

REPRODUCTIVE ECOLOGY OF DIPSADINE SNAKES, WITH EMPHASIS ON SOUTH AMERICAN SPECIES

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ABSTRACT: A relatively large amount of variation occurs in the reproductive ecology of tropical snakes, and this variation is generally regarded as being a consequence of seasonality in climate and prey availability. In some groups, even closely related species may differ in their reproductive ecology; however, in others it seems to be very conservative. Here we explore whether characters related to reproduction are phylogenetically constrained in a monophyletic group of snakes, the subfamily Dipsadinae, which ranges from Mexico to southern South America. We provide original data on reproduction for *Leptodeira annulata*, *Imantodes cenchoa*, and three species of *Sibynomorphus* from southern, southeastern and central Brazil, and data from literature for other species and populations of dipsadines. Follicular cycles were seasonal in *Atractus reticulatus*, *Dipsas albifrons*, *Hypsiglena torquata*, *Leptodeira maculata*, *L. punctata*, *Sibynomorphus* spp. and *Sibon sanniola* from areas where climate is seasonal. In contrast, extended or continuous follicular cycles were recorded in *Dipsas catesbyi*, *D. neivai*, *Imantodes cenchoa*, *Leptodeira annulata*, and *Ninia maculata* from areas with seasonal and aseasonal climates. Testicular cycles also varied from seasonal (in *H. torquata*) to continuous (in *Dipsas* spp., *Leptodeira annulata*, *L. maculata*, *N. maculata* and *Sibynomorphus* spp.). Most dipsadines are small (less than 500 mm SVL), and females attain sexual maturity with similar relative body size than males. Sexual dimorphism occurred in terms of SVL and tail length in most species, and clutch size tended to be small (less than five eggs). Combat behavior occurs in *Imantodes cenchoa*, which did not show sexual size dimorphism. Reproductive timing, for both females and males, varied among species but in general there were no differences between the tribes of Dipsadinae in most of the reproductive characteristics, such as mean body size, relative size at sexual maturity, sexual size and tail dimorphism, duration of vitellogenesis or egg-carrying in oviducts.

Key words: Dipsadinae; Fecundity; Follicular cycle; Reproduction; Sexual size dimorphism; Sexual tail dimorphism; Testicular cycle

REPRODUCTIVE cycles of snakes vary from highly seasonal to continuous. In temperate areas, snakes usually reproduce only during the warmer months (usually spring) and many species present nonannual cycles. In tropical areas, however, cycles tend to be more variable (Fitch, 1982; Seigel and Ford, 1987). This higher variability can be partially explained by greater climatic complexity (Greene, 1997) and food availability in tropical areas (Santos et al., 2005; Seigel and Ford, 1987). Climatic factors may be an important variable affecting seasonality in reproductive cycles of tropical snakes (Pizzatto and Marques, 2002, 2006). For example, Brown and Shine (2006) provided evidence that, for a

colubrid snake from tropical Australia (*Tropidonophis mairii*), abiotic factors such as seasonal availability of moist incubation conditions were more important than biotic factors (e.g., higher predation on eggs or hatchlings, or food availability for hatchlings) on influencing reproductive timing.

Recent studies on the evolution of ecological characters in Neotropical snakes have shown that characters related to defense against predators seem to have diversified apparently quickly in Neotropical snakes, with a large amount of variation within clades (e.g., Martins, 1996). In contrast, habitat and microhabitat use, as well as diet and many other characters related to feeding, seem to be conservative, i.e., they have experienced few changes during the lineage's history and, consequently, the snake groups studied show

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little contemporary variation in these characters (e.g., Martins et al., 2001, 2002). Characters related to reproduction in Neotropical snakes seem to be relatively conservative in some phylogenetic lineages (Almeida-Santos and Salomão, 2002; Almeida Santos et al., 2006; Marques, 1996; Marques et al., 2006; Pizzatto and Marques, 2007; Pizzatto et al., 2007a, 2008), although in other groups even closely related species may differ widely in their reproductive ecology (e.g., Marques, 1996). Despite the efforts to study the reproductive biology of tropical snakes in the last few decades (e.g., Balestrin and Di-Bernardo, 2005; Marques, 1996; Pizzatto and Marques, 2002; Vitt, 1987), it is still not possible to recognize patterns in many groups, especially in areas where species diversity is high, such as in the Neotropics (but see Almeida-Santos and Salomão, 2002).

The subfamily Dipsadinae (Vidal et al., 2000; Zaher, 1999) is composed of small, slender snakes which occur from Mexico to southern South America (Ferrarezzi, 1994; Zaher, 1999). The monophyly of Dipsadinae is suggested by both morphological and molecular data (Cadle, 1984; Vidal et al., 2000; Wallach, 1995; Zaher, 1999), and the subfamily is apparently the sister group of all other xenodontines (Vidal et al., 2000). Two apparently monophyletic clades comprise the Dipsadinae: the tribes Dipsadini, composed of aglyphous, relatively smaller, earthworm/mollusk-eating snakes (e.g., *Adelphicos*, *Atractus*, *Geophis*, *Ninia*, *Tropidodipsas*, *Sibon*, *Dipsas* and *Sibynomorphus*), and Leptodeirini, which is composed of aglyphous or opisthoglyphous, relatively larger, lizard/frog-eating snakes (e.g., *Eridiphas*, *Hypsiglena*, *Imantodes*, *Leptodeira* and *Pseudoleptodeira* (see Cadle, 1984; Cadle and Greene, 1993; Ferrarezzi, 1994; Martins and Oliveira, 1999; Rodríguez-Robles et al., 1999; Vidal et al., 2000; Vitt, 1996; Zaher, 1999)).

As a further attempt to understand the extent to which reproductive characters of Neotropical snakes are conservative (cf. Almeida-Santos and Salomão, 2002), we here explored the variation in reproductive ecology in the subfamily Dipsadinae based on original and literature data. Specifically, our aim is to: (1) conduct an overview of reproductive

characters, such as sexual maturity and dimorphism, body sizes, reproductive cycles and clutch size in snakes of the tribe Dipsadini; and (2) investigate how those characters differ between the tribes Dipsadini and Leptodeirini.

MATERIALS AND METHODS

Original data on adult *Leptodeira annulata* ($n = 181$), *Imantodes cenchoa* ($n = 36$), *Sibynomorphus mikanii* ($n = 144$), *S. newwiedi* ($n = 126$), and *S. ventrimaculatus* ($n = 111$) were obtained from specimens deposited in the collections of Instituto Butantan (IB), Museu de História Natural da Universidade Estadual de Campinas (ZUEC), Universidade Federal de Santa Maria (ZUFMS), Pontifícia Universidade Católica do Rio Grande do Sul (MCP), and Museu de História Natural do Capão da Imbuia (MHNCI). Specimens of *L. annulata* were collected in a range of localities between $11^{\circ} 47' N$ and $23^{\circ} 35' S$, and $39^{\circ} 43' E$ and $56^{\circ} 05' W$; those of *I. cenchoa* are from $21^{\circ} 11' N$ to $26^{\circ} 55' S$ and $45^{\circ} 24' E$ to $52^{\circ} 06' W$; *S. mikanii* from $20^{\circ} 16' N$ to $23^{\circ} 58' S$ and $45^{\circ} 42' E$ to $51^{\circ} 20' W$; *S. newwiedi* from $20^{\circ} 21' N$ to $25^{\circ} 00' S$ and $40^{\circ} 39' E$ to $49^{\circ} 42' W$; and *S. ventrimaculatus* from $27^{\circ} 28' N$ to $30^{\circ} 52' S$ and $51^{\circ} 01' E$ to $54^{\circ} 28' W$. For each snake we collected data on: (1) snout-vent length (SVL), (2) length of the right testis, (3) diameter of deferent duct, proximal to the cloaca, (4) diameter of the largest ovarian follicle or oviductal egg, and (5) number of well developed follicles in secondary vitellogenesis (>10 mm) and eggs.

Gravid *S. mikanii* and *S. newwiedi* received at Instituto Butantan (IB) were kept in captivity until oviposition. Data on other species of dipsadines were obtained from published papers. In these cases we used only information that confirmed reproductive timing and fecundity in each species. Many published sources were not used because they represent only a few, or casual, records that were not conclusive or comparable to our data. Data on testicular cycles of *Hypsiglena torquata*, *Leptodeira maculata*, *L. punctata* and *Ninia maculata* came from histological analyses (Diller and Wallace, 1986; Goldberg, 2001, 2004a,b).

Females were considered mature if they had follicles in secondary vitellogenesis, oviductal eggs (cf. Shine, 1978) or folded oviducts (which indicate recent oviposition). Males were considered mature when they had turgid testes and convoluted deferent ducts (cf. Shine, 1980; Slip and Shine, 1988). A sexual size dimorphism index (SSD) was calculated according to Shine (1994): mean body size of the largest sex divided by mean body size of the smallest sex, minus one. By convention, positive values represent females larger than males and negative values represent males larger than females (Shine, 1994).

Size at maturity, represented by the SVL of the smallest mature snake in the samples, and relative tail length were presented as the proportions of the mean body size and analyzed after transformation to the arcsine of their squared root. All variables were tested for normality and homoscedasticity prior to analyses (Zar, 1999).

Sexual dimorphism was investigated in terms of mean SVL, proportional size at maturity (PSM) and relative tail length (RTL). We compared these variables between sexes, using two-tailed *t*-Student test (Zar, 1999). Sexual dimorphism in tail length was analyzed in *L. annulata*, *I. cenchoa* and *Sibynomorphus* spp. with ANCOVA, using tail length as the dependent variable, SVL as the covariate, and sex as the factor (Zar, 1999). This analysis was not performed for the other species because we did not have access to the raw data sets.

We used the Student's *t*-test (Zar, 1999) to test for differences in mean SVL, PSM, RTL, SSD, clutch size, and duration of reproductive cycles between the tribes and RTL between habitat use categories (terrestrial/fossorial and arboreal/semi-arboreal). To test whether SSD was affected by body size, we used linear regressions, separately for males and females (Zar, 1999). To test whether clutch size is affected by body size in *L. annulata*, *I. cenchoa* and *Sibynomorphus* spp., we used linear regressions. Data were log-transformed as required (Zar, 1999).

Testis length indicates sperm production (cf. Volsøe, 1944), and deferent duct diameter can indicate sperm storage (Almeida-Santos et al., 2006; Sever et al., 2002; Yokoyama and

Yoshida, 1993). Variation in testis length and diameter of deferent duct (dependent variables) were compared among seasons (factors) using ANCOVA because both variables were significantly correlated to snake SVL (covariate) (Zar, 1999).

RESULTS

Mean body sizes of adult snakes differed among species in the dipsadines (Table 1). All species, except *I. cenchoa* had a mean SVL < 600 mm, and the smallest species was *N. maculata* (mean SVL = 226 mm; Table 1). When mean SVL is compared between the Dipsadina and the Leptodeirina, neither those of females (means 403.6 and 517.6 mm, respectively) nor those of males (means 372.7 and 457.8 mm, respectively) were significantly different ($t = -1.50$, $P = 0.156$; $t = -1.04$, $P = 0.318$; respectively). Males were significantly smaller than females in all species (*L. annulata*, $t = 8.09$, $df = 179$, $P < 0.001$; *S. mikanii*, $t = 9.05$, $df = 147$, $P < 0.001$; *S. neuwiedi*, $t = 9.25$, $df = 125$, $P < 0.001$; *S. ventrimaculatus*, $t = 9.48$, $df = 110$, $P < 0.001$; see original papers for results for other species), except for *I. cenchoa* ($t = 0.25$, $df = 34$, $P = 0.801$).

Sexual size dimorphism ranged from 0.009 in *I. cenchoa* to 0.27 in *S. ventrimaculatus*. The value of SSD was lower than 0.1 in all species of *Dipsas*, in *I. cenchoa* and in a population of *L. annulata* from the Brazilian Amazon (Table 1). Sexual size dimorphism was not significantly different between Dipsadini and Leptodeirini (means 0.159 and 0.156; $t = 0.06$, $P = 0.955$). Sexual size dimorphism decreased with increasing snake size; snake size explained about one third of the variation in SSD in males ($r^2 = 0.35$, $P = 0.034$) and one fifth in females ($r^2 = 0.18$, $P < 0.001$). Females of most species attained sexual maturity at 75–85% of mean adult SVL and males at 70–80% (Table 1), and this intersexual difference was not significant ($t = 1.42$, $P = 0.168$). When the proportion of mean adult SVL at which sexes attained sexual maturity is compared between the Dipsadini and the Leptodeirini, neither females (means 79.3 and 77.3%, respectively) nor males (means 77.0 and 73.1%) were significantly different ($t = 0.49$, $P = 0.640$, $t = -0.70$, $P = 0.500$; respectively).

TABLE 1.—Mean snout–vent length (SVL) in adult females and males, sexual maturity and sexual size dimorphism index (SSD) in dipsadine snakes. Means are followed by standard deviation, range in parenthesis and sample size (*n*). All measurements are in mm.

Species	SVL adult ♀♀ (mean ± SD)	SVL adult ♂♂ (mean ± SD)	Proportional SVL at maturity	SSD	Range	Reference
Dipsadini						
<i>Atractus reticulatus</i>	300.1 ± 30.0 (242–370, <i>n</i> = 43)	249.9 ± 24.4 (198–295, <i>n</i> = 58)	♀♀: 80.6% ♂♂: 79.2%	0.20	Southern Brazil (29° 39' N, 30° 04' S, 50° 31' E, 51° 13' W)	Balestrin and Di Bernardo, 2005
<i>Dipsas albifrons</i>	470.5 ± 45.5 (400–590, <i>n</i> = 63)	435.9 ± 57.7 (325–540, <i>n</i> = 50)	♀♀: 85.0% ♂♂: 74.6%	0.08	Southern Brazil (26° 18' N, 22° 56' S, 48° 50' E, 49° 14' W)	Hartmann et al., 2002
<i>Dipsas catesbyi</i>	494.19 ± 63.91 (331–640, <i>n</i> = 54)	463.69 ± 53.78 (341–575, <i>n</i> = 65)	♀♀: 67.0% ♂♂: 73.5%	0.06	Northeastern Brazil (14° 00' N, 18° 00' S, 39° 00' E, 41° 00' W)	Alves et al., 2005
<i>Dipsas catesbyi</i>	402.1 ± 48.6 (338–542, <i>n</i> = 51)	—	♀♀: 84.0%	—	Amazonia and tropical Forest region	Zug et al., 1979
<i>Dipsas neivai</i>	584.41 ± 86.67 (432–820, <i>n</i> = 91)	521.79 ± 81.29 (298–702, <i>n</i> = 99)	♀♀: 73.9% ♂♂: 57.1%	0.05	Northeastern Brazil (14° 00' N, 18° 00' S, 39° 00' E, 41° 00' W)	Alves et al., 2005
<i>Geophis brachycephalus</i>	333.6 ± 26.4 (295–365, <i>n</i> = 12)	—	♂♂: 88.4%	—	Costa Rica (10° 16' N, 9° 33' S, 83° 30'E, 84° 48' W)	Sasa, 1993
<i>Ninia maculata</i>	226.0 ± 22.0 (175–275, <i>n</i> = 25)	201.0 ± 15.0 (179–228, <i>n</i> = 16)	♀♀: 77% ♂♂: 89%	0.12	Costa Rica (11° 00' N, 9° 00' S, 83° 00' E, 85° 30' W)	Goldberg, 2004b
<i>Sibynomorphus mikamii</i>	437.6 ± 61.3 (339–580, <i>n</i> = 92)	352.8 ± 37.7 (280–510, <i>n</i> = 52)	♀♀: 77.5% ♂♂: 79.4%	0.24	Southeastern Brazil (20° 16' N, 23° 58' S, 45° 42' E, 51° 20' W)	This work
<i>Sibynomorphus newiiedi</i>	526.4 ± 58.9 (415–660, <i>n</i> = 72)	422.5 ± 66.8 (254–541, <i>n</i> = 54)	♀♀: 78.8% ♂♂: 60.1%	0.25	Southern and Southeastern Brazil (20° 21' N, 25° 00' S, 40° 39' E, 49° 42' W)	This work
<i>Sibynomorphus ventrimaculatus</i>	422.4 ± 48.4 (345–577, <i>n</i> = 71)	333.9 ± 45.0 (240–413, <i>n</i> = 40)	♀♀: 81.7% ♂♂: 71.9%	0.27	Southeastern Brazil (27° 28' N, 30° 52' S, 51° 01' E, 54° 28' W)	This work
<i>Sibon sannitola</i>	240.6 ± 22.6 (201–292, <i>n</i> = 42)	?	♀♀: 83.5%	—	Yucatan Peninsula, Mexico (22° 00' N, 20° 00' S, 87° 00' E, 90° 00' W)	Kofron, 1983
Leptodeirini						
<i>Hypsiglena torquata</i>	360.0 ± 45.4 (310–503, <i>n</i> = 42)	300.0 ± 27.2 (237–368, <i>n</i> = 67)	♀♀: 86% ♂♂: 79%	0.20	Arizona, EUA (37° 00' N, 31° 30' S, 109° 00' E, 114° 30' W)	Goldberg, 2001
<i>Imantodes cenchoa</i>	715.9 ± 67.7 (621–901, <i>n</i> = 33)	—	♀♀: 86.7%	—	Equatorial and Tropical Forest region (15° 53' N, 0° 03' S, 73° 15' E, 92° 48' W)	Zug et al., 1979
<i>Imantodes cenchoa</i>	771.2 ± 67.9 (640–880, <i>n</i> = 18)	764.2 ± 95.0 (601–972, <i>n</i> = 18)	♀♀: 83.0% ♂♂: 78.6%	0.009	S, SE Brazil (21° 11' N, 26° 55' S, 45° 24' E, 52° 06' W)	This work
<i>Leptodeira annulata</i>	595.2 ± 89.1 (454–841, <i>n</i> = 105)	502.2 ± 60.2 (367–644, <i>n</i> = 80)	♀♀: 76.3% ♂♂: 73%	0.19	Central and Southeastern Brazil (11° 47' N, 23° 35' S, 39° 43' E, 56° 05' W)	This work
<i>Leptodeira annulata</i>	545.6 ± 11.5 (497–609, <i>n</i> = 12)	498.6 ± 12.6 (431–584, <i>n</i> = 18)	♀♀: 91.1% ♂♂: 86.4%	0.09	Amazon region (0° 00' N, 10° 00' S, 50° 00' E, 78° 00' W)	Vitt, 1996
<i>Leptodeira maculata</i>	470.1 ± 82.8 (317–630, <i>n</i> = 19)	384.4 ± 52.7 (280–444, <i>n</i> = 27)	♀♀: 67% ♂♂: 73%	0.22	SW Mexico (26° 00' N, 16° 00' S, 98° 00' E, 109° 00' W)	Goldberg, 2004a
<i>Leptodeira punctata</i>	391.5 ± 59.6 (292–523, <i>n</i> = 26)	338.2 ± 41.1 (276–451, <i>n</i> = 41)	♀♀: 75% ♂♂: 82%	0.16	W Mexico (26° 00' N, 21° 00' S, 103° 00' E, 109° 00' W)	Goldberg, 2004a

TABLE 2.—Tail length (as % of SVL) in males and females, mean clutch size and habitat of dipsadine snakes.

Species	Tail length (as % of SVL)	Mean clutch size (\pm SD)	Habitat	Reference
Dipsadini				
<i>Atractus reticulatus</i>	♀♀: 11.6%, ♂♂: 15.7% ¹	2.7 \pm 0.8 (1–3, n = 6)	Fossorial	Balestrin and Di-Bernardo, 2005
<i>Dipsas albifrons</i>	—	3.9 \pm 1.8 (1–8, n = 33)	Arboreal	Hartmann et al., 2002
<i>Dipsas catesbyi</i>	♀♀: 36.5%, ♂♂: 39.0% ²	2.0 \pm 0.82 (1–3, n = 10)	Arboreal	Zug et al., 1979
<i>Dipsas catesbyi</i>	—	3.63 \pm 1.66 (1–6, n = 13)	Arboreal	Alves et al., 2005
<i>Dipsas neivai</i>	—	3.91 \pm 1.95 (1–8, n = 22)	Arboreal	Alves et al., 2005
<i>Geophis brachycephalus</i>	♀♀: 17.3%, ♂♂: —	4.2 \pm 1.17 (3–6, n = 6)	Terrestrial-fossorial	Sasa, 1993
<i>Ninia maculata</i>	—	2.9 \pm 1.1 (1–5, n = 14)	Semi-fossorial	Goldberg, 2004b
<i>Sibynomorphus mikanii</i>	♀♀: 20.4%, ♂♂: 24.8% ¹	5.7 \pm 1.7 (3–10, n = 29)	Terrestrial	This work
<i>Sibynomorphus newwiedi</i>	♀♀: 26.9%, ♂♂: 31.1% ¹	6.4 \pm 2.4 (4–12, n = 14)	Semi-arboreal	This work
<i>Sibynomorphus ventrimaculatus</i>	♀♀: 22.7%, ♂♂: 26.8% ¹	4.8 \pm 1.0 (3–7, n = 33)	Terrestrial	This work
<i>Sibon sanniola</i>	—	3.1 \pm 0.70 (2–5, n = 28)	?	Kofron, 1983
Leptodeirini				
<i>Hypsiglena torquata</i>	♀♀: 15.0%, ♂♂: 20.0% ²	3.2 \pm 1.5 (1–6, n = 9)	Terrestrial	Goldberg, 2001; Runquist, 2002
<i>Imantodes cenchoa</i>	—	2.0 \pm 0.71 (1–3, n = 5)	Arboreal	Zug et al., 1979
<i>Imantodes cenchoa</i>	♀♀: 45.0%, ♂♂: 47.0% ¹	3.3 \pm 1.70 (1–7, n = 13)	Arboreal	This work
<i>Leptodeira annulata</i>	♂♂: 30.0%, ♂♂: 39.0% ¹	7.3 \pm 2.53 (3–13, n = 23)	Arboreal	This work, but see also Duellman, 1958
<i>Leptodeira maculata</i>	—	8.7 \pm 1.5 (7–11, n = 7)	Arboreal	Goldberg, 2004a
<i>Leptodeira punctata</i>	—	7.8 \pm 1.7 (6–11, n = 9)	Arboreal	Goldberg, 2004a

¹ Statistically significant differences.² No statistical tests performed, but differences are apparent.

Relative tail length of male and female snakes did not differ significantly between Dipsadini and Leptodeirini (means 22.6% and 30.0% of body length for females, and 27.5% and 35.3% for males; $t = -0.92$, $P = 0.388$, and $t = -0.966$, $P = 0.371$, respectively; Table 2). When all species of Dipsadinae are considered together, tails were significantly longer in arboreal and semi-arboreal species than in fossorial and terrestrial species, both for females and males (medians 34.5% and 17.4% of body length for females, and 39.0% and 21.8% for males; $t = -4.03$, $P = 0.005$, and $t = -4.18$, $P = 0.004$, respectively; Table 2). Tails were also significantly longer in males than in females of *L. annulata*, *I. cenchoa*, *S. mikanii*, *S. newwiedi*, and *S. ventrimaculatus* (ANCOVA, all $F > 2.0$, all $P < 0.025$) and in other dipsadines (Table 2, for statistical analyses, see data in original papers).

Among the Leptodeirina, in *Leptodeira annulata*, follicles in secondary vitellogenesis were found from late February and March to early December and oviductal eggs from May

to August (Fig. 1A). In *I. cenchoa*, vitellogenic follicles were found in September and eggs were recorded from November to January (Fig. 1B). Among the Dipsadina, seasonal vitellogenesis was recorded for *S. mikanii* and *S. newwiedi* mostly from July to December and eggs were recorded from late August to February (Fig. 1C,D). In *S. ventrimaculatus*, vitellogenesis was shorter, occurring mostly from October to December, and eggs were recorded from October to February (Fig. 1E). Thus, a seasonal reproductive cycle, with vitellogenesis restricted to the warmer and rainier months of the year, was observed in *Sibynomorphus* spp. in our analyses, and also in *Atractus reticulatus*, *Dipsas albifrons* (from coastal Atlantic Forest in southern Brazil), *H. torquata*, *L. maculata*, *L. punctata* and *Sibon sanniola* in literature data (see Fig. 2). In *Dipsas catesbyi* and *D. neivai* from the coastal Atlantic Forest in northeastern Brazil and in *N. maculata* from Costa Rica cycles were continuous (Fig. 2). *Leptodeira annulata*, *Geophis brachycephalus* and prob-

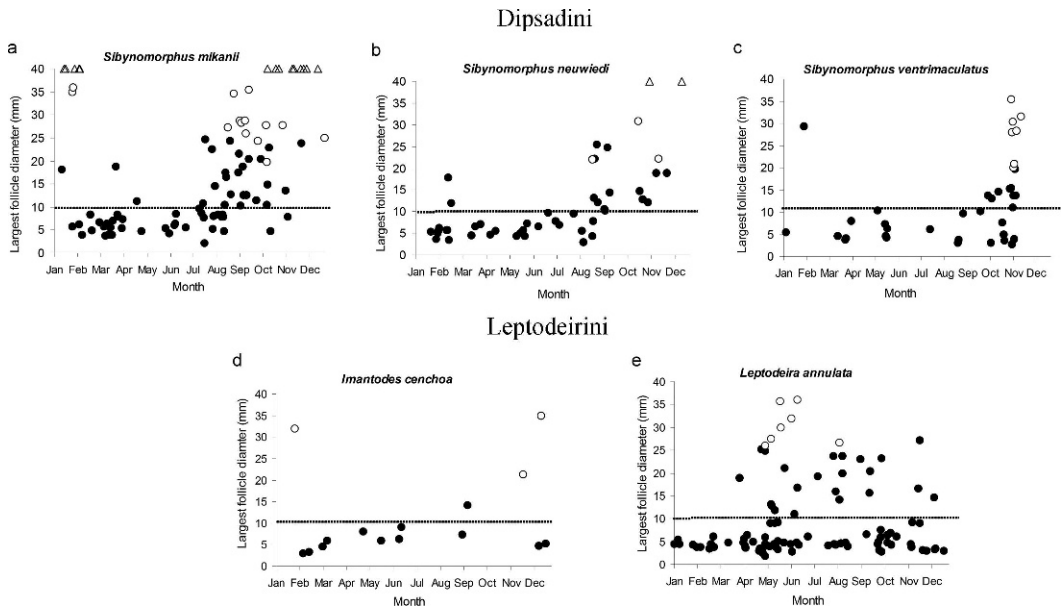


FIG. 1.—Seasonal variation in the diameter of the largest ovarian follicle (full circles) and oviductal eggs (empty circles) in *Leptodeira annulata*, *Imantodes cenchoa* and *Sibynomorphus* spp. from Brazil. Triangles represent egg-laying in snakes received gravid at IB. Follicles above dotted line were in secondary vitellogenesis.

ably *I. cenchoa* had extended cycles (about eight months; Fig. 2). Duration of vitellogenesis, occurrence of oviductal eggs or the duration of complete reproductive period (months in which vitellogenesis and/or presence of oviductal eggs occurred) did not differ between Dipsadinae (means 8.4, 7.1 and 15.5 mo, respectively) and Leptodeirinae (5.8, 5.0 and 10.8 mo, respectively; $t = 1.82$, $P = 0.093$ for vitellogenesis duration, $t = 1.37$, $P = 0.194$ for duration of eggs in oviducts, and $t = 1.63$, $P = 0.127$ for the complete cycle).

Clutch size is relatively small in the dipsadines (Table 2) and is not significantly different between the Dipsadini and the Leptodeirini (means 5.3 and 3.9 eggs, respectively; $t = 1.47$, $P = 0.160$). Clutch size was not different between terrestrial/fossorial snakes and arboreal/semiarboreal ones ($t = 0.45$, $P = 0.656$). Snout-vent length was significantly related to clutch size in *S. mikanii* ($r^2 = 0.39$, $P = 0.037$; Fig. 3A), *S. neuwiedi* ($r^2 = 0.63$, $P = 0.015$; Fig. 3B), *S. ventrimaculatus* ($r^2 = 0.59$, $P < 0.001$; Fig. 3C) and *I. cenchoa* ($r^2 = 0.68$, $P = 0.010$; Fig. 3E), but not in *L. annulata* (data log-transformed, $r^2 = 0.34$, $P = 0.101$; Fig. 3D). When all species are considered together, clutch size seems not

to be a function of female SVL (Fig. 4). When *I. cenchoa* populations and *D. neivai* (all with low relative fecundity) are removed from the analysis the relationship between SVL and clutch size become positive and significant ($r^2 = 0.33$, $P = 0.025$, Fig. 4).

Testis length and deferent duct diameter did not differ significantly among seasons in *L. annulata* and *Sibynomorphus* spp. (Table 3), which indicates continuous sperm production and absence of sperm storage by males. Data on *I. cenchoa* were not sufficient to compare either right testis length or deferent duct diameter among seasons.

Sperm production occurred throughout the year in the Dipsadini and in spring-summer in the only species of Leptodeirini studied. Sperm was found in the deferent duct throughout the year in all Dipsadini except *N. maculata* (in which it occurred in spring-autumn), and in spring-summer in both species of Leptodeirini studied (Table 4).

DISCUSSION

In all species of the subfamily Dipsadinae for which data on size at sexual maturity were available, males and females attained sexual

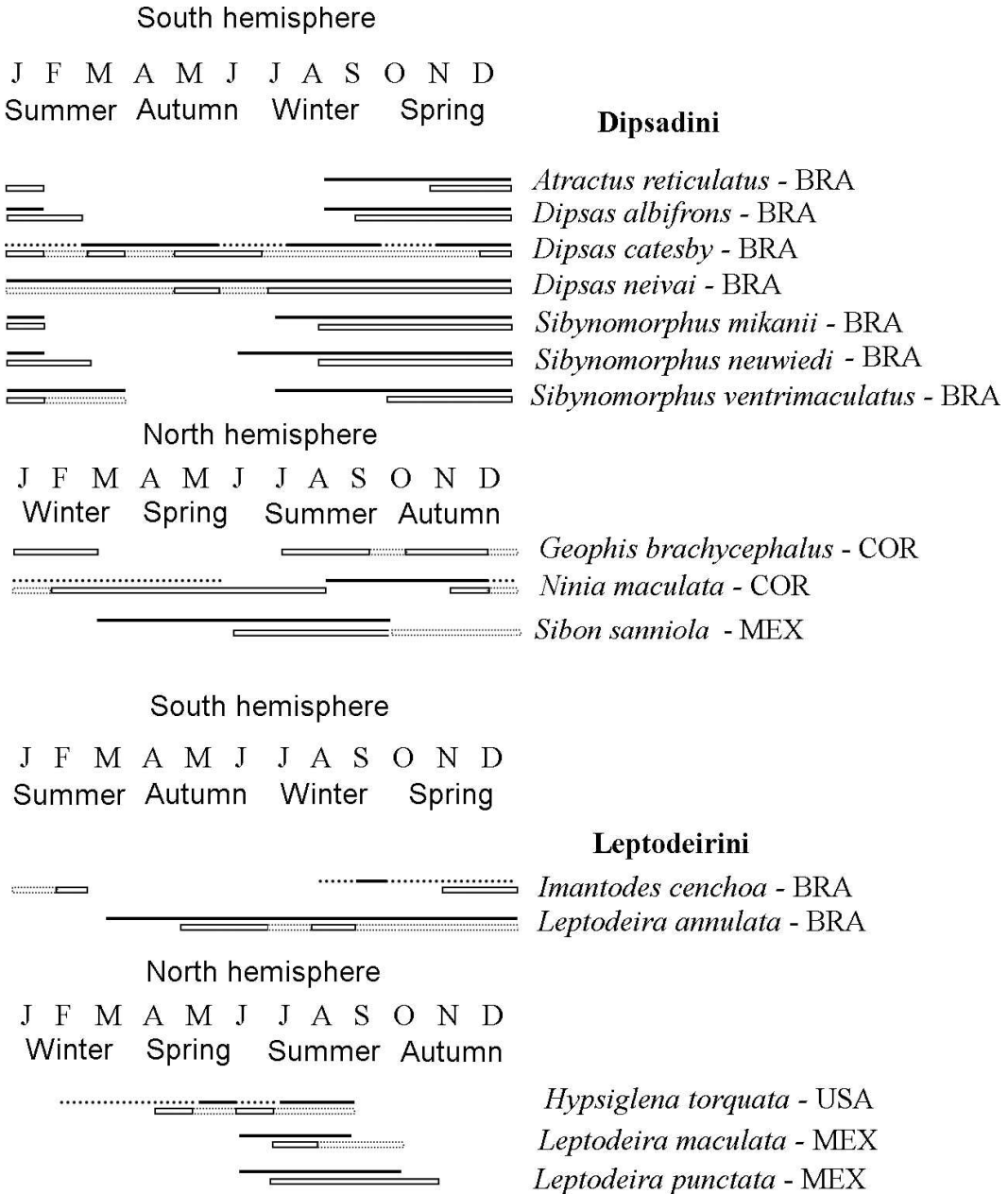


FIG. 2.—Reproductive cycles in Dipsadinae snakes. Lines: Vitellogenesis time. Boxes: Oviductal eggs or egg-laying. BRA = Brazil, USA = United States of America, MEX = Mexico, COR = Costa Rica. Full lines and boxes = observed, dotted lines and boxes = inferred.

maturity at similar relative body sizes. The degree of sexual size dimorphism (SSD) decreased with increasing body size in the dipsadines. This pattern is opposite to that found in the tribe Xenodontini (Pizzatto et al.,

2008), a clade within the Xenodontinae (Vidal et al., 2000; Zaher, 1999). Males larger than females or absence of sexual dimorphism usually occurs in species in which males exhibit combat behavior during the mating

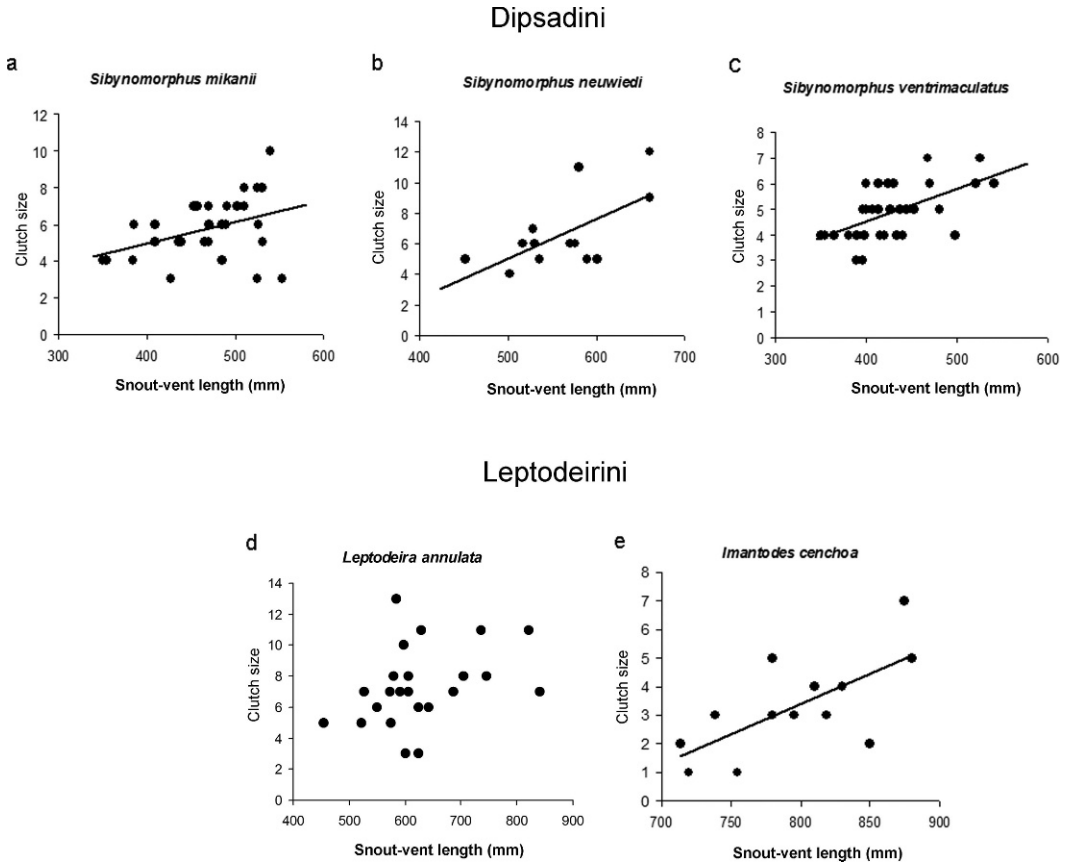


FIG. 3.—Relationship between clutch size and female snout–vent length in *Leptodeira annulata*, *Imantodes cenchoa* and *Sibynomorphus* spp. from Brazil.

season (Shine, 1994). The lowest SSD occurs in *Imantodes cenchoa* and this is the only species in which the largest body size is attained by males and not females. Male–male fighting behavior and mating was recorded in this species in October (spring) in the Brazilian Amazon (see Santos-Costa and Prudente, 2005) and, an aggregation of three males and one female in a Peruvian rainforest in May (spring) (Doan and Arriaga, 1999) also suggest combat. Male–male ritual combat has not been reported in any other dipsadine, xenodontines, nor in the *Heterodon-Farancia* group, the basal lineage of both clades (see Vidal et al., 2000). Thus, either ritual combat remains unnoticed due to elusive habits of the snakes and suboptimal research efforts or it is an autapomorphy of *Imantodes cenchoa* within this large clade of colubrids.

Sexual dimorphism also occurs in tail length in all species in both tribes (Dipsadini: *A. reticulatus*, Balestrin and Di-Bernardo, 2005; *D. albifrons*, Hartmann et al., 2002; *D. catesbyi*, Zug et al., 1979; *Sibynomorphus* spp., this study; Leptodeirini: *H. torquata*, Runquist, 2002; *I. cenchoa*, Zug et al., 1979, this study; *L. annulata*, Vitt, 1996, this study). A longer tail is expected in males due to the presence of the hemipenes and their retractor muscles (King, 1989). However, in many arboreal snakes this dimorphism is absent (Fowler and Salomão, 1994; Pizzatto and Marques, 2007) probably because a long tail may be advantageous for arboreal life (Lillywhite and Henderson, 1993; Martins et al., 2001). Tail dimorphism occurs in both terrestrial and arboreal dipsadines, but tail is proportionally much longer in arboreal and

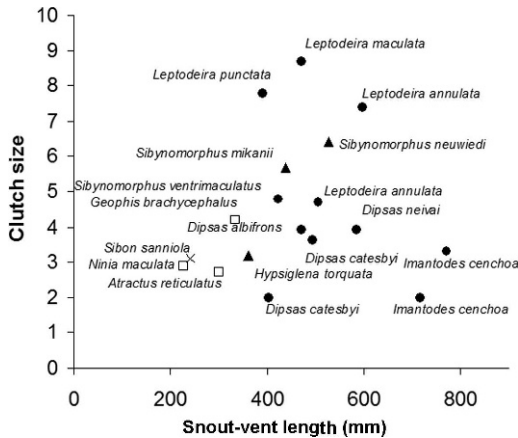


FIG. 4.—Relationship between mean clutch size and mean female snout-vent length in Dipsadinae snakes. Circles = arboreal/semi-arboreal species, triangles = terrestrial, squares = fossorial. Data from: Alves et al., 2005; Balestin and Di-Bernardo, 2005; Goldberg, 2001, 2004a,b; Hartmann et al., 2002; Kofron, 1983; Sasa, 1993; Vitt, 1996; Zug et al., 1979; this work.

semi-arboreal species of dipsadines than in terrestrial and fossorial species, as observed in other studies (e.g., Hartmann and Marques, 2005; Martins et al., 2001; Pizzatto and Marques, 2007; Pizzatto et al., 2007b).

Reproductive cycles vary among snake species and also can differ between females and males (Seigel and Ford, 1987). Dipsadines usually show seasonal reproductive cycles in females, but duration is variable among species. Some species occurring in areas with a seasonal climate exhibit cycles restricted to the warm and rainier seasons, but *L. annulata* seems to have extended follicular cycles even in areas where climate is seasonal (e.g., southeastern and central Brazil between 9° 34' N and 23° 35' S). In contrast, more

seasonal climates seem to restrict the female cycles in some species, such as *D. albifrons* and *S. ventrimaculatus* from southern Brazil. These species show more restricted timing of vitellogenesis than their congeners from lower latitudes.

Testicular cycles are not available for most species of dipsadines; however, our data indicate that it is variable within this subfamily. *Hypsiglena torquata* from temperate areas has a seasonal sperm production, occurring in the warmest periods of the year. Despite the records of seasonal sperm production in many tropical snakes (Fitch, 1982; Shine, 1977), most tropical species of dipsadines show continuous testicular activity. Cycles also differed among sexes in the same species. For example, while females of *Sibynomorphus* spp. have seasonal cycles, males produce sperm continuously, indicating that sperm production is less costly than egg production (Trivers, 1972), at least in tropical snakes.

In general, dipsadine snakes produce small clutches, probably because of the small size of these snakes. Also, the very slender body in arboreal species such as *L. annulata* and *I. cenchoa* can strongly reduce body cavity space to carry eggs, resulting in smaller clutches (see Pizzatto et al., 2007b). Thus, although female body size is important in determining clutch size for some species, other factors may influence this trait (e.g., habitat use, feeding habits, phylogeny).

Most reproductive characters we analyzed for the dipsadines seem to be conservative within the tribe. The tribes Dipsadini and Leptodeirini did not differ in the amount of SSD, the proportion of mean SVL at which sexes attained sexual maturity, relative tail

TABLE 3.—Statistical results of variation in right testis length and diameter of deferent duct among seasons in four dipsadine snakes from Brazil.

Species	Right testis length ANCOVA	Deferent duct diameter ANCOVA
Dipsadini		
<i>Sibynomorphus mikanii</i>	Slopes: $F_{3,32} = 0.11, P = 0.954$ Intercept: $F_{3,33} = 2.22, P = 0.102$	Insufficient data
<i>Sibynomorphus neuwiedi</i>	Slopes: $F_{3,25} = 1.01, P = 0.403$ Intercept: $F_{3,26} = 0.96, P = 0.423$	Slopes: $F_{3,22} = 0.20, P = 0.827$ Intercept: $F_{3,23} = 2.58, P = 0.076$
<i>Sibynomorphus ventrimaculatus</i>	Slopes: $F_{3,22} = 0.95, P = 0.434$ Intercept: $F_{3,23} = 1.07, P = 0.379$	Slopes: $F_{3,21} = 1.48, P = 0.248$ Intercept: $F_{3,22} = 0.08, P = 0.967$
Leptodeirini		
<i>Leptodeira annulata</i>	Slopes: $F_{3,71} = 0.74, P = 0.530$ Intercept: $F_{3,72} = 0.80, P = 0.495$	Slopes: $F_{3,69} = 1.86, P = 0.144$ Intercept: $F_{3,70} = 0.49, P = 0.688$

TABLE 4.—Male reproductive cycles in dipsadine snakes.

Species	Sperm production	Sperm in deferent duct	Location of collection	Reference
Dipsadini				
<i>Dipsas neivai</i>	Throughout the year	Throughout the year	Northeastern Brazil (14° 00' N, 18° 00' S, 39° 00' E, 41° 00' W)	Alves et al., 2005
<i>Dipsas catesbyi</i>	Throughout the year	Throughout the year	Northeastern Brazil (14° 00' N, 18° 00' S, 39° 00' E, 41° 00' W)	Alves et al., 2005
<i>Hypsiglena torquata</i>	Spring–summer	Spring–Summer	Arizona – USA (37° 00' N, 31° 30' S, 109° 00' E, 114° 30' W), Idaho – USA (49° 00' N, 42° 00' S, 112° 30' E, 116° 30' W)	Diller and Wallace, 1986; Goldberg, 2001,
<i>Ninia maculata</i>	Throughout the year	Spring–Autumn	Costa Rica (11° 00' N, 9° 00' S, 83° 00' E, 85° 30' W)	Goldberg, 2004b
<i>Sibynomorphus mikanni</i>	Throughout the year	Throughout the year	Southeastern Brazil (20° 16' N, 23° 58' S, 45° 42' E, 51° 20' W)	This work
<i>Sibynomorphus neucaedii</i>	Throughout the year	Throughout the year	Southeastern Brazil (20° 21' N, 25° 00' S, 40° 39' E, 49° 42' W)	This work
<i>Sibynomorphus ventrimaculatus</i>	Throughout the year	Throughout the year	Southern Brazil (27° 28' N, 30° 52' S, 51° 01' E, 54° 28' W)	This work
Leptodeirini				
<i>Leptodeira annulata</i>	Throughout the year	Throughout the year	Southeastern and Central Brazil (11° 47' N, 23° 35' S, 39° 43' E, 56° 05' W)	This work
<i>Leptodeira maculata</i>	Spring–Autumn	Spring–Autumn	SW Mexico (26° 00' N, 16° 00' S, 98° 00' E, 109° 00' W)	Goldberg, 2004a
<i>Leptodeira punctata</i>	—	Spring–Summer	W México (26° 00' N, 21° 00' S, 103° 00' E, 109° 00' W)	Goldberg, 2004a

length of both sexes, duration of vitellogenesis, egg-carrying period, duration of the complete reproductive cycle, and clutch size. However, tribes differ in the timing of reproductive cycles in females and, apparently, in the duration of sperm production in males. Thus, reproduction as a whole seems to have changed relatively little during the history of the dipsadines, as already observed in other monophyletic lineages of Neotropical snakes, e.g., the genera *Bothrops* (Almeida-Santos and Salomão, 2002) and *Micrurus* (Almeida-Santos et al., 2006).

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