Investigating Diet Shifts of *Tropidurus torquatus* in the Rainy Season Based on Age, Sex, and Pregnancy in a Coastal Habitat of Southeastern Brazil

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Abstract.—We analyzed the diet of the Collared Lizard (Tropidurus torquatus), characterizing it at a population level. Our study aimed to elucidate the differences in diet among three population classes: adult males, females (gravid and non-gravid), and juveniles. This study was conducted within Restinga habitat located in the state of Rio de Janeiro, southeastern Brazil. We sampled the four distinct vegetation zones of the habitat and collected 69 individuals during the rainy season, recorded their body size, and identified sex and ontogeny using laboratory-based procedures. We removed the stomach contents, documenting the number, volume, and frequency of each item. Our analysis within this sampling period revealed 28 distinct food items. Arthropods were the principal diet component, with Formicidae being the most consumed food item in terms of number and frequency, while Coleoptera dominated in volume. We also analyzed the proportion of plant material, which showed a substantial number of leaves and fruits in the diet. Moreover, we found differences in the number and frequency of food items among the three population classes. We also found significant volume-based disparities between males and females, and between females and juveniles. Gravid and non-gravid females, in this context, differed in diet composition, suggesting different foraging intensities. Our results suggest that the population presented an intermediate foraging strategy with a tendency to ambush, although we recognize our results were derived during only one season in one year. Additional research is needed to confirm our results.

Key Words.—Arthropoda; foraging strategy; ontogenetic variation; sexual dimorphism; trade-offs

INTRODUCTION

Understanding the dietary patterns of free-ranging animals is crucial for understanding their ecological functioning and their function in the environment allowing for appropriate conservation efforts (Losos and Greene 1988; Costa et al. 2008; Parker et al. 2009). Lizards generally exhibit a diverse diet, spanning from arthropods to vertebrates, including plant material (Rocha 1994). Thus, lizard dietary patterns can elucidate ecosystem dynamics and optimize species-specific systematic planning. Classical foraging theory assumes that the diet composition of lizard species is related to their foraging activity, constrained by morphological features and evolutionary history (Huey and Pianka 1981). The theory assumes that foraging activity is a continuum, with two extreme types: the active foragers, which often target less mobile prey, and ambush foragers, which await passing prey (Huey

and Pianka 1981). Usually, lizard species alternate foraging forms (mixed foraging), depending on resource exploitation, habitat structure, and species diversity (Huey and Pianka 2007).

More recently Pianka et al. (2017) suggested that lizard species can be organized into five major niche dimensions (e.g., habitat, life history, metabolism, defense, and diet) that seem to evolve in concert. Their recent findings suggest simultaneous shifts in both life-history and trophic traits, with certain groups of lizards exhibiting significant diversity in their diets and life histories, whereas others do not. If there is covariance between diet and life history across different dimensions, it indicates that much of the diversity in lizard ecology can be explained within a relatively concise dimensional space.

Intrapopulation variation is also found, mostly related to body size, reproductive state, and body condition (Bonine 2007). Ontogeny also plays a role, as adult lizards frequently consume distinct prey,

236

compared to juveniles (Rocha 1989; 1998; Fialho et al. 2000; Zaluar and Rocha 2000), while sex-related differences have been observed in some species, including prey type, size, and quantity (e.g., Schluter 1984; Zaluar and Rocha 2000). Also, in some cases, lizards can select a habitat for plants that are qualitatively more advantageous for their nutrition (Rocha 2000). Hence, it is possible to infer intra or interspecific foraging mode variations within the foraging theory context by analyzing dietary patterns.

The Collared Lizard (*Tropidurus torquatus*), a diurnal lizard found in open habitats (Rodrigues 1987) in coastal areas of Rio de Janeiro state, Brazil, ranges in body size from 28 mm snout-vent length (SVL) juveniles to 111 mm SVL adult females and 130 mm SVL adult males (Bergallo and Rocha 1993; Siqueira et al. 2010, 2013). This lizard is usually abundant in their habitats and displays a high rate of movement throughout the day (Kiefer et al. 2007). Notably, the species is sexual dimorphic, with males typically larger than females, and their reproductive activities span the entire year, with gravid females observed across all seasons (Siqueira et al. 2007). This lizard primarily preys upon mobile and active organisms employing an ambush foraging strategy (e.g., Siqueira et al. 2013).

Some studies have characterized the species feeding habits as opportunistic and generalist, encompassing a diet ranging from invertebrates to plant material (Siqueira et al. 2013). Indeed, previous dietary investigations have shown its inclination toward consuming plant material, encompassing leaves, flowers, and fruits (Bergallo and Rocha 1994; Fialho et al. 2000; Dutra et al. 2011; Siqueira et al. 2010, 2013). Predation of small lizards (Kiefer et al. 2006), and even cannibalism (Siqueira and Rocha 2008; Siqueira et al. 2013) have also been documented. A relatively limited number of studies have comprehensively analyzed the stomach contents after their extraction, however, particularly when analyzing trends by sex and/or ontogeny (Rocha 1998).

One significant gap that our research addresses is the lack of comprehensive understanding about how age, sex, and pregnancy influence dietary patterns in *T. torquatus*. By investigating these aspects, we aim to provide valuable information about the trophic ecology of this species. Furthermore, understanding the dietary preferences and shifts can have direct implications for the conservation of the species and its habitats by identifying specific dietary requirements during crucial life stages, which can lead to conservation strategies aimed at preserving essential foraging resources. Moreover, by elucidating the dynamics of this trophic niche of this lizard, our research contributes to a more comprehensive understanding of its ecological requirements. This understanding is crucial for formulating effective conservation plans to safeguard not only for *T. torquatus* but also the entire ecosystem upon which it depends. Given this context, our study aimed to address the following questions regarding the *T. torquatus* diet at the Grussaí sandy coastal plain of Rio de Janeiro, Brazil: (1) What is the importance, quantity (number), frequency, and volume of prey in the diet of this species? (2) Are there discernible diet variations among the sexes? (3) How do juveniles and adults differ in their food consumption patterns? (4) Do gravid and non-gravid females differ in diet?

MATERIAL AND METHODS

Study site.—The Brazilian coastal plains comprise mainly beaches, dunes, sandy coastal plains (Restingas), and mangroves, with each Restinga habitat generally characterized by sandy and highly saline substrate, often dominated by herbaceous vegetation, shrubs (short and tall), and forests (Suguio and Tessler 1984). The vegetation formations within Restingas undergo a parallel substitution pattern from the shoreline, dictated by the gradient of oceanic influences such as wind and salinity levels. The study was carried out in the Grussaí Restinga (21°44'S, 41°02'W), located along the northern coastline of Rio de Janeiro state within the São João da Barra municipality. Spanning approximately 4,800 ha, the study area encompasses an extensive beach area devoid of dunes, extending linearly across parallel coastal ridges (Assumpção and Nascimento 2000). The regional climate is sub-humid to semi-arid tropical, with average annual precipitation between 800 and 1,200 mm. Notably, the highest precipitation rates occur during the summer months (December to March; Nunes 1998).

Data collection.—We collected specimens of *Tropidurus torquatus* in the Grussaí Restinga during the wet season (October-April) over an uninterrupted 24-d span in December 2010 and January 2011. Our six-member research team independently surveyed the four vegetation zones (Nunes 1998). To execute this study, each of the six researchers autonomously traversed the four distinct vegetation zones, covering the designated areas from 0600 to 2100. During

this phase, we employed 4.5 mm pressure rifles to capture the specimens. Lizards were fixed in 10% formalin, followed by preservation in a solution of 70% alcohol to facilitate further analysis. At the laboratory, we measured the snout-vent length (SVL) and tail length (TL) of each individual using a digital caliper (precision of 0.1 mm). We identified the sex by gonadal analysis and inspected for the presence of eggs. We methodically removed stomachs and stored them in tubes filled with 70% alcohol. We then analyzed these stomach contents under a Leica M205 stereomicroscope (Leica Microsystems, Wetzlar, Hesse, Germany). During this process, we recorded the number, frequency, and volume (mm³) of each food item. Furthermore, we measured the length and width of each item using a digital caliper (0.1 mm precision), identifying each prey down to the lowest possible taxonomic level. In addition to prey, we also recorded plant-derived components. We identified and quantified plant items found in the form of leaves, with the caveat that we only considered whole leaves in the quantification process. Similarly, we also cataloged and accounted for plant-based food items, such as fruits. While detected in digestive tracts, we

TABLE 1. Number (n), frequency (F), volume (V), and Relative Importance Index (RII) of Collared Lizards (*Tropidurus torquatus*) irrespective of sex for each consumed food item in the Grussaí Restinga, Rio de Janeiro, Brazil. For food items, L = larvae and N = nymph.

Food item	n	n%	F (%)	V (mm³)	V (mm³) %	RII
Acari	3	0.22	5.66	0.360	< 0.001	3.006
Apidae	1	0.07	1.89	36	0.042	12.962
Araneae	13	0.95	22.6	6,038.6	6.987	2,024.7
Blattodea	6	0.44	9.43	4,714.5	5.455	1,576.7
Bone fragment	1	0.07	1.89	122.3	0.141	41.715
Brachycera	1	0.07	1.89	13.24	0.015	5.375
Caelifera	1	0.07	1.89	29.02	0.0335	10.635
Chilopoda	2	0.15	1.89	508.2	0.588	170.702
Cicadellidae	14	1.03	24.5	2,064.5	2.389	701.016
Cicadidae	5	0.37	9.43	1,214.8	1.406	409.741
Cicadidae (N)	3	0.22	5.66	138.1	0.159	48.930
Coleoptera	60	4.40	62.3	26,455.2	30.612	8,859.2
Coleoptera (L)	94	6.90	26.4	1,148.4	1.329	422.948
Diptera (L)	3	0.22	5.66	461.9	0.534	156.850
Formicidae	971	71.29	88.7	22,697.1	26.263	7918.94
Fruit	10	0.73	15.1	1,553.6	1.798	526.244
Gastropoda	2	0.15	3.77	9.690	0.011	5.154
Heteroptera	15	1.10	20.8	6,456.4	7.471	2,164.0
Isoptera	55	4.04	9.43	877.3	1.015	313.921
Leaves	19	1.39	22.6	837.8	0.969	293.133
Lepidoptera (L)	13	0.95	15.1	1,228.3	1.421	418.804
Myriapoda (L)	1	0.07	1.89	7.800	0.009	3.562
Nematocera	6	0.44	7.55	22.87	0.026	12.139
Neuroptera	9	0.66	15.1	297.6	0.344	107.241
Neuroptera (L)	3	0.22	3.77	61.11	0.071	22.627
Orthoptera (N)	1	0.07	1.89	8.300	0.0096	3.728
Pseudoscorpiones	2	0.15	3.77	2.460	0.003	2.744
Unidentified Arthropod remains			56.6	4,805.8	5.561	
Vespidae	35	2.57	30.2	4,587.9	5.309	1,551.0
TOTAL	1362			86,420.7		

classified sand as an accidentally ingested item and, consequently we did not include this in our food item analysis.

Data analysis.—To estimate prey volume (V), we used the ovoid-spheroid formula (Vitt 1991):

$$V = 4/3\pi \ (L/2) \ (W/2)^2$$

where L = length and W = width of prey items. We used this method for prey volume because it is the most widely used method in dietary studies, both recent and older, which has the advantage of allowing comparison even with what was found in studies from several decades ago. We quantified unidentified prey, estimated the volume of prey, and labeled as unidentified arthropod remains (UAR). For diet analysis, we focused solely on individuals with stomach contents. We used the Relative Importance Index (RII; Howard et al. 1999):

$$RII = n + F + V / (N)$$

Where n = number of food items, F = frequency of food items, V = volume of food items, and N = number of categories. This index quantifies the significance of each food item within the diet. We analyzed whether there were quantitative differences (number, volume, and frequency) among population classes (males, females, and juveniles), and between gravid and non-gravid females. We checked data for parametric assumptions of normality and homoscedasticity. Because data met these assumptions, we used Analysis of Variance (ANOVA) tests to compare these classes: (1) females/males; (2) females/juveniles; (3) males/juveniles; and (4) gravid/non-gravid females. We also analyzed prey life habits, categorizing them as active or passive (Ruppert and Barnes 1996; Brusca and Brusca 2007; Triplehorn and Johnson 2011) and compared the volume ingested by males, females, and juveniles in terms of animal prey with passive or active habits (Supplemental Information Tables S1, S2).

Finally, we assessed an index of prey-item heterogeneity using the Simpson's Diversity Index (D; Simpson 1949):

$$D = 1 - (\textstyle\sum n \ (n-1) \ / \ N \ (n-1))$$

Where N = number of organisms of all species and n = number of organisms of a particular species. We determined the index for males, females, and

juveniles (Supplemental Information Tables S3, S4, and S5). We used the R platform (R core team 2021) for all statistical analyses.

RESULTS

We collected 69 *Tropidurus torquatus,* including 29 females (19 gravid and 10 non-gravid), 24 males, and 16 juveniles. We found 16 stomachs that were empty: six of which were from females, seven from males, and three from juveniles. Therefore, we analyzed stomach contents of 53 lizards. Numerically, 1,362 food items in 28 food types were consumed by lizards (Table 1). Formicidae predominated in the diet (n = 971), followed by Coleoptera larvae (n = 94). Formicidae frequency was 67.1%, followed by Coleoptera (47.1%), Vespidae (22.9%), and Coleoptera larvae (20%). Plant material was present in 28% of stomachs (n = 20), involving 19 leaves (17.1%) and 10 fruits (11.4%). Volumetrically, Coleoptera held the highest volume (V = 26,455.2 mm³), comprising 30.6% of the total amount of ingested volume (V = 86,420.7 mm³), followed by Formicidae (V = 22,697.1 mm³; 26.3%) and Heteroptera (V = 6,456.4 mm³; 7.5%). Plant material constituted 2.8% (V = 2,391.4 mm³) of the overall volume of food ingested by lizards, with fruits volume of 1,553.6 mm³ and leaves of 837.76 mm³.

The Relative Importance Index (RII) across all lizards ranked Coleoptera as the highest (RII = 8,854.1), followed by Formicidae (RII = 7,911.8), and Heteroptera (RII = 2,162.4). Among plant material, fruits are ranked as most important (RII = 525.02). A fragment of bone from a vertebrate was found in the stomach of a gravid female, but we could not identify the animal to which it belonged.
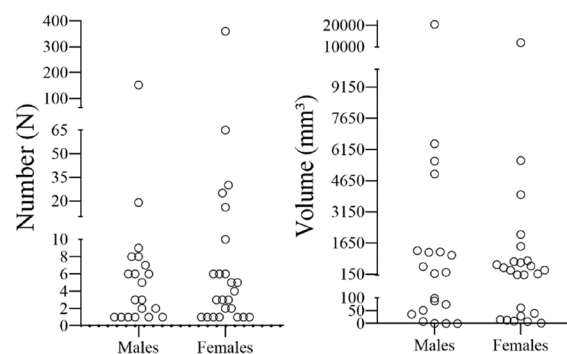

FIGURE 1. Prey number and volume consumed by adult female and male Collared Lizards (*Tropidurus torquatus*) in the Grussaí Restinga, Rio de Janeiro, Brazil.

Diet composition differed between adult males and females (Table 2). Females consumed 24 items, whereas males consumed 21 items with greater volume (Fig. 1). Formicidae was the most important food item for females (RII= 4,096.39), followed by Coleoptera (RII = 1,898.93) and Vespidae (RII = 1,338.14). For adult males, Coleoptera held the highest importance value (RII = 6,834.55), followed by Formicidae (RII = 2,212.06), and Araneae (RII = 1,873). Leaves were the main plant material for females (RII = 187.32), whereas fruits were more important for males (RII = 415.57). Plant material importance (RII) for adult females was 303.36, and for adult males was 502.43. Juveniles had a distinct food diet (Fig. 2, Table 3). Their diet included 16 food types, with all individuals sampled having ants in the stomach, which ranked as the most important (RII = 1,650.68) and frequent (81.25%) item. Coleoptera larvae (RII = 169.85) and Vespidae (RII = 162.15) were also important. In juveniles, leaves were the

TABLE 2. Number (n), frequency (F), volume (V), and Relative Importance Index (RII) of male and female Collared Lizards (*Tropidurus torquatus*) for each consumed food item in the Grussaí Restinga, Rio de Janeiro, Brazil. For food items, L = larvae and N = nymph.

| Food Item	Males						Females					
	n	n%	F (%)	V (mm³)	V (mm³) %	RII	n	n%	F (%)	V (mm³)	V (mm³) %	RII
Acari	1	0.410	5.880	0.330	0.0007	2.400	0	0	0	0	0	0
Apidae	1	0.409	5.880	36.00	0.082	14.29	0	0	0	0	0	0
Araneae	6	2.459	35.29	5,588.7	12.71	1,876.7	5	0.896	17.39	2,056.0	6.828	692.8
Blattodea	3	1.229	11.76	1,278.9	2.909	431.2	2	0.358	8.69	343.0	1.139	117.90
Bone fragment	0	0	0	0	0	0	1	0.179	4.35	122.3	0.406	42.54
Brachycera	0	0	0	0	0	0	1	0.179	4.35	13.24	0.044	6.20
Caelifera	0	0	0	0	0	0	1	0.179	4.35	29.02	0.096	11.46
Chilopoda	2	0.819	11.76	508.2	1.156	174.0	0	0	0	0	0	0
Cicadellidae	3	1.229	17.65	1,198.5	2.726	406.4	6	1.075	21.74	797.1	2.647	275.00
Cicadidae	2	0.819	11.76	512.3	1.165	175.4	3	0.537	13.04	702.5	2.333	239.5
Cicadidae (N)	2	0.819	11.76	98.45	0.224	37.40	1	0.179	4.35	39.68	0.132	15.01
Coleoptera	19	7.786	64.70	20,438.8	46.49	6,840.8	30	5.376	65.22	5615.1	18.65	1903.4
Coleoptera (L)	8	3.278	35.29	74.50	0.169	39.26	65	11.65	21.74	604.1	2.006	230.3
Diptera (L)	1	0.409	5.880	0.750	0.002	2.540	1	0.179	4.35	460.0	1.527	155.1
Formicidae	152	62.30	88.23	6,421.7	14.61	2,220.6	360	64.52	82.61	1,1863.7	39.40	4,102.1
Fruit	7	2.868	29.40	1,218.9	2.772	418.4	3	0.537	13.04	334.8	1.112	116.9
Gastropoda	0	0	0	0	0	0	2	0.358	8.69	9.69	0.032	6.80
Heteroptera	8	3.278	35.29	4,967.0	11.30	1,670.1	6	1.075	17.39	1,485.1	4.932	502.8
Isoptera	9	3.688	5.880	51.66	0.117	22.18	25	4.480	4.35	752.8	2.501	260.7
Leaves	5	2.049	23.53	238.9	0.543	89.15	10	1.792	17.39	538.2	1.787	188.5
Lepidoptera (L)	6	2.459	17.65	1,061.5	2.414	361.7	6	1.075	17.39	165.3	0.549	62.88
Myriapoda (L)	0	0	0	0	0	0	1	0.179	4.35	7.80	0.026	4.38
Nematocera	1	0.409	5.88	0.070	0.0002	2.320	4	0.716	8.69	14.91	0.049	9.20
Neuroptera	1	0.409	5.88	87.91	0.199	31.60	5	0.896	17.39	119.4	0.396	47.26
Neuroptera (L)	0	0	0	0	0	0	3	0.537	8.69	61.01	0.203	24.24
Orthoptera (N)	1	0.409	5.88	8.30	0.019	5.060	0	0	0	0	0	0
Pseudoscorpiones	0	0	0	0	0	0	1	0.179	4.35	1.78	0.006	2.38
Vespidae	6	2.459	17.65	177.6	0.404	67.10	16	2.867	30.43	3,974.3	13.20	1,340.2
TOTAL	244			43,969			558			30,110.5		
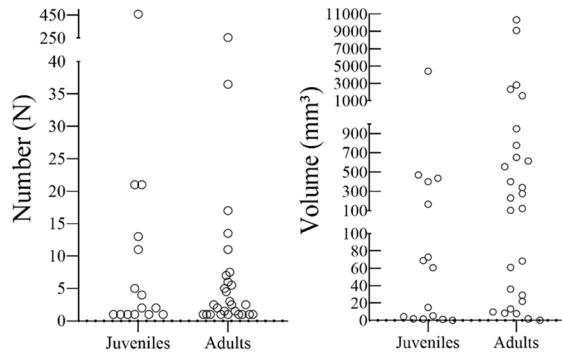
Figure 2. Prey number and volume consumed by adult and juvenile Collared Lizards (*Tropidurus torquatus*) in the Grussaí Restinga, Rio de Janeiro, Brazil.

sole plant part present, which we found in 25% of the stomachs (RII = 29.89).

The numbers of food items in stomachs differed significantly between males and females (SQ = 122.18; $P < 0.001$; GL = 1), males and juveniles (SQ = 21.50; $P < 0.001$; GL = 1), and females and juveniles (SQ = 122.49; $P < 0.001$; GL = 1). The frequency of food items in stomachs also differed significantly between females and males (SQ = 9,575.8; $P < 0.001$; GL = 1), females and juveniles (SQ = 7,715.1; $P < 0.001$; GL = 1), and males and juveniles (SQ = 7,456.4; $P < 0.001$; GL = 1). For volumes, males and females (SQ = 61,675.5; $P < 0.001$; GL = 1), and females and juveniles (SQ = 136,845.2; $P < 0.001$; GL = 1)

differed significantly, while males and juveniles did not differ (SQ = 42,667.9; $P = 0.106$; GL = 1). The RII values differed significantly between females and males (SQ = 18,833.7; $P < 0.001$; GL = 1), females and juveniles (SQ = 16,273.6, $P < 0.001$; GL = 1), but did not significantly differ between males and juveniles (SQ = 5,025.4; $P = 0.103$; GL = 1).

Further examination of gravid and non-gravid females disclosed significant diet differences (Fig. 3, Table 4). Gravid females consumed 63 Coleoptera larvae, 25 Coleopteran adults, and 25 Isopteran alongside their ant-based diet. Non-gravid females featured Vespidae (n = 11) as their second most consumed food. For gravid females, Formicidae (68.4%) and Coleoptera (57.9%) dominated as the most frequent items in stomachs, whereas 60% of stomachs of non-gravid females contained Formicidae, 40% contained Coleoptera, and 40% contained Vespidae. Formicidae also dominated as the highest volume in stomachs of gravid females (38.4%) and Coleoptera (27.3%), whereas stomachs of non-gravid females had Formicidae (31.9%), Vespidae (24.9%) and Blattodea (25.5%) with higher volumes. The highest values of RII for gravid females were Formicidae (RII = 2,605.08) and Coleoptera (RII = 1,823.76), whilst non-gravid females revealed Formicidae (RII = 1,512.28), Blattodea (RII = 1,146.64) and Vespidae (RII = 1,130.65) as the most

Table 3. Number (n), frequency (F), volume (V), and Relative Importance Index (RII) of juvenile Collared Lizards (*Tropidurus torquatus*) for each consumed food item in the Grussaí Restinga, Rio de Janeiro, Brazil. For food items, L = larvae and N = nymph.

| Food item	n	n%	F (%)	V (mm³)	V (mm³) %	RII	RII (Adults)
Acari	2	0.365	15.380	0.030	< 0.001	5.800	1.200
Araneae	2	0.365	15.380	167.10	2.695	61.50	1,284.7
Blattodea	1	0.182	7.690	5.280	0.085	4.660	274.57
Cicadellidae	5	0.914	38.460	68.93	1.112	37.46	340.67
Coleoptera	11	2.010	53.850	401.30	6.473	155.38	4,372.1
Coleoptera (L)	21	3.839	23.080	469.80	7.578	171.29	134.78
Diptera (L)	1	0.182	7.690	1.180	0.019	3.290	78.82
Formicidae	459	83.91	100	4,411.8	71.16	1,656.9	3,161.4
Heteroptera	1	0.182	7.690	4.300	0.069	4.330	1,086.5
Isoptera	21	3.839	23.080	72.88	1.175	38.99	141.45
Leaves	4	0.731	30.770	60.67	0.978	31.81	138.85
Lepidoptera (L)	1	0.182	7.690	1.610	0.026	3.430	212.29
Nematocera	1	0.182	7.690	7.890	0.127	5.530	5.760
Neuroptera	3	0.548	23.080	90.32	1.457	37.36	39.43
Pseudoscorpiones	1	0.182	7.690	0.680	0.011	3.120	1.190
Vespidae	13	2.376	46.150	435.95	7.032	165.03	703.67
TOTAL	547			6,199.7			
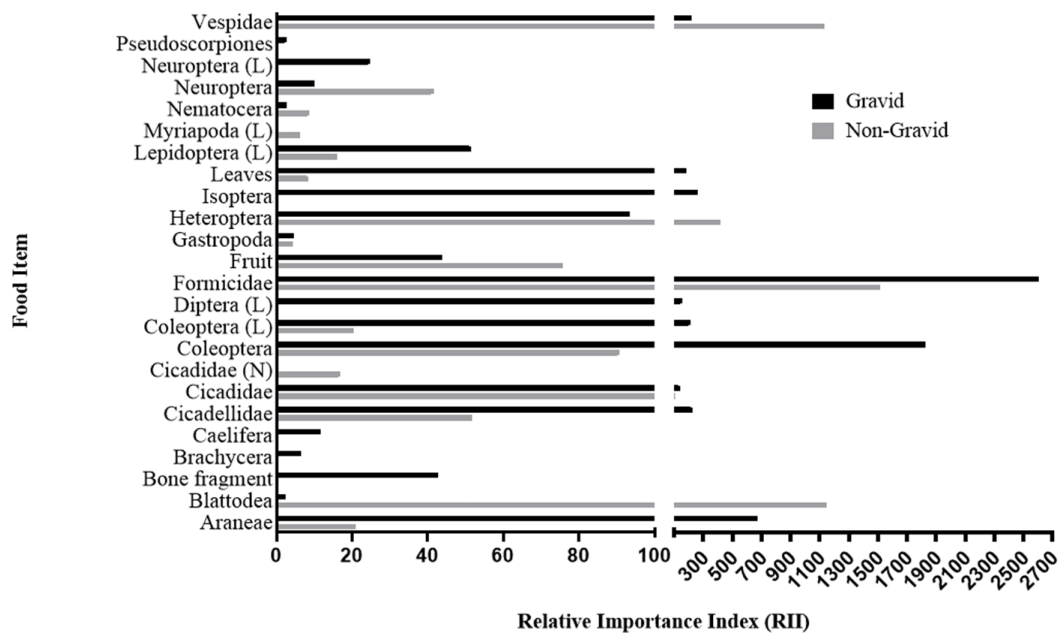
FIGURE 3. Diet of gravid and non-gravid female Collared Lizards (*Tropidurus torquatus*) in the Grussaí Restinga (Rio de Janeiro, Brazil). Relative Importance Values (RII) for each food item consumed by each of the two groups are shown.

important items. Gravid and non-gravid females diet differed significantly in terms of number (SQ = 23.25; $P < 0.001$; GL = 1), frequency (SQ = 5,926.2; $P < 0.001$; GL = 1), volumes (SQ = 18,745.2; $P = 0.013$; GL = 1), and RII (SQ = 2,361.0; $P = 0.010$; GL = 1).

DISCUSSION

Diet composition.—In the Grussaí Restinga, *Tropidurus torquatus* had a predominantly omnivorous diet, with arthropods being the primary component, but with substantial consumption of plant material. We identified 28 food items, revealing a generalist diet typical of ambush foragers. Such foraging behavior corresponds to species that tend to prey on passive prey and are less proactive in hunting (Huey and Pianka 1981). Numerically and in terms of frequency, Formicidae was the most common item for *T. torquatus*, ranking second in importance. The prevalence of Formicidae, driven by factors like their mobility and high local density, enhances encounter opportunities for ambush predators. Furthermore, we noted a significant occurrence of fossorial prey, particularly Coleoptera larvae, implying selective predation rather than random encounters. This implies occasional heightened foraging activity, possibly driven by the tradeoff between foraging effort and

energy gain (Drakeley et al. 2015). This selectivity may also be driven by the higher reproduction rate of arthropods during the rainy season, however, and, consequently, higher availability of larvae. Arthropod populations typically experience a decrease during dry seasons and an increase during rainy seasons, with significant correlations between arthropod numbers and environmental factors like precipitation and soil moisture levels (Vikram-Reddy and Venkataiah 1990). Also, the dietary preferences of *T. torquatus* change across its coastal distribution, with populations in the southern regions showing a preference for larger prey items such as larvae (Siqueira et al. 2013).

During foraging, a critical phase for most animals to obtain resources and avoid predation, important decisions arise. Dietary research provides insights into decision-making processes, exploring the foraging choices made based on environmental and social conditions (Hamilton 2010). Complexity arises because foraging decisions rely on both intrinsic factors (e.g., physiology, body condition, sex, ontogeny, animal personality) and extrinsic factors, such as food type, availability, structural habitat, and other environmental attributes (Stephens 2008). Moreover, evaluating the trade-offs of foraging decisions in their local surroundings, individuals must also anticipate the choices of competing conspecifics

and potential predators. Our findings indicate *T. torquatus* occupies an intermediate point on the spectrum of foraging strategies, with tendencies towards ambush foraging, albeit not exclusively. While characterized by an ambush-type lizard, this population deviates from pure ambush foraging due to the inclusion of passive prey in its diet (Huey and Pianka 1981). This strategic balance allows the species to adjust its foraging approach in response to varying prey density and resource availability within its habitats (Siqueira et al. 2013).

Herbivory is relatively rare in lizards, but most are classified within the Iguania clade, which includes Tropiduridae (Pyron et al. 2013). Although animal matter is readily digested and absorbed, the majority of energy within plant material resides in fibrous elements like cellulose, which vertebrates lack the

necessary enzymes to digest. Nonetheless, some species were observed consuming or avoiding plants containing significant plant secondary metabolites (PSMs). For some coastal populations of *T. torquatus*, the proportion of the volume of plant material in the diet varied from 2.1% to 58.0% of the total volume consumed, without variations in the volumetric proportion correlated with the body size of the lizard or the latitude of the population (Siqueira et al. 2010). We found plant parts in 37.7% of the examined stomachs of *T. torquatus* in Grussai. The high incidence of these items suggests their ingestion was deliberate and likely holds an important role in the diet of lizards in this population. It has been shown that some lizards (e.g., Lutz's Tree Iguana, *Liolaemus lutzae*; Rocha 2000) have a selective consumption of plants having the highest contents of water, total

TABLE 4. Number (n), frequency (F), volume (V), and Relative Importance Index (RII) of gravid and non-gravid female Collared Lizards (*Tropidurus torquatus*) for each consumed food item in the Grussaí Restinga, Rio de Janeiro, Brazil. For food items, L = larvae and N = nymph.

Food Items	Gravid n	F	V	V%	RII	Non-Gravid n	F	V	V%	RII
Acari	2	6.250	29.020	0.150	12.090	0	0	0	0.000	0
Araneae	4	18.75	2,003.8	10.14	674.53	1	14.28	52.14	0.390	28.48
Blattodea	1	6.250	1.370	0.010	2.540	1	14.28	3,428.9	25.52	1148.1
Bone fragment	1	6.250	122.26	0.620	42.84	0	0	0	0	0
Brachycera	1	6.250	13.24	0.070	6.500	0	0	0	0	0
Caelifera	1	6.250	29.02	0.150	11.76	0	0	0	0	0
Cicadellidae	4	18.75	663.92	3.360	227.90	2	28.57	133.21	0.990	54.59
Cicadidae	2	12.50	405.29	2.050	139.27	1	14.28	297.17	2.210	104.15
Cicadidae (N)	0	0	0	0	0	1	14.28	39.68	0.300	18.32
Coleoptera	25	68.75	5,388.4	27.27	1,823.8	5	57.14	226.69	1.690	96.28
Coleoptera (L)	63	18.75	564.80	2.860	214.53	2	28.57	39.33	0.290	23.30
Diptera (L)	1	6.250	459.96	2.330	155.41	0	0	0	0.000	0
Formicidae	162	81.25	7,584.8	38.38	2,605.1	198	85.71	4,278.9	1.610	1,520.9
Fruit	2	12.50	119.02	0.600	43.85	1	14.28	215.75	31.85	77.01
Gastropoda	1	6.250	7.840	0.040	4.700	1	14.28	1.850	0.010	5.71
Heteroptera	3	12.50	266.41	1.350	93.31	3	28.57	1,218.7	9.070	416.74
Isoptera	25	6.250	752.79	3.810	261.02	0	0	0	0.000	0
Leaves	8	18.75	524.98	2.660	182.92	2	14.28	13.19	0.100	9.83
Lepidoptera (L)	4	12.50	139.57	0.710	51.37	2	28.57	25.68	0.190	18.75
Myriapoda (L)	0	0	0	0.000	0	1	14.28	7.800	0.060	7.700
Nematocera	3	6.250	0.160	0.000	2.810	1	14.28	14.75	0.110	10.01
Neuroptera	2	12.50	17.88	0.090	10.14	3	28.57	101.52	0.760	44.36
Neuroptera (L)	3	12.50	61.01	0.310	24.85	0	0	0	0.000	0
Pseudoscorpiones	1	6.250	1.780	0.010	2.680	0	0	0	0.000	0
Vespidae	5	18.75	633.32	3.200	218.04	11	57.14	3,341.0	24.87	1,136.4
TOTAL	322		1,9761.6			236		13,436.1		

nitrogen, total sugar, and the lowest number of gross fibers (Rocha 2000). These plants might serve as an important water source, contributing to the water balance of the lizards (Fialho et al. 2000). This factor gains importance in environments with limited availability of free water, such as in Restingas, playing a role in population maintenance. Furthermore, a high number of fruits that we found in stomachs of *T. torquatus* retained their peduncles, indicating that the lizards did not consume fallen fruits but rather climbed plants to obtain them. In our analysis, fruits stood out as the most important vegetable item eaten; however, it is necessary to account for the slower digestion of plant items compared to animal items, which can lead to an apparent higher frequency, possibly resulting in its overestimation (Fialho et al. 2000). *Tropidurus torquatus* may play an important role in seed dispersal within the Restinga ecosystem. Another Tropidurid species, the Striped Lava Lizard (*T. semitaeniatus*), plays a crucial role as a double mutualist of a cactus plant in the Brazilian Caatinga, facilitating both the pollination and seed dispersal of this cactus (Gomes et al. 2014). This aspect in relation to *T. torquatus* still needs to be addressed in future research.

We observed a high occurrence of empty stomachs in our sample of *T. torquatus*. These instances of empty stomachs were observed throughout the entire day, with no distinct pattern in capture time. This implies that a substantial portion of the local population (approximately 25%) could be experiencing a negative energy balance (Huey et al. 2001). Of the 69 captured individuals, 16 stomachs contained no food (23%), a result that deviates from previously reported data for the same species in the literature (e.g., Fialho et al. 2000, one lizard; Siqueira 2007, 4.2%; Ribeiro et al. 2013, no lizards). In the Neotropical zone, around 11.8% of species exhibited empty stomachs on average, ranging from 0% to 44% (Huey et al. 2001). Examining ambush foraging species, the mean was comparable (11.7%), yet the range was wider, from 0% to 65.6% (Huey et al. 2001). Notably, specific top lizard predators showed a higher frequency of empty stomachs compared to lower trophic-level organisms (Huey et al. 2001). To gain deeper insight, a thorough assessment of the role of *T. torquatus* within the local trophic network would be useful.

Diet comparison between sexes.—Considering the number of food items, females had a slightly more diverse diet than males. Comparing the two diets, the most frequently consumed items were practically identical, although within the same category, males generally consumed a larger prey volume compared to females, albeit with a smaller number of items. In sexual dimorphic species based on size, such as *T. torquatus*, individuals tend to adopt a more generalist dietary approach to fulfill increased energy demands associated with reproductive activities, including male-male competition and territorial behavior (Schoener 1971). This phenomenon was not observed, however, when directly assessed in a prior study with an active forager lizard (Eifler et al. 2008).

Regarding plant material, females predominantly consumed leaves, while males favored fruits. This might result from higher energetic demand of males, as relying solely on animal prey may not fulfill their energy requirements. The observed diet disparities between males and females probably stem from distinct foraging preferences by each sex (Perez-Mellado and la Riva 1993). Hence, we suggest an intersexual variation in foraging intensity between males and females. Smaller female body sizes and mouth dimensions potentially led to more frequent consumption of smaller, highly active prey, whereas males seem to choose relatively larger prey, yielding higher energy intake. We speculate that *T. torquatus* diet variations between sexes stem from pronounced sexual size dimorphism, population structure, and dynamics, including the consequences of intrasexual competition on males due to reproductive pressure.

Diet comparison between juveniles and adults.— We found a lower number and volume of prey consumed by juveniles when compared to the diet of adults, with juveniles having a less diversified diet than adults. This variation likely results from a morphological limitation of juveniles, which, due to their smaller body and mouth size, are limited to capturing smaller prey and few items at one time, thus, the variety of possible prey decreases (Whitfield and Donnelly 2006). Juveniles can also be subjected to environmental pressures, such as predation by other species and/or even cannibalism, which means juveniles may need to hide more in the environment, decreasing the diversity of prey passing by them (Dutra 1996). The high incidence of Coleoptera larvae prey in the diet of juveniles suggests that ingestion was not accidental, and that this prey is part of their usual diet. Although larvae had a high importance value, all juveniles ingested ants, which were the food items most consumed by

them. Juveniles ingest smaller prey likely because eating smaller items requires substantially less energy expended than capturing, handling, and ingesting large prey, the energy of which may be higher than the energy gained from capturing and digesting larger items (Schoener 1971).

In terms of consumption of plant items, the results suggest that juveniles consume less plant material than adults, and do not consume fruits, only leaves. Animal food contains comparatively higher proportions of protein per unit of mass compared to plant food and, a higher amount of protein is of great importance allowing for fast growth by juveniles (Greene 1982; Rocha 1989, 2000). Also, because fruits are large, juveniles may not have mouths large enough to consume fruit. Juveniles also may not be able to ingest plant material or may not be able to pluck them from branches due to a lack of mechanical strength (Ribeiro et al. 2013).

Adult lizards catching and eating juveniles of the same or another species is relatively common (Sousa et al. 2021; Crespo-Pérez 2023). We found a bone fragment found in the stomach of a gravid female, but we could not identify it, so we cannot infer that it was the result of cannibalism or predation. This record does, however, indicate that females as well as males feed on vertebrates in the Grussaí Restinga.

Diet comparison between gravid and non-gravid females.—Our results indicated that gravid and non-gravid females did not differ in the number of food items consumed but in terms of diet composition. Our study suggests that gravid females ingest prey that does not require a high energy demand to be captured and handled, and may be easier to access (e.g., Formicidae and Coleoptera), because these preys are mobile and could inevitably enter their areas. Gravid females, being heavier due to the mass of the eggs, are limited in their movements, which reduces their escape time, and may require them to be a more focused forager (Bauwens and Thoen 1981). During gestation, female lizards often require additional nutrients to support the development of eggs (Wiederhecker et al. 2002) and Coleoptera might provide more essential nutrients than Vespidae and Blattodea. The preference for this food item could also be influenced by the abundance of those prey in their habitat, if Coleoptera are abundant and easily captured, gravid females might consume them more frequently simply due to their availability. Although non-gravid females also consume ants, they have a lower relative importance index when compared to gravid females, indicating that this class tend to have a more specific diet. As females have a more generalist diet than males, it can be suggested that foraging would be restricted to some degree during gestation. Vespidae and Blattodea may be preferred by non-gravid females to avoid intraspecific competition with gravid females, as these preys may present a higher risk of predation associated with capture. With the reduction in the rate of movement, gravid females become more vulnerable to predators than non-gravid females (Shine 2003). Therefore, a less generalist diet may reflect less exploration of the environment, balancing the relationship between exposure to predators and food acquisition. The prey consumed by gravid females come from the soil and vegetation, have diurnal activity and the habit of life can be active or passive. Similarly, the prey of non-gravid females comes from both the soil and the vegetation, however, they have diurnal or nocturnal activity and an active life habit (see Supplemental Information file).

Conclusions.—We conclude that *Tropidurus torquatus* in the Restinga of Grussaí has an omnivorous diet but is predominantly composed by arthropods. Diet varied among sexes, suggesting intersexual differences in the rate of foraging intensity. Adults consumed proportionally a greater amount of plant material compared to juveniles, which is suggestive of the occurrence of an ontogenetic variation in the diet of this species. Juveniles consumed a comparatively smaller amount of plant material and prey of smaller size compared to adults probably due to their higher need for a food source richer in protein by unit of mass to favor growth. Gravid and non-gravid females tended to consume similar numbers of prey but differed consistently in diet composition, which may be a result of a lower rate of movement that gravid females tend to maintain in the habitat. *Tropidurus torquatus* at the Grussaí sandy coastal plain of Rio de Janeiro presented a type of intermediate foraging strategy with a tendency to ambush.

Seasonal variations may exert influence on the observed patterns and dynamics elucidated in our study. While our research offers valuable insights into current patterns, it is important to acknowledge the potential impact of seasonality and short duration of our study on our findings. Addressing this concern, future studies should explore the potential variations that may occur over the entire year or during specific periods, such as the dry season. Investigating whether observed patterns remain consistent

across different seasons or exhibit variability under varying environmental conditions is crucial for interpreting our findings accurately and provide a deeper understanding of the dynamics that drive the ecological processes of this species.

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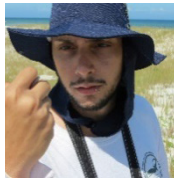
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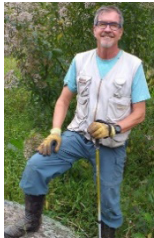
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