Feeding Ecology of the Endemic Rattleless Rattlesnake, *Crotalus catalinensis*, of Santa Catalina Island, Gulf of California, Mexico

Héctor Avila-Villegas, Marcio Martins, and Gustavo Arnaud

Crotalus catalinensis is a rattleless rattlesnake endemic to Santa Catalina Island, in the Gulf of California, Mexico. It has been hypothesized that the lack of a rattle in this species is a stealth adaptation for hunting birds in vegetation. We provide detailed data on the diet of *C. catalinensis* from samples obtained during nine trips to the island in 2002–2004. Over two-thirds (70%) of the diet of *C. catalinensis* was composed of the Santa Catalina Deer Mouse (*Peromyscus slevini*). The remaining prey were lizards (*Dipsosaurus catalinensis*, *Uta squamata*, and *Sceloporus lineatulus*). There was an ontogenetic shift in diet and higher feeding activity during the dry season. The diet of this species is only a small subset of the diet of its supposed closest relative, *C. ruber*, probably as a result of limited diversity of prey on the island. The lack of birds in the diet of *C. catalinensis* argues against the supposed importance of birds as an essential feature for the hypothesis relating the lack of a rattle with a stealth hunting technique for birds in vegetation. However, since *P. slevini* is partially arboreal, there remains the possibility that the lack of a rattle is an adaptation for stealth hunting for mice in vegetation.

THE rattleless rattlesnake, *Crotalus catalinensis*, is endemic to Santa Catalina Island, in the Gulf of California, Mexico. It is a slender, moderate-sized rattlesnake that is dimorphic in coloration, having an ashy gray phase and a brownish phase (Beaman and Wong, 2001; Grismer, 2002). The most remarkable feature of this rattlesnake is the lack of the rattle, which was hypothesized to be a consequence of the absence of natural predators on the island (Radcliffe and Maslin, 1975; Greene, 1997; Rubio, 1998), a stealth adaptation for hunting birds in vegetation (Ottley and Murphy, 1983; Greene, 1997; Grismer, 2002), or the result of random changes in genes controlling rattle formation (Greene, 1997).

Based on its phylogenetic affinity with the Red Diamond Rattlesnake, *C. ruber*, it is supposed that *C. catalinensis* originated from the isolation of a population of the former species on Santa Catalina Island during the Pleistocene (see Murphy and Crabtree, 1985; Murphy and Aguirre-León, 2002). Besides the lack of a rattle, another obvious difference between *C. ruber* and *C. catalinensis* is body length, up to 1.7 m in the former and 0.7 m in the latter (Grismer, 2002).

Information on the biology and ecology of *C. catalinensis* is limited. Previous work was reviewed by Beaman and Wong (2001), and recently Goldberg and Beaman (2003) presented information on reproduction. Regarding its diet, Grismer (2002) reported remains of Santa Catalina Deer Mouse (*Peromyscus slevini*), Black-Throated Sparrow (*Amphispiza bilineata*), and Santa Catalina Spiny Lizard (*Sceloporus lineatulus*) in scats. Grismer (2002) also suggested that juveniles may feed on small lizards, centerly the Santa Catalina Leaf-Toed Gecko, *Phyllodactylus bugastrolepis*. Avila-Villegas et al. (2004) found remains of *P. slevini* in the stomach contents of two snakes and Avila-Villegas et al. (2005) reported evidence of predation on Santa Catalina Desert Iguana (*Dipsosaurus catalinensis*). We here provide detailed data on the diet of *C. catalinensis* from samples obtained in the field in 2002–2004 and discuss the implications of our results to the ecology and evolution of this species.

MATERIALS AND METHODS

Santa Catalina (25°39′N, 110°49′W) is a granitic island with an area of 41 km² (Murphy et al., 2002). Its topography is characterized by rocky hillsides separated by wide and narrow sandy arroyos bearing the typical vegetation of the Sonoran Desert (Wiggins, 1980). The island is located within the protected area Parque Nacional Bahía de Loreto, off the coast of Loreto, in Baja California Sur. The climate of this region can be divided into three seasons according to patterns of precipitation: the dry season (March–June), characterized by the absence of rainfall; the summer rainy season (July–October), with a substantial increase in precipitation caused by the cyclonic activity of the tropical Pacific; and the winter rainy season (November–February), with a reduction of rainfall (Salinas-Zavala et al., 1990).

The vertebrate fauna of Santa Catalina Island is composed of nine reptile species besides the Rattleless Rattlesnake: the lizards *Dipsosaurus catalinensis*, *Sauromalus klauberi*, *Sceloporus lineatulus*, *Uta squamata*, *Aspidocelis catalinensis*, and

TABLE 1.   FREQUENCY OF OCCURRENCE OF PREY TYPES IN STOMACH CONTENTS AND FECES OF *C. catalinensis* COLLECTED DURING THE DRY (D) AND RAINY (R) SEASONS. Numbers in parentheses are values per taxonomic group.

	Stomach contents		Feces			
	D	R	D	R	Total	%
Mammals					(70)	(70.7)
Peromyscus slevini	5	6	18	41	70	70.7
Reptiles					(29)	(29.3)
Dipsosaurus catalinensis	2	1	3	10	16	16.2
Uta squamata	0	2	1	6	9	9.1
Sceloporus lineatulus	0	0	0	4	4	4.0
Total					99	100

Phyllodactylus bugastrolepis, and the snakes *Lampropeltis catalinensis, Hypsiglena torquata*, and *Leptotyphlops humilis* (Grismer, 1999, 2002; Murphy and Aguirre-León, 2002). Only one terrestrial mammal species occurs on the island, the Santa Catalina Deer Mouse, *Peromyscus slevini* (Hall, 1981), together with over 15 bird species (e.g., *Amphispiza bilineata, Carpodacus mexicanus, Cardinalis cardinalis, Auriparus flaviceps, Calypte costae*, Cody and Velarde, 2002).

We conducted nine visits to Santa Catalina Island from 2002 to 2004: three during the dry season (March–June) and six during the rainy season (July–October). In each field trip (3–5 days) we looked for snakes on the surface of arroyos and adjacent hillsides from 1900 to 2400 h, sampling a different locality each day. Captured snakes were searched for stomach contents and feces, which we obtained by forced regurgitation and gentle palpation of the last third of the body, respectively. When possible, we recorded direction of ingestion and sex of prey. We also recorded snout–vent length (SVL), sex (by cloacal probing; Schaefer, 1934), color pattern (gray phase or brown phase), and area of capture (arroyo or hillside) of each snake. Snakes were released immediately after data gathering. Prey samples were preserved in alcohol (70%), and prey remains (e.g., scales, fur) identified under a dissecting microscope. Lizard scales were identified by comparison with a reference collection of lizards from Santa Catalina Island or with the use of a scale identification key. Previous reports of our findings (Avila-Villegas et al., 2004, 2005) are also included in the analyses.

We tested for differences in diet between sexes, color patterns, seasons, and areas of capture by comparing the frequencies of prey types with a Chi-square test. Yates correction was applied when necessary (Zar, 1984). Ontogenetic shifts in diet were tested by comparing the SVL of snakes that consumed lizards with those of snakes that ate mammals using a Mann-Whitney *U*-test. We analyzed seasonal differences in foraging activity by comparing the proportion of snakes with stomach contents between the dry and rainy seasons with a Chi-square test. Statistica 7.0 was used for all statistical procedures.

RESULTS

We examined 193 live snakes for stomach contents, and 15 (12.8%) of them (seven males, six females, and two of unknown sex; SVL range 257–660 mm) had prey detectable by palpation. Sixteen prey items were found: 11 (68.8%) Santa Catalina Deer Mice, *Peromyscus slevini* (three males, two females, and six of unknown sex); three (18.8%) Santa Catalina Desert Iguana, *Dipsosaurus catalinensis* (sexes unidentified); and two (12.5%) Santa Catalina Side-Blotched Lizard, *Uta squamata* (one male and a lizard of unknown sex; Table 1). Only one snake had two prey items in its stomach (both *P. slevini*). All prey were ingested headfirst.

We searched for feces in 194 live snakes, which resulted in 93 samples. Of these, 75 snakes (80.6%, 35 males, 33 females, and seven of unknown sex; SVL range 279–762 mm) had identifiable remains. Eighty-three prey remains were found out of the 75 samples examined: 59 (71.1%) *P. slevini*; 13 (15.7%) *D. catalinensis*; seven (8.4%) *U. squamata*; and four (4.8%) *S. lineatulus* (Table 1). In eight cases, remains of two different prey species were found in the same sample: *P. slevini* and *U. squamata* (three times); *P. slevini* and *D. catalinensis* (twice); *P. slevini* and *S. lineatulus* (once); *D. catalinensis* and *S. lineatulus* (once); and *D. catalinensis* and *U. squamata* (once). We found no bird remains in scats or stomach contents of *C. catalinensis* in any year or season.

There were no significant differences in diet composition between sexes ($\chi^2 = 0.18$, df = 1, $P > 0.05$), color patterns ($\chi^2 = 2.77$, df = 1, $P > 0.05$), or seasons ($\chi^2 = 1.01$, df = 1, $P > 0.05$). However, there was a significant difference in the proportion of mice and lizards consumed by area

of capture (χ^2 = 6.41, df = 1, P < 0.05), with lizards being preyed at a higher proportion on streambeds than on hillsides. Snakes that consumed mammals (n = 64) were significantly larger (Z = 3.31, P < 0.001) than those that ate lizards (n = 32), showing a marked ontogenetic shift in diet, from ectothermic to endothermic prey. The proportion of fed snakes (in which we found feces or stomach contents) did not differ between dry and wet seasons (χ^2 = 0.83, df = 1, P = 0.361). However, the proportion of fed males was higher in the wet season than in the dry season (0.41 and 0.22, respectively), whereas for females this proportion was higher in the dry season (0.77) compared to the wet season (0.30); this difference between males and females was significant (χ^2 = 10.9, df = 1, P = 0.001).

DISCUSSION

Crotalus catalinensis exhibits the typical diet of most rattlesnakes, that is, a diet composed mainly of small mammals and lizards (Klauber, 1982; Ernst, 1992; Campbell and Lamar, 2004). The sister species of *C. catalinensis*, *C. ruber*, is a diet generalist and apparently a very opportunistic predator. Besides feeding frequently on locally abundant small mammals (including mice, rats, ground squirrels, tree squirrels, chipmunks, gophers, rabbits) and lizards of many different families, *C. ruber* occasionally feeds on frogs, toads, birds, and other snakes (Klauber, 1972; Ernst, 1992; Campbell and Lamar, 2004). Thus, the diet of *C. catalinensis* is only a fraction of the diet of its supposed closest relative (as observed in other island pitvipers like *Bothrops insularis* and *B. alcatraz*; Marques et al., 2002), probably as a result of limited prey diversity on Santa Catalina Island (especially the presence of only a single species of mouse). Indeed, the extremely generalist and opportunistic feeding habits of *C. ruber* may have facilitated the colonization and/or persistence of the ancestor of *C. catalinensis* on Santa Catalina Island, as suggested for the island species of the *Bothrops jararaca* group by Marques et al. (2002).

Boback (2003) showed that body length of island snakes is strongly affected by prey size availability: snakes that feed on small prey tend to become smaller than their closest relatives, while those that feed on large prey tend to become larger. Thus, dwarfism in *C. catalinensis* may reflect the relatively small size of the main prey of adults, the mouse *P. slevini* (see Álvarez-Castañeda and Cortés-Calva, 2002). This may also be the cause of dwarfism in the centipede-eating *Bothrops alcatraz* (Marques et al., 2002). Because there is only one mammalian prey (*P.

slevini) available to *C. catalinensis*, the maintenance of a viable population of that species is critical for the conservation of *C. catalinensis*.

Crotalus catalinensis preyed upon three of six lizard species that inhabit Santa Catalina Island: *Dipsosaurus catalinensis*, *Sceloporus lineatulus*, and *Uta squamata* (Grismer, 2002; Avila-Villegas et al., 2005). Although it is possible that the remaining lizard species (*Sauromalus klauberi*, *Aspidocelis catalinensis*, and *Phyllodactylus bugastrolepis*) were not observed as eaten prey due to our small sample size (29 individual lizards), it is also possible that they are not consumed for being energetically low profitable prey (hard-to-find, hard-to-catch, and/or hard-to-eat prey; Arnold, 2001) in relation to *P. slevini*.

Since bird remains (especially feathers) are easily detected in viper gut contents (pers. obs.) and our samples are relatively widespread throughout the year, the absence of birds in our samples strongly indicates that this prey is not important for *C. catalinensis*, although it may occasionally be taken (Grismer, 2002), as in many other rattlesnakes (Klauber, 1972; Ernst, 1992; Campbell and Lamar, 2004). This finding argues against the supposed importance of birds in the diet of *C. catalinensis*, an essential feature for the hypothesis relating the lack of a rattle with stealth hunting for birds in vegetation (Ottley and Murphy, 1983; Hollingsworth and Mellink, 1996; Greene, 1997; Grismer, 2002). However, there remains the possibility that the lack of a rattle may have been selected for stealth hunting for the partially arboreal mouse, *P. slevini*.

We did not find significant differences between sexes nor between color morphs in frequency of prey types. Shine (2001) argued that differences in diet between sexes are generally associated with sexual size dimorphism (SSD), primarily regarding head size (Camilleri and Shine, 1990); however, we do not have head measurements to check whether *C. catalinensis* is sexually dimorphic in head size or shape. Reinert (1984) stated that diet differences between sex, age, or morphological classes in a population may reflect differences in habitat use. Therefore, the lack of difference in diet between color morphs of *C. catalinensis* may indicate that these do not differ in habitat use.

The lack of seasonal differences in diet composition in *C. catalinensis* indicates that the most used prey types are available throughout the year. On the other hand, the higher proportion of fed females in the dry season indicates that males and females of *C. catalinensis* have different energy requirements in this part of the year, perhaps due to the fact that at least part of

the females are pregnant during the dry season (Grismer, 2002).

The ontogenetic shift from ectothermic to endothermic prey that we found in *C. catalinensis* is a common feature of vipers in general and most probably a plesiomorphic character in the Viperidae (Greene, 1997; Martins et al., 2002). Lizards were found at a significantly higher proportion in snakes sighted in arroyos, and this may reflect the fact that we found juveniles at a significantly higher proportion in arroyos than on hillsides (unpubl. data).

The feeding ecology of *C. catalinensis* is in general similar to that of its sister species, *C. ruber*, and the few differences we found are apparently due to particular environmental conditions found on Santa Catalina Island, such as reduced habitat and prey availability (especially the presence of only a single species of small mammal and its small size and partially arboreal habits). Efforts towards the conservation of habitats at Santa Catalina Island, as well as of *C. catalinensis* and its prey, would help to preserve this evolutionary heritage.

ACKNOWLEDGMENTS

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(HAV, GA) CENTRO DE INVESTIGACIONES BIOLÓGICAS DEL NOROESTE, MAR BERMEJO NO. 195, COL. PLAYA PALO DE SANTA RITA, C.P. 23090, LA PAZ, B.C.S., MÉXICO; AND (MM) DEPARTAMENTO DE ECOLOGIA, INSTITUTO DE BIOCIÊNCIAS, UNIVERSIDADE DE SÃO PAULO, 05508-090 SÃO PAULO, SP, BRAZIL. PRESENT ADDRESS: (HAV) INSTITUTO DEL MEDIO AMBIENTE DEL ESTADO DE AGUASCALIENTES, AVE. CONVENCIÓN PTE. #1626, FRACC. LA CONCORDIA, AGUASCALIENTES, AGS C.P. 20010, MEXICO. E-mail: (HAV) avila_hec@yahoo.com.mx; (GA) garnaud04@cibnor.mx; and (MM) jararaca@ib.usp.br. Send reprint requests to GA. Submitted: 23 Dec. 2005. Accepted: 12 Oct. 2006. Section editor: S. F. Fox.