Food Habits and Reproductive Biology of Tail-Luring Snakes of the Genus *Tropidodryas* (Dipsadidae, Xenodontinae) from Brazil

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ABSTRACT: The dipsadid snake genus *Tropidodryas* consists of two species that occur in the Atlantic Forest along Brazil's eastern coast, a conservation hot spot. Life-history information on pairs of sister species might allow insights into the evolutionary transitions that have occurred since the cladogenesis that putatively gave rise to them. We provide information on distribution, morphology, diet, reproduction, and seasonal activity of these species based on the examination of 624 specimens. The genus *Tropidodryas* occurs along a large extent of the Atlantic Forest of eastern Brazil, with *T. striaticeps* occurring at higher elevations, on average, than *T. serra*. These snakes forage by day either on the ground or in vegetation, consuming a wide variety of vertebrates, mainly mammals. Higher proportions of birds in the diet of *T. serra* and certain mammals in the diet of *T. striaticeps* probably reflect elevational differences in prey availability. An ontogenetic diet shift occurs in both species, with juveniles consuming mainly ectothermic prey (lizards and anurans), and adults preying predominantly on mammals. Caudal luring has been documented in juveniles, but the pale color and high frequency of injuries on the tail of larger individuals indicate that adult *T. striaticeps* also employ this technique to attract prey. Sexual dimorphism occurs in body size, tail size, and diameter of the eye. Female reproductive cycles are seasonal in both species, with egg laying occurring in warmer periods of the year. However, *T. striaticeps* seems to have a more extended reproductive cycle, with some females being able to lay eggs 1 or 2 mo earlier. Environmental differences between high and low altitudes in the Atlantic Forest are likely responsible for the slight ecological divergence between these two closely related snakes.

Key words: Diet; Distribution; Fecundity; Habitat; Reproductive cycle; Tropidodryadini

DIPSADIDAE is the largest radiation of colubroid snakes in the Neotropics, with approximately 700 species occurring mainly in Central and South America (Hedges et al. 2009; Zaher et al. 2009). Within this clade, the subfamily Xenodontinae has greater diversity in South America and includes almost 300 species in at least 10 distinct monophyletic lineages (Zaher et al. 2009; Grazziotin et al. 2012). The rear-fanged snakes of the genus Tropidodryas have been recognized as a monophyletic lineage within Xenodontinae (Vidal et al. 2010; Grazziotin et al. 2012), included in the tribe Tropidodryadini (Zaher et al. 2009; Grazziotin et al. 2012). The tribe contains only two extant species (T. serra and T. striaticeps; see images in Supplemental Material), both of them endemic to the Atlantic Forest of eastern Brazil. The two species are recognized by the conspicuous whitish or yellowish tail in juveniles, which can be used to lure prey (Sazima and Puorto 1993). Scarce data on museum specimens indicate that these snakes feed on a wide variety of vertebrates and exhibit an ontogenetic shift in diet (cf. Sazima and Puorto 1993). However, other aspects of their ecology are poorly known.

Ecological information on pairs of sister species might allow insights into the evolutionary transitions that have occurred since the cladogenesis that putatively gave rise to them. This is particularly true when sister species occur in sympatry, at least in part of their distribution, and when they occur along environmental gradients such as the mountainous regions of eastern Brazil. Furthermore, *Tropidodryas* spp. are endemic to the Atlantic Forest of coastal Brazil, a biodiversity hot spot (Myers et al. 2000) that has lost over 85% of its original vegetation cover in the last centuries. Therefore, studies aiming to increase knowledge of their natural history might provide important information for the conservation of the endemic fauna of this ecoregion. In this study, we provide information on geographic and altitudinal range, substrate use, morphology, reproductive biology, food habits, and activity of *T. striaticeps* and *T. serra*. Our intent is to elucidate important aspects of the ecology in a poorly known lineage of Neotropical dipsadids, comparing two sister species that are sympatric along part of their distribution in the Atlantic Forest of eastern Brazil.

MATERIALS AND METHODS

Our study is based on the dissection of preserved specimens from herpetological collections (see Appendix in Supplemental Material). We obtained data on locality, morphology, diet, and reproduction by analyzing specimens throughout their distribution in Brazil's Atlantic Forest. The Atlantic Forest covers an area that ranges from sea level to 2700 m above sea level (asl) and has a homogeneous climate characterized by high rainfall levels throughout the year (~2400–4000 mm annually; Fonseca 1985; Ab'Saber 1986; Nimer 1989). Nonetheless, two seasons are recognized: a rainy season (October–March) with higher rainfall (usually >1400 mm) and temperatures (mean = 25° C), and a dry season (April– September) with less rainfall (usually <800 mm) and lower temperatures (mean = 22° C; Nimer 1989).

We examined 187 *Tropidodryas serra* and 437 *T. striaticeps* from the collections of the Museu de Zoologia da Universidade Estadual de Santa Cruz (MZUESC, n =23), Comissão Executiva do Plano da Lavoura Cacaueira (CEPLAC, n = 14), Museu de Biologia Mello-Leitão (MBML, n = 9), Museu Nacional (MNRJ, n = 44), Instituto Butantan (IBSP, n = 441), Museu de História Natural da Universidade Estadual de Campinas (ZUEC, n = 19), Museu de História Natural Capão da Imbuia (MHNCI, n =34), and Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCP, n = 40). The following data were taken from each specimen: snout-

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FIG. 1.—Geographic and elevational distribution of *Tropidodryas serra* (open circles) and *T. striaticeps* (filled circles). The area delimited by the dotted line represents the extent of the Atlantic Forest biome.

vent length (SVL, ± 0.1 mm); tail length (TL, ± 0.1 mm); head length (HL, ± 0.01 mm); eye diameter (ED, ± 0.01 mm); mass (± 0.1 g, weighed after draining excess preservation liquid through a ventral incision; cf. Martins et al. 2001); sex; reproductive maturity (males were considered mature if they had enlarged testes or opaque deferent ducts; females were considered mature if they had either oviductal eggs or ovarian vitellogenic follicles >10 mm); length of largest ovarian follicle or size of all oviductal eggs, if present (mm); and gut contents. All food items were removed from the gut, identified to the lowest possible taxonomic level, and measured and weighed when intact or slightly digested.

The reproductive cycle of mature females was quantified by measuring the length of the largest ovarian follicle or oviductal egg throughout the year. Fecundity was assessed as the number of oviductal eggs and large vitellogenic ovarian follicles (>10 mm), and the relationship between maternal SVL and fecundity was analyzed by linear regression (Zar 1999). The sexes of each species were compared, and the degree of sexual size dimorphism (SSD) was calculated as:

1 - (mean adult SVL of the larger sex)

/mean adult SVL of the smaller sex).

This provides an index describing sexual dimorphism in snakes, which can be used in broader phylogenetic comparisons (see Shine 1994). We obtained data on oviposition from gravid females received at Instituto Butantan. We recorded the mass of the females and eggs within 12 h of oviposition and used these values to calculate the relative clutch mass (RCM; clutch mass/maternal body mass; Seigel and Ford 1987). The eggs were incubated in moist vermiculite at room temperature $(24-27^{\circ}C)$ until those that were viable hatched. We measured and weighed hatchling individuals that emerged from eggs within 24 h after hatching.

Morphology of the two species was compared with respect to body size, relative head length (HL/trunk length), relative eye diameter (ED/HL), relative tail length (TL/SVL), and stoutness (mass/total length). We tested for ontogenetic shift in prey type by comparing the SVL of snakes that consumed ectothermic and endothermic prey with a *t*-test (cf. Martins et al. 2002). Before using parametric tests, all variables were checked for violations of normality (using Kolmogorov– Smirnov tests) and homoscedasticity (visually). All statistical analyses were executed in Statistica (v6.0; Statsoft Inc., Tulsa, OK). Values are reported as means ± 1 SD, and differences are considered significant at $\alpha < 0.05$.

Results

Both species of the genus *Tropidodryas* are restricted to Brazil's Atlantic Forest (Fig. 1). *Tropidodryas serra* was

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		T. serra	T. striaticeps	Interspecific comparison
SVL	Male	732.5 ± 111.5	612 ± 73.6	t = 9.17, P < 0.001
		(513-960, n = 77)	(463-786, n = 122)	
	Female	843.6 ± 145.9	774.3 ± 96.2	t = 3.90, P < 0.001
		(497-1131, n = 54)	(508-974, n = 148)	
		t = 4.93, P < 0.001	t = 15.30, P < 0.001	
TL/SVL	Male	0.266 ± 0.021	0.314 ± 0.024	t = 13.93, P = 0.001
		(0.196-0.330, n = 75)	(0.217 - 0.367, n = 120)	
	Female	0.246 ± 0.022	0.269 ± 0.023	t = 5.87, P < 0.001
		(0.179-0.288, n = 50)	(0.167 - 0.340, n = 138)	
		t = 5.09, P < 0.001	t = 14.94, P = 0.001	
HL/TrL	Male	0.040 ± 0.003	0.043 ± 0.003	t = 8.10, P < 0.001
		(n = 79)	(n = 122)	
	Female	0.040 ± 0.003	0.040 ± 0.002	t = 1.69, P = 0.09
		(n = 54)	(n = 147)	
		t = 0.45, P = 0.64	t = 8.41, P < 0.001	
ED/HL	Male	0.156 ± 0.015	0.162 ± 0.012	t = 2.97, P = 0.003
		(n = 79)	(n = 120)	
	Female	0.148 ± 0.014	0.149 ± 0.011	t = 0.33, P = 0.73
		(n = 54)	(n = 145)	
		t = 3.14, P = 0.002	t = 9.17, P < 0.001	

TABLE 1.—Comparative morphology of two species of *Tropidodryas* with respect to snout–vent length (SVL), relative tail length (TL/SVL), relative head length (HL/trunk length [TrL]), and relative eye diameter (ED/HL). Values are reported as mean ± 1 SD. Range and sample size (*n*) in parentheses. All measurements are in millimeters; *t*-test results in the last row of each morphological category are for comparisons between the sexes within each species.

recorded from northern Espírito Santo State (~19°S) to eastern Santa Catarina State (~28°S; Fig. 1). It is more commonly found at sea level and lowland areas (83.5%, n =61), but also occurs in localities below 500 m asl. *Tropidodryas striaticeps* was recorded from southern Bahia State (~14°S) to northeastern Rio Grande do Sul State (30°S; Fig. 1). Most individuals (66%, n = 77) were collected at localities above 500 m asl. The two species can occur in sympatry, but the distribution of *T. striaticeps* extends more inland than that of *T. serra* (Fig. 1).

Sexual dimorphism was evident in adults of both species: Females were larger than males, but males had relatively longer tails and larger eyes than females (Table 1). Only in *T. striaticeps* did males have relatively longer heads than females. The degree of sexual size dimorphism was greater for *T. striaticeps* (0.26) than for *T. serra* (0.15). Both sexes of *Tropidodryas serra* had larger body size and smaller relative tail than those values for *T. striaticeps*. Males of *T. striaticeps* exhibited larger head and relative eye diameter than females of *T. serra* (Table 1).

Most juveniles of *T. serra* (96.5%, n = 56) and all juveniles of *T. striaticeps* (n = 168) had pale tail tips. The frequency of adults with pale tail tip was 37.2% (n = 48) in *T. serra*, and 84.9% (n = 220) in *T. striaticeps*. Tail tip mutilation was recorded for five juveniles (8.3%) and 12 adults (9.3%) of *T. serra*, and for nine juveniles (5.1%) and 40 adults (15.4%) of *T. striaticeps*.

Thirty-five out of 187 (18.6%) *T. serra* specimens, and 122 out of 437 (27.9%) *T. striaticeps* specimens contained identifiable prey in their guts. A wide variety of vertebrate prey was consumed (Table 2). Mammals were the most common prey of both species (46.0% for *T. serra*; 65.7% for *T. striaticeps*). Birds were the second most frequent item in both species (26.9% for *T. serra*; 18.2% for *T. striaticeps*). Ectothermic prey, such as lizards and anurans, were also consumed by both snake species (27.1% for *T. serra*; 16.1% for *T. striaticeps*), but mainly by juvenile individuals (Table 2). Only one juvenile of each species consumed endothermic prey, although those snakes were relatively large juveniles. The SVL values for snakes that consumed ectothermic prey $(\bar{X} = 429.0 \pm 87.9 \text{ mm}, n = 5 \text{ for } T. serra; \bar{X} = 439.6 \pm 169.3$ mm, n = 13 for T. striaticeps) were consistently smaller than for those snakes consuming endothermic prey (\bar{X} = 776.4 ± 153.5 mm, n = 17 for *T. serra*; $\bar{X} = 725.5 \pm 114.7$ mm, n = 82 for T. striaticeps; t = 6.42, P < 0.05 and t = 5.88, P < 0.05, respectively). We could only determine body mass for two items of prey of T. serra; mass ratios were 0.1 and 0.3. For T. striaticeps mass ratios ranged from 0.05 to 0.74 (\bar{X} = 0.25 ± 0.23, n = 13). The diet compositions of males and females of both species were similar. There were no differences between the frequencies of ectothermic and endothermic prey consumed by males and females in both species ($\chi^2 = 0.26$, df = 1, P = 0.61 for *Tropidodryas serra*; $\chi^2 = 1.88$, df = 1, P = 0.17 for T. striaticeps). None of the three T. serra females with oviductal eggs contained gut contents, and three of the nine females with oviductal eggs of *T. striaticeps* had mammal hair in the gut.

Ovaries of adult females of *T. serra* were inactive (diameter <10 mm) throughout much of the year, with vitellogenesis occurring from the end of the dry season to the middle of the rainy season (September–December), and ovulation in the middle of the rainy season (November–December; Fig. 2). A female (IB 56020) with one attrice ovarian follicle (18.2 mm) in secondary vitellogenesis and seven oviductal eggs was recorded in September. One female (SVL = 980 mm) collected in December 2006 laid 11 eggs in captivity in January 2007. All eggs deteriorated. Data on hatchlings of *T. serra* were not obtained, but the smallest specimen from a collection measured 251 mm SVL.

Analyses of ovarian follicle sizes in *T. striaticeps* revealed a more extended period of vitellogenesis that occurs throughout the dry season and lasts up to the middle of the rainy season (April–December); ovulation starts at the onset of the rainy season (October; Fig. 2). Data on three captive females (SVL = 886–995 mm) illustrated this pattern with clutches (from 4 to 12 eggs) being laid in October (n =2) and December (n = 1). One of the females (SVL = 900 mm) ovipositing in October produced her clutch in two

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TABLE 2.—Frequency of prey items in the gut of juvenile and adult *Tropidodryas serra* and *T. striaticeps*. Numbers in parentheses indicate percentage of the total number of prey.

stages; initially it laid four eggs and after 5 d it laid seven additional eggs. The RCM averaged 0.32 \pm 0.1 (range = 0.22–0.42) in *T. striaticeps*. Only one neonate (SVL = 231, tail = 71 mm, mass = 4.6 g, from a clutch deposited in October) hatched on 1 March. The smallest specimen from a collection measured 181 mm SVL. Based on preserved specimens, clutch size averaged 7.3 \pm 2.7 eggs (range = 2–11, n = 13) in *T. serra* and 9.5 \pm 3.7 eggs (range = 1–18, n = 41) in *T. striaticeps*, and was positively correlated with maternal SVL in both species ($r^2 = 0.34$, P = 0.03, and $r^2 = 0.24$, P = 0.001, respectively; Fig. 3). The clutch size of *T. striaticeps* is larger than that of *T. serra* (H = 4.61, df = 1, P = 0.03). The size of the eggs did not differ between species (*T. serra:* $\bar{X} = 22.9 \pm 9.9$ mm, range = 10.5–49.1 mm, n = 95; *T. striaticeps*: $\bar{X} = 21.3 \pm 7.8$ mm, range = 9.9–43.0 mm, n = 370; H = 0.53, df = 1, P = 0.46).

Females of *T. serra* were captured more frequently in the rainy season ($\chi^2 = 7.69$, df = 1, *P* = 0.005), and showed

apparent peaks in activity from October to January (Fig. 4). There was no seasonal difference in the number of males ($\chi^2 = 1.94$, df = 1, P = 0.16), however, despite a decrease in May to July (Fig. 4). Juveniles (SVL <500 mm) were collected throughout the year, but were encountered more frequently in the late rainy season and early dry season (comparing values for each 2-mo period: $\chi^2 = 13.2$, df = 5, P = 0.02; Fig. 4). Males and females of *T. striaticeps* showed no difference in the number of individuals collected in either of the two seasons ($\chi^2 = 0.04$, P = 0.84 and $\chi^2 = 0.11$, P = 0.74, respectively). We did not observe any peak in the encounter rates for juveniles of either snake species (Fig. 4).

DISCUSSION

Our distribution data confirm that the genus *Tropidodryas* is endemic to the Atlantic Forest. Records outside of that



FIG. 2.—Seasonal variation in the diameter of the largest follicle in adult females of *Tropidodryas serra* (upper panel) and *T. striaticeps* (lower panel) from southeastern Brazil.

region are adjacent to the geographical extent of that biome and appear to correspond with forest/open ecotones (Guedes and Marques 2011). Although the two species of *Tropidodryas* occur in sympatry, our data also corroborate previous reports (Argôlo 1999a,b; Marques et al. 2004; Guedes and Marques 2011) that these species are partially segregated by elevation—*T. striaticeps* occurs at higher elevations, in general, than *T. serra*. This segregation can be caused by various factors, including differences in the snakes' thermal preferences and in the structural complexity of forests at low elevation, as well as those along slopes and at greater altitudes (Lillywhite 1987; Leitão-Filho 1993).

Tropidodryas serra has been previously observed foraging by day in arboreal and terrestrial microhabitats (Sazima and Puorto 1993; Marques and Sazima 2004; Vrcibradic et al. 2012). Given that both terrestrial and arboreal prey were recovered from examined museum specimens, we feel confident that both species of *Tropidodryas* forage in these two microhabitat types. Birds appear to be important contributors to the diet of *Tropidodryas* because the frequency of occurrence (20–25% of identifiable gut content) is the highest value for this prey type among xenodontines (previously ~15% for *Philodryas olfersii*;



FIG. 3.—Relationship between snout–vent length and clutch size in adult female $Tropidodryas \ serra$ (upper panel) and $T. \ striaticeps$ (lower panel) from southeastern Brazil.

Hartmann and Marques 2005). In contrast to other xenodontine species that usually prey on nestlings (Sazima and Marques 2007), both species of Tropidodryas also feed on adult birds. Areas of low elevation in the Atlantic Forest show higher richness and abundance of birds than areas at high elevation (Goerck 1999), which could explain the slightly higher proportion of birds in the diet of T. serra in relation to that of *T. striaticeps*. Species composition of the small mammals also differs according to elevation. For instance, the genus Delomys (a frequent item in T. striaticeps, but absent in T. serra) is found at elevations >500 m asl, between 20 and 25° S (where most individuals of Tropidodryas were sampled). Thus, dietary differences between the two species might reflect differences in prey availability associated with the different elevational bands where the snakes occur. Previous descriptions of the diet of Tropidodryas reported only ectothermic prey in juveniles, and a predominance of mammals in adults (Sazima and Puorto 1993; Marques and Sazima 2004). Our data confirm the ontogenic shifts in the diet of both species of Tropidodryas suggested by Sazima and Puorto (1993).

Caudal luring has mainly been reported in juveniles, although it also occurs in adult snakes (Parellada and Santos



FIG. 4.—Seasonal abundance of *Tropidodryas serra* (upper panel) and *T. striaticeps* (lower panel) from southeastern Brazil, as indicated by collection date of museum specimens.

2002). Sazima and Puorto (1993) commented that it seems unlikely that adults of *Tropidodryas* lure prey. Adult specimens with pale tail tips are not uncommon, however, being particularly frequent in *T. striaticeps*. The tail tip of juveniles of both species has flared scales; this feature is ontogenetically lost in *T. serra*, but is retained in *T. striaticeps* (Thomas and Dixon 1977). The frequency of tail injuries is higher in adults of *T. striaticeps* compared to juveniles. Andrade et al. (2010) suggested that damaged tail tips in preserved snakes could indicate that they employ caudal luring, because certain prey that forage for insect larvae and other crawling invertebrates might damage the snake tail tip while the snake is luring. Thus, we do not discard the possibility that adult *T. striaticeps* use caudal luring to attract prey.

Male-male combat has not been recorded in Neotropical xenodontines, and the observed sexual size dimorphism in *Tropidodryas* being biased towards females supports this pattern (cf. Shine 1994). Both species of *Tropidodryas* have seasonal reproductive cycles, with egg laying occurring in warmer periods. A similar reproductive pattern has been reported in other snake species that occur in the Atlantic Forest (Marques 1996; Pizzatto and Marques 2002; Marques and Sazima 2004). A possible advantage of this strategy is that it allows clutches to attain higher temperatures for embryonic development (Vinegar 1974). In contrast, many colubrid and xenodontine snakes from the Atlantic Forest reproduce throughout the year, although with temporal peaks (cf. Pizzatto et al. 2008a,b). *Tropidodryas* is believed to form a monophyletic clade with the Tachymenini and Philodryadini tribes (cf. Grazziotin et al. 2012). Snakes of these two clades also exhibit a seasonal reproductive cycle (Fowler et al. 1998; Oliveira et al. 2003; Bizerra et al. 2005; Bellini et al. 2013); thus, seasonal reproductive cycle may be a conserved trait in this clade.

Seasonal variation in biotic factors can constrain the timing of reproduction in tropical snakes (Brown and Shine 2006). The species of Tropidoryas differ slightly in reproductive timing, and the distinct elevation distributions of the two species might explain this difference. Higher temperatures in lowland areas might ensure a short period of incubation for clutches of T. serra, which lay eggs in the middle of the rainy season. The greater number of juvenile T. serra collected in the late rainy season and early dry season indicate a short incubation period and a temporally limited reproductive cycle for T. serra. In contrast, T. striaticeps seems to have a protracted reproductive cycle. As in T. serra, egg laying in T. striaticeps can also occur in the middle of the rainy season (see also Cardoso and Albuquerque 2006). However, female T. striaticeps found at higher altitudes would avoid the risk of clutches being exposed to lower temperatures at the end of the rainy season by ovipositing at the onset of the rainy season (ensuring that all embryonic development occurs during the warmer periods of year). This pattern, along with other data reported here, indicates that differences in environmental conditions at high and low elevations might have produced divergent traits between these sister species.

Acknowledgments.—We thank A.T. Fellone, C.R. Martins, K. Kishi, and V.J. Germano for assistance in the laboratory; J. Quadros, F.C. Straube, and C.E. Conte for the identification of mammal, bird, and anuran prey; H.B.P. Braz and N.F.T. Vieira for generously providing data on clutches of captive snakes; and the curators of the following collections for loan or permission to study specimens: UESC, CEPLAC, MNRJ, IBUSP, ZUEC, MNHCI, and MCTPUCRS. This study is part of the following projects supported by FAPESP: grants 2011/50206-9, 2012/50206-9, and 2012/07334. The latter project is being carried out under permit SISBIO 36450-1 issued by ICMBio—Ministério do Meio Ambiente, and protocol 983/12 approved by the Animal Ethics Committee of Instituto Butantan. CNPq provided providential fellowships to OAVM and MM.

SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at http://dx.doi.org/10.1655/HERPETOLOGICA-D-14-00060.S1.

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Accepted on 30 October 2015 Associate Editor: Rulon Clark