. Demographics and diet results from a population of *C. viridis* collected near Ulysses, Kansas

Sex	Gravid	SVL	Month	Stomach or Intestine?	Prey ID	Timeline for eating (days)
M	NA	650	April	Stomach/Intestine	<i>Peromyscus</i>	2-3
F	N	632	April	Stomach	<i>Peromyscus</i>	1
F	Y	687	April	Stomach	<i>Peromyscus</i>	1
F	N	906	April?	Intestine	<i>Peromyscus</i>	4-6
F	Y	697	May	Intestine	<i>Sylvilagus</i>	4-6
M	NA	689	May	Intestine	<i>Reithrodontomys</i>	4-6
F	N	766	May	Intestine	<i>Sylvilagus</i>	4-6
F	Y	682	May	Intestine	Aves	4-6
F	N	763	May	Intestine	Soricidae	4-6
M	NA	1032	May	Intestine	<i>Peromyscus</i>	4-6
M	NA	744	May	Stomach	Aves	2-3
M	NA	650	May	Stomach	Aves	2-3
F	N	745	May	Stomach	<i>Sylvilagus</i>	1
F	N	749	May	Stomach	<i>Perognathus</i>	1
F	Y	810	May	Stomach	<i>Microtus</i>	2-3
F	N	730	May	Intestine	<i>Sylvilagus</i>	4-6
F	Y	739	May	Intestine	<i>Peromyscus</i>	4-6
F	Y	727	May	Intestine	<i>Sylvilagus</i>	4-6
F	N	720	May	Intestine	<i>Perognathus</i>	4-6
F	Y	840	May	Intestine	<i>Perognathus</i>	4-6
F	N	709	May	Intestine	Soricidae	4-6
F	N	673	May	Intestine	<i>Sylvilagus</i>	4-6
M	NA	694	June	Intestine	<i>Peromyscus</i>	4-6
F	Y	687	June	Intestine	<i>Sylvilagus</i>	4-6
F	N	742	June	Stomach	3-Muridae	1
F	Y	705	June	Stomach	<i>Microtus</i>	1
F	N	685	June	Stomach	<i>Peromyscus</i>	1
F	Y	724	June	Stomach	<i>Reithrodontomys</i>	1
M	NA	490	June	Intestine	<i>Onchomys</i>	4-6
F	N	713	June	Intestine	Soricidae	4-6
F	Y	715	June	Stomach AND Intestine	<i>Reithrodontomys</i> hair in stomach. <i>Sylvilagus</i> hair in intestine	R-2-3; S-4-6
M	NA	903	June	Stomach	<i>Plestiodon obsoletus</i>	1

Appendix A, continued. Demographics and diet results from a population of *C. viridis* collected near Ulysses, Kansas

Sex	Gravid	SVL	Month	Stomach or Intestine?	Prey ID	Timeline for eating (days)
F	Y	777	June	Stomach	<i>Microtus</i>	1
M	NA	904	June	Stomach	<i>Spermophilus</i>	2-3
F	N	696	June	Stomach	<i>Peromyscus</i>	1
F	Y	697	June	Stomach	Aves	1
F	N	570	June	Intestine	<i>Microtus</i>	4-6
M	NA	540	June	Stomach	<i>Peromyscus</i>	1
F	Y	685	July	Stomach	<i>Peromyscus</i>	2-3
M	NA	725	July	Intestine	Soricidae	4-6
M	NA	664	July	Animal in stomach; Hair in Intestine	<i>Peromyscus</i> in stomach <i>Chaetodipus</i> hair in intestine	P-1; C-4-6
F	Y	658	August	Stomach	<i>Peromyscus</i>	1
M	NA	550	August	Stomach	<i>Peromyscus</i>	1
M	NA	707	August	Stomach	<i>Reithrodontomys</i>	1
M	NA	562	September	Intestine	<i>Sylvilagus</i>	4-6