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Diet and Sexual Dimorphism of *Liophis poecilogyrus* (Serpentes, Dipsadidae) from the Wetland Regions of Northeast Argentina

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ABSTRACT.—**Feeding ecology is one of the most important aspects in the life history of snakes; however, studies about their trophic ecology are scarce and sometimes inaccurate. *Liophis poecylogyrus* is a medium-sized snake distributed widely in South America and relatively abundant in the study area. We describe the diet and sexual dimorphism of *L. poecilogyrus* from northeast Argentina based on the examination of museum specimens, and we compare our data with studies that include representative samples of this species. Amphibians were the most frequent prey (75%), but only one reptile was found (1%). Families represented were: Bufonidae (53%), Leiuperidae (19%), Leptodactylidae (14%), Hylidae (7%), Cycloramphidae (3%), Microhylidae (2%), and Gymnophthalmidae (2%). We observed that *L. poecilogyrus* has significant sexual size dimorphism in all morphometric characters analyzed but not in scalation variables. Despite the fact that *L. poecilogyrus* is considered by some to be an omni-carnivore, our data and other quantitative studies on distant populations from South America lead us to suggest that this species eats primarily anurans. The population studied has its own characteristics but retains similarities with geographically nearby and remote populations. This species is a specialist and its feeding habits seem to be conservative both in different populations of the same species and in phylogenetically related species. Sexual size dimorphism may be a common feature of the taxonomic group.**

Feeding ecology is one of the most important aspects in the life history of snakes (Shine, 1977; Bernarde et al., 2000; Gregory and Isaac, 2004; Hartmann and Marques, 2005), and because of associations between feeding strategies and other functions, nourishment is generally considered the key to animal ecology (Verwaijen and Van Damme, 2007). Most of the studies on snake feeding ecology and habitat use are generalizations and some authors have observed differences between those general studies and those that analyze representative samples of species (Giraudo et al., 2004; López and Giraudo, 2004). There have been recent studies focused on the feeding ecology of South American snakes, mainly in Brazil (e.g., Vitt and Vangilder, 1983; Di-Bernardo, 1998; Bernarde et al., 2000; Hartmann and Marques, 2005) and Argentina (López and Giraudo, 2004; Giraudo et al., 2008; López and Giraudo, 2008).

Liophis poecilogyrus is distributed broadly from Venezuela and Guyana to the central region of Argentina (Dixon and Markezich, 1992; Giraudo, 2001). It is a mid-sized snake, predominantly terrestrial and diurnal (Vitt and Vangilder, 1983). It is well represented in scientific collections but barely studied. Only a few studies have focused on diet and sexual dimorphism of *L. poecilogyrus* (e.g., Giraudo, 2001; Pinto and Fernandes, 2004). Generalized descriptions on snake diet show that *L. poecilogyrus* is an omni-carnivore species (e.g., Amaral, 1977; Michaud and Dixon, 1989; Cei, 1993), but most of the descriptions are based on small samples, with imprecise locations and no quantitative or qualitative analyses. However, some authors demonstrate that *L. poecilogyrus* feeds only on anuran amphibians (Vitt, 1983; Vitt and Vangilder, 1983; Dixon and Markezich, 1992; Pinto and Fernandes, 2004) or that amphibians are predominant in their diet (Carreira Vidal, 2002). Sexual dimorphism of *L. poecilogyrus* has been mentioned only by a few authors (Vitt, 1983; Vitt and Vangilder, 1983; Dixon and Markezich, 1992; Pinto and Fernandes, 2004). Many of these studies have been carried out in Brazilian and Uruguayan populations.

Herein we analyze diet and sexual dimorphism of *Liophis poecilogyrus* with the aim to compare diet characteristics of the species distributed in the northeast of Argentina with those from Uruguay, south and northeast of Brazil. We consider that the population of *L. poecilogyrus* studied here has its own characteristics but retains similarities with other geographically distant populations.

MATERIALS AND METHODS

Study Area.—The study area consists of the wetlands of the Chaco-Pampean plain and the alluvial floodplains of the Paraná, Paraguay, and Uruguay Rivers in northeastern Argentina. Those wetlands are made up of several regions: east Formosa, Chaco and Santa Fe, West Corrientes, Southwest Entre Ríos, and the Buenos Aires Delta. Vegetation is a mosaic of physiognomies ranging from wet savannahs and grasslands to subtropical dry forests, gallery forests, shrublands, and a wide variety of wetlands (López and Giraudo, 2008).

The study area is a subtropical-temperate region with a wet season from October to April. Annual mean temperatures range from 17°C to 21°C, with maximum temperatures close to 40°C in summer (between October and March) and minimum temperatures close to 0°C in winter (between April and September; Prado, 1993). Annual precipitation varies between 1,000 and 1,400 mm (Bó, 2005; Ginzburg and Adámoli, 2005). In the southern regions, rains are more intense in spring and autumn (Burkart et al., 1999) than in the north, where they occur mostly in summer, between October and April (Ginzburg and Adámoli, 2005).

Specimen Analysis.—We examined adult specimens belonging to herpetological collections from Instituto Nacional de Limnología (INALI), Museo Provincial de Ciencias Naturales “Florentino Ameghino” (MFA), Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN), Centro Nacional de Ictiología (CENAI) and Colección Félix de Azara (CFA).

Each specimen was sexed by a caudal incision to look for the presence of hemipenes. The specimens were also dissected to

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TABLE 1. Prey eaten by *Liophis poecilogyrus* of Northeast Argentina. Prey frequency is the total number of a particular prey type; parenthetical numbers are the total number of a particular prey type divided by the total number of prey; predator frequency is the number of snakes with each prey item. Argentine species in the *Leptodactylus ocellatus* group include *Leptodactylus chaquensis*, and *Leptodactylus ocellatus*, in the *Physalaemus biligonigerus* group include *Physalaemus biligonigerus*, and *Physalaemus santafecinus* and in the *Dendropsophus microcephalus* group include *Dendropsophus nanus* and *Dendropsophus sanborni*.

Prey taxon	Prey frequency	Predator frequency
Amphibia		
Bufonidae		
Rhinella fernandezae	5 (5.5)	4
Rhinella cf. *fernandezae*	2 (2.2)	2
Rhinella schneideri	22 (24.1)	6
Unidentified *Rhinella*	3 (3.3)	3
Leptodactylidae		
Leptodactylus cf. *latinasus*	1 (1.1)	1
Leptodactylus chaquensis	1 (1.1)	1
Leptodactylus ocellatus	1 (1.1)	1
Leptodactylus ocellatus group	3 (3.3)	3
Unidentified Leptodactylidae	2 (2.2)	2
Leiuperidae		
Physalaemus albonotatus	1 (1.1)	1
Physalaemus biligonigerus group	3 (3.3)	3
Physalaemus cf. *santafecinus*	2 (2.2)	2
Unidentified *Physalaemus*	4 (4.4)	4
Cycloramphidae		
Odontophrynus americanus	2 (2.2)	2
Hylidae		
Dendropsophus microcephalus group	1 (1.1)	1
Scinax acuminatus	1 (1.1)	1
Pseudis paradoxus	1 (1.1)	1
Unidentified Hylidae	1 (1.1)	1
Microhylidae		
Elachistochleis bicolor	1 (1.1)	1
Unidentified amphibians	11 (12.1)	11
Total amphibians	68	
Reptilia		
Gymnophthalmidae		
Cercosaura schreibersii	1 (1.1)	1
Unidentified vertebrates	3 (3.3)	3
Invertebrates	19 (20.9)	19
TOTAL	91 (100)	

determine reproductive status. Females were considered mature when the diameter of the ovarian follicles was >3 mm or if they had oviductal eggs. Males were considered mature if the deferent ducts were opaque and convoluted, indicating the presence of sperm (Shine, 1977; Pinto and Fernandes, 2004). We also considered the following variables: the number of ventral and subcaudal scales, snout–vent length (SVL), tail length (TL), head length (HL) taken from the rostral scale to the posterior extreme of the mandible, head width (HW) at the jaw base level, and mass. Morphometric measurements were recorded with a plastic commercial ruler and Vernier calipers, with 1-mm and 0.5-mm precision, respectively. An electronic balance of 1-g precision was used for determining mass. Counting of the ventral scales was performed from the first scale (which was wider than long) to the anal scute (not included; Gans, 1964). Counting of the subcaudal scales was performed from the first pair of subcaudal scales (immediately posterior to the anal scale) to the last pair of subcaudal scales (not including the terminal scale; Gans, 1964).

Diet.—Each specimen was dissected, and the prey items were extracted for assessment. Digestive content was removed after an incision in the ventral surface of the specimens (Gomes and Puorto, 1993; Salomão et al., 1995). Prey items were identified to the lowest possible taxonomic level by comparison with the material from the reference collection from Instituto Nacional de Limnología and published guides (Gallardo, 1974, 1987; Lavilla, 2005). Prey items were analyzed considering number of items per stomach and frequency of occurrence. Direction of ingestion (inferred from orientation in the stomach) was recorded whenever possible. Highly digested stomach contents (mainly small pieces of bones) were considered as unidentified vertebrates. Invertebrates were considered as secondary prey items, previously ingested by the lizards or amphibians eaten by the snake, because of their small size (Martins et al., 2002).

Statistical Analyses.—Differences between sexes on absolute morphometric and scalation variables were compared using Student's t-test and Mann-Whitney U-test. To analyze relative morphometric variables, we used analyses of covariance (ANCOVA) with SVL as a covariate, because TL, HL, HW, and mass may vary with the length of the body. The values for each morphological variable were converted to logarithm base 10. We performed all statistical analyses using Infostat software version 5.1 (Di Rienzo et al., 2005) with the significance level set at $\alpha = 0.05$.

RESULTS

Diet.—Of 151 specimens, 67 (44%) contained prey items in the gut, and 84 (56%) did not. We recovered 91 identifiable prey individuals. Amphibians were the most frequent prey (75%), but we also found identified (21%) and unidentified (3%) vertebrates and a reptile (1%). Representatives of six different amphibian families were identified: Bufonidae (53%), Leiuperidae (19%), Leptodactylidae (14%), Hylidae (7%), Cycloramphidae (3%), and Microhylidae (2%). The reptile (2%) was *Cercosaura schreibersii* (Gymnophthalmidae) (Table 1). Most snakes (88%) had one prey in their guts, although nine specimens had multiple prey items. We found three, four, and 12 *Rhinella schneideri* juveniles, respectively, in three snakes of similar size (about 22 mm). Also we found a specimen of *Rhinella fernandeza*e with a 24.1-mm-wide head, almost twice its predator's HW (12.25 mm) and an 84.1-mm-long body, representing over 15% of the predator's SVL (565 mm).

We were able to determine the direction of ingestion in 38 prey animals: 24 (63%) were swallowed head-first; and 14 (37%) were consumed tail-first. Prey items ingested head-first were significantly larger than prey items ingested tail-first ($W = 55.00$, $P = 0.0056$).

Sexual Dimorphism.—There were no statistical differences in ventral ($t = 0.19$, $P = 0.8505$) and subcaudal scales ($t = 0.18$, $P = 0.8590$), but sexual size dimorphism was evident in morphometric measurements (Table 2). Also, females had longer tails ($F_{2,135} = 99.02$, $P < 0.0001$), larger heads ($F_{2,135} = 246.96$, $P < 0.0001$), wider heads ($F_{2,122} = 113.65$, $P < 0.0001$), and were heavier ($F_{2,95} = 170.92$, $P < 0.0001$) than males with the same SVL.

DISCUSSION

Diet.—*Liophis poecilogyrus* is considered a generalist species by some authors (Amaral, 1977; Michaud and Dixon, 1989; Cei, 1993). This may be because items taken under particular environmental conditions or occasional items are named habitual prey items. By contrast, studies with representative samples have

TABLE 2. Variation and sexual size dimorphism of scale counts and size measurements (mm) in *Liophis poecilogyrus* examined. Abbreviations: TL = tail length, SVL: snout–vent length, HL: head length, HW: head width. An asterisk indicates significant differences on absolute measurements. SVL, HL, and HW were compared by the Student's *t*-test ($P \leq 0.0001$). LC and mass were compared by Mann-Whitney *U*-test ($P = 0.0001$ and $P \leq 0.0001$, respectively).

	Females			Males		
Variable	Range	Mean ± SD	*N*	Range	Mean ± SD	*N*
Ventrals	140–161	150.89 ± 4.25	85	141–163	150.76 ± 4.16	58
Subcaudals	37–5	43.71 ± 3.53	86	36–51	43.60 ± 3.60	52
TL*	41–181	77.26 ± 19.15	88	37–90	65.56 ± 11.84	53
SVL*	250–571	396.33 ± 74.94	87	211–451	325.46 ± 52.66	58
HL*	12.60–28.25	20.96 ± 3.03	83	12.40–22.77	17.18 ± 2.21	56
HW*	7.80–18.05	12.06 ± 2.27	76	6.25–15.35	9.78 ± 1.70	49
Mass (g)*	10–189	43.70 ± 28.70	54	3–53	22.93 ± 11.93	44

established that *L. poecilogyrus* consumes only amphibians (Vitt, 1983; Vitt and Vangilder, 1983; Dixon and Markezich, 1992; Pinto and Fernandes, 2004) or that amphibians are the predominant prey (Carreira Vidal, 2002). Our study agrees with these latter authors because we found that the population from northeastern Argentina feeds mainly on anurans with the occasional ingestion of alternative items. For example, one specimen, collected in an urban zone of Santa Fe during floods in 1982, had eaten a lizard (*Cercosaura schreibersii*), which coincides with Carreira Vidal's views (2002).

Based on our results and existing literature, we deduce that this snake is a specialist species. Their feeding habits seem to be conservative because there appears to be no major geographical variation in diet. Most families and genera of prey items found in other geographic regions were present in northeastern Argentina. Differences in the diets between populations were observed when prey species differed by region. With regard to the habits of the prey species, most were terrestrial (Vitt, 1983; this study), but Vitt (1983) also found prey items with entirely aquatic habits (e.g. *Pipa carvalhoi*).

There is also a similarity between the prey species of the genera *Liophis* and *Lygophis* (the latter recently resurrected and separated from the genus *Liophis* by Zaher et al., 2009). Several authors agree that this group feeds mainly on amphibians, for example, *Liophis jaegeri* (Di Bernardo, 1998), *Liophis semiaureus* (Carreira Vidal, 2002), and *Lygophis anomalus* (Michaud and Dixon, 1989; Carreira Vidal, 2002). It seems that the diet of *L. poecilogyrus* is conservative both in different populations of the same species and in phylogenetically related species.

In a study conducted in the Middle Paraná River, amphibians were included in the diets of about 50% of the species (Giraudo et al., 2007). It is likely that ecological factors such as the richness and abundance of amphibians (Manzano et al., 2004; Peltzer and Lajmanovich, 2007) may also influence the diet of predators. In the population studied, snakes primarily explore terrestrial environments surrounding water bodies (Giraudo, 2001). One of the main prey was amphibians of the genus *Rhinella*. Some anuran-eating xenodontine species show morphological specializations related to this diet. For example, *Waglerophis merremii* has large postdiastemal teeth and a short, rotating maxilla (Vitt, 1983). Vitt (1983) observed a specialized toad-eating behavior in *W. merremii*; individuals attempting to feed on extremely large toads would twist their necks and bodies during the strike so that the head of the snake was upside down when the toad was bitten. This behavior resulted in the air sacs of the toad being immediately punctured by the enlarged maxillary teeth of the snake, thus facilitating the swallowing of the large prey. We expect *L. poecilogyrus* to show some of these morphological or behavioral characteristics because of its dietary specialization and the presence of prey items larger than the snake.

Liophis poecilogyrus may have food strategies related to periods of amphibian reproduction, because some snakes had several *R. schneideri* juveniles of similar sizes in their stomachs. Feeding on juveniles may be advantageous, because large quantities of prey can often be consumed in a short period of time, with little exposure to predation.

Most prey were swallowed head-first, a behavior observed in most snakes (e.g., López and Giraudo, 2008; Albarelli and Santos-Costa, 2010). This minimizes the amount of time the predator is vulnerable during predation. Prey items ingested head-first were significantly larger than prey items ingested tail-first. These results may be explained by two hypotheses: (1) the snake manipulates large prey items in a way that results in head-first swallowing; or (2) biting the prey on the anterior portion of the body is more likely to result in successful ingestion by the snake (Albarelli and Santos-Costa, 2010). Consuming medium-sized prey animals in the right direction may reduce foraging effort and potential risks to predators.

We found prey items in 14 gravid females; this result is coincident with observations by Pinto and Fernandes (2004), which suggest that females do not reduce or stop feeding during the clutching season. Some snakes of the region, such as *Philodryas patagoniensis* (López and Giraudo, 2008) and *L. semiaureus* (Lopez et al., 2009), showed development of follicles and eggs in the rainy season (when amphibians are most abundant); this is likely similar in *L. poecilogyrus*.

Sexual Dimorphism.—Sexual size dimorphism is a common feature in colubrids (Shine, 1994; see *L. miliaris* in Giraudo et al., 2006 and López et al., 2009; *L. orinus* in Giraudo et al., 2006; and *L. lineatus*, *L. mossoroensis*, and *L. viridis* in Vitt, 1983). Previous works explain that this may be attributable to issues related to reproduction or snake diet. Usually, the females' larger body length increases fitness, because larger specimens have higher fecundity (Shine, 1994). Head size dimorphism may be associated with intersexual dietary divergence (Houston and Shine, 1993; Shetty and Shine, 2002). It is also possible that some snake species show head size dimorphism without any divergence in diet. In such cases, authors have attributed dimorphism to a "ghost of competition past" or to sexual selection (Luiselli et al., 2002; Pizzatto and Marques, 2006).

We found dimorphism in the study population was evident only in morphological variables. Females were larger than males in both absolute and relative measures with SVL as the covariate. Dixon and Markezich (1992) found no significant differences in these variables over the entire range of distribution of the species; Pinto and Fernandes (2004) reported differences only in gape and total length; and Vitt (1983) found no differences in absolute SVL, HL, and HW. However Vitt (1983) noted differences in HL related to SVL, coincident with our work, and Vitt and Vangilder (1983) found differences in HL and HW with SVL as the covariate, also coincident with the data reported here, indicating some agreement among studies that females are larger than males. In other species of the genera, results were variable. In *L. semiaureus*, significant differences were observed in SVL, TL (Giraudo et al., 2006; López et al., 2009), and mass (López et al., 2009); however, there were no differences in scalation (Giraudo et al., 2006). In *L. orinus*, differences were observed in TL as related to SVL, but there were no differences in ventral and subcaudal scales, total length, TL, and SVL (Giraudo et al., 2006). All species showed sexual dimorphism in any variable analyzed, which may be a common feature of the taxonomic group (Madsen and Shine, 1993; López et al., 2009).

With the recent emergence of studies on certain features of the life history of tropical snakes, strong similarities have been shown in association with a phylogenetic root, and differences related to their geographical characteristics have been highlighted (Vitt, 1983; López et al., 2009).

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Appendix 1

Specimens Examined

Buenos Aires Province: Distrito Federal MFA 256. Isla Martín García CENAI 2421. La Plata Department: CENAI 3028–3029; MACN 14993.

Corrientes Province: Berón de Astrada Department: INALI 73, 90, CFA 475; Capital Department: INALI 74, 78, 83, 94, 95, 104, 909, 910, 985, 1198, 1199,1659, 1660, 1676, 3025,3026; CFA 4, 5, 24, 36, 95,129,133, 151–153, 188, 189, 252, 280, 282, 296, 306, 307, 312, 318, 319, 402, 416, 419, 426, 468, 492, 519, 520, 603, 606, 632, 634, 635, 637, 638, 701, 702, 705, 706, 708. Mburucuyá Department CFA 281; Ñeembucú Department CFA 315. Sauce Department INALI 2870.

Entre Ríos Province: Colón Department: MACN 34789. Federal Department MACN 27464, 34530, 34610. Gualeguay Department: INALI 1471, 1476, 2376; MACN 2569. Gualeguaychú Department: INALI 2778. Islas del Ibicuy Department: INALI 1514, 1515, 2789. La Paz Department: INALI 2788. Paraná Department: INALI 1022, 1966, 2119, 2544, 2700.Formosa Province: Laishi Department: INALI 1129–1133, 1135–1141, 1144. Matacos Department: MACN 3752, 37355, 37356, 37358. Pirané Department: CFA 738.Provincia de Santa Fe: Garay Department: INALI 945, 1628, 1635, 1735, 2501. General Obligado Department: INALI 1260, 2079. La Capital Department: INALI 216, 984, 1593, 1594, 1631, 1849; CFA 72; MFA 136, 198, 395, 413, 538. Rosario Department MACN 27393. San Cristóbal Department INALI 919, 1300, 1301, 1968, 1969, 1982–1984, 2411. San Javier Department INALI 50, 601, 2220, 2304. San Justo Department INALI 986, 1367, 1368, 1370–1372. Vera Department INALI 210, 643, 650, 1061, MACN 36820. Río Salado MFA 187, 193. Sin localidad INALI 2651.