

# Diet and reproduction of the Western Indigo Snake *Drymarchon corais* (Serpentes: Colubridae) from the Brazilian Amazon

Ana Lúcia da Costa Prudente<sup>1,2,\*</sup>, Alessandro Costa Menks<sup>1,2</sup>, Fernanda Magalhães da Silva<sup>1,2</sup>  
and Gleomar Fabiano Maschio<sup>3</sup>

**Abstract.** *Drymarchon corais* is a diurnal species with semi-arboreal habits, which forages on both ground and vegetation in forested and open areas. The species occurs from Mexico to northern Argentina and Paraguay and, in Brazil, it was recorded in the northern, northeastern, and central regions. Information about diet and reproduction of this species is scarce, including only short notes about copulation of captive specimens. The few studies suggest that this species has a generalist diet, and can prey on amphibians, lizards, snakes, birds, eggs, and small mammals. The reproduction and diet of *D. corais* was studied in Amazonia, Brazil, based on 50 males and 26 females from museum species. The results show that anurans were the most frequent food items, followed by lizards and snakes. This is the first record of reptile eggs being preyed upon by *D. corais*. There was no relationship between body size of *D. corais* and their prey, except in the case of snakes and lizards ingested. The predominant direction of prey ingestion was antero-posterior. We have no conclusive results related to the ontogenetic diet of *D. corais*, but there was a tendency for the juveniles to feed on elongated items such as lizards and snakes. The low percentage of items in the mature female stomach of *D. corais* may be an indication of a tendency to decrease foraging during the breeding season. There is no sexual dimorphism in *D. corais* related to snout-vent length (SVL) and tail length, although dimorphism has been observed in other species of the genus. No significant relationship between the number of eggs and female SVL were observed, although there was a positive relationship between the number of secondary follicles and female SVL. Females with vitellogenic follicles observed throughout the year, with a tendency to a greater number of vitellogenic follicles and eggs in the dry season, suggest a sazonal reproductive cycle in *D. corais*.

**Keywords:** Natural history, Diet, Reproduction, Neotropics, Amazon, Serpentes.

## Introduction

Studies about diet and reproduction of snakes are becoming more frequent in the Neotropical region, especially over the last two decades, and have shown that feeding behavior and reproduction strategies have wide variation in some species (e.g., Hartmann, Hartmann and Martins, 2009; Orofino, Pizzatto and Marques, 2010; Pires et al., 2012).

Among Neotropical snakes, species of *Drymarchon* (Schlegel, 1837) are considered terrestrial and generalist, preying upon anurans, lizards, snakes, bird eggs,

and mammals (Duellman, 1990; Bernarde and Abe, 2006; Stevenson et al., 2009). Information regarding reproductive patterns of the genus is available only for captive specimens and restricted to some species and some regions, especially in North America (e.g., Gillingham and Chambers, 1980; Ernst and Barbour, 1989).

*Drymarchon* contains five species distributed in southeastern North America, Central America, and South America (Uetz and Hallermann, 2012): *D. caudomaculatus* Wüster, Yrausquin and Mijares-Urrutia, 2001 from Venezuela; *D. corais* (Boie, 1827) from southeastern North America to South America; *D. couperi* (Holbrook, 1842) from North American; *D. margaritae* Roze, 1958 from Venezuela; and *D. melanurus* (Duméril, Bibron and Duméril, 1854) from the west of the Andes and northern Venezuela (Peters and Orejas-Miranda, 1970; Stevenson et al., 2009).

*Drymarchon corais* has the widest distribution among species of the genus, with records from Mexico, Guatemala, Honduras, Belize, El Salvador, Nicaragua, Panama, Trinidad, Tobago, Guyana, Colombia, Venezuela, Ecuador, Peru, Argentina, Brazil, and

<sup>1</sup> Departamento de Zoologia, Museu Paraense Emílio Goeldi, 66077-530, Belém, Pará, Brazil.

<sup>2</sup> Programa de Pós-Graduação em Zoologia, Museu Paraense Emílio Goeldi, 66077-530, Belém, Pará, Brazil.

<sup>3</sup> Instituto de Ciências Biológicas, Universidade Federal do Pará, 66075-110, Belém, Pará, Brazil.

\* Corresponding Author. E-mail: prudente@museu-goeldi.br

Paraguay. In Brazil, it is recorded in northern, northeastern, and central regions in natural areas such as the Caatinga, Cerrado, and Amazonia (Frota *et al.*, 2005; Campos *et al.*, 2010). This species has both terrestrial and arboreal habits (Bernarde and Abe, 2006), foraging actively during the day in open and forested environments. The few studies about this species suggest that it has a generalist diet, which includes frogs, lizards, amphisbaenians, snakes, birds, eggs, and small mammals, such as rodents and marsupials (Bernarde and Abe, 2006; Campos *et al.*, 2010).

Herein we provide supplementary data on feeding (diet composition and frequency of food items) and new records of reproductive biology (sexual dimorphism, reproductive maturity, reproductive cycle, recruitment, and fecundity) of *Drymarchon corais* from Amazonia, Brazil.

## Material and Methods

We analyzed 76 specimens of *Drymarchon corais* (50 males and 26 females), collected between 1971 and 2010 in several localities in the states of Acre, Amazonas, Maranhão, Pará, Rondônia, and Roraima. These specimens are housed at the Herpetological Collection of the Museu Paraense Emílio Goeldi (MPEG), Belém, Pará, Brazil (Appendix 1).

Analysis of stomach contents was performed from direct observation of items consumed, found in the digestive tract of each specimen. The direction of prey ingestion was determined by the orientation of the prey head in relation to the body of the snake. Items were classified either as antero-posterior (AP) for those eaten head first, and postero-anterior (PA) for those ingested tail first. Quantitative analysis of the diet considered the number of prey inside the stomach and intestines, and qualitative analysis identified these prey to the lowest possible taxonomic level.

For each specimen, data about food items, snout-vent length (SVL to the nearest 1 mm), tail length (TL), total length (ToL), number of vitellogenic follicles larger than 10 mm (in secondary vitellogenesis), number of eggs, and the length of the largest follicle were collected. The total length of each food item was measured using calipers for small items (e.g., frogs and eggs), or a string for larger prey (e.g., lizards, snakes, amphisbaenians). Estimates of mean body size (SVL and TL) and mass of partially digested prey were obtained by comparing them with three similar-sized specimens from the same species housed in the collection of MPEG (Ruffato, Di-Bernardo and Maschio, 2003). Morphometric

measurements were log-transformed and tested for normality before analysis (Zar, 2010). A Spearman's rank correlation was used to test for a relationship between snake size and the size of prey groups.

The gonads of both males and females were analyzed macroscopically through a longitudinal incision in the abdominal region. The shape of the *ductus deferens* of males and the oviduct of females were assessed to infer the number and length of ovarian follicles (Shine, 1977a). All males with a coiled ductus deferens, and all females with either secondary follicles larger than 10 mm, or eggs in the oviducts or convoluted were considered mature specimens (Pizzatto, Almeida-Santos and Marques, 2007). Fecundity was inferred from the ratio between the number of follicles in secondary vitellogenesis and the number of oviductal eggs with snout-vent length of the female (Thompson and Speake, 2002; Santos and Llorente, 2004).

The reproductive cycle was analyzed using circular statistics (Zar, 2010), with ORIANA 4.02 (Kovach, 2009). Months were converted into angles (intervals of 30°) and number of vitellogenic follicles and eggs in each month were taken as frequencies of each angle (month) observed (see Prado *et al.*, 2005; Both *et al.*, 2008). Through this method we estimated: a) the mean vector ( $\mu$ ); b) the length of mean vector ( $r$ ); c) the circular standard deviation (SD) related to  $\mu$ ; d) the Rayleigh's Uniformity Test.

The Rayleigh's Uniformity Test (Zar, 2010) calculates the probability of the null hypothesis that the data are distributed in a uniform manner ( $P > 0.05$ ). A significant result of the Rayleigh's Uniformity Test ( $P < 0.05$ ) indicates that the data are not uniformly distributed and there is a significant mean angle or mean direction (Kovach, 2009).

A multiple linear regression was used to test for a relationship between female SVL (response variable), and the number of eggs and vitellogenic follicles (predictor variables). A Student t-test was performed to test for the presence of sexual dimorphism in relation to SVL. All data had normality and homogeneity of variance. In all tests of sexual dimorphism, only data from sexually mature females and males were used. Analyses were conducted using the software Statistica 7.0 (Statsoft, 2004).

## Results

A total of 25 specimens of *Drymarchon corais* had identifiable stomachal and intestinal contents (33% of 76 specimens; Appendix 2). The most frequent

food items were anuran amphibians (N = 9; 28.12%), followed by lizards (N = 5; 15.63%), snakes (N = 5; 15.63%), bird eggs (N= 5; 15.63%), and reptile eggs (N= 3; 9.38%; Table 1). A bird (*Gallus* sp.), amphisbaenids (*Leposternon polystegum*), and mammals (*Calomys expulsus*) were also recorded (Table 1). The following species were recorded for the first time in the diet of *D. corais*: *Bothrops taeniatus*, *Erythrolamprus reginae*, *Pseudoboa nigra*, *Tropidurus hispidus*, *Leposternon polystegum*, and *Calomys expulsus*.

**Table 1.** Frequency of items in the diet of 25 specimens of *D. corais*. SMPPr= Sex Maturity of Predator; SVLPr = Snout Vent Length (in mm) of *D. corais*; % = percentage of each group in relation to all items, DI = Direction of ingestion of prey; AP = Antero-posterior; PA = Postero-anterior; ToL = Total Length (in mm) of prey, Prop. ToL/SVL = ratio between total length of prey and *D. corais* SVL.

<i>Drymarchon corais</i>				Prey				
Voucher MPEG	Sex	SM	SVL	Item	%	DI	ToL	Prop. ToL/SVL
				<b>Amphibia</b>	<b>27</b>			
				<u>Anura</u>				
				BUFONIDAE				
14508	Female	Mature	1557	<i>Rhinella marina</i>		AP	45	0.028
14506	Female	Mature	1914	<i>Rhinella marina</i>		AP	98	0.051
7663	Male	Immature	1164	<i>Rhinella marina</i>		AP	-	-
15533	Male	Mature	1663	<i>Rhinella marina</i>		AP	83	0.05
15526	Male	Mature	1900	<i>Rhinella marina</i>		AP	60	0.031
15529	Male	Mature	1925	<i>Rhinella marina</i>		AP	92	0.047
				LEPTODACTYLIDAE				
15600	Female	Mature	1762	<i>Leptodactylus fuscus</i>		AP	43	0.024
15600	Female	Mature	1762	Undetermined		Undetermined	-	-
15600	Female	Mature	1762	Undetermined		Undetermined	-	-
				<b>Reptilia</b>	<b>34</b>			
				<u>Amphisbaenia</u>				
				AMPHISBAENIDAE				
13537	Male	Mature	1213	<i>Leposternon polystegum</i>		Undetermined	-	-
				<u>Sauria</u>				
				TEIIDAE				
15527	Female	Mature	1662	<i>Ameiva ameiva</i>		AP	422	0.254
12937	Male	Mature	1828	<i>Ameiva ameiva</i>		AP	437	0.239
6133	Male	Mature	1345	<i>Ameiva ameiva</i>		AP	-	-
6123	Male	Mature	1424	<i>Ameiva ameiva</i>		AP	-	-
				TROPIDURIDAE				
10829	Male	Immature	1004	<i>Tropidurus hispidus</i>		PA	215	0.214
				<u>Ophidia</u>				
				DIPSADIDAE				
14240	Male	Immature	904	<i>Atractus</i> sp.		Undetermined	-	-
14240	Male	Immature	904	<i>Erythrolamprus reginae</i>		Undetermined	301	0.332
14645	Male	Mature	1613	<i>Pseudoboa nigra</i>		AP	871	0.539
14645	Male	Mature	1613	Egg (Undetermined)		Undetermined	-	-
14645	Male	Mature	1613	Egg (Undetermined)		Undetermined	-	-
15194	Female	Mature	1655	Egg (Undetermined)		Undetermined	-	-
				VIPERIDAE				
23401	Male	Mature	1475	<i>Bothrops taeniatus</i>		AP	987	0.669
16880	Male	Mature	1757	<i>Bothrops taeniatus</i>		AP	802	0.456

Aves								27
Galliformes								
PHASIANIDAE								
3552	Male	Mature	1605	<i>Gallus sp.</i>	AP	116	0.072	
15193	Male	Mature	1720	Egg (Undetermined)	Undetermined	-	-	
15193	Male	Mature	1720	Egg (Undetermined)	Undetermined	-	-	
14506	Female	Mature	1914	Egg (Undetermined)	Undetermined	-	-	
14506	Female	Mature	1914	Egg (Undetermined)	Undetermined	-	-	
784	Female	Mature	1572	Egg (Undetermined)	Undetermined	-	-	
Mammalia								12
Rodentia								
CRICETIDAE								
14645	Male	Mature	1613	<i>Calomys expulsus</i>	PA	99	0.061	
15008	Male	Mature	1291	Bones and hair (Undetermined)	Undetermined	-	-	
16526	Male	Mature	1497	Bones and hair (Undetermined)	Undetermined	-	-	
13775	Male	Mature	1829	Bones and hair (Undetermined)	Undetermined	-	-	

No significant relationship between the SVL of *D. corais* and the total length of preys was observed ( $P=0.46$  for amphibians, birds, and mammals;  $P=0.58$  for snakes and lizards). However, there was a trend ( $r^2=0.41$ ) between the size of *D. corais* and the size of snakes and lizards ingested ( $P=0.87$  for amphibians, birds, and mammals;  $P=0.11$  for snakes and lizards; Figure 1A and 1B). Juveniles (SVL < 1.100 mm) ingested *Tropidurus hispidus*, *Atractus sp.*, and *Erythrolamprus reginae*. Generally, adults of *D. corais* seem to feed on the same prey as juveniles, but with a tendency to ingest larger prey (Figure 1).

The predominant direction of ingestion was antero-posterior (N = 15; 46%) and the prey ingested posterior-anteriorly accounted for were two (6%). We were unable to determine the direction of ingestion of 48% (N = 16) of the items analyzed, due to either advanced stage of digestion or the small size of the prey (Table 1).

The SVL of of mature individuals ranged from 1.201 to 2.005 mm in males (N= 33; mean = 1.595 mm; SD= 223.7) and from 1.155 to 1.914 mm in females (N= 16; mean = 1.597 mm; SD= 206.6). The TL of mature males ranged from 217 to 401 mm (N= 30; mean= 323 mm; SD = 47) and of females from 266 to 378 mm (N= 16; mean= 310 mm; SD = 29). No significant differences were found between adult males and females with regard to SVL ( $t = 0.02$ ;  $df = 47$ ;  $P = 0.97$ ) and TL ( $t = -0.94$ ;  $df = 42$ ;  $P = 0.34$ ).

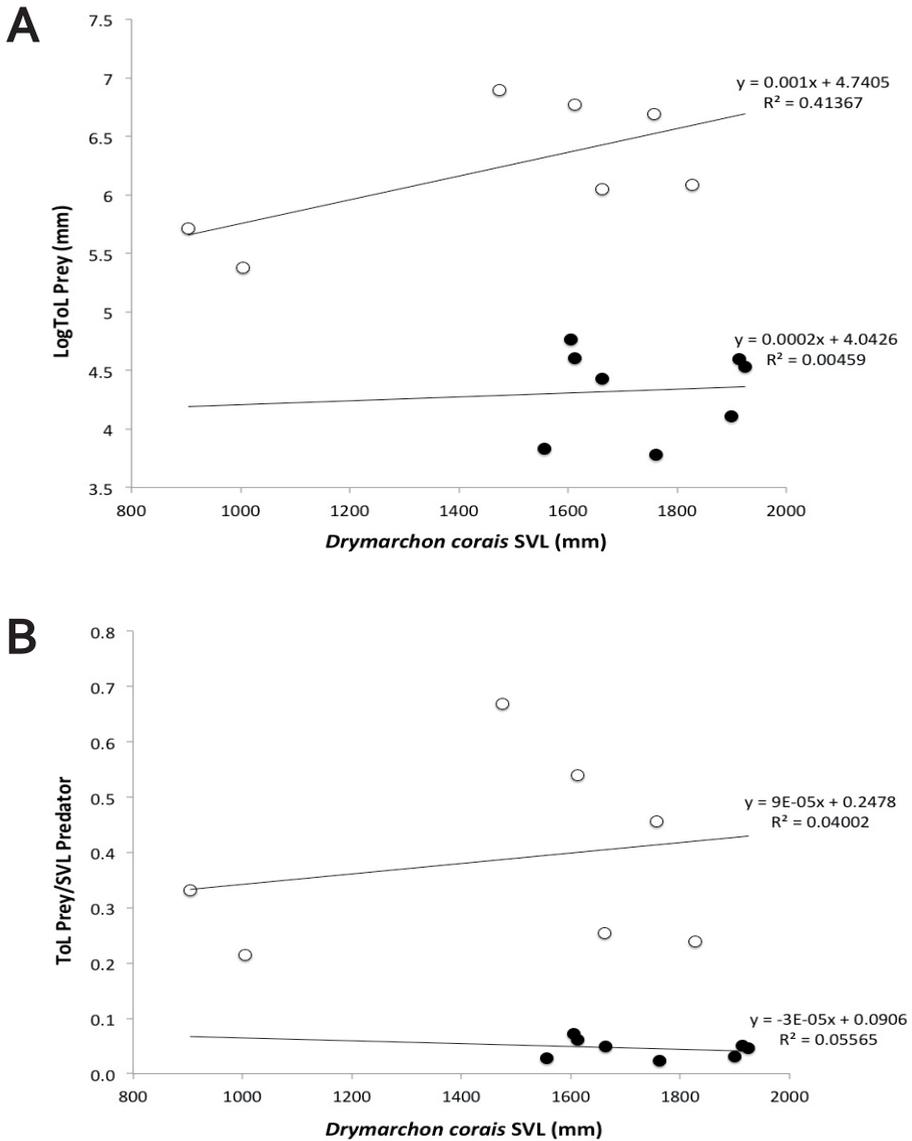
We found vitellogenic follicles throughout the year, from February to September, and November (Figure 2A), with a tendency to more vitellogenic follicles in

the dry season (between May and August), and eggs in June, July, and October (Figure 2B). The mean vector ( $r$ ) of the vitellogenic follicles occurred between June and July (Figure 2A), and the mean of eggs was recorded in August (Figure 2B). These results show strong concentration in the same direction as the studied cycle (Figure 2A, 2B; Table 2). The number of eggs in the oviduct ranged from 3 - 15 (females = 4), and vitellogenic follicles ranged from 6 - 28 (females = 10; Figure 2). No significant relationship between the number of eggs and female SVL ( $P=0.53$ ) was observed, but there was a positive relationship between the number of secondary follicles and female SVL ( $P=0.01$ ), with larger females bearing more secondary follicles (Figure 3).

## Discussion

The low percentage of items observed (33%) in the stomach of *Drymarchon corais* was similar to that found in some other studies of snake diets (Prudente *et al.*, 2007; Maschio *et al.*, 2010). Our results on the diet of *Drymarchon corais* corroborate the studies by Cunha and Nascimento (1993) and Bernade and Abe (2010), both of which state that the species is generalist, feeding on anurans, lizards, snakes, bird eggs, and mammals.

Predation of bird eggs is considered a rare event for Neotropical snakes, recorded for *Pseustes poecilonotus* (Greene, 1997), *Rhachidelus brazili* (Sawaya, Marques and Martins, 2008), and *Drymarchon corais* (Bernarde and Abe, 2006). Although this is the first record of reptile eggs being preyed upon by *D. corais*, we do



**Figure 1.** A- Relationship between snout-vent length (SVL, in mm) of *Drymarchon corais* and Log of total length (ToL, in mm) of its prey. B- Relationship between snout-vent length (SVL, in mm) of *D. corais* and the ratio of total length of prey (ToL, in mm) and SVL of *D. corais*. Legends: hollow circles = snakes and lizards; filled circles = amphibians, birds, and mammals.

not consider it an unexpected event, because there is a record of turtle eggs in the diet of *D. couperi* (Stevenson et al., 2010).

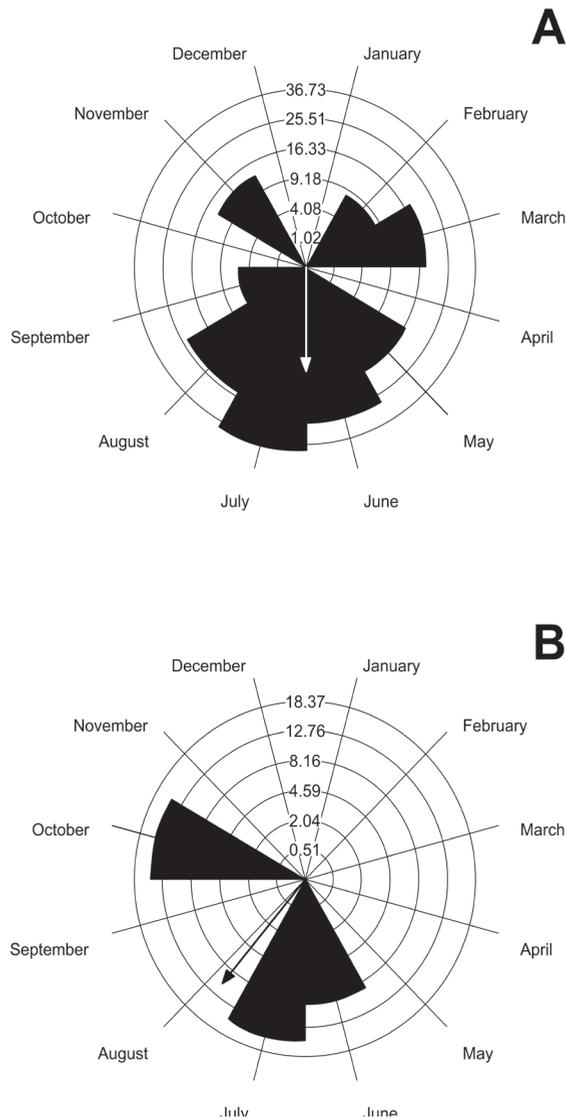
Predation of poisonous frogs (species of *Rhinella*) and venomous snakes (species of the genera *Sistrurus*, *Crotalus*, *Micrurus* and *Agkistrodon*) by *D. couperi* (see Stevenson, Dyer and Willis-Stevenson, 2003) was also observed in *D. corais*, which feeds on frogs of the genus

*Rhinella* and the poisonous snake *B. taeniata* (first record). As *D. couperi* is immune to the venom of North American rattlesnakes (Boos, 2001), we speculate that *D. corais* is immune to that of the South American pit vipers. However, physiological studies are required for this hypothesis to be tested.

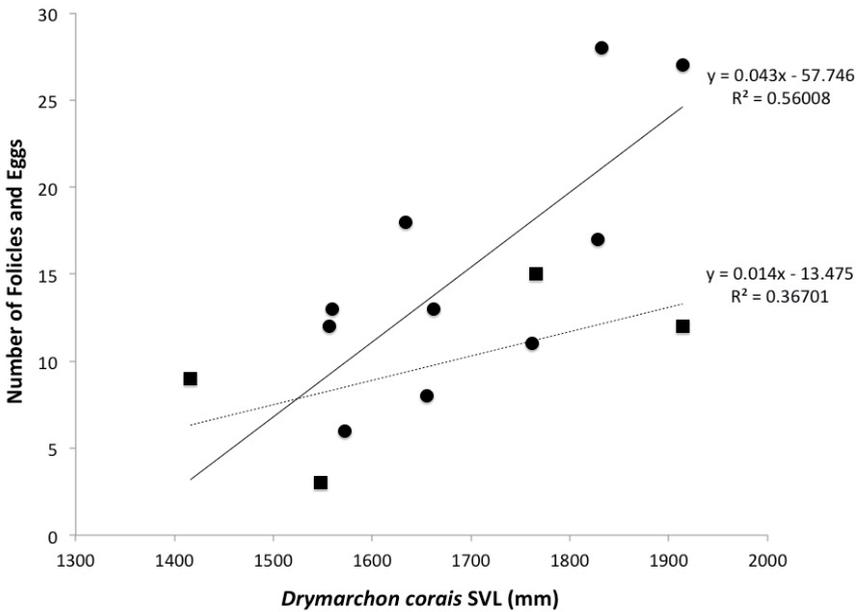
The presence of arboreal and terrestrial prey in the stomach of *D. corais* may indicate that foraging occurs

**Table 2.** Results of circular statistical analysis testing seasonality in reproductive cycle of the females of *Drymarchon corais* from the Brazilian Amazon.

Variables	Secondary follicles	Eggs
Observations (n)	153	36
Mean vector ( $\mu$ )	179.804°	222.944°
Length of mean vector (r)	0.501	0.63
Circular Standard Deviation (SD)	67.38°	55.118°
Rayleigh Test of Uniformity (P)	<0.001	<0.001



**Figure 2.** Rose diagram of circular analysis showing the seasonal distribution of the number of follicles (A) and eggs (B) in females of *Drymarchon corais* from the Brazilian Amazon. The numbers represent the frequency of vitellogenic follicles and eggs in each month. The length of the mean vector (r) is a measure of concentration of data around the year.



**Figure 3.** Relationship between the number of follicles/eggs and female SVL of *Drymarchon corais*. Legend: circles and solid line = vitellogenic follicles; squares and dashed line = eggs.

both in vegetation and on the ground (e.g., Duellman, 1990; Bernarde and Abe, 2006, 2010). *Drymarchon corais* is a diurnal snake that probably captures nocturnal prey when they are sheltered or resting (Bernarde and Abe, 2006).

As observed in *Anilius scytale* (Maschio et al., 2010), the low percentage of items in the mature female stomach of *D. corais* (N= 6; 37%) may indicate a tendency to decrease foraging during the breeding season (Shine, 1977b). This probably occurs due to decreased both of body space and agility of the snake during the gestation period (Shine, 1980). According to Gregory and Isaac (2004), the feeding gaps are smaller in oviparous than viviparous snakes, probably because they carry eggs for less time. At least 15 of 33 mature males of *D. corais* had items in the stomach, which may indicate that males do not make a high energetic investment in reproduction, as do some temperate-zone snakes (Gregory and Isaac, 2004). However, we cannot rule out the possibility that the absence of stomachal contents may be associated with advanced prey stage of digestion when the snakes were killed.

The low number of juveniles with food items in their digestive tracts can limit any comprehensive analyses of ontogenetic variation in the diet. However, our

results indicate a trend of juveniles to feed on elongated prey (lizards and snakes), while adults have a more generalized diet. This wider variety (wide size range and different shapes) of prey consumed by adults maximizes and optimizes the efficiency of their foraging strategy (Schoener, 1971; Maschio et al., 2010). As observed in *Thamnodynastes strigatus* (Bernarde, Kokubum and Marques, 2000), *D. corais* probably searches actively for prey in different substrates. This behavior can provide encounters with less common prey of different sizes, and may indicate the opportunistic character of *D. corais*, as observed in *T. strigatus* (Bernarde, Kokubum and Marques, 2000).

The prevalence of antero-posterior direction of ingestion observed in *D. corais* is a pattern commonly observed in several species of snakes (e.g., Maschio et al., 2010). This direction minimizes injury risk during feeding as it immobilizes the locomotor appendages of the prey, reducing handling time (Maschio et al., 2010).

The absence of sexual size dimorphism in the snout-vent and tail length of *D. corais* differs from the pattern observed for most colubrids, in which females grow larger than males in most species (Shine, 1978). The presence of sexual dimorphism in snakes of the

genus *Drymarchon* was reported by Stevenson *et al.* (2009), who noted a predominance of males larger than females and ritual combat between males of *D. couperi*, indicating that this behavior may be shared by other species of the genus *Drymarchon*.

In fact, the lack of sexual size dimorphism in body size, or males larger than females, may suggest a ritual combat between males (Shine, 1978; 1994), as observed in *Crotalus durissus* (Almeida-Santos, Laporta-Ferreira and Puerto, 1990), *Epicrates cenchria* (Schuett and Schuett, 1995), *Micrurus frontalis* (Almeida-Santos, Aguiar and Balestrin, 1998), *Chironius bicarinatus* (Almeida-Santos and Marques, 2002), *Bothrops moojeni* (Nogueira, Sawaya and Martins, 2003), and *Epicrates crassus* (Pizzatto, Haddad and Almeida-Santos, 2006). This aggressive behavior is related to the dispute for females, territory defense, and dominance establishment (e.g., Barker, Murphy and Smith, 1979; Gillingham, Carpenter and Murphy, 1983).

Females with vitellogenic follicles observed throughout the year, with a tendency to more vitellogenic follicles and eggs in the dry season (between May and August). This suggests that *D. corais* has a seasonal reproductive cycle, with juvenile recruitment occurring at the beginning of the rainy season (between October and November). Martins and Oliveira (1998) suggested that food availability might be higher for most snakes during the rainy season. Thus, young born at this time would face a higher food availability (see Maschio *et al.* (2007).

The data presented herein may help in the understanding the reproductive cycle and diet of this Neotropical snake. But this study is not exhaustive: studies using other microscopic techniques (e.g., Rojas *et al.*, 2013), such as scanning and transmission electron microscopy may reveal important details of *D. chorais* reproductive strategies. We hope that this study may open new perspectives and perhaps stimulate research on squamate reptiles in the Neotropics.

**Acknowledgements.** We thank Adriano Maciel, Alexandre Aleixo, Marinus Hoogmoed, and Silvia Pavan for the identification of food items. Financial support for A. Prudente was provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; grant number Pq, 308950/2011-9; PROTAX 36562171/2010-0). Financial support for Alessandro Menks and Fernanda Magalhães was provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), and Alcoa World Alumina Brasil Ltda (ALCOA). Diogo B. Provete and Anne Baldisseri helped with the English version.

## References

- Almeida-Santos, S.M., Laporta-Ferreira, I.L., Puerto, G. (1990): Ritual de combate em *Crotalus durissus*. *Anais da Academia Brasileira de Ciências* **62**: 418.
- Almeida-Santos, S.M., Aguiar, L.F.S.A., Balestrin, R.L. (1998): *Micrurus frontalis* (Coral snake), male combat. *Herpetological Review* **29**: 242.
- Almeida-Santos, S.M., Marques, O.A.V. (2002): Male-male ritual combat in the colubrid snake *Chironius bicarinatus* from the Atlantic Forest, southeastern Brazil. *Amphibia-Reptilia* **23**: 529-533.
- Barker, D.G., Murphy, J.B., Smith, K.W. (1979): Social behavior in a captive group of Indian Pythons, *Python molurus* (Serpentes, Boidae) with formation of a linear social hierarchy. *Copeia* 466-471.
- Bernarde, P.S., Abe, A.S. (2006): A snake community at Espigão do Oeste, Rondônia, southwestern Amazon, Brazil. *South American Journal of Herpetology* **1(2)**: 102-113.
- Bernarde, P.S., Abe, A.S. (2010): Hábitos alimentares de serpentes em Espigão do oeste, Rondônia, Brasil. *Biota Neotropica* **10(1)**: 167-173.
- Bernarde, P.S., Kokubum, M.N.C., Marques, O.A.V. (2000): Utilização de habitat e atividade em *Thamnodynastes strigatus* (Günther, 1858) no sul do Brasil (Serpentes, Colubridae). *Boletim do Museu Nacional* **428**: 1-8.
- Boos, H.E.A. (2001): The snakes of Trinidad and Tobago. College Station: Texas A & M University Press. 270 p.
- Both, C., Kaefer, I.L., Santos, T.G., Cechin, S.T.Z. (2008): An austral anuran assemblage in the neotropics: seasonal occurrence correlated with photoperiod. *Journal of Natural History* **42 (3-4)**: 205-222.
- Campos, V.A., Oda, F.H., Curcino, A.F., Curcino, A. (2010): An unusual prey item for the yellow tail cribro *Drymarchon corais* Boie, 1827, in the Brazilian Savannah. *Herpetology Notes* **3**: 229-231.
- Cunha, O.R., Nascimento, F.P. (1993): Ofídios da Amazônia. As cobras da região leste do Pará. *Boletim do Museu Paraense Emilio Goeldi* **9(1)**: 1-191.
- Duellman, W.E. (1990): Herpetofaunas in neotropical rainforests: comparative composition, history, and resource use. In: *Four Neotropical Rainforest*, p. 455-487. Gentry, A.H., Ed. Connecticut: Yale University Press.
- Ernst, C.H., Barbour, R.W. (1989): *Snakes of eastern North America*. George Mason University Press. Fairfax.
- Frota, J.G., Santos-Jr, A.P., Chalkidis, H.M., Guedes, A.G. (2005): As serpentes da região do baixo Rio Amazonas, oeste do Estado do Pará, Brasil (Squamata). *Biociências* **13**: 211-220.
- Gillingham, J.C., Chambers, J.A. (1980): Observations on the reproductive behaviour of the eastern indigo snake, *Drymarchon corais couperi*, in captivity. *British Journal of Herpetology* **6**: 99-100.
- Gillingham, J.C., Carpenter, C.C., Murphy, J.B. (1983): Courtship, male combat and dominance in the western diamondback rattlesnake (*Crotalus atrox*). *Journal of Herpetology* **17**: 265-270.
- Greene, H. (1997): *Snakes: the evolution of mystery in nature*. University of California Press, California.

- Gregory, P.T., Isaac, L.A. (2004): Food habits of the grass snake in southeastern England: is *Natrix natrix* a generalist predator? *Journal of Herpetology* **38**: 88–95.
- Hartmann, P.A., Hartmann, M.T., Martins, M. (2009): Ecologia e história natural de uma taxocenose de serpentes no Núcleo Santa Virgínia do Parque Estadual da Serra do Mar, no sudeste do Brasil. *Biota Neotropica* **9**(3).
- Kovach, W.L. (2009): Oriana – Circular Statistics for Windows, ver. 3. Kovach Computing Services, Pentraeth, Wales, U.K.
- Martins, M., Oliveira, M.E. (1998): Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. *Herpetological Natural History* **6** (2): 78-150.
- Maschio, G.F., Prudente, A.L.C., Lima, A.C., Feitosa, D.T. (2007): Reproductive biology *Anilius scytale* (Linnaeus, 1758) (serpentes, Aniliidae) from eastern Amazonia, Brazil. *South American Journal of Herpetology* **2**(3): 179-183
- Maschio, G.F., Prudente, A.L.C., Rodrigues, F.S., Hoogmoed, M.S. (2010): Food habits of *Anilius scytale* (Serpentes, Aniliidae) in the Brazilian Amazonia. *Zoologia* **27**: 184-190.
- Nogueira, C., Sawaya, R.J., Martins, M. (2003): Ecology of the pitviper, *Bothrops moojeni*, in the Brazilian Cerrado. *Journal of Herpetology* **37**(4): 653-659.
- Orofino, R.P., Pizzatto, L., Marques, O.A.V. (2010): Reproductive biology and food habits of *Pseudoboa nigra* (Serpentes, Dipsadidae) from the Brazilian Cerrado. *Phyllomedusa* **9**(1): 53-61.
- Peters, J.A., Orejas-Miranda, B. (1970): Catalogue of the Neotropical Squamata. Part I. Snakes. *United States National Museum Bulletin* **297**: 1-347.
- Pires, R.C., Borges, V.S., Souza, A.M., Eterovick, P.C. (2012): Natural history of a snakes assemblage alongside a river in south-eastern Brazil. *Journal of Natural History* **46**: 369-381.
- Pizzatto, L., Haddad, R.M., Almeida-Santos, S.M. (2006): Male-male ritualized combat in the Brazilian rainbow boa *Epicrates cenchria crassus*. *Herpetological Bulletin* **95**: 16-20.
- Pizzatto, L., Almeida-Santos, S.M., Marques, O.A.V. (2007): Biologia reprodutiva das serpentes brasileiras. In: Nascimento LB, Oliveira ME. (Org.). *Herpetologia no Brasil*. Belo Horizonte: Sociedade Brasileira de Herpetologia **2**: 201-221.
- Prado, C.P.A., Uetanabaro, M., Haddad, C.F.B. (2005): Breeding activity patterns, reproductive modes, and habit use by anurans (Amphibia) in a seasonal environment in the Pantanal, Brazil. *Amphibia-Reptilia* **26**: 211-221
- Prudente, A.L.C., Maschio, G.F., Yamashina, C.E., Santos-Costa, M.C. (2007): Morphology, reproductive biology and diet of *Dendrophidion dendrophis* (Schlegel, 1837) (Serpentes, Colubridae) in Brazilian Amazon. *South American Journal of Herpetology* **2**(1): 53-58.
- Rojas, C.A., Barros, V.A., Almeida-Santos, S.M. (2013): The reproductive cycle of the sleep snake *Sibynomorphus mikanii* (Schlegel, 1837) from southeastern Brazil. *Journal of Morphology* **274**:215-228.
- Ruffato, R., Di-Bernardo, M., Maschio, G.F. (2003): Dieta de *Thamnodynastes strigatus* (Serpentes, Colubridae) no sul do Brasil. *Phyllomedusa* **2**(1): 27-34.
- Santos, X., Llorente, G.A. (2004): Lipid dynamics in the viperine snake, *Natrix maura*, from the Ebro Delta (NE Spain). *Oikos* **105**: 132-140.
- Sawaya, R.J., Marques, O.A.V., Martins, M. (2008): Composition and natural history of a Cerrado snake assemblage at Itirapina, São Paulo state, southeastern Brazil. *Biota Neotropica* **8**: 129-151.
- Schoener, T.W. (1971): Theory of feeding strategies. *Annual Review of Ecology Evolution and Systematics* **11**: 69-404.
- Schuett, G.W., Schuett, S.P. (1995): *Epicrates cenchria cenchria*. Male combat. *Herpetological Review* **26**: 101.
- Shine, R. (1977a): Reproduction in Australian elapid snakes- I. Testicular cycles and mating seasons. *Australian Journal of Zoology* **25**: 647-653.
- Shine, R. (1977b): Reproduction in Australian elapid snakes- II. Female Reproductive Cycles. *Australian Journal of Zoology* **25**: 655-666.
- Shine, R. (1978): Sexual size dimorphism and male combat in snakes. *Oecologia* **33**: 269-277.
- Shine, R. (1980): Costs of reproduction in reptiles. *Eoecologia* **46**: 92-100.
- Shine, R. (1994): Sexual dimorphism in snakes revisited. *Copeia* **3**: 326-335.
- Statsoft. (2004): *Statistica* (data analysis software system), version 7. Statsoft. Inc.
- Stevenson, D.J., Dyer K.J., Willis-Stevenson B.A. (2003): Survey and monitoring of the Eastern Indigo Snake in Georgia. *Southeastern Naturalist* **2**: 393-408.
- Stevenson, D.J., Enge, K.M., Carlile, L.D., Dyer, K.J., Norton, T.M., Hyslop, N.L., Kiltie, R.A. (2009): An Eastern Indigo Snake (*Drymarchon couperi*) markrecapture study in southeastern Georgia. *Herpetological Conservation Biology* **4**: 30-42.
- Stevenson, D.J., Bolt, M.R., Smith, D.J., Enge, K.M., Hyslop, N.L., Norton, T.M., Dyer, K.J. (2010): Prey records for the Eastern Indigo Snake (*Drymarchon couperi*). *Southeastern Naturalist* **9**: 1–18.
- Thompson, M.B., Speake, B.K. (2002): Energy and nutrient utilization by embryonic reptiles. *Comparative Biochemistry and Physiology* **133**: 529-538.
- Uetz, P., Hallermann, J. (2012): The JCVI/TIGR Reptile Database. Available at: <http://www.reptile-database.org>. Last accessed on 11 July 2013.
- Zar, J.H. (2010): *Bioestatistical Analysis*. 5th edition. New Jersey: Prentice-Hall International.

**Appendix 1.**

Specimens examined, deposited in the Herpetological Collection of the Museu Paraense Emílio Goeldi:

BRAZIL. ACRE: Porto Walter (MPEG 20391); AMAZONAS: Manicoré (MPEG 20833); MARANHÃO: Arari (MPEG 5600, MPEG 13529, MPEG 13537, MPEG 14316, MPEG 14317, MPEG 14321, MPEG 14646, MPEG 15240, MPEG 15241, MPEG 16149, MPEG 16150, MPEG 14645), Nova Vida (MPEG 15008), Paruá (MPEG 14240), Sítio Novo (MPEG 18485), no data: (MPEG 13555, MPEG 13648, MPEG 10829); PARÁ: Almeirim (MPEG 20110), Belém (MPEG 1098), Cachoeira Porteira (MPEG 17676), Capitão Poço (MPEG 784), Castanhal (MPEG 2724), Chaves (MPEG 18672), Dom Eliseu (MPEG 14508, MPEG 15526, MPEG 15529, MPEG 15533, MPEG 14506, MPEG 13418, MPEG 14965, MPEG 15527, MPEG 15535), Juruti (MPEG 23401, MPEG 24282), Marabá (MPEG 15193, MPEG 15195, MPEG 16526, MPEG 15196, MPEG 15197, MPEG 15194, MPEG 16880, MPEG 16552, MPEG 16602, MPEG 16607, MPEG 16615, MPEG 16653, MPEG 16772, MPEG 16991), Moju (MPEG 17626), Palestina do Pará (MPEG 12937), Peixe-Boi (MPEG 1803); Santarém (MPEG 3935, MPEG 3936); Tucuruí (MPEG 16744), Vigia (MPEG 3978); Viseu (MPEG 1278, MPEG 1283, MPEG 2510, MPEG 3552, MPEG 3683, MPEG 6123, MPEG 6133, MPEG 7349, MPEG 7663, MPEG 10060, MPEG 12562, MPEG 12861, MPEG 13755, MPEG 16308); no data: (MPEG 16096); RONDÔNIA: Ji-Paraná (MPEG 16863); RORAIMA: no data: (MPEG 19010, MPEG 19011).

**Appendix 2.**

Stomach contents analyzed of *Drymarchon corais*, deposited in the Herpetological Collection of the Museu Paraense Emílio Goeldi:

*Ameiva ameiva* (MPEG 6123, MPEG 6133, MPEG 12937, MPEG 15527); *Leposternon polystegum* (MPEG 13537); *Atractus* sp. (MPEG 14240); *Bothrops taeniatus* (MPEG 16880, MPEG 23401); *Calomys expulsus* (MPEG 14645); *Gallus* sp. (MPEG 3552); *Leptodactylus fuscus* (MPEG 15600); *Erythrolamprus reginae* (MPEG 14240); *Pseudoboa nigra* (MPEG 14645); *Rhinella marina* (MPEG 7663, MPEG 14508, MPEG 15526, MPEG 15529, MPEG 15533, MPEG 14506); *Tropidurus hispidus* (MPEG 10829).