

## Reproduction and diet of *Imantodes cenchoa* (Dipsadidae: Dipsadinae) from the Brazilian Amazon

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**ABSTRACT.** *Imantodes cenchoa* (Linnaeus, 1758) is distributed from the east coast of Mexico to Argentina. In Brazil, it occurs in the north, central-west and northeast regions. We present information on the reproductive biology and diet of *I. cenchoa* from analysis of 314 specimens deposited in the Herpetological Collection of the Museu Paraense Emílio Goeldi (MPEG). *Imantodes cenchoa* displays sexual dimorphism in the snout-vent length, where sexually mature females are larger than mature males ( $t = 4.02$ ,  $p < 0.01$ ; N males = 150, N females = 71), head length ( $f_{1,218} = 98.29$ ,  $p < 0.01$ ; N males = 150, N females = 71), and head width ( $f_{1,218} = 112.77$ ,  $p < 0.01$ , N males = 150; N females = 71). Bi-sexual maturity is observed, with males becoming sexually mature earlier than females. Females with eggs were recorded from November to January (rainy season) and from April to July (dry season), suggesting two reproductive peaks throughout the year, with recruitment occurring mainly during the rainy season, when there is a greater supply of food. *Imantodes cenchoa* is a nocturnal active forager, capturing prey that are asleep on the vegetation. In 32.80% of the analyzed specimens, food contents were present, of which 84.11% were lizards of the genera *Norops* (69.16%, N = 74) and *Gonatodes* (14.95%, N = 16). The other 15.89% of the contents were made up of items in an advanced state of digestion, preventing their identification. Some specimens had more than one food item in their digestive tract, accounting for 107 prey items in total. There was no ontogenetic variation in the diet of *I. cenchoa*, and the predominant direction of prey ingestion was antero-posterior (71.96%). Larger snakes tended to feed on larger prey, although these did not exclude small prey from their diet.

**KEY WORDS.** Ecology; natural history; Neotropical; snakes.

Results obtained from natural history studies, and which investigate reproductive modes and strategies, habitat use, food habits, behavior and defensive tactics (according to GREENE 1986, 1994), can increase our knowledge of the local fauna (CUNHA & NASCIMENTO 1978).

Reproductive biology is widely discussed within the context of the natural history of snakes, mainly due to the great diversity of reproductive strategies in the group (SEIGEL & FORD 1987, SHINE 2003). These studies also include descriptions of reproductive mode, period of vitellogenesis, ovulation and gestation, period of spermatogenesis and mating, fecundity, maturation size and sexual dimorphism (PARKER & PLUMMER 1987, SEIGEL & FORD 1987, SHINE 1993). The trophic biology of snakes requires more detailed studies than those available in the literature, which consist mainly of taxonomic lists of ingested items. Since the 1990's, more detailed information has begun to emerge on predator-prey relationships, absolute and relative frequencies of food items in the diet, importance of food

items in the diet, ontogenetic variation, volume and calorific value (e.g., ARNOLD 1993, HENDERSON 1993, CUNDALL 1995, MARQUES & SAZIMA 1997, MASCHIO *et al.* 2010).

Despite the increasing number of ecological studies involving Neotropical snakes, mostly during the 21st century, (e.g., ALBUQUERQUE *et al.* 2007, LEITE *et al.* 2007, MARQUES & MURIEL 2007, MASCHIO *et al.* 2007, 2010, PRUDENTE *et al.* 2007, RIVAS *et al.* 2007a, b, PIZZATTO & MARQUES 2007, MARTINS *et al.* 2008, PARPINELLI & MARQUES 2008, PINTO *et al.* 2008, PIZZATTO *et al.* 2008a, b, 2009, SAWAYA *et al.* 2008; STURARO & GOMES 2008, TOZETTI & MARTINS 2008, HARTMANN *et al.* 2009a, b, MARQUES *et al.* 2009, SCARTOZZONI *et al.* 2009, TURCI *et al.* 2009, ALBARELLI & SANTOS-COSTA 2010, ÁVILA *et al.* 2010, BERNARDE & ABE 2010, OROFINO *et al.* 2010, ARAÚJO & ALMEIDA-SANTOS 2011, BERNARDE *et al.* 2011a, RODRIGUES & PRUDENTE 2011, BERNARDE & GOMES 2012, MARIA-CARNEIRO *et al.* 2012) and considering the great diversity and complexity of the snake fauna in the Amazon Biome (BERNARDE *et al.* 2011a, b, MENDES-PINTO *et al.* 2011, ARAÚJO *et al.* 2012), the reproductive and dietary patterns

of many species of snakes are still poorly known (MARTINS & OLIVEIRA 1999, BALESTRIN & DI-BERNARDO 2005, PIZZATTO *et al.* 2006, STURARO & GOMES 2008, MASCHIO *et al.* 2010).

Popularly known as vine-snakes, or tree-snakes (CUNHA & NASCIMENTO 1993), *Imantodes* (Duméril, 1853) includes six species with arboreal habits: *I. cenchoa* (Linnaeus, 1758), *I. gemmistratus* (Cope, 1861), *I. inornatus* (Boulenger, 1896), *I. lentiferus* (Cope, 1894), *I. phantasma* (Myers, 1982), *I. tenuissimus* (Cope, 1866). They are distributed between the Tropic of Cancer and the Tropic of Capricorn, from Mexico to Argentina, inhabiting very different environments, such as tropical forests and savannas (ZUG *et al.* 1979, MYERS 1982, COSTA *et al.* 2010).

*Imantodes cenchoa* is distributed from the tropical region of the island of Trinidad and Panama, through Mexico, Venezuela, Colombia, Guyana, Suriname, French Guiana, Bolivia and Brazil (north, central-west and northeast regions), reaching Paraguay and Argentina (CUNHA & NASCIMENTO 1978). It is an oviparous species and feeds on small frogs and lizards, mainly of *Norops* (Daudin, 1802) (ROBINSON 1977, ZUG *et al.* 1979, AVEIRO-LINS *et al.* 2006). Individuals can be seen foraging during the night on bromeliads, shrubs, in the underbrush, or on palm bracts, which during the day are primarily used for sleeping (HENDERSON & NICKERSON 1976, BARTLETT & BARTLETT 2003). Despite the arboreal habits of *I. cenchoa*, this snake has been observed on the ground of forests (HENDERSON & NICKERSON 1976, MARQUES & SAZIMA 2004) and dead on paved roads, killed by cars, indicating possible terrestrial foraging.

In this study, we present data to increase our understanding of the reproductive and dietary strategies of *I. cenchoa* from the Brazilian Amazon region.

## MATERIAL AND METHODS

We analyzed 314 specimens (200 males and 114 females) of *I. cenchoa*, from forested environments of the Brazilian Amazon. They are deposited in the Herpetological Collection of the Museu Paraense Emílio Goeldi (MPEG), state of Pará, Brazil (Appendix).

The Amazon region is formed mostly of constantly humid environments, with precipitation close to 3000 mm/year. The driest month never has less than 60 mm of rainfall and humidity is around 80%, with an average temperature of 25.9°C. The climate of this region is classified as type Af (according to Köppen's classification). The vegetation varies from a low-altitude forest (the Andean portion) to the Amazon rainforest, with predominance of the "terra firme" forests, flooded forests, "várzeas" and "igapós" (PNRH 2006).

For each specimen, the snout-vent length (SVL), tail length (TL), head width (HW), head length (HL), head height (HH) and distance between the eyes (DBE) were measured, as well as the mass.

Through a longitudinal incision in the abdominal region, the gonads of both males and females were analyzed

macroscopically, in order to assess the state of the vas deferens of the males and the oviduct of the females, and to infer the number and length of ovarian follicles. Thus, females with SVL equal to or larger than females having follicles in secondary vitellogenesis (diameter 10.0 mm), and/or oviductal eggs, and/or oviducts with evidence of eggs, were considered sexually mature. Males with SVL equal to or larger than the smallest male with turgid testes, convoluted and opaque efferent ducts, were considered sexually mature (SHINE 1977b, c, 1988, BALESTRIN & DI-BERNARDO 2005). Fecundity was inferred from the ratio of the number of follicles in secondary vitellogenesis and the number of oviductal eggs with snout-vent length of the female (ALDRIDGE 1979, DENARDO 1996, THOMPSON & SPEAKE 2002, SANTOS & LLORENTE 2004).

Analysis of the reproductive cycle was performed using adult (sexually mature) specimens, observing the temporal distribution of follicles in secondary vitellogenesis or the presence of oviductal eggs (SHINE 1977b, 1988).

Stomach contents were observed directly in the digestive tract of each specimen. The quantitative analysis of the diet was performed on the number of prey items observed in the stomach or intestine; in order to perform the qualitative analysis, we identified each prey item to the lowest possible taxonomic level, using the help of experts and the literature. Partially digested prey were measured (SVL and TL) and their mass was inferred from comparison with intact conspecific specimens of similar size (according to RODRIGUEZ-ROBLES & GREENE 1999) from nearby locations, and preserved in the Herpetological Collection of MPEG.

The direction of ingestion was classified according to the alignment of the head of the prey in relation to the body of the snake. Thus, the direction of items ingested head first was considered antero-posterior, and the direction of items ingested tail first was considered postero-anterior.

To verify the existence of ontogenetic variation in the diet, the types and size of prey found in the digestive tract of sexually immature and mature snakes were compared.

For data analyses, the program Statistica 7.1 was used. The significance level ( $\alpha$ ) used for all tests was 0.05. A Student t-test was performed to test for the presence of sexual dimorphism in the SVL (for data with normality and homogeneity of variance). To compare the sexual dimorphism in relation to the TL (excluding specimens with broken tails), a one-way ANCOVA was used, with sex as a factor and SVL as a covariate. To test the sexual dimorphism of the HL, a one-way ANCOVA was used with sex as a factor and HL subtracted from SVL as a covariate. In the case of HW, a one-way ANCOVA was used with sex as a factor and SVL as a covariate, with log-transformed data. All data submitted to ANCOVA were tested for normality and homogeneity of variance. Pearson correlation analysis was performed to find the relationships between SVL and HL, and SVL and HW. In all tests of sexual dimorphism, only data from sexually mature females and males were used. Pearson correla-

tion analysis was performed to find the ratio between the SVL of females and the number of eggs and vitellogenic follicles. Pearson correlation analysis was also used to find the relationship between predator-prey SVL, snake HL and prey SVL, and between mass of prey and mass of snake.

## RESULTS

### Reproductive aspects

The SVL of sexually mature females was significantly greater than that of sexually mature males ( $t = 4.02$ ,  $p < 0.01$ ; N males = 150, N females = 71). There was no significant difference between the TL of males and females ( $f_{1,196} = 2.40$ ,  $p = 0.12$ ; N males = 136, N females = 63). Sexual dimorphism of the HL was observed ( $f_{1,218} = 98.29$ ,  $p < 0.01$ ; N males = 150, N females = 71), with sexually mature females having a longer head than mature males (females = 11.60 to 15.91 mm; males = 10.20 to 15.50 mm). Sexual dimorphism was also present in the HW ( $f_{1,218} = 112.77$ ,  $p < 0.01$ ; N males = 150, N females = 71), with females having wider heads than males (females = 2.02 to 2.42 mm; males = 1.80 to 2.28 mm) (Table I).

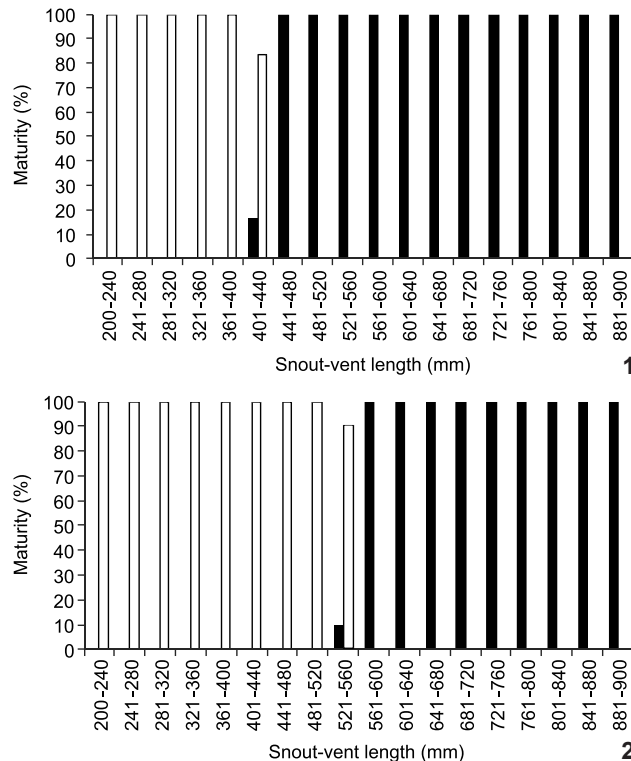
Table I. Morphometry of sexually mature females and males of *Imantodes cenchoa* from the Brazilian Amazon, showing the number of specimens examined (N), mean, standard deviation and range. (SVL) Snout-vent length (mm), (TL) tail length (mm), (HL) head length (mm), (HW) head width (mm).

	Number of specimens	Mean $\pm$ Standard Deviation	Range
<b>Female</b>			
SVL	71	731.53 $\pm$ 67.84	560.00-900.00
TL	63	333.60 $\pm$ 35.97	247.00-403.00
HL	71	14.04 $\pm$ 1.00	11.60-15.91
HW	71	2.21 $\pm$ 0.09	2.02-2.42
<b>Male</b>			
SVL	150	690.60 $\pm$ 71.86	498.00-829.00
TL	136	311.23 $\pm$ 38.74	220.00-395.00
HL	150	12.78 $\pm$ 0.99	10.20-15.50
HW	150	2.07 $\pm$ 0.08	1.80-2.28

A correlation was found between SVL and HL ( $r^2 = 0.68$ ,  $p < 0.01$ ) and between SVL and HW ( $r^2 = 0.44$ ,  $p < 0.01$ ), where individuals with larger snout-vent length had larger head length and width.

The SVL of sexually mature specimens ranged from 438 to 829 mm in males (Fig. 1) and between 560 and 900 mm in females (Fig. 2), emphasizing the sexual bi-maturity, with males reaching sexual maturity at a smaller size than females.

One to two follicles in secondary vitellogenesis (N = 8, mean = 1.87) and one to three eggs (N = 14, mean = 2.07) were found in mature females. The length of eggs ranged from 22.85 to 45.10 mm (N = 14, mean = 30.06 mm). Larger females had a



Figures 1-2. Percentage of sexually immature and mature males (1) and females (2) of *Imantodes cenchoa* from the Brazilian Amazon for the different size classes. (□) Immature, (■) mature.

greater number of follicles over 10 mm and a greater number of eggs ( $r^2 = 0.22$ ,  $p = 0.03$ ) (Fig. 3).

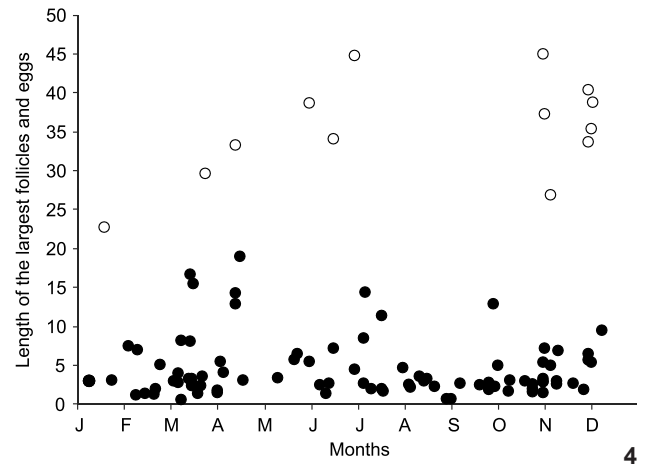
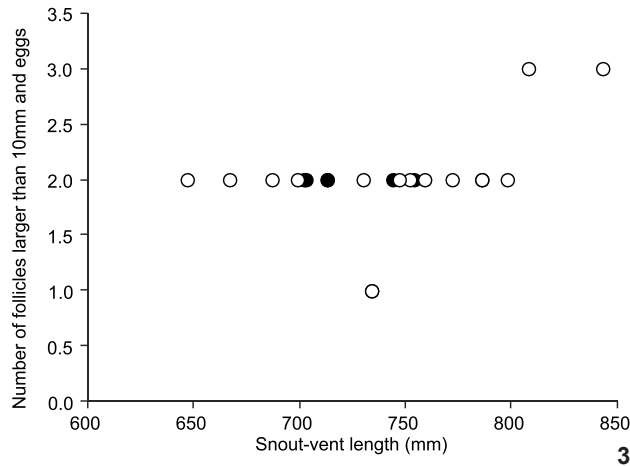
Females of *I. cenchoa* with eggs were found between November and January, during the rainiest season, and from April to July, during the dry season (Fig. 4).

### Diet

Of the 314 specimens of *I. cenchoa* analyzed, 32.80% (N = 103) had some type of content in the stomach and/or intestines. Among the females with secondary follicles and/or eggs (N = 21), six (28.57%) presented food contents.

Among the food items, 84.11% were *Norops* (69.16%, N = 74) and *Gonatodes* (Fitzinger, 1843) (14.95%, N = 16) lizards, and the other 15.89% was made up of insect wings, eggs, scales, tails, lizard skulls, and other items in an advanced state of digestion, preventing their identification. Seven specimens had two food items in their digestive tract, yielding a total of 107 preys (Table II).

The predominant direction of ingestion was antero-posterior (71.96%, N = 77), and prey ingested postero-anteriorly accounted for 1.87% (N = 2) of the total. The direction of ingestion could not be determined for 26.17% (N = 28) of the items (Table II).



Figures 3-4. (3) Fecundity of *Imantodes cenchoa*, from the Brazilian Amazon, indicating the relationship between the number of follicles in secondary vitellogenesis (●) and eggs (○) with female SVL. (4) Seasonal distribution of the largest follicles (●) and eggs (○) of *Imantodes cenchoa*, from the Brazilian Amazon.

Table II. Contents of the digestive tract of *Imantodes cenchoa* from the Brazilian Amazon. (N) Number of prey; Undetermined = food content in an advanced state of digestion; (Di) Direction of ingestion, (AP) antero-posterior, (PA) postero-anterior; Unidentified = food content for which the direction of ingestion was not verified due to its advanced state of digestion.

Prey/Item	N	(%)	Di
<b>Reptilia, Squamata</b>			
<i>Norops</i> sp. (Daudin 1802)	17	15.89	AP
<i>Norops</i> sp. (Daudin 1802)	1	0.93	PA
<i>Norops</i> sp. (Daudin 1802)	8	7.48	Unidentified
<i>Norops chrysolepis</i> (Duméril & Bibron, 1837)	3	2.80	AP
<i>Norops fuscoauratus</i> (D'Orbigny, 1837)	34	31.78	AP
<i>Norops fuscoauratus</i> (D'Orbigny, 1837)	2	1.87	Unidentified
<i>Norops punctatus</i> (Daudin, 1802)	2	1.87	AP
<i>Norops ortonii</i> (Cope, 1868)	6	5.61	AP
<i>Norops ortonii</i> (Cope, 1868)	1	0.93	PA
<i>Gonatodes</i> sp. (Fitzinger, 1843)	3	2.80	AP
<i>Gonatodes humeralis</i> (Guichenot, 1855)	12	11.21	AP
<i>Gonatodes humeralis</i> (Guichenot, 1855)	1	0.93	Unidentified
Undetermined	17	15.89	Unidentified
<b>Total</b>	<b>107</b>	<b>100.00</b>	

Both immature and mature females and males frequently preyed on *Norops fuscoauratus* and no evidence of ontogenetic variation was observed (Figs 5 and 6).

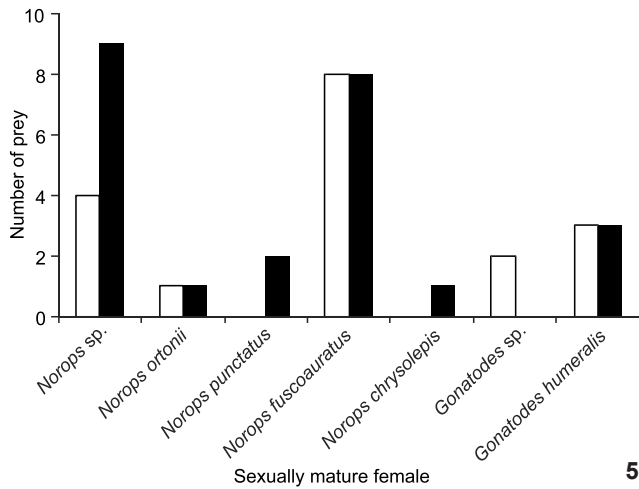
The results show that larger snakes tend to eat larger prey items with larger mass, although smaller prey with smaller mass were not eliminated from their diet, ( $r^2 = 0.13$ ,  $p = 0.01$ ;  $r^2 = 0.22$ ;  $p < 0.01$ , respectively) (Figs 7 and 8).

## DISCUSSION

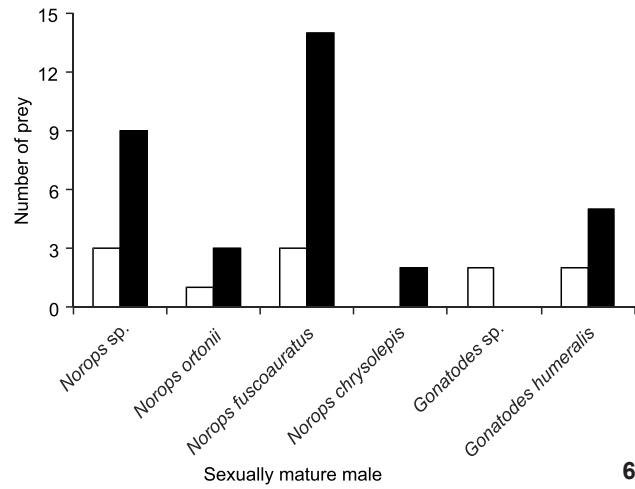
Sexual dimorphism in snakes can occur in characters such as size and/or body shape, color, position and/or size of organs, and behavior (KING 1989a, SHINE 1993, BONNET *et al.* 1998, KEOGH & WALLACH 1999, PIZZATTO & MARQUES 2006), as well as the relative size of the head (CAMILLERI & SHINE 1990). Most frequently sexually mature females have greater snout-vent length than their sexually mature male counterparts, as observed in this study, is (e.g., MARQUES & PUERTO 1998). This is related to the fact that there is a positive relationship between body size and the ability to produce and maintain a larger amount of eggs/embryos (SHINE 1994, PIZZATTO *et al.* 2006).

The absence of sexual dimorphism in the length of the tail of *Imantodes cenchoa*, observed in this study, had been previously reported by MYERS (1982), as was the exponential increase in length and width of the head of females relative to that of males. Adult males of *I. cenchoa* in Honduras and Costa Rica had a slightly longer tail than females. However, there was an absence of sexual dimorphism in tail length in specimens from Panama, Ecuador and Peru (ZUG *et al.* 1979). Sexual dimorphism in tail length occurs in most colubrids, in which males have larger tails than females. The larger tail of males is necessary to hold the copulatory organ and associated muscles. Conversely, females need a larger body in order to produce more offspring (KING 1989). The absence of sexual dimorphism in the tail of *I. cenchoa* can be related to its arboreal habit, since selection favors longer tails, which provide better balance and movement in trees (PIZZATTO *et al.* 2007).

Sexual dimorphism in head size, as found in *I. cenchoa*, has evolved, according to SHINE (1986), to enable males and females to feed on prey of different sizes, maximizing foraging efficiency and minimizing competition between the sexes. Simi-

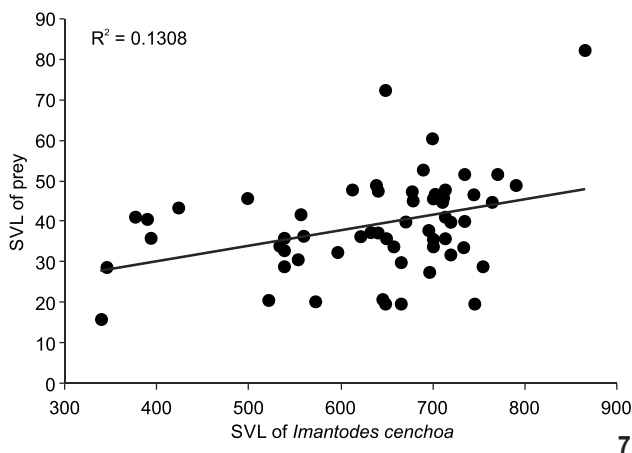


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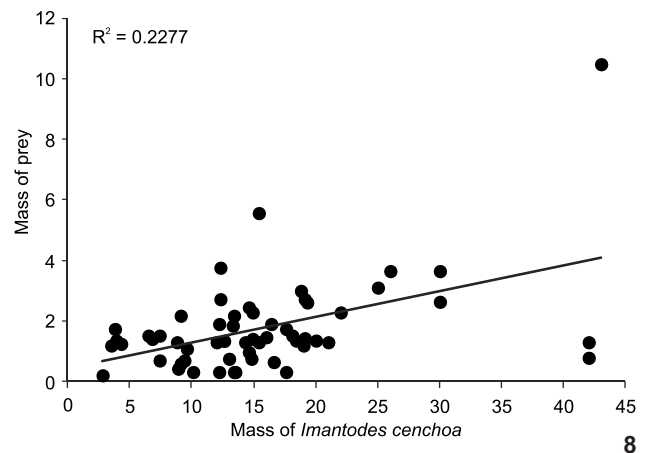


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Figures 5-6. Relationship between the number and type of prey consumed by sexually immature and mature females (5) and male (6) of *Imantodes cenchoa* from the Brazilian Amazon. (□) Immature, (■) mature.



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Figures 7-8. (7) Relationship between snout-vent length (SVL, in mm) of *Imantodes cenchoa*, and snout-vent length (SVL, in mm) of their prey, from the Brazilian Amazon. (8) Relationship between the mass (g) of *Imantodes cenchoa* and mass (g) of their prey, from the Brazilian Amazon.

larly, several authors (e.g., SHINE 1989, 1994, HOUSTON & SHINE 1993, PEARSON *et al.* 2002, SHETTY & SHINE 2002, SHINE *et al.* 2002) have suggested that head length dimorphism is related to intersexual resource competition instead of sexual selection, since head length is not crucial in mate choice or male fighting (SHINE 1991).

The fact that males reach sexual maturity earlier than females is probably related to energy cost, which is higher for females than for males of different sizes (PARKER & PLUMMER 1987, SANTOS-COSTA *et al.* 2006), but similar between large females and large males (MADSEN & SHINE 1993). Natural selection would favor of a more delayed sexual maturity in females. This results in larger females that are consequently more fertile (FITCH 1970,

1982, VITT & VANGILDER 1983, SHINE 1994) and could explain the bi-maturity in some species of snakes, such as *Erythrolamprus aesculapii* (Linnaeus, 1766) (MARQUES 1996), *Tantilla melanocephala* (Linnaeus, 1758) (MARQUES & PUERTO 1998, SANTOS-COSTA *et al.* 2006); *Helicops infrataeniatus* (Jan, 1865) (AGUIAR & DI-BERNARDO 2005), *Atractus reticulatus* (Boulenger, 1885) (BALESTRIN & DI-BERNARDO 2005), and as observed in *Imantodes cenchoa*.

The results on the fecundity of *Imantodes cenchoa*, presented in this study, are consistent with a trend found for most species of snakes, where larger females produce more eggs (FITCH 1970, SEIGEL & FORD 1987). The abdominal space may limit the reproductive investment relative to the size or the total mass of offspring, resulting, in many species, a strong relationship

between the body size of the mother and the size of the litter (FITCH 1981), emphasizing why larger females are favored. LILLYWHITE and HENDERSON (1993) speculated that the slender body shape of arboreal snakes may constrain the female's capacity to carry eggs. This hypothesis was strongly supported by the results of PIZZATTO *et al.* (2007), and would explain the small amount of eggs produced by *I. cenchoa*. Some previous studies (e.g., JAMES & JOHNSTON 1998, PLAUT 2002, GHALAMBOR *et al.* 2004) have demonstrated that the movement and escape ability of females is related to the habitat type and the offspring/egg weight. These results suggest that the weight of eggs has a significant cost. Likewise, the use of arboreal habitats by snakes could have provided selective advantages, such as a better ability to cradle and camouflage in between tree branches (POUGH *et al.* 1988, LILLYWHITE & HENDERSON 1993), along with the laterally compressed body shape, as in *I. cenchoa*.

Snakes have different reproductive cycles, and males and females of the same species may also have distinct cycles (SEIGEL & FORD 1987). PIZZATTO *et al.* (2008a) suggested that the cycle of *I. cenchoa* is continuous for about eight months, differing from that observed in this study, where females containing eggs were found in the beginning of the rainy season (November to January) and in the first months of the dry season (April to July), suggesting two reproductive peaks throughout the year, but with recruitment occurring mainly in the period (rainy season) when there seems to be more food available. A third pattern was observed by ZUG *et al.* (1979). In his data, females of *I. cenchoa* with eggs were found throughout the year, indicating a prolonged breeding season, which is correlated with the rainy season in the region.

In temperate regions, the period when the temperatures are higher influence the timing of the reproductive cycle of snakes. Higher temperatures are important not only for egg development, but are also associated with greater availability of food during recruitment (SHINE 1977a). In Iquitos, Peru, FITCH (1982) found no evidence that snake species reproduce only in certain seasons. DUELLMAN (1978), based on work carried out in Santa Cecilia, Ecuador, concluded that non-seasonal reproduction is a trend among Amazonian snakes. However, according to data obtained by MARTINS & OLIVEIRA (1999), recruitment for most species occurs during the rainy season, when there is a greater supply of food than in the dry season.

In the present study, only 32.8% of the specimens analyzed had food contents in their stomachs. These results were expected, since the frequency of specimens containing food items is usually low, ranging between 14 and 30% (MASCHIO *et al.* 2010). According to GREGORY & ISAAC (2004), this low frequency may be related to the period in which the specimen was collected. SHINE (1987) suggested that female snakes generally tend to reduce food consumption during their gestation period. This was observed in females of *Natrix natrix* (Linnaeus, 1758) and *Anilius scytale* (Linnaeus, 1758) (READING & DAVIES 1996, MASCHIO *et al.* 2010, respectively), which began to feed

again after the reproductive period. The small number of females of *I. cenchoa* containing eggs and/or follicles in this study does not allow us to draw conclusions about the influence of gestation on stomach contents.

Analyses of stomach contents of *I. cenchoa* showed that *Norops* lizards are the most frequent items in their diet, demonstrating that these are their main prey (see also STUART 1948, 1958, WEHERKIND 1955, LANDY *et al.* 1966, HENDERSON & NICKERSON 1976). This result is in agreement with the findings of ZUG *et al.* (1979), who stated that *I. cenchoa* forages actively during the night, feeding on small diurnal arboreal lizards (mainly *Norops*) that sleep on the vegetation (see ÁVILA-PIRES 1995).

In this study, no food item of *I. cenchoa* was identified as an anuran. Despite this result, it is possible that these amphibians may occasionally serve as food for this species, as noted by different authors, as follows: MARTINS & OLIVEIRA (1999) found *Pristimantis fenestratus* (Steindachner, 1864) in the digestive tract of an adult male and a gravid female; TEST *et al.* (1966), observed *I. cenchoa* under captivity feeding on *Pristimantis* sp. (Duméril & Bibron, 1841); and BEEBE (1946) observed an individual of *I. cenchoa* stalking an individual of *Oloolygon rubra* (Daudin, 1803).

According to MARTINS & GORDO (1993) the occurrence of arthropods in the digestive tract of snakes is the result of their anuran-based diets. In our study, arthropods were characterized as secondary stomach contents because they were always associated with lizard vestiges. This may be explained by the fact that *Norops* sp. and/or *Gonatodes* sp. are insectivorous (ARAÚJO 1991).

There is no record of *I. cenchoa* eating reptile eggs. Even though eggs have been found in the stomachs of these snakes by some studies (e.g. LANDY *et al.* 1966), these findings are associated with the ingestion of a gravid female lizard, where most of the prey was digested, except the eggs (HENDERSON & NICKERSON 1976).

The anteroposterior direction of ingestion, prevalent in this study, follows the pattern found in most species of snakes (PALMUTI *et al.* 2009), for example *Helicops infrataeniatus* (Jan, 1865) (AGUIAR & DI-BERNARDO 2004) and *Thammodon strigatus* (Günther, 1858) (RUFFATO *et al.* 2003). According to GREENE (1976), this direction prevents the limbs of the prey and the disposition of their scales from offering resistance to swallowing, and minimizes the potential risk of injuries caused by the claws or teeth of the prey. Consequently, intake by the head results in decreased time, effort and energy expenditure during the process of prey capture and ingestion (PINTO & LEMA 2002). Furthermore, the chances of prey escaping are minimized by ingesting the lizards head-first, since some species have caudal autotomy. Caudal autotomy is a successful defensive strategy used by many lizards (CHAPPLE & SWAIN 2002), including those of *Norops* (SCHOENER & SCHOENER 1980) and geckos (CONGDON *et al.* 1974), for instance species of *Gonatodes*, the main prey of *I. cenchoa*.

The specimens containing *N. fuscoauratus* and *G. humeralis* were recorded in almost every month of the year except May, September and November for *N. fuscoauratus* and April, August and December for *G. humeralis*. *Norops fuscoauratus*, the most consumed item by *I. cenchoa* in this study, can produce at least three clutches per year, laying one egg per clutch (VITT *et al.* 2008), indicating that this species has a continuous reproductive cycle (ÁVILA-PIRES 1995), which would justify the occurrence of *N. fuscoauratus* in the digestive tract of *I. cenchoa* throughout the year (see FITCH 1970, HOOGMOED 1973, DIXON & SOINI 1975, 1986, DUELLMAN 1978). Females of *Gonatodes humeralis* lay one egg at a time and may return a few days later to the same place to lay another egg (HOOGMOED 1973). Its reproduction also seems to occur throughout the year (DIXON & SOINI 1975, 1986) and it can lay up to twelve eggs (ÁVILA-PIRES 1995).

The selection of prey with specific sizes can be influenced by prey density and availability (PLUMMER & GOY 1984, SHINE 1987, 1991, MASCHIO *et al.* 2010). Although species normally have continuous reproductive cycles in the tropics, reproduction of some species may be seasonal (SHINE 2003, ALVES *et al.* 2005), with recruitment occurring mainly during the rainy season, when prey availability appears to be higher (MARTINS & OLIVEIRA 1999). This does not seem to be the case of *I. cenchoa*, for which both immature and mature males and females feed on common lizard species, as seen previously, in all seasons, in the studied area.

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

Acre: About 5 Km N. de Porto Walter, Juruá river: MPEG 20377.

Amapá: Jari, Santo Antônio waterfall: MPEG 17746. Km 95 of the BR-156: MPEG 16673. Macapá: MPEG 18945, MPEG 18948.

Amazonas: Carreiro da Várzea, Km 2 of the road for Autazes: MPEG 19533, MPEG 19534, MPEG 19535. Coari, Porto Urucu: MPEG 18851. Ituxi river, Madereira Scheffer: MPEG 20323, MPEG 20324, MPEG 20325. Maraã, Maguari: MPEG 18020, MPEG 18021. Maraã, Santa Rita, Left bank of Paricá river: MPEG 17865, MPEG 17867. Morrinho, Madeira River: MPEG 21108, MPEG 21109, MPEG 21110. Presidente Figueiredo, Uatumã river, UHE-Balbina: MPEG 17410, MPEG 17417, MPEG 17423, MPEG 17442, MPEG 17448, MPEG 17457, MPEG 17458, MPEG 17588.

Maranhão: BR-316, about 8 Km of the Bacabal, Mearim river: MPEG 18668. Highway Belém-Brasília: MPEG 306. Nova Vida, 25 Km away from the Gurupi river, BR-316: MPEG 10314, MPEG 10315, MPEG 10316, MPEG 10317, MPEG 10320, MPEG 10321, MPEG 10322, MPEG 11143, MPEG 11144, MPEG 12289, MPEG 12291, MPEG 12717, MPEG 12719, MPEG 13738, MPEG 15318. Paruá, BR-316: MPEG 13642, MPEG 13646, MPEG 14348. São Raimundo, BR-316: MPEG 10877. Urbano Santos, Fazenda Santo Amaro: MPEG 20543. Vila Nova, Pará: MPEG 24021.

Pará: Agropecuária WE, UHE-Belo Monte, Tapuamã, Altamira: MPEG 22402, MPEG 23097, MPEG 23101. Anajás, Ilha de Marajó: MPEG 320, MPEG 20674. Barcarena: MPEG 16471, MPEG 20035, MPEG 20036, MPEG 23432. Belém: MPEG 325, MPEG 358, MPEG 1524,

MPEG 2061, MPEG 20673. Benevides: MPEG 611, MPEG 612, MPEG 721, MPEG 854, MPEG 1006, MPEG 1856, MPEG 2602, MPEG 3976, MPEG 6029, MPEG 6019, MPEG 7567, MPEG 7584, MPEG 8410, MPEG 12574, MPEG 15482. Bragança: MPEG 2251, MPEG 2479, MPEG 2480, MPEG 4371, MPEG 7944, MPEG 8242, MPEG 8252, MPEG 8290, MPEG 8291, MPEG 8293, MPEG 8574, MPEG 8576, MPEG 11371. Cachoeira do Arari, Ilha do Marajó: MPEG 18317. Cacoal, Augusto Corrêa: MPEG 5389, MPEG 10771. Canaã dos Carajás: MPEG 16714, MPEG 20622. Capitão Poço: MPEG 1012, MPEG 6076, MPEG 8176, MPEG 11041, MPEG 15401. Castanhal: MPEG 530, MPEG 531, MPEG 712, MPEG 972, MPEG 2034, MPEG 2035, MPEG 2673, MPEG 2674, MPEG 2676, MPEG 2678, MPEG 4022, MPEG 4756, MPEG 4759, MPEG 4765, MPEG 6940, MPEG 10532, MPEG 10778, MPEG 11292, MPEG 19666. Chiqueirão: MPEG 16689, MPEG 16798. Colônia Nova, BR-316: MPEG 2971, MPEG 5176, MPEG 5202, MPEG 8211, MPEG 9562, MPEG 10305, MPEG 11464, MPEG 13961, MPEG 14806. Curuçá, Marauá: MPEG 7138, MPEG 7627. Distrito Industrial, Ananindeua: MPEG 19255. Faro, Flota Faro: MPEG 23080. Ilha Santa Rosa: MPEG 16413. Ipixuna do Pará: MPEG 21343. Km 23 to the road of Maracanã: MPEG 4819, MPEG 5812. Km 16 to the road of Acará: MPEG 8055, MPEG 8066, MPEG 8068, MPEG 8077, MPEG 12798, MPEG 13372. Bujarú: MPEG 16451. Juruti: MPEG 21026, MPEG 22410, MPEG 22411, MPEG 22413, MPEG 22414, MPEG 22415, MPEG 22412, MPEG 22416, MPEG 22679, MPEG 22690, MPEG 23283, MPEG 23284, MPEG 23285, MPEG 23367, MPEG 23376, MPEG 23377, MPEG 23398, MPEG 24286, MPEG 24321, MPEG 24341. Flona Tapirapé-Aquiri: MPEG 19364, MPEG 19374, MPEG 23894, MPEG 23895. Marabá, Carajás: MPEG 16491, MPEG 16897, MPEG 17231, MPEG 23808. Marituba: MPEG 16433. Melgaço, Caxiuanã: MPEG 18649, MPEG 18969, MPEG 19725, MPEG 19733, MPEG 19753, MPEG 19946, MPEG 20022, MPEG 20023, MPEG 20024, MPEG 20025, MPEG 20137, MPEG 20202, MPEG 20228, MPEG 20305, MPEG 20484, MPEG 20485, MPEG 20613, MPEG 20893, MPEG 20894, MPEG 20895, MPEG 20896, MPEG 20897, MPEG 20898, MPEG 20899, MPEG 20900, MPEG 20923, MPEG 20925, MPEG 20926, MPEG 20927, MPEG 20928, MPEG 21872, MPEG 21873, MPEG 21874, MPEG 21875, MPEG 21876, MPEG 21877, MPEG 21878, MPEG 21879, MPEG 21880, MPEG 21881, MPEG 21882, MPEG 21883, MPEG 21884, MPEG 21885, MPEG 21886, MPEG 21887, MPEG 21888, MPEG 21889, MPEG 21890, MPEG 21891, MPEG 21892, MPEG 21893, MPEG 21894, MPEG 21895, MPEG 21896, MPEG 21897, MPEG 21898, MPEG 21899, MPEG 21900, MPEG 21901, MPEG 21902. Monte Dourado, Almeirim: MPEG 21392. Óbidos, Flota Trombetas: MPEG 23659, MPEG 23660. Oriximiná, Porto Trombetas: MPEG 17030, MPEG 19668, MPEG 19798, MPEG 19800, MPEG 20788, MPEG 21564, MPEG 22174, MPEG 22319, MPEG 22320, MPEG 23504, MPEG 23507, MPEG 23846. Ourém, Limão Grande: MPEG 6138, MPEG 6181, MPEG 6190, MPEG 6200. Ourilândia do Norte, Serra do Granito: MPEG 20662. Parauapebas, Barragem da Pêra: MPEG 22916, MPEG 22917. Parque Indígena de Tumucumaque, Aldeia Apalaí, Parú do Leste river: MPEG 16374. Peixe Boi: MPEG 1411, MPEG 1416, MPEG 3911, MPEG 18775. Ponta de Pedras, Ilha de Marajó: MPEG 16461. Portel, Fazenda Riacho Monte verde. Precious Woods: MPEG 22705, MPEG 22706, MPEG 22707. Santarém: MPEG 19038, MPEG 19058, MPEG 19061, MPEG 19062, MPEG 19078, MPEG 19089, MPEG 19102, MPEG 19106. Santa Rosa. Road of Vigia: MPEG 4010, MPEG 9584, MPEG 11805. Viseu: MPEG 1038, MPEG 2550, MPEG 4422, MPEG 4428, MPEG 4454, MPEG 5251, MPEG 5252, MPEG 5253, MPEG 7322, MPEG 7335, MPEG 7656, MPEG 8928, MPEG 10188, MPEG 10881, MPEG 10882, MPEG 10883, MPEG 10885, MPEG 14133, MPEG 14929.

Rondônia: Espigão do Oeste: MPEG 21062. Parque Estadual de Guajará Mirim: MPEG 19492, MPEG 19493, MPEG 19494, MPEG 19495, MPEG 19496, MPEG 19497, MPEG 19498, MPEG 19499, MPEG 19500. Pimenta Bueno: MPEG 19397. Porto Velho, Jamari river: MPEG 17839, MPEG 17888, MPEG 17889, MPEG 17890, MPEG 17939.

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