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DIET OF ROADKILLED WESTERN RATTLESNAKES (*CROTALUS OREGANUS*) AND GOPHERSNAKES (*PITUOPHIS CATENIFER*) IN SOUTHERN BRITISH COLUMBIA

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ABSTRACT—A critical 1st step in understanding the basic ecology of any predator is to delineate their suite of prey species. In this paper we provide data on the diet of 2 threatened snake species in British Columbia, the Western Rattlesnake (*Crotalus oreganus*) and the Gophersnake (*Pituophis catenifer*). By dissecting the gastrointestinal tracts of roadkilled specimens, we identified a total of 11 different prey types. Unlike what has been previously reported elsewhere for the 2 species, we found a strikingly high degree of overlap between the diets, as shown through Morisita's similarity index ($\hat{C} = 0.98$). The Deer Mouse (*Peromyscus maniculatus*) was the most frequently identified prey type for both species, followed by shrews (*Sorex* spp.). Other prey species consumed by Western Rattlesnakes were approximately even in abundance and in low numbers. Gophersnakes had a wider range of prey consumed at moderate frequencies, including voles (*Microtus* spp.) and birds. We also detected prey in a relatively high percentage of our specimens, likely due to our method of analyzing roadkills rather than sampling live, free-ranging animals. These prey data contribute a better understanding of the natural history and conservation issues facing these 2 threatened snake species, providing insight into how they coexist in a habitat increasingly destroyed and fragmented by human development.

Key words: British Columbia, *Crotalus oreganus*, diet, gastrointestinal tract analysis, Gophersnake, Okanagan Valley, *Pituophis catenifer*, prey, roadkill, Western Rattlesnake

The diet of a predator is central to both the ecology of the species in question and the entire community to which it belongs (Iverson and others 2004; Jiang and Morin 2005). Studies designed to obtain dietary information not only contribute to the construction of food webs, but may also reveal the relative importance of different prey species or specific habitat types for a particular trophic level, even if prey availability is not a limiting factor. In addition, the types of prey consumed and where they are obtained may play an important role in interspecific and intraspecific interactions within a population and community (Marti and others 1993).

Difficulty in obtaining information on predator diets is variable and depends to a large extent on inherent characteristics of the focal organism. For instance, direct observation of feeding behavior in cryptic and smaller species is challenging and often limited to fortuitous

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encounters (Bhupathy and others 2014). Many, if not most, snake species fall into this category, and researchers have consequently developed a variety of methods for collecting dietary data on this taxon. One common method is to palpate feces from the lower abdomen of either an alert or sedated snake (Shewchuk 1996). Another method of collecting fecal matter is to capture snakes and wait for them to defecate (Macartney 1989; Diller and Wallace 1996); this approach may require an extended period of captivity, potentially resulting in stress and forgone opportunities such as breeding, basking, and hunting. As an alternative to the collection of feces, snakes can be forced to regurgitate their gut contents. All sampling methods involving live animals require ethical consideration, especially when animals are deprived of meals (Fauvel and others 2012). Once samples are in hand, however, various methods for identifying prey may be used, such as keying out mammalian hair, stable-isotope analysis (Gillespie 2013), DNA barcoding (Valentini and others 2009), enhanced microscopy, and x-ray microanalysis (Nadjafzadeh 2011).

Another method of obtaining diet information is gastrointestinal tract (GIT) content analysis (Diller and Wallace 1996; Rodriguez-Robles 1998). This technique relies on the availability of dead individuals, an unlikely or undesired resource in many cases (such as rare snake species). However, if carcasses are readily available they may provide a useful resource to study diet (Lee and others 2013). Dissection of deceased snakes provides an opportunity to thoroughly examine the GITs for prey remains and may offer data on multiple meals.

We analyzed the gut contents of roadkilled individuals to investigate the diet of 2 threatened snake species in south-central British Columbia (BC). The Western Rattlesnake (*Crotalus oreganus*) and the Gophersnake (*Pituophis catenifer*) have restricted and generally sympatric ranges in this region. These species are associated with semi-arid grasslands, a habitat type that occurs only in the warmer valley bottoms near the USA–Canada border. Data on the diet of these animals in this northern portion of their range are scant. Although there have been a number of studies on rattlesnakes in British Columbia (for example, Charland 1989; Charland and Gregory 1989; Brown and others 2009; Gomez and others 2015; Lomas and others 2015), only 1 study has investigated diet and prey composition (Macartney 1989). Similarly, information on the diet of Gophersnakes in BC also is limited, with data attained primarily from palpations of live animals at 1 location (Shewchuk 1996).

The limited range of both Western Rattlesnakes and Gophersnakes in BC largely includes the Okanagan Valley, a region experiencing one of the fastest rates of human population growth and development in Canada (Statistics Canada 2014). Thus, studies designed to gather data on the basic ecology and habitat requirements, including food, of these snakes in the Okanagan Valley are of paramount importance to their conservation in Canada. Herein, we present a detailed diet comparison of these 2 species in the south Okanagan Valley, using data obtained by GIT analysis of roadkilled specimens. Because these meso-predators have similar, overlapping ranges, comparative data on their diets will provide insight into the extent of niche overlap or separation along this aspect (Luiselli 2006) and contribute significantly to conservation planning.

Methods

Volunteers opportunistically collected roadkilled snakes in the southern region of the Okanagan Valley in BC from 2000 to 2013. Carcasses were stored in freezers at the Ministry of Forests, Lands and Natural Resource Operations office in Penticton, BC, until dissection. Initial dissections took place in November and December 2013. Carcasses were partially thawed to allow measurements of snout-vent length (SVL) and to remove GITs for storage and later examination in January and February 2014. Rattlesnakes <650-mm SVL were deemed juveniles, and all others considered adults (Macartney 1989; Macartney and others 1990). For Gophersnakes the criterion was 700-mm SVL (Shewchuk 1996).

During GIT dissections we recorded the presence-absence of food contents, the prey species, and whether food was found within the stomach or intestines of each individual snake. Because we dissected and analyzed entire GITs, we were able to identify the presence of food that was already well-digested and contained insubstantial amounts of prey remains (such as single strands of hair, eggshell remnants, and small feathers). We used key characteristics to identify eggshells, feathers, teeth, and

bones, such as dental formulas as well as foot and bone measurements (Nagorsen 2005). Our primary method of identifying prey was the analysis of mammalian guard hairs. We soaked guard hairs in 70% ethanol, then dried and mounted the hairs on labeled slides for inspection under a compound microscope (SPU24-105, B3 Professional Series, Motic). We then determined mammalian prey genus (and species where possible) by identifying important structural features of the hair following a modified dorsal guard-hair analysis methodology (Moore and others 1974). In addition, we cross-examined guard-hair characteristics described by Moore and others (1974) with reference slides sourced from the Royal British Columbian Museum (RBCM) and the Thompson Rivers University (TRU) mammal collections. To reduce the likelihood that multiple prey taxa went undetected, we examined several hairs from each sample. We also used tail and foot measurements as references for samples that contained intact prey body parts (Nagorsen 2005).

In 5 Gophersnake samples, we found small (5 mm by 5 mm) possible remnants of eggshells unaccompanied by more direct evidence of nest predation (such as nestling birds, feathers, etc.). To verify their identity, we conducted x-ray microanalysis using a scanning electron microscope (EVO LS 15, Zeiss) equipped with an energy dispersive x-ray detector system (EDS) (INCA x-act 10mm SDD, Oxford Instruments). We compared control samples (1 chicken eggshell and 2 quail eggshells) to the 5 putative eggshell samples. Spectral mapping of the samples followed standard procedures described in the Zeiss EVO Operational User Guide (Carl Zeiss 2008).

We followed Krebs (1998) and compared the diet overlap of the 2 snake species using Morisita's index of similarity ($\hat{C}$; Morisita 1959) which ranges from 0 (no similarity) to ≈1 (complete similarity). The Morisita index often has been recommended as the best overall measure of diet similarity in ecology, and works best when original data are expressed as proportions (Wolda 1981). Unless sample size is very small, $\hat{C}$ is independent of sample size.

RESULTS

We dissected a total of 50 GITs from roadkilled Western Rattlesnakes and 92 GITs from roadkilled Gophersnakes. Western Rattlesnake carcasses were consistently numerous during the months of June to August, whereas Gophersnake carcasses were most frequent in May–June, and dropped until another peak in September (Fig. 1). Fewer samples of both species were collected in October and November.

The percentage of snakes with GIT contents shifted through the active season, with Gophersnakes increasing one month then decreasing the next. Rattlesnake specimens outside of May followed the same pattern (Fig. 1). Although our sample of rattlesnakes collected in May was small ($n = 5$), all had GIT contents, whereas only half (10 of 20) of the Gophersnakes collected in the same month had GIT contents. Samples for both species collected in July produced low percentages (Western Rattlesnakes: 20%; Gopher Snakes: 40%) followed by a considerable increase in August (73 and 89%, respectively).

Fifty-two percent of the roadkilled Western Rattlesnake samples and 61% of roadkilled Gophersnakes contained detectable food items. For those rattlesnake specimens yielding diet information ($n = 26$), 14 had prey remains in the stomach, 8 in the intestine, and 4 in both. The respective numbers for the 56 Gophersnake samples were 16, 30, and 10. Overall, the lengths of animals with food in their GITs were not significantly different from specimens not containing detectable food items [Western Rattlesnakes: $t = 1.32$, $df = 47$ (unequal SDs), $P = 0.19$; Gophersnakes: $t = 0.88$, $df = 55$ (unequal SDs), $P = 0.38$].

For specimens with detectable food items in the GITs, we were able to identify the prey for 24 of 26 Western Rattlesnake samples, but only 35 of 56 Gophersnake samples. In total, we identified 11 different prey types (Fig. 2; scientific names and actual counts of prey species listed in Appendix). We detected multiple prey items in 2 Western Rattlesnake and 3 Gophersnake GITs. Based on our results, the diets of the 2 snake species are extremely similar ($\hat{C} = 0.98$). For both species, Deer Mice (*Peromyscus maniculatus*) were the most frequent prey species (approximately 42% in Western Rattlesnake prey samples, and approximately 31% in Gophersnake prey samples; Fig. 2). Shrews (*Sorex* spp.) also were commonly occurring prey items for both species, while voles (*Microtus* spp.) and birds were more often represented in the Gophersnake samples

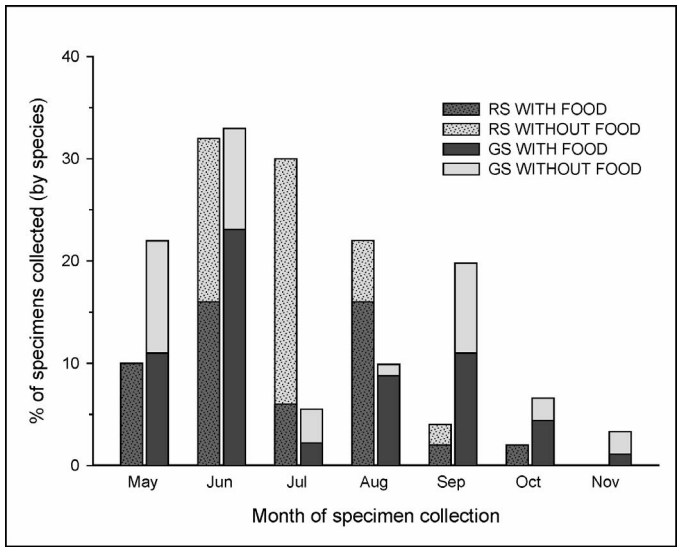

FIGURE 1. Percent of roadkilled Western Rattlesnakes ($n = 50$) and Gophersnakes ($n = 91$; 1 specimen with unknown month of collection) with and without detectable food in their gastrointestinal tracts, separated according to species and month of specimen collection.

(Fig. 2). Western Harvest Mice (*Reithrodontomys megalotis*) and Great Basin Pocket Mice (*Perognathus parvus*) were consumed by both Gophersnakes and Western Rattlesnakes and were approximately even in abundance and in low numbers. Prey species we identified exclusively in Western Rattlesnakes were the Yellow-Bellied Marmot (*Marmota flaviventris*), American Red

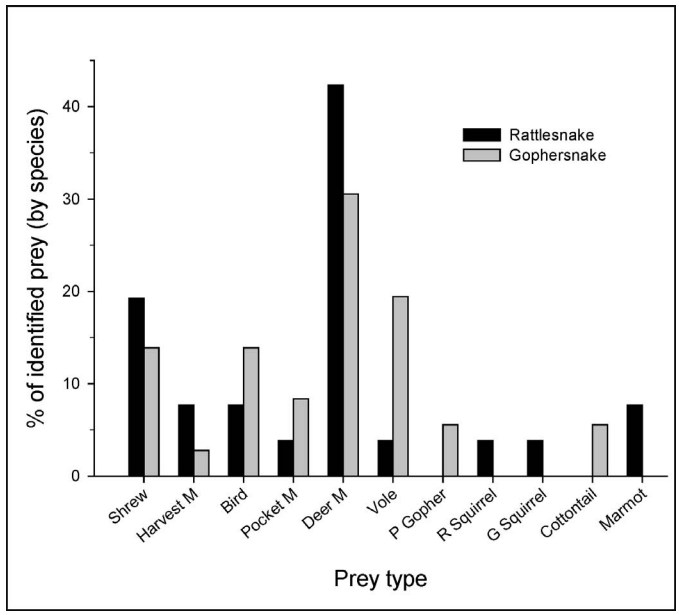

FIGURE 2. Prey species identified in the gastrointestinal tracts of Western Rattlesnakes and Gophersnakes in the Okanagan Valley region of British Columbia, Canada. Prey are arranged on the ordinate according to adult size (smaller to larger). See appendix for a complete list of scientific names of prey.

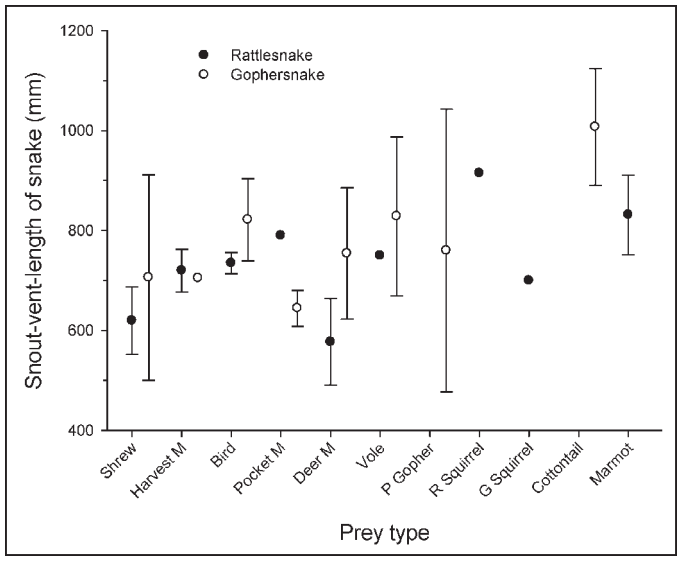

FIGURE 3. Average lengths of Western Rattlesnakes ($n = 49$; 1 specimen with unknown SVL) and Gophersnakes ($n = 92$) according to type of prey detected. Prey are arranged on the ordinate according to approximate adult size (smaller to larger). Error bars represent standard deviation from the mean; absence of an error bar indicates $n = 1$. See appendix for a complete list of scientific names of prey and sample sizes.

Squirrel (*Tamiasciurus hudsonicus*), and Columbian Ground Squirrel (*Urocitellus columbianus*) ($n =$ 1 detection each). Conversely, we detected Great Basin Pocket Gopher (*Perognathus parvus*) and Nuttall's Cottontail (*Sylvilagus nuttalli*) ($n = 2$ of each) only in the Gophersnake samples.

We found the largest prey species, cottontail and marmot, only in large snakes (Western Rattlesnakes: >775 mm SVL; Gophersnakes: >925 mm SVL). A reverse pattern for smaller prey was not clear for either snake species. We found pocket gophers, shrews, and voles in Gophersnakes with a wide range of SVLs. For both species, we identified Deer Mice in the GITs of snakes of varying length (Fig. 3). Still, within the sample of Western Rattlesnakes with identifiable GIT contents, Deer Mice more commonly appeared in smaller snakes (with Deer Mice: SVL = 577 mm, $SD = 86.3$, $n = 11$; without: SVL = 727 mm, $SD = 106.2$, $n = 13$; $t = 3.82$, $df = 22$, $P < 0.001$). This relationship was not apparent in the Gophersnake data ($t = 0.49$, $df = 24$ [unequal SDs], $P < 0.64$).

DISCUSSION

There are 2 notable facets to our results: (1) the percentage of snakes with food items in our roadkilled specimens (both species) was relatively high; and (2) the identification of the prey base for these animals in roadside habitats not only improves our understanding of the basic natural history of the species, but reveals overall similarity in the diet for the 2 species. This suggests a degree of niche overlap for these animals, albeit with some potentially important differences.

For both snake species, the percentage of individuals containing prey was higher than that reported elsewhere in the literature. The percentage of our Western Rattlesnake specimens with detectable prey (52%) was higher than reported by Fitch and Twinning (1946), Diller and Johnson (1988), Macartney (1989), and Wallace and Diller (1990); 15, 40, 5.2, and 12%, respectively. Similarly, the percentage for Gophersnakes containing prey (61%) in our sample was greater than that seen by Diller and Johnson (1988), Shewchuk (1996), and Rodriguez-Robles (2002); 25, 13, and 16%, respectively. Across these studies, various techniques were used to sample and detect prey in the snakes, and this discrepancy likely influenced the percentage of individuals with detectable food items. Our ability to draw samples from both the stomach and intestine in each specimen undoubtedly increased our prey-detection rates. Also, sam-

pling from different habitats, such as higher elevation pine forests and riparian habitats, may affect both the proportion and composition of prey detected. It is possible that roadside habitats may support more abundant small mammal communities (Rotholz and Mandelik 2013), thus increasing the likelihood that snakes containing prey, specifically mammalian prey, would be found on or near roads (assuming the snakes were hunting near the road — an untested assumption). Another possible explanation for the higher percentage of snakes with prey items sampled from roads is that snakes that have recently eaten may utilize roads as sources of heat more often than individuals that have not eaten, and individuals of both species may be more sluggish on heated roads after ingesting prey. The use of anthropogenic sources of heat by female snakes developing eggs or embryos has been examined (Löwenborg and others 2010), but to our knowledge, the relationship between such structures (particularly roads) and recently-fed snakes has not been considered in detail. Latitude may exert a strong influence on this relationship, as in temperate zones heat will become a more limiting resource, particularly at night.

The method of prey detection used by investigators also will affect the types of prey identified. For example, the method used to force regurgitation may only provide data on relatively undigested prey and likely would miss remnant evidence such as single hairs, bird shell fragments, or single feathers. The consumption of nestling mammals, amphibians, and other hairless prey also may go undetected by fecal analysis if guard-hair examination methods are used exclusively.

Another interesting aspect of our data is the difference in collection rates between the 2 species of snakes. The majority of Western Rattlesnake specimens were collected between June and August, dropping dramatically in September, whereas Gophersnake collection rates were bimodal, being most prominent in early summer (May–June) and in September, suggesting search effort was reasonably consistent throughout the active season for both species. Therefore, these data suggest different timing in the risk of road mortality for the 2 species (Jochimsen and others 2014). As diet was similar, more subtle factors relating to the natural history of the 2 species may be at play. Timing of mortality aside, the overall lower numbers of Western Rattlesnakes collected on the roads may also be explained by differences in the species that relate to movements and postures. Western Rattlesnakes are sedentary ambush hunters, whereas Gophersnakes are active and more vagile predators; if this results in the latter crossing roads more often, it would produce more roadkill events. Furthermore, rattlesnakes tend to coil their bodies, providing a smaller target, whereas Gophersnakes are more prone to stretching out and thus are more likely to be hit by a car if on a road (Jochimsen and others 2014).

The overall similarity of prey species we detected for the 2 snakes was striking. In a similar study of the ecology of the same animals in Idaho, using a combination of sampling methods, Diller and Wallace (1996) found food habits to be strongly partitioned: using data from their paper we calculate a value of $\hat{C} = 0.55$, substantially lower than we report herein. One notable difference in their study was that Townsend's Ground Squirrel (*Urocitellus townsendii*; absent from our study area) represented 54% of identified prey types for Western Rattlesnakes, with Deer Mice constituting 43% of detectable prey items in Gophersnakes. The authors suggested that the rattlesnake, being a sit-and-wait venomous predator, was better able to prey on larger ground squirrels than a constrictor (Gophersnakes). We also note that Western Rattlesnakes have been detected (using radiotelemetry) entering ground squirrel and marmot burrows (K Larsen, pers. obs.), both noticeably larger than those of other burrowing rodents in our study area. This suggests that subsurface predation on all sizes of marmots and ground squirrels would be possible. Although ground squirrels are rare in the South Okanagan Valley (O Dyer, pers. obs.), marmots and cottontails are present and were detected in our GIT analyses (in relatively large snakes), although we lack the resolution to distinguish between juvenile or adult prey. Certainly, very large individuals of both snakes are known to successfully prey on mid-sized cottontails and marmots in this region (K Larsen, pers. obs.).

It was not surprising that Deer Mice were the most prominent prey type in our data set, as this species is often the most abundant small mammal in the lower grassland habitats of southern BC (Hales 2011; K Larsen, unpubl.

data). Our results show that predation on this species likely spans all size classes, as Deer Mice were associated with small and large snakes in our sample. Diller and Wallace (1996) also reported high consumption rates of Deer Mice for both species of snakes. The aforementioned rarity of ground squirrels in our study area may result in Deer Mice being more common in the diet of both snakes. After the Deer Mouse, voles (*Microtus* spp.) were a major prey species for Gophersnakes (as per Shewchuk 1996), but not so for Western Rattlesnakes. This contrasts with previous reports of high vole consumption by rattlesnakes (Macartney 1989; Wallace and Diller 1990; Diller and Wallace 1996). Although voles are known to fluctuate considerably in the arid grasslands of southern BC (Hales 2011; K Larsen, unpubl. data), Gophersnakes clearly were encountering these types of small mammals, so abundance of voles alone cannot explain the discrepancy in our data from other studies.

The species we detected in this study should not be considered a definitive list of prey for the Western Rattlesnake and Gophersnake in the Okanagan Valley region. For example, other sampling near the USA–Canada border has detected pocket gophers (Geomyidae) and even Muskrat (*Ondatra zibethicus*) in the diet of rattlesnakes near Osoyoos Lake, yet neither of these appeared in our samples (K Larsen, unpubl. data). We presume that the snakes sampled in this study had hunted near their point of collection on the roads, and with these roads closely following the bottoms of valleys in the south Okanagan, prey species taken by snakes in higher-elevation forested habitats (Lomas and others 2015) may not be represented. Regardless, our data reveals a close similarity in the diet of the 2 snake species in our study area. Luiselli (2006) conducted a meta-review of niche partitioning (particularly diet) in sympatric species of snakes, and concluded the potential for interspecific competition was low in northern communities due to high prey species-specificity and low prey diversity. In contrast, our data suggest a higher potential for competition between these 2 northern snakes, due at least in part to a less diverse prey base. This occurs despite apparently different hunting techniques used by the 2 species. The degree that this competition affects individuals and populations may be alleviated by relatively low densities of snakes at this northern latitude. This finding and other more subtle effects, including prey distribution and abundance, need to be explored.

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APPENDIX. Common and scientific names of detected prey species for Western Rattlesnakes (*Crotalus oreganus*) and Gophersnakes (*Pituophis catenifer*) in the south Okanagan Valley region of British Columbia. RSn = number detections for Western Rattlesnakes, GSn = number detections for Gophersnakes.

Common name	Scientific name	RSn	GSn
Shrew	*Sorex* spp.	5	5
Western Harvest Mouse	*Reithrodontomys megalotis*	2	1
Bird	Class Aves	2	5
Great Basin Pocket Mouse	*Perognathus parvus*	1	3
Deer Mouse	*Peromyscus maniculatus*	11	11
Vole	*Microtus* spp.	1	7
Northern Pocket Gopher	*Thomomys talpoides*	0	2
North American Red Squirrel	*Tamiasciurus hudsonicus*	1	0
Columbian Ground Squirrel	*Urocitellus columbianus.*	1	0
Nuttall's Cottontail	*Sylvilagus nuttallii*	0	2
Yellow-Bellied Marmot	*Marmota flaviventris*	2	0