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Intraspecific Variation in Diet Composition and Morphology of Yucatecan Cantils (*Agkistrodon russeolus* Gloyd 1972 [Serpentes: Viperidae])

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ABSTRACT: Detailed studies on the natural history of snakes are essential for ecological hypothesis-driven research and effective conservation. Herein, we studied the diet composition and morphology of Yucatecan Cantils (*Agkistrodon russeolus* Gloyd 1972 [Serpentes: Viperidae]), an understudied viperid species endemic to the Yucatán Peninsula. We collected data from live free-ranging snakes; freshly road-killed snakes and snakes deliberately killed by local villagers; and museum specimens and literature sources. We compared their age classes, sexes, and color morphs. Data came from snakes from Yucatán, Quintana Roo, and Campeche in Mexico, and two records were from northern Belize, comprising most of the species' distribution range. Examination of 76 individuals resulted in 77 prey items from 68 snakes. Results indicated that *A. russeolus* is a generalist-opportunistic predator that feeds on a wide variety of vertebrates, but primarily on lizards and small mammals and less frequently on birds, snakes, and anurans. Geographic patterns in the diet and morphology of *A. russeolus* were evident: snakes from the coastal region were smaller in body size and less heavy bodied and with a heavily lizard-based diet, whereas snakes from both dry and moist forest regions were larger and heavier and their diet was primarily mammal based. We did not detect differences in diet composition among age classes because lizards and mammals were eaten at all stages of life, but an "ontogenetic telescope" was evident; that is, the importance of mammals increases with snake body size and the spectrum of prey types consumed also broadens. Males had longer tails than females, and females were light colored more often than males, but other morphological characteristics were similar between the sexes. The sexes and color morphs did not differ in diet composition. We did not detect dietary composition variations between seasons, and our data indicate that this species can feed year-round opportunistically. Because of increasing environmental pressures within its range, studies are urgently needed to elucidate other critical aspects of the ecology of this viperid species.

Key words: Feeding; Geographic variation; Ontogeny; Sexual dimorphism; Wolpoch

DETAILED studies of the natural history of snakes are essential for addressing broad ecological questions and identifying site-specific resources for the conservation of endangered species (Greene 1994; Webb and Shine 1998; Litvaitis 2000). Studies of snake diets are particularly important because they provide valuable insights into the ecological needs of the species and improve understanding of movement and habitat selection (Heard et al. 2004; Sperry and Weatherhead 2009), venom composition and variation (Casewell et al. 2020), evolution of natural populations (Shine and Madsen 1997), and effective snake habitat management strategies (Webb and Shine 1998). However, despite the importance of dietary studies and snake ecology, information on many snake species (including imperiled taxa) is still scarce.

Snakes are important predators in many terrestrial and aquatic communities. Some species are specialist feeders with narrow diets, but many others are generalists and exhibit substantial dietary variation at both inter- and intrapopulation levels (Greene 1997; Dugan and Hayes 2012). Species of the genus *Agkistrodon* are typically categorized as dietary generalists. Although the food habits of North American species such as *A. contortrix* and *A. piscivorus* have received considerable research attention (reviewed in Gloyd and Conant 1990), less is known about the diets of the species commonly known as cantils, which includes *A. bilineatus*, *A. howardgloydi*, *A. taylori*, and *A. russeolus*, found in Mexico and Central America (Gloyd and Conant 1990; Solórzano et al. 1999; Porras et al. 2013).

Because snakes are gape-limited predators, their morphology is highly relevant for—among other issues—prey acquisition. Consequently, morphological characteristics (e.g., age classes, sexes, and color morphs) may influence the prey acquisition capabilities of snakes. For example, diets of snakes can differ dramatically throughout ontogeny, typically from ectothermic to endothermic prey (as reported for many vipers, including *A. howardgloydi*; Solórzano et al. 1999), largely driven by size-related morphological constraints from newborns to adults (Shine 1991a; Arnold 1993; López et al. 2013). Similarly, sexual size and/or shape dimorphism often can result in dietary differences between sexes, wherein the larger sex consumes a greater spectrum of types of prey or larger prey that the other sex cannot consume due to gape-size limitations (e.g., *A. piscivorus*, Vicent et al. 2004; *Crotalus polystictus*, Meik et al. 2012). However, sexual size dimorphism has been reported in some species of *Agkistrodon* (e.g., *A. piscivorus* and *A. contortrix*), but not in others (e.g., *A. howardgloydi* and *A. taylori*; Gloyd and Conant 1990).

Coloration is another component of snake morphology reported in some cantil species (*A. howardgloydi* and *A. taylori*; Gloyd and Conant 1990) that could be a potential source of variation in diet. For example, snakes with distinct color morphs within a population may use different microhabitats (e.g., for foraging or thermoregulatory purposes), which may lead to different rates of prey encounters and prey types (Reinert 1984, 1993; Shine et al. 1998).

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In addition, snake populations exposed to heterogeneous environmental conditions (e.g., seasonal or geographic) may experience different habitat interactions that can lead to dependence on alternative prey (Boback 2003; Amarello et al. 2010). In fact, evidence indicates that the diet of Eastern Copperheads (*A. contortrix*) varies seasonally and in different geographic areas along its range (Garton and Dimmick 1969; Gloyd and Conant 1990). Seasonal and geographical variation in diet composition of snakes suggests plasticity in feeding behavior and may be driven by prey availability, resource competition, and/or habitat structure (e.g., Rodríguez-Robles et al. 1999; Luiselli 2006; Reinert et al. 2011). Detailed information on geographic dietary variation can also support venom research and enhance understanding of how the local environment influences body size and sexual size dimorphism in snakes (Daltry et al. 1996; Boback 2003; Amarello et al. 2010).

Yucatecan Cantils (*Agkistrodon russeolus* Gloyd 1972 [Serpentes: Viperidae], or Wolpoch, the Mayan name), are medium-sized (total length up to 1050 mm), relatively uncommon pitviper snakes, endemic to the Yucatán Peninsula (YP; Porras et al. 2013). The species is represented apparently by disjunct populations, with most known records from the dry northern portion of the YP and few records from relatively moist areas in the southern and northeastern portions (Gloyd and Conant 1990; Lee 1996; Rautsaw et al. 2022). In the most recent reassessment of the conservation status of the cantils, Porras et al. (2013) classified *A. russeolus* as an endangered species applying International Union for Conservation of Nature criteria and placed it in the high vulnerability category to extinction according to the environmental vulnerability score index. The authors assigned these conservation categories to *A. russeolus* primarily due to its limited geographic distribution, the considerable growth of the human population density in its range (that leads to the destruction of natural habitats), and the direct human persecution of this snake species (that leads to killing on sight; Porras et al. 2013). For instance, *A. russeolus* populations outside protected areas from the northern coast of the YP are under immense human pressure by tourism-related infrastructure and urbanization. As of 2010, more than half of the original territorial extension of the coastal dune scrub vegetation has been lost due to the alarming increase in anthropogenic development (Andrade-Hernández 2010; Durán et al. 2010), which has accelerated noticeably in recent years (J.A. Ortiz-Medina, personal observation).

Agkistrodon russeolus is an understudied and scarcely collected species; thus, current knowledge on its natural history and ecology is considerably limited (Gloyd and Conant 1990; Lee 1996; Heimes 2016). For example, there are only three anecdotal reports on its feeding habits (Hoevers and Henderson 1974; Henderson 1978; Lee 1996), all reporting unidentified mammals as prey items, although it has been suggested that much like other cantils it possibly feeds on other types of prey (Gloyd and Conant 1990; Lee 1996; Heimes 2016). In this study, we investigated the dietary composition of *A. russeolus* and examined how it varies within and among populations according to snake morphological characteristics (age, body size, sex, and color morph), climatic season, and geographical region across much of its range. Thus, we also provide detailed information on the morphology of *A. russeolus*, with emphasis on sexual dimorphism and geographic variation.

Based on natural history data from other cantils (*A. bilineatus*, *A. howardgloydi*, and *A. taylori*; see Gloyd and Conant 1990, and references therein; Solórzano et al. 1999) and our previous observations in the field, we specifically tested the following hypotheses: (1) *A. russeolus* has a generalist diet; (2) there is a habitat-associated geographic influence on the diet composition and morphology of *A. russeolus*, such that snakes from coastal populations are smaller in body size and consume proportionally more ectothermic prey than other habitat populations, because the availability of rodents is lower on the coast; (3) an ontogenetic shift in the diet composition occurs, such that smaller *A. russeolus* mainly feed on ectothermic prey (anurans and lizards) and gradually switch to a diet dominated by endothermic prey (mammals) with age; (4) *A. russeolus* exhibits relatively little sexual difference in morphology; thus, diet composition is similar between the sexes; and (5) *A. russeolus* decreases its activity in the dry season and therefore its feeding frequency, and the composition of its diet is expected to vary seasonally; that is, the consumption of ectothermic prey is greater in the rainy season when these prey are more active.

MATERIALS AND METHODS

Most dietary and morphological data of *A. russeolus* were obtained from 33 live free-ranging individuals, 21 freshly road-killed individuals, and 12 individuals that were deliberately killed by local villagers. All individuals were collected from August 2017 to April 2022 through intensive direct searches in the field, night-driving road surveys, and opportunistic encounters, following the methods suggested by Fitch (1987). We also examined eight preserved voucher specimens from the herpetological collection of El Colegio de la Frontera Sur (ECOSUR) at Chetumal, Quintana Roo (ECO-CH-H), deposited from 1993 to 2015 (Appendix). Most snake samples are from Yucatán ($n = 69$), with a few from Quintana Roo ($n = 4$) and Campeche ($n = 1$), in Mexico. In addition, data on the diet of two *A. russeolus* from northern Belize (see Hoevers and Henderson 1974; Henderson 1978) were included (Fig. 1).

Fecal material was obtained from live snakes in situ (when possible) through gentle palpation on the last third of the body, although some individuals were kept in plastic containers at the laboratory until they defecated voluntarily. An adult female snake voluntarily regurgitated a juvenile Black Spiny-tailed Iguana (*Ctenosaura similis*) 1 d after capture. All snakes were implanted with a subcutaneous passive integrated transponder tag (Avid Identification Systems, Inc.) for future identification and later released at the place of capture. An adult male snake (ID *303) from the northern coastal dune scrub region (NCR; see below for regions) was caught twice, 70 d apart, and provided a fecal sample each time. The road-killed and deliberately killed snakes, as well as voucher specimens, were examined by making a midventral incision to obtain prey remains in their digestive tracts. Upon removal, all prey remains were stored individually in 70% ethanol for subsequent identification.

Prey items were identified to the lowest possible taxonomic level based on the degree of digestion. Claws,

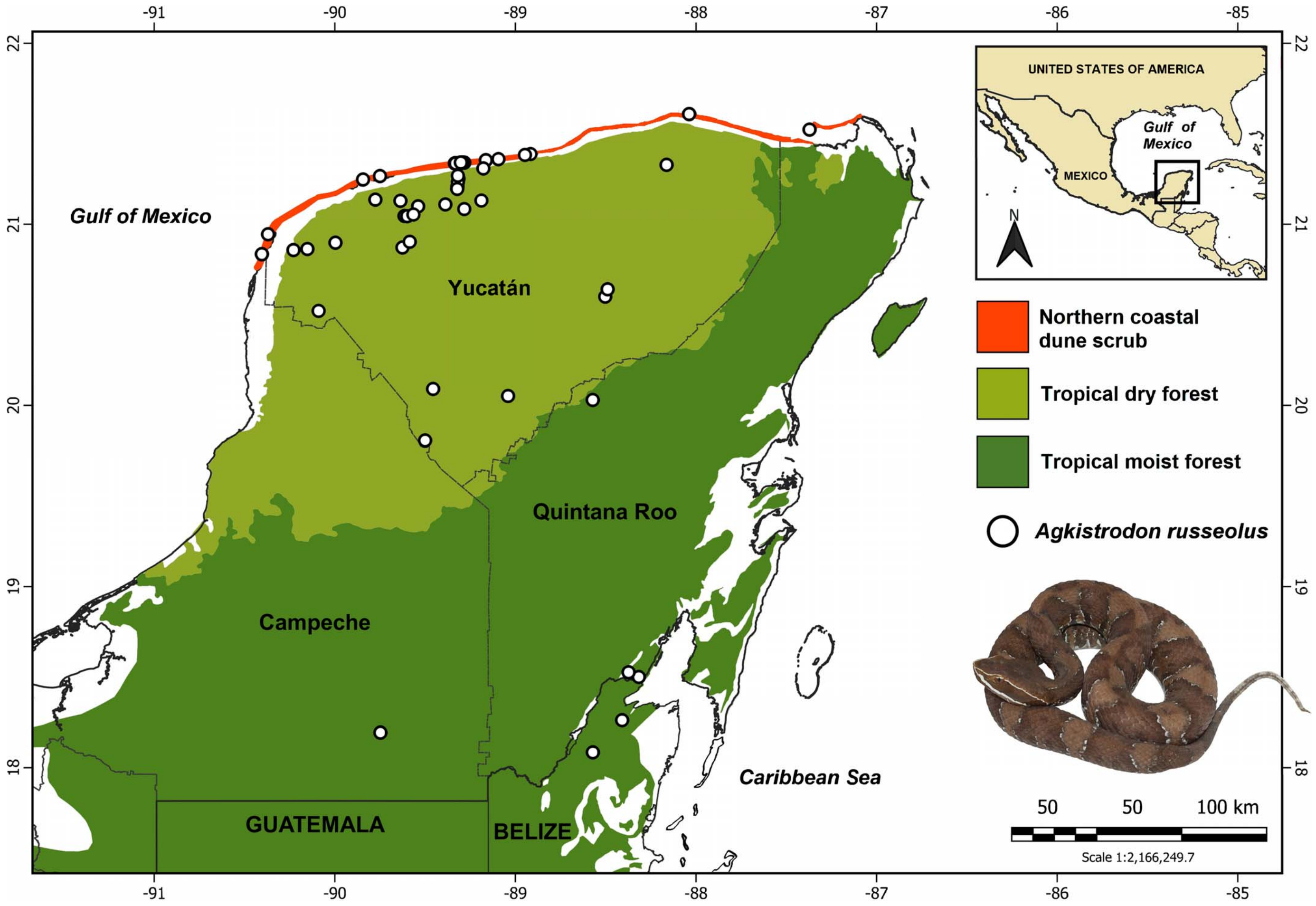

FIG. 1.—Collection sites on the Yucatán Peninsula from which dietary samples and morphological data of *Agkistrodon russeolus* were obtained. Geographic regions are adapted from Olson et al. (2001). Each dot might represent more than one snake. A color version of this figure is available online.

bones, teeth, hind limbs, hairs, and tails were used to identify mammal prey items. Dorsal guard hairs were prepared according to the method described by Monroy-Vilchis and Rubio-Rodríguez (2003) and then compared (gross morphology, medulla configuration, and scale patterns) with reference to premounted guard hairs of small mammals of the YP from the mammal collection of ECOSUR (ECO-SC-M) and pertinent literature (e.g., Pech-Canché et al. 2009). Nonavian reptile (lizards and snakes) and amphibian (anurans) remains were identified through their morphology (e.g., diagnostic scale characteristics, color pattern, tails, limbs, and toes) by using dichotomous keys of sympatric species (see Lee 1996) and by comparing them directly with specimens from ECO-CH-H. Birds were diagnosed based on complete or fragmented feathers. Because the recognition of primarily or secondarily invertebrate ingestion can be problematic (see Neill and Allen 1956), they were excluded from our analyses because they were always found in conjunction with vertebrate prey remnants in feces. Furthermore, invertebrate remains found in feces belonged to very small insects (e.g., ants, termites, mosquitoes, and small beetles), so it is unlikely that they could be ingested intentionally by the snakes. Plant material was occasionally found in feces and also considered as accidental or secondary intake. We recognize that our methods may lead to natural biases because larger, more difficult-to-digest prey are more likely to be detected than soft-bodied, easy-to-digest prey, as demonstrated by Glaudas et al. (2017) with Puff Adders (*Bitis arietans*). Therefore, the interpretation of our results should be taken with caution, particularly in the proportion of amphibian prey that we recorded.

Locality data, date of collection, sex, snout–vent length (SVL; ±1 mm), total length (TTL; ±1 mm), tail length (TL; ±1 mm), head length (from tip of rostral scale to angle of jaw, HL; ±0.01 mm), head width (widest part of head, HW; ±0.01 mm), interocular width (minimal distance between eyes, IW; ±0.01 mm), direction of prey ingestion, taxonomic identity of prey, and number of prey items of each snake were recorded. HL, HW, and IW were taken mostly from dead snakes, but we excluded those measures affected by crushed heads. Body mass was obtained (weighing on an electronic scale, ±0.2 g) only from live and freshly dead snakes; museum snakes were not weighed due to the inaccuracy associated with preserved specimens. We classified alive and freshly dead snakes into two general dorsal color categories: dark and light, wherein dark corresponds to dark brown and light to reddish brown; all museum specimens were excluded from this classification due to the loss of original pigmentation. Sex identification of snakes was achieved by either probing in alive snakes (Schaefer 1934) or by making a small incision in the base of the tail of dead specimens to check for the presence of the hemipenes (Keogh et al. 2000). In some dead specimens, the sex was corroborated by examination of the gonads. For identification of possible ontogenetic shifts in diet, we classified snakes as newborns (<380 mm SVL), juveniles (380–500 mm SVL), and adults (>500 mm SVL), following the age class criteria used by Solórzano et al. (1999) for *A. howardgloydi*, a closely related species and of similar size as *A. russeolus* (Gloyd and Conant 1990; Alencar et al. 2016). We did not analyze the prey–predator size or mass relationships because most of our samples came from feces and prevented us from collecting those data. To assess geographic variation in diet and morphology, we assigned individual snakes into three regions of the YP according to their general vegetation types as follows: NCR ($n = 42$), tropical dry forest region (DFR; $n = 28$), and tropical moist forest region (MFR; $n = 6$), following a modified map from Olson et al. (2001; Fig. 1). To assess temporal variation in diet, we considered three climatic seasons: dry season (March–May), rainy season (June–October), and northerlies (cold fronts) season (November–February; Enriquez et al. 2013).

Statistical Analyses

Differences in diet composition were analyzed using Fisher's exact tests to determine frequencies of utilization of distinct prey types according to snake age class, sex, color morph, geographic region, and climatic season. The same test was used to assess differences in the proportion of snakes with and without prey (digestive tract or feces) and to examine whether color morph was linked to the sex and/or region of the snake. Because the consumption of different prey items is unlikely to represent a single predation event, we treated each prey item as a separate event; therefore, snakes with food remains involving more than one prey item are thus reflected in our data in accordance with the number of predation events (i.e., prey; Mociño-Deloya et al. 2015).

We use one-way analysis of variance (ANOVA) with post hoc pairwise least-significant difference (LSD) tests to compare SVL of adult snakes among geographic regions and SVL of snakes eating different prey types. We tested for differences in body mass between snakes from different regions by using independent-samples *t*-tests. We performed two-factor ANOVAs (with sex and region as factors) to examine sexual differences in SVL, TTL, and body mass (as dependent variables), as well as analysis of covariance (with sex and region as factors, using SVL as covariate) to examine differences in TL, HL, HW, and IW (as dependent variables) between sexes in adult snakes.

All statistical analyses were performed using SPSS Statistics v20 (IBM, Armonk, NY). Parametric tests were done after verifying that data met the assumptions. Values given are mean ± 1 SD, and total range with minimum–maximum values. *P* values are two tailed, and the significance level for all tests was determined at $\alpha \leq 0.05$.

RESULTS

Prey Items

Of the 76 *A. russeolus* in this study (12 newborns, 13 juveniles, and 51 adults), 68 (89%) contained 77 partially identifiable prey items; 9 (12%) of these prey items were recovered from stomach contents and 68 (88%) from feces (defecated or in intestine). The remaining eight snakes (one juvenile and seven adults) had no prey remains. Overall, prey items were represented by 36 (47%) lizards, 31 (40%) mammals, 5 (6%) birds, 3 (4%) snakes, and 2 (3%) anurans, of which 43 came from NCR, 27 from DFR, and 7 from MFR (Table 1). We were able to determine the direction of ingestion of only eight prey contained in stomachs, of which six (75%) were ingested headfirst (two lizards, two mammals, one snake, and one bird) and two (25%) tailfirst (both lizards).

TABLE 1.—Prey items identified from fecal and stomach contents of *Agkistrodon russeolus* obtained from live free-ranging snakes, freshly road-killed snakes, snakes that were deliberately killed by local villagers (2017–2022), museum specimens (1993–2015), and literature sources (Hoevers and Henderson 1974; Henderson 1978). NCR = northern coastal dune scrub region, DFR = tropical dry forest region, MFR = tropical moist forest region. Asterisk indicates invasive species.

		Frequency		
Prey type		NCR	DFR	MFR
Anurans	Unidentified anuran	0	2	0
Lizards	*Anolis* sp.	1	0	0
	*Hemidactylus frenatus**	15	1	0
	Ctenosaura similis	2	1	0
	Sceloporus chrysostictus	0	1	0
	Sceloporus cozumelae	7	0	0
	Aspidoscelis angusticeps	2	0	0
	Holcosus gaigeae	2	1	0
	Unidentified lizard	1	1	1
Snakes	*Conophis lineatus*	1	0	0
	Mastigodryas melanolomus	0	1	0
	Stenorrhina freminvillii	0	1	0
Mammals	*Cryptotis mayensis*	0	4	0
	Heterogeomys hispidus	2	1	0
	Heteromys gaumeri	0	1	0
	Heteromys sp.	0	0	1
	Reithrodontomys gracilis	2	1	0
	Sigmodon toltecus	0	0	2
	*Mus musculus**	5	5	1
	*Rattus rattus**	0	2	0
	Unidentified mammal	1	1	2
Birds	*Tringa semipalmata*	1	0	0
	Sternula antillarum	1	0	0
	Quiscalus mexicanus	0	1	0
	Unidentified bird	0	2	0

Geographic Variation

The probability of snakes containing prey items was similar among regions (NCR = 86% of 42 snakes, DFR = 93% of 28 snakes, and MFR = 100% of 6 snakes; $P = 0.614$). We found geographic differences in the diet composition ($P < 0.001$): *A. russeolus* from NCR fed mainly on lizards (70%), followed by mammals (23%), birds (5%), and snakes (2%); snakes from DFR fed mainly on mammals (56%), followed by lizards (19%), birds (11%), snakes (7%), and anurans (7%); and our small sample from MFR showed that these snakes consumed mostly mammals (86%) and lizards in lesser proportion (14%; Fig. 2; Table 1). Pairwise comparisons showed that the lizard-based diet of NCR snakes differed from the mammal-based diet of DFR ($P < 0.001$) and MFR ($P = 0.009$) snakes and that the diets of the latter showed no differences ($P = 0.931$). The most frequently consumed prey species according to region were as follows: *Hemidactylus frenatus* (Common House Gecko

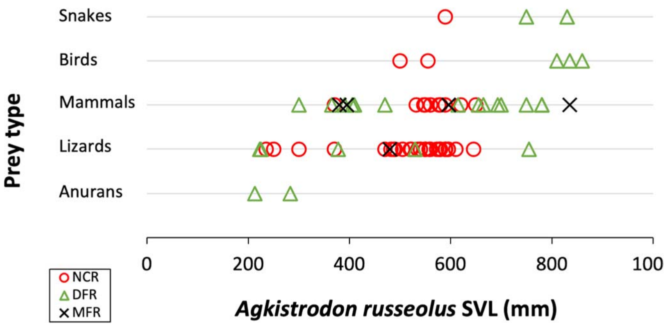

FIG. 2.—Association between prey types and snout–vent length (SVL) of *Agkistrodon russeolus*. NCR = northern coastal dune scrub region, DFR = tropical dry forest region, MFR = tropical moist forest region. A color version of this figure is available online.

[invasive species], $n = 15$; 35% of total prey) and *Sceloporus cozumelae* (Cozumel Spiny Lizard, $n = 7$; 16% of total prey) from NCR, *Mus musculus* (House Mouse [invasive species], $n = 5$; 19% of total prey) and *Cryptotis mayensis* (Yucatán Small-eared Shrew, $n = 4$; 15% of total prey) from DFR, and *Sigmodon toltecus* (Toltec Cotton Rat, $n = 2$; 29% of total prey) from MFR (see Table 1).

The SVL of *A. russeolus* ranged 213–860 mm (mean = 545.43 ± 158.325 mm), whereas TTL ranged 265–1050 mm (mean = 663.376 ± 190.674 mm). The SVL significantly differed among regions ($F_{2,47} = 39.58$, $P < 0.001$). Adult snakes from NCR had smaller mean body size (mean = 568.94 ± 38.21 mm, range = 505–650 mm) than those from DFR (mean = 736.94 ± 86.702 mm, range = 530–860 mm; LSD, $P < 0.001$) and MFR (mean = 715.5 ± 168.99 mm, range = 596–835 mm; LSD, $P = 0.003$); the snakes from DFR and MFR were similar in size (LSD, $P = 0.656$). The NCR adult snakes were also less heavy bodied (mean = 172.98 ± 53.25 g, range = 100–303.8 g) than those from DFR (mean = 431.3 ± 156.89 g, range = 121.6–646.4 g; $t_{37} = 7.716$, $P < 0.001$; snakes from MFR were excluded from this analysis because of the lack of body mass data). Because differences between sexes in SVL and body mass were nonsignificant (see below), we pooled male and female data for the above-mentioned analyses. There were no differences in color morphs exhibited by snakes between regions (NCR × DFR only, $P = 1$).

Ontogenetic Variation

Prey presence was independent of age class ($P = 0.485$). Proportions of prey types consumed among all three age classes did not differ ($P = 0.24$), even when regions were separately analyzed (for each region, $P > 0.05$). However, differences in SVL among *A. russeolus* that consumed different prey types were found ($F_{4,71} = 6.700$, $P < 0.001$; Fig. 2). Individuals that fed on anurans (mean = 248 ± 49.497 mm, range = 213–283 mm) were smaller than those that ate lizards (mean = 503.5 ± 124.55 mm, range = 223–755 mm; LSD, $P = 0.01$), mammals (mean = 571.17 ± 145.66 mm, range = 300–835 mm; LSD, $P = 0.002$), birds (mean = 712 ± 170.46 mm, range = 500–860 mm; LSD, $P < 0.001$), and snakes (mean = 723 ± 122.748 mm, range = 589–830 mm; LSD, $P < 0.001$). Those that preyed on lizards were smaller than those that ate mammals (LSD, $P = 0.047$), birds (LSD, $P = 0.002$), and snakes (LSD, $P = 0.009$). Individuals that consumed mammals, birds, and snakes were similar in size (for all pairwise comparisons: LSD, $P > 0.05$).

Only adult snakes (550–780 mm SVL; $n = 7$) presented multiple prey items: one snake contained remains of both a lizard and a snake, two snakes contained remains of two mammals, two snakes contained remains of a mammal and a lizard, and one snake contained remains of a mammal and two lizards. Identifying multiple prey items was possible only if remains of different species were found, except for one killed snake containing a freshly eaten Black Rat (*Rattus rattus*) and hair remnants of another digested one in the lower intestine, which led to a possible underestimation.

Sexual Variation

Prey presence was independent of sex ($P = 0.456$) or color morph ($P = 0.67$). Prey types consumed did not vary between the sexes ($P = 0.53$) or color morphs ($P = 0.96$).

The sample of adult MFR snakes was too small ($n = 1$ for each sex); thus, morphological comparisons between sexes were made only between adult snakes from NCR and DFR. No differences between sexes in SVL ($F_{1,44} = 0.000$, $P = 0.996$) or TTL ($F_{1,44} = 0.290$, $P = 0.593$) were found. After controlling for body size, adult males had longer tails than females ($F_{1,42} = 19.546$, $P < 0.001$), but did not differ in HL ($F_{1,16} = 2.360$, $P = 0.144$), HW ($F_{1,6} = 0.105$, $P = 0.757$), or IW ($F_{1,16} = 0.463$, $P = 506$). No differences between sexes in body mass ($F_{1,35} = 0.098$, $P = 0.757$) were found in adults (see Table 2). The interaction sex × region was not significant for any of the morphological variables (for all cases, $P > 0.05$), indicating that patterns of sexual variation in morphology were consistent between regions. Color morphs occurred in both sexes, although females were more often lighter than males (males: 15 presented dark color and 24 light color; females: 2 presented dark color and 22 light color; using snakes of all age classes pooled, $P < 0.001$). All newborns were light in color, as well as all but two juvenile males (Table 3).

Seasonal Variation

The dietary composition in the regions did not vary between seasons (for all cases, $P > 0.05$). The proportion of snakes with and without prey also did not vary seasonally ($P = 0.772$): we obtained prey remains from snakes in all months except April (only one snake, no prey). The greatest number of snakes and prey items were registered in the rainy (36 prey from 33 snakes) and the northerlies (31 prey from 32 snakes) seasons, whereas the lowest number occurred in the dry season (10 prey from 12 snakes). Of the nine prey items obtained from the stomachs, one (11%) came from dry, three (33%) from rainy, and five (56%) from northerlies seasons.

DISCUSSION

As predicted, results indicate that *A. russeolus* is a generalist predator that feeds on a wide variety of vertebrates across its distribution: mainly on lizards and small mammals and less frequently on birds, snakes, and anurans. Some authors in regional field guides (e.g., Lee 1996, 2000; Campbell 1998; Díaz-Gamboa et al. 2021) speculatively mentioned fish and invertebrates as other possible prey of *A.*

TABLE 2.—Sample size (*n*), mean ± 1 SD, and range minimum–maximum of morphological data of adult *Agkistrodon russeolus* from the different geographic regions: NCR = northern coastal dune scrub region, DFR = tropical dry forest region, MFR = tropical moist forest region. See main text for statistical analyses.

	NCR			DFR			MFR		
Trait	*n*	Mean ± 1 SD	Range	*n*	Mean ± 1 SD	Range	*n*	Mean	Range
Snout–vent length (mm)									
Males	17	573.06 ± 46.86	505–650	13	734.85 ± 93.25	530–860	1	835	—[a]
Females	14	563.93 ± 24.83	520–610	4	743.75 ± 72.27	665–810	1	596	—
Total length (mm)									
Males	17	694.88 ± 52.02	625–782	13	896.67 ± 109.74	645–1050	1	1001	—
Females	14	672.07 ± 31.58	617–720	4	893.75 ± 80.14	800–970	1	724	—
Tail length (mm)									
Males	16	124 ± 11.82	96–150	13	168.37 ± 21.03	115–193	1	166	—
Females	14	108.14 ± 9.44	93–125	4	150 ± 10.8	135–160	1	128	—
Head length (mm)									
Males	6	33.6 ± 1.64	31.4–36.3	7	41.1 ± 3.47	34.4–44.6	1	44.5	—
Females	4	34.77 ± 2.74	32.5–38.6	4	42.47 ± 3.67	37.5–46.3	1	40.2	—
Head width (mm)									
Males	2	24.7 ± 1.13	23.9–25.5	5	34 ± 2.73	31.5–38	1	33.4	—
Females	1	26.6	—	3	30.4 ± 2.02	28.6–32.6	—	—	—
Interocular width (mm)									
Males	6	12.81 ± 1.29	10.3–13.9	8	16.66 ± 1.52	15.1–19.8	1	17.6	—
Females	3	13.3 ± 0.2	13.1–13.5	4	16.95 ± 2.16	14.6–19.7	1	13.6	—
Body mass (g)									
Males	15	189.6 ± 63.83	100–303.8	10	420.7 ± 168.79	121.6–646.4	—	—	—
Females	12	152.21 ± 25.86	116.2–190.8	2	484.3 ± 87.25	422.6–546	—	—	—

[a] A dash indicates not applicable.

russeolus. Nevertheless, our data revealed the absence of fish, and indeed, they are highly unlikely prey because *A. russeolus* appears to avoid aquatic habitats even in coastal areas, as supported by our own fieldwork. The erroneous assumption of semiaquatic habits on other cantils was also refuted by Burchfield (1982), Gloyd and Conant (1990), and Solórzano et al. (1999) for *A. taylori*, *A. bilineatus*, and *A. howardgloydi*, respectively. We also found no substantial evidence that *A. russeolus* feeds on invertebrates, contrary to its congeners *A. contortrix* and *A. piscivorus* (reviewed in Gloyd and Conant 1990; Lagesse and Ford 1996). However, the absence of invertebrates seems to be consistent in the diet of other cantil species. For instance, Solórzano et al. (1999) did not report them in the diet of *A. howardgloydi* from Costa Rica, and West (1981) stated that young captive *A. bilineatus* refused to eat insects. Burchfield (1982) found grasshoppers in feces of wild *A. taylori*, although it is unclear whether it was the result of secondary ingestion as mammals were also reported.

Agkistrodon russeolus ate its prey mainly headfirst, which is common among snakes because it facilitates the passage of the limbs of the prey and reduces the swallowing time (Greene 1997; Glaudas et al. 2008). However, some lizards were eaten tailfirst, presumably because of their small sizes and slender bodies such that they can be easily eaten from any direction. *Agkistrodon russeolus* is an opportunistic feeder consuming both diurnal and nocturnal prey (see Table 1). Cantils are considered to be sit-and-wait (ambush) predators and use their tails to lure prey (Gloyd and Conant 1990); the latter behavior linked with feeding on ectothermic prey as in many vipers (e.g., genus *Bothrops*, Martins et al. 2002). For example, we observed radio-tracked adult snakes at NCR during daytime displaying caudal luring, which may be associated with the high frequency of lizard consumption by adults. Thus, prey consumed might reflect that *A. russeolus*' daytime-active prey (such as most predated lizard species, and possibly some birds; Table 1) may be attracted by caudal luring, whereas nocturnal prey such as geckos and mammals may be ambushed at night.

TABLE 3.—Color morphs (light, dark) presented by age classes and sexes from 63 alive and freshly dead *Agkistrodon russeolus* in this study.

	Males		Females	
Age class	Dark	Light	Dark	Light
Newborn	—[a]	3	—	5
Juvenile	2	5	—	2
Adult	13	16	2	15
Total	15	24	2	22

[a] A dash indicates not applicable.

Geographic differences in the diet and the morphology of *A. russeolus* were evident. Specifically, the NCR adult snakes differed markedly from the other populations, being smaller in body size, less heavy bodied, and with a heavily lizard-based diet, whereas both DFR and MFR snakes were larger, heavier (more robust), and their diets were primarily mammal based. Differences in prey consumption surely reflect the dietary plasticity of this opportunistic predator as result of local availability of those prey in the regions, probably driven by the particularly low abundance of rodents in the coastal dune scrub vegetation (e.g., Cimé-Pool et al. 2006) compared with the other regions (e.g., Hernández-Betancourt et al. 2008a, b), and also the high abundance of Asian invasive geckos (*H. frenatus*) in NCR. Indeed, the large number of invasive geckos found in the diet of coastal snakes was surprising. The high abundance of these geckos in NCR, certainly enhanced by the alarming increase in anthropogenic development in the region (e.g., hotel complexes, luxury beachfront developments, summer houses, and coconut plantations), could make them a readily available food source for coastal *A. russeolus*.

Geographic variation in body size in *A. russeolus* is more difficult to interpret because many habitat-associated factors that we did not analyze can drive geographic differences in snake body size (e.g., Amarello et al. 2010). However, we suspect that differences in the snakes' diet among regions could be a potential factor related to adult body size variation. For example, the diet alteration hypothesis predicts that conspecific snakes will be larger in areas where larger types of prey, usually mammals or birds, are available, and smaller where only or largely small types of prey, typically squamates (e.g., lizards), are present (Forsman 1991; Boback 2003). Thus, *A. russeolus* from DFR and MFR could reach larger body sizes by consuming a higher proportion of mammals than snakes from NCR feeding predominantly on lizards. However, because our data provide no direct evidence on prey size/mass differences consumed among each population (as we caution in the methods), more studies testing this hypothesis in *A. russeolus* are required.

Our failure to find differences in the consumption of prey types according to snake age class was mainly due to *A. russeolus*' consumption of lizards and mammals (the two main prey) in all stages of life (Fig. 2). Nevertheless, when we looked at the relationship between the body size of snakes and the type of prey that they consume, an ontogenetic telescope is evident (Arnold 1993). As snakes get larger, the importance of mammals increases and the spectrum of prey types broadens to comprise other prey that smaller *A. russeolus* do not eat, such as birds and snakes (Fig. 2). The size of the snake head is the major determinant of the prey type and size that snakes can consume. Head size contributes to the maximum gape size; therefore, it is easier for larger snakes to exploit available prey than their smaller conspecifics (Shine 1991a; Arnold 1993). For example, *A. russeolus* did not consume birds until the snakes reached a size of 500 mm SVL (the upper limit for juveniles). Birds have a bulky shape due to their wings and feathers that makes them difficult to handle and swallow; therefore, snakes may require a larger gape to deal with such prey (Arnold 1993; Greene 1997). Larger snakes may also be physically more capable of consuming prey that are long relative to their own body size, such as other snakes (Shine 1991a). In addition, multiple prey items observed only in adults may indicate that larger snakes may feed more frequently.

Our results indicate that males and females of *A. russeolus* do not vary much in their morphology, except that males have longer tails (which is common among snakes; see King 1989). Also, females are more often lighter in color regardless of population and geographic distribution. Likewise, Burchfield (1982) and Gloyd and Conant (1990) for *A. taylori* and *A. howardgloydi*, respectively, reported a comparable pattern wherein females were often lighter in color than males, but similar in size. In addition, our color morph data on newborns and juveniles of *A. russeolus* apparently support the trend observed by Gloyd and Conant (1990) that usually males darken with age. The color morph, however, seems to be irrelevant in the intraspecific feeding behavior of *A. russeolus* because no differences were found in the diet between color morphs. In fact, intraspecific dietary differences related to color morphs in snakes are rarely reported, but it occurs in some species (e.g., *Python brongersmai*; Shine et al. 1998). Furthermore, given that *A. russeolus* did not show sexual morphological differences in body and head size, it is possible that both sexes consume prey of the same type, which was supported by our results wherein they had a similar diet composition. By contrast, in other species of *Agkistrodon*, for example *A. piscivorus*, a sexual dimorphism exists in body size and head shape, with males being larger than females, which contributes to differences in prey consumption (Vicent et al. 2004). Nevertheless, variation in the degree of sexual dimorphism between closely related taxa is common in snakes, even among populations of widely distributed species (Shine 1991b, 1993; Pearson et al. 2002).

Our failure to detect variation in diet composition between seasons may suggest that common prey in the regions are available throughout the year, as suggested by Carbajal-Márquez et al. (2020) for the Yucatán endemic pitviper *Crotalus tzabcan*. However, we observed a decline in the number of snakes collected and prey during the dry season. In an ongoing radio telemetry study with *A. russeolus*, we observed an almost complete cessation of activity in radio-telemetered snakes during the dry months that also corresponded to the hottest period of the year (J.A. Ortiz-Medina, personal observation). This possibly leads to a low rate of prey encounters during the drought, but the record of a snake with prey in its stomach indicates that snakes could still continue to feed opportunistically. A similar pattern of temporal feeding decline related to unfavorably high temperatures was reported for *A. contortrix* by Garton and Dimmick (1969).

Even though our sample size was relatively small, it also reflects the relative rarity of *A. russeolus*, especially for MFR, which also was supported by the scarce number of known records in the literature pertaining to that region (see Gloyd and Conant 1990; Lee 1996; Porras et al. 2013). For example, in a long-term study (2010–2018) involving road-killed snakes near Chetumal (on the Mexico–Belize border), Cedeño-Vázquez et al. (2021) recorded 742 snakes belonging to 31 species, but none included *A. russeolus*. Our data significantly expand the knowledge on the natural history of this viperid snake and at the same time highlight the need for additional studies to elucidate other critical aspects of the ecology of this endemic species amid the increasing environmental pressures taking place in the YP.

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APPENDIX

Preserved voucher specimens examined from the herpetological collection of ECOSUR (ECO-CH-H) at Chetumal, Quintana Roo, deposited from 1993 to 2015.

MEXICO: CAMPECHE: Calakmul, Road to the Archaeological Zone of Calakmul, Calakmul Biosphere Reserve (ECO-CH-H-1261). QUINTANA ROO: José María Morelos, 3 km N Sacalaca (ECO-CH-H-3824); Lázaro Cárdenas, Holbox (ECO-CH-H-2592); Othón P. Blanco: Centro de Investigaciones de Quintana Roo, Chetumal (ECO-CH-H-0418); Camino a Tres Ríos (ECO-CH-H-2724). YUCATÁN: Celestún, Rancho Xixim, Hotel Ecoparaiso (ECO-CH-H-1744); Chankom: Road to Chankom (ECO-CH-H-3515); Chankom (ECO-CH-H-3823).