



RESEARCH ARTICLE

Reproductive and fat body cycles of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata, Tropiduridae) in a caatinga area of northeastern Brazil

Ciclos reproductivos y de grasa corporal de *Tropidurus hispidus* y *Tropidurus semitaeniatus* (Squamata, Tropiduridae) en una área de caatinga del nordeste de Brasil

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ABSTRACT

This study assessed the reproductive and fat body cycles of *Tropidurus hispidus* (Spix, 1825) and *T. semitaeniatus* (Spix, 1825) in an area of caatinga in the Seridó of Rio Grande do Norte, Brazil, from October 2006 to May 2008. In both species, the females were reproductively active from the middle of the dry season to the beginning of the rainy season. Female reproductive activity was influenced by precipitation, whereas males exhibited spermatozoa in their testes throughout the year, and their reproductive activity was not related to any of the climatic variables analyzed. Mean clutch size (\pm SD) was 8.1 ± 2.0 and 2.1 ± 0.6 eggs in *T. hispidus* and *T. semitaeniatus*, respectively, and was significantly related to female body size only in *T. hispidus*. The fat stock varied inversely with reproductive activity in the two species, and there was no difference in fat body mass between females and males. The effects of precipitation on the length of the breeding season of these two *Tropidurus* species suggest that their reproductive cycles are related to the microclimatic conditions suitable for embryo development, as well as for the neonates' emergence and survival especially during the rainy season, which may offer greater food availability to the hatchlings.

Key words: body size-fecundity, clutch size, minimum size at maturity, reproduction, semiarid.

RESUMEN

Este estudio evaluó los ciclos reproductivos y de grasa corporal de *Tropidurus hispidus* (Spix, 1825) y *T. semitaeniatus* (Spix, 1825) en una área de caatinga en el Seridó de Rio Grande do Norte, Brasil, de octubre de 2006 a mayo de 2008. En ambas especies, las hembras se encontraron reproductivamente activas a partir de mediados de la estación seca para el inicio de la temporada de lluvias. La actividad reproductiva de las hembras fue influenciada por las precipitaciones, mientras que los machos presentaron espermatozoides en los testículos durante todo el año, y su actividad reproductiva no fue relacionada con ninguna de las variables climáticas analizadas. El tamaño medio (\pm DE) de la nidada fue de 8.1 ± 2.0 y 2.1 ± 0.6 huevos en *T. hispidus* y *T. semitaeniatus*, respectivamente, y se relacionó significativamente con el tamaño corporal de la hembra solo en *T. hispidus*. La reserva de grasa varió inversamente con la actividad reproductiva en las dos especies, y no hubo diferencia en la cantidad de grasa corporal entre hembras y machos. Los efectos de la precipitación sobre la duración de la temporada reproductiva de estas dos especies de *Tropidurus* sugieren que sus ciclos reproductivos están relacionados con las condiciones microclimáticas adecuadas para el desarrollo del embrión, así como para la emergencia de los recién nacidos y su supervivencia, especialmente durante la temporada de lluvias, que es la que puede ofrecer una mayor disponibilidad de alimentos para las crías.

Palabras clave: relación tamaño corporal y fecundidad, reproducción, tamaño de la postura, tamaño mínimo de madurez, semiárido.

INTRODUCTION

A diversity of reproductive strategies occurs among Squamata (Tinkle et al. 1970, Fitch 1982,

Zug et al. 2001), involving a set of elements promoting variation of these strategies within and between species, such as phylogeny, morphological characteristics of lineages,

and adaptive responses to environmental conditions; these factors may act alone or in combination (Ballinger 1983, Vitt 1992, Colli et al. 1997, Ramírez-Bautista et al. 2002). The temporal pattern of reproduction in Squamata is often associated with limiting environmental conditions. In temperate regions, reproductive activity is seasonal and dictated by temperature and day length (Fitch 1970, Duvall et al. 1982, Meshaka et al. 2006). In tropical regions, Squamata exhibit a wide range of reproductive patterns, from continuous reproductive cycles to strictly seasonal reproduction, making it difficult to identify the environmental factors that may be limiting (Vitt 1992, Clerke & Alford 1993). However, the reproductive cycles of tropical species living in environments with seasonal variation have been connected to the effects of precipitation (Van Sluys et al. 2002, Ávila et al. 2008), i.e., the reproductive activities of a large number of tropical lizard species are reduced or interrupted during the dry season (Fitch 1970, 1982).

Traditionally, two hypotheses are used to explain reproductive seasonality in tropical oviparous lizards: (1) the restriction of microhabitats with adequate moisture for egg development (Sexton et al. 1971, Andrews 1988, Wiederhecker et al. 2002), and (2) the lack of food resources for reproduction, offspring development, or both, during adverse seasonality (Rocha 1992, Van Sluys 1993, Vrcibradic & Rocha 1998). Additionally, a number of studies show the influence of temperature, precipitation, and day length on the reproduction of lizards (Adolph & Porter 1993, Smith 1996, Ramírez-Bautista et al. 1998, Wiederhecker et al. 2002). For the genus *Tropidurus* (sensu Frost et al. 2001), which includes oviparous and heliophyllous species (Rocha & Bergallo 1990, Van Sluys 1992, Vitt 1995) and typical of open habitats in South America (Rodrigues 1987, 1988, Frost et al. 2001), the reproductive cycle is usually seasonal in habitats that are also seasonal. This type of reproductive cycle is recorded for *T. spinulosus* (Cope) (Cruz et al. 1997), *T. itambere* Rodrigues (Van Sluys 1993), *T. montanus* Rodrigues (Van Sluys et al. 2002), and *T. torquatus* (Wied) (Wiederhecker et al. 2002).

Studies on the reproduction of *T. hispidus* (Spix, 1825) and *T. semitaeniatus* (Spix, 1825) were previously conducted in one caatinga

area in the state of Pernambuco, Brazil (Vitt 1981, Vitt & Goldberg 1983) and on *T. hispidus* in Venezuela (Prieto et al. 1976). Considering the influence of environmental factors on the reproductive cycles of lizards, including populations of the same species in different geographical regions (Howland 1992, Benabib 1994, Vitt & Colli 1994), coupled with the fact that precipitation in the caatingas is strongly seasonal, scarce, and irregular (Nimer 1972), our initial prediction was that the extent of the reproductive activity of *T. hispidus* and *T. semitaeniatus* in the caatinga of the present study should be affected by local environmental conditions. From this perspective, we conducted seasonal analyses of reproductive activity and fat body mass in female and male *T. hispidus* and *T. semitaeniatus* in sympatry, and their associations with environmental variables, in an area of caatinga in the state of Rio Grande do Norte, Brazil.

METHODS

Study area

The study was conducted at the Ecological Station of the Seridó (ESEC Seridó, 06°34'36.2" S, 37°15'20.7" W, datum: WGS84; altitude: 192 masl), which encompasses a caatinga area of 1166.38 hectares located in the municipality of Serra Negra do Norte, Rio Grande do Norte, Brazil. The climate is semiarid (Ab'Sáber 1974), with a short wet season concentrated between March and May and rainfall ranging between 500 and 700 mm year⁻¹. Mean annual temperatures vary from 28 to 30 °C, but can exceed 40 °C; the minimum ranges between 17 and 20 °C. Relative air humidity oscillates around 30-50 % in the dry season, reaching 80-90 % in the wet season (Nimer 1972). The vegetation of ESEC Seridó is arboreal-bushy hyperxerophilous (Varela-Freire 2002). Amidst this vegetation, various rocky extrusions are found that remain covered by the vegetation during the wet season, resulting in partially shaded areas. During the dry season these rocky outcrops become exposed after leaf fall (Velloso et al. 2002).

Lizard sampling and data analyses

Fieldwork was conducted on monthly excursions, each lasting three consecutive days, during two periods: from October 2006 to September 2007 to identify the reproductive period of *T. hispidus* and *T. semitaeniatus*; and from October 2007 to May 2008 to investigate the reproductive activity of these species, looking at a larger sample size. To make a comparison between the reproductive cycles and seasonality, the dry and rainy seasons were considered. The dry season lasted from October 2006 to February 2007 (dry season 2006/2007; mean monthly rainfall: 56.0 mm) and from July 2007 through January 2008 (dry season 2007/2008; mean monthly rainfall: 5.8 mm). The rainy season lasted from March to June 2007 (wet season 2007; mean monthly

rainfall: 101.5 mm) and between February and May 2008 (wet season 2008; mean monthly rainfall: 236.7 mm).

An area of ESEC Seridó composed of five rocky outcrops, each with an average distance of 20 m from the others, was designated for the collection. The lizards were captured between 0700 and 1800 h, using air rifles, and in some cases glue traps strategically placed in the crevices of rocks. At the end of each collection day, the lizards were dissected for gonad removal. In all the collected specimens snout-vent length (SVL) was measured using a manual caliper (to the nearest 0.1 mm), and body mass with Pesola® scale (to the nearest 0.2 g). The lizards were deposited in the Herpetological Collection of the Department of Botany, Ecology, and Zoology (CHBEZ) at the Federal University of Rio Grande do Norte.

Reproductive condition of females was determined based on the presence and number of vitellogenic follicles, eggs in the oviducts, and/or corpora lutea (Van Sluys 1993). Follicles were considered vitellogenic when yellow and larger than 2.0 mm in diameter, in accordance with Galdino et al. (2003). Clutch size was estimated by counting the number of vitellogenic follicles or eggs in the oviducts. The simultaneous occurrence of vitellogenic follicles and eggs in the oviducts or corpora lutea was considered indicative of the production of more than one clutch for the female per breeding season. For females in this condition, clutch size was estimated only by the number of oviductal eggs. The diameter of the vitellogenic follicles and the length and width of the eggs in the oviducts were measured with a manual caliper (0.1 mm). The SVL of the smallest female containing vitellogenic follicles or eggs in the oviducts was considered as the minimum SVL for sexual maturity. The effect of female SVL on clutch size (\log_{10} -transformed) was tested using simple regression analysis (Zar 1999).

To describe the male reproductive condition, the length and width of the left testis were measured with a manual caliper (0.1 mm), and the volume was estimated using the ellipsoid formula: $V = \frac{\pi}{6} (W^2) L$ (6⁻¹), in accordance with Wiederhecker et al. (2002), where V = testis volume, W = testis width and L = testis length. Subsequently, the testes and their respective epididymides were fixed in Bouin's fixative, dehydrated in ascending series of alcohol, cleared in xylene, and embedded in paraffin. Then they were sectioned at 5 mm, stained with hematoxylin-eosin, and mounted on slides. The slides were analyzed under an Olympus® BX41 microscope coupled with a Nikon® DXM 1200 digital camera, and the images were captured using the Nikon ACT-1 program. For each individual, 10 measurements in different fields of the seminiferous tubule diameter (STD) and germinative epithelium height (GEH) were obtained using Image-Pro Plus 4.5.0.29 software. The maturation stages used were those defined by Vieira et al. (2001) and the more advanced cell types of the spermatogenic lineage were recorded. Males were considered reproductively active when they had spermatozoa in the testes or epididymides. Averages for STD and GEH were used as secondary estimators of the reproductive activity of each individual. The minimum size at sexual maturity was determined as the SVL of the smallest male with spermatozoa, and all males with SVL equal or greater than the minimum were regarded as adults.

For fat body cycle analysis, the abdominal fat bodies were removed and weighed with an electronic scale (to the nearest 0.001 g; Gehaka® model BG200). To obtain the caloric content of fat bodies, the average composition

of 90 % lipids (Brian et al. 1972) and an equivalence of 37.656 kJ (9 kcal) to 1 g of lipids (Berne & Levy 1993) were considered.

To satisfy the normality conditions of the statistical analyses, some variables were transformed: square root of the arcsine of the monthly frequency of reproductive individuals, and logarithm (base 10) of testis volume and fat body mass. The effects of SVL on fat body mass were removed using the residuals of the simple linear regressions of this variable against SVL. To test the difference in fat body mass between the sexes, an ANCOVA was conducted with SVL as the covariate (Zar 1999). The effects of precipitation, air humidity, air temperature, and solar radiation (Fig. 1A, 1B) (obtained from the Laboratório de Recursos Hídricos e Saneamento Ambiental - LARHISA) on the frequency of reproductive individuals were tested using multiple regression analysis between these climatic variables, with an interval of one month. Data were analyzed using SPSS version 13.0. The significance level adopted for obtaining critical values on the tests was 0.05, and descriptive statistics are given as mean \pm 1 SD.

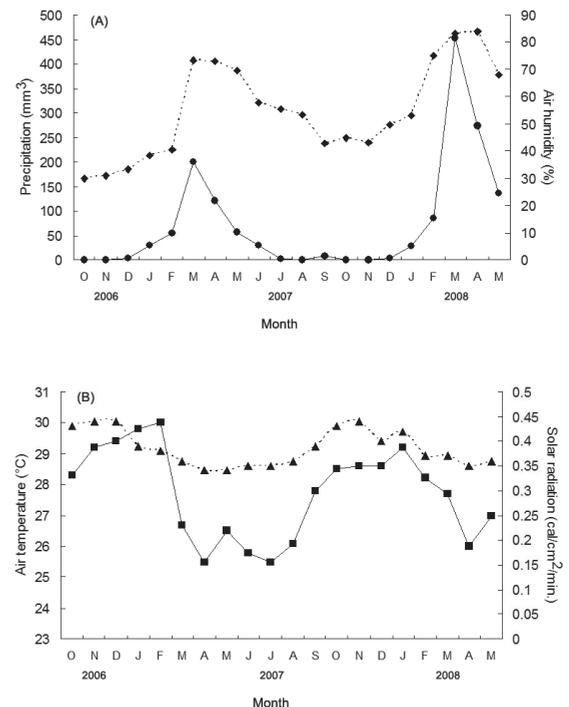


Fig. 1: Monthly values of climatic variables in the ESEC Seridó between October 2006 and May 2008, Serra Negra do Norte municipality, Rio Grande do Norte, Brazil. (A) total precipitation (—●—) and relative air humidity (---○---); (B) average air temperature (—■—) and solar radiation (---▲---).

Valores mensuales de las variables climáticas en la ESEC Seridó entre octubre de 2006 y mayo de 2008, Serra Negra do Norte, Rio Grande do Norte, Brasil. (A) precipitación total (—●—) y humedad relativa del aire (---○---); (B) temperatura media del aire (—■—) y radiación solar (---▲---).

RESULTS

Female reproductive cycle

In *T. hispidus*, SVL varied from 56.1 mm to 113.3 mm (86.8 ± 13.2 mm; $n = 51$), with the smallest reproductive female collected in January 2008 displaying vitellogenic follicles and measuring 65.0 mm. In *T. semitaeniatus*, SVL ranged from 38.3 mm to 87.4 mm (63.3 ± 7.6 mm; $n = 71$), and the smallest reproductive female containing follicles in vitellogenesis had a SVL of 59.0 mm and was collected in March 2007. All reproductive females of both species were collected from November 2006 to March 2007 (reproductive season I) and from November 2007 to April 2008 (reproductive season II) (Figs. 2A and 2B). Females containing vitellogenic follicles and oviductal eggs, indicating production of multiple clutches during the breeding season, occurred in January 2007 and in February and March 2008 for *T. hispidus* (Fig. 2A), and in January and February 2007 and March 2008 for *T. semitaeniatus* (Fig. 2B).

The mean diameter of the vitellogenic follicles and the mean egg volume were, respectively, 4.2 ± 2.6 mm ($n = 21$); 711.7 ± 107.1 mm³ ($n = 4$) for *T. hispidus*, and 4.8 ± 2.7 mm ($n = 29$), 595.8 ± 103.1 mm³ ($n = 3$) for *T. semitaeniatus*. These two estimates were calculated from individual female means, instead of the vitellogenic follicles and the eggs, grouped respectively. Clutch size estimated by the number of vitellogenic follicles did not differ from clutch size estimated by the number of eggs in the oviducts of both species (Mann-Whitney U test, $P > 0.05$). For this reason, data from both sources were combined to calculate clutch size, but when the females simultaneously contained vitellogenic follicles and eggs in the oviducts, only the number of eggs was used to preserve the independence of the data. Thus, the mean clutch size for *T. hispidus* was 8.1 ± 2.0 (range 6-13; $n = 22$) and was significantly correlated with SVL ($R^2 = 0.65$, d.f. = 1, $\beta_{\text{standardized}} = 0.70$, $P = 0.0001$). In *T. semitaeniatus* mean clutch size was 2.1 ± 0.6 (range 1 - 3; $n = 29$) and was not significantly correlated with SVL ($R^2 = 0.07$, d.f. = 1, $\beta_{\text{standardized}} = 0.16$, $P = 0.125$). In *T. hispidus*, a clutch size composed of six eggs was the most common, while in *T. semitaeniatus*, 96 % of females had clutches with two eggs.

The monthly frequency of reproductive females of *T. hispidus* was significantly related to climatic variables both in reproductive

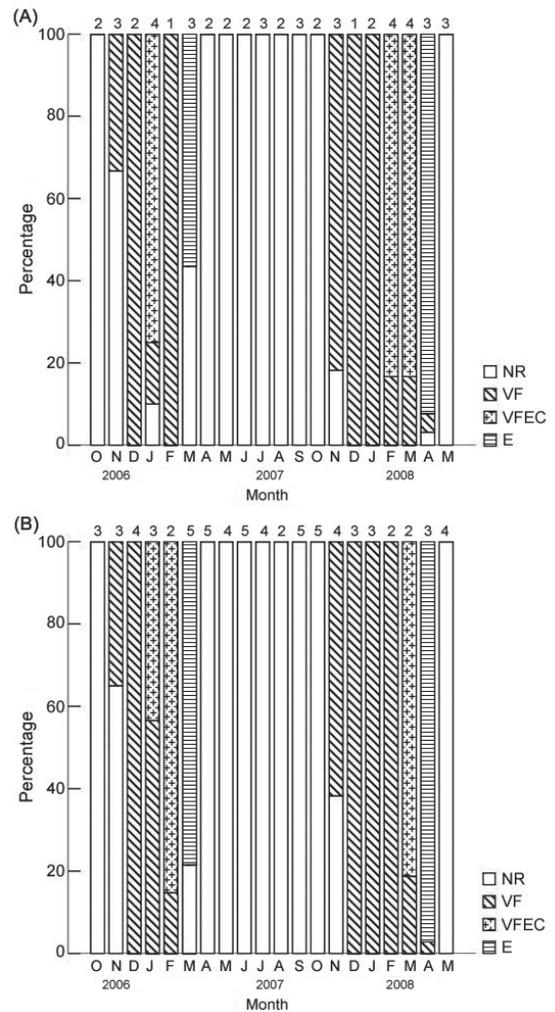


Fig. 2: Female reproductive condition of *Tropidurus hispidus* (A) and *Tropidurus semitaeniatus* (B) from October 2006 to May 2008 in the ESEC Seridó, Serra Negra do Norte municipality, Rio Grande do Norte, Brazil. NR = nonreproductive female; VF = presence of vitellogenic follicles; VFEC = simultaneous presence of vitellogenic follicles and eggs or vitellogenic follicles and corpora lutea; E = presence of eggs in the oviducts. Numbers above bars indicate sample size.

Condição reprodutiva de hembras de *Tropidurus hispidus* (A) y *Tropidurus semitaeniatus* (B) de octubre 2006 a mayo 2008 en la ESEC Seridó, Serra Negra do Norte, Rio Grande do Norte, Brasil. NR = hembra no reproductiva; VF = presença de folículos vitelogênicos; VFEC = presença simultânea de folículos vitelogênicos y huevos o folículos vitelogênicos y cuerpo lúteo; E = presença de huevos en los oviductos. Los números sobre las barras indican el tamaño de la muestra.

season I ($R^2 = 0.87$, $F_{3,8} = 11.8$, $P = 0.001$) and reproductive season II ($R^2 = 0.82$, $F_{3,11} = 19.3$, $P = 0.0001$), and in both seasons precipitation explained most of the variation in female reproductive activity (I: $\beta_{\text{standardized}} = 0.79$, $P = 0.0001$; II: $\beta_{\text{standardized}} = 0.77$, $P = 0.0001$). Similar results were recorded for *T. semitaeniatus*

in reproductive seasons I ($R^2 = 0.71$, $F_{3,15} = 15.6$, $P = 0.001$) and II ($R^2 = 0.83$, $F_{3,21} = 22.9$, $P = 0.0001$), when the monthly frequency of reproductive females was most strongly correlated with precipitation (I: $\beta_{\text{standardized}} = 0.73$, $P = 0.0001$; II: $\beta_{\text{standardized}} = 0.71$, $P = 0.0001$).

Male reproductive cycle

In *T. hispidus*, SVL ranged from 45.3 mm to 139.1 mm (97.6 ± 26.7 mm; $n = 34$), and the smallest reproductive male with a SVL of 68.0 mm, collected in February 2007, displayed testes and epididymides with mature spermatozoa in the lumen. In *T. semitaeniatus*, SVL varied from 27.7 mm to 86.7 mm (68.8 ± 14.7 mm; $n = 63$), and the smallest reproductive male, with a SVL of 68.5 mm, was collected in February 2007. Adult males of *T. hispidus* were collected with no spermatozoa in June, July, and September 2007, but adult males collected from October 2006 to May 2007, in August 2007 and between October 2007 and May 2008 were reproductively active (Fig. 3A). For *T. semitaeniatus*, males bearing spermatozoa were collected in all months except October 2006 (Fig. 3B). For nonreproductive adult males of both species, spermatocytes or spermatids were the most advanced cell types in the testes; for the young males, it was spermatogonia or spermatocytes.

According to the stages of spermatogenic activity, the testes of *T. hispidus* and *T. semitaeniatus* in stage I displayed most of the seminiferous tubules with no lumen, containing spermatogonia as the predominant cell type, especially in young specimens (Figs. 4A and 5A). Subsequently, stage II was characterized by the opening of the seminiferous tubules with the presence of spermatocytes in their margins and, in stage III, by the presence of spermatids in the luminal margins. Stage IV marked the peak of reproductive activity with the accumulation of spermatozoa in the lumen of the seminiferous tubules, which were commonly surrounded by Leydig cells (Figs. 4C and 5C). Finally, in Stage V the spermatogenic lineage cells became detached from the epithelium and scattered throughout the lumen of the seminiferous tubules (Figs. 4E and 5E), representing the regression phase of the germinative epithelium.

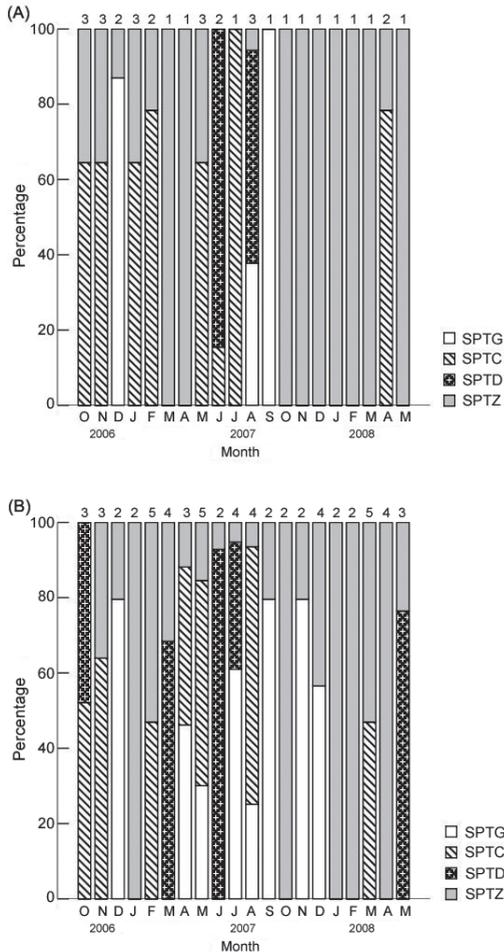


Fig. 3: Male reproductive condition of *Tropidurus hispidus* (A) and *Tropidurus semitaeniatus* (B) from October 2006 to May 2008 in the ESEC Seridó, Serra Negra do Norte municipality, Rio Grande do Norte, Brazil. The most advanced cell types in the testes: SPTG = spermatogonia; SPTC = spermatocytes; SPTD = spermatids; SPTZ = spermatozoa. Numbers above bars indicate sample size.

Condición reproductiva de machos de *Tropidurus hispidus* (A) y *Tropidurus semitaeniatus* (B) de octubre 2006 a mayo 2008 en la ESEC Seridó, Serra Negra do Norte, Rio Grande do Norte, Brasil. Los tipos celulares más avanzados en los testículos: SPTG = espermatogonia; SPTC = espermatocitos; SPTD = espermatidas; SPTZ = espermatozoides. Los números sobre las barras indican el tamaño de la muestra.

In the epididymal cycle, the epididymides in stages I, II and III displayed empty lumen and a low epithelium formed by cuboidal cells (Figs. 4B and 5B). Together with the testes in stage IV, the epididymides in stage IV displayed lumen completely filled with spermatozoa (Figs. 4D and 5D). All adult males of *T. hispidus* and *T. semitaeniatus* collected from November 2006 to March 2007 and November 2007 to April 2008 were in stage IV of the testicular and epididymal cycles. During these same periods, females of both species were also able to reproduce, thus indicating the extent of the breeding season of these species in the study area. Finally, during their regression in stage V the epididymides were characterized by lumen containing amorphous material, sometimes with few spermatozoa (Figs. 4F and 5F). Histologically, the epithelium of the epididymal ducts in stages

IV and V were formed by columnar cells with stereocilia.

For males of both species, the testicular parameters STD, GEH, and TV differ significantly among the stages of spermatogenic activity (Table 1). For all these parameters, the highest means occurred in stage IV of maturity, whereas in stage V of the regression, the means were intermediate between stages III and IV, based on multiple comparisons by the Tukey post-test ($P < 0.05$). Male reproductive activity in *T. hispidus* was not significantly related to any climatic variables in reproductive season I ($R^2 = 0.27$, $F_{1,11} = 1.18$, $P = 0.31$), nor in reproductive season II ($R^2 = 0.13$, $F_{1,27} = 0.19$, $P = 0.71$). The same was true for males of *T. semitaeniatus* in reproductive seasons I ($R^2 = 0.31$, $F_{1,22} = 1.56$, $P = 0.51$) and II ($R^2 = 0.23$, $F_{1,13} = 0.17$, $P = 0.19$).

TABLE 1

Testicular parameters for the stages of spermatogenic activity in *Tropidurus hispidus* and *Tropidurus semitaeniatus*. STD = seminiferous tubule diameter, GEH = germinative epithelium height, TV = testis volume. Data are mean \pm standard deviation. F values are for ANOVA in the case of GEH, and for ANCOVA (with SVL as covariate) in the cases of STD and TV.

Parámetros testiculares para los estadios de la actividad espermatogénica en *Tropidurus hispidus* y *Tropidurus semitaeniatus*. STD = diámetro del túbulo seminífero, GEH = altura del epitelio germinativo, TV = volumen de los testículos. Los datos se presentan como promedio \pm desviación estándar. Los valores de F son de ANOVA en el caso de GEH, y de ANCOVA (con SVL como covariable) en los casos de STD y TV.

<i>Tropidurus hispidus</i>								
Parameters	Stages					N	F	P
	I	II	III	IV	V			
STD (mm)	0.06 \pm 0.02	0.10 \pm 0.06	0.14 \pm 0.03	0.30 \pm 0.08	0.20 \pm 0.06	34	18.9	0.0001
GEH (mm)	—	0.03 \pm 0.01	0.06 \pm 0.02	0.09 \pm 0.01	0.07 \pm 0.02	25	21.7	0.0001
TV (mm ³)	1.0 \pm 0.7	8.4 \pm 4.1	15.7 \pm 2.1	77.1 \pm 39.6	25.7 \pm 18.7	34	11.6	0.0001
<i>Tropidurus semitaeniatus</i>								
Parameters	Stages					N	F	P
	I	II	III	IV	V			
STD (mm)	0.05 \pm 0.02	0.06 \pm 0.02	0.11 \pm 0.01	0.31 \pm 0.07	0.14 \pm 0.05	63	71.4	0.0001
GEH (mm)	—	0.02 \pm 0.01	0.03 \pm 0.003	0.09 \pm 0.02	0.04 \pm 0.01	47	37.5	0.0001
TV (mm ³)	0.56 \pm 0.15	1.7 \pm 1.3	7.0 \pm 4.0	34.7 \pm 18.3	8.4 \pm 5.6	63	20.7	0.0001

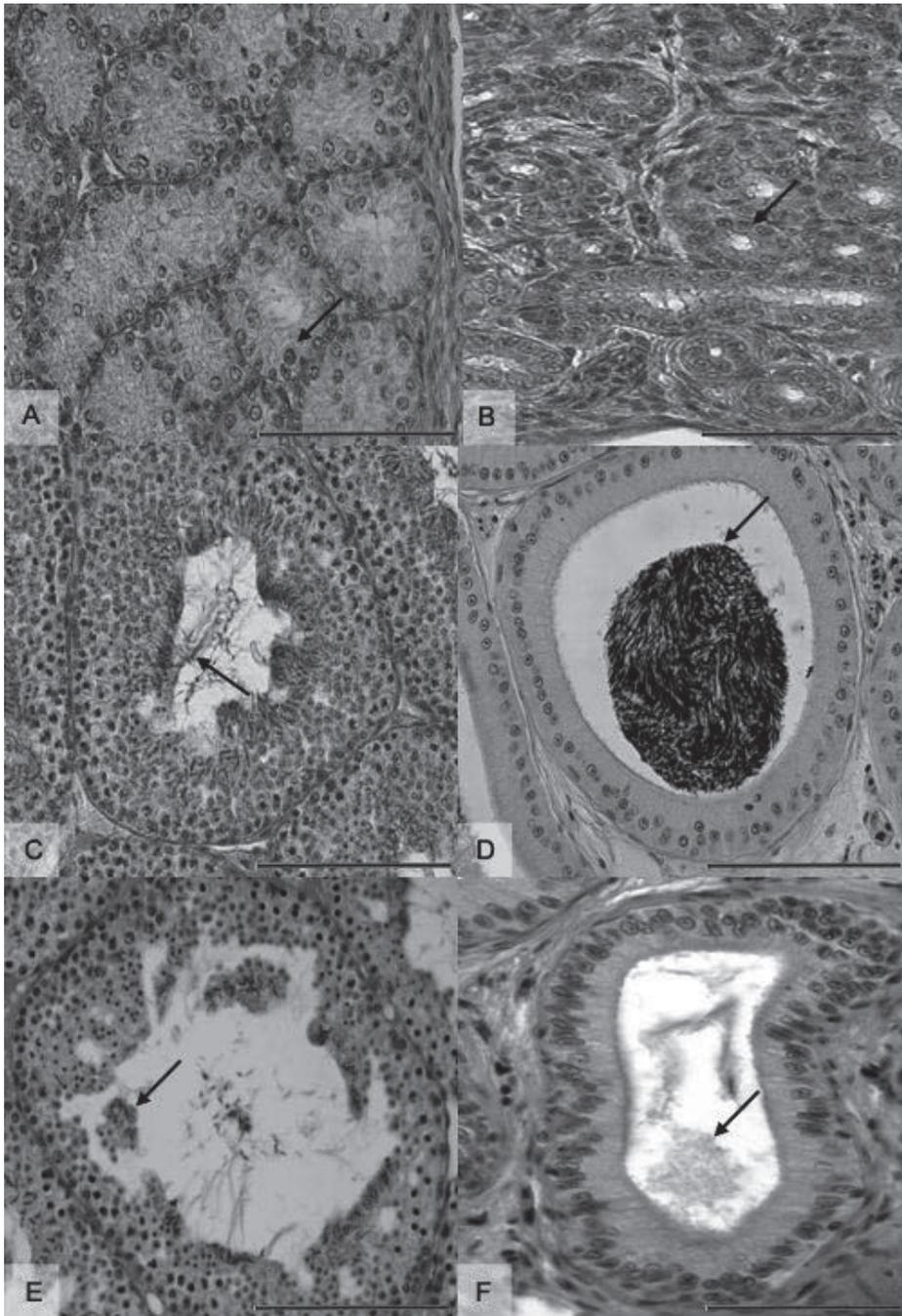


Fig. 4: Testicular and epididymal cycle in *Tropidurus hispidus*. Seminiferous tubules: (A) stage I of the spermatogenic lineage, highlighting spermatogonia (arrow) as the predominant cell type; (C) stage IV, luminal margin with spermatozoa (arrow); (E) stage V, germinative cells detached from the epithelium (arrow). Epididymal ducts: (B) stage I-III, low epithelium with cuboidal cells (arrow); (D) stage IV, lumen with spermatozoid storage (arrow); (F) stage V, lumen containing amorphous material (arrow). A-B: young individuals, C-F: adult individuals. Bar: 40 μ m (A-F).

Ciclos testicular y epididimal en *Tropidurus hispidus*. Túbulos seminíferos: (A) estadio I de la linaje espermatogénica, destacando las espermatogonias (flecha) como el tipo celular predominante; (C) estadio IV, margen luminal con espermatozoides (flecha); (E) estadio V, células germinativas destacadas del epitelio (flecha). Conductos del epidídimo: (B) estadios I-III, epitelio bajo con células cúbicas (flecha); (D) estadio IV, lumen con estoque de espermatozoides (flecha); (F) estadio V, lumen conteniendo material amorfo (flecha). A-B: individuos jóvenes, C-F: individuos adultos. Barra: 40 μ m (A-F).

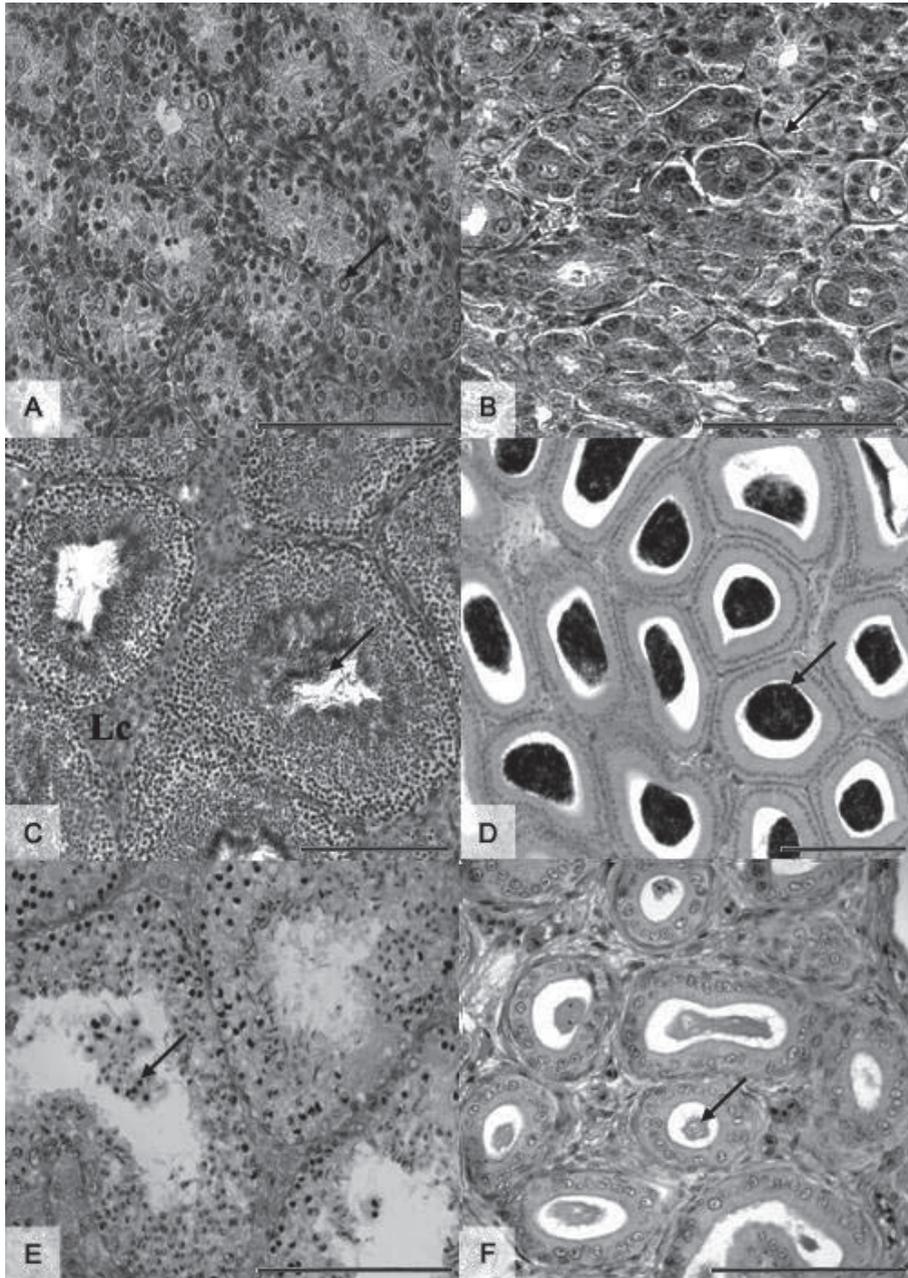


Fig. 5: Testicular and epididymal cycle in *Tropidurus semitaeniatus*. Seminiferous tubules: (A) stage I of the spermatogenic lineage, highlighting spermatogonia (arrow) as the predominant cell type; (C) stage IV, luminal margin with spermatozoa (arrow) and interstitial spaces with a concentration of Leydig cells (Lc); (E) stage V, germinative cells detached from the epithelium (arrow). Epididymal ducts: (B) stage I-III, low epithelium with cuboidal cells (arrow); (D) stage IV, lumen with spermatozoid stock (arrow); (F) stage V, lumen containing amorphous material (arrow). A-B: young individuals, C-F: adult individuals. Bar: 40 μm (A, B, E, F), 20 μm (C), 10 μm (D).

Ciclos testicular y epididimal en *Tropidurus semitaeniatus*. Túbulos seminíferos: (A) estadio I de la linaje espermatogénica, destacando las espermatogonias (flecha) como el tipo celular predominante; (C) estadio IV, margen luminal con espermatozoides (flecha) y los espacios intersticiales con una concentración de células de Leydig (Lc); (E) estadio V, células germinativas destacadas del epitelio (flecha). Conductos del epidídimo: (B) estadios I-III, epitelio bajo con células cúbicas (flecha); (D) estadio IV, lumen con estoque de espermatozoides (flecha); (F) estadio V, lumen conteniendo material amorfo (flecha). A-B: individuos jóvenes, C-F: individuos adultos. Barra: 40 μm (A, B, E, F), 20 μm (C), 10 μm (D).

Fat body cycle

Fat body mass was similar between the sexes in *T. hispidus* (females: 0.561 ± 0.071 g; males: 0.643 ± 0.090 g; ANCOVA, $F_{1,83} = 0.82$, $P = 0.36$), as well as in *T. semitaeniatus* (females: 0.201 ± 0.022 g; males: 0.225 ± 0.026 g; ANCOVA, $F_{1,134} = 2.97$, $P = 0.087$). The lowest residual values for fat body mass of female and male *T. hispidus* and *T. semitaeniatus* occurred from December 2006 to March 2007 and from January to April 2008 (Fig. 6). These results coincided with peaks of breeding season. On the other hand, between April and December 2007 there was an increase in fat body mass in both sexes and both species, coinciding with the reduction in reproductive activity.

During the reproductive period, female *T. hispidus* stored an average of 14402 kJ in

fat bodies; in the first reproductive season (November 2006 to March 2007) the equivalent of 10539 kJ and in the second (November 2007 to April 2008) an average of 16334 kJ. For female *T. semitaeniatus* the average was 2952 kJ; in the first reproductive season the mean value was 2948 kJ and in the second corresponded to 2955 kJ. In the period between reproductive seasons, the average values reached 25667 kJ and 11970 kJ, respectively, for females of *T. hispidus* and *T. semitaeniatus*.

DISCUSSION

The reproduction of *T. hispidus* and *T. semitaeniatus* in the caatinga of the ESEC Seridó occurs during a well-defined period of the year, between the last months of the dry season (November to January) and the

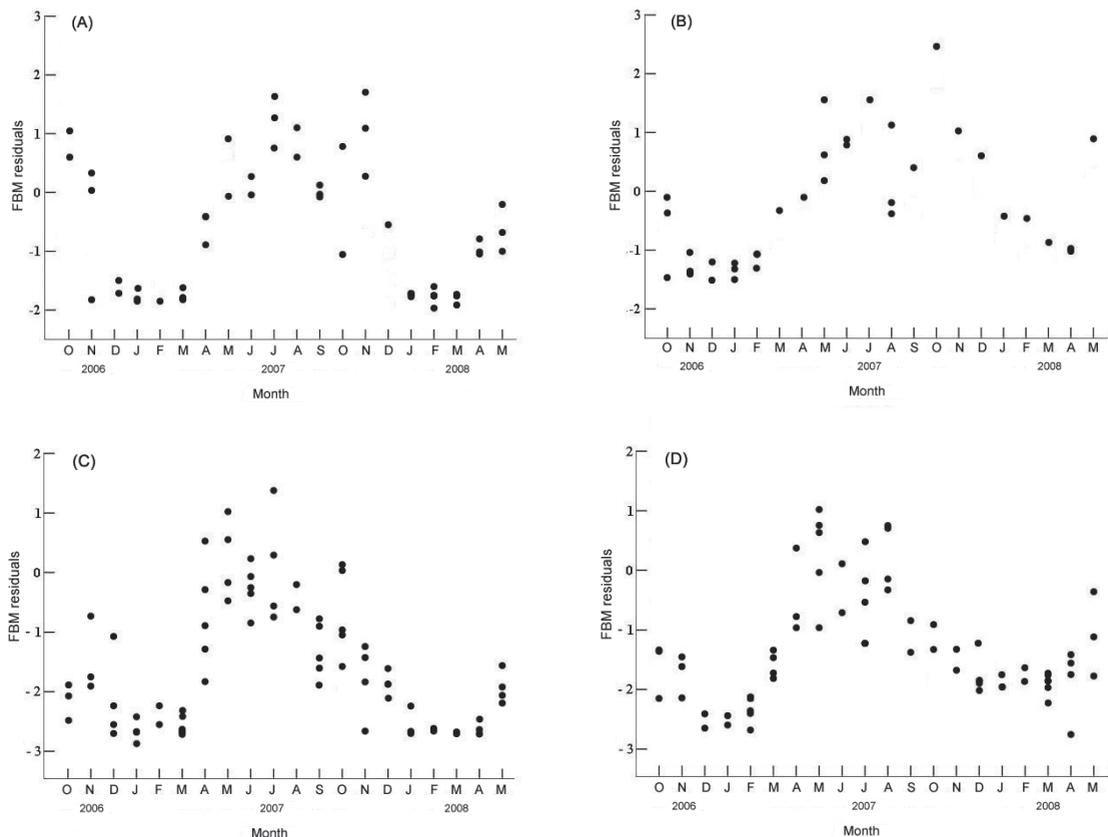


Fig. 6: Monthly means of the regression residuals of fat body mass versus snout-vent length in females (A) and males (B) of *Tropidurus hispidus*, and in females (C) and males (D) of *Tropidurus semitaeniatus*, from October 2006 to May 2008 in the ESEC Seridó, Serra Negra do Norte municipality, Rio Grande do Norte, Brazil.

Medias mensuales de los residuos de la regresión de la masa de grasa corporal versus longitud hocico-cloaca en hembras (A) y machos (B) de *Tropidurus hispidus*, y en hembras (C) y machos (D) de *Tropidurus semitaeniatus*, de octubre 2006 a mayo 2008 en la ESEC Seridó, Serra Negra do Norte, Rio Grande do Norte, Brasil.

beginning of the rainy season (February to April). In the caatinga of the state of Pernambuco, although Vitt & Goldberg (1983) have collected adult females of *T. hispidus* with increased vitellogenic follicles over 11 months, most reproduction in this species and in *T. semitaeniatus* occurred during the dry season (July to November), and a large proportion of females of both species were breeding at the beginning of the rainy season (December and January). Seasonal reproductive activity is typical of tropidurid lizards that live in seasonally variable environments, such as *T. itambere* (Van Sluys 1993, Ferreira et al. 2009), *T. montanus* (Van Sluys et al. 2002), *T. torquatus* (Wiederhecker et al. 2002), and *Eurolophosaurus nanuzae* (Rodrigues) (Galdino et al. 2003). Although adult males of *T. hispidus* and *T. semitaeniatus* displayed spermatozoa in the testes in almost every month of this study, the variation in testicular parameters (STD, GEH, and TV) indicates variation in the reproductive activity of these males, with the peak of spermatogenic activity coinciding with the period in which the females were reproductively active. Thus, although longer, male reproductive activity is synchronous with that of females.

In lizards with synchronous reproductive cycles, male spermatogenesis and aggressive behaviors are often associated with the production of testosterone (Moore & Lindzey 1992, Tokarz 1995). Given that *T. hispidus* and *T. semitaeniatus* are territorial, as are other *Tropidurus* species (e.g., *T. itambere*, Van Sluys 1997; *T. torquatus*, Ribeiro et al. 2009), the production of sperm in months when no receptive females are available may result from minimum levels of testosterone to defend territories. We observed agonistic encounters intramales of *T. hispidus* and *T. semitaeniatus* in the field in all months, but they were most evident in the reproductive season. Similar results were observed in males of *T. torquatus* that defended high quality territories having large numbers of females (Pinto 1999). Alternatively, Wiederhecker et al. (2002) suggest that the continuous sperm production by male lizards during females' nonreproductive season may represent a remnant of spermatogenic activity, or a result of low costs of producing sperm. Nevertheless, the spermatogenic activity cycle in *T. hispidus*

and *T. semitaeniatus* followed the pattern of other *Tropidurus* species (e.g., *T. itambere*, Van Sluys 1993; *T. torquatus*, Vieira et al. 2001), in which the regenerative phase occurred during female reproductive activity and the degenerative phase during the course of the female nonreproductive phase.

The accumulation of energy in fat bodies of *T. hispidus* and *T. semitaeniatus* was seasonal, varying inversely with reproductive activity. In this form of storage, both sexes showed the highest values of fat body mass in the period between breeding seasons, corresponding to the driest months (July to October 2007). This result indicates that energy accumulation in fat bodies plays an important role in the gonad maturation process and in the subsequent maintenance of reproductive activity. Larger fat body masses during the nonbreeding season and smaller fat body masses during the breeding season have also been described for *T. hispidus* and *T. semitaeniatus* in the state of Pernambuco (Vitt & Goldberg 1983). Additionally, the cyclic accumulation of fat and its importance in reproduction have been observed in tropical lizard species living in seasonal environments (Rocha 1992, Van Sluys et al. 2002, Wiederhecker et al. 2002, Galdino et al. 2003).

The minimum sizes at sexual maturity in *T. hispidus* in the ESEC Seridó, equivalent to 65 and 68 mm, for females and males, respectively precede the previous minima described by Vitt (1995) for females by 5 mm and for males by 3 mm (see also Ribeiro & Freire 2009). However, in *T. semitaeniatus* minimum sizes at maturity were above the SVLs of 58 mm for females and 64 mm for males, as established by Vitt (1995). Our data showed that clutch size in *T. hispidus* at ESEC Seridó (6 - 13 eggs) was similar to that found for this species in another area of caatinga (3-14 eggs; Vitt & Goldberg 1983), and also to that observed for the congeneric species *T. torquatus*, in the cerrado biome (3-10 eggs; Wiederhecker et al. 2002). On the other hand, compared with the clutch size of *T. torquatus* populations in restingas on the Brazilian coast (1-4 eggs; Kiefer et al. 2008), clutch size in *T. hispidus* at ESEC Seridó was considerably higher.

According to Kiefer et al. (2008), different clutch sizes are influenced by differences in female body size, as well as extrinsic factors

related to local environmental features (e.g., the structural complexity of the areas), climatic factors (e.g., precipitation, temperature, photoperiod), and ecological factors (e.g., escape from predators, breeding sites, food availability). In fact, species occurring in habitats with a high degree of psammophily, such as *T. torquatus* in restingas (Kiefer et al. 2008), tend to produce smaller clutches compared to those of terrestrial and saxicolous species (Dunham et al. 1988). Behavioral acts such as movement on sand and quick escape from predators may be affected by a greater clutch size, representing important evolutionary pressures for reduction in clutch size (Shine 1980). In some tropidurid species, clutch size is positively related to female body size (Van Sluys 1993, Cruz 1998, Wiederhecker et al. 2002), and in many lizard species, larger females tend to produce larger clutches (Tinkle et al. 1970, Rocha 2008). *Tropidurus hispidus* is apparently not an exception, since female SVL explained 65 % of the variation in clutch size. Vitt and Goldberg (1983) argue that in species such as *T. hispidus*, whose clutch size is related to body size, larger females can produce larger clutches and selection should favor an increase in body growth after reaching maturity.

Although clutch size in reptiles generally has a direct relationship with female body size (King 2000), in *T. semitaeniatus*, this did not occur, as was also observed for another population of this species (Vitt & Goldberg, 1983). The prevalence of a small clutch size (usually 2 eggs) recorded for *T. semitaeniatus* was in agreement with previous descriptions (Vitt 1981, Vitt & Goldberg 1983). The small clutch size in this species was explained by Vitt (1981) in the context of the ecological adaptations of this habitat specialist species, with a predominantly saxicolous way of life. Therefore, production of a smaller number of eggs per clutch would enhance efficiency in the use of rock crevices during escape from predators, resulting in an increase in the life expectancy of the female. Similarly in *E. nanuzae*, a small tropidurid whose clutch usually has two eggs and also displays no significant relationship with female body size, Galdino et al. (2003) considered that carrying larger clutches and using refuges in rocky microhabitats could potentially reduce the ability to escape. Some lizards have a fixed

clutch size (e.g., one egg in *Anolis* (Andrews & Rand 1974) and *Coleodactylus* (Vanzolini et al. 1980; Lisboa et al. 2008)); in *T. semitaeniatus* the most common clutch of two eggs, suggests that this size would not be constrained only by the effect of phylogeny, but also by ecological factors.

Regarding the temporal pattern of reproductive activity in tropical areas, some authors have reported the influence of precipitation on reproduction in seasonal environments (Fitch 1982, Rocha 1992, Van Sluys et al. 2002). Although interannual rainfall in the caatingas is unpredictable (Nimer 1972), they exhibit extremely different landscapes, characterized by low rainfall in the dry season and the vitality of the vegetation in the rainy season. In the ESEC Seridó, the rise in rainfall was the factor that best explained cyclical reproduction in *T. hispidus* and *T. semitaeniatus*, starting in the middle of the dry season and declining before the end of the rainy season. The reduction in the abundance of arthropods in the dry season is indicated by some authors (Vitt & Goldberg 1983, Anderson 1994) as an important factor regulating reproduction in lizards, especially for sit-and-wait foragers such as those of the genus *Tropidurus*. However, our results showed that the highest fat body mass in *T. hispidus* and *T. semitaeniatus* occurred in the driest months (July to December 2007), indicating that food availability may not have been a factor regulating reproduction in these two species. Similar results were also found when reproduction in tropidurid species in seasonal habitats was studied (e.g., *T. torquatus*, Wiederhecker et al. 2002; *E. nanuzae*, Galdino et al. 2003). In accordance with Colli et al. (1997), compared with active foragers, the largest accumulation of fat in sit-and-wait foragers during the dry season is a result of increased production efficiency as a consequence of lower maintenance costs. If fat body mass, used as a main indicator of food availability (Derickson 1976), showed that this was not a factor restricting reproduction in *T. hispidus* and *T. semitaeniatus* in the caatinga of the ESEC Seridó, what would have influenced the reduction in their reproductive activities in part of the dry season, when there was greater energy storage?

The answer to that question finds support in the two hypotheses referenced above, which

are the lack of microhabitats with adequate humidity for egg development, and the lack of food resources for the development of newborns. In the context of the first statement, the nest environment is referred to as a critical factor for egg survival, where humidity conditions are important, especially for increasing embryo mass and hatching success (Packard & Packard 1988, Overall 1994). Adult females of *T. hispidus* and *T. semitaeniatus* containing oviductal eggs between the months of January and April, respectively, when approaching and during the peak of the humid season in the Northeastern caatinga (Nimer 1972), especially in the area studied, suggest that egg deposition and incubation primarily occur outside the arid period of the dry season, characterizing above all the seasonal reproductive cycle of these species.

The reproductive cycle of the teiid lizard *Ameiva ameiva* (Linnaeus) was described as continuous in an area of caatinga (Vitt 1982), and attributed by the author to the active foraging mode that allows for the exploration of a wider range of microhabitats than the sit-and-wait foragers, ensuring sufficient food to enable reproduction. However, our results based on fat body mass discussed above, and those described by other authors (Colli et al. 1997, Wiederhecker et al. 2002, Galdino et al. 2003), showed that reproductive seasonality in sit-and-wait foraging lizards is not constrained by food limitation. Thus, Wiederhecker et al. (2002) contend that active foragers such as *A. ameiva* have access to better breeding sites or eggs that are more resistant to dehydration, favoring reproduction throughout the year, even in the driest months. As to the second hypothesis about the scarcity of food for offspring development limiting reproduction, the recruitment period of *T. hispidus* and *T. semitaeniatus* in the ESEC Seridó, identified as the months of May and June, shows an adjustment of their reproductive cycles. This adjustment favors early newborn development under the milder conditions of the rainy season, when they might be better served by the greater abundance of food typical of this period (Janzen & Schoener 1968), thereby improving their likelihood of survival. Finally, our results on the reproductive and fat body cycles in *T. hispidus* and *T. semitaeniatus* suggest that reproduction in these species is

related to microclimatic conditions suitable for both embryo development and the hatching and survival of newborns, especially during the rainy season, which may offer greater food availability to the offspring.

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LITERATURE CITED

- AB'SÁBER AN (1974) O domínio morfoclimático semiárido das Caatingas brasileiras. *Geomorfologia* 43: 1-139.
- ADOLPH SC & WP PORTER (1993) Temperature, activity and lizard life histories. *American Naturalist* 142: 273-295.
- ANDERSON RA (1994) Functional and population responses of the lizard *Cnemidophorus tigris* to environmental fluctuations. *American Zoologist* 34: 409-421.
- ANDREWS RM (1988) Demographic correlates of variable egg survival for a tropical lizard. *Oecologia* 76: 376-382.
- ANDREWS RA & AS RAND (1974) Reproductive effort in anoline lizards. *Ecology* 55: 1317-1327.
- ÁVILA RW, LR CUNHA-AVELLAR & VL FERREIRA (2008) Diet and reproduction of the lizard *Tropidurus etheridgei* in rocky areas of central Brazil. *Herpetological Review* 39: 430-433.
- BALLINGER ER (1983) Life-history variations. In: Huey RB, ER Pianka & TW Schoener (eds) *Lizard ecology: Studies of a model organism*: 241-260. Harvard University Press, Cambridge.
- BENABIB M (1994) Reproduction and lipid utilization of tropical populations of *Sceloporus variabilis*. *Herpetological Monographs* 8: 160-180.
- BERNE RM & MN LEVY (1993) *Physiology*. Third edition. Mosby-Year Book Inc, Saint Louis, MO.
- BRIAN BL, FG GAFFNEY, LC FITZPATRICK & VE SCHOLE (1972) Fatty acid distribution of lipids from carcass, liver, and fat bodies of the lizard *Cnemidophorus tigris* prior to hibernation. *Comparative Biochemistry and Physiology* 41B: 661-664.
- CLERKE RB & RA ALFORD (1993) Reproductive biology of four species of tropical Australian lizards and comments on the factors regulating lizard reproductive cycles. *Journal of Herpetology* 27: 400-406.
- COLLI GR, AK PERES JR & MG ZATZ (1997) Foraging mode and reproductive seasonality in tropical lizards. *Journal of Herpetology* 31: 490-499.
- CRUZ FB (1998) Natural hystory of *Tropidurus spinulosus* (Squamata: Tropiduridae) from the dry

- Chaco of Salta, Argentina. *Herpetological Journal* 8: 107-110.
- CRUZ FB, E TEISAIRE & L NIETO (1997) Reproductive biology of the lizard *Tropidurus spinulosus* in the chaco of Salta, Argentina. *Studies on Neotropical Fauna and Environment* 32: 28-32.
- DERICKSON WK (1976) Lipid storage and utilization in reptiles. *American Zoologist* 16: 711-723.
- DUNHAM AE, DB MILES & DN REZNICK (1988) Life history patterns in squamate reptiles. In: Gans C & RB Huey (eds) *Biology of the Reptilia*: 441-522. Alan R. Liss, Inc, New York.
- DUVALL D, LJ GUILLETTE JR & RE JONES (1982) Environmental control of reptilian reproductive cycles. In: Gans C & FH Pough (eds) *Biology of the Reptilia*: 201-231. Academic Press, New York.
- FERREIRA A, DN SILVA, M VAN SLUYS & H DOLDER (2009) Seasonal changes in testicular and epididymal histology of the tropical lizard, *Tropidurus itambere* (Rodrigues, 1987), during its reproductive cycle. *Brazilian Journal of Biology* 69: 429-435.
- FITCH HS (1970) Reproductive cycles in lizards and snakes. *Miscellaneous Publications of the Museum of Natural History, University of Kansas* 52: 1-247.
- FITCH HS (1982) Reproductive cycles in tropical reptiles. *Occasional Papers of the Museum of Natural History, University of Kansas* 96: 1-53.
- FROST DR, MT RODRIGUES, T GRANT & TA TITUS (2001) Phylogenetics of the lizard genus *Tropidurus* (Squamata: Tropiduridae: Tropidurinae): Direct optimization, descriptive efficiency, and sensitivity analysis of congruence between molecular data and morphology. *Molecular Phylogenetics and Evolution* 21: 352-371.
- GALDINO CAB, VB ASSIS, MC KIEFER & M VAN SLUYS (2003) Reproduction and fat body cycle of *Eurolophosaurus nanuzae* (Sauria; Tropiduridae) from a seasonal montane habitat of Southeastern Brazil. *Journal of Herpetology* 37: 687-694.
- HOWLAND JM (1992) Life history of *Cophosaurus texanus* (Sauria: Iguanidae): Environmental correlates and interpopulational variation. *Copeia* 1992: 82-93.
- JANZEN DH & TW SCHOENER (1968) Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* 49: 96-110.
- KIEFER MC, M VAN SLUYS & CFD ROCHA (2008) Clutch and egg size of the tropical lizard *Tropidurus torquatus* (Tropiduridae) along its geographic range in coastal eastern Brazil. *Canadian Journal of Zoology* 86: 1376-1388.
- KING RB (2000) Analyzing the relationship between clutch size and female body size in reptiles. *Journal of Herpetology* 34: 148-150.
- LISBOA, CMCA, PAG SOUSA, LB RIBEIRO & EMX FREIRE (2008) *Coleodactylus natalensis* (NCN). Clutch size; hatchling size. *Herpetological Review* 39: 221-221.
- MESHAKA, WE JR, HT SMITH & CL DEAN (2006) Gonadal cycle and growth of a West Indian Lizard, the Northern Curlytail Lizard (*Leiocephalus carinatus armouri*), in southern Florida. *Herpetological Conservation and Biology* 1: 109-115.
- MOORE MC & J LINDZEY (1992) The physiological basis of sexual behavior in male reptiles. In: Gans C & D Crews (eds) *Biology of the Reptilia*: 70-113. University of Chicago Press, Chicago.
- NIMER E (1972) Climatologia da região Nordeste do Brasil. Introdução à climatologia dinâmica. *Revista Brasileira de Geografia* 34: 3-51.
- OVERALL KL (1994) Lizard egg environments. In: Vitt LJ & ER Pianka (eds) *Lizard ecology: Historical and experimental perspectives*: 51-72. Princeton University Press, Princeton.
- PACKARD GC & MJ PACKARD (1988) The physiological ecology of the reptilian eggs and embryos. In: Gans C & RB Huey (eds) *Biology of the Reptilia*: 523-606. Alan R. Liss Inc, New York.
- PINTO ACS (1999) Dimorfismo sexual e comportamento sexual em *Tropidurus torquatus* (Squamata, Tropiduridae) no Brasil Central. Master thesis, Universidade de Brasília, Brasília, Brazil.
- PRIETO AS, JR LEON & O LARA (1976) Reproduction in the tropical lizard *Tropidurus hispidus* (Sauria: Iguanidae). *Herpetologica* 32: 318-323.
- RAMÍREZ-BAUTISTA A, J BARBA-TORRES & LJ VITT (1998) Reproductive cycle and brood size of *Eumeces lynxe* from Pinal de Amoles, Queretero, Mexico. *Journal of Herpetology* 32: 18-24.
- RAMÍREZ-BAUTISTA A, O RAMOS-FLORES & JW SITES JR (2002) Reproductive cycle of the spiny lizard *Sceloporus jarrovi* (Sauria: Phrynosomatidae) from north-central México. *Journal of Herpetology* 36: 225-233.
- RIBEIRO LB & EMX FREIRE (2009) *Tropidurus hispidus* (NCN). Minimum size at maturity; Maximum body size. *Herpetological Review* 40: 350-351.
- RIBEIRO LB, BM SOUSA & SC GOMIDES (2009) Range structure, microhabitat use, and activity patterns of the saxicolous lizard *Tropidurus torquatus* (Tropiduridae) on a rock outcrop in Minas Gerais, Brazil. *Revista Chilena de Historia Natural* 82: 577-588.
- ROCHA CFD (1992) Reproductive and fat body cycles of the tropical sand lizard (*Liolaemus lutzae*) of southeastern Brazil. *Journal of Herpetology* 26: 17-23.
- ROCHA CFD (2008) Body size, female reproduction and sexual dimorphism in the lizard *Ameiva ameiva* (Teiidae) in a restinga of southeastern Brazil. *Revista Brasileira de Zoologia* 25: 370-372.
- ROCHA CFD & HG BERGALLO (1990) Thermal biology and flight distance of *Tropidurus oreadicus* (Sauria: Iguanidae) in an area of Amazonian Brazil. *Ethology, Ecology & Evolution* 2: 263-268.
- RODRIGUES MT (1987) Sistemática, ecologia e zoogeografia dos *Tropidurus* do grupo *torquatus* ao Sul do Rio Amazonas (Sauria, Iguanidae). *Arquivos de Zoologia do Estado de São Paulo* 31: 105-230.
- RODRIGUES MT, S KASAHARA & Y YONENAGA-YASSUDA (1988) *Tropidurus psammonastes*: Uma nova espécie do grupo *Torquatus* com notas sobre seu cariótipo e distribuição (Sauria, Iguanidae). *Papéis Avulsos de Zoologia* 36: 307-313.
- SEXTON OJ, EP ORTLEB, LM HATHAWAY, RE BALLINGER & P LICHT (1971) Reproductive cycles of three species of anoline lizards from the Isthmus of Panama. *Ecology* 52: 201-215.
- SHINE R (1980) "Costs" of reproduction in reptiles. *Oecologia* 46: 92-100.
- SMITH GR (1996) Annual life-history variation in the striped plateau lizard, *Sceloporus virgatus*. *Canadian Journal of Zoology* 74: 2025-2030.

- TINKLE DW, HM WILBUR & SG TILLEY (1970) Evolutionary strategies in lizard reproduction. *Evolution* 24: 55-74.
- TOKARZ RR (1995) Importance of androgens in male territorial acquisition in the lizard *Anolis sagrei*: An experimental test. *Animal Behaviour* 49: 661-669.
- VAN SLUYS M (1992) Aspectos da ecologia do lagarto *Tropidurus itambere* (Iguanidae) em uma área do sudeste do Brasil. *Revista Brasileira de Biologia* 52: 181-185.
- VAN SLUYS M (1993) The reproductive cycle of *Tropidurus itambere* (Sauria, Tropiduridae) in southeastern Brazil. *Journal of Herpetology* 27: 28-32.
- VAN SLUYS M (1997) Home range of the saxicolous lizard *Tropidurus itambere* (Tropiduridae) in southeastern Brazil. *Copeia* 1997: 623-628.
- VAN SLUYS M, HM MENDES, VB ASSIS & MC KIEFER (2002) Reproduction of *Tropidurus montanus* Rodrigues, 1987 (Tropiduridae), a lizard from a seasonal habitat of south-eastern Brazil, and a comparison with other *Tropidurus* species. *Herpetological Journal* 12: 89-97.
- VANZOLINI PE, AMM RAMOS-COSTA & LJ VITT (1980) Répteis das Caatingas. Academia Brasileira de Ciências, Rio de Janeiro, Brasil.
- VARELA-FREIRE AA (2002) A caatinga hiperxerófila Seridó: A sua caracterização e estratégias para sua conservação. Academia de Ciências do estado de São Paulo, São Paulo, Brasil.
- VELLOSO AL, EVSB SAMPAIO & FGC PAREYN (2002) Ecorregiões: Propostas para o bioma caatinga. Instituto de Conservação Ambiental. The Nature Conservancy do Brasil, Recife, Brasil.
- VIEIRA GHC, HC WIEDERHECKER, GR COLLI & SN BÃO (2001) Spermiogenesis and testicular cycle of the lizard *Tropidurus torquatus* (Squamata, Tropiduridae) in the Cerrado of central Brazil. *Amphibia-Reptilia* 22: 217-233.
- VITT LJ (1981) Lizard reproduction: Habitat specificity and constraints on relative clutch mass. *American Naturalist* 117: 506-514.
- VITT LJ (1982) Reproductive tactics of *Ameiva ameiva* (Lacertilia: Teiidae) in a seasonally fluctuating tropical habitat. *Canadian Journal of Zoology* 60: 3113-3120.
- VITT LJ (1992) Diversity of reproductive strategies among Brazilian lizards and snakes: The significance of lineage and adaptation. In: Hamlett WC (ed) *Reproductive biology of South American vertebrates*: 135-149. Springer-Verlag, New York.
- VITT LJ (1995) The ecology of tropical lizards in the caatinga of northeast Brazil. *Occasional Papers of the Oklahoma Museum of Natural History* 1: 1-29.
- VITT LJ & GR COLLI (1994) Geographical ecology of a neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. *Canadian Journal of Zoology* 72: 1986-2008.
- VITT LJ & SR GOLDBERG (1983) Reproductive ecology of two tropical iguanid lizards: *Tropidurus torquatus* and *Platynotus semitaeniatus*. *Copeia* 1983: 131-141.
- VRCIBRADIC D & CFD ROCHA (1998) Reproductive cycle and life-history traits of the viviparous skink *Mabuya frenata* in southeastern Brazil. *Copeia* 1998: 612-619.
- WIEDERHECKER HC, ACS PINTO & GR COLLI (2002) Reproductive ecology of *Tropidurus torquatus* (Squamata: Tropiduridae) in the highly seasonal Cerrado biome of Central Brazil. *Journal of Herpetology* 36: 82-91.
- ZAR JH (1999) *Biostatistical analysis*. Fourth edition. Prentice-Hall Inc, Upper Saddle River, NJ.
- ZUG GR, LJ VITT & JP CALDWELL (2001) Reproductive ecology and life histories. In: Zug, GR, LJ Vitt & JP Caldwell (eds) *Herpetology: An introductory biology of amphibians and reptiles*: 135-153. Academic Press, San Diego.

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