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Comparative ecology of three species of *Thamnodynastes* (Serpentes, Dipsadidae) in subtropical-temperate South America

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Two hypotheses have been proposed to explain the differences among species within present-day communities: the competition-predation hypothesis (CPH) and the deep history hypothesis (DHH). However, the lack of information about the ecology of many species hinders clarification of the role of these different, though not mutually exclusive, hypotheses. We compared ecological data of three species of snakes (genus *Thamnodynastes*) in their subtropical-temperate geographical distributions, evaluating the reproductive biology, sexual dimorphism, feeding ecology and habitat use of *T. hypoconia* and *T. strigatus*, and providing the first ecological data of *T. chaquensis*. Females attained sexual maturity at larger sizes than males. Unusually for viviparous snakes, males and females had similar body sizes although males had more ventral scales than females. The reproductive cycle of females was seasonal (not annual), with parturition occurring in summer. Males of *T. chaquensis* and *T. strigatus* were characterised by continuous reproductive cycles, while males of *T. hypoconia* showed differences between seasons. All three species mainly fed on amphibians. *Thamnodynastes strigatus* also fed on fishes, lizards and mammals, *T. hypoconia* occasionally fed on lizards, while *T. chaquensis* was an amphibian specialist. *Thamnodynastes hypoconia* lived in lentic aquatic habitats, *T. strigatus* was the most aquatic species, and *T. chaquensis* was the most terrestrial species. We propose that most of the ecological traits examined are phylogenetically conservative within the Tachymenini, supporting the DHH.

Key words: competition-predation hypothesis, deep history hypothesis, reproduction ecology, feeding ecology, habitat use, niche overlap, Tachymenini

INTRODUCTION

Studies on the ecology of Neotropical communities of snakes have played an important role in generating different hypotheses to explain the coexistence of the different species in present-day communities (Cadle & Greene, 1993; Colston et al., 2010). Two of these hypotheses are the competition-predation hypothesis (CPH) and the deep history hypothesis (DHH). According to the CPH, ecological differences result from recent factors that promote interactions among species at a local scale, causing divergence in niche characteristics (Colston et al., 2010). The DHH, in turn, asserts that ecological differentiation is caused by pre-existing differences, the similarity among species being associated with shared ancestry (Webb et al., 2002; Vitt & Pianka, 2005; Colston et al., 2010). However, the hypotheses are not mutually exclusive, and phylogenetic structure and ecological interactions may both act to determine community structure (França et al., 2008; Colston et al., 2010).

In snakes, previous studies have suggested that ecological traits (e.g., diet, reproductive mode and habitat use) have shifted during the evolutionary history of the clades (Martins et al., 2002; Vitt et al., 2003;

Shine, 2005). Some traits exhibit few changes during the diversification of a lineage, resulting in snakes with little present-day variation (Vitt & Vangilder, 1983). However, other traits are less conservative and differ widely within a clade (Pizzatto et al., 2008a). Consequently, many present-day species maintain the same traits as their ancestors, regardless of current environmental constraints (Colston et al., 2010). Vitt & Pianka (2005) proposed that partitioning of currently available niche space could still be strongly affected by the relative competitive abilities of current taxa that retain ancient differences. They argued that historical effects are most important among phylogenetically distant species, and minimal among phylogenetically similar species sharing the same environment. The development of the "Niche overlap theory" has shown that resource partitioning is a major determinant of the diversity of coexisting species. Most sympatric species differ in at least one of the three niche dimensions; diet, habitat and/or activity pattern, reducing competition and facilitating coexistence (Pianka, 1974). In snakes, diet is the most important dimension in reducing ecological overlap among species (Pianka, 1974; Goodyear & Pianka, 2008). Resource partitioning may not be a consequence of

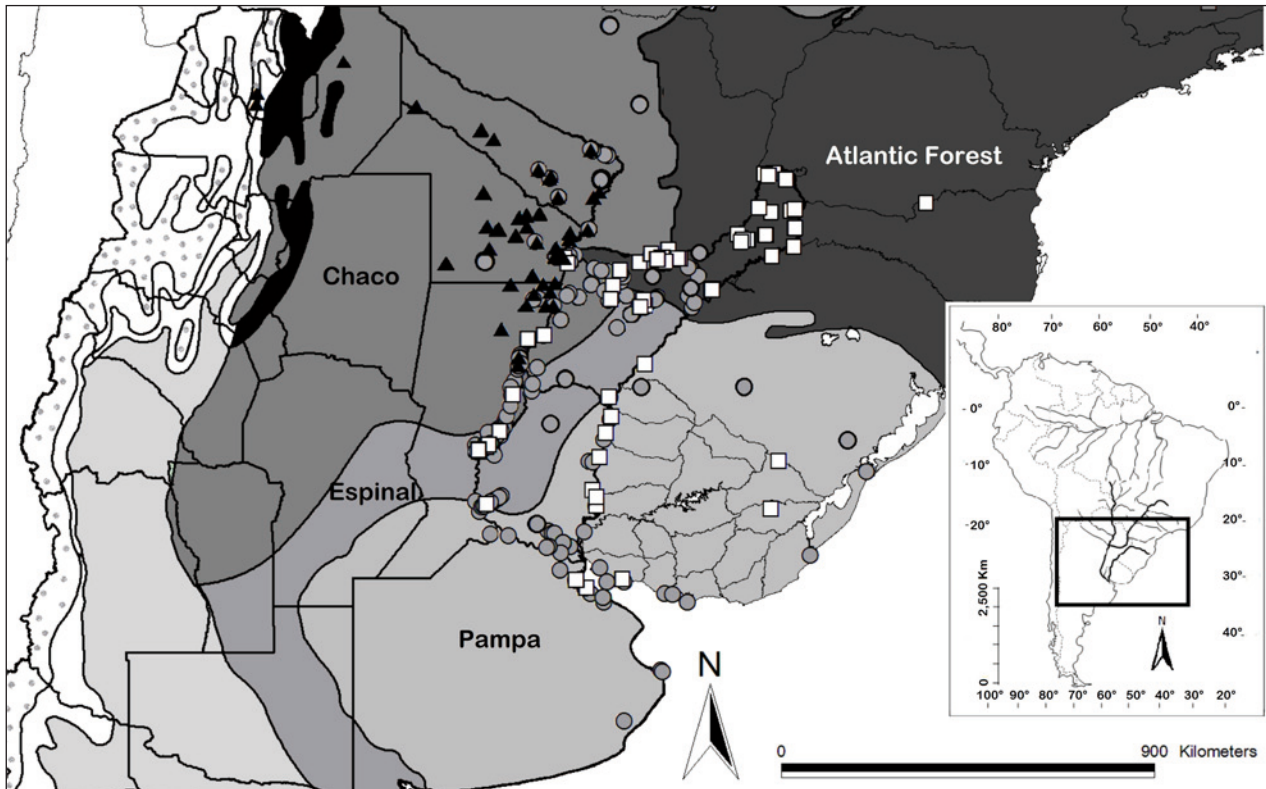*Correspondence:* Gisela P. Bellini (giselabellini@yahoo.com.ar)

Fig. 1. Distribution of the three species of *Thamnodynastes* (grey circles: *T. hypoconia*, empty squares: *T. strigatus*, black triangles: *T. chaquensis)* in the subtropical-temperate region of South America. The phytogeographic provinces covering the study area are indicated.

competition alone but may be influenced by variation in physiological and morphological constraints, response to predators and historical constraints (Goodyear & Pianka, 2008). Moreover, if a resource is not in short supply, two organisms can share it without detriment to one other (Pianka, 1974).

One of the biggest gaps in the study of ecological differences among species within present-day communities of snakes is the lack of information about the ecology of many species (Martins et al., 2002), with most studies having been conducted in North America, Australia and Europe (e.g., Madsen & Shine, 1993; Webb et al., 2003). The genus *Thamnodynastes* comprises poorly known and widely distributed Neotropical snakes of the tribe Tachymenini (Zaher et al., 2009; Grazziotin et al., 2012), subfamily Xenodontinae (*sensu* Cadle & Greene, 1993). Currently, this genus comprises 19 species distributed between the Caribbean coast and central Argentina (Bailey et al., 2005). Four species reach the subtropical-temperate region in South America: *Thamnodynastes chaquensis, T. hypoconia, T. strigatus* and *T. lanei* with records in the province of Formosa (Argentina) and Paraguay (Giraudo, 2001; Bailey et al., 2005). The poorly resolved taxonomy of the genus has given rise to several problems and confusion about its distribution, ecology and natural history (Franco & Ferreira, 2002; Bailey et al., 2005; Barbosa et al., 2006; Bellini et al., 2013). For example, *T. hypoconia* (Cope, 1860) was mentioned in the literature as *T. nattereri* (Mikan, 1828), and for decades was confused with *T. chaquensis* (Bergna & Alvarez, 1993) and *T. strigilis* (Thunberg, 1787; e.g., Serié, 1915; Gudynas, 1981). Ecological data are

available for *T. hypoconia* and *T. strigatus* (Bernarde et al., 2000b; Carreira, 2002; Ruffato et al., 2003; Sawaya et al., 2008; Bellini et al., 2013), although the ecology of *T. chaquensis* is largely unknown (Scrocchi et al., 2006).

Herein, we compare the ecological data of *T. chaquensis, T. hypoconia* and *T. strigatus*. We used data about reproductive biology, sexual dimorphism, feeding ecology and habitat use collected in a long-term study. We also discuss main ecological traits in the context of the DHH and CPH. Since *T. chaquensis, T. hypoconia* and *T. strigatus* have a common phylogenetic history (Grazziotin et al., 2012) and share part of their distribution area (Giraudo, 2001), we expect to find differences in diet and habitat use but similar sexual dimorphism reproductive traits, since the latter are more conservative than the former (Bailey et al., 2005).

MATERIALS AND METHODS

Area of study

We examined the ecology of *T. chaquensis, T. hypoconia* and *T. strigatus* throughout their distribution in eastern Argentina, southern Paraguay, southeastern Brazil, and Uruguay (Fig. 1). We analysed specimens collected by us, specimens from collections and data from the literature. The field study was carried out in eastern Argentina and southern Paraguay, an area with a mosaic of vegetation ranging from wet savannas and grasslands to subtropical forests, gallery forests and a wide variety of wetlands. The region encompasses four phytogeographical provinces: the Atlantic Forest (dominated by subtropical humid forest), Chaco (subtropical and temperate dry

Table 1. Meristic and morphometric variation in mature individuals of *Thamnodynastes chaquensis, T. hypoconia* and *T. strigatus*. *n*: Number of individuals, *X*: Mean, SE: Standard Error, R: Range, VS: Ventral scales, SC: Subcaudal scales, SVL: Snout-vent-length, TL: Tail length, BM: Body mass, HL: Head length, *: *p*< 0.05, NS: Not significant.

		T. chaquensis		T. hypoconia		T. strigatus	
		Males	Females	Males	Females	Males	Females
VS	n	28	48	78	67	32	16
	X	145.85	142.29	146.83	143.52	141.18	136.12
	SE	9.05	4.93	3.77	5.50	6.57	4.56
	R	113–166	128–149	138–155	135–154	131–155	130–147
		* H=7.16		* H=27.67		* H=5.19	
SS	n	24	44	74	63	27	15
	X	62.62	54.31	75.95	69.63	65.51	62.26
	SE	4.67	4.40	4.13	5.14	4.01	4.54
	R	54–73	47–67	64–82	53–79	59–75	56–72
		* H=32.17		* H=48.51		* H=12.02	
SVL	n	27	37	67	35	25	8
	X	422.14	425.4	399.37	395.34	477.8	517.44
	SE	80.13	63.04	66.75	32.87	102.55	153.73
	R	315–590	314–619	256–537	341–475	341–685	403–795
		NS		NS		NS	
TL	n	25	35	63	33	22	9
	X	124.48	106.88	145.84	136.6	151.54	132.25
	SE	24.91	21.08	25.57	37.89	28.39	15.40
	R	83–174	69–166	87–193	93–329	95–204	112–158
		* F=29.43		* F=22.18		* F=9	
BM	n	22	35	62	33	19	7
	X	43.79	58.09	21.66	25.27	62.27	90.57
	SE	19.52	19.41	9,00	7.96	30.45	33.53
	R	17–91	28.5–105	7–52	9–45	21.75–125	32–134
		* F=9.45		* F=16.76		* F=8.36	
HL	n	25	35	48	28	20	7
	X	22.72	24.43	17.63	18.13	26.17	27.82
	SE	2.95	2.37	2.54	1.84	3.79	2.92
	R	17–28.1	20.35–29.09	12.85–26.71	14.68–21.86	20.65–35.95	22.83–31.22
		* F=6.87		* F=5.22		NS	

forest and savannas), Espinal (savannas, grassland and dry shrublands) and Pampa (steppes) (Cabrera, 1994; Arzamendia & Giraudo, 2009, Fig. 1). The climate is seasonal, with a hot and rainy spring and summer (mean temperature: 25–27.5°C) and a dry autumn and winter (mean temperature: 10–15°C). Precipitation decreases from northeast to southeast and annual precipitation is around 1800–800 mm (Iglesias de Cuello, 1982; Paoli et al., 2000).

Snake collection
We sampled the study area from January 1991 to April 2012, mainly by means of road sampling in different habitats (López & Giraudo, 2008). Road sampling allowed us to cover large distances and detect both road-killed and live snakes. We also conducted time constrained searches and opportunistic encounter surveys (see Scott 1994; Valdujo et al., 2002). The sampling was carried out both day and night. For each specimen, we recorded the exact location (using a Garmin eTrex Legend Global Positioning System device), habitat use, date and, whenever possible, the time of activity. Live snakes were measured and subsequently released at the capture site. We preserved recently road-killed snakes that were in good condition for collecting dietary, reproductive and morphological data. All collected specimens are housed in the collection of the Instituto Nacional de Limnología (INALI, Santa Fe, Argentina).

The reproductive and feeding ecological data were supplemented with original data from specimens deposited in the following scientific collections: Museo Argentino de Ciencias Naturales "Bernadino Rivadavia" (MACN, Buenos Aires), Centro Nacional de Investigaciones Iológicas (currently deposited in the MACN), Colección del Museo de La Plata (MLP, Buenos Aires), Museo Antonio Serrano, (MAS, Entre Ríos), Universidad Nacional del Nordeste, (UNNE, Corrientes). We also used feeding ecological data from literature (Carreira, 2002; Bernarde et al., 2000b; Ruffato et al., 2003; Winkler et al., 2011).

Ecological data collection and analysis

The following morphometric variables were recorded: snout–vent length (SVL), tail length (TL) and head length (HL), measured with a flexible ruler (in mm); number of ventral and subcaudal scales according to Gans' (1964) technique; body mass (nearest 0.1 g); the length, width and thickness of the right testis (in mm, Feriche, 1998); and diameter of the largest ovarian follicles (in primary or secondary vitellogenesis) or oviductal egg (length and width in mm), using a digital calliper.

Females were considered mature if they had follicles in secondary vitellogenesis, oviductal eggs or folded oviducts which indicate recent parturition (see Pizzatto et al., 2007a, 2008a; Leite et al., 2009b). Males were considered mature when they had turgid testes and opaque and convoluted deferent ducts (Shine, 1978; Pizzatto et al., 2008b; Leite et al., 2009b). We recorded males and females with SVLs larger than that of the smallest mature specimen as adults (Hartmann & Marques, 2005). In males, increased size and mass of the testes probably reflect spermiogenesis (Pizzatto et al., 2007a), so we calculated the volume of the testis using the ellipsoid formula (Pleguezuelos & Feriche, 1999). We defined the reproductive season as the period from secondary vitellogenesis to the bearing of young (Leite et al., 2009a). We evaluated the presence of sexual dimorphism for SVL, and the number of ventral and subcaudal scales with a Kruskal-Wallis test. In the analyses of covariance (ANCOVA), we used SVL and trunk (SVL-head length) as covariates for TL, mass and head length. Reproductive frequency was estimated by the percentage of reproductive females (with ovarian follicles >5 mm or oviductal eggs). Oviductal eggs, corpora lutea and neonates were counted to estimate fecundity (Pizzatto, 2005). We compared fecundity among species with an ANOVA test and performed a Spearman Rank Correlation to test for the relationship between SVL and fecundity in females. The reproductive potential, which shows the number of potential neonates of one species per female per year, was estimated as mean fecundity × reproductive frequency (Trauth, 1978). The index of sexual size dimorphism (SSD) was calculated according to Shine (1994) as mean SVL of the largest sex/(mean SVL of the smallest sex)-1. This index is positive if females are the largest sex. To determine reproductive activity in males, we compared variation in testicular volume of each species between seasons using an ANCOVA with SVL as a covariate.

We dissected the digestive tracts to analyse their contents. We identified prey items to the lowest possible taxonomic group by comparing them with material of the reference collection of the Instituto Nacional de Limnología and the literature (Lavilla, 2005). Highly digested stomach contents (primarily small pieces of bone) were recorded as unidentified vertebrates. Small insects were deemed secondary prey having been ingested by amphibians because hair, feathers and scales were evident when present in the hindgut (Martins et al., 2002; López & Giraudo, 2008). We tested for differences in the frequency of prey categories to the level of higher groups (fishes, amphibians, reptiles and mammals) using a chi-square test.

We recorded the habitat in which each snake occurred. The relative importance of resource (diet and habitat use) was determined by comparing niche overlaps as calculated by Pianka (1973) using the program EcoSim v.7.0 (Gotelli & Entsminger, 2001) with randomisation algorithm three (RA3) and 1,000 randomisations of the original matrix. RA3 retained the niche breadth of each species, but randomised which particular resource states were utilised (Winemiller & Pianka, 1990). Pianka's niche overlap index varies between 0 (non-overlapping) and 1 (full overlap). We compared the dietary niche overlap among *T. chaquensis*, *T. hypoconia* and *T. strigatus* at two levels: higher groups, with four states (fishes, amphibians, reptiles and mammals); and taxonomic families, with fourteen states (Poeciliidae, Characidae, Hylidae, Leptodactylidae, Cycloramphidae, Bufonidae, Brachycephalidae, Leiuperidae, Gekkonidae, Dipsadidae, Rodentia, Cricetidae, Hylodidae and Scincidae). Habitat use was analysed with seven states (dry forest, lentic wetlands on the floodplains of the Paraná and Paraguay Rivers, wet savannahs, marshes, human-altered habitats, forests in gallery - riparian forest, lotic aquatic environments). Dimensions having less overlap identify dimensions that may be key to phenotypic divergence among species and, hence, ecological diversification. All statistical analyses, with the exception of niche overlap analyses, were performed using Infostat software v. 5.1 (Di Rienzo et al., 2005) with $p < 0.05$.

Table 2. Comparisons of morphological variables among *Thamnodynastes chaquensis*, *T. hypoconia* and *T. strigatus*. Upper panel: males; lower panel: females. VS: Ventral scales, SS: Subcaudal scales, SVL: Snout-Vent-Length, TL: Tail length, BM: Body mass, HL: Head length. A<B<C for parameters measured. All comparisons are significantly different at $p < 0.05$.

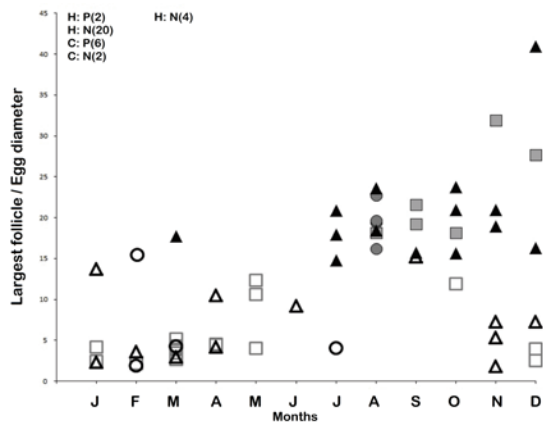| Species	VS	SS	SVL	TL	BM	HL
T. chaquensis	B	A	A	A	B	B
T. hypoconia	B	B	A	C	A	A
T. strigatus	A	A	B	B	C	C
	$H=20.69$	$H=70.97$	$F=9.05$	$F=16.93$	$F=54.88$	$F=89.44$
T. chaquensis	B	A	A	A	B	B
T. hypoconia	B	C	A	C	A	A
T. strigatus	A	B	B	B	C	C
	$H=17.14$	$H=70.91$	$F=11.18$	$F=20.94$	$F=35.32$	$F=92.66$

Fig. 2. Seasonal variation in the diameter of the largest ovarian follicle (empty square: *T. hypoconia*, empty circle: *T. strigatus*, empty triangle: *T. chaquensis*), oviductal eggs (full square: *T. hypoconia*, full circle: *T. strigatus*, full triangle: *T. chaquensis*), parturition (P), and neonates (N) of *Thamnodynastes chaquensis* (C) and *T. hypoconia* (H) in subtropical-temperate South America.

RESULTS

Morphology and Sexual Dimorphism
We analysed 88, 154 and 58 specimens of *T. chaquensis*, *T. hypoconia* and *T. strigatus*, respectively (Table 1). Juveniles of *T. strigatus* had the longest SVL (H=8.83; p<0.001) and were also the heaviest (H=26.92; p=0.012). Among the adults, *T. strigatus* were the longest (SVL and head length) and the heaviest species (Table 2). *Thamnodynastes chaquensis* were heavier and had longer heads than *T. hypoconia*, but were similar in SVL. *Thamnodynastes hypoconia* had the longest tail, followed by *T. strigatus* and *T. chaquensis* (Table 2).

In all three species, males had more subcaudal and ventral scales than females (Table 1). Males had the longest tails while the females were heaviest, without dimorphism in SVL for any of the three species (Table 1). Females of *T. chaquensis* and *T. hypoconia* but not *T. strigatus* had longer heads than males (Table 1). SSD for adults was 0.0002, -0.0035 and 0.082 for *T. chaquensis*, *T. hypoconia* and *T. strigatus,* respectively.

Reproductive Ecology
Females (*T. chaquensis* SVL=325 mm; *T. hypoconia* SVL=358 mm; *T. strigatus* SVL=403 mm) attained sexual maturity at a larger body size than males (*T. chaquensis* SVL=315 mm; *T. hypoconia* SVL=256 mm; *T. strigatus* SVL=341 mm). Mature females of *T. chaquensis* (*n*=38) and *T. hypoconia* (*n*=35) had vitellogenic follicles (5–13 mm) from March to June, and oviductal eggs (14–32 mm) from July to December, with a single record of *T. chaquensis* with oviductal eggs in March. Parturition occurred in January, indicating a seasonal reproductive cycle (Fig. 2). We found newborns with umbilical scars from December to March. For *T. strigatus* we found vitellogenic follicles from February to July, oviductal eggs in August and parturition in January (Fig. 2). Fecundity did not differ among the three species of *Thamnodynastes* (*F*=2.67, *p*=0.08). Litter size was 2–18 individuals for *T. chaquensis*

(*X*=10.5; *n*=20), 4–13 individuals for *T. hypoconia* (*X*=7.6; *n*=12) and 9–16 individuals for *T. strigatus* (*X*=11; *n*=4). Reproductive frequency was 0.81 in *T. chaquensis*, 0.48 in *T. hypoconia* and 0.5 in *T. strigatus*, suggesting a biennial reproductive cycle for the latter two species. This is confirmed by the simultaneous occurrence of gravid females and females without vitellogenic follicles or eggs in equal proportions (Fig. 2). The reproductive potential was 5.87, 3.22 and 8.00 neonates per female and year for *T. chaquensis*, *T. hypoconia* and *T. strigatus*, respectively. The relationship between the number of embryos and SVL was not significant for any species (*T. chaquensis:* ρ=0.30; p=0.23; *T. hypoconia*: ρ=-0.21, p=0.51; *T. strigatus*: ρ=0.80; p=0.17)

Males of *T. chaquensis* and *T. strigatus* showed no significant difference in testicular volume between seasons. For *T. hypoconia*, the largest testicular volume was found in spring and the smallest in autumn and summer (ANCOVA *F*=3.2, df=3, p=0.04, *n*=30).

Feeding Ecology
We dissected the digestive tracts of 154 *T. hypoconia*, 64 *T. chaquensis,* and 50 *T. strigatus* specimens. Of all individuals examined, 25 specimens (16%) of *T. hypoconia*, 9 specimens (18%) of *T. strigatus,* and 4 specimens (6.25%) of *T. chaquensis* had gut content. Fishes and mammals were recorded only in the diet of *T. strigatus,* and lizards were preyed on mainly by *T. strigatus*. Amphibians were the main prey of all species, and the only prey found for *T. chaquensis* (*n*=6); *T. hypoconia* consumed amphibians (97.33 %, *n*=34) and lizards (2.77 %, *n*=1) and *T. strigatus* consumed amphibians (69.47 %, *n*=66), fishes (21.05 %, *n*=20), mammals (7.37 %, *n*=7) and lizards (2.11 %, *n*=2, Table 3). The preference for amphibians was significant for *T. hypoconia* (χ^2=89.33; p<0.001) and *T. strigatus* (χ^2=113.12; p<0.001). Niche overlaps were high for *T. chaquensis* and *T. hypoconia* (0.99), *T. chaquensis* and *T. strigatus* (0.94) and *T. hypoconia* and *T. strigatus* (0.94). At the level of families, the dietary niche overlap was 0.87 for *T. strigatus* and *T. hypoconia*, 0.26 for *T. chaquensis* and *T. hypoconia*; and 0.20 for *T. chaquensis* and *T. strigatus*.

Habitat Use
Thamnodynastes chaquensis inhabits dry forest (*n*=41, 51%), wetlands (*n*=13, 16%), wet savannahs (*n*=11, 14%) and marshes (*n*=8, 10%). We recorded seven specimens (9%) of *T. chaquensis* in human-altered habitats in suburban areas. *Thamnodynastes hypoconia* inhabits mainly lentic aquatic environments and the wetlands surrounding large rivers (*n*=147, 68%). We found 41 snakes (18%) in wet savannahs close to wetlands or temporary ponds. We obtained five records (2%) from forests, most of them in riparian forest near wetlands. We recorded 29 specimens (13%) of *T. hypoconia* around farmland, urban and suburban areas. We recorded 61 specimens (79%) of *T. strigatus* in lotic aquatic habitats, 15 (19%) in marshes and one specimen (1%) in human-altered habitat. Niche overlap was low (*T. chaquensis/T. hypoconia*: 0.35, *T. chaquensis/T. strigatus*: 0.043, *T. hypoconia/T. strigatus*: 0.0003).

Table 3. Diet of *Thamnodynastes chaquensis, T. hypoconia* and *T. strigatus*. *Data from the literature.

Prey category	Prey taxon	T. chaquensis		T. hypoconia		T. strigatus	
		n	%	n	%	n	%
FISHES	Unidentified Fishes					1	1.05
	Poeciliidae						
	Poecilia sp.*					3	3
	*Phalloceros caudimaculatus**					1	1.05
	Characidae						
	Unidentified Characidae*					1	1.05
	Unidentified Tetragonopterinae*					4	4.21
	*Hyphessobrycon luetkenii**					8	8.42
	Thoracocarax sp.					2	2.11
AMPHIBIA	Unidentified Amphibia	1	16.6	11	28.95	9	9.47
	Hylidae						
	Unidentified Hylidae			2	5.26	6	6.32
	Dendropsophus nanus			1	2.63		
	Dendropsophus sp.			2	5.26		
	*Hypsiboas latistriatus**					1	1.05
	*Hypsiboas pulchellus**			1	2.63	1	1.05
	*Scinax aromothyella**					2	2.11
	Scinax cf. *berthae*			6	15.8		
	*Scinax fuscovarius**					11	11.58
	*Scinax squalirostris**			1	2.63		
	Scinax sp.					5	5.26
	Hylodidae						
	Crossodactylus cf. *bokermanni**					1	1.05
	Leptodactylidae						
	Unidentified Leptodactylidae			2	5.26	5	5.26
	Leptodactylus chaquensis	1	16.6				
	*Leptodactylus gracilis**					1	1.05
	Leptodactylus latrans group*			1	2.63		
	Leptodactylus latrans	1	16.6	2	5.26	8	8.42
	Leptodactylus sp.			1	2.63	1	1.05
	Cycloramphidae						
	*Lymnomedusa macroglossa**			1	2.63		
	*Odontophrynus americanus**					5	5.26
	Bufonidae						
	Rhinella cf. *fernandezae*			2	5.26		
	*Rhinella ictericus**					1	1.05
	Rhinella sp.	3	50			1	1.05

Table 3. *Continued*.

Prey category	Prey taxon	T. chaquensis		T. hypoconia		T. strigatus	
		n	%	*n*	%	*n*	%
	*Melanophryniscus moreirae**					1	1.05
	Brachycephalidae						
	*Ischnocnema holti**					3	3.16
	Leiuperidae						
	Physallaemus cf. *albonotatus*			2	5.26		
	*Physalaemus cuvieri**					2	2.11
	Physalaemus rodrigoi					1	1.05
	Physalaemus sp.*			2	5.26	1	1.05
REPTILIA	**Scincidae**						
	Mabuya sp.			1	2.63		
	Gekkonidae						
	*Hemidactylus mabouia**					1	1.05
	Dipsadidae						
	*Sibynomorphus ventrimaculatus**					1	1.05
MAMMALIA	**Rodentia**						
	Unidentified Rodentia					4	4.21
	Cricetidae					1	1.05
	*Oligoryzomys nigripes**					2	2.11
TOTAL		6	100	38	100	95	100

DISCUSSION

Contrary to the pattern commonly recorded in snakes, *T. chaquensis, T. hypoconia* and *T. strigatus* exhibited male-biased sexual dimorphism in the number of ventral scales (for other examples on *Thamnodynastes* see Franco, 1999; Franco & Ferreira, 2002; Bailey et al., 2005). Vincent & Herrel (2007) proposed that aquatic and semi-aquatic snakes have relatively large females with big heads to consume larger prey than conspecific males. In our study, none of three species showed sexual dimorphism in SVL, and *T. strigatus* did not exhibit any head sexual dimorphism. Our data were however insufficient to test for sexual differences in diet.

Female body size determines litter mass if females delay reproduction until they have enough energy to fill their body cavity with eggs or embryos (Shine, 2003). Accordingly, females of all three species attained sexual maturity at longer SVL than males, with the SVL difference disappearing later in life. The lack of a relationship between the number of embryos and SVL contradicts an otherwise common pattern in viviparous snakes (Martins et al., 2002; Leite et al., 2009a). Females of all studied species had seasonal reproductive cycles. Pizzatto et al. (2008b) suggest that the duration of the reproductive

cycles in South American Xenodontines is conserved in many lineages. We propose that this holds true for *Thamnodynastes*, and the seasonal reproductive cycle seems to be generally conservative in many species of Tachymenini (Bizerra et al., 2005; Pizzatto et al., 2008b). The relatively low number of embryos per female and year as well as the biennial reproductive frequency is probably a consequence of viviparity and late parturition. The latter limits post-partum feeding opportunities and the ability to store reserves for reproducing in the following year, resulting in a largely biennial cycle (see also Shine, 2003; Ibarguengoytía & Casalins, 2007). The suggested annual reproductive frequency of *T. chaquensis* may be due to different energy acquisition or a potential sampling bias. Males of *T. chaquensis* and *T. strigatus* showed a continuous cycle, whereas males of *T. hypoconia* had seasonally-dependent testes volumes. However, macroscopic structures are not always good indicators of spermiogenesis (Mesquita et al., 2013), and a truly continuous cycle has so far not yet been convincingly been demonstrated in neotropical snakes (Almeida-Santos et al., 2006; López & Giraudo, 2008).

In agreement with our study, *T. strigatus* has previously been documented as predating predominately on anurans and occasionally rodents, fish, and lizards

(Bernarde et al., 2000b; Ruffato et al., 2003). For *T. hypoconia*, prey such as lizards, snakes, anurans, coleoptera and insect larvae were previously recorded based on anecdotal information (Miranda et al., 1983; Cei et al., 1992; Cei, 1993; Achaval & Olmos, 1997), and more quantitative studies confirm that the species is primarily batrachophagous (Carreira, 2002; Sawaya et al., 2008; Bellini et al., 2013). No data were previously available for *T. chaquensis*. Our data point towards a similar diet than the other studied congeners, however, at a low sample size. The body size of a predator limits prey size (Cadle & Greene, 1993), and how a snake uses the habitat is related to prey availability (Ruffato et al., 2003). *Thamnodynastes strigatus* was the only species that consumed fish and mammals, in accordance with its larger size (Bernarde et al., 2000a, b; Giraudo, 2001; Ruffato et al., 2003). *Thamnodynastes hypoconia* is the most slender species, associated with aquatic habitats (Arzamendia & Giraudo, 2009). Accordingly, its diet was mainly composed of hylids which are regionally abundant in wetlands. Conversely, *T. chaquensis* is the most terrestrial species and its diet is based on the more terrestrial Leptodactylidae and Bufonidae. Despite its toxicity, *Rhinella* was consumed by all studied species, and toxic *Melanophryniscus* have previously been reported as prey of *T. strigatus*, reinforcing the idea that these species may be tolerant against anuran toxins (Winkler et al., 2011).

The three species of *Thamnodynastes* showed a high overlap in their diets. Pianka (1974) stated that sympatric species with high overlap along one dimension often show little overlap along other dimensions, and that resources can be shared if they are not in short supply. Anurans are indeed abundant in the regional wetlands, although dietary niches varied at the level of families. Habitat use was characterised by low overlap and seems to be conservative in most Xenodontinae in general and within the Tachymenini in particular (Bernarde et al., 2000a). In agreement with previous studies, we found that *T. hypoconia* predominately occupies open, lentic habitats (Sawaya et al., 2008; Arzamendia & Giraudo, 2009; Bellini et al., 2013), whereas *T. strigatus* has commonly been found in streams of the Atlantic or the dense Paraná forest (Giraudo, 2001; Giraudo et al., 2009). In the floodplain of the Middle Paraná river dominated by lentic wetlands with open vegetation, Giraudo et al. (2007) assigned 212 (93%) and 16 (7%) specimens to *T. hypoconia* and *T. strigatus*, respectively. Little was previously known about the habitat of *T. chaquensis* (but see Giraudo, 2001). Based on our records and its body structure, we considered *T. chaquensis* to be the most terrestrial of the three species. This is supported by its geographical distribution, which includes xeric areas in the dry Chaco ecoregion (Giraudo, 1996, 2001; Akmentins et al. 2010; Arzamendia & Giraudo, pers. obs.).

Consistent with the DHH, the three studied *Thamnodynastes* species were similar in sexual dimorphism, duration of vitellogenesis, egg-carrying period and clutch size. The duration of the reproductive cycle and the reproductive potential as well as frequency may however be influenced by environmental factors food availability and habitat use, in agreement with the CPH. Our results also reinforce that the diet is a conservative trait in *Thamnodynastes* (Bernarde et al., 2000a, b; Ruffato et al., 2003, Bailey et al., 2005), although the diet of *T. strigatus* particularly is also shaped by morphology and lifestyle. Similarities in diet may reflect close phylogenetic relatedness, while differences in habitat use may be related to differences in prey type frequencies or spatial niche partitioning. The same pattern was found for coexisting Neotropical dipsadids such as *Philodryas olfersii* and *P. patagoniensis* (Hartmann & Marques, 2005).

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