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Diet of the Northern Pacific Rattlesnake (*Crotalus o. oreganus*) in California

Data from museum specimens are used to inform a wide range of studies from taxonomy and physiology, to how climate change affects animal distributions (e.g., Moritz et al. 2008; Suarez and Tsutsui 2004; see Pyke and Ehrlich 2010 for review). Analysis of the gut contents of museum specimens is a straightforward and low-cost method of determining the dietary habits of species in the wild, and these data may then be used to help inform conservation programs of at-risk species.

The feeding habits of many species of rattlesnakes have been elucidated with museum studies (for recent examples see Glaudas et al. 2008; Dugan and Hayes 2012). These studies provide initial data that form the backbone for other lines of inquiry such as the relationship between diet and venom composition (Mackessy 1988; Mackessy et al. 2003) and the evolutionary arms race between rattlesnakes and their prey (Biardi et al. 2005; Barlow et al. 2009). We analyzed data on the diet of Northern Pacific Rattlesnakes (*Crotalus o. oreganus*) from California by identifying prey items recovered from dissection of museum specimens. *Crotalus o. oreganus* ranges from central California to northern British Columbia (Stebbins and McGinnis 2012). Several field studies on diet have been conducted near the northern boundary of the range (Macartney 1989; Wallace and Diller 1990), and several were centered closer to the southern edge of the range (Fitch and Twining 1946; Mackessy 1988). Ernst and Ernst (2011) provide an extensive review of the diets of many North American rattlesnakes, including *Crotalus o. oreganus* in various parts of its range. Our museum study included specimens from throughout the California range of this taxon with the goal of filling in a geographical gap. Combined with other published dietary accounts, our study helps contribute to a more robust understanding of the feeding habits of *C. o. oreganus*.

ALISON M. SPARKS
CRAIG LIND[1]
EMILY N. TAYLOR*
Biological Sciences Department, California Polytechnic State University, San Luis Obispo, California 93407-0401, USA

[1] Present address: Stetson University, DeLand, Florida 32723, USA
** Corresponding author; e-mail: etaylor@calpoly.edu*

Methods.—Remains of prey were present in the gastrointestinal tracts (stomach and intestines) of 85 specimens of *Crotalus o. oreganus* collected in California and deposited in the Museum of Vertebrate Zoology (MVZ, Berkeley, California) and the Santa Barbara Natural History Museum (SBNHM, Santa Barbara, California). In some cases prey had already been removed from snakes, and in other cases we removed prey items from the stomach and intestines and stored them in ethanol in glass vials. We attempted to avoid snakes from possible intergrade zones with other subspecies (based on range maps). The snout–vent length (SVL) of each snake was measured with a cloth measuring tape. Each snake was categorized as male (N = 45), female (N = 30), or neonate (N = 10). Neonate snakes were identified based on their single rattle segment and uniform small size (range: 245–290 mm SVL).

Prey items were identified to the lowest possible taxon level. In the 85 snakes, 88 prey items (3 snakes had two different prey types present) could be positively identified at least to the level of vertebrate class. These prey items were categorized as amphibians based on presence of identifiable amphibian tissue (e.g., bones),

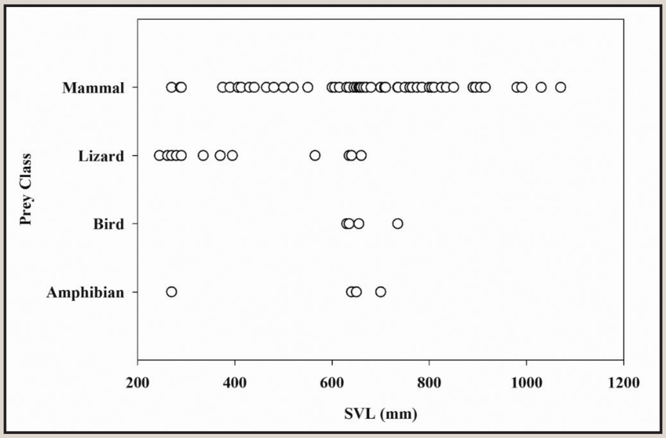

FIG. 1. Prey type distribution based on snout–vent length (SVL) of *Crotalus o. oreganus* in the present study. Each data point represents an individual snake. Snakes that ate lizards were smaller in SVL than snakes that ate mammals and birds; snakes that ate amphibians were not different in size from those that ate other prey types.

as mammals based on presence of hair and/or mammalian teeth, as lizards based on presence of lizard scales, and as birds based on presence of feathers. The majority of prey items were found highly digested in the intestines. However, in cases where prey items were intact or other reliable structures (e.g., teeth) were well preserved (N = 52), we identified prey to taxonomic levels below class (e.g., order, family, genus, or species).

The size of snakes that consumed each prey class was compared by ANOVA on square-root-transformed snake SVL. Post hoc Tukey's tests were used for pairwise comparisons. To test the hypothesis that juvenile snakes consumed lizards more frequently than adults, snakes were assigned to two groups: immature/juvenile (< 520 mm [Diller and Wallace 2002], including neonates) and adult (520 mm or greater). Chi-square likelihood-ratio tests were used to compare the proportion of individuals containing lizard prey within the two groups. The effect of sex on diet composition was also examined using likelihood-ratio tests using adults only. The presence of sexual size dimorphism was tested using a student's t-test on log-transformed data. All analyses were conducted in JMP Pro 11 (SAS Institute Inc.).

Results.—Prey from three vertebrate classes were represented: Amphibia, Reptilia (lizards and birds), and Mammalia (Table 1). We broke down reptilian prey into lizards and birds for the purpose of analysis. Mammal prey were most common (76.1%), followed by lizards (14.8%), birds (4.5%), and amphibians (4.5%). Only 3 snakes contained prey items from more than one prey class; we treated them as independent samples because deleting these data did not affect the results of the analysis. There was a significant difference in the size of individuals that preyed upon the different prey classes ($F_{3,87} = 11.06$, $P < 0.001$; Fig. 1). Post-hoc analyses showed that snakes that consumed lizards were significantly smaller compared to those that ate mammals and birds, which were not different in size from each other or from those that consumed amphibians. Compared to adults, snakes classified as juveniles based on SVL preyed more on lizards ($\chi^2 = 15.0$, $P < 0.001$). Adult males and females did not significantly differ in size (T = 1.45, P = 0.15), or diet (All classes: $\chi^2 = 2.44$, $P = 0.49$, Proportion lizard: $\chi^2 = 2.15$, $P = 0.14$). The majority of neonates (60%, 6 of 10) examined had consumed lizard prey, followed by small mammals (30%, 3 of 10) and amphibians (10%, 1 of 10).

Of the 88 prey items, we were able to identify the following specific prey taxa (See Table 1 for details): Anuran (species not identified), Arboreal Salamander, *Aneides lugubris*, Gilbert's Skink, *Plestiodon gilberti*, Western Skink, *P. skiltonianus*, Sagebrush Lizard, *Sceloporus graciosus*, Western Fence Lizard, *S. occidentalis*, *Sceloporus* sp., Side-blotched Lizard, *Uta stansburiana*, Warbler, family Paruidae, Rabbit, *Sylvilagus* sp., American Pika, *Ochotona princeps*, Mountain Beaver, *Aplodontia rufa*, California Vole, *Microtus californicus*, *Microtus* sp., Dusky-footed Woodrat, *Neotoma fuscipes*, Southern Grasshopper Mouse, *Onychomys torridus*, *Onychomys* sp., Deer Mouse, *Peromyscus maniculatus*, Western Harvest Mouse, *Reithrodontomys megalotis*, Kangaroo Rat, *Dipodomys* sp., and California Ground Squirrel, *Otospermophilus beecheyi*.

Discussion.—The diet of *C. o. oreganus* has been studied in several field studies (Fitch and Twining 1946; Macartney 1989; Wallace and Diller 1990). Each of these studies examined one or a small group of populations in restricted geographic localities (central California: Fitch and Twining 1946, northern Idaho: Wallace and Diller 1990; British Columbia, Canada: Macartney 1989; Central Washington: Weaver and Lahti 2005). Our goal in the present study was to conduct an investigation of the diet of *C. o. oreganus* in its range throughout California (central California to the Oregon border) using museum specimens, which will help to fill in gaps in our knowledge of types of prey consumed by *C. o. oreganus* in the southern part of its range.

Our study agrees with previous field studies that the majority of the diet of *C. o. oreganus* consists of small rodents. A report on diet in central Washington shows a similar prey class distribution compared to our results for California populations (74% mammal, 20% lizard, and 6% bird; Weaver and Lahti 2005). Studies at the far northern part of the range found that the diet consists almost entirely of mammals, primarily rodents, and a small number of birds and lizards (Macartney 1989; Wallace and Diller 1990). In these studies, neonates ate mainly small mammals such as shrews; in our study, neonates also ate small mammals but ate lizards at a higher frequency than mammals. The higher prevalence of lizard prey found in our California snakes compared to snakes in northern populations could reflect a greater abundance of lizards in California than in northern parts of the range. Mackessy (1988) also found that lizards made up a large portion of the diet of juvenile *C. o. helleri* in central California, and that snakes larger than 500 mm total length ate mammals rather than lizards. In our study, we found that some juvenile *C. o. oreganus* (< 520 mm SVL) ate mammals and some snakes larger than 520 mm ate lizards; nevertheless, the general trend of an ontogenetic shift from a diet primarily of lizards to one primarily of mammals is supported (Fig. 1). Mackessy (1988) also showed that the venom composition of *C. o. helleri* and *C. o. oreganus* changes ontogenetically, with smaller snakes having higher venom toxicity. The ontogenetic shift in venom composition in *C. o. oreganus* may relate to a change in diet from primarily lizards to primarily mammals. Such a shift in diet was first suggested by Fitch and Twining (1946) and is evidenced in our study by the fact that neonates ate many lizards but adults did not. It is therefore possible that neonate *C. o. oreganus* at the southern part of the range have evolved venom more suited towards eating lizards compared to neonates at the northern end of the range, which may encounter lizards more rarely. This hypothesis could be tested by obtaining data on lizard densities as well as the toxicity of neonate venom along a latitudinal cline from central California to southern Canada.

Table 1. List of food items consumed by *Crotalus o. oreganus* throughout its range summarized from four studies conducted on populations throughout the range, including this study on California snakes. Prey taxa are listed within vertebrate class, alphabetically by family and then genus and species. Percentages in bold are range-wide percentages for each vertebrate class. Percentages not in bold are those reported in each study. Blank values indicate information was not available.

Class	Order	Lowest taxonomic rank identified	Family	N	% of diet	Source	State/province
Amphibia			Total	4	**0.8**		
	Anura						
		Spadefoot Toad, *Spea hammondii*	Scaphiopodidae		2	1.1	Fitch and Twining 1946
CA							
		Unidentified anuran		2	3.8	This study	CA
	Caudata						
		Arboreal Salamander, *Aneides lugubris*	Plethodontidae		1	1.9	This study CA
Reptilia			Total	37	**7.1**		
	Squamata						
		Sagebrush Lizard, *Sceloporus graciosus*	Phrynosomatidae	4	7.7	This study	CA
		Western Fence Lizard, *Sceloporus occidentalis*	Phrynosomatidae	7	4.0	Fitch and Twining 1946	CA
		Western Fence Lizard, *Sceloporus occidentalis*	Phrynosomatidae	8	15.4	This study	CA
		Sceloporus sp.	Phrynosomatidae	1	1.9	This study	CA
		Side-blotched Lizard, *Uta stansburiana*	Phrynosomatidae	2	3.8	This study	CA
		Side-blotched Lizard, *Uta stansburiana*	Phrynosomatidae	5	2.8	Fitch and Twining 1946	CA
		Gilbert's Skink, *Plestiodon gilberti*	Scincidae	2	1.1	Fitch and Twining 1946	CA
		Gilbert's Skink, *Plestiodon gilberti*	Scincidae	1	1.9	This study	CA
		Western Skink, *Plestiodon skiltonianus*	Scincidae	1	0.9	Wallace 1990	ID
		Western Skink, *Plestiodon skiltonianus*	Scincidae	2	3.8	This study	CA
		Whiptail Lizard, *Aspidoscelis tigris*	Teiidae	4	2.3	Fitch and Twining 1946	CA
Aves			Total	≥ 12	**2.3**		
	Passerifomes						
		Bushtit, *Psaltriparus minimus**	Aegithalidae	≥1		Macartney 1989	BC
		Dark-eyed Junco, *Junco hyemalis**	Emberizidae	≥1		Macartney 1989	BC
		California Towhee, *Melozone crissalis*	Emberizidae	2	1.1	Fitch and Twining 1946	CA
		Song Sparrow, *Melospiza melodia*	Emberizidae	1	1.1	Wallace 1990	ID
		Spotted Towhee, *Pipilo maculatus**	Emberizidae	≥1		Macartney 1989	BC
		Warbler, family Parulidae	Parulidae	1	1.9	This study	CA
		European Starling, *Sturnus vulgaris**	Sturnidae	≥1		Macartney 1989	BC
	Galliformes						
		California Quail, *Callipepla californica*		2	1.1	Fitch and Twining 1946	CA

Table 1. Continued.

Class	Order	Lowest taxonomic rank identified	Family	N	% of diet	Source	State/province
Mammalia			Total	466	**89.8**		
	Lagomorpha						
		Desert Cottontail, *Sylvigagus auduboni*	Leporidae	17	9.6	Fitch and Twining 1946	CA
		Mountain Cottontail, *Sylvilagus nuttallii*	Leporidae	5	4.7	Wallace 1990	ID
		Sylvilagus sp.	Leporidae	1	1.9	This study	CA
		American Pika, *Ochonta princeps*	Ochotonidae	1	1.9	This study	CA
	Rodentia						
		Mountain Beaver, *Aplodontia rufa*	Aplodontiidae	2	3.8	This study	CA
		California Vole, *Microtus californicus*	Cricetidae	7	13.5	This study	CA
		California Vole, *Microtus californicus*	Cricetidae	4	2.3	Fitch and Twining 1946	CA
		Vole, *Microtus* sp.	Cricetidae	2	3.8	This study	CA
		Vole, *Microtus* sp.	Cricetidae	56	52.8	Wallace 1990	ID
		Vole, *Microtus* sp.	Cricetidae	86	46.3	**Macartney 1989	BC
		Bushy-tailed Woodrat, *Neotoma cinerea*	Cricetidae	1	0.5	**Macartney 1989	BC
		Dusky-footed Woodrat, *Neotoma fuscipes*	Cricetidae	5	2.8	Fitch and Twining 1946	CA
		Dusky-footed Woodrat, *Neotoma fuscipes*	Cricetidae	1	1.9	This study	CA
		Southern Grasshopper Mouse, *Onychomys torridus*	Cricetidae	1	1.9	This study	CA
		Grasshopper Mouse, *Onychomys* sp.	Cricetidae	1	1.9	This study	CA
		Deer Mouse, *Peromyscus maniculatus*	Cricetidae	7	13.5	This study	CA
		Deer Mouse, *Peromyscus maniculatus*	Cricetidae	24	22.6	Wallace 1990	ID
		Deer Mouse, *Peromyscus maniculatus*	Cricetidae	41	22.1	**Macartney 1989	BC
		White-footed mouse, *Peromyscus* sp.	Cricetidae	14	7.9	Fitch and Twining 1946	CA
		Western Harvest Mouse, *Reithrodontomys megalotis*	Cricetidae	3	5.8	This study	CA
		Western Harvest Mouse, *Reithrodontomys megalotis*	Cricetidae	3	2.8	Wallace 1990	ID
		Pocket gopher, *Thomomys bottae*	Geomyidae	10	5.6	Fitch and Twining 1946	CA
		Northern Pocket Gopher, *Thomomys talpoides*	Geomyidae	2	1.9	Wallace 1990	ID
		Northern Pocket Gopher, *Thomomys talpoides*	Geomyidae	19	10.3	**Macartney 1989	BC
		Heermann's Kangaroo Rat, *Dipodomys heermanni*	Heteromyidae	29	16.4	Fitch and Twining 1946	CA
		Kangaroo Rat, *Dipodomys* sp.	Heteromyidae	1	6.8	This study	CA
		Great Basin Pocket Mouse, *Perognathus parvus*	Heteromyidae	3	1.5	**Macartney 1989	BC
		Pocket mouse, *Perognathus* sp.	Heteromyidae	12	6.8	Fitch and Twining 1946	CA
		California Ground Squirrel, *Otospermophilus beecheyi*	Sciuridae	60	33.9	Fitch and Twining 1946	CA
		California Ground Squirrel, *Otospermophilus beecheyi*	Sciuridae	3	5.8	This study	CA
		Yellow Pine Chipmunk, *Tamias amoenus*	Sciuridae	4	2.0	**Macartney 1989	BC
		Yellow Pine Chipmunk, *Tamias amoenus*	Sciuridae	1	0.9	Wallace 1990	ID
		Red Squirrel, *Tamiasciurus hudsonicus*	Sciuridae	14	7.3	**Macartney 1989	BC
		Yellow-bellied Marmot, *Marmota flaviventris*	Sciuridae	1	0.5	**Macartney 1989	BC
		Vagrant Shrew, *Sorex vagrans*	Soricidae	13	12.3	Wallace 1990	BC
		Cinerus Shrew, *Sorex cinereus*	Soricidae	9	4.9	**Macartney 1989	BC
		Unidentified "mouse"		2	1.1	Fitch and Twining 1946	CA

*Sample size was not reported in the study.
**Raw sample sizes not reported, numbers were back-calculated from reported percentages and rounded to the nearest whole number.

Several unusual prey records have been recorded for *C. o. oreganus*. Bullard and Fox (2002) report an adult male *C. o. oreganus* that had eaten a Rubber Boa (*Charina bottae*). Cannibalism has not been reported in *C. o. oreganus*, but there are several reports of closely related species eating conspecifics (Gloyd 1933; Lillywhite 1982). Our study revealed two new prey genera for *C. o. oreganus*: Mountain Beavers, *Aplodontia rufa*, and Grasshopper Mice, *Onychomys*. Two individuals consumed Mountain Beavers (based on identification of claws in gut contents). That Mountain Beavers have not previously been identified in studies of *C. o. oreganus* diet is likely because few field studies have been conducted at montane sites within the range of this prey taxon. This highlights the importance of museum studies in filling in the gaps in our knowledge of the feeding habits of species over large geographic areas. Taken together, the results of range-wide studies (summarized from four comprehensive studies in Table 1 and reviewed in detail in Ernst and Ernst 2011 and Klauber 1956), reveal that adult *C. o. oreganus* prey upon diverse mammalian taxa throughout their range and that juveniles in the central and southern portions of the range prey more frequently on lizards compared to adults and juveniles from northern populations.

Specimens examined.—MVZ 747-48, 2079, 2772-73, 2775-76, 2778-79, 2781, 2783, 2785, 3820, 5326-27, 5561, 6839, 6841-42, 6845, 8651, 9469, 9989, 10215, 10537-38, 11190, 11428, 12364, 13099, 14597, 14599-600, 15208, 16339, 16341, 16422, 16439, 16461, 16463-64, 16855, 17572, 17585, 17619, 18191, 18405–07, 20562, 21380–82, 21574, 21917, 24125, 24253-54, 24398, 24840, 29281, 29335, 33913, 34111, 34116-17, 34936, 35358, 35466, 37131, 39057, 43709, 45739, 50213, 50974, 51708-09, 58265, 62064, 64143, 64148, 66426-27, 75833, 78072, 80771, 80933, 83654-55, 85225, 85486, 92684, 92685, 149388, 158972, 170801, 176163-64, 179788, 179969, 191384, 191413, 191863, 192218, 193426–30, 193432-33, 193435, 202295, 204238–40, 204243-44, 206223, 215726, 217434, 223168, 228714, 229507, 229847–49, 244367, 370905; SBMNH 983, 1351, 2346.

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