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Ontogenetic Variation in Head Morphology and Diet in Two Snakes (Viperidae) from Northeastern Argentina

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ABSTRACT.—Snakes are highly diverse in head morphology and in the types of prey they eat. Species of the Viperidae family have a high degree of morphological specialization; however, some species specialize in feeding on a single or a few prey species whereas closely related organisms take a diverse array of prey taxa. We compared head morphology and diet throughout ontogeny in two species of the family Viperidae. *Rhinocerothis alternatus* (Yarará grande) had a highly specialized diet, feeding exclusively on mammals throughout its life. *Bothropoides diporus* (Yarará chica) fed on small prey such as amphibians and reptiles and on large prey such as mammals. Mature specimens differed significantly in snout–vent length (SVL) between species whereas juvenile specimens did not. A statistical comparison of head morphology showed differences between species in both juvenile and mature specimens. Linear regression analysis showed that head variability throughout ontogeny was greater in *R. alternatus* than in *B. diporus*. There were significant positive correlations between total length of prey in relation to SVL, head length, and head width of predator and they were higher in *R. alternatus* than in *B. diporus*. Our findings suggest ontogenetic morphological variation between *R. alternatus* and *B. diporus* and that this variation could be related to interspecific differences in eating habits. Therefore, our results agree with the hypotheses postulating that differences in morphology and diet between species could be influenced by genetic and phylogenetic constraints. However, further studies comparing sympatric species or species with their ancestors in terms of morphology and diet are necessary to confirm these results.

RESUMEN.—Las serpientes presentan gran variabilidad tanto en la morfología de la cabeza como en los tipos de presas que consumen. Las especies de la familia Viperidae tienen un alto grado de especialización morfológica; sin embargo algunas de ellas son especialistas en su alimentación, consumiendo solo un tipo de presas, mientras que otras se alimentan de variadas presas. En éste trabajo se comparó la morfología de la cabeza y dieta a lo largo de la ontogenia en dos especies de la familia Viperidae. *Rhinocerothis alternatus* se alimentó exclusivamente de mamíferos a lo largo de su vida. *Bothropoides diporus* presentó una dieta generalista, consumiendo presas pequeñas como anfibios y reptiles, y presas grandes como mamíferos. Los ejemplares maduros presentaron diferencias significativas entre las especies en la distancia entre el hocico y la cloaca (LHC), mientras que los individuos juveniles no presentaron diferencias. La morfología de la cabeza presentó diferencias entre las especies tanto en los ejemplares juveniles como en los maduros. Los análisis de regresión lineal mostraron que las variables de la cabeza analizadas presentaron mayores dimensiones a lo largo de la ontogenia en *R. alternatus*. Las correlaciones entre el largo total de las presas y el LHC, largo de la cabeza y ancho de la cabeza de los predadores fueron positivas y significativas, y fueron mayores en *R. alternatus*. Nuestros resultados sugieren que existe una variación morfológica ontogénica entre *R. alternatus* y *B. diporus*, y que dicha variación podría estar relacionada con diferencias en los hábitos alimentarios entre las especies. En consecuencia, nuestros resultados concuerdan con las hipótesis que plantean que las diferencias en morfología y dieta entre las especies podrían estar influenciadas por factores genéticos y filogenéticos. Sin embargo, son necesarios futuros estudios que comparen especies simpátricas o especies con sus ancestros, en relación a la morfología y dieta para poder corroborar éstos resultados.

Snakes are the only terrestrial vertebrates that can ingest whole prey larger in both mass and diameter than themselves (Greene, 1997). Most living snakes differ from other tetrapods in their ability to transport entire prey through their oral cavities using alternate movements of the left and right jaw elements (Cundall and Greene, 2000). Because of their specialized cranial morphology and dentition, most snakes are unable to reduce large prey items into smaller fragments before ingestion; thus, head size may well set an upper limit on the size of prey items that can be ingested (Shine, 1991; but see Jayne et al., 2002). Indeed, previous studies based on the feeding apparatus hypothesized that adaptations to ingest large prey would have played a central role in the evolutionary and ecological success of snakes (Gans, 1961; Cundall and Greene, 2000; Aubret et al., 2004b; Vincent et al., 2006b).

A relationship between morphological variation and dietary requirements in snakes has been suggested (Greene, 1983). Pough and Groves (1983) found morphological and dietary differences among species of Viperidae, Dipsadidae, Boidae, and Elapidae involving differences in head width, mandible length, and circumference at the quadrates, among others. In

addition, a clear relationship between head length and prey size has been documented frequently in snakes (Vitt, 1983; Forsman, 1991; Shine, 1991; Forsman, 1996; Cundall and Greene, 2000).

Differences in the diet can also occur throughout ontogeny. Several snake families show ontogenetic diet shifts, often from ectothermic to endothermic prey (Martins and Oliveira, 1999; Nogueira et al., 2003; López and Giraudo, 2008). Ontogenetic changes in the diet are generally attributed to changes in morphological, behavioral, and physiological characteristics (Martins et al., 2002; Herrel and Gibb, 2006). This change has been also related to a difference in prey availability in the habitats used by juveniles and adults (García and Drummond, 1988; Lind and Welsh, 1994). In addition, when both age classes occupy the same habitats, ontogenetic diet shift might be a strategy to reduce interspecific competition (Meik et al., 2010). Within the family Viperidae, some species show ontogenetic variation in the diet while others eat the same type of prey as juveniles and as mature individuals (Martins et al., 2002; Valdujo et al., 2002; Nogueira et al., 2003; Monteiro et al., 2006). However, few studies have examined how head shape changes during ontogeny and how such changes may influence prey selection (Vincent et al., 2004).

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Within the family Viperidae, the genus *Bothrops* was subdivided recently into new genera (*Bothrops*, *Bothropoides*, and *Rhinocerothis*) based on morphological and molecular evidence (Fenwick et al., 2009). Most species have a generalist diet (e.g., *Bothropoides neuwiedi pauloensis*, Valdujo et al. 2002; *Bothropoides pubescens*, Hartmann et al., 2005; *Bothropoides matogrossensis*, Monteiro et al., 2006; *Bothrops mojeni*, Nogueira et al., 2003; *Bothrops atrox*, *Bothropoides jararaca*, *Bothropoides neuwiedi*, and *Bothrops taeniatus*, Martins et al., 2002). Only the species *Rhinocerothis alternatus*, *Rhinocerothis fonsecai*, and *Rhinocerothis cotiara* are mammal specialists and *Bothropoides insularis* specializes in birds (Martins et al., 2002). Both genera include species with generalist and specialist feeding habits and a generalist diet was regarded as plesiomorphic within the group (genus *Bothrops*, Martins et al., 2002). Generalist species may feed on a wide range of prey including invertebrates, amphibians, reptiles, birds, and mammals. However, head morphology in species with different food habits within Viperidae has received little attention.

We studied two related snakes belonging to the Viperidae family, a group of snakes with a high degree of morphological specialization: *R. alternatus* and *B. diporus*. Both species are terrestrial and sympatric in several regions of South America: *R. alternatus* is distributed from southern Brazil to Paraguay, Uruguay, and central Argentina; *B. diporus* is distributed from Mato Grosso do Sul and Paraná in Brazil to the south and east of Paraguay and central Argentina (Ceï, 1993; Giraudo and Scrocchi, 2002). *Rhinocerothis alternatus* is a dietary specialist feeding exclusively on mammals throughout its life (Martins et al., 2002; Giraudo et al., 2008; Nunes et al. 2010); *B. diporus* is a dietary generalist feeding on lizards, amphibians, and rodents (Giraudo et al., 2008; López, 2010). Literature cited here suggests that head shape might impose constraints on dietary habits. Accordingly, the aim of our work was to compare ontogenetic morphological variation in the head of these two viper species in relation to their diets.

MATERIALS AND METHODS

Morphological Measurements.—We examined 170 specimens from herpetological collections; 123 specimens of *R. alternatus* (24 juveniles and 99 mature specimens) and 47 of *B. diporus* (15 juveniles and 32 mature specimens) from northeastern Argentina. The preserved, analyzed specimens belong to the collections held at national museums (see Appendix 1). We discarded individuals that were grossly distorted by preservation. For each specimen we took six morphological measurements: 1) snout–vent length (SVL), distance between rostral scale and the posterior edge of the anal scute; 2) head length (HL), distance from the articulation of the lower jaw with the quadrate bone to the anteriormost point of the rostral scale; 3) right lower jaw length (JL), distance from the articulation of the lower jaw with the quadrate bone to the anteriormost point of the labial scale on the ventral side of the head; 4) head width (HW), distance between both articulations of the lower jaw with the quadrate bone; 5) interocular width (IW), measured at the point of minimum distance between the eyes; and 6) eye to snout length (ESL), distance from the front of the eye to the rostral scale. We selected these head measurements because they have been associated with feeding behavior. HL, HW, and ESL contribute to maximum gape size in snakes; HW is also associated with the space available for food passage through the buccal cavity and JL is presumably related to both jaw opening-closing velocity and maximum gape size (Vincent et al.,

2006a); lower ESL increases snout mobility or may decrease snout size to give greater freedom of maxillary motion (Gans, 1961; Cundall and Irish, 2008). Measurements were taken with a ruler or calipers.

Individuals were classified as juveniles or mature specimens based on gonad examination. Males with umbilical scars or nonconvoluted vas deferentia were classified as juveniles whereas those with convoluted vas deferentia, indicating the presence of sperm, were considered mature (Aguar and Di-Bernardo, 2005). Females with umbilical scars or ovaries with follicular growth <5 mm were classified as juveniles whereas females with vitellogenic follicles >5 mm were considered mature (Saint Girons, 1985; Marques and Puerto, 1998). We were unable to characterize the gonads of 29 individuals. In those cases we used TL of the smallest mature female and TL of the smallest mature male (based on the measurement of 143 specimens that could be recognized by the analysis of gonads) to determine the reproductive status (juvenile or mature individuals). In *R. alternatus* the TL of the smallest mature female and smallest mature male was 853 mm and 603 mm, respectively; in *B. diporus* TL of the smallest mature female and male was 695 mm and 578 mm, respectively.

Diet Analysis.—We analyzed stomach and intestine contents by making an incision in the ventral surface of the specimens. We identified prey items to the class taxonomic level (amphibians, reptiles, mammals). Prey that had been slightly digested were measured in TL from the tip of the snout to the tip of the legs. Measurement of TL of rodents did not include the tail. A high number of prey could not be identified to species or genus level, or measured in TL, because they had been largely deteriorated by the digestive process. Highly digested stomach contents (mainly small pieces of bones) were considered nonidentified vertebrates. The number of prey items and the direction (head- or tail-first) in which prey was ingested were recorded when possible, and the stomach contents of juveniles and mature specimens were analyzed separately.

Statistical Analysis.—SVL was compared between species, considering age classes and sex (the latter only in adult individuals), using a Mann-Whitney test. Head measurements were compared individually, considering age classes and sex (the latter only in adults), by ANCOVA with SVL as covariable. We tested data normality and homogeneity of variances using Shapiro-Wilks and F test, respectively. All variables together were compared between species using a multivariate analysis (MANCOVA) with SVL as covariable. We performed a MANCOVA considering age class and sex as alternative criteria. We considered sex because both species show sexual dimorphism (Giraudo et al., 2008). The relationship between head variables (HL, JL, ESL, HW, and IW) and SVL in each species was assessed with regression analyses. To assess the relationship between TL of the prey and SVL, HL, and HW of the predator, the Pearson correlation coefficient was used. All analyses were performed on log₁₀-transformed variables. We performed all statistical analyses using Infostat software version 2011 (Di Rienzo et al., 2011).

RESULTS

Morphological Analyses.—Mature specimens differed significantly in SVL between species, *R. alternatus* being larger than *B. diporus*; juvenile specimens were not statistically different. Most of the head measurements were different between species, being larger in *R. alternatus*, considering SVL as a covariable, in both juvenile and mature specimens (Table 1).

TABLE 1.— Morphological characteristics of juvenile and mature specimens of *R. alternatus* and *B. diporus*. The mean values of head morphology are absolute values and are not size corrected. The ANCOVA compares mean values of head morphology (HL, JL, ESL, IW, HW) between species considering SVL as covariable. Mature males and females are reported separately. All measurements are given in millimeters.

Measurement ^a	<i>Rhinocerothis alternatus</i>		<i>Bothropoides diporus</i>		P	Statistics	df
	N	Mean ± SD	N	Mean ± SD			
Juvenile specimens							
SVL	23	455 ± 147.95	16	389 ± 99.65	0.2151	W = 0.11	1
HL	21	29.39 ± 9.63	16	21.36 ± 3.38	<0.0001	F = 26.97	1
JL	15	26.3 ± 7.33	16	19.99 ± 3.38	0.0758	F = 3.42	1
ESL	18	8.19 ± 2.18	15	6.92 ± 1.6	0.0853	F = 3.17	1
IW	20	9.8 ± 3.12	16	8.73 ± 1.75	0.3509	F = 0.90	1
HW	20	18.32 ± 7.06	16	13.82 ± 3.21	0.0107	F = 7.38	1
Mature specimens							
SVL							
Female	48	958,52 ± 145,39	16	836,93 ± 145,70	0.0146	W = 296	1
Male	46	725,26 ± 155,15	16	601,38 ± 94,49	0.0002	W = 181.5	1
HL							
Female	40	48.39 ± 6.32	16	39.53 ± 5.83	0.0002	F = 16.28	1
Male	34	37.01 ± 3.89	16	29.46 ± 3.22	0.0006	F = 13.75	1
JL							
Female	35	45.5 ± 5.05	16	37.34 ± 5.68	<0.0001	F = 20.32	1
Male	25	34.28 ± 3.8	16	27.43 ± 3.15	0.0101	F = 7.40	1
ESL							
Female	40	14.39 ± 2.07	14	11.74 ± 1.7	0.0008	F = 12.93	1
Male	33	11.5 ± 1.33	12	9.33 ± 0.84	0.0073	F = 7.97	1
IW							
Female	38	16.21 ± 2.57	16	13.94 ± 1.98	0.1193	F = 2.52	1
Male	34	12.47 ± 1.56	16	10.68 ± 1.56	0.7240	F = 0.13	1
HW							
Female	41	32.3 ± 5.58	16	25.76 ± 5.1	0.0235	F = 5.46	1
Male	34	23.24 ± 3.15	16	19.03 ± 2.78	0.1050	F = 2.74	1

^a SVL = snout-vent length; HL = head length; JL = right lower jaw length; ESL = eye to snout length; IW = interocular width; HW = head width.

There was a positive and linear relationship between head variables (HL, JL, ESL, HW, and IW) and SVL in each species. Linear regressions for head measurements showed different slopes between species (Fig. 1A,B,C,E). Regression lines of IW had similar slopes (Fig. 1D).

Results of the multivariate analysis comparing head morphology were significantly different between species in mature females, mature males, and juvenile males ($P = 0.0376$, $F = 2.54$, Pillai = 0.17, $df = 61$; $P = 0.0039$, $F = 3.94$, Pillai = 0.26, $df = 57$; $P = 0.0160$, $F = 3.95$, Pillai = 0.55, $df = 16$, respectively) whereas juvenile females did not differ between species ($P = 0.1564$, $F = 2.05$, Pillai = 0.51, $df = 10$).

Diet Analysis.—We found prey items in the stomach of 35 individuals of *R. alternatus* (28.45% of the total analyzed) and in 16 *B. diporus* individuals (29.78%). In *R. alternatus*, 100% of the prey were mammals (Table 2); 11 prey were swallowed head-first and one tail-first (*Monodelphis dimidiata*, Colicorto pampeano). The diet of *B. diporus* comprised mammals (38.8%), amphibians (33.33%), reptiles (16.6%), and nonidentified vertebrates (11.11%, Table 2); six items were swallowed head-first and one tail-first (*Cercosaura schreibersii*, Lagartija parda). Each individual of both snake species had a single prey item in the stomach.

There was a significant positive correlation between TL of the prey and SVL of the predator ($r = 0.90$, $n = 9$; Fig. 2A), TL of prey and HL predator ($r = 0.88$, $n = 6$; Fig. 2B), and TL of prey and HW of predator ($r = 0.92$, $n = 6$; Fig. 2C); the highest values were recorded in *R. alternatus*.

DISCUSSION

Studies on the morphology and diet of snakes frequently evaluated differences between sexes (Shetty and Shine, 2002; Vincent et al., 2004), analyzed allometric coefficients between

predator and prey size (Pough and Groves, 1983; King, 2002; Aubret et al., 2004a), ontogenetic variation in diet (Lind and Welsh, 1994; Daltry et al. 1998; López and Giraud, 2008), and head morphology and prey selection in different populations of a single species (Forsman, 1991; Forsman, 1996; Aubret et al., 2004a). Comparisons of head morphology and prey selection between snake species, however, have received less attention. For example, Wuster et al. (2005) studied the morphological differences between two semi-arboreal, bird-eating island pitvipers, *B. insularis* and *Gloydus shedaoensis*. The authors found that the greater head length of *B. insularis* was more similar to head length of *G. shedaoensis* than to that of *B. jararaca*, a species closely related to *B. insularis*. Wuster et al. (2005) concluded that increased head size might represent an adaptation to the abundance of larger food items (migratory passerine birds), providing a selective advantage to snakes able to switch to larger prey at an earlier age. By contrast, other work postulates that morphology and diet of a species (or population) might be determined by genetic or phylogenetic factors (Cadle and Greene, 1993; Aubret et al., 2004a).

We found variation in head morphology and diet between *R. alternatus* and *B. diporus*. Most of the head variables differed between species both in juveniles and mature individuals and were higher in *R. alternatus* than in *B. diporus*. Several authors have studied how the shape and size of the snakes' head determines the type of prey they are able to eat (large vs. small). In functional terms head size limits prey size, taking into account that head length contributes to maximum gape size and thus facilitates the ingestion of large prey. Shine (1991) demonstrated a strong and consistent relationship between head length of snakes and their ability to manipulate and swallow prey items. Taxa for which rodents or birds predom-

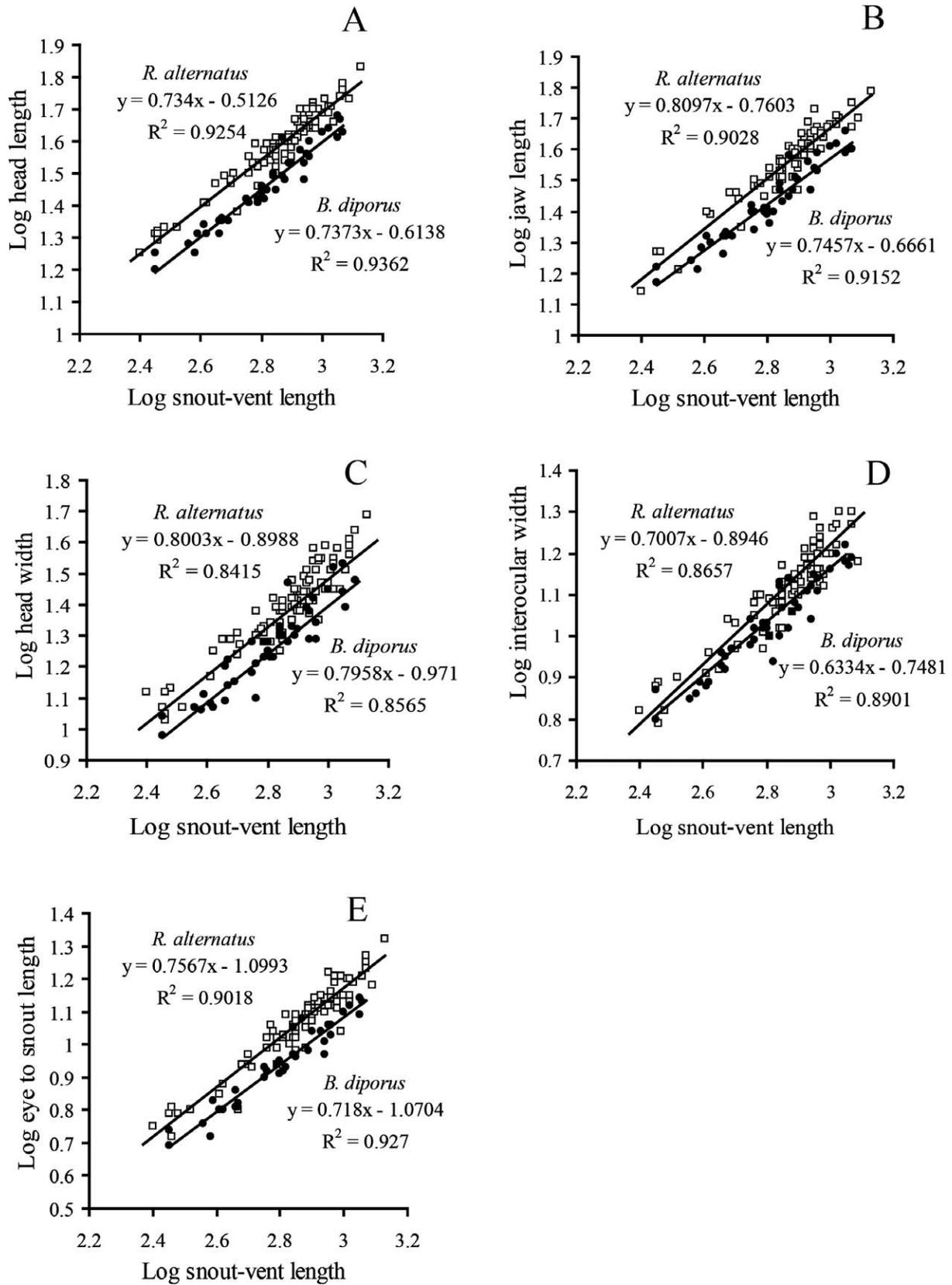


FIG 1.— Linear regression of the relationship between total length and (A) head length; (B) jaw length; (C) eye to snout length; (D) interocular width; (E) head width. The squares represent individuals of *R. alternatus* and the circles individuals of *B. diporus*. Measurements were taken in millimeters and log-transformed.

TABLE 2.—Prey consumed by juveniles and mature specimens of *B. diporus* and *R. alternatus*. Percentage of each prey class with respect to total prey per each age class and species is indicated in parentheses.

Species and prey	Amphibians	Reptiles	Mammals	Nonidentified vertebrates	Total prey
Juveniles					
<i>B. diporus</i>	2 (40%)	1 (20%)	2 (40%)		5
<i>R. alternatus</i>			3 (100%)		3
Matures					
<i>B. diporus</i>	2 (22.22%)	2 (22.22%)	5 (55.55%)	2 (100%)	11
<i>R. alternatus</i>			32 (100%)		32

inate in the diet should require adaptations for increased gape compared to those that eat prey of relatively small mass and diameter (worms, amphibians, and other snakes or lizards). Snakes that regularly eat rodents have longer quadrates and mandibles than do species feeding on small and elongated items (Cundall and Greene, 2000; Aubret et al., 2004a). Our results are consistent with these observations and show that *R. alternatus*, which feeds exclusively on mammals (Martins et al., 2002; Giraud et al., 2008; Nunes et al., 2010), has a larger head than *B. diporus* throughout ontogeny. The diet of *B. diporus* consisted of 38.8% rodents, the remaining items being amphibians and reptiles; other authors found between 33%–50% of rodents (Giraud et al., 2008; López, 2010). Serie (1919) reported the presence of invertebrates in the diet of *B. diporus* (*Scolopendra* spp., centipedes); we found no invertebrate remains in the specimens analyzed.

For evolutionary biology, specialization (e.g., diet specialization) usually implies modifications in an organism's design relative to some particular task (Rodríguez-Robles and Greene, 1999). Aubret et al. (2004a) studied two populations of Tiger Snake (*Notechis scutatus*) with different feeding habits: a mainland population that usually feeds on small prey (frogs and mice) and an island population usually consuming large prey (Silver Gull chicks, *Chroicocephalus novaehollandiae*). Under laboratory conditions, the authors observed that exposure to large prey increased the head size of the island snakes to a greater extent than that of the mainland snakes; in addition, they found that neonates of island snakes had larger heads than did neonates of mainland snakes, despite their similar body sizes. They concluded that island Tiger Snakes can consume larger prey than can mainland conspecifics for two reasons: first,

they may carry genes that determine a larger relative head size; and second, their head sizes enlarge facultatively if they eat large prey. Accordingly, differences in relative head size found between *R. alternatus* and *B. diporus* might be due to genetic differences between species. The species studied in our study are sympatric and terrestrial; hence, the same prey types are available to them. However, *B. diporus* feeds on smaller prey than does *R. alternatus*, which might indicate a phylogenetic constraint. Comparisons among species suggest that different head sizes may have evolved to allow differences in foraging behavior and diet (Pough and Groves, 1983; Vitt, 1983; Seib, 1984; Vincent et al., 2006a) and that the species diet might be genetically determined and influenced by phylogenetic factors (such as morphology or taxonomic group, Cadle and Greene, 1993; Vincent et al., 2006a). However, other authors have argued that ecological aspects (e.g., prey abundance or presence of certain prey type) are the factors determining the diet of predators (Vitt and Vangilder, 1983; Wuster et al., 2005).

Among the prey that we were able to identify, one of the most frequent in the diet of *R. alternatus* was *Cavia aperea* (Cuis), a grassland herbivorous mammal of medium to large size (between 196–320 mm of TL) that can occur in high densities (Redford and Eisenberg, 1992). *R. alternatus* also fed on the abundant Black Rat, *Rattus rattus* (Mills et al., 1991; Novillo and Ojeda, 2008) and on the abundant rodent *Akodon azarae* (Ratón de Azara) (Mills et al., 1991). We also found some species of amphibians in the stomachs of *B. diporus*. The snakes we studied live in areas influenced by the Paraná River, which includes a variety of aquatic environments such as temporary and permanent ponds, main water courses, and riparian areas (Paira and Drago, 2007). This area is appropriate environment

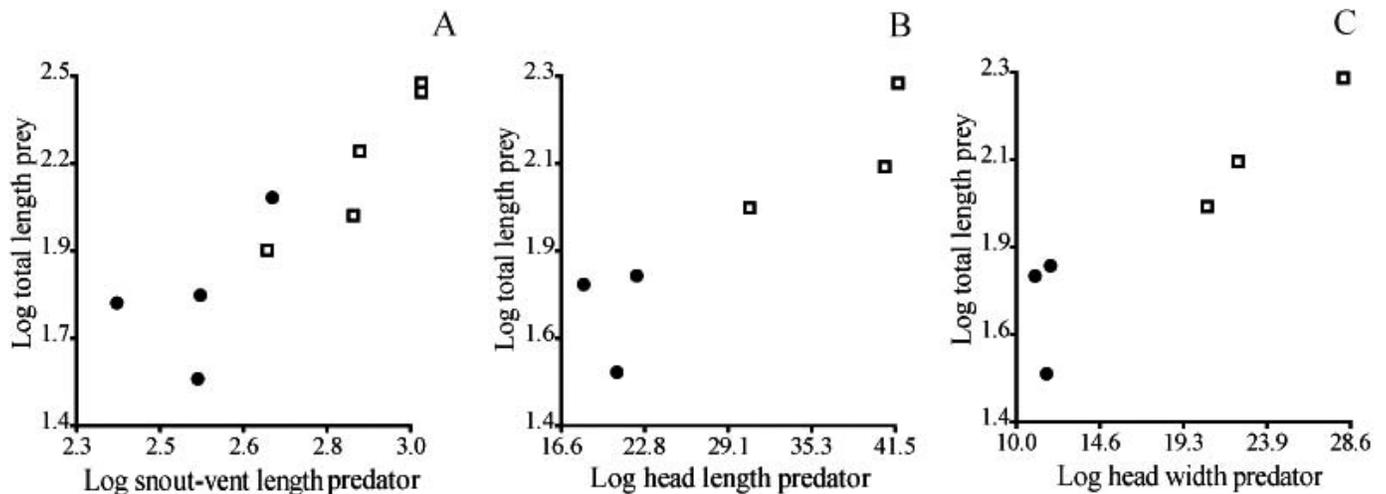


FIG. 2.—Relationship between TL of prey and SVL, HL, and HW of predator. Squares correspond to *R. alternatus* and circles to *B. diporus*. Measurements were taken in millimeters and log-transformed.

for amphibian reproduction (Manzano et al., 2004; Peltzer and Lajmanovich, 2007) and amphibians, especially anurans, are abundant, accessible, and smaller than most of the rodents (Achaval and Olmos, 1997; Lavilla, 2005; López et al., 2011). Therefore, both of the studied snake species feed on apparently abundant prey.

Most prey items were swallowed head-first in both species, possibly to facilitate ingestion as previously reported for other snakes (Valdujo et al., 2002; Bizerra et al., 2005; Prieto et al., 2012). Our results also show a significant correlation between prey and predator size; hence, large predators tend to exclude small prey from their diets. Costa et al. (2008) found that the dietary niche breadth of predatory lizards decreased with body size, suggesting that consuming small prey when larger and probably more profitable prey are available is not an optimal foraging strategy; large predators should target large prey while avoiding small prey. Females of both *R. alternatus* and *B. diporus* were larger than males, which suggests that females of both species might consume large prey than males.

Our findings suggest ontogenetic morphological variation among *R. alternatus* and *B. diporus* and that this variation could be related to interspecific differences in eating habits. Therefore, our results support the hypotheses that differences in morphology between species could be influenced by genetic and phylogenetic constraints. Further studies with a greater number of species are necessary to test our results.

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APPENDIX 1

Museum Acronyms

Centro Nacional de Investigaciones Iológicas (CENAI), in Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; Colección Felix de Azara (CFA), in Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; Instituto Nacional de Limnología (INALI), Santa Fe, Santa Fe, Argentina; Museo Argentino de Ciencias Naturales (MACN), Bernardino Rivadavia, Buenos Aires, Argentina; Museo Provincial de Ciencias Naturales Florentino Ameghino (MFA), Santa Fe, Santa Fe, Argentina.

Specimens Examined

Bothropoides diporus.—Juveniles: CENAI 455; CFA 155, 380, 803; INALI 577, 876, 1156, 2921; MACN 1907, 4874, 23940, 24028, 32424; MFA 373, 118. Mature specimens: CENAI 452, 454, 457, 458; CFA 53, 228, 339, 491, 804; INALI 841, 875, 1051, 1157, 1828, 1978, 2425; MACN 35350, 39002, 39003, 39004, 39006, 39015, 39017, 39018, 39019, 39020, 39021; MFA 79, 241, 438, 456, 568.

Rhinocerophis alternatus.—Juveniles: MFA 515, 616, 617, 618; INALI 153, 192, 535, 549, 572, 1010, 1106, 1161, 1212, 1528, 1772, 2166, 2379, 2380, 2404, 2446, 2666, 2771, 3181, 3182. Mature specimens: MFA 70, 76, 181, 254, 326, 331, 388, 441, 442, 446, 447, 448, 450, 453, 502, 514, 525, 591, 615; INALI 35, 221, 444, 457, 573, 719, 815, 859, 860, 918, 987, 1043, 1101, 1102, 1118, 1210, 1211, 1239, 1274, 1277, 1281, 1282, 1540, 1671, 1689, 1979, 1998, 2007, 2008, 2009, 2073, 2104, 2105, 2120, 2204, 2335, 2400, 2403, 2407, 2416, 2421, 2458, 2495, 2502, 2505, 2517, 2533, 2562, 2664, 2665, 2702, 2703, 2716, 2717, 2718, 2720, 2769, 2770, 2772, 2857, 2858, 2863, 2864, 2865, 2900, 2901, 2903, 2905, 2906, 2935, 2915, 2941, 3281, 3285, 3417, 3418, 3462, 3463, 3464, 3579.