

## Feeding Ecology of Sidewinder Rattlesnakes, *Crotalus cerastes* (Viperidae)

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**21** **ABSTRACT:** Dietary studies are important for understanding predator–prey relationships and species interactions because they provide information on the trophic resources available to predators and their potential impact on prey populations. We relied on stomach contents of museum specimens and literature records to examine ontogenetic (size-related), sexual, seasonal, and geographic variation in the feeding habits of Sidewinders, *Crotalus cerastes*. Sidewinders fed primarily on lizards and slightly less frequently on mammals; birds and snakes were rarely consumed. The vast majority of *C. cerastes* consumed single prey items ingested head-first. Juvenile and adult female Sidewinders consumed lizards and mammals with similar frequency. We observed an ontogenetic shift in feeding patterns of adult male *C. cerastes* because they included more mammals in their diets, compared with juvenile males. Sidewinders are classic ambush (sit-and-wait) predators and, as predicted by theory, actively foraging lizards and mammals comprise a considerable fraction of their prey. We documented seasonal shifts in the feeding patterns of Sidewinders, with snakes consuming a greater proportion of lizards during early spring and autumn, and a greater percentage of mammals during late spring and summer. This dietary shift likely results from seasonal changes in the activity patterns of *C. cerastes*, because individuals can be diurnally active during early spring and autumn but are predominantly nocturnal during late spring and summer. Adult male and female Sidewinders from the Mojave and the Sonoran deserts consumed similar proportions of lizards and mammals. Our findings regarding the trophic habits of *C. cerastes* contribute to our understanding of the ecology of terrestrial, venomous predators.

**Key words:** Diet; Foraging; Mojave Desert; Prey; Serpentes; Sonoran Desert; Variation

DIET is a fundamental aspect of an animal's biology. Foraging and feeding are critical ecological tasks that supply the energy required for growth, maintenance, and reproduction (Pianka 2000). Dietary studies are important for understanding predator–prey relationships because they provide information on predators' fundamental trophic resources and their potential impact on prey populations (Martínez-Gutiérrez et al. 2015). Foraging and feeding behavior influence basic organismal features, including habitat selection (Custer and Galli 2002), movement patterns (Vedder 1984; Kreiter and Wise 2001), thermoregulatory regimes (Regal 1966; Lang 1979), and ultimately fitness (Selman and Houston 1996). Elucidating the underlying causes of variation in these traits thus provides valuable information regarding the overall biology of a predator and its trophic niche within an ecosystem (Young et al. 2010; Brasil et al. 2011; Thorén et al. 2011; Roşca et al. 2013).

Sidewinders, *Crotalus cerastes* Hallowell 1854, are relatively small-bodied serpents (50–60-cm adult snout–vent length [SVL]; Ernst and Ernst 2003) that inhabit sandy washes, dunes, and flatlands of the warm deserts of southwestern North America (Campbell and Lamar 2004; Fig. 1). The species is reported to be moderately sexually dimorphic, with females attaining larger body sizes than males (Reiserer 2001; Campbell and Lamar 2004). Males achieve sexual maturity at a smaller body size (SVL = 34 cm) than females (SVL = 38 cm), based on the body size of the smallest reproductive individual of each sex (Reiserer 2001). Sidewinders can be found near or within rodent burrows, or coiled in self-constructed depressions (a behavior known as “cratering”) beneath desert vegetation (Secor 1994a; Stebbins 2003). The snakes are usually considered nocturnal;

almost all summer activity takes place at night, but diurnal movements occur in early spring and in the autumn, particularly during the morning or late in the afternoon (Ernst and Ernst 2003). Sidewinders exhibit a classic ambush foraging strategy in which they wait in a cratered or coiled position for suitable prey to come into close proximity (Secor 1994a).

Herein, we tested specific hypotheses regarding the feeding ecology of *C. cerastes*, and assessed geographic variation in the diet of this snake. Several species of large-bodied snakes incorporate a greater proportion of larger prey in their diets, compared with smaller-bodied individuals (e.g., Mackessy 1988; Santos et al. 2007; Glaudas et al. 2008). Accordingly, we predicted that Sidewinders experience an ontogenetic (size-related) shift in feeding behavior, in which snakes incorporate larger prey into their diets as the serpents increase in body size (Klauber 1972; Secor 1994a). Knowledge of the predominant foraging mode of a predator allows assessments of how aspects of the animal's feeding biology may covary with foraging mode (Huey and Pianka 1981). Sidewinders are ambush foraging predators; therefore, we predicted that they predominantly feed upon actively foraging (mobile) species. The aforementioned temporal change in the activity patterns of Sidewinders led to the prediction that they primarily eat diurnal prey (lizards) when the snakes are active during the day, and switch to mainly crepuscular and nocturnal prey (mammals) when the serpents are predominantly active at night. Finally, we investigated geographic variation in the feeding ecology of *C. cerastes*.

### MATERIALS AND METHODS

We checked the stomach contents of individual *C. cerastes* by making a midventral incision in 1086 specimens from the following institutions: California Academy of Sciences, San Francisco (CAS;  $n = 142$ ); Natural History Museum of Los Angeles County, Los Angeles, California

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(LACM;  $n = 344$ ); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ;  $n = 295$ ); and the Department of Ecology and Evolutionary Biology, University of Arizona, Tucson (UAZ;  $n = 305$ ). We did not examine type specimens or especially soft, brittle, or otherwise fragile specimens, and we excluded individuals that might have been fed in captivity before being preserved. Our data set also incorporates published dietary reports of *C. cerastes* (cf. Rodríguez-Robles 1998) after accounting for redundancy between accounts (e.g., Klauber 1931, 1972). When possible for each snake, we recorded the following variables: locality data, date of collection, body size (SVL,  $\pm 1.0$  cm), body mass ( $\pm 0.1$  g), sex (determined by inspection of the reproductive tract), taxonomic identity of the prey, direction of prey ingestion (inferred from orientation in the gut), number of prey items, and prey mass ( $\pm 0.1$  g).

We weighed snakes and their intact or slightly digested prey after blotting and draining them briefly in a towel to remove excess fluid. Body measurements of partially digested items were estimated by comparison with intact conspecifics of similar size available at the Marjorie Barrick Museum of Natural History, University of Nevada, Las Vegas (MBM; the MBM collection was acquired by the MVZ in September 2009). We relied on this limited data set ( $n = 15$ ) to obtain an estimate of mean relative prey mass (RPM), the ratio of prey mass to predator mass. Most prey items were considerably digested, and in those instances we assigned an average adult mass obtained from preserved specimens or from literature records to species of lizards (Miller 1951; Vitt et al. 1981; Degenhardt et al. 1996; Turner 1998; Wright 2002; Newbold 2005; Mosher and Bateman 2014), mammals (Burt and Grossenheider 1980; Jameson and Peeters 2004), and birds (Alsop 2001) consumed by *C. cerastes*, an approach used in prior studies (e.g., Clark 2002; Weatherhead et al. 2009; Dugan and Hayes 2012). Based on the distribution of these estimates of prey mass, we divided prey into smaller ( $<30$  g) and larger ( $\geq 30$  g) prey, irrespective of prey type. The smaller prey category consisted of lizards (e.g., *Coleonyx variegatus* [Western Banded Gecko], 2.7 g; *Urosaurus* spp. [tree and brush lizards],  $<3.8$  g), mammals (e.g., *Chaetodipus* spp. [Pocket Mice],  $<23$  g; *Reithrodontomys megalotis* [Western Harvest Mice], 11.5 g), and birds (e.g., *Cardellina pusilla* [Wilson's Warblers], 8.5 g). The larger prey category included lizards (e.g., *Dipsosaurus dorsalis* [Desert Iguanas], 39.8 g; *Gambelia wislizenii* [Long-nosed Leopard Lizards], 36.4 g), mammals (e.g., *Dipodomys* spp. [Kangaroo Rats],  $>45$  g), and birds (*Campylorhynchus brunneicapillus* [Cactus Wrens], 39.7 g). Assigning an average adult mass to all prey items of a given species might have overestimated prey mass for smaller Sidewinders and might have underestimated prey mass for larger snakes. We used this expanded data set to assess the relationship between snake body size and prey mass.

We assessed ontogenetic, sexual, temporal, and geographic variation in the feeding habits of *C. cerastes*. To evaluate temporal variation in diet, we divided the active season into two components: diurnal season (March, April, October) and nocturnal season (May, June, July, August, September; cf. Ernst and Ernst 2003), and compared the frequency of lizards and mammals eaten in each season. Three previous studies on the food habits of Sidewinders were based on

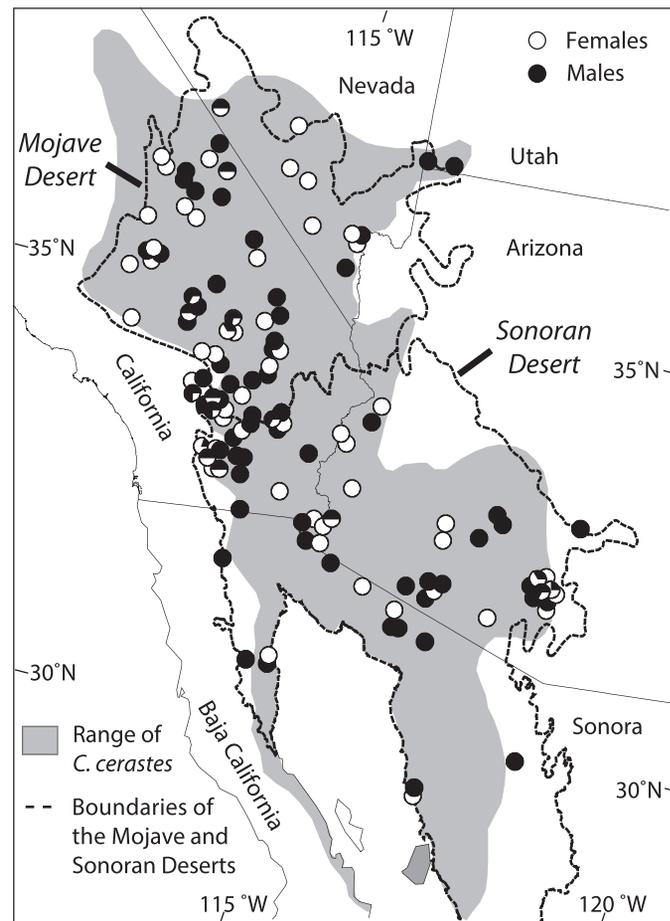


FIG. 1.—Approximate distribution of Sidewinders, *Crotalus cerastes* (grey shading; after Campbell and Lamar 2004), and approximate boundaries of the Mojave and Sonoran deserts (dotted lines) in southwestern North America. Circles indicate the georeferenced locations of male (filled circles) and female (open circles) snakes that contained prey in their stomachs.

restricted segments of the snakes' range: Yuma County, southwestern Arizona (Funk 1965), southern Nevada (Clark 1968), and southeastern California (Secor 1994a). We combined these data with records from our examination of a larger number of specimens from across the species' distribution to investigate geographic variation in feeding patterns of Sidewinders. Specifically, the distribution of *C. cerastes* extends into two physiographic regions of southwestern North America, the Mojave and the Sonoran deserts (Brown et al. 1979; Campbell and Lamar 2004; Fig. 1). We tested for spatial differences in the diet of Sidewinders by comparing the numbers of lizards and mammals eaten by snakes from the two deserts.

We checked all data for normality prior to analysis. We assessed differences in snake body size (SVL) using analysis of variance (ANOVA), and removed the nonsignificant interaction terms from the final model (Engqvist 2005). We relied on the  $G$ -test of goodness-of-fit (also known as the likelihood ratio test, or the log-likelihood ratio test) to determine whether the number of observations in particular categories (i.e., prey size, prey type) fits theoretical expectations. We performed all statistical analyses using SPSS Statistics (v20, SPSS Inc., Chicago, IL, USA). Values

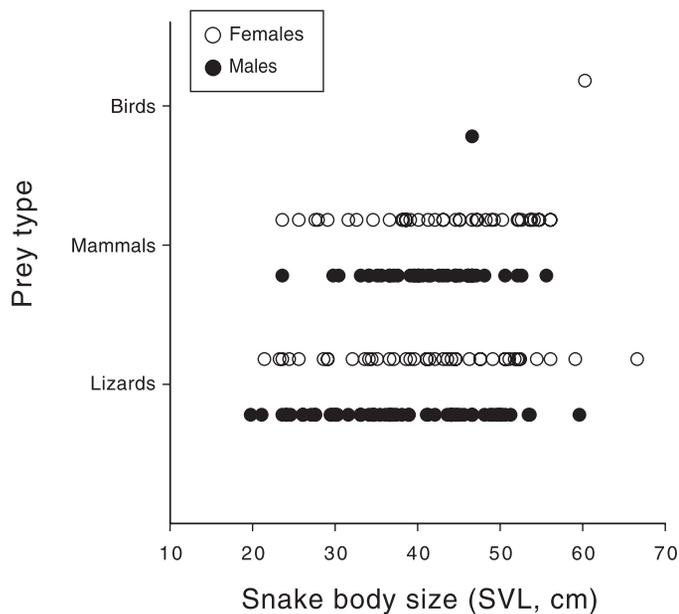


FIG. 2.—Relationship between prey type (lizards, mammals, birds) and snake body size (snout–vent length [SVL], cm) in *Crotalus cerastes* males (filled circles) and females (open circles). See Table S1 (in Supplemental Material available on-line) for sample sizes depicted in this graph.

are reported as means  $\bar{X} \pm 1$  SE, and all *P*-values are two-tailed.

## RESULTS

We examined 1086 individuals of *C. cerastes*, 209 (19.2%) of which contained prey. Of the 215 total prey items recovered, 118 were lizards, 82 were mammals, 2 were birds, and 2 were unidentified squamate reptiles; we could not identify the remaining 11 items. Combining our records with previous dietary accounts for Sidewinders ( $n = 267$ ; see Table S1 in the Supplemental Material available on-line), lizards were the most frequent prey type consumed (247/482, 51.2%), followed by mammals (206/482, 42.7%), birds (11/482, 2.3%), and snakes (5/482, 1%); 2 prey (0.4%) were unidentified squamate reptiles. The most commonly eaten lizards were *Aspidoscelis tigris* (Tiger Whiptails,  $n = 57$ ) and *Uta stansburiana* (Common Side-blotched Lizards,  $n = 39$ ). The mammals most frequently taken by *C. cerastes* were heteromyid rodents (*Dipodomys merriami* [Merriam's Kangaroo Rats],  $n = 29$ ; *Perognathus longimembris* [Little Pocket Mice],  $n = 28$ ; *D. deserti* [Desert Kangaroo Rats],  $n = 20$ ; and *Chaetodipus penicillatus* [Desert Pocket Mice],  $n = 19$ ). In some instances, we could not determine the frequency of certain prey species reported in dietary accounts of *C. cerastes*, specifically *A. tigris*, *A. t. tigris* (Great Basin Whiptails), *Callisaurus draconoides* (Zebra-tailed Lizards), *Uma inornata* (Coachella Fringe-toed Lizards), *Uma notata* (Colorado Desert Fringe-toed Lizards), *Uta stansburiana stejnegeri* (Eastern Side-blotched Lizards), *Chaetodipus* sp. or *Perognathus* sp. (Pocket Mice), and *Dipodomys* sp. (Kangaroo Rats; Cunningham 1959; Klauber 1972). Additionally, Secor (1994a) reported that, at a locality in the eastern Mojave Desert, several juvenile *C. cerastes* fed upon small *P. longimembris*; and Nabhan (2003) stated that Seri Indians from Sonora, Mexico, claim that they

have seen Sidewinders eat marine isopods (Crustacea: Isopoda) along rocky beaches and on the edge of tidepools. Lastly, Klauber (1972) reported a *C. cerastes* feeding on carrion (*Dipodomys* sp.).

The vast majority of *C. cerastes* that we examined had consumed single prey items (203/209, 97.1%); only six (2.9%) snakes had two items in their stomachs. Of the six Sidewinders that had eaten two prey items, two were adult males and four were females (one juvenile, three adults). One adult male (CAS 229244, SVL = 49.5 cm) contained one *A. tigris* and one *Sceloporus magister* (Desert Spiny Lizards), whereas the other (MVZ 193506, SVL = 34.5 cm) contained two unidentified lizards. The juvenile female (MVZ 3718, SVL = 35.0 cm) had ingested a *Sceloporus* sp. (Spiny Lizards) and an unidentified lizard. One adult female (LACM 104604, SVL = 56.0 cm) contained a *Dipsosaurus dorsalis* (Desert Iguanas) and a *Dipodomys merriami*, whereas another one (MVZ 228655, SVL = 38.5 cm) had consumed an unidentified lizard and a *Chaetodipus* sp. (Pocket Mice). The remaining adult female (LACM 104713, SVL = 52.2 cm) contained an unidentified lizard and an unidentified mammal. Additionally, Klauber (1972) reported an adult (SVL = 54.3 cm) *C. cerastes* that had consumed an *Aspidoscelis* sp. and an unidentified mouse, and a juvenile individual (SVL = 29.2 cm) that contained a caterpillar and an *Uma notata*, although it was unclear whether the larva represented a primary prey item for the Sidewinder, or whether the lizard had eaten the caterpillar. Funk (1965) stated that a juvenile male (total length = 31.7 cm) had ingested three young *Chaetodipus penicillatus*, all from one nest.

We inferred direction of ingestion for 52 items, 49 (94.2%) of which were ingested head-first while 3 (5.8%) were swallowed tail-first. The three prey ingested tail-first were lizards (*Coleonyx variegatus*, *Uta stansburiana*, and an unidentified lizard). Funk (1965) reported four prey items, all mammals (*Chaetodipus penicillatus*, *D. deserti*, *Mus musculus* [House Mice], and *Spermophilus tereticaudus* [Round-tailed Ground Squirrels]), that were also consumed tail-first.

For all snakes examined (irrespective of whether or not they had stomach contents), male (SVL =  $40.8 \pm 0.4$  cm, range = 16.0–59.5 cm,  $n = 601$ ) and female *C. cerastes* (SVL =  $41.0 \pm 0.50$  cm, range = 17.8–68.5 cm,  $n = 432$ ) had similar body sizes (single-factor ANOVA;  $F_{1,1031} = 0.12$ ,  $P = 0.73$ ), contrary to reports that the species exhibits sexual dimorphism in body size with females being the larger sex (Reiserer 2001; Campbell and Lamar 2004; but see below). Male (64 lizards, 41 mammals) and female *C. cerastes* (42 lizards, 41 mammals) consumed lizard and mammal prey with similar frequency ( $G = 2.02$ ,  $df = 1$ ,  $P = 0.16$ ). The two adult snakes (1 male, 1 female) that took birds had body sizes of 46.5 cm, and 60.2 cm, respectively (Fig. 2). Klauber (1972) reported an adult Sidewinder (SVL = 53.0 cm, unknown sex) that fed on a *Setophaga aestiva brewsteri* (California Yellow Warblers). Birds were excluded from further analyses because of their small sample size.

Of the 1086 *C. cerastes* we dissected, 122 were juvenile males (SVL < 34 cm), whereas 477 were adult males (SVL  $\geq$  34 cm; Reiserer 2001). Twenty-eight (23%) juveniles had prey in their stomachs, compared with 83 (17.4%) adults. Immature males fed predominantly on lizards (22/28,

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TABLE 1.—Two-factor analysis of variance of sexual variation in body size in *Crotalus cerastes* that consumed lizards and mammals. The interaction term (in parentheses) was nonsignificant, and thus it was excluded from the final model.

Parameter/Factor	Snake body size (snout-vent length; cm)	
	Males that preyed on lizards	Females that preyed on lizards
$\bar{X} \pm SE$	37.9 $\pm$ 1.3	37.9 $\pm$ 1.3
Range	19.7–59.5	21.3–66.5
<i>n</i>	61	42
	Males that preyed on mammals	Females that preyed on mammals
$\bar{X} \pm SE$	41.5 $\pm$ 1.0	42.9 $\pm$ 1.4
Range	23.5–55.5	23.5–56.0
<i>n</i>	41	41
Sex : $F_{1,182} = 3.3, P = 0.07$		
Prey type : $F_{1,182} = 3.80, P = 0.05$		
(Sex $\times$ Prey type : $F_{1,181} = 0.55, P = 0.46$ )		

78.6%), and less frequently on mammals (4/28, 14.3%). Two prey items (7.1%) consumed by juvenile males were unidentifiable. Mature males consumed a slightly greater proportion of lizards (41/85, 48.2%) than of mammals (37/85, 43.5%), and ate one bird (1/85, 1.2%). Two (2.4%) prey consumed by adult males could only be identified as squamate reptiles, and four (4.7%) were unidentifiable. Adult males fed on a greater proportion of mammals, compared with immature males ( $G = 9.82, df = 1, P = 0.002$ ).

Of the 1086 Sidewinders examined, 154 were juvenile females (SVL < 38 cm), and 278 were adult females (SVL  $\geq$  38 cm; Reiserer 2001). Twenty-five (16.2%) juveniles and 60 (21.6%) adults contained prey. Most prey ingested by immature females were lizards (16/26, 61.5%), with the remaining items being mammals (9/26, 34.6%) and one unidentifiable prey item (1/26, 3.8%). Mature females mainly fed upon mammals (32/63, 50.8%), followed by lizards (27/63, 42.9%), and birds (1/63, 1.6%); three (4.8%) items were unidentified. Nevertheless, differences in the proportions of lizards and mammals consumed by the two age classes were absent ( $G = 1.93, df = 1, P = 0.17$ ).

Disregarding the age class distinction (i.e., juveniles, adults) in snakes that contained lizards and/or mammals, a two-factor ANOVA indicated a trend for snake body size to vary in relation to sex. Specifically, females tended to be larger than males (Table 1). The analysis also revealed that snakes that consumed mammals were larger than those that took lizards, a pattern mainly driven by the differences in body size between males that preyed on lizards and those that ate mammals.

The estimates of body mass for the limited number of intact or partially digested prey items that we recovered indicated that average relative prey mass was  $26.6 \pm 8.0\%$  of Sidewinders' body mass (range = 1.5–114.9%,  $n = 15$ ). Based on the data set assigning prey species to size categories according to their average body mass, larger male and female *C. cerastes* fed on heavier prey (Table 2).

*Crotalus cerastes* exhibited temporal, but not geographic, variation in overall food habits. The proportion of mammalian prey consumed by Sidewinders was greater during the months when the snakes are predominantly active at night (May through September: 66 mammals, 77 lizards), compared with the months when they can be active during the day (March, April, October: 13 mammals, 35 lizards;  $G = 5.59, df = 1, P = 0.02$ ). There was no difference in the proportion of lizards and mammals consumed by snakes from the Mojave Desert (48 lizards, 34 mammals) and the Sonoran Desert (66 lizards, 48 mammals;  $G = 0.008, df = 1, P = 0.93$ ).

## DISCUSSION

Our study provides an inclusive and detailed account of the feeding habits of *C. cerastes* across its distribution. We used our data set to characterize taxonomic composition of the diets, as well as ontogenetic, sexual, temporal, and geographic variation in the feeding ecology of this snake species.

In general, Sidewinders preyed on lizards, less frequently on mammals, and only occasionally on birds and snakes. In studies of feeding ecology, evidence for intraindividual dietary variation comes from multiple prey types in the same specimen (Greene 1989). For Sidewinders, this

TABLE 2.—Two-factor analysis of variance of sexual variation in body size in *Crotalus cerastes* that consumed "smaller" (lighter; <30 g) and "larger" (heavier;  $\geq$ 30 g) prey. The interaction term (in parentheses) was nonsignificant, and thus it was excluded from the final model.

Parameter/Factor	Snake body size (snout-vent length; cm)	
	Males that consumed smaller prey	Females that consumed smaller prey
$\bar{X} \pm SE$	37.6 $\pm$ 1.5	35.9 $\pm$ 1.9
Range	19.7–55.5	21.3–53.9
<i>n</i>	37	29
	Males that consumed larger prey	Females that consumed larger prey
$\bar{X} \pm SE$	45.6 $\pm$ 1.8	46.6 $\pm$ 1.8
Range	33.0–53.3	38.5–56.0
<i>n</i>	12	10
Sex : $F_{1,85} = 0.32, P = 0.58$		
Prey size : $F_{1,85} = 18.40, P < 0.001$		
(Sex $\times$ Prey size : $F_{1,84} = 0.41, P = 0.53$ )		

variability encompasses at least lizards and mammals. Juveniles and adult males of *C. cerastes* fed most frequently on lizards, although mature individuals ate a greater proportion of mammals. These findings indicate that male Sidewinders exhibit an ontogenetic change in the proportion of different prey types in their diets, with mammals being more frequently consumed by larger individuals. The increase in consumption of mammalian prey by adult male *C. cerastes* might be facilitated by the larger gape attained by males as they grow, because an increased gape would allow the ingestion of bulkier prey, such as rodents (Forsman and Lindell 1993; Rodríguez-Robles et al. 1999a,b; Meik et al. 2012; Fabre et al. 2016). Moreover, during the reproductive season, adult males increase the distances traveled in search for mates (Secor 1994b). This heightened activity is almost certainly energetically expensive, and male Sidewinders increase the frequency with which they eat during this period (Webber et al. 2012). Consuming a larger proportion of rodents, and feeding upon mammals and other prey types more often, might allow mature males to more quickly replenish the energetic reserves needed to support the more extensive movements associated with their breeding activities. Similar size-related changes in diet, in which young snakes predominantly feed on lizards and adults switch to a diet mainly consisting of mammals, have been documented in various other serpents such as *Vipera berus* (Common European Adders; Kjørsgaard 1981), *C. catalinensis* (Santa Catalina Island Rattlesnakes; Ávila-Villegas et al. 2007), and *Morelia viridis* (Green Pythons; Natusch and Lyons 2012).

In similar fashion, juvenile female Sidewinders preyed more commonly on lizards, whereas adult females incorporated a larger number of mammals in their diets. In fact, mammals were the most frequent prey type eaten by mature females. Despite these contrasting food habits, the proportions of lizards and mammals consumed by juvenile and adult female snakes were similar, likely because male and female Sidewinders attain sexual maturity at different body sizes (SVL = 34 cm and SVL = 38 cm, respectively; Reiserer 2001). Nevertheless, the trend for adult *C. cerastes* to incorporate a larger percentage of mammals in their diets is qualitatively the same for male and female snakes. As in males, consuming more mammals, particularly during the early stages of a reproductive cycle, likely provides valuable energetic resources for fueling a female's breeding activities (gestation, parturition, maternal care; Webber et al. 2012).

Only larger *C. cerastes* (SVL > 46.0 cm) fed on birds. Snakes that eat avian prey require a larger gape than that required by snakes that consume lizards or mammals of similar body size or mass (Greene 1997). Birds have low densities for their diameter (because of their feathers), but they are relatively bulky items because of their protruding wings, which might explain why only larger Sidewinders preyed on birds. A similar pattern occurs in *C. willardi obscurus* (New Mexico Ridge-nosed Rattlesnakes), where individuals that consumed birds had the greatest body sizes (Holycross et al. 2002).

Larger male and female *C. cerastes* fed on heavier prey. Despite their relatively small body size among North American vipers (Campbell and Lamar 2004), *C. cerastes* consumed prey that averaged 26.6% of their body mass. Predation on relatively large prey has been documented in various snake species (Shine 1991; Greene 1997), particu-

larly viperids (Pough and Groves 1983; Martins et al. 2002; Glaudas et al. 2008). Indeed, viperid snakes are distinctive in their ability to subdue, ingest, and digest prey items that occasionally exceed RPM of 1.0 (Greene 1992). For instance, we dissected a 17.3-g juvenile male *C. cerastes* (MVZ 176134) that had consumed a 19.88-g *Callisaurus draconoides* (RPM = 1.15). Nevertheless, larger individuals continue to feed on relatively small prey (e.g., adult snakes containing prey with RPM ranging from 0.02 to 0.07). Therefore, in *C. cerastes*, the lower limit of prey mass does not appear to increase with snake mass (Shine 1991). In contrast, in *C. lutosus* (Great Basin Rattlesnakes), heavier individuals also take heavier prey, but tend to drop smaller items from their diets (Glaudas et al. 2008).

Foraging theory suggests that sit-and-wait predators feed predominantly on actively foraging species, because of the greater encounter rates facilitated by the frequent movements of the latter (Reilly et al. 2007). The lizards most frequently consumed by *C. cerastes* were *A. tigris* (Tiger Whiptails) and *U. stansburiana* (Common Side-blotched Lizards). Tiger Whiptails forage widely (Anderson and Karasov 1981), a behavior that increases the chance that Sidewinders will encounter them. *Uta* generally uses an ambush foraging strategy, although occasionally they employ more active foraging methods (Parker and Pianka 1975). Common Side-blotched Lizards are one of the most abundant lizards in southwestern North America, reaching maximum densities of >110 individuals/ha in different parts of their range (Turner et al. 1970; Parker 1974; Gadsden and Castañeda 2012). Accordingly, Sidewinders probably encounter *Uta* often when either species is moving about, and the abundant lizards likely constitute an energetically profitable prey item for Sidewinders. Further, the relatively small girth of lizards such as younger *A. tigris* and *Uta* may account for the great frequency of these species in the diet of juvenile and smaller bodied *C. cerastes* (Secor 1994a). The mammals most frequently taken by Sidewinders were *Chaetodipus* spp. (Pocket Mice), *Dipodomys* spp. (Kangaroo Rats), and *Perognathus* spp. (Pocket Mice), all of which are active foragers. Thus, widely foraging species comprise a considerable fraction of the prey taken by *C. cerastes*.

There was a temporal shift in the types of prey consumed by *C. cerastes*. Sidewinders ate a greater proportion of mammals from late spring to summer, compared with early spring and autumn. This pattern coincides with detailed observations of the foraging behavior of a population of *C. cerastes* in the eastern Mojave Desert, in which snakes mostly fed on diurnal lizards during the spring and autumn, but incorporated more nocturnal mammals in their diets during the summer (Secor 1994a). This change in the feeding behavior of *C. cerastes* likely results from temporal changes in surface activity; Sidewinders can be diurnally active during March, April, and October, but become largely nocturnal during late spring and especially summer, when daytime temperatures can exceed their critical thermal maximum (Secor 1994a). We did not detect geographic differences in the general diets of *C. cerastes* from the Sonoran and the Mojave deserts, because Sidewinders from the two deserts preyed on lizards and mammals with similar frequency.

In conclusion, we assembled a comprehensive data set of the food habits of *C. cerastes* rattlesnakes to examine aspects

of the feeding ecology of these ambush predators. Our observations regarding patterns of ontogenetic, sexual, temporal, and spatial variation in diet provide insight into the trophic niche of these snakes within their ecosystems. Our findings provide additional context on which to base further predictions regarding the feeding ecology of terrestrial predators, and help elucidate factors that lead to variation in life history patterns.

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#### SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at <http://dx.doi.org/10.#####/MS#.S#>

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