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RESEARCH ARTICLE

Feeding and reproduction ecology of the lizard *Tropidurus torquatus* (Squamata: Tropiduridae) in a rock outcrop area in southeastern Brazil

Ecología de la alimentación y reproducción del lagarto *Tropidurus torquatus* (Squamata: Tropiduridae) en un afloramiento rocoso en el sureste de Brasil

SAMUEL C. GOMIDES[1,4*], LEONARDO B. RIBEIRO[2], VERA M. PETERS[3] & BERNADETE M. SOUSA[1]

[1]Universidade Federal de Juiz de Fora, Instituto de Ciências Biológicas, Departamento de Zoologia, Campus Universitário Martelos, 36036-900, Juiz de Fora, MG, Brazil

[2]Universidade Federal do Vale do São Francisco - UNIVASF, Campus Ciências Agrárias, Colegiado de Ciências Biológicas, 56300-990, Petrolina, Pernambuco, Brazil

[3]Universidade Federal de Juiz de Fora, Centro de Biologia da Reprodução, Campus Universitário Martelos, 36036-900, Juiz de Fora, MG, Brazil

[4]Present Address: Programa de Pós-Graduação em Zoologia, Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Av. Antônio Carlos, 6627, CEP: 31270-901, Belo Horizonte, MG, Brazil

*Corresponding author: samuelbio@hotmail.com

ABSTRACT

This work evaluates the diet and the reproductive cycle of *Tropidurus torquatus* in relation to seasonality in a rock outcrop formations in a remaining area of Atlantic Rainforest. The data indicate that the lizards feed mainly on arthropods and plant material. The female reproductive activity varies between seasons, while males contain spermatozoids throughout the year. The minimum body size at maturity of the individuals was larger when compared to other population of the same species studied by other authors. The data obtained in the present study confirm previous observations about the different patterns in diet composition and reproductive cycles of each population of this species in different latitude and occurrence areas, and provide the first study about this theme for *T. torquatus* in rock outcrops in Atlantic Forest of Minas Gerais state.

Key words: diet, follicular cycle, reproductive ecology, seasonal changes, testicular cycle.

RESUMEN

En este estudio se evalúa la dieta y el ciclo reproductivo de *Tropidurus torquatus* en relación con la estacionalidad en en un afloramiento rocoso de la Mata Atlántica. Los datos recogidos indican que los lagartos se alimentan principalmente de artrópodos y materia vegetal. La actividad reproductiva de las hembras varía entre temporadas, mientras que los machos contenía esperma durante todo el año. El tamaño mínimo de ejemplares reproductivamente activos fue mayor en comparación a la encontrada por otros autores para esta especie en otras localidades. Los datos obtenidos en este estudio confirman observaciones previas sobre los diferentes patrones en composición de dieta y ciclos reproductivos de cada población de esta especie en diferentes latitudes y áreas de ocurrencia, y proporcionan el primer estudio sobre este tema para *T. torquatus* en un afloramiento rocoso de la Mata Atlántica del estado de Minas Gerais.

Palabras clave: cambios estacionales, ciclo folicular, ciclo de los testículos, dieta, ecología reproductiva.

INTRODUCTION

The *Tropidurus* of the *torquatus* group from South America (sensu Frost et al. 2001) comprises mainly heliophilous species, living in open areas such as semi-arid caatingas (shrublands), cerrados (savannas), chacos (lowlands), restingas (coastal sand dune habitats), savanna enclaves, clearings within mesic lowland forest, and rock outcrop formations (Rodrigues 1987, Vitt 1993, Vitt et al. 1996, Kolodiuk et al. 2009). *Tropidurus torquatus* (Wied 1820) is a common species which has a wide distribution in Brazil (Rodrigues 1987, Frost et al. 2001). This diurnal species is predominantly insectivorous, and their diet composition can vary both ontogenetically (Fialho et al. 2000) and seasonally (Fialho 1990, Araújo 1991). Their diet is subject to seasonal variations due to food availability and juveniles tend to eat less plant material than adults (Fialho et al. 2000). In restinga areas, their diet is basically composed of arthropods, although larger specimens may eat considerable amounts of plant material (Araújo 1987, Bergallo & Rocha 1994, Teixeira & Giovanelli 1999).

The availability and composition of diet can interfere in reproductive cycles of neotropical lizards (Colli et al. 1997). Some tropidurid species in semiarid caatingas (Vitt & Goldberg 1983) and rock outcrop formations in southeastern Brazil (Van Sluys 1993) were documented as clearly seasonal in their reproduction. The reproductive activities (e.g. sperm production, follicles increase, egg laying) of many tropical species can decline or cease during the dry months (Fitch 1970, 1982), either for lack of environmental conditions for development of embryos or scarcity of food for adults and juveniles in this season (Colli et al. 1997). In cerrado areas in central Brazil, *T. torquatus* reproductive activity is seasonal, apparently constrained during the dry season by the scarcity of microhabitats suitable for egg development (Vieira et al. 2001, Wiederhecker et al. 2002). In restinga areas, *T. torquatus* reproduces almost year-round, but the proportion of reproductive individuals varies through the year (Van Sluys et al. 2010). Apparently females have a more pronounced reproductive cycle than males, which seem to reproduce continuously (Van Sluys et al. 2010). Male lizards apparently have continuous spermatozoa production, but the peak reproductive activity in males and females is very synchronized (Wiederhecker et al. 2003).

Variations in reproductive patterns of *T. torquatus* appear to be linked to different latitudes and vegetation types in which the species occurs (Ribeiro et al. 2008b, Kiefer et al. 2008). The clutch size (average of two eggs) of coastal populations of *T. torquatus* (Kiefer et al. 2008) is smaller than that from the inland population (six eggs) in cerrado (Wiederhecker et al. 2002). Despite being the most widely distributed species in the genus, detailed data on reproduction of different *T. torquatus* populations are still scarce. The exceptions are Wiederhecker et al. (2002) for cerrado and Kiefer et al. (2008) and Van Sluys et al. (2010) for restinga areas. Virtually nothing is known about inland populations found in the Atlantic Rainforest biome.

For lizards in tropical areas, whose reproductive cycles can be both continuous and seasonal, it is difficult to identify the environmental factors that may be related or limit reproductive cycles. The most probable factors affecting reproduction in tropidurid lizards are: rain, temperature, photoperiod, adequate microhabitat availability and food availability for fat storage (Van Sluys 1993, Wiederhecker et al. 2002, 2003). Variation in reproductive strategies among lineages has been attributed to phylogenetic or adaptative responses to environmental factors or combination of both (Wiederhecker et al. 2002, 2003). The influence by environmental factors is evident when different reproductive tactics occur among populations of the same species inhabiting different regions (Wiederhecker et al. 2002, 2003). Fat storage patterns, resource acquisition, fat body mass variation and their relationships with reproduction are difficult to elucidate, and a pattern for tropical species is not evident (Vitt & Goldberg 1983).

Some reproductive parameters of *T. Torquatus*, such as minimum size at reproductive maturation (from 51.1 to 74.8 cm for females), number of eggs (from two to six) per nest and breeding season vary between the different Brazilian biomes, as observed among cerrado (Wiederhecker et al. 2002, 2003, Pinto et al. 2005), restinga (Teixeira & Giovanelli 1999, Kiefer et al. 2008, Van Sluys et al. 2010) and pampas (southern grasslands) (Arruda 2009). Therefore, this study aims to assess (i) the diet composition of *T. torquatus* according to sex, evaluating the diversity, amount and size of the consumed prey items, and (ii) the reproductive conditions of the specimens in relation to seasonality, in an area of rock outcrop formations in an Atlantic Rainforest fragment located in the southeastern Brazil. Additionally, we investigated whether the reproductive patterns of the studied population of *T. torquatus* differed from those reported for the species in other biomes, to increase understanding of the parameters regulating this species' reproductive cycle.

METHODS

Study area

The specimens were collected in a quartzite outcrop area (approximately 60 x 90 m) on the left bank of the Rio do Peixe in the Toledos district, defined as a rural area of Juiz de Fora municipality, located in the "Zona da Mata mineira", state of Minas Gerais in southeastern Brazil (21°48'27.5"S; 43°35'31.7"W, altitude: 697 m). The study area is located in the domain of the Atlantic Rainforest, and is characterized by bush vegetation and small sparse trees that grow inside the blocks of quartzite rocks. The floristic composition of the place consisted mainly of plants of the families: Apocynaceae (*Mandevilla tenuifolia*), Asteraceae (*Eremanthus erithropappus*), Bromeliaceae (*Dyckia* sp.), Leguminosae (*Centrosema coriaceum*), Melastomataceae, Myrtaceae, and Velloziaceae (*Vellozia* sp.) (Salimena, com. pers. 2005). According to the classification of Koëppen, the region has Cwa climate, that is, a humid subtropical (generically defined as "tropical de altitude"), with two well-defined seasons, one hot and rainy (October to April) and another mild and dry (May to September). The average annual precipitation is 1.536 mm and the average annual temperature is 19.4 °C. The hottest month is February, with an average of 23.6 °C and the coolest months are July and August, with an average of 15.8 °C (DEGEO - ICH/UFJF 2008).

Fieldwork procedures

The lizards were collected randomly with glue traps (Victor Mouse™ glue traps) and by noosing, in the daytime, from March 2005 to July 2007, in dry season (n = 55) and rainy season (n = 55). We performed bi-weekly excursions to the study area during the indicated periods, from 08:00 – 17:00 h. The specimens were weighed (Pesola™ [Baar, Switzerland] balance, precision = 0.25g), snout-vent-length (SVL) and jaw length (JL) were measured (digital caliper [Mitutoyo™, Tokyo, Japan], precision = 0.01 mm), and then killed with sodium pentobarbital overdosis. The reproductive organs were removed, fixed in 10 % formalin and conserved in 70 % alcohol. Monthly air temperature, relative humidity and precipitation averages were obtained from the Laboratory of Climatology and Environmental Analysis of the Federal University of Juiz de Fora and corresponded to the study period.

Identification of diet composition and assessment of the reproductive parameters

Dissections for stomach content analysis were performed in the same University's Herpetology Laboratory. With the aid of a stereoscopic microscope, the contents of each stomach were examined separately in Petri dishes containing physiological solution. The stomach contents were identified and the samples that presented prey items in advanced digestion stage not allowing identification were discarded. The rest of the unknown vegetable material was recorded as "unidentified plant material".

The food items were quantified using the frequency of occurrence and numerical frequency. The entire preys were counted and measured (total length and width in mm) with a digital caliper to estimate the stomach content volume in mm^3, through the ellipsoid formula:

$$v = (\pi w^2 l)/6,$$

where v = prey volume, w = prey width and l = prey length). The entire preys were measured and used to estimate the prey's size that was found in pieces or missing body parts. Any preys found that could be identified reliably was included in analyzes. The volume of plant material identifiable and those unidentifiable were also included in the analysis. In order to identify the invertebrates we used the keys in Borror & DeLong (1988) and Buzzi (2002). Prey items were identified to the lowest taxonomic category possible (usually order or family).

To describe the female reproductive activity, we registered the presence and diameter of vitellogenic follicles and the number of eggs in the oviduct and corpora lutea. Females with developed yellow vitellogenic follicles or with eggs in the oviduct were considered mature adults. Females without eggs in the oviduct or with milky-white ovarian follicles were considered juveniles (Sodeinde & Kuku 1989) or inactive. The fat bodies were removed and weighed for seasonal variance analyses.

The reproductive activity of males was determined by the presence of spermatozoids in the testes and/or epididymides, according to Van Sluys (1993). The length and width of the left testis of each male specimen was measured immediately after death and dissection. Later all the gonads were fixed in Bouin's solution, sectioned at 7 µm and stained in toluidine blue according to Luna (1960). Based on the analysis of the gonads, the animals were grouped into juvenile and adult categories. The smallest sizes of individuals (male and female) in reproductive condition in this population were compared in relation to other populations from different biomes. Voucher specimens were deposited in the Herpetological Collection of the Zoology Department of Federal University of Juiz de Fora.

Data analysis

Accumulation curves of prey species were plotted from the average of 1000 randomizations with EstimateS version 8.2.0 through the bootstrap method (Colwell 2006) for each sex and for each season, to estimate the richness of prey and to evaluate whether sampling of the work covered most of the prey. To analyze the similarities of preys consumed between juvenile and adult individuals, as well as between sexes throughout the seasons, the Shannon diversity index and the Evenness index were used, calculated with the Past program (version 1.85; Hammer et al. 2001). The Mann-Whitney U test was used to compare the average vitellogenic follicle size and the fat body weight between the dry and rainy seasons, as well as to compare sex difference in SVL and JL. Spearman's correlation was used to test the relationship between follicle *vs.* animal size and clutch size vs. animal size. We also correlated reproductive aspects (vitellogenic follicles size, clutch size, testis volume, fat body mass) and abiotic aspects (temperature, humidity, precipitation). The significance level was α = 0.05. The descriptive statistics are expressed in the text as mean ± SD.

RESULTS

A total of 55 individuals were collected in the dry season (14 males, 25 females and 16 juveniles, for statistical purposes juveniles were grouped into one category regardless of sex) and 55 in the rainy season (15 males, 31 females and nine juveniles), totalizing to 110 individuals.

The adult males (defined by the smallest individual who was in reproductive condition, assessed by dissection of specimens) were larger and heavier than adult females and juveniles in the dry season and in the rainy season (Table 1). Males were significantly different from females in SVL both in the dry (U = 3.6011; P = 0.0003) and the rainy season (U = 3.9952; P = 0.0001). The JL of adults (15.16 ± 2.75 mm; range = 11.3 – 24.4 mm; n = 85) and juveniles (10.66 ± 1:49 mm; range = 8.0 - 13.8 mm; n = 25) were significantly different (U = 6,818, P < 0.0001).

Composition of stomach contents

The accumulation curve of prey species (Fig. 1) shows that an asymptote was not reached for either sex and in either season. Only females and juveniles in the dry season tended to the asymptote of the curve. The other curves showed that greater prey richness can be achieved.

The *T. torquatus* specimens in overall fed on a variety of prey types. All lizards examined had food in their stomachs. They fed mainly on arthropods but differed in the relative proportion of the different food categories consumed. Ants were the most frequently consumed food items. In terms of volume, flowers were the more important food item for adults. Animals and plant items of 28 different categories were ingested (Table 2). The plant material encountered consisted mainly of *Centrosema coriaceum* Bentham, 1837 flowers, a Leguminosae that is abundant in the region and that flowers during the rainy season. A piece of bryophyte was also found in one individual.

TABLE 1

Comparison of snout-vent length (SVL), body mass, diet diversity, evenness and volume of *Tropidurus torquatus* in an area of rocky outcrops in southeastern Brazil (mean ± SD).

Comparación de los valores de longitud hocico-cloaca (LHC), peso, diversidad, uniformidad y volumen de dieta de *Tropidurus torquatus* en un área de afloramientos rocosos en el sureste de Brasil (media ± DE).

	Dry season			Rainy Season		
	Males (n = 14)	Females (n = 25)	Juveniles (n = 16)	Males (n = 15)	Females (n = 31)	Juveniles (n = 09)
SVL (mm)	98.5 ± 10.9; range = 86.6 - 127.2	84.3 ± 8.8; range = 70.5 - 101.3	53.5 ± 6.0; range = 42.1 - 67.0	98.7 ± 17.1; range = 77.9 - 122.6	78.3 ± 7.2; range = 69.5 - 93.5	65.8 ± 4.3; range = 59.2 - 71.8
Body mass (g)	35.09 ± 15.4; range = 21.9 - 78.5	21.5 ± 6.5; range = 12.0 - 33.4	8.5 ± 5.1; range = 2.3 - 15.4	36.8 ± 18.1; range = 17.0 - 71.4	17.1 ± 4.7; range = 10.7 - 28.5	9.9 ± 2.3; range = 6.8 - 12.7
Shannon diversity Index	1.466	1.695	1.166	1.568	1.149	1.685
Evenness index	0.2548	0.3403	0.2467	0.3197	0.1752	0.599
Diet volume (mm^3)	1535.00 ± 1980.78; range = 116.18 - 7068.14	458.27 ± 560.63; range = 0.0 - 2070.83	149.93 ± 187.04; range = 13.6 - 744.93	817.03 ± 829.80; range = 43.95 - 2300.56	703.46 ± 960.00; range = 1.57 - 4653.44	181.36 ± 177.26; range = 3.14 - 404.01
Fat body mass (g)	0.543 ± 0.907	0.614 ± 0.414	0.106 ± 0.025	1.140 ± 0.844	0.674 ± 0.306	0.311 ± 0.145

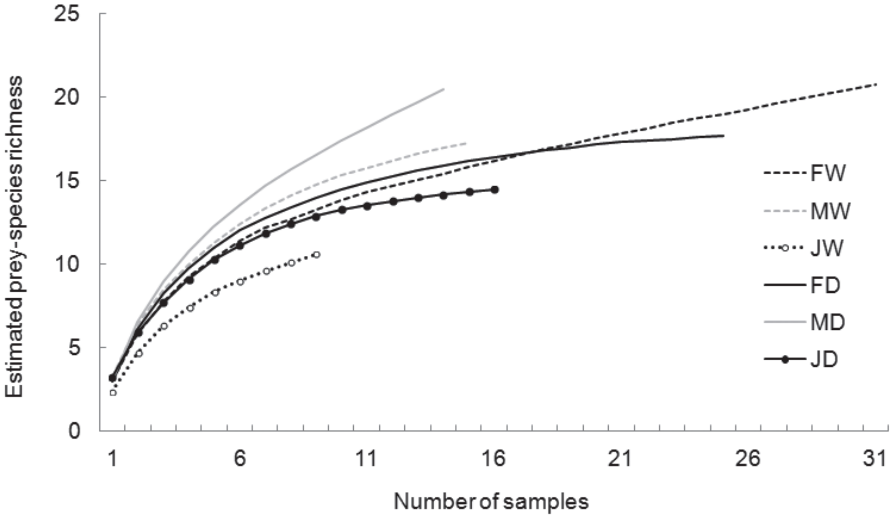

Fig. 1: Accumulation curve of food items recorded in stomach contents of *Tropidurus torquatus* in the dry season and the rainy season in an area of rocky outcrops in southeastern Brazil. Female in wet season (FW); Male in wet season (MW); Juvenile in wet season (JW); Female in dry season (FD); Male in dry season (MD); Juvenile in dry season (JD).

Curva de acumulación de los alimentos registrados en los contenidos estomacales de *Tropidurus torquatus* en la estación seca y la estación de lluvias en un área de afloramientos rocosos en el sureste de Brasil. Hembra en la estación húmeda (FW), Macho en la estación húmeda (MW), Juvenil en la estación húmeda (JW); Hembra en la estación seca (FD); Macho en la estación seca (DM); Juvenil en la estación seca (JD).

TABLE 2

Comparison of numerical frequencies (F. N.) and the frequency of occurrence (F. O.) of food items recorded in the stomach contents of *Tropidurus torquatus* in an area of rocky outcrops in southeastern Brazil. (Female = F, Male = M; Juvenile = J).

Comparación de las frecuencias numéricas (F.N.) y la frecuencia de ocurrencia (F. O.) de los alimentos registrados en los contenidos estomacales de *Tropidurus torquatus* en un área de afloramientos rocosos en el sureste de Brasil. (Hembra = F, Macho = M, Juvenil = J).

	Dry Season						Wet Season					
	F. N. (%)			F. O. (%)			F. N. (%)			F. O. (%)		
Taxon	F	M	J	F	M	J	F	M	J	F	M	J
Apidae	16.26	50.6	1	40	50	18.75	2.37	6.75	5.76	19.35	53.33	33.33
Formicidae	53.17	31.7	41.65	64	57.14	100	75.46	61.48	36.53	87.09	73.33	66.66
Vespidae	1.98	-	-	12	-	-	0.79	2.02	-	9.67	13.33	-
Other Hymenoptera	6.74	2.43	1.57	28	28.57	31.25	4.22	6.08	13.46	29.03	20	22.22
Coleoptera larvae	-	0.6	-	-	7.14	-	0.52	-	1.92	6.45	-	11.11
Elateridae	-	-	-	-	-	-	-	0.67	-	-	6.66	-
Carabidae	1.19	1.21	1	8	14.28	25	0.26	2.7	-	3.22	20	-
Curculionidae	-	0.6	-	-	7.14	-	0.26	1.35	1.92	3.22	13.33	11.11

TABLE 2. Continuation.

	Dry Season						Wet Season					
	F. N. (%)			F. O. (%)			F. N. (%)			F. O. (%)		
Coccinellidae	0.39	-	-	4	-	-	-	-	-	-	-	-
Scarabaeidae	-	-	0.2	-	-	6.25	-	-	-	-	-	-
Other Coleoptera	3.96	1.82	0.6	28	21.42	18.75	1.84	4.05	26.92	22.58	33.33	33.33
Odonata	0.79	0.6	-	8	7.14	-	-	-	-	-	-	-
Diptera	0.79	0.6	0.4	8	7.14	12.5	0.79	-	-	3.22	-	-
Orthoptera	1.58	-	3.5	16	-	56.25	2.11	1.35	1.92	22.58	13.33	11.11
Blattaria	2.77	-	-	24	-	-	0.79	-	-	9.67	-	-
Araneae	0.79	0.6	0.6	4	7.14	18.75	4.74	0.67	9.61	29.03	6.66	33.33
Araneae egg sac	-	-	-	-	-	-	0.26	-	-	3.22	-	-
Homoptera	-	-	0.4	-	-	12.5	-	1.35	-	-	6.66	-
Lepidoptera	-	0.6	-	-	7.14	-	-	-	-	-	-	-
Lepidoptera caterpillars	2.77	2.43	1	20	28.57	18.75	2.11	6.08	-	16.12	20	-
Gastropoda	-	0.6	-	-	7.14	-	0.26	-	-	3.22	-	-
Heteroptera	0.39	-	0.2	4	-	6.25	-	-	-	-	-	-
Isoptera	-	-	48	-	-	6.25	-	-	-	-	-	-
Opiliones	-	0.6	-	-	7.14	-	0.26	-	-	3.22	-	-
Collembola	-	1.21	-	-	14.28	-	-	-	-	-	-	-
Unidentified plant material	5.55	1.82	-	20	21.42	-	0.26	0.67	-	3.22	6.66	-
Flowers	0.79	1.82	-	8	21.42	-	2.63	4.05	1.92	29.03	33.33	11.11
Bryophyta	-	-	-	-	-	-	-	0.67	-	-	6.66	-

Numerically, the most significant items for adults in the dry season were ants and bees, followed by plant material, beetles and caterpillars. Juveniles consumed mainly termites and ants. Although termites had a more representative numerical frequency, they had one of the lowest frequencies of occurrence, that is, few individuals ingested large amounts of this item. In the rainy season, once again ants were most abundant in the adult lizard diet, and secondarily other Hymenoptera. Beetles, Lepidoptera caterpillars and plant material, besides arachnids, stood out in the diet during the most humid period of the year. Females from dry season diet showed the highest Shannon diversity indices, and the highest Evenness indices were obtained for females during the dry season (Table 1). Concerning stomach volume, males always had larger amounts of food (Table 1).

The lizards consumed numerically more ants. But in terms of volume, flowers along with other items of animal origin were more represented in the diet in the dry season (Table 3). Juveniles, however, contained mainly ants in their stomach volume, but also termites. In the rainy season, the volume importance of plant material increased even more for the adult animals in relation to other items (Fig. 2). In this period, ants were the main volume component of the juvenile diet and, secondarily Coleoptera.

Reproduction and fat body cycles

The diameter of the vitellogenic follicles was significantly correlated with the SVL in the

TABLE 3

Proportion of volume of food items (in %) recorded in stomach contents of *Tropidurus torquatus* during dry and wet seasons in an area of rocky outcrops in southeastern Brazil. Females (F), males (M), juveniles (J).

Porcentaje del volumen de los productos alimenticios (em %) registrado en el contenido estomacal de *Tropidurus torquatus* durante las estaciones secas y húmedas en un área de afloramientos rocosos en el sureste de Brasil. Hembras (F), machos (M), juveniles (J).

	Dry Season			Wet Season		
Taxon	F	M	J	F	M	J
Formicidae	11.16	4.12	28.31	12.01	8.93	29.22
Other Hymenoptera	30.18	42.06	15.07	2.7	12.43	18.2
Blattaria	6.43	-	-	21.3	-	-
Coleoptera	7.45	2.25	8.72	3.1	12.11	29.2
Larvae	5.98	1.22	7.76	1.33	8.31	4.32
Odonata	0.04	0.77	-	-	-	-
Diptera	1.26	0.96	0.04	0.02	-	-
Orthoptera	8.55		15.7	5.86	0.46	5.77
Araneae	0.41	2.8	1.3	6.4	1.84	1.24
Araneae egg sac	-	-	-	6.91	-	-
Homoptera	-	-	1.37	-	0.03	-
Lepidoptera	-	0.13	-	0.77	-	-
Gastropoda	-	0.3	-	0.15	-	-
Hemiptera	0.2	-	0.43	-	-	-
Isoptera	-	-	21.25	-	-	-
Opiliones	-	0.04	-	0.34	-	-
Collembola	-	0.01	-	-	-	-
Plant Material	28.29	45.28	-	39.04	55.87	12.02

dry season ($r_S = 0.775$; $P < 0.001$; $n = 25$) and in the rainy season ($r_S = 0.525$; $P < 0.001$; $n = 31$). The size of the vitellogenic follicles was also correlated with the SVL, irrespective of the seasons ($r_S = 0.740$; $P < 0.001$; $n = 56$) and did not show significant variations between the seasons ($U = 1.260$; $P = 0.208$; $n = 56$), though there was a tendency for the size to increase as the rainy season advances. There was no correlation between SVL and clutch size ($r_S = 0.322$; $P = 0.333$; $n = 11$). The average number of eggs per individual was of 4.3 ± 0.7. The eggs (n = 45) had an average length of 20.8 ± 1.2 mm and an average width of 10.2 ± 0.9 mm. Among the females that contained eggs in their oviducts (n = 11), one was captured in May (dry season), while all others were captured in the rainy season. The smallest female with eggs in the oviducts measured 69.5 mm of SVL and was found in the rainy season. The shortest SVL for the male specimens with spermatozoa in the testes and epididymides was 77.9 mm. There was no significant difference in the frequency of males' reproductively active and inactive

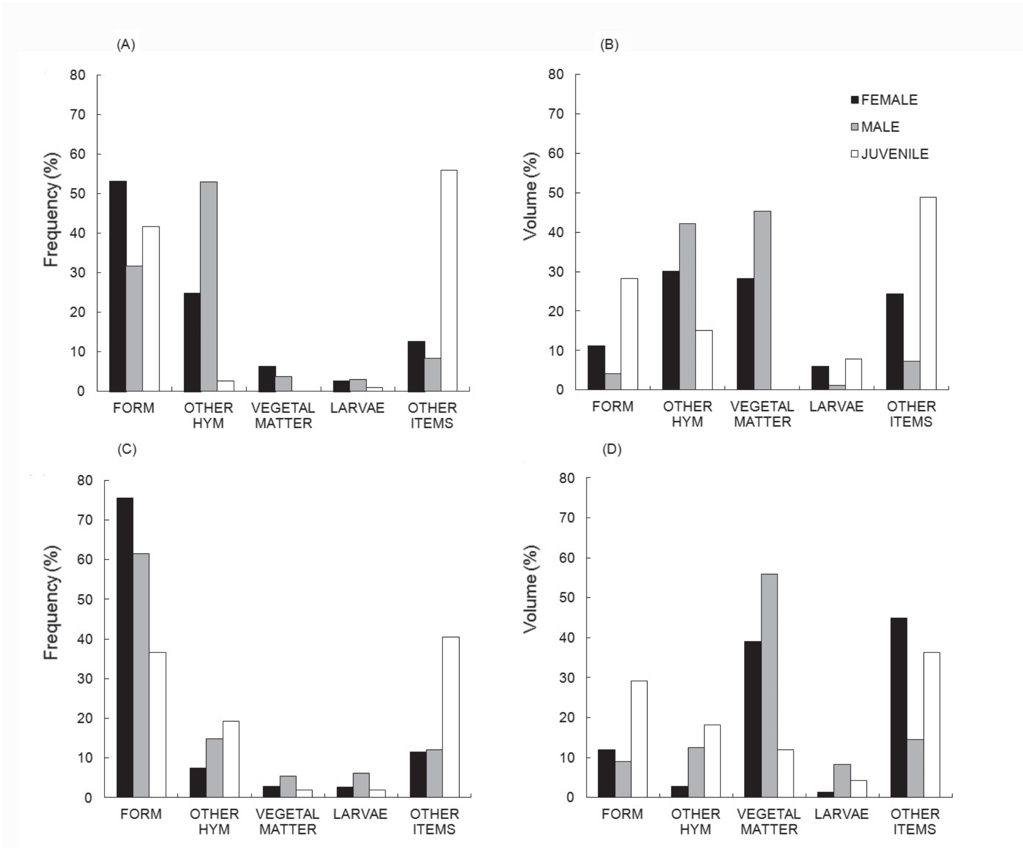

Fig. 2: Comparison between the number of food items recorded in the stomach contents of female, male and juvenile *Tropidurus torquatus* in the dry season (A and B) and the rainy season (C and D) in an area of rocky outcrops in southeastern Brazil. FORM = Formicidae; OTHER HYM = Other Hymenoptera.

Comparación entre el número de alimentos registrados en los contenidos estomacales de hembras, machos y juveniles de *Tropidurus torquatus* en la estación seca (A y B) y la estación de lluvias (C y D) en un área de afloramientos rocosos en el sureste de Brasil. FORM = Formicidae; OTHER HYM = Otro himenópteros.

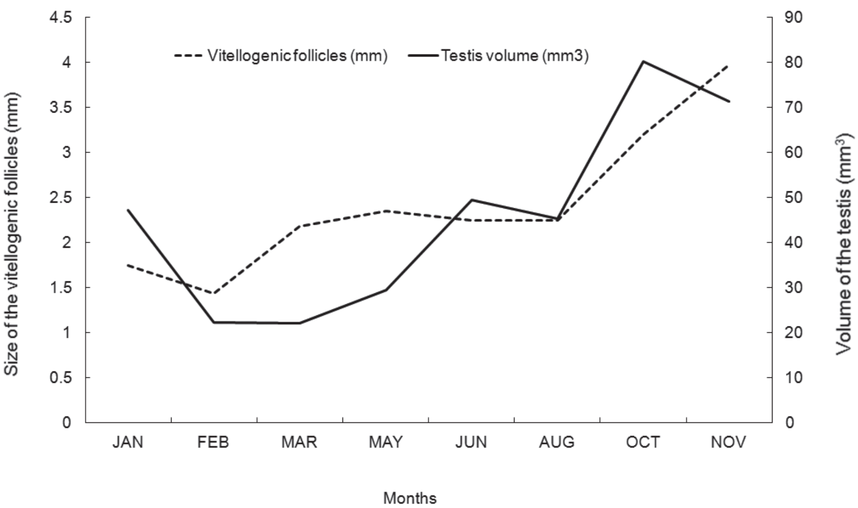

Fig. 3: Seasonal variation of the size of the vitellogenic follicles of females and the volume of the testes of males of *Tropidurus torquatus* in an area of rocky outcrops in southeastern Brazil.

Variación estacional del tamaño de los folículos vitelogénicos de las hembras y el volumen de los testículos de los machos de *Tropidurus torquatus* en un área de afloramientos rocosos en el sureste de Brasil.

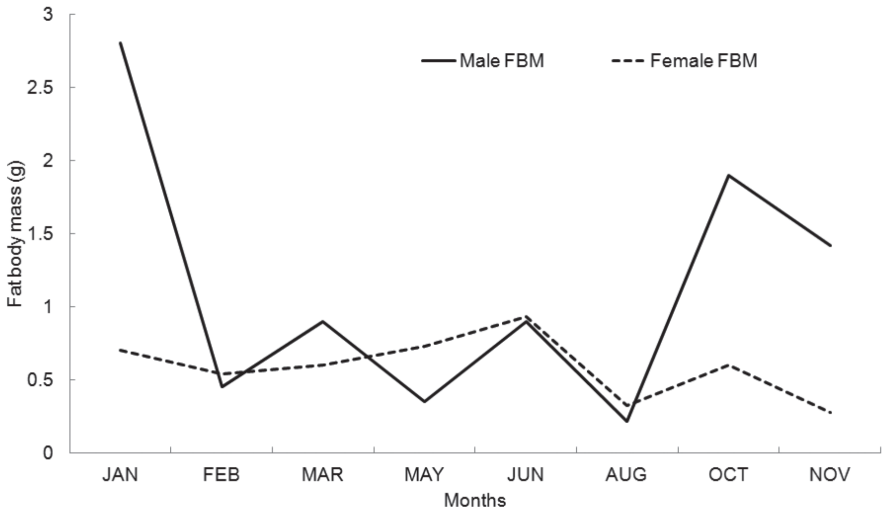

Fig. 4: Comparison between the seasonal patterns of fat body mass in male and female *Tropidurus torquatus* in an area of rocky outcrops in southeastern Brazil.

Comparación entre los patrones estacionales de la masa del cuerpo grasa en machos y hembras de *Tropidurus torquatus* en un área de afloramientos rocosos en el sureste de Brasil.

between the dry and the rainy seasons. In both seasons, adult males were reproductively active or beginning this activity, although the testicular volume tended to increase as females entered the reproductive period (Fig. 3).

The fat body weight (Table 1) did not significantly vary between the seasons for females (U = 0.9698; P = 0.3322; n = 56), while for males the changes were more accentuated (U = 1.9203; P = 0.0548; n = 29; Fig. 4). The juveniles had a very significant variation in their fat body mass (U = 3.876; P < 0.0001; n = 25). The reproductive parameters (size of vitellogenic follicles, clutch size, volume of testes and fat body mass) were not correlated with the environmental variables (temperature, humidity and precipitation) (Table 4). In other words, the increase in size of these structures was not related to the variation of environmental variables.

DISCUSSION

Diet composition

Our data show that the population exhibits sexual size dimorphism, as expected for the species, with males being significantly larger and heavier than females (Rodrigues 1987, Bergallo & Rocha 1993). The population of *T. torquatus* at Toledos feeds mainly on arthropods and plant material. This result corroborates the findings reported for *T. torquatus* populations in restinga areas, where the numerical frequency of arthropods in diet corresponded to more than 80 % of total prey (Bergallo & Rocha 1994, Teixeira & Giovanelli 1999). In our study the volumetric stomach content consisted mainly of plant material. Some authors have previously described omnivore habits for *T. torquatus* (Araújo 1987, Van Sluys 1993, 1995), which was also observed in this work. Based on the volume of material consumed, our results suggest that adults focus more on particular plants (almost all plants consumed were *Centrosema coriaceum*) than on a carnivorous diet (which was general in relation to taxa).

Tropidurus torquatus often feeds on arthropods, a basal condition in neotropical lizards (Vitt et al. 2003), and this work showed that the prey item ants had the highest numerical frequency in the lizards' diet. Most of the ants eaten by the lizards were worker ants, probably ingested while foraging. Worker ants are often small and with lower nutritional value for predators than alate ants and other invertebrates (Redford & Dorea 1984). For this reason, this prey item, although widely consumed, probably does

TABLE 4

Spearman's correlation between parameters associated with reproduction of *Tropidurus torquatus* and climate variables in an area of rocky outcrops in southeastern Brazil.

Correlación de Spearman entre los parámetros asociados con la reproducción de *Tropidurus torquatus* y las variables climáticas en un área de afloramientos rocosos en el sureste de Brasil.

	Temperature (°C)	Humidity (%)	Precipitation (mm)
Vitellogenic follicles size	r_S = -0.5749; P = 0.1360	r_S = 0.1317; P = 0.7578	r_S = -0.1796; P = 0.6703
Testis volume	r_S = -0.4048; P = 0.3198	r_S = 0.00; P = 1.0	r_S = -0.0476; P = 0.9108
Male fat body mass	r_S = 0.2874; P = 0.4900	r_S = 0.4671; P = 0.2432	r_S = 0.6347; P = 0.0908
Female fat body mass	r_S = -0.3832; P = 0.3486	r_S = -0.958; P = 0.8215	r_S = -0.3353; P = 0.4168
Juvenile fat body mass	r_S = 0.5643; P = 0.3217	r_S = 0.6156; P = 0.2689	r_S = 0.7182; P = 0.1717
Clutch size	r_S = -0.1911; P = 0.5519	r_S = 0.2113; P = 0.5097	r_S = 0.1703; P = 0.5966

not provide adequate nutrition. Lizards are able to capture the most abundant preys in the environment (personal observation), showing wide trophic niche with generalized diet, reducing the hunting period, while also they are able to perform other functions, such as thermoregulation and territorial defense. The sit-and-wait foraging behavior described for this species (Araújo 1987, Van Sluys 1993, 1995, Teixeira & Giovanelli 1999, Carvalho et al. 2007) is a strategy that occurs in opportunist and generalist predators (Jaksic 2001).

The most diverse and uniform diet was observed in females captured during the dry season. The juveniles preferably consumed ants and other insects. The volume of plant material was very important for the adults, because this was their main diet component in the rainy season, the same as encountered by Fialho et al. (2000) and Carvalho et al. (2007). These research groups observed that the ingestion of plant material can constitute more than 50 % of the diet of adults, contrasting to the low amount of material ingested by juvenile individuals. In this work, probably the low occurrence of flowers of *Centrosema coriaceum* in the stomach contents of juvenile lizards was probably due to an anatomical restriction to ingest these plants, i.e., the jaw length was a limiting factor for juvenile lizards to eat flowers or they did not have the strength to pull flowers out. Adults have greater mouth openings, facilitating the ingestion of flowers. The flowers of this herb commonly occur in the study area and measure about 35-50 mm in length. Some specimens were observed competing for flowers as food.

Adults, mainly males, ingested larger volumes of plant material. The food pattern where adults ingest mostly vegetable parts and the juveniles consume preferentially ants and secondarily other insects was also reported for *T. psammonastes* in dunes of the São Francisco River flowing through a Brazilian caatinga (Lima & Rocha 2006) and for *T. torquatus* in restinga habitats in southeastern Brazil (Carvalho et al. 2007). According to Frost et al. (2001) and Vitt et al. (2003), ingestion of both ants and plants is plesiomorphic for the Tropidurinae, occurring from basal branches (*Eurolophosaurus* spp.) up to the most derived branches (*T. oreadicus* and *T. hispidus*). Plants are a source of water in dry environments or dry seasons (Fialho et al. 2000, Lima & Rocha 2006, Ribeiro et al. 2008a) and may also represent a source of important nutrients for growth. Juvenile lizards are unable to digest (or swallow) plant material and therefore consume more animal protein than vegetable protein (Pough 1973).

Other authors also reported the presence of plant material in the *T. torquatus* stomach content, suggesting that it is not accidental (Bergallo & Rocha 1994, Teixeira & Giovanelli 1999). For *T. torquatus* in this study, the selectivity for certain plant species in its diet is evident, because most of the vegetable material ingested was *Centrosema coriaceum* flowers. It is a creeping herb with flowers that can be reached from the ground by the lizards. Flowers are easily digestible and do not require morphological specialization or associated intestinal flora and fauna to aid in cellulose digestion (Cooper & Vitt 2002). This plant may possess anthelmintic properties, as observed by Pereira et al. (2012), because the consumption of *C. coriaceum* had a negative effect on the abundance of nematode parasite species of *T. torquatus*.

It has been observed that only the largest lizard species that lived in warm climates are successful as herbivores (Pough 1973). However, small body size lizards, as some liolaemids, that live in cold-climate are herbivores successful (Espinoza et al. 2004; Valdecantos et al. 2012). It is explained by a unique combination of climatic conditions, ecophysiological constraints and opportunities, and phylogenetic history (Espinoza et al. 2004). *Tropidurus torquatus* consumes a large volume of plant material, so it is reasonable to speculate that the lizards can digest and use this food item. In environments with little availability of arthropods, as reported by Fialho et al. (2000), *T. torquatus* consumes large amounts of vegetable material.

Lizards are able to change their foraging strategy according to food availability (Huey & Pianka 1981), or to some characteristics of each habitat, varying the types of prey consumed and their reproductive pattern, as also observed in other *Tropidurus* species (Vitt 1993, Cruz et al. 1998, Ávila et al. 2008, Ribeiro & Freire 2011). Probably the plasticity of the species is enough to change the hunting strategy according food supply, which varies throughout the year, as observed for two tropidurid lizards in Brazilian caatinga (Kolodiuk et al. 2009). As shown in Fig. 2 and Table 1, this species have a wide food niche and adapt its diet according to the availability of the environment. The accumulation curve of prey species shows that an asymptote was not reached for either sex and in either season, showing that the species can feed on a wide range of taxa, and is likely to feed on almost all species it can swallow. Basically, *T. torquatus* can eat wide range of food items.

Reproductive aspects

The data on the female reproductive activity of *T. torquatus* showed a difference between the seasons, but not as noticeable in relation to the seasonal reproduction observed by Wiederhecker et al. (2002) in the cerrado biome. The high frequency of reproductive females in the rainy season, as observed by Kiefer et al. (2008) in restinga environments, was not observed in our study. According to these authors, different patterns in reproductive cycles may originate from the different resources and microhabitats availability for development of juvenile individuals.

The absence of significant differences in the fat body mass of males and females, and in the size of the follicles between seasons in the analyzed sample cannot be explained by environmental factors. There was no influence of seasonality on the fat body size in females. Vitt & Goldberg (1983) and Ribeiro et al. (2012) observed for *T. hispidus* in Brazilian caatinga biome that fat body mass decreased as the reproductive period advanced. Our data for *T. torquatus* do not demonstrate this same process. In relation to juveniles, according to Wiederhecker et al. (2002), this increase in the fat body mass can be explained by the food abundance in the rainy season, since fat body mass can indirectly indicate food availability. As we found no variation in fat bodies mass between the seasons, our data suggest that food is not an important factor in the study area between seasons.

Females presented reproductive conditions at the end of the dry season and during the rainy season (August to December), similar to that registered for the inland populations in the cerrado region of central Brazil (Vieira et al. 2001, Wiederhecker et al. 2002, 2003), not throughout the year, as reported for the coastal region of southeastern Brazil (Teixeira & Giovanelli 1999). These adjustments in behavior patterns may result from acclimation mechanism from this species that presents a wide geographic distribution and a range of body temperatures in different populations (Ribeiro et al. 2008b).

In our study, though there was no significant difference in the size of the vitellogenic follicles between seasons, females which effectively had eggs in their oviducts were found from the beginning of October to the beginning of December, that is, in the spring and early summer, and oviposition was more restricted to this part of the year. The hatchling seasonality may be an evolutionary adaptation to achieve better offspring success, and may be influenced by better thermal conditions (Murphy et al. 2006). We cannot say that the reproduction of *T. torquatus* usually occurs in the dry season based only on the finding of one female (size = 88.3 mm) containing eggs in the oviducts during the month of May. Nevertheless, since female lizards can accumulate sperm during many months or years in their seminal receptacles (Ferreira & Dolder 2003b), delay in fertilization can occur and cause the formation of eggs some time after copulation or some females can reproduce more than one occasion per season (Teixeira & Giovanelli 1999, Wiederhecker et al. 2002, 2003, Kiefer et al. 2008). However, for Tropiduridae species, studies on these structures are still scarce, with reports only for *T. itambere* (Ferreira & Dolder 2007), which shows the female's ability to keep spermatozoids inside folds of the vaginal epithelium. This fact was not investigated in the present study, but it may also happen with *T. torquatus*.

Adult males of *T. torquatus* at Toledos contained spermatozoa throughout the year and for this reason were potentially reproductive during the entire year, a pattern that seems to be common for the genus (Ferreira & Dolder 2003a, Vitt & Goldberg 1983, Van Sluys 1993, Van Sluys et al. 2010). However, during the female reproductive period, an increase in the cell division of germinal epithelium was observed in males in our study. Although there is continuous spermatozoa production, the peak of the reproductive activity in males and females is very synchronized (Wiederhecker et al. 2003). The males that did not show spermatozoids in our study were juveniles or recent adults that had not begun to produce gametes. According to Wiederhecker et al. (2002), continuous spermatozoa production guarantees the males a minimum testosterone production along the year, which influences agonistic encounters, since *T. torquatus* is considered a highly territorial species (Wiederhecker et al. 2002, Ribeiro et al. 2009), thus ensuring success by keeping or conquering a good site for reproduction, reflecting directly on this species' reproductive fitness.

In this study we did not find any correlations between environmental variables and reproductive parameters of *T. torquatus*. Although Colli et al. (1997) and Wiederhecker et al. (2002, 2003) considered that reproduction is affected by resource availability and environmental conditions, the relationship between these variables is not clearly defined for any species. In this study, it was also difficult to correlate environmental conditions with the reproductive processes. Many of the differences encountered reflect different climatic conditions of each region and *T. torquatus* is found in a wide range of regions and with different body temperatures (Bergallo & Rocha 1993, Teixeira-Filho et al. 1996, Gandolfi & Rocha 1998, Hatano et al. 2001, Rocha et al. 2002, Kiefer et al. 2005, Ribeiro et al. 2008b). Therefore, different reproductive strategies have been observed in populations of *T. torquatus* (Wiederhecker et al. 2002, Kiefer et al. 2008). Our study site is located near thick vegetation and beside a river, and the *T. torquatus* specimens presented lower average body temperatures than individuals from other areas where this species occurs (see Ribeiro et al. 2008b for the thermal ecology of the population of this study). The minimum reproductive size, the number of clutches per breeding season, the number of eggs per brood, the number of days estimated to reach sexual maturity, and survival of *T. torquatus* vary enormously between the different biomes of Brazil as already demonstrated for the cerrado (Wiederhecker et al. 2002, 2003, Pinto et al. 2005), restingas (Teixeira & Giovanelli 1999, Kiefer et al. 2008), pampas sulinos (Arruda 2009) and Atlantic Rainforest (this study). Therefore, changes in reproductive strategies are essential to adjust the life cycle of the species to the highly diverse environments in which it occurs. The patterns reproductive biology of *T. torquatus* is variable.

The body temperatures may influence the minimum reproductive size of the individuals from this population in relation to populations from other areas. The minimum reproductive size of the individuals analyzed in the study area was larger than that described by Wiederhecker et al. (2002), who registered reproductive males of *T. torquatus* with SVL of 70 mm and females with 65 mm in cerrado. In restingas areas, the smallest reproductive female was 51.1 mm and the smallest reproductive male was 49.7 mm (Van Sluys et al. 2010). *Tropidurus torquatus* populations usually have different minimum reproductive size patterns, probably due to differences of environmental temperatures between those saxicolous and psammophilous populations (see Kiefer et al. 2008) and also among those populations from different latitude, altitude, vegetation units or resource availability (Wiederhecker et al. 2002, 2003).

The average number of eggs per female in our study corroborates the findings in a coastal area of Espírito Santo state (Teixeira & Giovanelli 1999). The same occurs for the average size of the eggs (Rodrigues 1987, Bergallo & Rocha 1993, 1994), which does not seem to be influenced by the female body size, but the number of eggs did not match that observed in most coastal areas, where females usually only invested in two eggs per clutch (Kiefer et al. 2008).

The relationship between reproductive aspects and the environmental factors are not yet clear. More studies are still needed to relate the parameters that act as triggers of reproductive processes. Our results corroborate the observations made by Kiefer et al. (2008) in different coastal areas, where the patterns of each population vary according to latitude and the area of occupation. Thus, species with wide geographic distribution, such as *T. torquatus,* may present high plasticity and adaptability in relation to the peculiar conditions of each region where it occurs.

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LITERATURE CITED

ARAÚJO AFB (1987) Comportamento alimentar dos lagartos: o caso dos *Tropidurus* do grupo *torquatus* da Serra de Carajás, Pará (Sauria: Iguanidae). Anais de Etologia (Brazil) 5: 189-197.

ARAÚJO AFB (1991) Structure of a white sand-dune lizard community of coastal Brazil. Revista Brasileira de Biologia (Brazil) 51: 857-865.

ARRUDA JLS (2009) Ecologia de *Tropidurus torquatus* (Squamata: Tropiduridae) no bioma pampa, extremo sul do Brasil. MSc. Dissertation, Universidade Federal de Santa Maria, Santa Maria, Brazil.

ÁVILA RW, LR CUNHA-AVELAR & VL FERREIRA (2008) Diet and reproduction of the lizard *Tropidurus etheridgei* in rocky areas of Central Brazil. Herpetological Review 39: 430-433.

BERGALLO HG & CFD ROCHA (1993) Activity patterns and body temperatures of two sympatric lizards (*Tropidurus torquatus* and *Cnemidophorus ocellifer*) with different foraging tactics in southeastern Brazil. Amphibia-Reptilia 14: 312-315.

BERGALLO HG & CFD ROCHA (1994) Spatial and trophic niche differentiation in two sympatric lizards (*Tropidurus torquatus* and *Cnemidophorus ocellifer*) with different foraging tactics. Australian Journal of Ecology 19: 72-75.

BORROR DJ & DM DELONG (1988) Introdução ao estudo dos insetos. First edition. Editora Edgard Blücher Ltda, São Paulo.

BUZZI ZJ (2002) Entomologia didática. Fouth edition. Editora UFPR, Curitiba.

CARVALHO ALG, HR SILVA, AFB ARAÚJO, R ALVES-SILVA & RR SILVA-LEITE (2007) Feeding ecology of *Tropidurus torquatus* (Wied) (Squamata, Tropiduridae) in two areas with different degrees of conservation in Marambaia Island, Rio de Janeiro, Southeastern Brazil. Revista Brasileira de Zoologia (Brazil) 24: 222-227.

COLLI GR, AK PÉRES-JR & MG ZATZ (1997) Foraging mode and reproductive seasonality in tropical lizards. Journal of Herpetology 31: 490-499.

COLWELL RK (2006) EstimateS: Statistical estimation of species richness and shared species from samples. Version 8. (accessed June 20, 2009).

COOPER WE & LJ VITT (2002). Distribution, extent, and evolution of plant consumption by lizards. Journal of Zoology 257: 487-517.

CRUZ FB, S SILVA & GJ SCROCCHI (1998) Ecology of the lizard *Tropidurus etheridgei* (Squamata: Tropidurudae) from the dry Chaco of Salta, Argentina. Herpetological Natural History 6: 23-31.

DEGEO - ICH/UFJF (2008) Laboratório de Climatologia Geográfica e Análise Ambiental. Estação Climatológica Principal de Juiz de Fora; Centro de Pesquisas Sociais /Anuário 2008.

ESPINOZA RE, JJ WIENS & CR TRACY (2004) Recurrent evolution of herbivory in small, cold-climate lizards: Breaking the ecophysiological rules of reptilian herbivory. Proceedings of the National Academy of Sciences 101: 16819-16824.

FERREIRA A & H DOLDER (2003a) Sperm ultrastructure and spermatogenesis in the lizard, *Tropidurus itambere*. Biocell 27: 353-362.

FERREIRA A & H DOLDER (2003b) Cytochemical study of spermiogenesis and mature spermatozoa in the lizard *Tropidurus itambere* (Reptilia, Squamata). Acta Histochemica 105: 339-352.

FERREIRA A & H DOLDER (2007) Histochemistry and ultrastructure of the oviducts and seminal receptacle of *Tropidurus itambere* (Rodrigues, 1987) (Reptilia: Tropiduridae). Brazilian Journal of Morphology Science (Brazil) 24: 29-38.

FIALHO RF (1990) Seed dispersal by a lizard and a treefrog: effect of dispersal site on seed survivorship. Biotropica 22: 423-424.

FIALHO RF, CFD ROCHA & D VRCIBRADIC (2000) Feeding ecology of *Tropidurus torquatus*: ontogenetic shift in plant consumption and seasonal trends in diet. Journal of Herpetology 34: 325-330.

FITCH HS (1970) Reproductive cycles in lizards and snakes. University of Kansas, Museum of Natural History, Miscellaneous Publication 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 RD, 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.

GANDOLFI SM & CFD ROCHA (1998) Orientation of thermoregulating *Tropidurus torquatus* (Sauria: Tropiduridae) on termite mounds in an open area of south–eastern Brazil. Amphibia-Reptilia 19: 319-323.

HAMMER Ø, DAT HARPER & PD RYAN (2001) PAST: Paleontological Statistics Software Package for Education and Data Analysis. URL: http://palaeo-electronica.org/2001_1/past/issue1_01.htm (accessed September 20, 2007).

HATANO FH, D VRCIBRADIC, CAB GALDINO, M CUNHA-BARROS, CFD ROCHA & M VAN SLUYS (2001) Thermal ecology and activity patterns of the lizard community of the restinga of Jurubatiba, Macaé, RJ. Revista Brasileira de Biologia (Brazil) 61: 287-294.

HUEY RB & ER PIANKA (1981) Ecological consequences of foraging mode. Ecology 62: 991-999.

JAKSIC F (2001) Ecología de comunidades. First edition. Ediciones Universidad Católica de Chile, Santiago.

KIEFER MC, M VAN SLUYS & CFD ROCHA (2005) Body temperatures of *Tropidurus torquatus* (Squamata, Tropiduridae) from coastal populations: Do body temperatures vary along their geographic range? Journal of Thermal Biology 30: 449-456.

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.

KOLODIUK MF, LB RIBEIRO & EMX FREIRE (2009) The effects of seasonality on the foraging behavior of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata, Tropiduridae) living in sympatry in the Caatinga of northeastern Brazil. Zoologia 26: 581-585.

LIMA AFB & PLB ROCHA (2006) Ontogenetic change in plant consumption by *Tropidurus psammonastes*, Rodrigues, Kasahara & Yonenaga-Yassuda, 1988 (Tropiduridae), a lizard endemic to the dunes of the São Francisco River, Bahia, Brazil. Revista Brasileira de Zoociências (Brazil) 8: 67-75.

LUNA LG (1960) Histologic Staining Methods of the Armed Forces Institute of Pathology. Third edition. McGraw Hill, New York.

MURPHY K, S HUDSON & G SHEA (2006) Reproductive seasonality of three cold-temperature viviparous skinks from southeastern Australia. Journal of Herpetology 40: 454-464.

PEREIRA FB, SC GOMIDES, BM SOUSA, SS LIMA & JL LUQUE (2012) The relationship between nematode infections and ontogeny and diet of the lizard *Tropidurus torquatus* (Wied, 1820) (Squamata: Tropiduridae) from the Atlantic Rainforest in southeastern Brazil. Journal of Helminthology. URL: doi:10.1017/S0022149X12000466 (accessed October 15, 2012).

PINTO CS, HC WIEDERHECKER & GR COLLI (2005) Sexual dimorphism in the neotropical lizard, *Tropidurus torquatus* (Squamata: Tropiduridae). Amphibia-Reptilia 26: 127-137.

POUGH FH (1973) Lizard energetics and diet. Ecology 54: 837- 844.

REDFORD KH & JG DOREA (1984) The nutritional value of invertebrates with emphasis on ants and termites as food for mammals. Journal of Zoology 203: 385-395.

RIBEIRO LB & EMX FREIRE (2011) Trophic ecology and foraging behavior of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata, Tropiduridae) in a caatinga area of northeastern Brazil. Iheringia Série Zoologia (Brazil) 101: 225-232.

RIBEIRO LB, M GOGLIATH & EMX FREIRE (2008a) *Tropidurus semitaeniatus* (Squamata: Tropiduridae) as a seed disperser of the plant *Commiphora leptophloeos* (Burseraceae) in the caatinga of northeastern Brazil. Cuadernos de Herpetología (Argentina) 22: 91-94.

RIBEIRO LB, SC GOMIDES, AO SANTOS & BM SOUSA (2008b) Thermoregulatory behavior of the saxicolous lizard, *Tropidurus torquatus* (Squamata, Tropiduridae), in a rocky outcrop in Minas Gerais, Brazil. Herpetological Conservation and Biology (USA) 3: 63-70.

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.

RIBEIRO LB, NB SILVA & EMX FREIRE (2012) Reproductive and fat body cycles of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata, Tropiduridae) in a caatinga area of northeastern Brazil. Revista Chilena de Historia Natural 85: 307-320.

ROCHA CFD, GF DUTRA, D VRCIBRADIC & VA MENEZES (2002) The terrestrial reptile fauna of the Abrolhos archipelago: species list and ecological aspects. Brazilian Journal of Biology 62: 285-291.

RODRIGUES MT (1987) Sistemática, ecologia e zoogeografia dos *Tropidurus* do grupo *torquatus* ao sul do Rio Amazonas (Sauria, Iguanidae). Arquivos de Zoologia (Brazil) 31: 105-230.

SODEINDE AO & OA KUKU (1989) Aspects of the morphometry, growth-related parameters and reproductive condition of *Agama* lizards in Ago-Iwoye, Nigeria. Herpetological Journal 1: 386-392.

TEIXEIRA-FILHO PE, CFD ROCHA & SC RIBAS (1996) Aspectos da ecologia termal de *Tropidurus torquatus* (Sauria: Tropiduridae) em uma área de restinga do sudeste do Brasil. In: Péfaur JE (ed) Herpetologia Neotropical: 255-267. Consejo publicaciones, Universidad de Los Andes, Merida.

TEIXEIRA RL & M GIOVANELLI (1999) Ecologia de *Tropidurus torquatus* (Sauria: Tropiduridae) da restinga de Guriri, São Mateus, ES. Revista Brasileira de Biologia (Brazil) 59: 11-18.

VALDECANTOS MS, F ARIAS & RE ESPINOZA (2012) Herbivory in *Liolaemus poecilochromus*, a small, cold-climate lizard from the Andes of Argentina. Copeia 2012: 203-210.

VAN SLUYS M (1993) The reproductive cycle of *Tropidurus itambere* (Sauria: Tropiduridae) in Southeastern Brazil. Journal of Herpetology 27: 28-32.

VAN SLUYS M (1995) Seasonal variation in prey choice by the lizard *Tropidurus itambere* (Tropidurudae) in southeastern Brazil. Ciência e Cultura (Brazil) 47: 61-65.

VAN SLUYS M, SB MARTELOTTE, MC KIEFER & CFD ROCHA (2010) Reproduction in neotropical *Tropidurus* lizards (Tropiduridae): evaluating the effect of environmental factors on *T. torquatus*. Amphibia-Reptilia 31: 117-126.

VIEIRA GHC, HC WIEDERHECKER, GR COLLI & SN BÁO (2001) Spermiogenesis and testicular cycle of the lizard *Tropidurus torquatus* (Tropiduridae, Squamata) in the Cerrado of central Brazil. Amphibia-Reptilia. 22: 217-233.

VITT LJ & SR GOLDBERG (1983) Reproductive ecology of two tropical iguanid lizards: *Tropidurus torquatus* and *Platynotus semitaeniatus*. Copeia 1983: 131-141.

VITT LJ (1993) Ecology of isolated open-formation *Tropidurus* (Reptilia: Tropiduridae) in Amazonian lowland rain forest. Canadian Journal of Zoology 71: 2370- 2390.

VITT LJ, PA ZANI & JP CALDWELL (1996) Behavioral ecology of *Tropidurus hispidus* on isolated rock outcrops in Amazonia. Journal of Tropical Ecology 12: 81-101.

VITT LJ, ER PIANKA, WE COOPER-JR & K SCHWENK (2003) History and the global ecology of squamate reptiles. American Naturalist 162: 44-60.

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.

WIEDERHECKER HC, ACS PINTO, MS PAIVA & GR COLLI (2003) The demography of the lizard *Tropidurus torquatus* (Squamata, Tropiduridae) in a highly seasonal Neotropical Savanna. Phyllomedusa 2: 9-19.

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