

# Ecology and natural history of *Tropidurus hispidus* (Squamata, Tropiduridae) from an area of Caatinga, Northeastern Brazil

## Ecología e historia natural de *Tropidurus hispidus* (Squamata, Tropiduridae) de un área de Caatinga, en el Noreste de Brasil

Tatiana Feitosa Quirino <sup>1\*</sup>, Ronildo Alves Benício <sup>2</sup>, and Robson Waldemar Ávila <sup>3</sup>

- Received: 20/Oct/2023
- Accepted: 20/Mar/2025
- Online Publishing: 01/Dic/2025

**Citation:** Feitosa Quirino T, Alves Benício R, Waldemar Ávila R. 2025. Ecology and natural history of *Tropidurus hispidus* (Squamata, Tropiduridae) from an area of Caatinga, Northeastern Brazil. *Caldasia* 47:e108040. doi: <https://doi.org/10.15446/caldasia.v47.108040>

### ABSTRACT

The study of common and widely distributed species can help us understand how their ecology and natural history may vary across their range and respond to local ecological factors. Here, we studied the ecological and natural history aspects of the lizard *T. hispidus* at Estação Ecológica de Aiuaba, an Integral Protection Conservation Unit, in an area of Caatinga, state of Ceará, Northeastern Brazil. Our objective was to analyze the diet, foraging, sexual dimorphism, reproductive biology and helminthofauna associated with *T. hispidus*. We collected the specimens between the years 2012 and 2015 through active search, time-limited visual search, and pitfall traps. Overall, we collected 103 specimens of *T. hispidus*. There was sexual dimorphism, with males showing greater head and body width. Reproduction occurred between the middle of the dry season and the beginning of the rainy season. The diet was composed of 18 categories of food items, consisting mainly of ants, in addition to important amounts of plant material. The helminthofauna was composed of ten taxa, with the first occurrence of *Oochoristica travassosi* and *O. vanzolinii* infecting *T. hispidus*. Despite being a generalist species and one of the most common in the Neotropics, here, we present some unprecedented information about the ecology and natural history of *T. hispidus*, and we compared our results with data from other populations in the Caatinga.

**Keywords:** diet, lizards, parasites, reproductive biology, sexual dimorphism.

1 Laboratório de Herpetologia, Programa de Pós-Graduação em Sistemática, Uso e Conservação da Biodiversidade, Universidade Federal do Ceará, Fortaleza, Ceará, Brazil; [tata\\_tatifeitosa@hotmail.com](mailto:tata_tatifeitosa@hotmail.com)

2 Núcleo Regional de Ofiologia, Departamento de Biologia, Universidade Federal do Ceará, Fortaleza, Ceará, Brazil; [benicio.herpeto@gmail.com](mailto:benicio.herpeto@gmail.com)

3 Núcleo Regional de Ofiologia, Departamento de Biologia, Universidade Federal do Ceará, Fortaleza, Ceará, Brazil; [robsonavila@gmail.com](mailto:robsonavila@gmail.com)

\* Corresponding author



## RESUMEN

El estudio de especies comunes y ampliamente distribuidas puede ayudarnos a comprender cómo su ecología e historia natural pueden variar a lo largo de su área de distribución y responder a factores ecológicos locales. Aquí estudiamos los aspectos ecológicos y de historia natural del lagarto *T. hispidus* en la Estação Ecológica de Aiuaba, una Unidad de Conservación de Protección Integral, en un área de Caatinga, estado de Ceará, noreste de Brasil. Nuestro objetivo fue analizar la dieta, forrajeo, dimorfismo sexual, biología reproductiva y fauna de helmintos asociados a *T. hispidus*. Recolectamos los especímenes entre los años 2012 y 2015 mediante búsqueda activa, búsqueda visual por tiempo limitado y trampas de interceptación y caída. En total, recolectamos 103 especímenes de *T. hispidus*. Hubo dimorfismo sexual, presentando los machos mayor anchura de cabeza y cuerpo. La reproducción se produjo entre mediados de la estación seca y el inicio de la estación lluviosa. La dieta estaba compuesta por 18 categorías de alimentos, principalmente hormigas, además de cantidades importantes de material vegetal. La fauna de helmintos estaba compuesta por diez taxones, siendo la primera aparición de *Oochoristica travassosi* y *O. vanzolinii* infectando a *T. hispidus*. A pesar de ser una especie generalista y una de las más comunes en el Neotrópico, aquí presentamos información importante sobre la ecología e historia natural de esta especie para la región noreste de Brasil.

**Palabras clave:** biología reproductiva, dieta, dimorfismo sexual, lagartos, parásitos.

## INTRODUCTION

Some lizard taxa have been considered excellent experimental models for ecology and natural history studies because they are abundant, easy to observe, capture, handle, have relatively well-known taxonomy, host a wide variety of parasites, and respond strongly to local ecological and environmental factors (Pianka 1978, Rocha 1994, Anderson 2000, Ávila and Silva 2010, de Andrade 2020, Passos *et al.* 2021).

Among the most common lizards in the Neotropical region, *Tropidurus hispidus* (Spix, 1825) is the largest species of the genus, reaching 35 cm in total length, and has a wide geographic distribution in Brazil (Rodrigues 1987, 1988, Ávila-Pires 1995, Carvalho 2013). It is a relatively well-known species, compared to the others in the group, with studies on its ecology and natural history in the Amazon (e.g., Rodrigues 1987, Vitt *et al.* 1996, Figueiredo *et al.* 2020), Atlantic Forest (e.g., Santana *et al.* 2014, Lima *et al.* 2017), Cerrado (e.g. Van Sluys *et al.* 2004), and Caatinga (Vitt 1995, Ribeiro and Freire 2010, Ribeiro and Freire 2011, Anjos *et al.* 2013, Gomes *et al.* 2015, Maia-Carneiro and Rocha 2021). Despite the large number of studies conducted on *T. hispidus*, there are still gaps in knowledge about the ecology and natural history of some regions, such as the

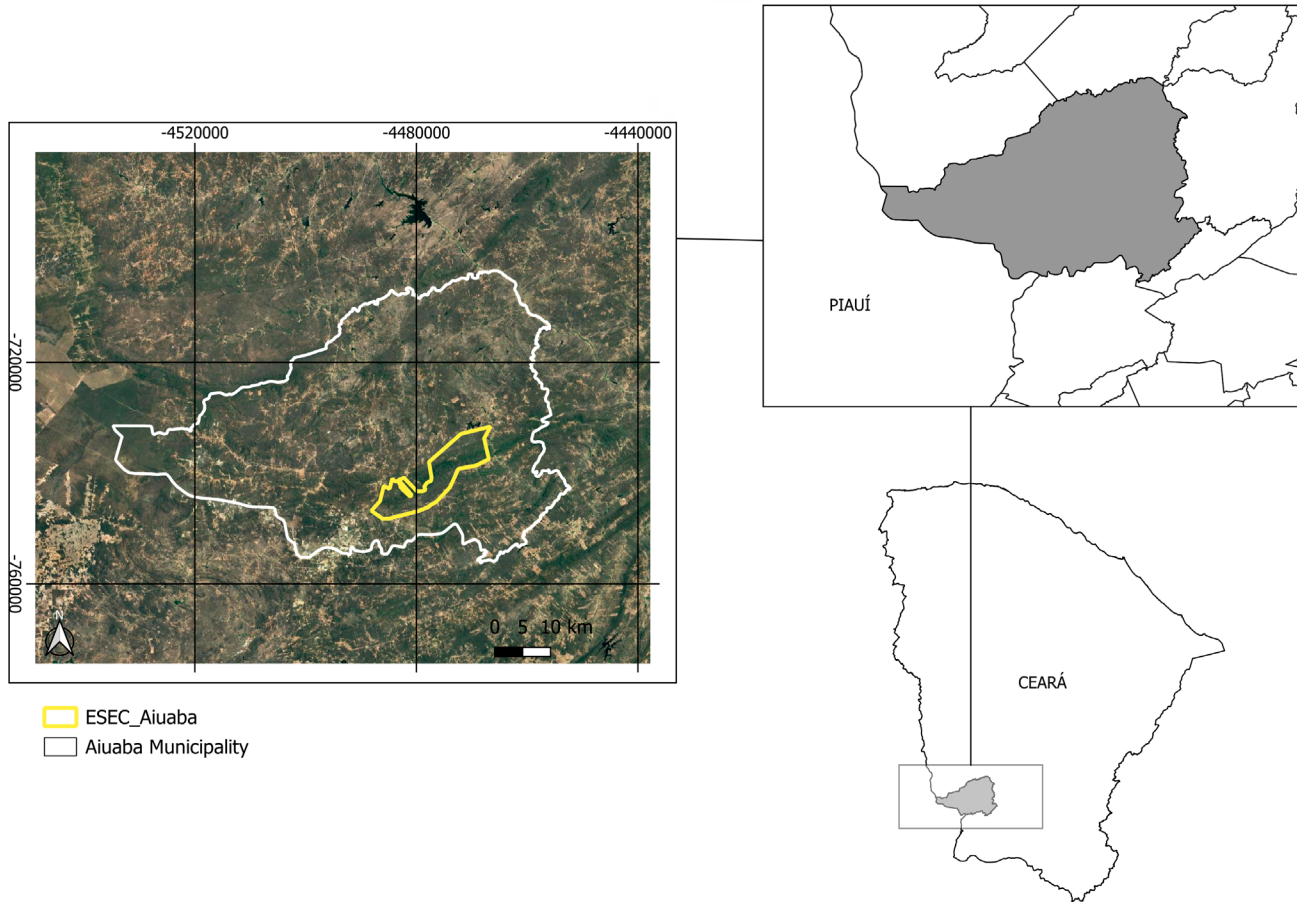
Caatinga ecoregion in northeastern Brazil. Furthermore, the study of common and widely distributed species can help us understand how their ecology and natural history may vary across their range and respond to local ecological factors (Albuquerque *et al.* 2018, Benício *et al.* 2019). Thus, here, we hypothesize that local environmental factors may produce variations in responses among the studied populations within the Caatinga.

Our objective was to study the ecology and natural history of the lizard *T. hispidus* in an area of Caatinga in Northeastern Brazil. The aspects analyzed were sexual dimorphism, diet, reproductive cycle, and associated parasites. Despite being an abundant and widely distributed species, we present some unprecedented information about the ecology and natural history of *T. hispidus*, and we compared our results with data from other populations in the Caatinga.

## MATERIAL AND METHODS

### Study area

The study was carried out at the Estação Ecológica de Aiuaba (Fig. 1) (6°49'S 40°44'W), an Integral Protection Conservation Unit, located in the municipality of Aiuaba, southwest of the State of Ceará, Northeastern Brazil. The



**Figure 1.** Location of Aiuaba

region's climate is defined as hot and semi-arid, with an average temperature around 24° C to 26° C in the rainy season between February and April, and in the dry season it reaches over 40° C (CEARÁ 2012). The Conservation Unit presents low average annual precipitation around 562.4 mm<sup>3</sup> per year (IPECE 2012).

#### Data collection

We collected specimens between the years 2012 and 2015 through active search, time-limited visual search, and pit-fall traps, during the daytime period from 8:00 am to 5:00 pm (Cechin and Martins 2000, Franco *et al.* 2002). All specimens captured had their mass measured using precision dynamometers (Pesola®, 0.1 g precision) and, with the aid of a digital caliper (Mitutoyo®, 0.01 mm precision) had the following morphometric variables taken: snout-vent length (SLV), body width (BW), body height (BH), head length (HL), head width (HW) head height (HH), and tail length (TL).

The specimens were euthanized by anesthetic injection following all ethical procedures and, after that, fixed in 10 % formalin and preserved in 70 % alcohol (Franco *et al.* 2002). All specimens are deposited in the Herpetological Collection of the Universidade Regional do Cariri (URCA-H). All collections were authorized by the Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio (SISBIO 32758-1).

#### Reproductive biology

The reproductive condition was verified through direct examination of the gonads. Females were considered adults due to the presence of vitellogenic follicles and/or eggs in the oviduct. The simultaneous presence of eggs and follicles in the oviduct was considered indicative of the production of more than one litter during the breeding season. As for males, they were considered reproductive when the testes were developed and at the same time the epididymis were curled (Bal estrin *et al.* 2010). The smallest SLV of

males and females with the characteristics previously reported were considered the minimum size at maturity.

Diet

To analyze the diet, we removed the stomach and intestines of the collected lizards and content was analyzed using a stereoscopic magnifier. Intact items were identified to the lowest possible taxonomic level, usually up to Order. The length and width of the prey were also measured with a digital caliper ( $\pm 0.01$  mm) and the volume was estimated using the ellipsoid formula:  $V = (4\pi/3)(L/2)(W/2)^2$ , where  $V$  = volume,  $L$  = length, and  $W$  = width (Magnusson *et al.* 2003). The food niche overlaps ( $\emptyset$ ) between males and females, and between juveniles and adults were calculated by the symmetric overlap index (Pianka 1973). Values close to zero indicate no similarity in diets, while values close to one indicate similar diets. The Index of Relative Importance (IRI) was also calculated to verify the proportion of each item in the diet of males and females of *Tropidurus hispidus*, using the following equation:  $IRI = F\% + N\% + V\%$ , where IRI = Index of Relative Importance,  $F$  = frequency,  $N$  = number, and  $V$  = volume (Powell *et al.* 1990).

Parasitism

The parasitological examination was performed in the gastrointestinal tract, lungs, liver and kidneys, where the helminths found were counted and identified. Prevalence ( $P$ ), mean abundance ( $MA$ ), and mean infection intensity ( $MII$ ) indices were calculated according to Bush *et al.* (1997). To assess the effect of host size on infection intensity, we use linear regression. Differences in the prevalen-

ce and intensity of infection between genders were tested using the chi-square method.

Foraging

For foraging data, lizards were observed in different transects distant from each other, and only once each, in order to avoid pseudo-replicates. The indices used were: the proportion of time spent moving (PTM), number of movements per minute (MPM) and proportion of attacks on prey discovered while moving (PAM) (Huey and Pianka 1981, Cooper *et al.* 1997, 1999, 2001, Perry 1999). The proportion of attacks initiated when moving (PAM) provides a measure independent of the mode of foraging, which is much less subject to variations in factors such as temperature and satiety (Cooper *et al.* 2001). Feeding attempts were observed by checking whether the attacks were initiated by lizards that detected prey while they were immobile, or by lizards that moved when they detected prey. The relationships between these variables were examined using simple linear regression and correlation (Zar 1996) as well as the independent contrast method (Felsenstein 1985).

Data analyses

We evaluated the sexual difference between the size (SLV) of adult males and females using analysis of variance (ANOVA). To remove the effect of size on the variables (BW, BH, HL, HW, HH, TL) we performed a regression analysis. To verify which of the variables contributed to the dimorphism, the step-by-step method of discriminant analysis was used with the residuals of the regressions using Wilk's Lambda as an indicator of discriminatory power. We excluded from the analysis individuals with au-

**Table 1.** Discriminant Analysis of *Tropidurus hispidus* morphometric variables in an area of Caatinga, Northeastern Brazil. All measurements are in millimeters. In bold, characters with significant values.

Variable	Males (n = 32)	Females (n = 54)	Wilk's Lambda	F	p
<b>Snout-vent length</b>	86.5 $\pm$ 14.6	67.7 $\pm$ 8.6	0.8	85.7	<b>0.001</b>
Head length	21.2 $\pm$ 3.5	16.3 $\pm$ 1.9	0.4	3.4	0.07
<b>Head width</b>	18.2 $\pm$ 3.3	13.5 $\pm$ 1.5	0.4	8.9	<b>0.001</b>
Head height	12.2 $\pm$ 2.4	9.2 $\pm$ 1.2	0.4	0.00	0.98
<b>Body width</b>	23.1 $\pm$ 5.0	19.8 $\pm$ 3.8	0.5	20.6	<b>0.001</b>
Body height	12.7 $\pm$ 3.2	10.2 $\pm$ 2.7	0.4	0.09	0.76



totomized tails or with any of the variables compromised due to the collection process. The significance level used was 5 %.

## RESULTS

We collected 103 specimens of *T. hispidus*, being 32 adult males, 54 adult females, and 17 juveniles.

### Sexual dimorphism

Males have greater body size ( $x = 86.5 \pm 14.6$  mm) than females ( $x = 67.7 \pm 8.6$  mm) (ANOVA  $F = 6.8$ ;  $p < 0.001$  for SLV). They also presented greater head width and larger body width (Wilk's Lambda = 0.4 and 0.5;  $p = 0.000$  and  $<0.001$ , respectively) (Table 1). All adult males analyzed presented secondary sexual characters of easy observation, through black ellipsoid spots present in the pelvic region (Fig. 2).

### Reproductive biology

Reproductive females were found in January, February and September. Females that presented eggs and follicles were captured in January and February. The smallest ma-

ture female had SLV = 59.1 mm. The litter size, based on the presence of vitellogenic eggs or follicles, was on average  $4.65 \pm 1.28$  (range 2 – 7,  $n = 34$ ). There was no correlation between SLV and mean egg volume ( $p = 0.2$ ), nor with secondary follicles ( $p = 0.1$ ). The mean egg volume was  $391.6 \pm 46.4$  mm<sup>3</sup> ( $n = 10$ ) and for secondary follicles  $105.4 \pm 16.3$  mm<sup>3</sup> ( $n = 24$ ). In relation to males, from January to April the proportion of breeding males increased ( $n = 26$ ), with the highest peak in January. The sexually mature male measured 50.7 mm. The mean volume of the testes was  $35.1 \pm 4.3$  mm<sup>3</sup>. There was no correlation between SLV and mean testicle volume ( $p = 0.6$ ).

### Diet

We analyzed 103 stomachs, and 89.3 % ( $n = 92$ ) had food content. The diet consisted of 18 categories of food items. Ants (22.8 %) and plant material (20.5 %) were the most frequent items in the diet of *T. hispidus*. Numerically, ants (64.4 %) and other Hymenoptera (14.9 %) were the predominant items in the species' diet (Table 2).

Diet was compared between males ( $n = 31$ ), females ( $n = 48$ ) and juveniles ( $n = 13$ ), and the number of categories found



Figure 2. Specimens of *Tropidurus hispidus*. A. Male, B. female.

**Table 2.** Frequency (F%), Number (N%) and Index Relative Importance (IRI) of each prey category in the diet of females, males and juveniles of *Tropidurus hispidus* in an area of Caatinga, northeastern Brazil. In bold, the highest values.

Categories	Females			Males			Juveniles		
	F%	N%	IRI	F%	N%	IRI	F%	N%	IRI
ARACHNIDA									
Araneae	3.3	0.4	2.1	1.9	0.2	1.6	5.0	1.7	2.8
CRUSTACEA									
Isopoda	0.7	0.1	0.7	0.9	0.1	1.2	2.5	0.4	2.8
INSECTA									
Blattaria	3.9	0.3	7.1	4.7	0.5	6.3	7.5	1.7	5.7
Coleoptera	9.2	2	8.6	8.5	2.1	6	5	0.9	3.3
Dermaptera	1.3	0.1	1.9	–	–	–	–	–	–
Diptera	–	–	–	1.9	0.5	1.1	–	–	–
Formicidae	<b>21.7</b>	<b>61.8</b>	<b>28.8</b>	<b>24.5</b>	<b>68.3</b>	<b>32.2</b>	<b>22.5</b>	<b>62.9</b>	<b>29.4</b>
Other Hymenoptera	11.8	<b>15.3</b>	<b>14.2</b>	7.5	<b>16.5</b>	10.7	10.0	2.2	<b>15.9</b>
Isoptera	5.9	14.9	7.2	3.8	3.0	2.4	2.5	<b>22.3</b>	8.3
Lepidoptera	10.5	2.4	11.3	9.4	5.7	<b>17.6</b>	5.0	0.9	4.0
Orthoptera	3.9	0.3	6.2	5.7	0.6	9.1	5.0	0.9	14.1
VEGETABLE MATERIAL									
Flower/Leaves/Fruits	<b>18.4</b>	1.5	6.6	<b>21.7</b>	1.8	7.8	<b>25</b>	4.4	9.8
Wood	0.7	0.1	0.2	1.9	0.2	0.7	–	–	–
MOLLUSCA									
Gastropoda	2.0	0.2	2.4	–	–	–	–	–	–
OTHERS									
Unidentified arthropod	–	–	–	0.9	0.3	0.7	–	–	–
Ecdysis (lizards)	0.7	0.1	0.5	0.9	0.1	0.5	2.5	0.4	1.1
Cricket eggs	2.0	0.2	0.7	1.9	0.2	0.7	2.5	0.4	1.0
Stone	3.9	0.3	1.4	3.8	0.3	1.4	5.0	0.9	2.0

were 17, 16 and thirteen, respectively. Again, Formicidae and plant material were the most frequent items for males, females and juveniles. Numerically, Formicidae and other Hymenoptera predominated for males and females, while Formicidae and Isoptera predominated for juveniles (Table 2).

The trophic niche width was 2.3 for females, 2.0 for males and 2.2 for juveniles in number, and 6.9, 4.5 and 3.6 for volume, respectively. The overlap analysis based on feed composition showed high overlap between males and females ( $\emptyset = 0.97$ ), males and juveniles ( $\emptyset = 0.91$ ), and females and juveniles ( $\emptyset = 0.94$ ). The items with the highest

Index of Relative Importance (IRI) were Formicidae and Lepidoptera for males, and Formicidae and other Hymenoptera for females and juveniles (Table 2).

### Parasitism

We examined 103 lizards, of which 76 were infected with at least one species of parasite, the total prevalence was 73.7 %. A total of 669 helminths were collected, with a mean abundance of  $6.49 \pm 0.81$  (range 0 – 42) and mean infection intensity was  $8.80 \pm 0.97$  (range 1 – 42) (Table 3).

The helminthofauna of the *T. hispidus* population examined was composed of ten taxa (Table 3). *Parapharyngodon*

**Table 3.** Helminths, number of helminths (NH), mean abundance (MA), mean infection intensity (MII) with standard error (SE), range of infection intensity (RII) and site of infection (SI) of associated helminths to *Tropidurus hispidus* in an area of Caatinga, northeastern Brazil. \* New record.

S – stomach, SI – small intestine, LI – large intestine, GC – general cavity.

Helminths	NH	MA ± SE	MI I ± SE	RII	SI
CESTODA					
<i>Oochoristica travassosi</i> *	20	0.2 ± 0.1	2.2 ± 0.8	(1–8)	S/SI/LI
<i>Oochoristica vanzolinii</i> *	23	0.2 ± 0.1	3.3 ± 1.5	(1–12)	SI
NEMATODA					
<i>Physaloptera lutzi</i>	119	1.2 ± 0.3	4.3 ± 0.8	(1–18)	S/SI
<i>Physaloptera retusa</i>	86	0.8 ± 0.3	5.1 ± 1.4	(1–24)	S/SI
<i>Physaloptera</i> sp.	1	0.01 ± 0.01	1 ± 0	(1–1)	S
<i>Physalopteroides venancioi</i>	11	0.1 ± 0.1	5.5 ± 3.5	(2–9)	S/LI
<i>Strongyluris oscar</i>	130	1.2 ± 0.5	6.5 ± 2.0	(1–40)	S/SI/LI
<i>Parapharyngodon largitor</i>	239	2.3 ± 0.4	5.2 ± 0.7	(1–21)	S/SI/LI
<i>Oswaldofilaria</i> sp.	20	0.2 ± 0.1	6.7 ± 1.5	(4–9)	GC
<i>Spauligodon oxkutzcabensis</i>	20	0.2 ± 0.1	6.7 ± 1.5	(4–9)	LI

*largitor* Albo & Rodrigues, 1963 was the most prevalent taxon ( $P = 47.4\%$ ) and the most abundant ( $n = 239$ ) (Table 3). Mean richness was  $1.3 \pm 0.1$  helminths / host, and the highest richness ( $S = 5$ ) was found in only one host specimen. There was no significant difference in the prevalence of parasites between females and males ( $Z = 1.5$ ;  $p = 0.2$ ) and adults and juveniles ( $Z = 1.7$ ;  $p = 0.1$ ). However, the mean abundance of helminths differed between males and females ( $U = 1206.5$ ;  $p = 0.01$ ) and between adults and juveniles ( $U = 656$ ;  $p = 0.02$ ). There was a difference in the intensity of infection between genders ( $U = 1726.5$ ;  $p = 0.001$ ), but not between adults and juveniles ( $U = 300$ ;  $p = 0.9$ ).

Host size (SLV) and mass were positively correlated with parasite richness and abundance (abundance vs. SLV:  $rs = 0.5$ ;  $p = 0.05$ ;  $n = 103$ ; abundance vs. weight:  $rs = 0.4$ ;  $p = 0.05$ ;  $n = 103$ ; richness vs. SLV:  $rs = 0.5$ ;  $p = 0.001$ ;  $n = 103$ ; richness vs. weight:  $rs = 0.4$ ;  $p = 0.001$ ;  $n = 103$ ). On the other hand, mean infection intensity was not correlated with SLV and weight (mean infection intensity vs. SLV:  $rs = 0.2$ ;  $p = 0.05$ ;  $n = 76$ ; mean infection intensity vs. weight:  $rs = 0.1$ ;  $p = 0.05$ ;  $n = 76$ ).

### Foraging

*Tropidurus hispidus* had a very low proportion of time spent in movement (PTM = 0.02) and number of movements per minute (MPM = 0.04), characteristic values of a sit-and-wait forager, spending most of the time immobile, waiting for prey. Despite this, when *T. hispidus* saw it, it moved quickly in search of its prey, returning to its initial starting point. Feeding attempts observed were from ambush, with a proportion of attacks initiated when moving (PAM) more successful than failure (15:1).

## DISCUSSION

Sexual size dimorphism (SLV) with males larger than females, in addition to other attributes such as color (black ellipsoid spots in males) and body shape are factors commonly related to sexual selection in short-lived polygamous species such as *T. hispidus* (Emlen and Oring 1977). On the one hand, traits that allow high reproductive performance are selected in females, resulting in energy allocation directed towards early reproduction rather than growth (Smith and Ballinger 1994, Van Sluys 1998). On

the other hand, the characteristics that allow the control of high quality territories are selected in males (Pinto *et al.* 2005). In addition to these characteristics, males have black spots in adults, and yellowish spots in youngsters, on the ventral surface of the thigh and anal flap (Rodrigues 1987, Pinto *et al.* 2005). These color changes may be socially recognized signs associated with varying hormonal rates of sexual maturity (Díaz *et al.* 1994, Morrison *et al.* 1995, Lemos-Espinal *et al.* 1996). Here, this combination of characters (i.e., color markings, body size, head size, and body width) can likely be selected and guarantee success in intrasexual conflicts.

The reproduction of *T. hispidus* is possibly influenced by the unpredictability of rainfall regimes (Albuquerque *et al.* 2018), starting their reproduction at the end of the dry season and peaking in the rainy season (Rocha 1994, Colli *et al.* 1997). In this study, females with eggs and follicles and breeding males were found from January to April, which corresponds to the beginning of the rainy season in the collection area (ESEC Aiuaba). The mean number of eggs (4.6, range 2 – 7) found in this population of *T. hispidus* from the Caatinga is also similar to that found in previous studies for the same species (e.g., mean 5.5, range 1 – 8, Prieto *et al.* 1976), and comparable to sympatric species such as *T. semitaeniatus* (Spix, 1825); also ranging from two to seven eggs (Vitt 1981, Vitt and Goldberg 1983). With the peak of egg deposition in the rainy season, females tend to improve their reproductive success, reducing losses caused by dissection, as this period is the most favorable for the development of eggs, due to the high humidity (Rocha 1994). It also concentrates a greater availability of food and water necessary for the development of newly hatched ones (Van Sluys 1993b, Meira *et al.* 2007), since moisture is a critical factor for egg survival (Wiederhecker *et al.* 2002). On the other hand, the mean number of eggs for other populations of *T. hispidus* in the Caatinga can also vary greatly compared to the results found here (e.g., mean of 7.4, range 3 – 14, Vitt and Goldberg 1983, mean of 8.1, range 6 – 13, Ribeiro *et al.* 2012; mean of 7.5, range 2 – 16, Albuquerque *et al.* 2018). Thus, due to this large variation in clutch size among populations of *T. hispidus*, it is possible that other functional characteristics of the species, in addition to the number of eggs, which respond to local environmental factors and/or characteristics intrinsic to the population, have a greater effect on the reproductive biology of these local populations.

Most tropidurids are “sit-and-wait” foragers (Schoener, 1971, Rocha, 1994). In this study, *Tropidurus hispidus* was observed feeding on both active (Formicidae and Orthoptera) and sedentary (termites, insect larvae) prey. Usually, species that adopt this type of strategy tend to have greater food niche width, being more generalist (Dias and Lira-da-Silva 1998), as also observed for other populations of this species in other locations (e.g., Vitt 1995, Vitt *et al.* 1996, Van Sluys *et al.* 2004, Ribeiro and Freire 2011, Gomes *et al.* 2015, Ferreira *et al.* 2017, Maia-Carneiro *et al.* 2017, Pelegrin *et al.* 2017, Albuquerque *et al.* 2018, Figueiredo *et al.* 2020, Maia-Carneiro and Rocha 2021). Despite being a generalist, the most important items in the diet of *T. hispidus* did not differ from other populations within the Caatinga. Most studies have shown that Formicidae are among the main items consumed in this ecoregion (Van Sluys *et al.* 2004, Ribeiro and Freire 2011, Ferreira *et al.* 2017, Maia-Carneiro *et al.* 2017, Pelegrin *et al.* 2017, Oliveira *et al.* 2024). This pattern - “sit-and-wait” foragers with a wide range of food niches - is also found for a number of other *Tropidurus* species (Colli *et al.* 1992, Van Sluys 1993a; Vitt 1993, Teixeira and Giovanelli 1999, Faria and Araújo 2004, Meira *et al.* 2007, Carvalho *et al.* 2007, Rocha and Siqueira 2008, Gomes *et al.* 2015, Drago *et al.* 2020, Maia-Carneiro and Rocha 2021).

The types of prey consumed by males, females and juveniles of *T. hispidus* were similar; only the proportion with which some of them occurred varied, changing their importance in the diet of this lizard. In addition to having a diet with several categories of arthropods, *T. hispidus* also consumed a significant amount of plant material (more than 20 %), items that are part of the diet during the dry season, a fact that can be related to scarcity of other resources and/or greater availability of leaves in the environment, resulting from the deciduous vegetation process. It is possible that, in addition to the energy return provided by these items, the consumption of plants complements the water needs, a scarce resource in Caatinga environments. There is support in the literature that suggests such hypotheses (e.g., Van Sluys 1993a; Vitt 1995, Rocha 1996, Kolodiuk *et al.* 2009). For some studies (e.g., Kolodiuk *et al.* 2009) plant material was the main food item consumed by *T. hispidus* (volume = 84.4 %, Index Relative Importance = 47.5) and congeneric species. Ingestion of plant material in *Tropidurus* and other lizards is relatively common (Araújo 1987, Dias and Lira-da-Silva



1998, Rocha and Bergallo 1992, Rocha 1994, Colli *et al.* 1992, Van Sluys 1993a, 1993b, Cooper and Vitt 2002, Faria and Araujo 2004), but not in this amount. Thus, it is necessary to evaluate in future studies the importance of this item in the diet of Caatinga lizards.

*Tropidurus hispidus* was parasitized by ten species of helminths, and its helminthofauna resembles that found in other neotropical lizards. For example, *Physaloptera lutzi* Guimaraes, Cristófaró and Rodrigues, 1976 has been found infecting several lizards of the Leiosauridae, Teiidae, and Tropiduridae families (Ávila and Silva 2010). *Strongyluris oscar* Travassos, 1923 is known to be a common parasite of *Tropidurus* lizards (Ávila and Silva 2010) and has also been found infecting many species in the Leiosauridae, Teiidae, Liolaemidae, Polychrotidae, and Scincidae families (Ávila and Silva 2010, Ávila *et al.* 2012). Although most helminths found in *T. hispidus* are commonly recorded in other lizard species, *Oochoristica travassosi* Rego & Ibanez, 1965 and *O. vanzolinii* Rego & Rodrigues, 1965 represent the first record of *T. hispidus* as a host for these parasites. Furthermore, two taxa (*Physaloptera* sp., *Oswaldofilaria* sp.) could not be identified down to the species level, as they are species complexes. An effect of host size (SLV) and weight on parasite richness and abundance was also observed. This same pattern, i.e., larger and heavier lizards presented greater species richness and parasite abundance, was recorded for some species of lizards (Neta and Ávila 2018, Amorim and Ávila 2019), including *T. hispidus* (Araujo-Filho *et al.* 2017).

Ambush foragers have a lower proportion of time spent moving (PTM) than active foragers, but the number of movements per minute (MPM) is more variable within foraging modes. The PTM and MPM recorded in *T. hispidus* for this area showed very low values ( $n = 0.02$  and  $n = 0.04$ , respectively) in ambush foragers and an increase is expected with the degree of active foraging, such tendency is consistent to categorize foraging as sedentary (Huey and Pianka 1981, Vitt *et al.* 1996). According to Perry (1990), ambush foragers are considered to be those with  $PTM < 0.100$ . Thus, for this population of *T. hispidus*, the recorded values reinforce the sit-and-wait foraging, as demonstrated in other studies with tropidurids, including for this same species (e.g., Kolodiuk *et al.* 2009, Ribeiro and Freire 2011, Alcantara *et al.* 2018, Maia-Carneiro and Rocha 2021, Oliveira *et al.* 2024). Possibly, these characteristics

related to few movements of *T. hispidus* may be related to niche divergence - which would favor its local coexistence (syntopy) with congeneric species (e.g., *T. semitaeniatus*), in addition to other factors, such as phylogeny and thermal conditions (Maia-Carneiro and Rocha 2021).

The population of *T. hispidus* examined in this area of Caatinga in Northeastern Brazil showed sexual size dimorphism, with males having greater head and body width; reproduction occurred between the middle of the dry season and the beginning of the rainy season; the diet, with a high niche overlap value, consisting of a wide variety of food items, in addition to expressive amounts of plant material; and helminthofauna composed of ten taxa, with the first occurrence of *O. travassosi* and *O. vanzolinii* infecting *T. hispidus*.

Thus, despite numerous studies on *Tropidurus* in the Caatinga, we do not know how the studied characteristics vary among populations throughout this ecoregion. Our results, such as variation in clutch size and new parasite records, reinforce the need to study common and widely distributed species. Furthermore, with the increasing effect of climate change and the intrinsic characteristics of the Caatinga biome – such as high temperatures and low annual precipitation, our results provide updated data to test new approaches and hypotheses.

## AUTHOR CONTRIBUTIONS

TFQ: conception, project, field collection, laboratory sample processing, data analysis and document writing. RAB: data analysis and document writing. RWA: data analysis and document Writing.

## ACKNOWLEDGMENTS

The authors thank the administrators of the Estação Ecológica de Aiuaba (ESEC) for granting permission to conduct this study. We are also grateful to Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico (FUNCAP) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Proc. 151124/2020-5) for their financial support. The collection permit was issued by the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis – IBAMA (SISBIO No. 32758-1).

## CONFLICT OF INTERESTS

The authors declare that they have no conflict of interest.

## REFERENCES

- Albuquerque RL, dos Santos Protázio A, Cavalcanti LBQ, Lopez LCS, Mesquita DO. 2018. Geographical ecology of *Tropidurus hispidus* (Squamata: Tropiduridae) and *Cnemidophorus ocellifer* (Squamata: Teiidae) in a Neotropical region: a comparison among Atlantic Forest, Caatinga, and coastal populations. *J. Herpetol.* 52(2): 145–155. doi: <https://doi.org/10.1670/16-018>
- Alcantara EP, Ferreira-Silva C, Sousa JGG, Ávila RW, Morais DH. 2018. Ecology and parasitism of the lizard *Tropidurus jaguaribanus* (Squamata: Tropiduridae) from northeastern Brazil. *Phyllomedusa*. 17(2): 195–210. doi: <https://doi.org/10.11606/issn.2316-9079.v17i2p195-210>
- Amorim DM, Ávila RW. 2019. Infection patterns of helminths in *Norops brasiliensis* (Squamata, Dactyloidae) from a humid forest, Northeastern Brazil and their relation with body mass, sex, host size, and season. *Helminthologia*. 56(2): 168–174. doi: <https://doi.org/10.2478/helm-2019-0011>
- Anderson RC. 2000. Nematode parasites of vertebrates: Their development and transmission. 2 ed. CABI International, Wallingford.
- Anjos LA, Ávila RW, Ribeiro SC, Almeida WO, da Silva RJ. 2013. Gastrointestinal nematodes of the lizard *Tropidurus hispidus* (Squamata: Tropiduridae) from a semi-arid region of north-eastern Brazil. *J. Helminthol.* 87(4): 443–449. doi: <https://doi.org/10.1017/S0022149X12000491>
- Araújo JA, Brito SV, Lima VF, Pereira AMA, Mesquita DO, Albuquerque RL, Almeida WO. 2017. Influence of temporal variation and host condition on helminth abundance in the lizard *Tropidurus hispidus* from north-eastern Brazil. *J. Helminthol.* 91(3): 312–319. doi: <https://doi.org/10.1017/S0022149X16000225>
- Ávila RW, Silva RJ. 2010. Checklist of helminths from lizards and amphisbaenians (Reptilia, Squamata) of South America. *J. Venom. Anim. Toxins Incl. Trop. Dis.* 16(4): 543–572. doi: <https://doi.org/10.1590/S1678-91992010000400005>
- Ávila RW, Anjos LA, Ribeiro SC, Morais DH, Da Silva RJ, Almeida WO. 2012. Nematodes of lizards (Reptilia: Squamata) from Caatinga biome, northeastern Brazil. *Comparative Parasitology*. 79(1): 56–63. doi: [10.1654/4518.1](https://doi.org/10.1654/4518.1)
- Avila-Pires TCS. 1995. Lizards of Brazilian Amazonia (Reptilia: Squamata). *Zool. Verh.* 299: 1–706.
- Balestrin RL, Cappellari LH, Outeiral AB. 2010. Reproductive biology of *Cercosaura schreibersii* (Squamata, Gymnophthalmidae) and *Cnemidophorus lacertoides* (Squamata, Teiidae) in Sul-Riograndense Shield, Brazil. *Biota Neotrop.* 10(1): 31–140. doi: <https://doi.org/10.1590/S1676-06032010000100013>
- Benício RA, Ortega Z, Mencia A, Passos DC. 2019. Microhabitat selection of *Ameiva ameiva* (Linnaeus, 1758), in the Brazilian Pantanal. *Herpetozoa*. 31(3/4): 211–218.
- Bush AO, Lafferty KD, Lotz JM, Shostak AW. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *J. Parasitol.* 83(4): 575–583. doi: <https://doi.org/10.2307/3284227>
- Carvalho ALG. 2013. On the distribution and conservation of the South American lizard genus *Tropidurus* Wied–Neuwied, 1825 (Squamata: Tropiduridae). *Zootaxa* 3640(1): 42–56. doi: <https://doi.org/10.11646/zootaxa.3640.1.3>
- Carvalho ALG, Silva HR, Araújo AFB, Alves-Silva R, Silva-Leite RR. 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. *Rev. Bras. Zool.* 24(1): 222–227. doi: <https://doi.org/10.1590/S0101-81752007000100029>
- Cechin SZ, Martins M. 2000. Eficiência de armadilhas de queda (pitfalltraps) em amostragens de anfíbios e répteis no Brasil. *Rev. Bras. Zool.* 17(3): 729–740. doi: <https://doi.org/10.1590/S0101-81752000000300017>
- Colli GR, Araújo AFB, Silveira R, Roma F. 1992. Niche partitioning and morphology of two syntopic *Tropidurus* (Sauria: Tropiduridae) in Mato Grosso, Brazil. *J. Herpetol.* 26(1): 66–69. doi: <https://doi.org/10.2307/1565023>
- Colli GR, Peres AKJR, Zatz MG. 1997. Foraging Mode and Reproductive Seasonality in Tropical Lizards. *J. Herpetol.* 31(4): 490–499. doi: <https://doi.org/10.2307/1565600>
- Cooper Jr. WE, Hiting MJ, Van Wyk JH. 1997. Foraging modes of cordyliform lizards. *S. Afr. J. Zool.* 32(1): 9–13. doi: <https://doi.org/10.1080/02541858.1997.11448420>
- Cooper Jr. WE, Whiting MJ, Van Wyk JH, le FN Mouton P. 1999. Movement-and attack-based indices of foraging mode and ambush foraging in some gekkonid and agamine lizards from southern Africa. *Amphib.-Reptil.* 20(4): 391–399. doi: <https://doi.org/10.1163/156853899X00439>
- Cooper Jr. WE, Vitt LJ, Caldwell JP, Fox SF. 2001. Foraging modes of some American lizards: Relationships among measurement variables and discreteness of modes. *Herpetologica* 57(1): 65–67.
- Cooper Jr. WE, Vitt LJ. 2002. Distribution, extent, and evolution of plant consumption by lizards. *J. Zool.* 257(4): 487–517. doi: <https://doi.org/10.1017/S0952836902001085>
- Drago MC, Kato MM, Koster R, Vrcibradic D. 2020. How Does Habitat Anthropization Influence Lizard Diets? An Analysis Comparing Two Populations of *Tropidurus torquatus* (Iguania). *J. Herpetol.* 54(2): 144–150. doi: <https://doi.org/10.1670/18-148>
- de Andrade AC. 2020. Metropolitan lizards? Urbanization gradient and the density of lagartixas (*Tropidurus hispidus*) in a tropical city. *Ecol. Evol.* 10(4): 1740–1750. doi: <https://doi.org/10.1002/ece3.5518>

- Dias EDR, Lira-da-Silva RM. 1998. Utilização dos recursos alimentares por quatro espécies de lagartos (*Phyllorhynchus pollicaris*, *Tropidurus hispidus*, *Mabuya macrorhyncha* e *Vanzosaura rubricauda*) da Caatinga (Usina Hidroelétrica do Xingo). *Braz. J. Ecol.* 2: 97–101.
- Díaz JÁ, Alonso-Gómez AL, Delgado MJ. 1994. Seasonal variation of gonadal development, sexual steroids, and lipid reserves in a population of the lizard *Psammotriton algirus*. *J. Herpetol.* 28(2): 199–205. doi: <https://doi.org/10.2307/1564621>
- Emlen ST, Oring LW. 1977. Ecology, sexual selection and the evolution of mating systems. *Science*. 197(4300): 215–223. doi: <https://doi.org/10.1126/science.327542>
- Faria RG, Araújo AFB. 2004. Syntopy of two *Tropidurus* lizard species (Squamata: Tropiduridae) in a rocky cerrado habitat in central Brazil. *Braz. J. Biol.* 64(4): 775–786. doi: <https://doi.org/10.1590/S1519-69842004000500007>
- Felsenstein J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125(1): 1–15. doi: <https://doi.org/10.1086/284325>
- Figueiredo VA, Souza NS, Anaissi JS, Sanches PR, Costa-Campos CE. 2020. Diet of four lizards from an urban forest in an area of amazonian biome, eastern amazon. *Cuad. herpetol.* 34(2): 231–237.
- Franco FL, Salomão MG, Auricchio P. 2002. Répteis. In: Auricchio P, Salomão MG, editors. *Técnicas de coleta e preparação de vertebrados para fins científicos e didáticos*. Arujá: Instituto Pau Brasil de História Natural; p. 95–124.
- Gomes FFA, Caldas FLS, dos Santos RA, da Silva BD, Santana DO, Rocha SM, Ferreira AS, Faria RG. 2015. Patterns of space, time and trophic resource use by *Tropidurus hispidus* and *T. semitaeniatus* in an area of Caatinga, northeastern Brazil. *Herpetol. J.* 25(1): 27–39.
- Huey RB, Pianka ER. 1981. Ecological consequences of foraging mode. *Ecology* 62(4): 991–999. doi: <https://doi.org/10.2307/1936998>
- Kolodiy MF, Ribeiro LB, Freire EM. 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(3): 581–585. doi: <https://doi.org/10.1590/S1984-46702009000300026>
- Lemos-Espinal JA, Smith GR, Ballinger RE. 1996. Ventral blue coloration and sexual maturation in male *Sceloporus gadowiae* lizards. *J. Herpetol.* 30(4): 546–548. doi: <https://doi.org/10.2307/1565702>
- Lima DSDS, Siqueira RS, Dias EJDR, Lira-da-Silva RM. 2017. Atividades diárias de *Tropidurus hispidus* (Squamata: Iguania: Tropiduridae) na Ilha do Monte Cristo, Baía de Todos-os-Santos, Bahia, Brasil. *Rev. Bras. Zoo.* 18(2): 55–70. doi: <https://doi.org/10.34019/2596-3325.2017.v18.24610>
- Magnusson WE, Lima AP, Silva WA, Araújo MC. 2003. Use of geometric forms to estimate volume of invertebrates in ecological studies of dietary overlap. *Copeia*. 2003(1): 13–19. doi: [https://doi.org/10.1643/0045-8511\(2003\)003\[0013:UOGFTE\]2.0.CO;2](https://doi.org/10.1643/0045-8511(2003)003[0013:UOGFTE]2.0.CO;2)
- Maia-Carneiro T, Motta-Tavares T, Ávila RW, Rocha C FD. 2017. Helminth infections in a pair of sympatric congeneric lizard species. *Parasitology Research*, 117(1): 89–96. doi: <https://doi.org/10.1007/s00436-017-5672-y>
- Maia-Carneiro T, Rocha CD. 2021. Diverging temporal and thermal niche dimensions favor syntopy of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata: Tropiduridae). *Biologia* 76: 133–146. doi: <https://doi.org/10.2478/s11756-020-00523-w>
- Meira KTR, Faria RG, Silva MDM, Miranda VT, Zahn-Silva W. 2007. História natural de *Tropidurus oreadicus* em uma área de cerrado rupestre do Brasil Central. *Biota Neotrop.* 7(2): 155–163. doi: <https://doi.org/10.1590/S1676-06032007000200018>
- Morrison RL, Sand MS, Frost-Mason SK. 1995. Cellular basis of color differences in three morphs of the lizard *Sceloporus undulatus erythrocheilus*. *Copeia* 1995(2): 397–408. doi: <https://doi.org/10.2307/1446903>
- Neta AS, Ávila R. 2018. Helminths of the lizard *Colobosauroides cearensis* (Squamata, Gymnophthalmidae) in an area of Caatinga, Northeastern Brazil. *Acta Herpetol.* 13(1): 95–100.
- Oliveira PMDA, Feitosa JLL, Nunes PMS. 2024. Seasonal Influence on the Feeding Patterns of Three Sympatric *Tropidurus* Lizards (Squamata: Tropiduridae) of the Caatinga, in the Brazilian Semi-Arid Region. *South Am J Herpetol.* 31(1): 56–64. doi: <https://doi.org/10.2994/SAJH-D-21-00043.1>
- Passos DC, Benício RA, Mência A, Ortega Z. 2021. Microhabitat selection of the poorly known lizard *Tropidurus lagunablanca* (Squamata: Tropiduridae) in the Pantanal, Brazil. *Pap. Avulsos Zool.* 61: e2021611. doi: <https://doi.org/10.11606/1807-0205/2021.61.18>
- Pelegrin N, Mesquita DO, Albinati P, Caldas FLS, Cavalcanti LBQ, Costa TB, Falico DA, Galdino JYA, Tucker DB, Garda AA. 2017. Extreme specialization to rocky habitats in *Tropidurus* lizards from Brazil: Trade-offs between a fitted ecomorph and autoecology in a harsh environment. *Austral Ecol.* 42(6): 677–689. doi: <https://doi.org/10.1111/aec.12486>
- Perry G. 1990. Foraging mode in lacertid lizards: variation and correlates. *Amphib.-Reptil.* 11(4): 373–384. doi: <https://doi.org/10.1163/156853890X00069>
- Perry G. 1999. The evolution of search modes: ecological versus phylogenetic perspectives. *Am. Nat.* 153(1): 98–109. doi: <https://doi.org/10.1086/303145>
- Pianka ER. 1973. The structure of lizard communities. *Annu. Rev. Ecol. Evol. Syst.* 4(1): 53–74. doi: <https://doi.org/10.1146/annurev.es.04.110173.000413>
- Pianka ER, Huey RB. 1978. Comparative ecology, resource utilization and niche segregation among gekkonid lizards in the southern Kalahari. *Copeia*, 691–701. doi: <https://doi.org/10.2307/1443698>
- Prieto AS, León JR, Lara O. 1976. Reproduction in the tropical lizard, *Tropidurus hispidus* (Sauria: Iguanidae). *Herpetologica* 32(3): 318–323.
- Pinto ACS, Wiederhecker HC, Colli GR. 2005. Sexual dimorphism in the Neotropical lizard, *Tropidurus torquatus* (Squamata,

- Tropiduridae). Amphib.-Reptil. 26(2): 127–137. doi: <https://doi.org/10.1163/1568538054253384>
- Powell R, Parmelee JS, Rice MA, Smith DD. 1990. Ecological observations of *Hemidactylus brooki haitianus* Meerwath (Sauria: Gekkonidae) from Hispaniola. Caribb. J. Sci. 26:67–70.
- Ribeiro LB, Silva NB, Freire EMX. 2012. Reproductive and fat body cycles of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata, Tropiduridae) in a caatinga area of northeastern Brazil. Rev. Chil. Hist. Nat 85(3): 307–320. doi: <https://doi.org/10.4067/S0716-078X2012000300005>
- Ribeiro LB, Freire EMX. 2011. Trophic ecology and foraging behavior of *Tropidurus hispidus* and *Tropidurus semitaeniatus* (Squamata, Tropiduridae) in a caatinga area of northeastern Brazil. Iheringia Ser. Zool. 101(3): 225–232. doi: <https://doi.org/10.1590/S0073-47212011000200010>
- Ribeiro LB, Freire EMX. 2010. Thermal ecology and thermoregulatory behaviour of *Tropidurus hispidus* and *T. semitaeniatus* in a caatinga area of northeastern Brazil. Herpetol. J. 20(3): 201–208.
- Rocha CFD, Bergallo HG. 1992. Thermal biology and flight distance of *Tropidurus oreadicus* (Sauria, Iguanidae) in an area of Amazonian Brazil. Ethology, Ecology & Evolution. 2(3): 263–268.
- Rocha CFD. 1994. Ecologia de lagartos no Brasil: status e perspectivas. In: Nascimento LB, Bernardes AT, Cotta GA, editors. Herpetologia no Brasil I. Belo Horizonte: Pontifícia Universidade Católica, Fundação Biodiversitas e Fundação Ezequiel Dias; p. 39–57.
- Rocha CFD, Siqueira CC. 2008. Feeding ecology of the lizard *Tropidurus oreadicus* Rodrigues 1987 (Tropiduridae) at Serra dos Carajás, Pará state, northern Brazil. Braz. J. Biol. 68(1): 109–113. doi: <https://doi.org/10.1590/S1519-69842008000100015>
- Rodrigues MT. 1987. Sistemática, ecologia e zoogeografia dos *Tropidurus* do grupo *torquatus* ao Sul do Rio Amazonas (Sauria, Iguanidae). Arq. Zool. S. Paulo 31(3): 105–230. doi: <https://doi.org/10.11606/issn.2176-7793.v31i3p105-230>
- Rodrigues MT. 1988. Distribution of lizards of the genus *Tropidurus* in Brazil (Sauria, Iguanidae). In: Heyer WR, Vanzolini PE, editors. Proceeding of a Workshop on Neotropical Distribution Patterns. Rio de Janeiro: Academia Brasileira de Ciências; p. 305–315.
- Santana DO, Caldas FLS, Gomes FFA, dos Santos RA, da Silva BD, Rocha SM, Faria RG. 2014. Aspectos da história natural de *Tropidurus hispidus* (Squamata: Iguania: Tropiduridae) em área de Mata Atlântica, nordeste do Brasil. Neotrop. Biol. Conserv. 9(1): 55–61. doi: <https://doi.org/10.4013/nbc.2014.91.07>
- Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2: 369–404. doi: <https://doi.org/10.1146/annurev.es.02.110171.002101>
- Smith GR, Ballinger RE. 1994. Temporal and spatial variation in individual growth in the spiny lizard, *Sceloporus jarrovi*. Copeia 1994(4): 1007–1013. doi: <https://doi.org/10.2307/1446724>
- Teixeira RL, Giovanelli M. 1999. Ecologia de *Tropidurus torquatus* (Sauria: Tropiduridae) da restinga de Guriri, São Mateus, ES. Rev. Bras. Biol. 59(1): 11–18. doi: <https://doi.org/10.1590/S0034-71081999000100002>
- Van Sluys M. 1993a. Food habitats of the lizard *Tropidurus itambere* (Tropiduridae) in Southeastern Brazil. J. Herpetol. 27(3): 347–351. doi: <https://doi.org/10.2307/1565162>
- Van Sluys M. 1993b. The Reproductive Cycle of *Tropidurus itambere* (Sauria: Tropiduridae) in Southeastern Brazil. J. Herpetol. 27(1): 28–32. doi: <https://doi.org/10.2307/1564901>
- Van Sluys M. 1998. Growth and body condition of the saxicolous lizard *Tropidurus itambere* in southeastern Brazil. J. Herpetol. 32(3): 359–365. doi: <https://doi.org/10.2307/1565450>
- Van Sluys M, Rocha CFD, Vrcibradic D, Galdino CAB, Fontes AF. 2004. Diet, Activity, and Microhabitat Use of Two Syntopic *Tropidurus* Species (Lacertilia: Tropiduridae) in Minas Gerais, Brazil. J. Herpetol. 38(4): 606–611. doi: <https://doi.org/10.1670/218-03N>
- Vitt LJ. 1981. Lizard reproduction: habitat specificity and constraints on relative clutch mass. Am. Nat. 117(4): 506–514. doi: <https://doi.org/10.1086/283731>
- Vitt LJ. 1993. Ecology of isolated open-formation *Tropidurus* (Reptilia: Tropiduridae) in Amazonian lowland rain forest. Can. J. Zool. 71(12): 2370–2390. doi: <https://doi.org/10.1139/z93-333>
- Vitt LJ. 1995. The ecology of tropical lizards in the Caatinga of Northeast Brazil. Occas. pap. Mus. Nat. Hist. 1: 1–29.
- Vitt LJ, Goldberg SR. 1983. Reproductive ecology of two tropical iguanid lizards: *Tropidurus torquatus* and *Platynotus semitaeniatus*. Copeia 1983(1): 131–141. doi: <https://doi.org/10.2307/1444707>
- Vitt LJ, Zani PA, Caldwell JP. 1996. Behavioural ecology of *Tropidurus hispidus* on isolate rock outcrops in Amazônia. J. Trop. Ecol. 12(1): 81–101. doi: <https://doi.org/10.1017/S0266467400009329>
- Wiederhecker HC, Pinto ACS, Colli GR. 2002. Reproductive ecology of *Tropidurus torquatus* (Squamata: Tropiduridae) in the highly seasonal cerrado biome of central Brazil. J. Herpetol. 36(1): 82–91. doi: [https://doi.org/10.1670/0022-1511\(2002\)036\[0082:REOTTS\]2.0.CO;2](https://doi.org/10.1670/0022-1511(2002)036[0082:REOTTS]2.0.CO;2)
- Zar JH. 1996. Biostatistical Analysis, 3rd ed. New Jersey: Prentice Hall, Upper Saddle River.