

**Diet and food ontogeny of the lizard *Tupinambis matipu* Silva et al. 2018 (Squamata:
Teiidae) in Central Brazil**

**Dieta e ontogenia alimentar do lagarto *Tupinambis matipu* Silva et al. 2018 (Squamata:
Teiidae) no Brasil Central**

**Dieta y ontogenia alimentaria del lagarto *Tupinambis matipu* Silva et al. 2018
(Squamata: Teiidae) en el Brasil Central**

Received: 11/10/2020 | Reviewed: 11/16/2020 | Accept: 11/20/2020 | Published: 11/25/2020

Odair Diogo da Silva

ORCID: <https://orcid.org/0000-0002-5271-2849>

Universidade do Estado de Mato Grosso, Brazil

E-mail: odair_diogo@hotmail.com

Thatiane Martins da Costa

ORCID: <https://orcid.org/0000-0001-7560-8828>

Universidade do Estado de Mato Grosso, Brazil

E-mail: thaticpcl@gmail.com

Vancleber Divino Silva-Alves

ORCID: <https://orcid.org/0000-0002-0730-5101>

Universidade do Estado de Mato Grosso, Brazil

Eder Correa Fermiano

ORCID: <https://orcid.org/0000-0002-1465-0675>

Universidade do Estado de Mato Grosso, Brazil

E-mail: edderfermiano@gmail.com

Mariany de Fatima Rocha Seba

ORCID: <https://orcid.org/0000-0002-5128-1530>

Universidade do Estado de Mato Grosso, Brazil

E-mail: marianyrocha6@gmail.com

Olinda Maíra Nogueira

ORCID: <https://orcid.org/0000-0002-1829-9325>

Universidade do Estado de Mato Grosso, Brazil

E-mail: olindamaria@gmail.com

Jessica Rhaiza Mudrek

ORCID: <https://orcid.org/0000-0001-8452-2946>

Universidade do Estado de Mato Grosso, Brazil

E-mail: jessicamudrek@gmail.com

Ana Paula Dalbem Barbosa

ORCID: <https://orcid.org/0000-0002-6282-4799>

Universidade do Estado de Mato Grosso, Brazil

E-mail: pauladalbem11@gmail.com

Almério Câmara Gusmão

ORCID: <https://orcid.org/0000-0002-5450-5392>

Universidade do Estado de Mato Grosso, Brazil

E-mail: almeriocg@hotmail.com

Claumir César Muniz

ORCID: <https://orcid.org/0000-0002-2082-2234>

Universidade do Estado de Mato Grosso, Brazil

E-mail: claumir@unemat.br

Maria Antônia Carniello

ORCID: <https://orcid.org/0000-0002-7474-4227>

Universidade do Estado de Mato Grosso, Brazil

E-mail: carniello@unemat.br

Manoel dos Santos-Filho

ORCID: <https://orcid.org/0000-0002-9784-7114>

Universidade do Estado de Mato Grosso, Brazil

E-mail: msantosfilho@gmail.com

Dionei José da Silva

ORCID: <https://orcid.org/0000-0002-6189-9756>

Universidade do Estado de Mato Grosso, Brazil

E-mail: dioneijs@unemat.br

Abstract

The tegus are generalists lizards that use large amounts of prey in its diet, providing environmental services as a biological controller and seed disperser, which reveals how important diet studies are to understand ecological relationships related to a particular species. So the objective of this study was to analyze diet and food ontogeny of *T. matipu*, investigating changes in the pattern and composition of food items in different age classes and

how the species shares its intraspecific niche. The captured specimens had the contents of their digestive tracts were analysed qualitatively and quantitatively. Our results indicate that *T. matipu* is a generalist lizard, consuming many food items, which fruits are the most important item in its diet. However, the species uses food resources in different importance proportions, according to its age class. Fruit consumption tends to increase and arthropods consumption decline as the age class increase. Thus, *T. matipu* performs an intraspecific sharing of feeding niche between the age classes and constitutes potential seed dispersers in its populations distributed along the Upper Course of the Paraguai River.

Keywords: Reptiles; Tegu; Food item; Frugivory; Floodplain.

Resumo

Os teiús são lagartos generalistas que utilizam grande quantidade de presas em sua dieta, prestando serviços ambientais como controlador biológico e dispersor de sementes, o que revela a importância dos estudos dietéticos para entender as relações ecológicas relacionadas a uma determinada espécie. Assim, o objetivo deste estudo foi analisar a dieta e a ontogenia alimentar de *T. matipu*, investigando mudanças no padrão e na composição de alimentos em diferentes classes de idade e como a espécie compartilha seu nicho intraespecífico. Os espécimes capturados tiveram os conteúdos de seus tratos digestórios analisados qualitativamente e quantitativamente. Nossos resultados indicam que *T. matipu* é um lagarto generalista, consumindo diversos itens alimentares, sendo as frutas os mais importantes em sua dieta. No entanto, a espécie utiliza recursos alimentares em diferentes proporções de importância, de acordo com sua classe de idade. O consumo de frutas tende a aumentar e o consumo de artrópodes diminui com o aumento da classe de idade. Assim, *T. matipu* realiza um compartilhamento intraespecífico de nicho alimentar entre as classes de idade e se constitui em potenciais dispersores de sementes em suas populações distribuídas ao longo do Alto Curso do Rio Paraguai.

Palavras-chave: Répteis; Teiú; Item alimentar; Frugivoria; Planície de inundação.

Resumen

Los teiús son lagartos generalistas que utilizan grandes cantidades de presas en su dieta, brindando servicios ambientales como controladores biológicos, que pueden actuar como potenciales dispersores de semillas, lo que revela la importancia de los estudios sobre la dieta para comprender las relaciones ecológicas en estas especies. Así, el objetivo de este estudio fue analizar la dieta y la ontogenia alimentaria de *T. matipu*, investigando cambios en el

patrón y composición de los alimentos en diferentes clases de edad y cómo la especie comparte su nicho intraespecífico. Los especímenes capturados tenían el contenido de sus tractos digestivos analizados cualitativa y cuantitativamente. Nuestros resultados indican que *T. matipu* es un lagarto generalista, que consume una gran cantidad de alimentos, siendo las frutas el elemento más importante en su dieta. Sin embargo, la especie utiliza recursos alimentarios en diferentes proporciones de importancia, según su clase de edad. El consumo de frutas tiende a aumentar y los artrópodos disminuyen con la edad. Así, *T. matipu* realiza un reparto intraespecífico de nicho alimentario entre las clases de edad, y constituyen potenciales dispersores de semillas en sus poblaciones distribuidas a lo largo del curso superior del río Paraguai.

Palabras clave: Reptiles; Teiú; Alimento; Frugivoria; Lianura aluvial.

1. Introduction

Within the group of reptiles Squamata, the tegus (Teiidae) constitute the largest predatory lizards in South America (Maffei et al., 2007), being distributed in two genera, *Tupinambis* and *Salvator* (Harvey et al., 2012). The species of the genus *Tupinambis* are distributed in the northern and central portion of Cis-Andean South America, including Venezuela, Ecuador, Peru, Bolivia, Trinidad and Tobago, Guyana, eastern Colombia and Brazil (Silva et al., 2018). To Brazil, Costa & Bernils (2018) consider the records of seven species, *T. cryptus*, *T. cuzcoensis*, *T. longilineus*, *T. teguixin*, *T. palustres*, *T. quadrilineatus* and *T. matipu*. Although the wide occurrence, species number and several ecological aspects of the tegus are still unknown (Winck, 2007).

The literature points out that these animals have an active terrestrial habit (Pough, 1999). The tegus diet can be quite varied, including eggs, vegetables, arthropods, and even small vertebrates (Mecolli & Yanosky, 1994). Due to the diverse consumption of food items, they can act as predators and potential seed dispersers (Castro & Galetti, 2004), playing an important role in the ecosystem balance (Maffei et al., 2007). Described by Silva et al. (2018), mainly with specimens from the state of Mato Grosso, *T. matipu* has a distribution that ranges the states of Mato Grosso, Mato Grosso do Sul and Goiás (Silva et al., 2018; Costa & Bernils, 2018). The species inhabits the transition area between the Amazon, Cerrado and the Pantanal, with the vegetation forming a mosaic of dense tropical forest, savanna areas and

wetlands in the Brazilian Pantanal (Silva et al., 2018). Ecological data on the species are rare, and their diet has not yet been investigated.

Food is a fundamental component in structuring the interaction dynamics of a given lizards population with its habitat (Duffield & Bull, 1998), making it a fundamental aspect of these organisms (Colli et al., 1992). Therefore, knowing the role of this species and how it uses the environment to obtain its food resources is essential to understand its relationship with the ecosystem. However, in the diet, the items used by a given species may have qualitative and quantitative variations (Van Sluys, 1993; Duffield & Bull, 1998), according to different influences. These influences can be caused by biotic factors such as physiological or resource availability (Vitt & Caldwell, 2009), and abiotic factors, such as temperature (Rocha et al., 2009). Furthermore, tegus present an ontogenetic change in their dentition (Dessem, 1985; Presch, 1974), this fact has been associated with differences in the composition of the diet, between different age classes (Presch, 1974).

In any case, the environment structure in which these animals live is fundamental to the nutritional life of the species, since the environment is the food source. Therefore, changes in the biotic structure of different environments can promote changes in food availability for different organisms in the community. Thus, the environmental changes caused by the implementation of agricultural activities, for instance, are described as the main threats to Brazilian reptiles (ICMbio, 2018), not only by the direct changes in its preferred habitats but indirectly by disrupting important food sources.

However, reptiles such as tegus can contribute to agricultural activities, since they ingest large amounts of arthropods (e.g. Williams et al., 1993; Mercolli & Yanoski, 1994; Kiefer & Sazima, 2002), and many of these are considered agricultural pests. It is also noteworthy that tegus are generalist animals and feed on many fruits, swallowing whole parts of it and, therefore, can be potential seed dispersers (Castro & Galetti, 2004). The fact that lizards are not demanding, in habitat structures, can facilitate fruit consumption in areas where it is available and disperse seeds to impacted areas, where other potential dispersers, such as birds, and other large dispersers would not be. In addition, studies with diet (e.g. Mercolli & Yanosky, 1994; Kiefer & Sazima, 2002; Castro & Galleti, 2004) have revealed relevant information on the natural history of tegus, thus enabling the understanding of the ecological relationships of these species with their environment.

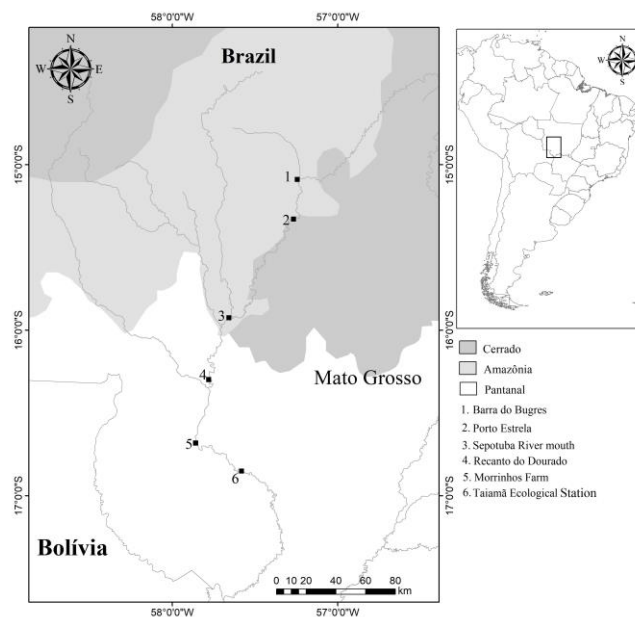
Given these factors, in this study we evaluated the *T. matipu* diet, investigating changes in the pattern and composition of food items in different age groups (juveniles, sub-adults and adults) and its intraspecific partitioning strategies of feeding niche, in the riparian

forest in the Upper Course of the Paraguay River. Understanding this species eating behavior, constitutes a knowledge basis to better understand these reptile's importance for the environment structure and its ecological roles in this portion of Mato Grosso.

2. Methodology

The study area is located in the Upper Course of the Paraguay River, from the municipality of Barra do Bugres ($15^{\circ} 05' 41.66''$ S; $57^{\circ} 14' 30.08''$ W) to Taiamã Ecological Station ($16^{\circ} 51' 54.20''$ S; $57^{\circ} 33' 11''$ W) (Figure 1), in a gradient of approximately 200 km extension. The region's climate is Aw, with a rainy season between October and April and a dry season between May and September (Amaral & Fonzar, 1982). The vegetation present in this location differs between Cerrado, Amazon Forest, Pantanal and ecotonal zones (Mourão et al., 2002).

Figure 1 - Study area identifying the sampling modules. Upstream to downstream in riparian vegetation of Upper Course of the Paraguay River. 1- Barra do Bugres; 2- Porto Estrela; 3- Sepotuba River mouth; 4- Recanto do Dourado Hotel; 5- Morrinhos Farm; 6- Taiamã Ecological Station.



Source: Almério C. Gusmão.

Six modules were established along the sampling area, in which each module had four sampling points, two on the right bank and two on the left bank of the Paraguay River, with the exception of Taiamã, which for logistical reasons and the absence of riparian forest on the left bank of the river, the four areas were implemented on the right bank (Figure 1), with a minimum distance of 2 km from each other. The traps were arranged in a "Y" shape, using four 60 L buckets, 15 meters from the center and interconnected by a 70 cm height guide

fence. The traps were open for ten days at each sampling point and were inspected daily in the morning. In the same areas, at points close to the pitfalls, there was also mammals sampling, using live traps (Sherman and Tomahawk), where the *T. matipu* captured in these traps were included as an occasional capture in our sample.

The sampling occurred in two dry seasons from 07/07/2017 to 11/18/2017 and 07/16/2018 to 07/26/2018. The captured specimens were euthanized with an injectable solution of lidocaine hydrochloride 2 % (Xylestesin®), fixed in 10 % formalin, preserved in 70 % alcohol and subsequently registered in the collection of the Limnology, Biodiversity and Ethnobiology Research Center of the Pantanal (CELBE), State University of Mato Grosso (UNEMAT), Cáceres, Mato Grosso, Brazil. The samplings were conducted under permanent collection license SISBIO number 8849-1, expedition registration number 10128 and 59443-1, and Opinion of the Ethics Committee on the Use of Animals of the State University of Mato Grosso CEUA / UNEMAT.

In the laboratory, all collected individuals were measured using tape to obtain head length (HL), rostrum-cloacal length (RCL) and tail length (TL). To identify the age group of *T. matipu* individuals, we observed the reproductive development of the specimens, together with morphological characters reported by Silva et al. (2018). Where adult males have well-developed testicles, female follicles are well developed, in juveniles, these reproductive structures are in development. In Silva et al. (2018) the authors relate that the species has the dorsum predominantly dark brown, with small elongated spots with black edges, forming irregular paravertebral and dorsolateral stripes from the nape to the base tail. This pattern can be overlapped on cream and black transverse stripes, which is visible in juveniles and sub-adults and disappears or becomes less evident in adults. Considering these criteria, we observed that juvenile had a maximum SVL of 250 mm and weight up to 320 g, sub-adults with SVL between 251 and 290 mm and weight between 321 to 490 g and adults with SVL above 290 mm and weight above 490 g.

The animals were dissected through a ventral incision to remove the digestive tract. Subsequently, the content analysis was made with the help of a stereoscopic microscope. The food items found were quantified and organized into categories, identified at the lowest taxonomic level possible and stored separately in ergometric flasks with a solution containing 70 % alcohol. The arthropods were identified by the morphological characteristics of the exoskeleton and specific literature. To identify the fruits consumed by the species, including seed fragments, we used literature and consulted the collection of fruits from the Herbarium of Pantanal “Vali Joana Pott” (HPAN) of the State University of Mato Grosso, in addition to

specialists in the area (Maria Antonia Carniello). The volume of food items was obtained using the liquid displacement in a graduated cylinder, adapted from Magnusson et al. (2003).

To determine the importance of each prey category, three different quantities were used: (i) numerical percentage (N %); (ii) percentage of frequency (F %) and (iii) percentage of volume (V %). To show the most important items in the diet, the Importance Value Index (IVI) of the food item was calculated based on the model proposed by Meira et al. (2007), $IVI = (N \% + F \% + V \%)/3$. The Niche Overlap Index (Pianka, 1973) was calculated using the *Spaa* package (Zhang & Zhang, 2016) in R (R Core Team, 2016). To demonstrate the species feeding strategy in its different age groups (juvenile, sub-adult and adult) we used Costello's (1990) graphic method.

3. Results

With a sampling effort of 2.880 buckets/nights, 46 specimens of *Tupinambis matipu* were collected, of which 26 were females and 20 males (Figure 2A and 2B). The specimens were identified according to age, being 17 juveniles, 10 sub-adults and 19 adults. The specimens were collected in five of the six modules sampled: Taiamã Ecological Station (n = 15), Morrinhos Farm (n = 15), Recanto do Dourado (n = 7), Sepotuba River mouth (n = 3) and Barra do Bugres (n = 6). The exception was the Porto Estrela module, however, the species was observed at this site.

Figure 2 - 2a) *Tupinambis matipu* captured in Tomahawk trap in Taiamã Ecological Station; 2b) Adult *T. matipu* registered in Morrinhos Farm area.



Source: Dionei J. Silva and Odair D. Silva.

All analysed stomachs showed at least one item inside, totalling 435 items registered, distributed in 36 different food categories (Table 1). In the composition of the species diet, considering the 46 specimens, the arthropod category was the most frequent, occurring in

78.26 % of the stomachs, however, fruits were the most representative item in terms of the numerical percentage (73.33 %), volumetric (60.77 %) and with the highest importance value (75.86 %; Figure 3). Among the fruits, the most representative were the species *Brosimum guianense* (Aubl.) Huber (V % = 24.92 % and IVI = 25.59) and *Ocotea diospyrifolia* (Meisn.) Mez (V % = 20.88 % and IVI = 16.47). In the arthropod category, Coleoptera with a volume of 6.18% and IVI = 16.98 and Decapoda with a volume of 2.47 % and IVI = 13.22 was the most expressive items. Among vertebrates, reptiles with the volume of 5.09 % and IVI = 7.46 and small mammals with the volume of 5.63 % and IVI = 5.16 were the most representative items in *T. matipu* diet (Table 1).

In Table 1, we present the food categories consumed by the species *T. matipu*, as well as the total of items consumed by the different age groups throughout the study area.

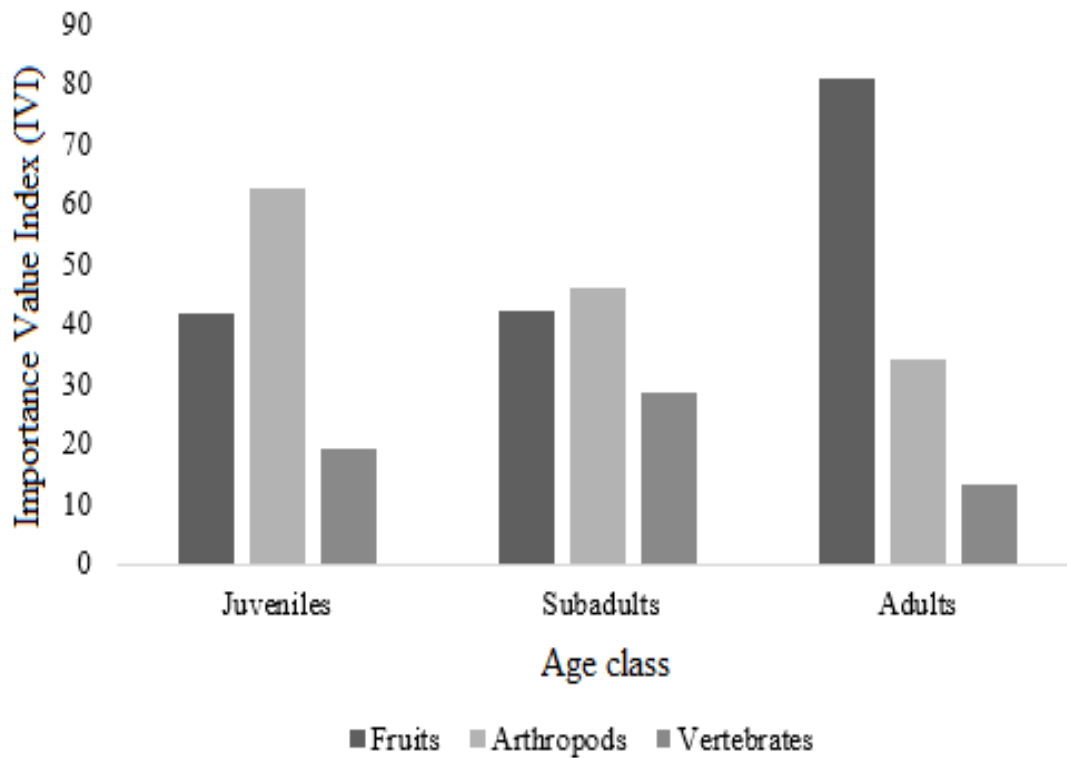
Table 1 - Composition of the food content found in the stomachs of 46 individuals of *Tupinambis matipu* collected on the banks of the Upper Paraguay River. N % = Numeric percentage of the item in the stomachs; F % = Percentage of the frequency of the item in the stomachs; V % = Volumetric percentage of the stomach item; IVI = Importance value index.

Prey Category	Total (n = 46)				juvenile (n = 17)				Sub-adults (n = 10)				Adults (n = 19)			
	N %	F %	V %	IVI	N %	F %	V %	IVI	N%	F%	V %	IVI	N %	F %	V %	IVI
Fruits (Total)	73.3	56.5	60.8	63.5	43.4	41.2	40.2	41.6	72	40	14.5	42.2	83.7	79	80.5	81.1
<i>Ficus</i> sp.	15.4	8.7	0.37	8.15	2.41	5.88	2.64	3.64	55	10	0	21.67	3.97	10.53	0.02	4.84
<i>Brosimum guianense</i> (Aubl.) Huber	30.12	21.74	24.92	25.59	7.23	17.65	11.89	12.25	0	0	0	0	49.6	36.84	35.96	40.8
<i>Cissus</i> cf. <i>spinosa</i> Cambess.	0.46	2.17	0.18	0.94	2.41	5.88	1.32	3.2	0	0	0	0	0	0	0	0
<i>Unonopsis guatterrioides</i> (A.DC.) R.E.Fr.	1.38	4.35	1.76	2.49	1.2	5.88	2.64	3.24	5	10	6.45	7.15	0	0	0	0
<i>Trichilia catigua</i> A.Juss.	1.38	4.35	0.28	2	7.23	11.76	2.11	7.04	0	0	0	0	0	0	0	0
Poaceae 1	0.23	2.17	0	0.8	0	0	0	0	1	10	0	3.67	1.98	5.26	1.95	3.07
Poaceae 2	1.15	2.17	1.27	1.53	0	0	0	0	0	0	0	0	0.4	5.26	0.01	1.89
Poaceae 3	0.23	2.17	0.01	0,8	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vitex cymosa</i> Bertero ex Spreng.	0.92	2.17	5.97	3.02	0	0	0	0	0	0	0	0	1.59	5.26	9.2	5.35
<i>Alchornea castaneifolia</i> (Willd.) A.Juss.	1.38	2.17	1.76	1.77	0	0	0	0	0	0	0	0	2.38	5.26	2.71	3.45
Euphorbiaceae 1	0.69	2.17	0.18	1.01	0	0	0	0	0	0	0	0	1.19	5.26	0.27	2.24
Fabaceae 1	0.92	2.17	1.27	1.45	0	0	0	0	0	0	0	0	1.59	5.26	1.95	2.93
<i>Piper callosum</i> Ruiz & Pav.	0.46	2.17	0.01	0.88	2.41	5.88	0.06	2.78	0	0	0	0	0	0	0	0
<i>Piper</i> sp.	0.23	2.17	0	0.8	1.2	5.88	0.01	2.36	0	0	0	0	0	0	0	0
<i>Ceiba</i> cf. <i>pentandra</i> (L.) Gaertn.	0.23	2.17	0.35	0.92	0	0	0	0	0	0	0	0	0.4	5.26	0.54	2.07

<i>Cecropia pachystachya</i> Trécul	2.99	2.17	0.14	1.77	15.66	5.88	1.06	7.53	0	0	0	0	0	0	0	0
<i>Mouriri</i> sp.	0.46	2.17	0.7	1.11	0	0	0	0	0	0	0	0	0.79	5.26	1.08	2.38
<i>Trema micranta</i> (L.) Blume	2.99	4.35	0.71	2.68	0	0	0	0	10	10	3.23	7.74	1.19	5.26	0.01	2.15
Polygonaceae 1	2.76	2.17	0.04	1.66	0	0	0	0	0	0	0	0	4.76	5.26	0.05	3.36
<i>Ocotea diospyrifolia</i> (Meisn.) Mez	8.97	19.57	20.88	16.47	3.61	11.76	18.49	11.29	1	10	4.84	5.28	13.89	31.58	26.75	24.07
Arthropods (Total)	22.1	78.3	26.3	42.2	47	88.2	52.7	62.7	22	70	45.8	45.9	13.9	73.7	14.3	33.9
Coleoptera	7.82	36.96	6.18	16.98	15.66	47.06	6.74	23.15	4	30	0.13	11.38	6.75	31.58	8.09	15.47
Isoptera	0.23	2.17	0	0.8	0	0	0	0	1	10	0	3.67	0	0	0	0
Orthoptera	2.76	21.74	4.48	9.66	6.02	29.41	1.91	12.45	4	20	19.36	14.45	1.19	15.79	0.01	5.66
Belostomatidae	0.23	2.17	0.7	1.04	1.2	5.88	5.28	4.12	0	0	0	0	0	0	0	0
Blattodae	0.69	4.35	1.48	2.17	0	0	0	0	0	0	0	0	1.19	10.53	2.28	4.66
Lepidoptera	0.23	2.17	2.11	1,5	0	0	0	0	0	0	0	0	0.4	5.26	3.25	2.97
Hymenoptera	0.69	6.52	0.07	2.43	0	0	0	0	3	30	0.33	11.11	0	0	0	0
Larvas ssp.	1.38	6.52	2.29	3.4	1.2	5.88	0.01	2.36	4	10	9.68	7.89	0.4	5.26	0.27	1.98
Araneae	2.99	21.74	5.71	10.15	9.64	35.29	21.77	22.24	3	20	12.91	11.97	0.79	10.53	0	3.77
Scorpiones	0.23	2.17	0.07	0.82	1.2	5.88	0.53	2.54	0	0	0	0	0	0	0	0
Thelyphonida	0.23	2.17	0.7	1.04	0	0	0	0	1	10	3.23	4.74	0	0	0	0
Decapoda	4.6	32.61	2.47	13.22	12.05	35.29	16.5	21.28	2	20	0.16	7.39	3.17	36.84	0.36	13.46
Vertebrates (Total)	4.6	37	13	18.2	9.64	41.2	7.04	19.3	6	40	39.7	28.6	2.38	31.6	5.23	13.1
Reptiles	2.07	15.22	5.09	7.46	3.61	11.76	0.64	5.34	3	20	17.1	13.37	1.19	15.79	1.97	6.32
Mammals	1.15	8.7	5.63	5.16	1.2	5.88	5.28	4.12	3	20	22.58	15.19	0.4	5.26	0.01	1.89
Fish	0.69	6.52	0.78	2.66	3.61	17.65	1.11	7.46	0	0	0	0	0.4	5.26	1.08	2.25
Birds	0.69	6.52	1.48	2.9	1.2	5.88	0.01	2.36	0	0	0	0	0.4	5.26	2.17	2.61

Source: Authors.

Figure 3 - Importance of food items related to the different age class of *Tupinambis matipu* in the Upper Paraguay River.

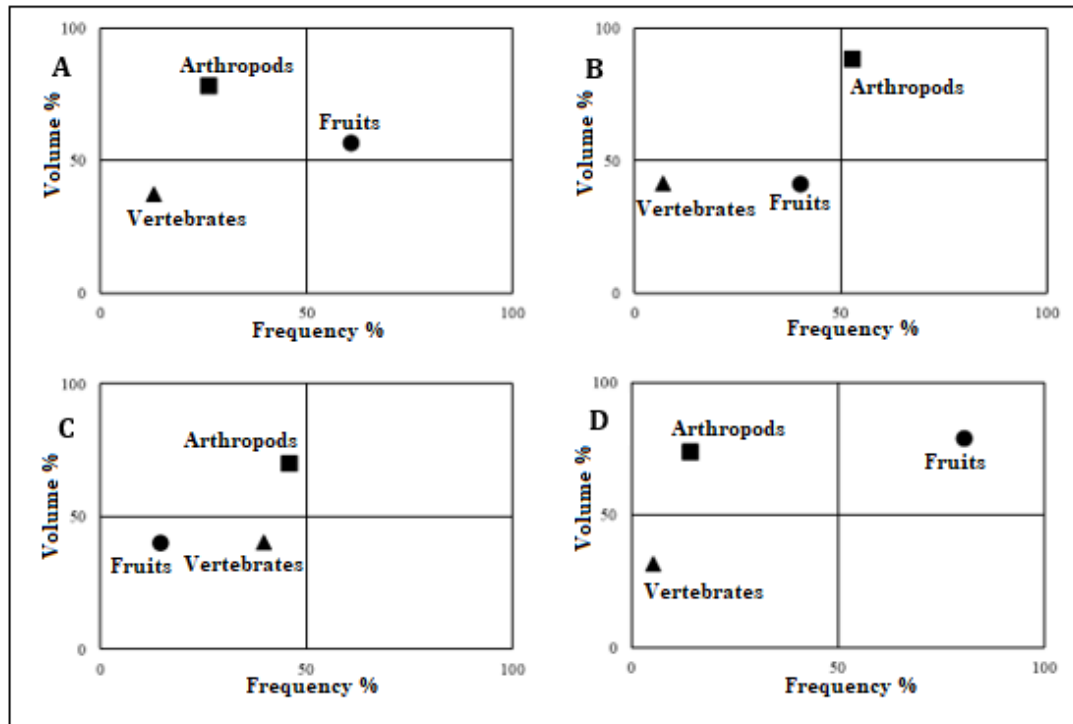


Source: Authors.

As for the feeding strategy, the species showed dominant fruit consumption, rare consumption of vertebrates and specialist consumption of arthropods, as showed by the analysis of the Costello diagram (Figure 4).

Juveniles showed specialist and dominant consumption of arthropods, while fruits and vertebrates were rare items. The sub-adults showed a diet specialized in arthropods, while fruits and vertebrates were rare, with a slight predominance of vertebrates. Among adult individuals, fruit consumption was dominant, while vertebrates were rare and the specialist consumption of arthropods (Figure 4).

Figure 4 - *Tupinambis matipu* feeding strategy diagram, in riparian forest areas in the Upper Paraguay River region, based on the Costello graphic method. A) The 46 individuals sampled; B) Juveniles; C) Sub-adults; D) Adults.



Source: Authors.

As regards the ontogeny, arthropods were the most important items for juvenile individuals ($n = 17$), with the volume of 52.74 % and $IVI = 88.15$ followed by fruits with the volume of 40.22 % and $IVI = 53.35$. For sub-adult individuals ($n = 10$), arthropods with a volume of 45.79% and $IVI = 72.60$ was the most representative category.

For this development stage, the vertebrate category constituted the second-largest volume (39.68 %), and the second-largest IVI was fruits, with (45.51). For adults ($n = 19$), the largest volume (80.51 %) and IVI (98.60) were fruits, followed by arthropods with a volume of 14.26 % and $IVI = 47.98$ (Table 1).

The Pianka Niche Overlap Index showed that juvenile and sub-adults had greater niche overlap (0.79), followed by the overlap between juvenile and adults (0.74). Sub-adults and adults showed the lowest index value (0.40).

4. Discussion

Our results show that in the riparian forest of upper Paraguay River region, *T. matipu* has a generalist feeding habit, with a diversified diet, including items such as vertebrates, invertebrates, and fruits (Table 1). This diversification may be related to the Teiidae's active foraging manner (Pianka, 1966; Schoener 1971; Huey & Pianka, 1981; Pough, 1999), which the predator consumes a large number of food items compensating the energy expenditure in the search of food (Anderson & Karasove, 1981; Nagy et al., 1984). In this way, the species reset the expenses used in the food search by diversifying its diet with the resources available in the environment.

Although amphibians are commonly reported in the tegus' diet (Mecolli & Yanosky, 1994; Kiefer & Sazima, 2002; Silva, 2013), in our sample we did not find it. This fact may be related to the unpalatability that some anurans have or the total digestion of bones of these prey (Yáñez et al., 1980). However, Huey & Pianka (1981), reported that there may be plasticity in the foraging mode of a given species of lizard, influenced by factors such as predation risk and/or resources availability. Greff & Whiting (2000) describe that, if food is abundant, lizards can be more selective and focus on more rewarding prey. Thus, *T. matipu* can have a certain selectivity, discarding items such as amphibians, consuming items of easier capture and greater compensation, such as fruits, once amphibians were abundant in the sampled areas (Silva-Alves, 2019; personal observation).

As regards fish consumption, Mecolli & Yanosky (1994) have already observed its occurrence in *T. teguixin* diet and suggest that this species go to shallow waters to search this food item. However, it was not possible to observe this behavior for *T. matipu*. Individuals of this species were observed in the vicinity of fishermen's campsites consuming leftover food, and in one of the sampling points, the ingestion of fish scraps was observed. Thus, it is more likely that this item is related to fish carcasses left by fishermen since we found fish only in the stomachs of individuals collected near a fishermen's camp.

The consumption of plant material, mainly fruits, seems common for the *Tupinambis* genus species. Williams et al. (1993) point out that items of plant origin were the most found for the species *T. rufescens* in northwestern Argentina. Mecolli & Yanosky (1994), detected plant material as the most abundant item in the diet of *T. teguixin* in the Argentine Chaco. As in these studies, plant material (fruits) also constituted the most important items in the diet of *T. matipu*.

The preference for fruit, or at least the willingness for high fruit consumption, can make *Tupinanbis matipu* an important seed disperser since tegus act in the dispersion of seeds (Castro & Galletti, 2004). Unlike birds, which shed their feces in a random manner in the environment (Francisco & Galetti, 2002), reptiles, in general, eliminate feces in places with a higher incidence of light where they thermoregulate (e.g. clearings and edges) and these places have better conditions for seed germination (Rosa et al., 2012). Thus, the role of *T. matipu* as a potential seed disperser in this portion of Mato Grosso state may be relevant, since the species uses anthropized areas, borders, clearings, moving between fragments (personal observation), and can be important to recolonize areas where other large frugivores dispersers would not be able to access.

Regarding the hypothesis that this species contributes to the control of agricultural pests, our data indicate that a large part of the total volume of arthropods consumed by the species belongs to the Coleoptera, Lepidoptera, Orthoptera, Hymenoptera and Isoptera orders. Some species of these orders can be considered important agricultural pests (Fujihara, 2008) and can compromise the production of cultivated plants, causing significant economic losses (De Medeiros, 2011). Thus, although we have not measured these effects, cultivars located close to areas of *T. matipu* occurrence may be benefiting from ecosystem services of a natural pest controller.

As for food ontogeny, the relation of the arthropod item consumption, for instance, between the age groups tended to be an inverse relation, that is, with the increase of the age group (juvenile to adults) the consumption of this item decreases. For fruits, the trend was to increase the consumption of this item according to animal growth. These changes in the composition of the diet are directly associated with an ontogenic change in the tegus dentition, where juveniles have teeth adapted to perforate chitinous exoskeleton, which facilitates the consumption of small invertebrates (Presch, 1974). In the following phases, their dentition is altered, with dental structures linked to the consumption of harder foods, such as mollusks (Presch, 1974), in these phases, there is an increase in the consumption of foods of plant origin, especially fruits (Milstead, 1961; Mercolli & Yanosky, 1994). This variation in the predominance of food items according to the individuals' age group is important for species since it reduces intraspecific competition.

Change in the tegus' feeding pattern was also observed by Kiefer & Sazima (2002) when they reported that juvenile individuals of *Salvator merianae* in southeastern Brazil used invertebrates more frequently in its diet, while adults in Argentina presented plant material as the most representative item in its diet (Mercolli & Yanosky, 1994). These changes in the *T.*

matipu diet can offer advantage related to the different nutritional needs during the stages of its development, as some lizards such as *Tropidurus*, in the early stages of their development, invest more during the growth (Meira et al., 2007), already after the sexual maturity a change occurs, and its energy is turned to reproduction activities (Fitch, 1981).

Thus, for *T. matipu*, in the early stages (juvenile and sub-adult) arthropods provide a greater amount of protein, while fruits provide more energy for reproductive activities in adulthood. The sub-adults presented fruits and arthropods consumption in similar proportion. However, this age class presented the highest index of importance for vertebrate consumption. It may be related to the fact that this age group is an intermediate phase between juvenile and adult, so their protein needs may increase, focusing on the increase in vertebrate intake, as an important extra source of proteins.

Although there are changes in the proportion of food intake in different age groups, our results showed a marked sharing of food resources. Considering that at the species level the resources sharing occurs according to the type of food, habitat and time (Pianka, 1969), differentiating their needs in minimal quantities (Pianka, 1974), our intraspecific approach shows that the segregation of trophic niche also occurs on this scale.

5. Conclusion

We observed that *T. matipu* shares food resources between the age classes adopting physiological/temporal criteria, with strategies where the different age classes use the resources in different proportions throughout their development. This mechanism can be an important strategy for the recruitment of new individuals in these populations, since it relieves competition for resources, and can even avoid cannibalism, considering that reptiles were the most important item within vertebrates for the species.

The *T. matipu* diet reveals that the species uses a wide variety of items, taking advantage of available resources in the environment, and may have selectivity according to the development phase, opting for items that have a higher cost-benefit. Fruits were the most important items, showing that the species can be an important seed disperser. *T. matipu* also consumes many arthropods that can be considered agricultural pests, reinforcing its role as a natural controller of these organisms in the environment. In short, this species plays an important role in the transport of native seeds, contributing to the regeneration of the disturbed area and can assist production systems by consuming potentially harmful arthropods. Despite sharing food resources between the different stages of development, *T.*

matipu has a greater predominance of one or the other category in these phases, avoiding intraspecific competition, keeping populations stable and well distributed in the Upper Course of the Paraguay River. Future studies are encouraged mainly by including the seasonality variable in the sample, allowing greater knowledge about the feeding behavior of this species as a result of a change in food availability.

Acknowledgements

The development of this research was possible through the project " Erosão da biodiversidade na bacia do Alto Paraguai: impactos do uso da terra na estrutura da vegetação e comunidade de vertebrados terrestres e aquáticos "- Rede Erosão (UNEMAT/UFMT/UEA-UK) - which has financial support from FAPEMAT (call no. 037/2016 - Research Networks in Mato Grosso with concession term under no. 0589188/2016).

We would also like to thank the field team of the "Erosão" project, ICMBio, UNEMAT, Porto Estrela City Hall, Recanto do Dourado Hotel, Morrinhos Farm, fishermen Reis and Jânio for their support and infrastructure in conducting field research. The Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the doctoral scholarships of the author ACG, for the master scholarships to the authors ODS, OMAN, ECF, APDB and TMC and the Fundação de Amparo à Pesquisa do Estado de Mato Grosso (FAPEMAT) for the master's degree scholarship to the author VDSA, and doctoral scholarship to JRM. The Taiamã Ecological Station in the person of Daniel Kantek.

References

Amaral, D. L., & Fonzar, B. C. (1982). Levantamento de Recursos Naturais. Págs. 401-52 em: Brasil. *Ministério das Minas e Energia*. Secretaria Geral. Projeto Radambrasil. Folha SD.21. Cuiabá. 4. Rio de Janeiro.

Anderson, R. A., & Karasove, W. H. (1981). Contrast in energy intake and expenditure in sit-and-wait and widely foraging lizards. *Oecologia* (Berlin), 49, 67–72.

Castro, E. D. R., & Galetti, M. (2004). Frugivoria e dispersão de sementes pelo lagarto teiú *Tupinambis merianae* (Reptilia: Teiidae). *Papéis Avulsos de Zoologia São Paulo*, 44(6), 91–4.

Colli, G. R., Araújo, A. F. B., Silveira, R., & Roma, F. (1992). Niche partitioning and morphology of two syntopic *Tropidurus* (Sauria: Tropiduridae) in Mato Grosso, Brazil. *Journal of Herpetology*, 26(1), 66–9.

Costa, H. C., & Bérnils, R. S. (2018.) Répteis do Brasil e suas Unidades Federativas: Lista de espécies. *Herpetologia Brasileira*, 7(1), 1–58.

Costello, M. J. (1990). Predator feeding strategy and prey importance: a new graphical analysis. *Journal Fish Biology*, 36, 261–3.

De Medeiros, M. A., Harterreiten, S. E. S., Togni, P., Milane, P., Pires, C., Carneiro, R., & Sujii, E. (2011). Princípios e práticas ecológicas para o manejo de insetos-praga na agricultura. Embrapa Recursos Genéticos e Biotecnologia-Livro técnico (INFOTECA-E).

Dessem, D. (1985). Ontogenetic changes in the dentition and diet of *Tupinambis* (Lacertilia: Teiidae). *Copeia*, 1985(1), 245–7.

Duffield, G. A., & Bull, C. M. (1998). Seasonal and ontogenetic changes in the diet of the Australian skink *Egernia stokesii*. *Herpetologica*, 54(3), 414–9.

Fitch, H. S. (1981). Sexual size differences in reptiles. *Miscellaneous publication - University of Kansas, Museum of Natural History*, 70, 1–72.

Francisco, M. R., & Galetti, M. (2002). Aves como potenciais dispersores de sementes de *Ocotea pulchella* Mart. (Lauraceae) numa área de vegetação de cerrado do Sudeste Brasileiro. *Revista Brasileira de Botânica*, 25(1), 11–7.

Fujihara, R. T. (2008). Chave pictórica de identificação de famílias de insetos-pragas agrícolas. *Dissertação*. Universidade Estadual Paulista, Botucatu, São Paulo. 71.

Greff, J. F., & Whiting, M. J. (2000). Foraging-mode plasticity in the lizard *Platysaurus broadleyi*. *Herpetologica*, 56, 402–7.

Harvey, M. B., Ugueto, G. N., & Gutberlet JR, R. L. (2012). Review of teiid morphology with a revised taxonomy and phylogeny of the Teiidae (Lepidosauria: Squamata). *Zootaxa*, 3459(1), 1–156.

Huey, R. B., & Pianka, E. R. (1981). Ecological consequences of foraging mode. *Ecology*, 62, 991–9.

ICMBio. Instituto Chico Mendes de Conservação da Biodiversidade. (2018). Livro Vermelho da Fauna Brasileira Ameaçada de Extinção: Volume IV - Répteis. In: Instituto Chico Mendes de Conservação da Biodiversidade. (Org.). Livro Vermelho da Fauna Brasileira Ameaçada de Extinção. Brasília: ICMBio. 252.

Kiefer, M. C., & Sazima, I. (2002). Diet of juvenile tegu lizard *Tupinambis merianae* (Teiidae) in southeastern Brazil. *Amphibia-Reptilia*, 23, 105–8.

Maffei, F., Heubel, M. T. C. D., & Silva, F. B. (2007). Genética e hematologia de lagartos do gênero *Tupinambis* (Sauria: Teiidae). *Salusvita*, Bauru, 26(3), 337–46.

Magnusson, W. E., Lima, P. A., Silva, W. A., & Araújo, M. C. (2003). Use of geometric forms to estimate volume of invertebrates in ecological studies of dietary overlap. *Copeia*, 2003(1), 13–9.

Meira, K. T. R., Faria, R. G., Silva, M. D. M., Miranda, V. T., & Zahn-Silva, W. (2007). História natural de *Tropidurus oreadicus* em uma área de cerrado rupestre do Brasil Central. *Biota Neotropica*, 7(2), 155–63.

Mercolli, C., & Yanosky, A. A. (1994). The diet of adult *Tupinambis teguixim* (Sauria, Teiidae), in the eastern chaco of Argentina. *Journal of Herpetology*, 4, 15–9.

Milstead, W. (1961). Notes on teiid lizards in southern Brazil. *Copeia*, 1961(4), 493–5.

Mourão, G., Oliveira, M. D., Calheiros, D. F., Padovani, C. R., Marques, E. J. & Uetanabaro, M. (2002). O Pantanal Mato-grossense. In: Seeliger, U., Cordazzo, C., & Barbosa, F. A. R.

(eds.). In: Os sites e o Programa Brasileiro de Pesquisas Ecológicas de Longa Duração. Belo Horizonte, Brasil: *Universidade Federal de Minas Gerais (UFMG)*, 29–49.

Nagy, K. A., Huey, R. B., & Bennett, A. F. (1984). Field energetics and foraging mode of Kalahari lacertid lizards. *Ecology*, 65, 588–596.

Pianka, E. R. (1966). Convexity, desert lizard, and spatial heterogeneity. *Ecology*, 47, 1053–59.

Pianka, E. R. (1969). Sympatry of desert lizards (*Ctenotus*) in Western Australia. *Ecology*, 50, 1012–30.

Pianka, E. R. (1973). The structure of lizard communities. *Annual Review of Ecology and Systematics*, 4, 53–74.

Pianka, E. R. (1974). Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences*, 71(5), 2141–5.

R Core Team. (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from: <http://www.R-project.org/>

Pough, F. H. (1999). A Vida dos vertebrados. São Paulo, Brasil: Atheneu, 1999.

Presch, W. (1974). A Survey of the Dentition of the Macroteiid Lizards (Teiidae: Lacertilia). *Herpetologica*, 30(4), 344–9.

Rocha, C. F. D. (1994). Introdução à Ecologia de Lagartos Brasileiros. In: Nascimento, L.B., Bernardes, A. T., & Cotta, G. A (Eds.). *Herpetologia no Brasil* (1st ed., pp. 39-57). Belo Horizonte: Fundação Biodiversitas & Fundação Ezequiel Dias, 1994. 134.

Rocha, C. F. D., Van Sluys, M., Vrcibradic, D., Kiefer, M. C., Menezes, V. A., & Siqueira, C. C. (2009). Comportamento de termorregulação em lagartos brasileiros. *Oecologia brasiliensis*, 13(1), 115–131.

Rosa, V. G. S., Do Rosário, I. R., & Dias, E. J. R. (2012). Zoocoria com o lagarto *Cnemidophorus abaetensis*. Dias, Rocha & Vrcirbradic 2002 na restinga de Abaeté (29th ed., pp. 53–63), Salvador, Bahia, Brasil: Bol. Mus. Biol. Mello Leitão.

Schoener, T. W. (1971). Theory on feeding strategies. *Annual Review of ecology and systematics*, 2, 369–405.

Silva, J. S. (2013). Conhecimento ecológico local sobre aspectos alimentares e reprodutivos de *Tupinambis merianae* (Duméril e Bibron, 1839) e *Hoplias malabaricus* (Bloch, 1794) no semiárido do nordeste brasileiro. Dissertação, 63.

Silva, M. B., Ribeiro-Júnior, M. A., & Ávila-Pires, T. C. (2018). A New Species of *Tupinambis* Daudin, 1802 (Squamata: Teiidae) from Central South America. *Journal of Herpetology*, 52(1), 94–110.

Silva-Alves, V. D. (2019). Anuros na região do alto curso do rio Paraguai e a herpetofauna da Estação ecológica de Taiamã, Mato Grosso, Brasil. 2019. *Programa de Pós-Graduação em Ciências Ambientais*. Universidade do Estado de Mato Grosso, Cáceres-MT, 92.

Van Sluys, M. (1993). The reproductive cycle of *Tropidurus itambere* (Sauria: Tropiduridae) in Southeastern Brazil. *J. Herpetol.*, 27(1), 28–32.

Vitt, L. J., & Caldwell, J. P. (2009). *Herpetology: an introductory biology of amphibians and reptiles*. (3rd ed) Amsterdam: Academic Press.

Williams, J. D., Donadío, O. E., & Ré, I. (1993). Notas relativas a la dieta de *Tupinambis rufescens* (Reptilia: Sauria) del noroeste argentino. *Neotropica*, 39, 45–51.

Winck, G. R. (2007). História Natural de *Tupinambis merianae* (Squamata, Teiidae) na Estação Ecológica do Taim, extremo sul do Brasil. *Dissertação*, 59.

Yáñez, J. L., Núñez, H., Schlatter, R. P., & Jaksić, F. M. (1980). Diet and weight of American Kestrels in central Chile. *The Auk*, 97(3), 629–63.

Zhang, J., & Zhang, M. J. (2016). Package 'spaa'. R package version, v: 0.2.2.1.

Percentage of contribution of each author in the manuscript

Odair Diogo da Silva – 15%

Thatiane Martins da Costa – 7%

Vancleber Divino Silva-Alves – 7%

Eder Correa Fermiano – 8%

Mariany de Fatima Rocha Seba – 5%

Olinda Maíra Nogueira – 5%

Jessica Rhaiza Mudrek – 6%

Ana Paula Dalbem Barbosa – 6%

Almério Câmara Gusmão – 6%

Claumir César Muniz – 6%

Maria Antônia Carniello – 9%

Manoel dos Santos-Filho – 8%

Dionei José da Silva – 12%