Feeding ecology of the Great Basin Rattlesnake (*Crotalus lutosus*, Viperidae)

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Abstract: Documenting variation in organismal traits is essential to understanding the ecology of natural populations. We relied on stomach contents of preserved specimens and literature records to assess ontogenetic, intersexual, temporal, and geographic variations in the feeding ecology of the North American Great Basin Rattlesnake (*Crotalus lutosus* Klauber, 1930). Snakes preyed mainly on rodents, occasionally on lizards, and less frequently on birds; squamate eggs and frogs were rarely eaten. There was a positive relationship between predator and prey size. The best predictors of this relationship were prey diameter as a function of snake body length and head size, underscoring the importance of prey diameter for gape-limited predators such as snakes. *Crotalus lutosus* displayed ontogenetic, sexual, and seasonal variations in diet. Smaller rattlesnakes fed predominantly on lizards, whereas larger individuals mostly fed on mammals. Females fed on lizards more often than males. The proportion of mammals in the diet was highest during the summer, a temporal variation that may be related to behavioral shifts in the diel activity and prey selectivity of *C. lutosus*, and (or) to differential abundance of rodents between seasons. Great Basin Rattlesnakes also displayed geographic variation in feeding habits, with snakes from the Great Basin Desert eating a higher proportion of lizards than serpents from the more northern Columbia Plateau.

Résumé : Il est nécessaire de connaître la variation des traits des organismes pour comprendre l'écologie des populations naturelles. Nous avons examiné les contenus d'estomacs de spécimens de collection et consulté la littérature pour quantifier les variations ontogénétiques, sexuelles, et saisonnières dans le régime alimentaire du crotale du Grand Bassin (*Crotalus lutosus* Klauber, 1930) en Amérique du Nord. Ce crotale se nourrit principalement de rongeurs, parfois de lézards, et moins fréquemment d'oiseaux. Les œufs de squamates et les amphibiens sont très rarement consommés. Il y a une relation positive entre la taille des proies et celle des serpents. La meilleure variable prédictive de cette relation est le diamètre de la proie en fonction de la taille du corps et de la tête du crotale, ce qui démontre l'importance du diamètre de la proie pour des prédateurs qui avalent leurs proies entières comme les ophidiens. Les habitudes alimentaires de ce crotale varient en fonction de l'ontogenèse, du sexe et de la saison. Les juvéniles consomment une plus grande proportion de lézards que les adultes, qui se nourissent principalement de petits rongeurs. Les femelles mangent plus de lézards que les mâles. La proportion de mammifères dans le régime alimentaire de *C. lutosus* est plus importante en été qu'au printemps et en automne. Cette variation saisonnière est peut-être due à des changements d'activité journalière ou de sélectivité de proies du crotale et/ou à des abondances variables des divers types de proies entre les saisons. Finalement, le régime alimentaire de *C. lutosus* varie géographiquement : les crotales du Plateau du fleuve Columbia, situé au nord du Grand Bassin, consomment moins de lézards que ceux du Grand Bassin.

Introduction

Variability is widespread in nature (Darwin 1859; Endler 1977, 1986; Foster and Endler 1999; Grant and Grant 2002, 2006; Epperson 2003). Documenting variation in organismal traits is therefore essential to understanding the ecology and evolution of natural populations. For example, studies that quantify within and among individual and population variations can elucidate different patterns of spatial ecology and habitat selection (Gibbons and Semlitsch 1987; Austin et al. 2004; Glaudas et al. 2007), thermoregulatory behavior (Peterson et al. 1993; Dorcas and Peterson 1998), reproductive ecology (Seigel and Ford 1987; Christians 2002; Chiaraviglio and Bertona 2007), antipredator behavior (Greene 1988; Leal and Rodríguez-Robles 1997; Glaudas et al. 2006), feeding ecology (Arnold 1977; Forsman and Lindell 1993; Poulsen et al. 2001; Rodríguez-Robles 2002), and local adaptation (Laugen et al. 2003; Forde et al. 2004).

Among these biological attributes, feeding occupies a central role because individuals must acquire nutrients for growth, maintenance, and reproduction. Furthermore, foraging can affect other characteristics of an organism's biology, such as activity patterns (Cooper et al. 2001), habitat use (Fedriani et al. 1999; Lombardini et al. 2001), defensive behavior (Cooper et al. 1990), and ecosystem biodiversity and productivity (Schmitz 2008). Although the importance of food resources in biological systems has long been established (Hutchinson 1959; Weatherley 1963), comprehensive ecological studies of the dietary habits of free-ranging animals remain relatively rare.

Snakes are excellent model systems for conducting studies of feeding ecology (Seigel 1993). These animals are major predators in many terrestrial and aquatic communities, and documenting their feeding preferences can provide valuable

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information on predator–prey relationships in ecological assemblages (Vitt 1987; Henderson and Crother 1989; Cadle and Greene 1993; Rodríguez-Robles and Greene 1996; Luiselli 2006). Therefore, our main objective in this study was to assess ontogenetic, intersexual, temporal, and geographic patterns of variation in the feeding habits of the Great Basin Rattlesnake (*Crotalus lutosus* Klauber, 1930), a snake that predominantly feeds on lizards and rodents (this study).

In gape-limited predators such as snakes, head size affects the size and type of prey consumed (Shine 1991*a*; Shine et al. 1996; Rodríguez-Robles et al. 1999; Holycross et al. 2002). Juvenile snakes have smaller gapes than adults, a trait that may preclude younger individuals from ingesting prey of relatively large diameter. Therefore, we hypothesized that smaller *C. lutosus* mainly feed on smaller prey (e.g., small lizards), and gradually switch to a diet dominated by larger items (e.g., mammals) as the snakes increase in size. Additionally, because *C. lutosus* males grow larger than females and possess proportionally longer heads (this study), we predicted that males eat larger prey than females. Third, the diel activity of *C. lutosus* varies seasonally; the snakes are active during the day in the spring and fall, but become nocturnal in the summer (Bryan T. Hamilton, personal communication). Because the main prey types of *C. lutosus* differ in their activity patterns (rodents are mainly nocturnal, whereas lizards are mostly diurnal), we expect Great Basin Rattlesnakes to eat a higher proportion of lizards in the spring and fall, and a higher proportion of rodents in the summer. In addition to testing these hypotheses, herein we report the taxonomic composition of the diet of *C. lutosus* and document geographic differences in the feeding ecology of this rattlesnake.

Materials and methods

Study species

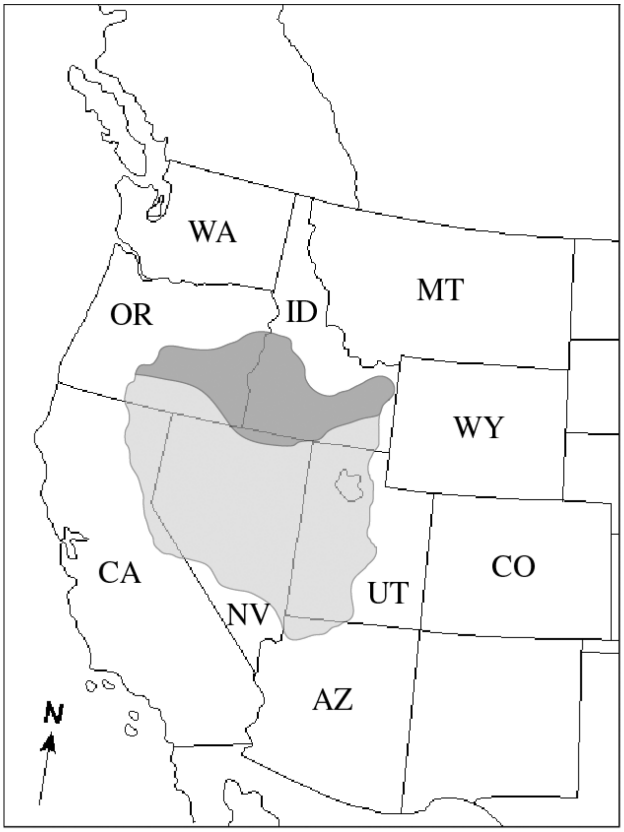
Crotalus lutosus is the only rattlesnake that is widely distributed in the cold deserts of North America. The Great Basin Rattlesnake ranges from central and southeastern Oregon, southern Idaho, and northeastern California south through Nevada and western Utah to northwestern Arizona (Fig. 1). The species usually inhabits arid and semiarid plains, desert areas, and talus slopes of mountainous, rocky areas (Klauber 1972). (The systematic relationships of *C. lutosus*, a taxon belonging to the Prairie Rattlesnake (*Crotalus viridis* (Rafinesque, 1818)) species complex, have been recently studied by several authors (Pook et al. 2000; Ashton and de Queiroz 2001; Douglas et al. 2002), and herein we recognize this snake at the species level, following the recommendation of Douglas et al. (2002).) Individuals can grow up to 135 cm in total length (Ernst and Ernst 2003), although adult body sizes average 73.9 and 65.3 cm in snout-to-vent length (SVL) in males and females, respectively. As most viperid snakes (Old World vipers and adders and Old and New World pitvipers, including rattlesnakes), *C. lutosus* is a sit-and-wait predator that typically selects an ambush site based on the presence of chemical cues left by potential prey (Reinert et al. 1984; Greene 1992, 1997; Secor and Nagy 1994).

Data collection

We relied on examination of preserved specimens and on published and unpublished records to document the dietary habits and assess patterns of variation in the feeding ecology of *C. lutosus*. We checked the stomach contents of individual snakes by making a mid-ventral incision in 659 specimens from the following institutions: Monte L. Bean Life Science Museum, Brigham Young University (BYU), Provo, Utah; California Academy of Sciences (CAS), San Francisco, California; Field Museum of Natural History (FMNH), Chicago, Illinois; Los Angeles County Museum of Natural History (LACM), Los Angeles, California; Museum of Vertebrate Zoology (MVZ), University of California, Berkeley, California; San Diego Natural History Museum (SDSNH), San Diego, California; Utah Museum of Natural History (UMNH), University of Utah, Salt Lake City, Utah; Marjorie Barrick Museum of Natural History (MBM), University of Nevada, Las Vegas, Nevada; and Museum of Biology, University of Nevada, Reno (UNR), Nevada. We avoided type and especially soft, brittle, or otherwise fragile specimens. We dissected 15 additional specimens collected by Bryan T. Hamilton (BTH 87–91, 96, 108–110, 112–116, 119).

Whenever possible, for each snake containing prey we recorded the following variables: complete locality data, date of collection, body size (SVL, ±1 cm), head length (from the tip of the rostral scale to the retroarticular process of the

Fig. 1. Approximate distribution of the Great Basin Rattlesnake, *Crotalus lutosus* (after Stebbins 2003), indicating the segments of the species' range in the Columbia Plateau (dark gray) and Great Basin Desert (light gray). AZ, Arizona; CA, California; CO, Colorado; ID, Idaho; MT, Montana; NM, New Mexico; NV, Nevada; OR, Oregon; UT, Utah; WA, Washington; WY, Wyoming.



right mandible, ±1 mm), maximum head width (±1 mm), body mass (±0.1 g), sex (determined by inspection of the reproductive tract), taxonomic identity of the prey, prey mass (±0.1 g), prey length (±1 mm), and prey diameter (±1 mm). We counted all squamate eggs in the stomach or intestine of a snake as one prey item because they may represent a single feeding event. We weighed snakes and their intact or slightly digested prey after blotting and draining them briefly in paper towel to remove excess fluid. Our data set also incorporates published and unpublished dietary reports of *C. lutosus*. We accounted for redundancy among literature records (i.e., Diller and Johnson 1988, with Diller and Wallace 1996). We performed statistical tests using STATISTICA® version 6.0 (StatSoft Inc. 2000) and StatView® version 5.0.1 (SAS Institute Inc. 1998). Values are means ± 1 SD; all P values are two-tailed unless otherwise indicated. Significance level for all tests was determined at $\alpha = 0.05$.

Results

Feeding habits and predator–prey size relationships

Of the 659 *C. lutosus* examined by us, 144 contained 167 at least partially identifiable prey items. We combined these data with literature records to gain a more accurate assessment of the feeding ecology of the Great Basin Rattlesnake (cf. Rodríguez-Robles 1998). Overall, 85% (301/354) of the prey eaten by *C. lutosus* were mammals, 11.6% (41/354) were squamates, 2.3% (8/354) were birds, 0.8% (3/354) were squamate eggs (one single egg and two clutches of five eggs each), and 0.3% (1/354) were amphibians (Table 1). Among mammals, murid (29.7%, 105/354), sciurid (28.2%, 100/354), and heteromyid (13%, 46/354) rodents were the most commonly eaten prey. Because we also found the scales of sceloporine lizards (genera *Uta* Baird and Girard, 1852 and *Sceloporus* Wiegmann, 1828) in two of the three snakes that ate squamate eggs, it is possible that these eggs were secondarily ingested (i.e., the snakes ate gravid females). The third snake had only squamate eggs in its digestive tract, which suggests that the eggs were consumed directly. Three of the five eggs taken by the latter snake were in the anterior section of the small intestine, which is consistent with the observation that the egg shells of squamate eggs are not easily digested (Harry W. Greene, personal communication).

Most snakes (86.1%, 124/144) contained single prey, whereas 17 (11.8%) and 3 (2.1%) individuals had consumed two and three prey items, respectively. Males and females ate single and multiple prey with similar frequency (single:multiple prey; males, 72:15; females, 48:4; χ^2 test, $\chi^2 = 2.52$, df = 1, $P = 0.11$). We found no significant differences in body size (SVL) between snakes that contained single (61.5 ± 17.9 cm, range = 20.6–102.1 cm, $n = 121$) and multiple (65.0 ± 12.8 cm, range = 42.0–88.8 cm, $n = 19$) prey (ANOVA, $F_{[1,138]} = 0.68$, $P = 0.41$). In studies of food habits, evidence for intraindividual dietary variation comes from multiple prey types in the same specimen (Greene 1989). For Great Basin Rattlesnakes, this variability encompasses at least lizards and mammals, and mammals and squamate eggs.

We could reliably estimate direction of ingestion for 65 prey items, of which 93.8% (61/65) were ingested head-first and 6.2% (4/65) were ingested tail-first. Snakes ingested mammals head-first (98%, 49/50) significantly more frequently than lizards (78.6%, 11/14; $\chi^2 = 7.05$, df = 1, $P = 0.008$). The three lizards eaten tail-first are relatively small species (Common Sagebrush Lizard, *Sceloporus graciosus* Baird and Girard, 1852; Common Side-blotched Lizard, *Uta stansburiana* Baird and Girard, 1852) that were taken by adult (larger) snakes. One passerine bird was swallowed head-first.

The variables describing snake morphology (SVL, head length, head width, body mass) are highly correlated among themselves (linear regressions, ln-transformed data, $r^2 \geq 0.94$, $P < 0.0001$ for all possible pairwise comparisons). The best predictors of the predator–prey size relationship were prey diameter as a function of (*i*) snake body size ($r^2 = 0.78$, $F_{[1,18]} = 27.2$, $P < 0.0001$), (*ii*) snake head length ($r^2 = 0.77$, $F_{[1,16]} = 23.8$, $P = 0.0002$), and (*iii*) snake head width ($r^2 = 0.70$, $F_{[1,17]} = 16.2$, $P = 0.0009$; all linear regressions were performed on ln-transformed data). Prey mass was 12.6% ± 9.1% ($n = 22$) of the predator's body mass and varied from 3.2% to 44%. Prey mass was positively related to predator's body mass (Fig. 2).

Ontogenetic, intersexual, temporal, and geographic variations in feeding habits

Snakes that fed on mammals (SVL, 65.8 ± 14.1 cm, range = 35.1–102.1 cm, $n = 111$) were significantly larger than those that ate lizards (48.9 ± 19.1 cm, range = 20.6–83.2 cm, $n = 34$; $F_{[1,143]} = 31.24$, $P < 0.001$; Fig. 3). Indeed, juveniles (SVL < 54 cm; X. Glaudas, unpublished data) preyed more commonly on lizards than did adults: 45.2% (14/31) of the prey taken by juveniles were lizards compared with 17.5% (20/114) for adults (one-tailed χ^2 test; $\chi^2 = 11.24$, df = 1, $P = 0.0008$). We classified snakes that contained food into four size categories (SVL: 20–40, 40.1–60, 60.1–80, >80 cm). The proportion of lizards in the diet of *C. lutosus* consistently decreased in each of these size categories (20–40 cm: 66.7% (14/21); 40.1–60 cm: 20% (10/51); 60.1–80 cm: 16.1% (9/57); >80 cm: 6.3% (2/33); $\chi^2 = 31.14$, df = 3, $P < 0.0001$). Therefore, our prediction that smaller snakes mainly feed on smaller (lizard) prey is supported by the data.

Crotalus lutosus is sexually dimorphic. Males have larger bodies (SVL, body mass), longer tails, and larger heads (head length, head width; Table 2) than females. Tail length, head dimensions, and body mass are positively correlated with SVL (linear regressions, $P < 0.0001$ for all possible pairwise comparisons). Because males grow larger than females, the differences in tail length, head dimensions, and body mass can simply be a consequence of the size disparity between the sexes. After controlling for sexual differences in body size (SVL) using ANCOVAs, males had relatively longer tails ($F_{[1,133]} = 143.7$, $P < 0.0001$) and heads ($F_{[1,122]} = 5.73$, $P = 0.02$) and were heavier than females ($F_{[1,129]} = 5.52$, $P = 0.02$; excluding three gravid females), but the sexes did not differ in head width ($F_{[1,121]} = 1.94$, $P = 0.16$).

Despite their differences in head length and body size (SVL, body mass), males (15.0% ± 11.7%, range = 4.7%–44.4%, $n = 10$) and females (10.6% ± 6.0%, range = 3.2%–

Table 1. Prey eaten by *Crotalus lutosus*.

Prey taxon	Frequency	Percentage of total number of prey	Sources
Amphibia	**1**	**0.3**	
Anura			
Pelobatidae			
Spea intermontana (Cope, 1883) (Great Basin Spadefoot)	1	0.3	Diller and Wallace 1996
Reptilia	**41**	**11.6**	
Squamata			
Crotaphytidae			
Crotaphytus bicinctores Smith and Tanner, 1972 (Great Basin Collared Lizard)	2	0.6	This study
Gambelia wislizenii (Baird and Girard, 1852) (Long–nosed Leopard Lizard)	1	0.3	This study
Unidentified crotaphytids	1	0.3	This study
Phrynosomatidae			
Phrynosoma platyrhinos Girard, 1852 (Desert Horned Lizard)	2	0.6	Diller and Wallace 1996; this study
Sceloporus graciosus Baird and Girard, 1852 (Common Sagebrush Lizard)	6	1.7	Klauber 1972; Pack 1930; this study
Sceloporus cf. *Sceloporus magister* Hallowell, 1854 (Desert Spiny Lizard)	1	0.3	This study
Sceloporus sp. (Spiny Lizards)	8	2.3	This study
Uta stansburiana Baird and Girard, 1852 (Common Side-blotched Lizard)	3	0.8	This study
Unidentified sceloporine lizards	8	2.3	This study
Teiidae			
Aspidoscelis tigris (Baird and Girard, 1852) (Tiger Whiptail)	4	1.1	Diller and Wallace 1996; this study
Unidentified lizards	5	1.4	This study
Squamate eggs	**3**	**0.8**	This study
Mammalia	**301**	**85.0**	
Lagomorpha			
Leporidae			
Sylvilagus nuttallii (Bachman, 1837) (mountain cottontail)	9	2.5	Diller and Wallace 1996
Rodentia			
Geomyidae			
Thomomys bottae (Eydoux and Gervais, 1836) (Botta's pocket gopher)	2	0.6	Woodbury 1931; this study
Thomomys sp. (pocket gophers)	1	0.3	This study
Heteromyidae			
Dipodomys merriami Mearns, 1890 (Merriam's kangaroo rat)	1	0.3	This study
Dipodomys ordii Woodhouse, 1853 (Ords's kangaroo rat)	16	4.5	Diller and Wallace 1996; Jenkins and Peterson 2005; this study
Dipodomys sp. (kangaroo rats)	8	2.3	Fautin 1946; this study
Perognathus longimembris (Coues, 1875) (little pocket mouse)	3	0.8	This study
Perognathus parvus (Peale, 1848) (Great Basin pocket mouse)	17	4.8	Diller and Wallace 1996; Jenkins and Peterson 2005; this study
Perognathus sp. (pocket mice)	1	0.3	This study

Table 1 (*continued*).

Prey taxon	Frequency	Percentage of total number of prey	Sources
Muridae			
Arvicollinae			
Lemmiscus curtatus (Cope, 1868) (sagebrush vole)	2	0.6	Jenkins and Peterson 2005
Microtus montanus (Peale, 1848) (montane vole)	3	0.8	This study
Microtus sp. (meadow voles)	6	1.7	This study
Unidentified arvicolline rodent	7	2.0	This study
Murinae			
Mus musculus L., 1758 (house mouse)	1	0.3	This study
Sigmodontinae			
Neotoma cinerea (Ord, 1815) (bushy-tailed woodrat)	2	0.6	Jenkins and Peterson 2005; this study
Neotoma lepida Thomas, 1893 (desert woodrat)	2	0.6	Diller and Wallace 1996; this study
Neotoma sp. (woodrats)	2	0.6	This study
Peromyscus crinitus (Merriam, 1891) (canyon mouse)	1	0.3	This study
Peromyscus maniculatus (Wagner, 1845) (deer mouse)	49	13.8	Diller and Wallace 1996; Jenkins and Peterson 2005; Bryan T. Hamilton, personal communication; this study
Peromyscus cf. *P. maniculatus*	2	0.6	This study
Peromyscus truei (Shufeldt, 1885) (pinyon mouse)	1	0.3	Bryan T. Hamilton, personal communication
Peromyscus sp. (deer mice)	13	3.7	This study
cf. *Peromyscus* sp.	1	0.3	This study
Reithrodontomys megalotis (Baird, 1858) (western harvest mouse)	2	0.6	Jenkins and Peterson 2005; this study
Unidentified sigmodontine rodents	11	3.1	This study
Sciuridae			
Ammospermophilus leucurus (Merriam, 1889) (white-tailed antelope squirrel)	5	1.4	Diller and Wallace 1996; Hall 1946; this study
Spermophilus mollis Kennicott, 1863 (Piute ground squirrel)	90	25.4	Diller and Wallace 1996; Fautin 1946; Hall 1929; Pack 1930; Richardson 1915
Spermophilus sp. (ground squirrels)	1	0.3	This study
Tamias minimus Bachman, 1839 (least chipmunk)	2	0.6	Jenkins and Peterson 2005; this study
cf. *Tamias minimus*	1	0.3	This study
Unidentified sciurid rodent	1	0.3	This study
Unidentified rodents	16	4.5	This study
Unidentified mammals	22	6.2	This study
Aves	**8**	**2.3**	
Galliformes			
Odontophoridae			
Callipepla californica (Shaw, 1798) (California Quail)	1	0.3	Jewett 1939
Passeriformes			
Alaudidae			
Eremophila alpestris (L., 1758) (Horned Lark)	1	0.3	Fautin 1946
Corvidae			
Aphelocoma californica (Vigors, 1839) (Western Scrub-Jay)	1	0.3	Woodbury 1933

Table 1 (*concluded*).

Prey taxon	Frequency	Percentage of total number of prey	Sources
Emberizidae			
Pooecetes gramineus (Gmelin, 1789) (Vesper Sparrow)	1	0.3	Fautin 1946
Spizella passerina (Bechstein, 1798) (Chipping Sparrow)	1	0.3	Woodbury 1933
Icteridae			
Euphagus cyanocephalus (Wagler, 1829) (Brewer's Blackbird)	1	0.3	LaRivers 1944
Unidentified passerine bird	1	0.3	This study
Unidentified bird	1	0.3	This study
Total	**354**		

Note: "Sceloporine lizard" refers to species of *Uta*, *Urosaurus*, or *Sceloporus*. "Frequency" refers to the number of times each prey taxon was found in the entire data set. Values in boldface type are subtotals within taxon groups.

Fig. 2. Ln-transformed prey mass (g) as a function of ln-transformed snake mass (g) in *Crotalus lutosus* ($r^2 = 0.45$, $F_{[1,20]} = 16.21$, $P = 0.0007$).

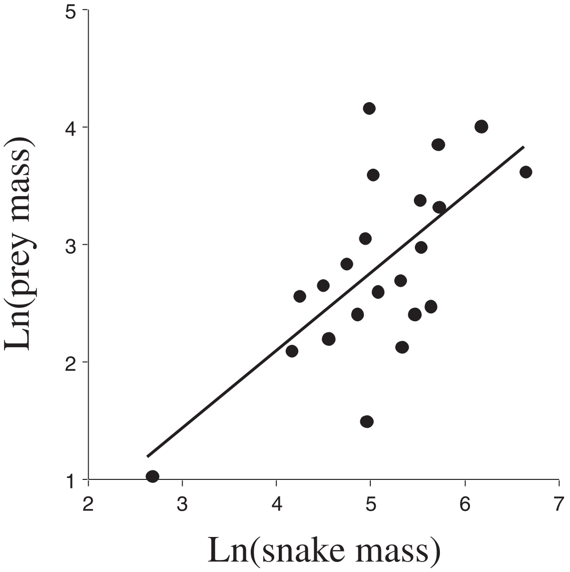
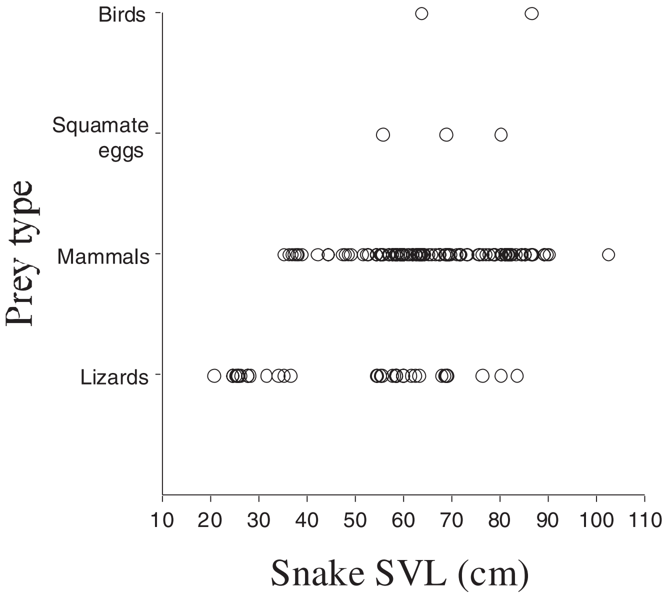


Fig. 3. Relationship between prey type and snake body size (snout-to-vent length, SVL) in *Crotalus lutosus* ($n = 150$).



24.2%, $n = 12$) consumed animals of similar relative prey mass (one-tailed ANOVA; $F_{[1,20]} = 2.49$, $P = 0.13$). Female Great Basin Rattlesnakes fed on lizards more often than males: 30% (15/50) of prey taken by females were lizards compared with 17.8% (16/90) for males (one-tailed χ^2 test; $\chi^2 = 3.84$, df = 1, $P = 0.05$). This pattern can result from sexual differences in body size (see above), or from variation in dietary preferences between males and females. To distinguish between these two alternatives, we assigned males and females (independently) to four size categories (SVL: 20–40, 40.1–60, 60.1–80, >80 cm). Because males grow larger than females (see above), the proportion of individuals in the size categories varied by sex (increasing size categories; males, 9:18:33:23; females, 10:21:16:3; χ^2 =

Table 2. Sexual dimorphism in body size (snout-to-vent length, SVL), tail length, head length, head width, and body mass in *Crotalus lutosus*.

Trait	Mean ± 1 SD	Range	*n*	*F*	df	*P*
SVL (cm)						
Males	66.9±17.0	24.5–102.1	84	16.86	1, 134	<0.0001
Females	55.4±14.2	24.5–83.2	52			
Tail length (cm)						
Males	5.1±1.3	1.7–8.5	84	74.09	1, 134	<0.0001
Females	3.3±0.9	1.5–5.0	52			
Head length (cm)						
Males	3.2±0.7	1.6–4.4	75	17.9	1, 123	<0.0001
Females	2.7±0.5	1.5–3.8	50			
Head width (cm)						
Males	2.4±0.6	1.0–3.9	75	15.66	1, 123	<0.0001
Females	2.1±0.4	1.1–3.1	50			
Body mass (g)						
Males	261.9±167.3	9.5–767.0	84	25.4	1, 134	<0.0001
Females	135.7±85.9	10.8–372.3	52			

Note: The differences between the sexes in tail length, head length, and body mass remained significant after controlling for differences in body size between males and females (see text for details).

15.47, df = 3, $P = 0.001$). After excluding the largest size category (>80 cm) to eliminate this statistical difference, we determined that the proportion of lizards taken by male and female snakes was similar (males, 22.7%, 15/66; females, 29.8%, 14/47; $\chi^2 = 0.71$, df = 1, $P = 0.4$). This result supports the idea that the different percentage of lizards in the diet of male and female *C. lutosus* is caused by the variation in body size between the sexes; that is, smaller snakes (i.e., females) predominantly feed on smaller prey (i.e., small lizards).

The proportion of mammals preyed upon was highest during the summer months of July and August (91.9%, 34/37) compared with the rest of the year (May, June, September, October; 72.1%, 80/111; one-tailed χ^2 test; $\chi^2 = 7.55$, df = 1, $P = 0.006$). However, larger *C. lutosus* consume fewer lizards than smaller snakes (see above), and because North American rattlesnakes typically give birth in late summer (Aldridge and Duvall 2002), younger (smaller) snakes are more likely to be collected later in the year. Therefore, body size may be a confounding variable in this analysis of seasonal variation in dietary habits. After repeating the previous contingency test including only adult snakes (SVL > 54 cm; X. Glaudas, unpublished data), we determined that the proportion of mammals eaten was still higher during July and August (93.9%, 31/33) compared with May, June, September, and October (77%, 67/87; one-tailed χ^2 test; $\chi^2 = 6.63$, df = 1, $P = 0.01$). Further, the body size of the snakes that contained prey was similar between July and August versus May, June, September, and October (ANOVA, $F_{[1,103]} = 0.10$, $P = 0.75$). Collectively, these results support the prediction that Great Basin Rattlesnakes exhibit temporal variation in their diet.

Crotalus lutosus occurs in two physiographic regions of North America, the Great Basin Desert and the Columbia Plateau (Fig. 1). Snakes from the two regions have similar body sizes ($F_{[1,142]} = 0.01$, $P = 0.91$) and head sizes (head length, $F_{[1,127]} = 0.0003$, $P = 0.98$; head width, $F_{[1,126]} = 0.32$, $P = 0.36$). We assessed geographic variation in diet by comparing the proportion of lizards and mammals taken by snakes from the two physiographic regions (we excluded birds and squamate eggs from this analysis because of low sample size). Snakes from the Great Basin Desert ate significantly more lizards (21.7%, 35/161) than snakes from the Columbia Plateau (1.7%, 3/175; $\chi^2 = 33.52$, df = 1, $P < 0.0001$). We also examined whether *C. lutosus* from the two physiographic regions differed in the kind of mammalian prey they consumed. We classified mammals into five families: Geomyidae (*Thomomys* Wied-Neuwied, 1839), Heteromyidae (*Dipodomys* Gray, 1841; *Perognathus* Wied-Neuwied, 1839), Muridae (*Lemmiscus* Thomas 1912; *Microtus* Schrank, 1798; *Mus* L., 1758; *Neotoma* Say and Ord, 1825; *Peromyscus* Gloger, 1841; *Reithrodontomys* Giglioli, 1874), Sciuridae (*Ammospermophilus* Merriam, 1892; *Spermophilus* F. Cuvier, 1825; *Tamias* Illiger, 1811), and Leporidae (*Sylvilagus* Gray, 1867). However, we excluded geomyids (pocket gophers) and leporids (hares and rabbits) from the comparison because of insufficient sample size. Snakes from the Great Basin Desert ate proportionally more murids and fewer heteromyids and sciurids compared with snakes from the Columbia Plateau (number of murid:heteromyid:sciurid rodents eaten; Great Basin Desert, 60:18:13; Columbia Plateau 44:28:87; $\chi^2 = 44.17$, df = 2, $P < 0.0001$). Thus, the feeding habits of *C. lutosus* vary geographically.

Discussion

Feeding habits and predator–prey size relationships

Our study indicates that *Crotalus lutosus* feeds mainly on mammals, occasionally on lizards, and less frequently on birds; squamate eggs and frogs are only rarely eaten. Although rodents clearly are the dominant prey type of Great Basin Rattlesnakes, lizards are important prey items for smaller individuals. To our knowledge, our discovery of squamate eggs in the stomachs of three snakes represents the first published report of a rattlesnake species eating this type of prey.

Most *C. lutosus* contained single prey that was consumed head-first. Direction of ingestion was influenced by the type of prey taken; snakes ingested mammals head-first significantly more frequently than lizards, which generally have a smaller maximum diameter than mammals and therefore can be more easily swallowed from either direction. Swallowing vertebrate prey head-first may also be easier, because the front and hind limbs more easily fold against the body, offering less resistance during consumption (cf. Greene 1976). Accordingly, head-first ingestion of larger prey may reduce swallowing time (Vincent et al. 2006; Mori 2006).

We documented a positive relationship between predator and prey size in *C. lutosus*. The best predictors of this relationship were prey diameter as a function of snake body length and snake head dimensions (head length and head width). Many studies of snake feeding ecology only describe the relationship between size and (or) body mass of the predator and its prey. Nonetheless, items of similar mass can have different shapes (e.g., elongate versus bulky prey), and thus differ significantly in maximum girth (Greene 1983). In gape-limited predators such as snakes that swallow their prey whole, prey diameter can be an important constraint on swallowing performance (Cundall and Greene 2000), but this variable is seldom reported. Because investigating the relationship between predator and prey size is relevant to understanding the ecology and evolution of gape-limited predators (Greene 1997; Schwenk 2000), documenting the correlation between snake size and prey diameter will facilitate gaining a deeper understanding of the trophic ecology of these predators.

Larger (heavier) Great Basin Rattlesnakes consumed larger (heavier) prey, which suggests that as snakes grow larger they tend to drop relatively small items from their diet. In other words, *C. lutosus* exhibits an ontogenetic shift in the lower size limit of its prey (Arnold 1993). Two scenarios may account for this observation. First, the cost of capturing and ingesting smaller animals may be too high in relation to their energy content (Arnold 1993). Alternatively, the observed pattern may not be directly related to an energetic cost–benefit relationship; rather, sit-and-wait predators such as rattlesnakes may simply not be efficient at accurately striking and capturing relatively small prey items (“hard to catch prey”, Arnold 1993) from an ambush posture. It will be informative to determine whether a correlation exists between foraging modes (active vs. ambush foraging) and predator–prey size attributes (e.g., amount of variance in prey mass explained by predator mass).

Foraging theory and empirical evidence (Huey and Pianka 1981; Shine 1991*b*; Secor and Nagy 1994; Greene 1997; Secor and Diamond 2000) indicate that ambush predators (e.g., boas, pythons, and vipers, including rattlesnakes) generally consume fewer but relatively larger items than active foragers (e.g., cobras, racers), which actively investigate the habitat in search of potential prey. Our findings are not consistent with this tenet. Relative prey mass in *C. lutosus* averaged 12.6%, a lower percentage than in several actively foraging snakes (Rodríguez-Robles 2002). Further, in a multiyear study conducted at a locality in southwestern Idaho, *C. lutosus* ate, on average, proportionally smaller prey than the sympatric, widely foraging Gophersnake, *Pituophis catenifer* (Blainville, 1835) (Diller and Wallace 1996).

Ontogenetic, intersexual, temporal, and geographic variations in feeding habits

Crotalus lutosus displayed ontogenetic variation in diet. In ontogenetic shifts in food habits, the diet of a species changes as a function of its body size. This phenomenon occurs in many predators, including snakes (e.g., Godley 1980; Rodríguez-Robles 2002; Greene and Rodríguez-Robles 2003; Graham et al. 2007). Our data suggest that Great Basin Rattlesnakes feed predominantly on lizards until they reached ca. 34 cm in SVL. Although larger snakes continue to eat reptiles, they switch to a diet that mainly consists of mammals. Being gape-limited predators, smaller snakes are presumably physically incapable of ingesting prey of a larger maximum diameter such as mammals and birds, and thus younger snakes feed on lizards until an increase in absolute gape size allows them to take larger prey (Rodríguez-Robles and Greene 1999, and references therein). This pattern is prevalent in many rattlesnake species and may be the ancestral condition for these snakes (Greene 1997). Consistent with the idea that body size is an important factor influencing selection of prey type in gape-limited predators, neonates of larger rattlesnake species (e.g., Timber Rattlesnake (*Crotalus horridus* L., 1758), Clark 2002; Neotropical Rattlesnake (*Crotalus durissus* L., 1758), Salomão et al. 1995) feed on small mammals shortly after birth.

Reports of intersexual variation in feeding ecology are relatively common in sexually dimorphic snakes (Mushinsky et al. 1982; Shine 1991*c*; Houston and Shine 1993; Shetty and Shine 2002). Female *C. lutosus* are smaller and have relatively shorter heads than males. Accordingly, we expected females to eat smaller prey (e.g., lizards; cf. Shine 1989; Forsman 1991). Females indeed ate a significantly higher proportion of lizards compared with males, although relative prey mass did not vary between the sexes. Because males and females of similar body size ate a similar proportion of lizards and mammals, the higher percentage of lizards taken by female *C. lutosus* is likely due to the smaller size of these snakes. This sexual variation in feeding habits is consistent with the ontogenetic shift exhibited by the species in which smaller snakes feed more often on lizards compared with larger individuals (see above).

Crotalus lutosus also displayed temporal variation in feeding habits. The proportion of mammals in the diet of Great Basin Rattlesnakes was highest during the summer months of July and August. This variation may be due to at least three nonexclusive factors. First, Great Basin Rattlesnakes develop nocturnal habits during the hottest part of the year (Bryan T. Hamilton, personal communication). Because lizards are mainly diurnal, they may not be as accessible to sit-and-wait predators such as *C. lutosus* at night. On the other hand, with the exception of sciurids (e.g., genera *Ammospermophilus*, *Spermophilus*, *Tamias*), rodents are primarily nocturnal, and these mammals may be the most available prey type to *C. lutosus* during summer months. Second, activity levels of potential prey may fluctuate across seasons, and snakes may feed on the more readily available food resources at any given time of the year. There is some support for this scenario. Kenagy (1973) documented that activity patterns of a small rodent community peaked during the summer. However, another study revealed that only 1 of 12 species of nocturnal rodents (*Perognathus longimembris* (Coues, 1875), a mammal rarely consumed by *C. lutosus*; Table 1) increased its activity levels during the summer (O'Farrell 1974). Third, Great Basin Rattlesnakes may be less selective at certain periods of the year, such as shortly after leaving or shortly before going into hibernacula in the spring and fall, respectively. For instance, *C. lutosus* may feed more opportunistically (e.g., eat more lizards) during these periods to obtain the food resources necessary to sustain the energetically demanding activities associated with the beginning and the end of the activity season (e.g., migration between hibernacula and active season habitats, mating activities).

Range-wide analyses of feeding ecology allow us to investigate variation in dietary habits across physiographic regions. *Crotalus lutosus* from the Great Basin Desert and the Columbia Plateau differed in the proportion of prey types (lizards vs. mammals) they consumed. Rattlesnakes from the Great Basin Desert ate a higher proportion of lizards compared with snakes from the Columbia Plateau, which almost exclusively fed on mammals. The Columbia Plateau is located north of the Great Basin Desert (Fig. 1), and because in North America lizard species diversity decreases with increasing latitude (Pianka 1967; Kiester 1971), there may be fewer lizard species available as potential prey for rattlesnakes from the Columbia Plateau. However, lizard abundance, rather than species diversity, is probably the variable that determines the rate at which a predator encounters potential lizard prey. Therefore, data on overall lizard density in the Great Basin Desert and the Columbia Plateau are needed to assess whether rattlesnakes from the latter region indeed encounter lizard prey less often than those from the Great Basin Desert.

Snakes from the two physiographic regions also differed in the kind of mammals they consumed. Rattlesnakes from the Great Basin Desert primarily ate murid rodents (mainly *Peromyscus* deer mice), whereas those from the Columbia Plateau mostly fed on sciurid rodents (mainly *Spermophilus* ground squirrels). This pattern is probably not caused by differential abundance of these rodents, for at least in parts of the Columbia Plateau *Peromyscus* is more abundant than *Spermophilus* (Diller and Wallace 1996). Instead, snakes from the Columbia Plateau may forage more extensively during the day than snakes from the Great Basin Desert, and hence encounter the diurnal *Spermophilus* more frequently.

In conclusion, our investigation of the food habits of *C. lutosus* documented interesting patterns of intraspecific variation in the feeding ecology of this venomous snake. Ecological studies such as this one are valuable because they provide basic information about the biology of a species and reveal patterns that can subsequently be placed in a broader context. For example, gathering dietary data for sympatric and congeneric species would allow the assessment of trait variation across taxa. Additionally, these findings can be analyzed in an explicit phylogenetic context to gain a better understanding of the evolution of ecological traits in closely related species.

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