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Reproductive biology and food habits of *Pseudoboa nigra* (Serpentes: Dipsadidae) from the Brazilian cerrado

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Abstract

Reproductive biology and food habits of *Pseudoboa nigra* (Serpentes: Dipsadidae) from the Brazilian cerrado. Herein we provide data on body size, sexual size dimorphism, reproductive cycle, and food habits of the pseudoboini snake *Pseudoboa nigra*, which is distributed mainly in central South America throughout the Cerrado domain. Based on dissections of 147 preserved specimens, it is shown that females attain, and mature at, larger body sizes than males. There is no significant sexual dimorphism in head length, but males have longer tails relative to their body sizes. Vitellogenesis, egg-laying, and sperm production occur throughout the year, but males do not exhibit long-term sperm storage. The main prey of *P. nigra* is lizards; there is no evidence of ontogenetic change or sex differences in the diet of this species.

Keywords: Serpentes, Colubridae, Pseudoboini, South America, sexual dimorphism snake, reproductive cycles, diet.

Resumo

Biologia reprodutiva e hábitos alimentares de *Pseudoboa nigra* (Serpentes: Dipsadidae) do cerrado brasileiro. Neste trabalho fornecemos informações sobre tamanho corporal, dimorfismo sexual, ciclo reprodutivo e hábitos alimentares da serpente Pseudoboini *Pseudoboa nigra*, que ocorre no domínio do Cerrado na região central da América do Sul. Com base na dissecção de 147 espécimes preservados, mostramos que as fêmeas são em média maiores e atingem maturidade sexual com maior tamanho corporal que os machos. O dimorfismo sexual não foi significativo para o tamanho da cabeça, mas os machos possuem caudas relativamente mais longas que as fêmeas. A vitelogênese, a postura de ovos e a espermatogênese ocorrem durante todo o ano, e os machos não armazenam esperma no ducto deferente por longos períodos. A principal presa dessa espécie são lagartos; não há evidências de variação ontogenética ou de diferenças relacionadas ao sexo na dieta dessa espécie.

Palavras-chave: Serpentes, Colubridae, Pseudoboini, América do Sul, dimorfismo sexual, ciclo reprodutivo, dieta.

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Introduction

Adaptationist ecologists argue that most characters of an organism are shaped by natural selection, and that they represent environmental adaptations and confer fitness advantages to the organism. Natural selection can affect many life history traits of the organisms, including reproduction and diet. For example, the tropical snakes *Tropidonophis mairii* have reproductive peaks during the early dry season when the eggs experience lower risks of both water logging and dehydration (Brown and Shine 2006). In garter snakes (*Thamnophis elegans* and *T. sirtalis*), diet varies geographically and may be related to prey availability (Arnold 1977, Kephart 1982). However, phylogenetic conservatism may have considerable influence on life history traits (Gould and Lewontin 1979). Conserved intrageneric patterns in the reproductive traits (e.g., seasonality, sexual dimorphism, clutch size, egg size) and diet have been observed in snakes (e.g., Shine 1989, Martins *et al.* 2002) and also occur in higher taxonomic levels (e.g., Pizzatto and Marques 2007, Pizzatto *et al.* 2008a,b). Diet also may be strongly influenced by phylogeny (Greene 1983, Martins *et al*. 2002), although in many cases, it depends on prey availability (Shine 1993, Hartmann and Marques 2005). In most instances, dietary and reproductive patterns of snakes only become evident once there is an accumulation of published data on life history traits of individual species.

Pseudoboa comprises six species of dipsadid snakes that belong to the monophyletic tribe Pseudoboini (Zaher *et al.* 2009). New species of *Pseudoboa* are still being discovered and described (Zaher *et al*. 2008), suggesting that this group is poorly known. Some data on natural history are available for few members of the tribe (e.g., *Oxyrhopus guibei:* Andrade and Silvano 1996, Pizzatto and Marques 2002; *Clelia* spp. and *Boiruna maculata:* Pinto and Lema 2002, Pizzatto 2005; *Siphlophis* spp.: Prudente *et al*. 1998). However, limited information is available for species of *Pseudoboa* (e.g., Cunha and Nascimento 1983, Martins and Oliveira 1998), and none of these snakes has been specifically investigated in ecological studies. Published information on *Pseudoboa* reveals that these snakes are nocturnal, terrestrial, and feed mostly on lizards (Vanzolini *et al*. 1980, Pérez-Santos and Moreno 1988, Cei 1993, Murphy 1997, Martins and Oliveira 1998), but data on morphometrics, food habits, and reproductive cycles of males and females remain scarce for most species, especially *P. nigra*.

Unlike its congeners, *Pseudoboa nigra* inhabits open-vegetation formations, and is widely distributed throughout the Caatinga, Cerrado, and Chaco (Bailey 1970, Zaher *et al.* 2008), but the species occurs mainly in Cerrado areas. In this study, we present data from preserved specimens on sexual dimorphism, diet, and the reproductive cycle of female and male *Pseudoboa nigra* from the cerrado. Our findings are compared with those from studies of other pseudoboini.

Materials and Methods

We examined a total of 147 Brazilian specimens of *Pseudoboa nigra* housed in the collection of Instituto Butantan, São Paulo, Brazil. According to the current taxonomy, this species has two color morphs in adults—one is plain black and the other is black with irregular white patches (Figure 1). However, because the second morph may represent a different species (*P. albimaculata* see Marques *et al*. 2005), only the former was considered in this study. The specimens were collected throughout Brazilian Cerrado domain that includes 12 states of Brazil (between 2°53'39" N and 22º11'15" S, 35°19'46" E and 57°52'57" W), but most originated from the states of São Paulo (29.3%) and Mato Grosso do Sul (24%). The states of Goiás, Mato Grosso, Minas Gerais, Tocantins, and Maranhão are underrepresented in our samples (voucher numbers and localities in Appendix I). The cerrado is covered by a mosaic of savanna-like vegetation, with interspersed patches of grasslands, woodlands, and gallery forests along

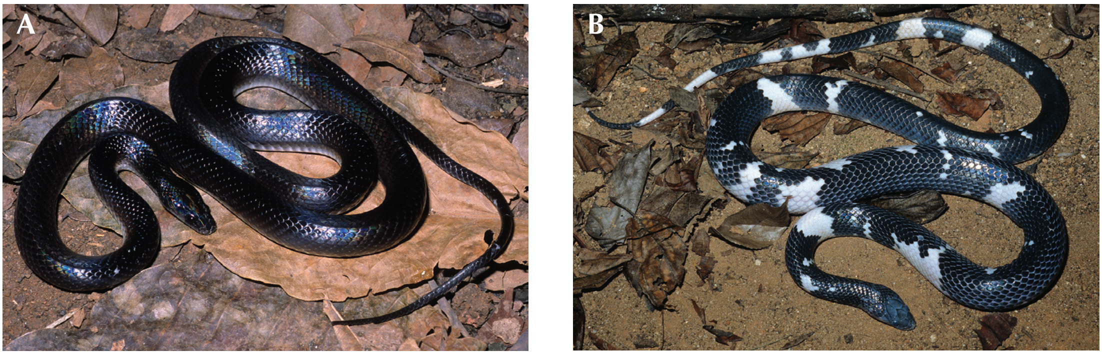

Figure 1. The two morphological variants of *Pseudoboa nigra*. (**A**) Black pattern, (CT = 675 + 185 mm, m = 85 g, IB66356, UHE Luiz Eduardo Magalhães, Porto Nacional, TO). (**B**) Black with white spots pattern (CT > 800 mm, UHE Sérgio Motta, Presidente Epitácio, SP/Anaurilândia, MS).

river courses (Silva and Bates 2002). Climate is diverse throughout the biome, but seasonality is marked, with most of the 750–2000 mm of rainfall occurring between October and March, depending on the region (Adámoli *et al.* 1987).

A mid-ventral incision was made in each specimen and the following data were recorded: (1) sex; (2) snout–vent length (SVL in mm, with a ruler); (3) head length (mm, with Vernier calipers); (4) tail length (mm, with a ruler); (5) body mass after draining the preservative liquid (g, with PESOLA® scale); (6) reproductive maturity or immaturity based on the presence of large testes or an opaque, convoluted vas deferens in males, and the presence of eggs, ovarian follicles in secondary vitellogenesis (>5 mm), or folded oviducts in females (Shine 1980); (7) diameter (mm) of the largest ovarian follicle or largest egg (with Vernier calipers); (8) length (mm) of the right testis (with Vernier calipers); (9) vas deferens diameter (mm) close to the cloaca (with Vernier calipers; Almeida-Santos *et al*. 2006); and (10) gut contents, which were removed and identified to the lowest possible taxonomic category.

The sexual size dimorphism (SSD) index (Shine 1994) was calculated as:

(mean SVL of the larger sex/mean SVL of the smaller sex) – 1.

Differences in mean SVLs between males and females were compared using a *t*-test. Sexual dimorphisms (in head and tail lengths), and seasonal variation (wet season: Oct.–Mar., dry season: Apr.–Sept.) in testis size and diameter of vas deferens were analyzed by ANCOVA, using SVL as a covariate. Means presented are always followed by standard deviations. Statistical tests were performed using Statistica6® with alpha-value set at 0.05.

Results

Adult females are larger (881.3 ± 149.2 mm SVL; range: 561–1261 mm; n = 68) and heavier (267.9 ± 125.9 g, n = 68) than males (736.7 ± 114.28 mm SVL; range: 548–1046 mm; n = 42; t = 5.37; df = 108; $p < 0.0001$; 175.6 ± 85.2 g, n = 42; t = 4.19, df = 108, $p < 0.0001$). The SSD index is 0.30. Females have shorter tails relative to body size than males do (ANCOVA: log-transformed variables; slopes $F_{(1,103)} = 1.36$, $p = 0.204$, sex $F_{(1,103)} = 58.07$, $p < 0.0001$). Relative head size is the same in both sexes (ANCOVA: slopes $F_{(1,101)} = 0.022$, $p = 0.883$; sex $F_{(1,101)} = 0.02$, $p = 0.970$). Newborn snakes (SVL < 340 mm; the maximum newborn size considered to be 50% larger the smallest snake sampled) were collected in March (n = 1; SVL = 308 mm), April (n = 2; SVL = 268 and 234 mm), May (n = 1; SVL = 298), July (n = 3; SVL = 234; 296 and 303 mm), August (n = 1; SVL = 311 mm), and October (n = 2; SVL = 292 and 324 mm).

Three females had oviducal eggs (6, 7, and 8, respectively), in February and September (Figure 2). Females with ovarian follicles in secondary vitellogenesis were found throughout the year. Minimally, about 30% of the females in our sample may be reproductive (i.e., individuals having oviductal eggs or follicles larger than 10 mm; Pizzatto 2005). No seasonal variation was detected in testis length (variables log-transformed; slopes $F_{(1,34)}$ = 0.183, p = 0.671; sex $F_{(1,34)}$ = 0.001, p = 0.973; Figure 3) or diameter of the vas deferens (variables log-transformed; slopes $F_{(1,32)}$ = 0.922, p = 0.344; sex $F_{(1,32)}$ = 1.49, p = 0.232; Figure 3).

Forty-two snakes (28.6% of the total 150) had food in the gut. Lizards are the most frequent prey item (92.9% of total; Table 1). One snake ingested two lizard eggs and another had mammal fur in the intestine (Table 1). One immature snake had snake and anuran remains in its guts (Table 1). However, the latter specimen was collected from a habitat that was being flooded as part of a new hydroelectric installation. Under these circumstances, the natural microhabitat of the animals may change and they are likely exhibit atypical behavior, capturing unusual prey. All lizards except one were ingested head-first. We did not detect dietary differences between immature and mature snakes, or between males and females in the types of prey ingested (Table 1). Because most of the gut contents were vestigial, we could not analyze relationships between prey and predator sizes.

Discussion

The reproductive traits of *Pseudoboa nigra* are similar to those recorded for other pseudoboini snakes. Sexual dimorphism in size with females being larger than males is characteristic of snakes lacking male-male ritual combat (Shine 1994), and also characterizes *Clelia* and *Oxyrhopus*. The SSD index of 0.3 is similar to the values reported for *Oxyrhopus guibei* and the larger species of *Clelia* (Pizzatto and Marques 2002, Pizzatto 2005). Just as in most non-arboreal snakes, male *P. nigra* have relatively longer tails than females to accommodate the hemipenis in males (King 1989).

The occurrence of eggs and neonates throughout the year suggests a continuous female reproductive cycle. This may ubiquitous among members of the pseudoboini tribe, save for those species inhabiting high altitudes (Pizzatto and Marques 2002, Pizzatto 2005). Our data on clutch size are limited, but, when the average body length is considered, *Pseudoboa nigra* apparently has smaller clutches than *Oxythopus guibei* and *Clelia rustica,* but similar-sized clutches to large species of *Clelia* (Pizzatto and Marques 2002, Pizzatto 2005). The percentage of reproductive females during the reproductive season indicates reproductive frequency (Blem 1982). Other pseusoboini seem to have annual reproduction (50% or more females reproductive; see Pizzatto and Marques 2002, Pizzatto 2005), but *P. nigra* may reproduce less often.

Data on male reproductive cycles of tropical snakes are fewer than for females because the morphological changes in the male reproductive tract are less obvious macroscopically than those of females. Therefore, large sample sizes are needed to detect significant changes. Testicle dimensions (length, surface, or diameter) reflect cell activities (Volsøe 1944, Clesson *et al.* 2002, Schuett *et al.* 2002); thus, testes increase in size during sperm production. The sperm are released into the vas deferens, where they are stored until mating occurs, and the diameter of the vas deferens is correlated with the amount of sperm it contains (Yokoyama and Yoshida 1993, Almeida-Santos *et al.* 2004, Sever *et al.* 2004). These variations in morphology are significant, especially when cycles are seasonal. The lack of variation in the sizes of male testis or the vas deferens in *Pseudoboa nigra* indicates a continuous male reproductive cycle, in which sperm are continuously produced and released into the

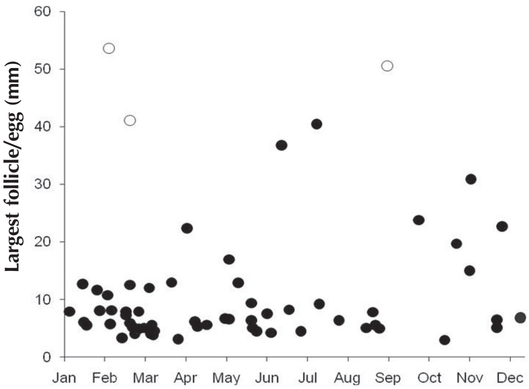

Figure 2. Seasonal variation in the diameter of ovarian follicles (solid circles) and oviducal eggs (open circles) of *Pseudoboa nigra*.

vas deferens, or at least a low seasonality. The absence of seasonal variation in the diameter of the vas deferens suggests there is no long-term storage of sperm and the snakes may copulate throughout the year. Continuous reproductive cycles in males are common in tropical snakes and occur in *O. guibei* and other tribes of xenodontinae (such as xenodontini: Pizzatto *et al.* 2008a).

Phylogeny has an important role in reproductive patterns. Pizzatto (2005) and Pizzatto *et al*. (2008a) used the same methods as we did in this study and reported that Neotopical endemic xenodontine snakes of the tribes Pseudoboini and Xenodontini have the potential to reproduce continually. As in most studies based on museum specimens, our study includes animals from several localities and collected in different years; thus, we are able to characterize the general reproductive pattern for this species. The methodology that we used did not permit us to identify interpopulational, geographic, or annual variations in the reproductive cycles or small variations in sperm production that are not reflected by changes in the size of the testis. Other studies of Neotropical snakes suggest that minor climate changes can modify the length of reproductive cycle, but only major climate changes are likely to be sufficient to change a seasonal cycle to a continuous one (e.g., Seigel and Ford 1987, Pizzatto 2005, Pizzatto and Marques 2006). Histological studies of male reproductive structures also can reveal minor seasonal variation in sperm production and storage. Clutch size and reproductive frequency are likely to be influenced by prey availability and minor climatic fluctuations. These less significant variations in reproductive cycles still require further investigation in snakes from tropical areas, where climatic patterns are complex.

Most snakes in the Tribe Pseudoboini feed on lizards (including their eggs), snakes, and mammals; anurans are unusual prey items.

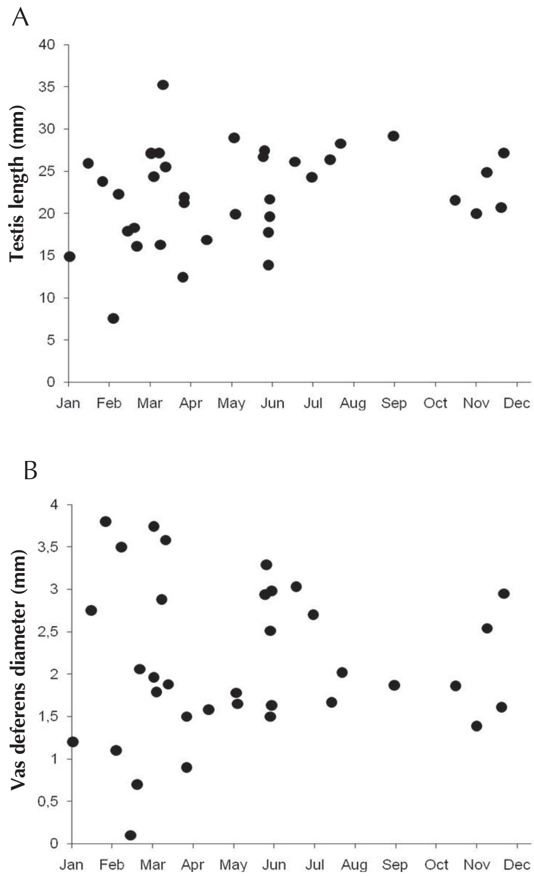

Figure 3. Seasonal variation in the relative testis length (**A**) and diameter of vas deferens (**B**) in *Pseudoboa nigra*.

Table 1. Prey items extracted from preserved specimens of *Pseudoboa nigra* from Brazil. Total of 43 prey items from 42 snakes.

Prey type	Number of records		
	Juvenile	Female	Male
Reptilia			
Ameiva ameiva	7	4	2
Cnemidophurus sp.	1	–	–
Tropidurus sp.	5	2	1
Tropidurus hispidus	–	2	2
Tropidurus cf. *itambere*	1	1	–
Tropidurus torquatus	2	3	1
Teiidae unidentified	4	–	–
Unidentified lizard	1	–	–
Lizard eggs	1	–	–
Unidentified snake[1]	1	–	–
Anura			
Unidentified species[1]	1	–	–
Mammalia			
Cricetidae: Sigmodontinae: unidentified	–	1	–
Totals	**24**	**13**	**6**

[1] Prey ingested under unnatural conditions; see text for explanation.

Pseudoboine species vary in degree of diet specialization (Sazima and Haddad 1992, Cei 1993, Andrade and Silvano 1996, Martins and Oliveira 1998, Prudente 1998, Prudente *et al*. 1998, Marques and Sazima 2004). This study confirms that *Pseudoboa nigra* is a lizard specialist (Vanzolini *et al.* 1980), and that it consumes mammals and lizard eggs only rarely. Lizards are the main prey for other species of *Pseudoboa* (Vanzolini *et al.* 1980, Pérez-Santos and Moreno 1988, Cei 1993, Martins and Oliveira 1998), as well as members of two other genera of Pseudoboini *Siphlophis* and *Phimophis* (Rodrigues 1993, Prudente *et al*. 1998, Marques and Sazima 2004, Schrocchi *et al*. 2006, Sawaya *et al*. 2008). Like other species in the tribe, species of *Pseudoboa* are mainly nocturnal (Martins and Oliveira 1998); thus, *P. nigra* may actively search for resting prey, because all lizards we recorded in the diet of this snake are diurnal.

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Appendix I. Specimens examined organized alphabetically by Brazilian states. The abbreviations for the state names are, as follow: AL = Alagoas, BA = Bahia, CE = Ceará, GO = Goiás, MA = Maranhão, MG = Minas Gerais, MS = Mato Grosso do Sul, PA = Pará, PI = Piauí, RN = Rio Grande do Norte, SP = São Paulo, TO = Tocantins.

Alagoas: Maceió (09°39′ S, 35°44′ W): IBSP 48449, 48989, 48990.

Bahia: Belmonte (15°51′ S, 38°52′ W): IBSP 50604; Brumado (14°12′ S, 41°39′ W): IBSP 32053, 40821, 42164; Itaetê (13°03′ S, 41°09′ W): IBSP 66390; Itaparica (12°53′ S, 38°40′ W): IBSP 52105; Muritiba (12°37′ S, 38°59′ W): IBSP 49306–307, 49336; Poções (14°31′ S, 40°31′ W): IBSP 28169; Porto Seguro (16°26′ S, 39°03′ W): IBSP 54380, 54394, 54433, 54528, 54597, 56438, 61099.

Ceará: Crato (07°14′ S, 39°24′ W): IBSP 20130, 20139; Fortaleza (03°43′ S, 38°32′ W): IBSP 19822–23, 20000, 43073, 43616; Unknown: IBSP 19819, 20054–55, 20058, 20086–87, 20091, 20202–03, 20253.

Goiás: Alto Paraíso de Goiás (14°07′ S, 47°30′ W): IBSP 62523; Campinorte (14°18′ S, 49°09′ W): IBSP 5688, 7772; Leopoldo de Bulhões (16°37′ S, 48°44′ W): IBSP 9971; Minaçu UHE (13°30′ S, 48°21′ W): IBSP 9134–35, 56724.

Maranhão: São Bento (02°41′ S, 44°49′ W): IBSP 56908, 56918; São Vicente Ferrer (07°35′ S, 35°30′ W): IBSP 56914.

Minas Gerais: Araguari (18°38′ S, 48°11′ W): IBSP 58317, 67000; Engenheiro Lisboa (19°48′ S, 47°36′ W): IBSP 5870; Passos (20°43′ S, 46°36′ W): IBSP 22869, 28401–02.

Mato Grosso do Sul: Anaurilândia (22°11′ S, 52°43′ W): IBSP 59427, 63874; Aquidauana (20°28′ S, 55°47′ W): IBSP 33457, 63665; Bodoquena (20°32′ S, 56°42′ W): IBSP 16768, 24468; Brasilândia (21°15′ S, 52°02′ W): IBSP 8937, 18474, 24902, 63297, 63666; Garcias (20°36′ S, 52°13′ W): IBSP 7780, 14368, 15572; Miranda (20°14′ S, 56°22′ W): IBSP 6243, 6290, 31734; Parnaíba (19°40′ S, 51°11′ W): IBSP 45974; Porto Murtinho (21°14′ S, 56°22′ W): IBSP 8994; Rio Pardo – O Rio, MS: IBSP 63080; Santa Rita do Pardo UHE (21°18′ S, 52°49′ W): IBSP 63826– 27; Três Lagoas (20°45′ S, 51°40′ W): IBSP 15287, 24707, 24893, 25009–10, 25029, 25072, 25073, 27380, 29054, 29364, 33150.

Pará: Cameta (02°14′ S, 49°29′ W): IBSP 2217.

Piauí: Teresina (05°05′ S, 42°48′ W): IBSP 48747, 49810, 50263.

Rio Grande do Norte: São Gonçalo do Amarante (05°46′ S, 35°19′ W): IBSP 53850.

São Paulo: Altinópolis (21°01′ S, 47°22′ W): IBSP 32874; Andradina (20°53′ S, 51°22′ W): IBSP 32681, 32699, 32861; Araçatuba (21°12′ S, 50°25′ W): IBSP 24681, 28441, 31635, 32442; Araraquara (21°47′ S, 48°10′ W): IBSP 50405; Barretos (20°33′ S, 48°34′ W): IBSP 16013; Barrinha (21°11′ S, 48°09′ W): IBSP 16726; Birigui (21°17′ S, 50°20′ W): IBSP 24954, 33355; Boribi (22°34′ S, 48°58′ W): IBSP 15916; Brodowski (20°59′ S, 47°39′ W): IBSP 10339; Igarapava (20°02′ S, 47°44′ W): IBSP 8241; Lavínia (21°10′ S, 51°02′ W): IBSP 29593, 63509; Marília (22°12′ S, 49°56′ W): IBSP 46662; Matão (21°36′ S, 48°21′ W): IBSP 52429–30; Morro Agudo (20°43′ S, 48°03′ W): IBSP 10328; Orlândia (20°43′ S, 47°53′ W): IBSP 4756, 9297, 44528, 55413; Palestina (20°23′ S, 49°25′ W): IBSP 5917; Pitangueiras (21°00′ S, 48°13′ W): IBSP 9311; Pontal (21°01′S , 48°02′ W): IBSP 9288, 9305; Presidente Epitácio (21°45′ S, 52°06′ W): IBSP 10277, 16667; Sales de Oliveira (20°46′ S, 47°50′ W): IBSP 29641, 32623; São Joaquim da Barra (20°34′ S, 47°51′ W): IBSP 9247, 18772; Uchoa (20°57′ S, 49°10′ W): IBSP 17362, 28239, 30171; Valentim Gentil (20°25′ S, 50°05′ W): IBSP 28610; Votuporanga (20°25′ S, 49°58′ W): IBSP 32192, 32336, 33921.

Tocantins: Alvorada (12°28′ S, 49°07′ W): IBSP 5611; Lageado UHE (09°45′ S, 48°21′ W): IBSP 66265–66; P. Nacional UHE (10°42′ S, 48°25′ W): IBSP 65904, 65930, 66083–84, 66170; Palmas UHE (10°12′ S, 48°21′ W): IBSP 65403; Sandolândia (12°32′ S, 49°55′ W): IBSP 56562.