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RESEARCH ARTICLE

Trophic ecology of *Thoropa miliaris* (Anura: Cycloramphidae) in two mountain ranges of south-eastern Brazil

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Abstract

Among populations of the same species, the diet composition varies depending on the environment, given the variation in diversity and abundance of available prey. Since *Thoropa miliaris* is a habitat specialist in reproduction, we tested the hypothesis that this specialization is also verified in its diet. We carried out the work in 10 localities in Serra do Mar and Serra da Mantiqueira, south-eastern Brazil, where we collected frogs and evaluated prey availability. The environment did not provide significant variation in the diet of *T. miliaris*, and Formicidae was the prey category selectively consumed in greater volume, frequency and abundance in both mountain ranges. Therefore, we can state that *T. miliaris* has a selective diet on ants.

KEYWORDS
Amphibia, Atlantic Forest, diet, Eltonian shortfall, prey availability

INTRODUCTION

Many species lack information regarding their ecological interactions (Eltonian shortfall) and sensitivity to abiotic conditions (Hutchinsonian shortfall) (Hortal et al., 2015). The diet of a species is determined by the conditions and limitations of the environment in which it lives (Parker & Goldstein, 2004), and information on trophic ecology contributes to reducing knowledge gaps on biodiversity (Hortal et al., 2015). The diet of a species may differ among its populations due to variations in environmental features and prey availability (Bonansea & Vaira, 2007; Lima & Magnusson, 1998). The composition of communities can be influenced by primary productivity, climate and elevation, among other factors (Davey et al., 2013; Perillo et al., 2021; Siemann, 1998). For example, primary productivity affects the richness of invertebrates, particularly arthropods, such that more productive environments provide a greater variety of prey for secondary consumers (Huckembeck et al., 2020). In addition, arthropod consumer populations can exhibit significant variations in diet in environments with different elevation gradients, as the diversity of arthropods decreases at higher elevations (Galetti et al., 2000).

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Observations along mountain ranges in south-eastern Brazil have revealed that differences in climate, elevation and vegetational cover can impact habitat complexity and species composition (Cruz & Feio, 2007). The Serra do Mar mountain range is home to a greater number of species of plants (Marchiori et al., 2016; Pompeu et al., 2014), arthropods (Pinto-da-Rocha et al., 2005; Siegloch et al., 2012) and anurans (Malagoli et al., 2018; Silva et al., 2018) compared to the Serra da Mantiqueira mountain range. Anurans, known for their generalist and opportunistic feeding habits, prey on almost all kinds of invertebrates in their habitat (López et al., 2009; Rodrigues et al., 2004; Solé et al., 2009). Their diet composition is influenced by habitat, seasonality and prey availability (Ceron et al., 2022; Rosa et al., 2002). Regardless of their generalist feeding habit, anurans are capable of recognizing and selecting their prey, displaying preference for some resources over others and consuming them in different proportions than found in their habitat (Attademo et al., 2007; López et al., 2007).

Despite the high degree of endemism observed among anurans in the Serra do Mar and Serra da Mantiqueira (Cruz & Feio, 2007), several species are found in both mountain ranges, including the rock river frog, *Thoropa miliaris* (Spix, 1824) (Cruz & Feio, 2007; Malagoli et al., 2018; Silva et al., 2018). From the larval stage to adult life, individuals of this species inhabit rocky habitats in the Atlantic Rainforest (Feio et al., 2006; Giaretta & Facure, 2004), from sea level to almost 1500 m a.s.l. (above sea level) (Feio et al., 2006). Although previous studies suggest that *T. miliaris* primarily feeds mostly on arachnids and insects, particularly ants (Pertel et al., 2010; Sazima, 1971; Siqueira et al., 2006), the role of prey availability in shaping the species' diet has not yet been explored, making it difficult to draw accurate conclusions about whether the species actively selects its prey or consumes them at randomly, or whether certain preys are avoided altogether (Ceron et al., 2019; Moroti et al., 2021). Moreover, it remains unclear whether populations of *T. miliaris* from different mountain ranges have distinct dietary compositions due to regional environmental differences. Therefore, in this study, we aim to address the following questions:

1. Does the Serra do Mar range have a greater prey availability and prey diversity consumed by *T. miliaris* compared to the Serra da Mantiqueira range due to environmental differences between the two mountain ranges? We predict that the Serra do Mar will have a larger taxonomic diversity of invertebrates, resulting in a higher number of prey categories available for *T. miliaris* in that range.
2. Do individuals of *T. miliaris* actively select their prey or consume them randomly based on availability? We hypothesize that *T. miliaris* is a generalist and opportunistic feeder, as described in most anuran species (Pertel et al., 2010; Sazima, 1971; Siqueira et al., 2006; Solé & Rödder, 2010).

MATERIALS AND METHODS

Study area

The present study was carried out in the Atlantic Forest, a biodiversity hotspot (Zachos & Habel, 2011), encompassing various locations in the Serra do Mar and Serra da Mantiqueira mountain ranges, south-eastern Brazil (Table 1, Figure 1). The Serra do Mar stretches ranges for approximately 1500 km, from the state of Rio de Janeiro to the north of the state of Santa Catarina, and reaching elevations over 2000 m a.s.l. (Almeida & Carneiro, 1998; Gontijo-Pascutti et al., 2012). In contrast, the Serra da Mantiqueira is

TABLE 1 Collection sites for *Thoropa miliaris* and prey availability in Serra da Mantiqueira and Serra do Mar, Atlantic Forest of south-eastern Brazil.

Mount. Range	State	Municipality	Locality	Elevation	Latitude	Longitude	*T. miliaris* collected
Mantiqueira	MG	Antônio Prado de Minas	Pedra Elefantina	754	−20.9758	−42.1658	18
Mantiqueira	MG	Cataguases	Sinimbu	302	−21.3390	−42.7616	25
Mantiqueira	MG	Juiz de Fora	Bairro Retiro	633	−21.7766	−43.2911	09
Mantiqueira	MG	Muriaé	Macuco	300	−21.1582	−42.5234	10
Mantiqueira	MG	Muriaé	Usina da Fumaça	474	−21.0142	−42.4459	23
Serra do Mar	RJ	Cachoeiras de Macacu	REGUA	396	−22.3950	−42.7377	14
Serra do Mar	RJ	Campos dos Goytacazes	Morangaba	54	−21.8674	−41.7215	15
Serra do Mar	RJ	Campos dos Goytacazes	Morro do Itaoca	399	−21.7935	−41.4486	05
Serra do Mar	RJ	Campos dos Goytacazes	Rio Preto	56	−21.7061	−41.6299	24
Serra do Mar	RJ	Santa Maria Madalena	Sossego do Imbé	100	−21.9075	−41.8116	20

Abbreviations: Mount., mountain; REGUA, Reserva Ecológica de Guapiaçu.

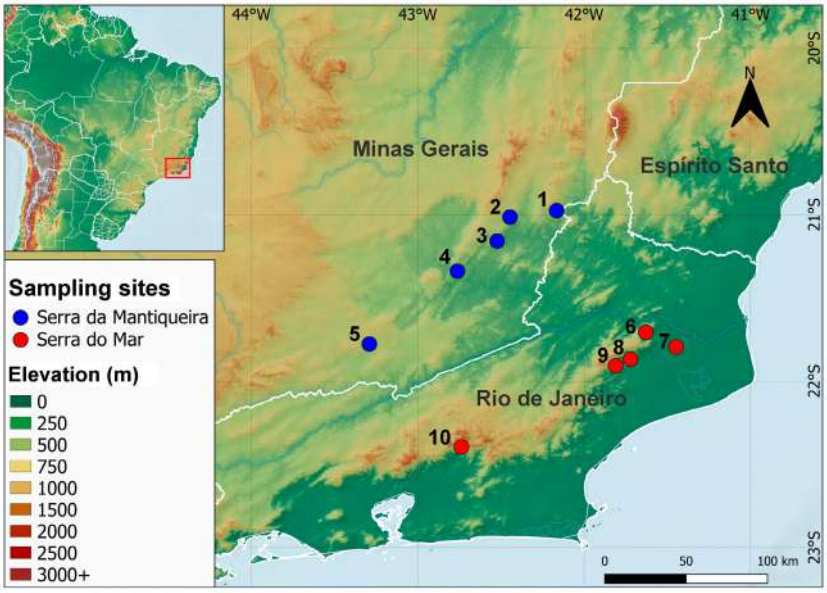

FIGURE 1 A map showing the locations where *Thoropa miliaris* and prey availability were sampled in Serra da Mantiqueira and Serra do Mar, Atlantic Forest of south-eastern Brazil.

almost 900 km long, with elevations above 2800 m a.s.l., and spans across the states of Minas Gerais, São Paulo, Rio de Janeiro and Espírito Santo (Gontijo-Pascutti et al., 2012).

Field sampling

We conducted the study in 10 different locations in Minas Gerais and Rio de Janeiro states. The sampling sites varied from 54 to 754 m a.s.l., in both mountain ranges (Table 1, Figure 1). Our fieldwork took place between November 2021 and January 2022, during which we actively searched for and captured individuals of *T. miliaris* by hand (SISBIO #72874-4 and

SISBIO #77181-2) in nocturnal surveys. We then placed the captured individuals in plastic bags, along with moist substrate from the collection site, and killed them using a cutaneous anaesthetic of 5% lidocaine (Heyer et al., 1994). We collected tissue samples (liver or muscle, preserved in 100% ethanol) before fixing the specimens in 10% formalin and storing them in 70% ethanol (Heyer et al., 1994) at the Zoological Collection from Universidade Federal de Mato Grosso do Sul (ZUFMS-AMP) (Appendix S1). All procedures were carried out in compliance with the ethical guidelines provided by the Ethics Commission on Animal Use from the Universidade Federal de Juiz de Fora (CEUA – UFJF; protocol n°. 007/2021).

Prey availability sampling

We sampled available prey at each sampling point using pitfall traps with ten 500 mL plastic buckets buried at ground level (Díaz et al., 2020). We installed the traps evenly spaced 2 m apart and placed them next to rocks in the sampling habitat. Inside each plastic bucket, we added a solution of 70% ethanol and drops of dishwashing liquid to break the water surface tension and preserve any captured potential prey (Steyskal et al., 1986). The pitfall traps were left open for approximately 2 h. Additionally, we collected 0.005 m^2 of leaf litter from a 2 square metre quadrat as a complementary method to identify any potential prey (Rafael et al., 2012).

Diet and prey availability analyses

Using surgery scissors, we did an inverse 'C' shaped cut on the ventral region of preserved *T. miliaris* specimens to remove the stomach. We then preserved the stomachs in 70% ethanol and examined their contents under a stereo microscope. We identified prey items found in the stomachs and those collected from the environment to the lowest possible taxonomic rank, usually the order, using specialized taxonomy ID books (Fransozo & Negreiros-Fransozo, 2016; Giupponi et al., 2017; Rafael et al., 2012). We separated ants from the rest of the Hymenoptera due to their high abundance found in the stomachs and identified them up to the genus rank (Baccaro et al., 2015). To estimate the volume (V) of each prey item, we measured their width (W) and length (L) using the ellipsoid formula: $V = 4\pi/3 * L/2 * (W/2)^2 * N$ (Griffiths & Mylotte, 1987; Santana et al., 2019).

To determine the importance of each prey category consumed by *T. miliaris*, we calculated an index of relative importance (IRI) using abundance (N%), frequency (F%) and volume (V%) as follows: IRI = F% * (N% + V%) (Pinkas, 1971). We calculated the IRI separately for the genera of Formicidae. To evaluate the feeding strategy of *T. miliaris* and the distribution of prey categories, we created a graph as proposed by Costello (1990), modified by Amundsen et al. (1996). The Y-axis represented the specific abundance (P_i), calculated with the equation: $P_i = (\Sigma\, S_i/\Sigma\, S_{ti}) * 100$, where S_i is the number of individuals from a specific category of consumed prey and S_{ti} is the total amount of prey found only in the stomachs which this prey was found. The X-axis represented the frequency of occurrence for consumed prey categories (F_i), calculated using the equation: $F_i = N_i/N$, where N_i represents the number of stomachs in which the prey category was present, and N is the total number of analysed stomachs (Amundsen et al., 1996; Costello, 1990; Oliveira et al., 2019).

To assess if *T. miliaris* exhibits a preference for a particular type of prey, we used a selective index (LI) calculated as follows: $LI = r_i - p_i$, where r_i and p_i

represent the occurrence frequencies (*F*%) of the prey category in the stomachs and the environment respectively (Díaz et al., 2020; Strauss, 1979). The LI index is crucial for determining a species' diet selectivity, with positive values indicating a preference, values close to zero suggesting random consumption and negative values indicating prey avoidance or non-encounters (Strauss, 1979). The LI values are presented as percentages (%).

Statistical analyses

To investigate whether the diet of *T. miliaris* varied between the two sampled mountain ranges (Serra do Mar and Serra da Mantiqueira), we conducted a permutational analysis of variance (PERMANOVA) using the abundance (*N*) of each consumed prey category (Santana et al., 2019). This method enables testing of hypotheses and comparing species abundance across different environments using non-normally distributed data (Silva et al., 2022). To assess whether the geographic distance influenced prey availability in the environments, we performed a Mantel test using the frequency (*F*) data for each prey category found in the sampling points for both mountain ranges. This involved using a distance matrix, which contained the geographic coordinates in decimal degrees as the predictor, and a similarity matrix of diets as the response variable. We conducted statistical analyses using the "vegan" package (Oksanen et al., 2015) in R v. 4.2.1 software (R Core Team, 2022).

RESULTS

Diet analyses

We collected 163 specimens of *T. miliaris*, 85 from Serra da Mantiqueira (35 males, 42 females and eight juveniles) and 78 from Serra do Mar (20 males, 32 females and 26 juveniles). During fieldwork, we observed many individuals dwelling in gullies around rocks, presumably foraging on the leaf litter. Of the 163 stomachs examined, only 4 were empty (2.45%). We found 1158 prey items, comprising 25 prey categories, besides plant matter (Table 2). Individuals from Serra do Mar consumed a greater number of prey categories (24) than individuals from Serra da Mantiqueira (16). Annelida, Collembola, Dermaptera, Hemiptera, Coleoptera (larval stage), Nematoda, Odonata, eggs of Arthropoda and Scolopendromorpha were consumed only by individuals from Serra do Mar, while Pseudoscorpiones were exclusively consumed by individuals from Serra da Mantiqueira (Table 2).

The diet composition of *T. miliaris* did not differ between populations from both mountain ranges ($F = 0.79$; $p = 0.74$). The most notable prey category in both environments was Formicidae (IRI = 72.7% and 83.3% for Serra do Mar and Serra da Mantiqueira, respectively), which also accounted for the highest volume, abundance and frequency in the diet for both mountain ranges. We identified 20 genera of Formicidae in the examined stomachs, with *Odontomachus* Latreille, 1804 (Ponerinae) being the most important genus for Serra da Mantiqueira (IRI% = 19.4) and *Solenopsis* Westwood, 1840 (Myrmicinae) for Serra do Mar (IRI% = 42.5) (Table 2). Coleoptera was the second most consumed prey category (IRI = 9.6% and 8.6% for Serra do Mar and Serra da Mantiqueira, respectively) followed by Isoptera, which showed greater importance for Serra do Mar (IRI = 9.2%) compared to Serra da Mantiqueira (IRI = 1.3%).

Regarding feeding strategy and prey categories, we observed that Formicidae is most dominant family in the diet of *T. miliaris*, with the top

TABLE 2 Comparison of the diet of *Thoropa miliaris* between Serra do Mar and Serra da Mantiqueira, Atlantic Forest of south-eastern Brazil.

Preys consumed by *Thoropa miliaris*	Serra do Mar				Serra da Mantiqueira			
	V%	*N*%	*F*%	IRI%	*V*%	*N*%	*F*%	IRI%
Arachnida								
Araneae	1.390	2.449	7.921	0.933	1.405	2.128	5.488	0.383
Pseudoscorpiones	–	–	–	–	0.024	0.473	1.220	0.012
Hexapoda								
Blattodea	0.215	0.272	0.990	0.015	0.370	0.709	1.829	0.039
Coleoptera	16.617	6.122	13.861	9.675	18.404	9.220	15.854	8.640
Coleoptera (larvae)	0.473	0.136	0.495	0.009	–	–	–	–
Collembola	0.012	0.136	0.495	0.002	–	–	–	–
Dermaptera	0.301	0.136	0.495	0.007	–	–	–	–
Diptera	0.181	0.272	0.990	0.014	0.053	0.236	0.610	0.003
Diptera (larvae)	3.068	2.721	2.475	0.440	0.345	0.473	1.220	0.020
Formicidae	20.219	48.163	34.653	**72.739**	22.906	70.686	45.122	**83.318**
Dolichoderinae								
Azteca Forel, 1878	–	–	–	–	2.950	2.326	3.448	1.120
Dolichoderus Lund, 1831	0.390	0.216	0.877	0.026	0.346	1.744	0.862	0.111
Tapinoma Förster, 1850	7.231	0.864	1.754	0.694	1.500	1.453	3.448	0.627
Dorylinae								
Eciton Latreille, 1804	–	–	–	–	0.432	0.581	0.862	0.054
Labidus Jurine, 1807	0.256	0.864	0.877	0.048	–	–	–	–
Neivamyrmex Borgmeier, 1955	1.636	2.592	0.877	0.181	0.020	0.291	0.862	0.016
Ectatomminae								
Ectatomma F. Smith, 1858	3.019	0.432	1.754	0.296	–	–	–	–
Formicinae								
Camponotus Mayr, 1861	7.096	2.808	4.386	2.121	3.478	4.651	5.172	2.588
Myrmicinae								
Acromyrmex Mayr, 1865	4.635	4.536	5.263	2.357	6.624	12.791	9.483	11.331
Atta Fabricius, 1804	5.949	5.832	5.263	3.028	10.509	13.372	7.759	11.403
Blepharidatta Wheeler, 1915	0.035	0.216	0.877	0.011	–	–	–	–
Carebara Westwood, 1840	0.793	8.207	7.018	3.085	1.481	4.070	7.759	2.651
Cephalotes Latreille, 1802	3.462	0.864	2.632	0.556	1.598	0.872	2.586	0.393
Crematogaster Lund, 1831	1.001	2.592	4.386	0.770	1.085	1.163	2.586	0.358
Cyatta Sosa-Calvo et al. 2013	0.474	1.080	1.754	0.133	0.531	0.872	1.724	0.149
Pheidole Westwood, 1839	2.646	4.536	6.140	2.154	1.021	3.779	4.310	1.273
Solenopsis Westwood, 1840	4.517	35.205	21.930	**42.542**	8.542	13.663	12.931	17.671
Trachymyrmex Forel, 1893	2.552	0.216	0.877	0.119	8.463	1.163	2.586	1.532
Ponerinae								
Anochetus Mayr, 1861	7.816	6.695	6.140	4.352	14.628	14.826	7.759	14.064

TABLE 2 (Continued)

Preys consumed by *Thoropa miliaris*	Serra do Mar				Serra da Mantiqueira			
	V%	*N*%	*F*%	IRI%	*V*%	*N*%	*F*%	IRI%
Hypoponera Santschi, 1938	27.910	10.151	12.281	22.827	16.139	6.686	9.483	13.321
Odontomachus Latreille, 1804	13.696	10.799	11.404	13.642	12.866	11.628	12.931	**19.493**
Pachycondyla F. Smith, 1858	4.885	1.296	3.509	1.059	7.691	3.779	2.586	1.826
Pseudomyrmecinae								
Pseudomyrmex Lund, 1831	–	–	–	–	0.095	0.291	0.862	0.020
Hemiptera	0.011	0.136	0.495	0.002	–	–	–	–
Hym. not Formicidae	1.235	0.408	1.485	0.075	0.748	0.709	1.220	0.035
Isopoda	1.558	1.361	3.960	0.355	0.129	0.709	1.829	0.030
Isoptera	14.655	26.122	7.426	9.295	7.585	6.619	4.878	1.367
Lepidoptera	0.170	0.408	0.990	0.018	0.876	0.236	0.610	0.013
Lepidoptera (larvae)	2.482	0.136	0.495	0.040	4.226	0.473	1.220	0.113
Mantodea	0.095	0.136	0.495	0.004	0.118	0.236	0.610	0.004
Odonata	0.038	0.136	0.495	0.003	–	–	–	–
Orthoptera	4.134	1.633	5.446	0.964	1.187	0.946	2.439	0.103
Others								
Annelida	0.447	0.136	0.495	0.009	–	–	–	–
Diplopoda	0.201	0.136	0.495	0.005	0.468	0.236	0.610	0.008
Gastropoda	0.058	0.136	0.495	0.003	0.918	0.473	1.220	0.033
Fragments	19.930	1.088	3.960	2.555	32.719	2.364	6.098	4.221
Nematoda	1.052	2.721	3.960	0.459	–	–	–	–
Arthropoda eggs	0.314	3.129	0.495	0.052	–	–	–	–
Scolopendromorpha	0.016	0.136	0.495	0.002	–	–	–	–
Plant matter	11.127	1.633	5.941	2.327	7.521	3.073	7.927	1.657

Note: Higher values are in bold.

Abbreviations: *F*%, frequency; Hym., Hymenoptera; IRI%, index of relative importance; *N*%, abundance; *V*%, volume.

position in the graphs of both Serra do Mar and Serra da Mantiqueira. Although Formicidae was the primary prey category for all individuals, we also noted occasional ingestion of other prey categories in smaller proportions (Figure 2). The graphs for both mountain ranges displayed several points at the bottom left corner, indicating rare consumption of those prey categories in the diet composition of *T. miliaris*. In Serra do Mar, only specimens from the Reserva Ecológica de Guapiaçu (REGUA) consumed termites (Isoptera), and their stomachs presented a higher abundance for this type of prey (P_i = 53.4%). This is represented by a point at the upper left corner of the Serra do Mar graph (Figure 2).

Prey availability analyses

In the sampling of prey availability, we collected 790 items from 22 prey categories (20 for Serra do Mar and 21 for Serra da Mantiqueira) (Table 3). While we found Anura and Pseudoscorpiones in Serra do Mar, *T. miliaris* did not consume these prey categories there. Similarly, although Anura, Collembola, Dermaptera, Hemiptera and Scolopendromorpha were

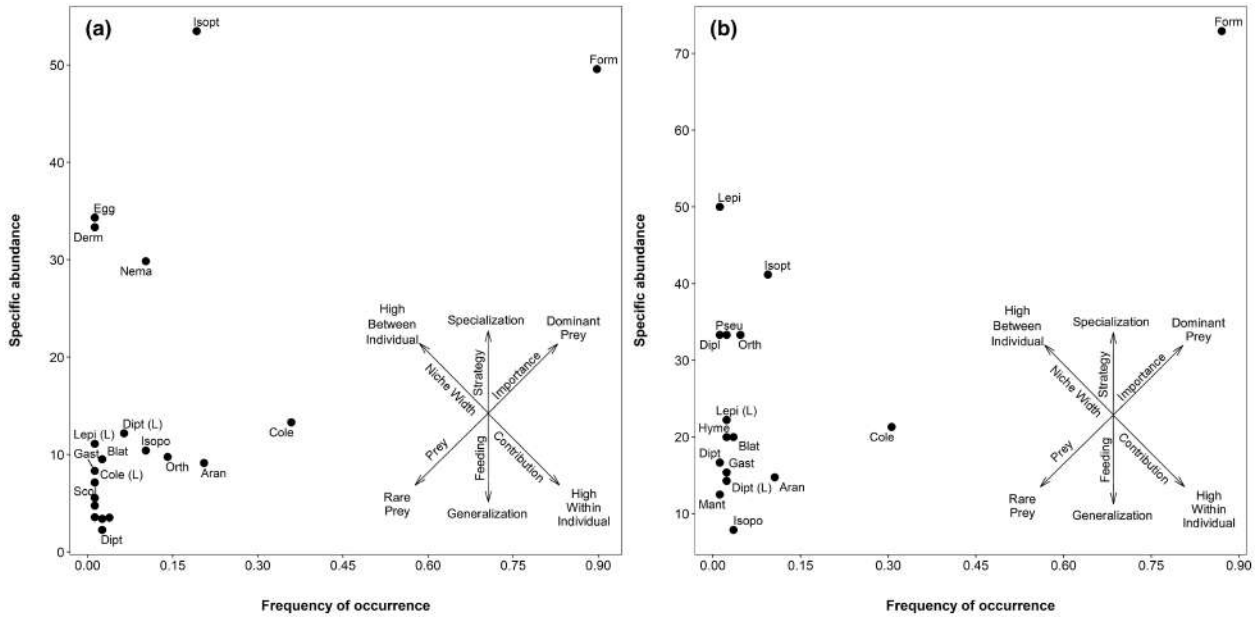

FIGURE 2 Feeding strategy of *Thoropa miliaris* and distribution of prey categories consumed in Serra do Mar (a) and Serra da Mantiqueira (b), Atlantic Forest of south-eastern Brazil. Aran, Araneae; Blat, Blattodea; Cole, Coleoptera; Cole (l), Coleoptera (Larvae); Coll, Collembola; Derm, Dermaptera; Dipl, Diplopoda, Dipt, Diptera; Dipt (L), Diptera (Larvae); Gast, Gastropoda; Form, Formicidae; Hyme, Hymenoptera; Isopo, Isopoda; Isopt, Isoptera; Lepi, Lepidoptera; Lepi (l), Lepidoptera (Larvae); Mant, Mantodea; Nema, Nematoda; Odon, Odonata; Orth, Orthoptera; Egg, Arthropod egg; Pseu, Pseudscorpiones; Scol, Scolopandromorpha. For details, see (Amundsen et al., 1996).

available in Serra da Mantiqueira, *T. miliaris* from this environment did not consume these prey categories. Some prey categories (Coleoptera larvae, Gastropoda, Mantodea, Nematoda and Odonata) were found in the stomachs of *T. miliaris* from Serra do Mar but were not recorded in our sampling across the environment.

Formicidae was the most abundant and frequent prey category available in both Serra do Mar (*N*% = 26.9, *F*% = 10.2) and Serra da Mantiqueira (*N*% = 41.3, *F*% = 9.6), and represented the greatest volume in Serra da Mantiqueira (*V*% = 36.0). Orthoptera presented greater volume (*V*% = 72.2) in Serra do Mar. We identified 15 genera of Formicidae, 11 of which were recorded in Serra do Mar and 13 in Serra da Mantiqueira (Table 3). *Carebara* Westwood, 1840 (Myrmicinae) was the most abundant genus in both Serra do Mar (*N*% = 34.3) and Serra da Mantiqueira (*N*% = 66.7), while *Tapinoma* Förster, 1850 (Dolichoderinae), represented the greatest volume in Serra do Mar (V% = 33.4) and *Carebara* in Serra da Mantiqueira (*V*% = 45.02). *Carebara* and *Solenopsis* were the most frequent genus in Serra do Mar (*F*% = 17.6) and Serra da Mantiqueira (*F*% = 18.2).

We did not find a correlation between geographic distance and prey availability (Mantel statistic $r = 0.09$; $p = 0.26$), indicating that even sampling points that were geographically close had dissimilar compositions of available prey. *Thoropa miliaris* selectively foraged for Formicidae (LI = 35.51% to the Serra da Mantiqueira and 24.45% to the Serra do Mar) and Coleoptera (LI = 8.16% to the Serra da Mantiqueira and 5.70% to the Serra do Mar), while consuming other prey randomly or rejecting them. Although we recovered Nematoda and Isoptera with positive values of LI to the Serra do Mar (3.96% and 1.30%, respectively), we believe that Nematoda may have been present in the stomachs as a result of a parasitism association with other ingested prey (Figure 3).

TABLE 3 Comparison of prey availability sampled in Serra do Mar and Serra da Mantiqueira, Atlantic Forest of south-eastern Brazil.

Availability of environmental prey	Serra do Mar			Serra da Mantiqueira		
	***V*%**	***N*%**	***F*%**	***V*%**	***N*%**	***F*%**
Arachnida						
Araneae	3.727	7.623	**10.204**	0.780	1.940	7.692
Pseudoscorpiones	0.061	1.794	6.122	0.010	0.176	1.923
Hexapoda						
Blattodea	2.930	1.345	4.082	2.302	0.882	5.769
Coleoptera	4.601	13.453	8.163	6.664	5.996	7.692
Collembola	0.353	4.933	8.163	0.800	22.928	7.692
Dermaptera	1.538	1.345	4.082	1.092	0.176	1.923
Diptera	0.142	3.139	2.041	0.968	5.467	**9.615**
Diptera (larvae)	0.045	0.448	2.041	0.070	0.176	1.923
Formicidae	4.702	**26.906**	**10.204**	**36.012**	**41.270**	**9.615**
Dolichoderinae						
Linepthema Mayr, 1866	–	–	–	3.262	0.521	4.545
Tapinoma Förster, 1850	**33.392**	8.955	5.882	2.369	0.521	4.545
Ectatomminae						
Ectatomma F. Smith, 1858	0.111	1.493	5.882	11.101	0.521	4.545
Formicinae						
Camponotus Mayr, 1861	–	–	–	9.927	1.042	4.545
Myrmicinae						
Atta Fabricius, 1804	2.283	1.493	5.882	5.644	2.604	9.091
Carebara Westwood, 1840	2.077	**34.328**	**17.647**	**45.022**	**66.667**	**18.182**
Cyphomyrmex Mayr, 1862	0.055	1.493	5.882	–	–	–
Pheidole Westwood, 1839	1.977	4.478	5.882	2.350	3.646	9.091
Solenopsis Westwood, 1840	3.800	29.851	**17.647**	3.006	8.333	**18.182**
Strumigenys F. Smith, 1860	0.323	4.478	11.765	–	–	–
Wasmannia Forel, 1893	–	–	–	1.826	12.500	4.545
Ponerinae						
Anochetus Mayr, 1861	28.958	7.463	5.882	4.301	1.042	4.545
Hypoponera Santschi, 1938	–	–	–	4.848	1.563	9.091
Odontomachus Latreille, 1804	3.855	1.493	5.882	6.055	0.521	4.545
Pachycondyla F. Smith, 1858	23.167	4.478	11.765	0.290	0.521	4.545
Hemiptera	1.120	7.175	4.082	0.470	1.940	7.692
Hym. not Formicidae	0.009	0.448	2.041	0.512	0.176	1.923
Isopoda	3.175	5.830	8.163	0.114	0.529	1.923
Isoptera	1.654	3.139	6.122	1.553	3.175	7.692
Lepidoptera	0.215	1.794	4.082	3.431	0.705	3.846
Lepidoptera (larvae)	0.651	0.448	2.041	7.041	0.705	3.846
Mantodea	–	–	–	0.548	0.176	1.923
Orthoptera	**72.239**	16.143	8.163	32.145	12.169	7.692
Others						
Annelida	0.523	0.448	2.041	–	–	–
Anura	1.528	0.448	2.041	0.957	0.176	1.923

(Continues)

TABLE 3 (Continued)

Availability of environmental prey	Serra do Mar			Serra da Mantiqueira		
	V%	*N*%	*F*%	*V*%	*N*%	*F*%
Diplopoda	0.105	0.897	2.041	3.065	0.176	1.923
Gastropoda	–	–	–	0.261	0.176	1.923
Scolopendromorpha	0.432	0.448	2.041	1.206	0.882	3.846

Note: Higher values are in bold.

Abbreviations: *F*%, frequency; Hym., Hymenoptera; *N*%, abundance; *V*%, volume.

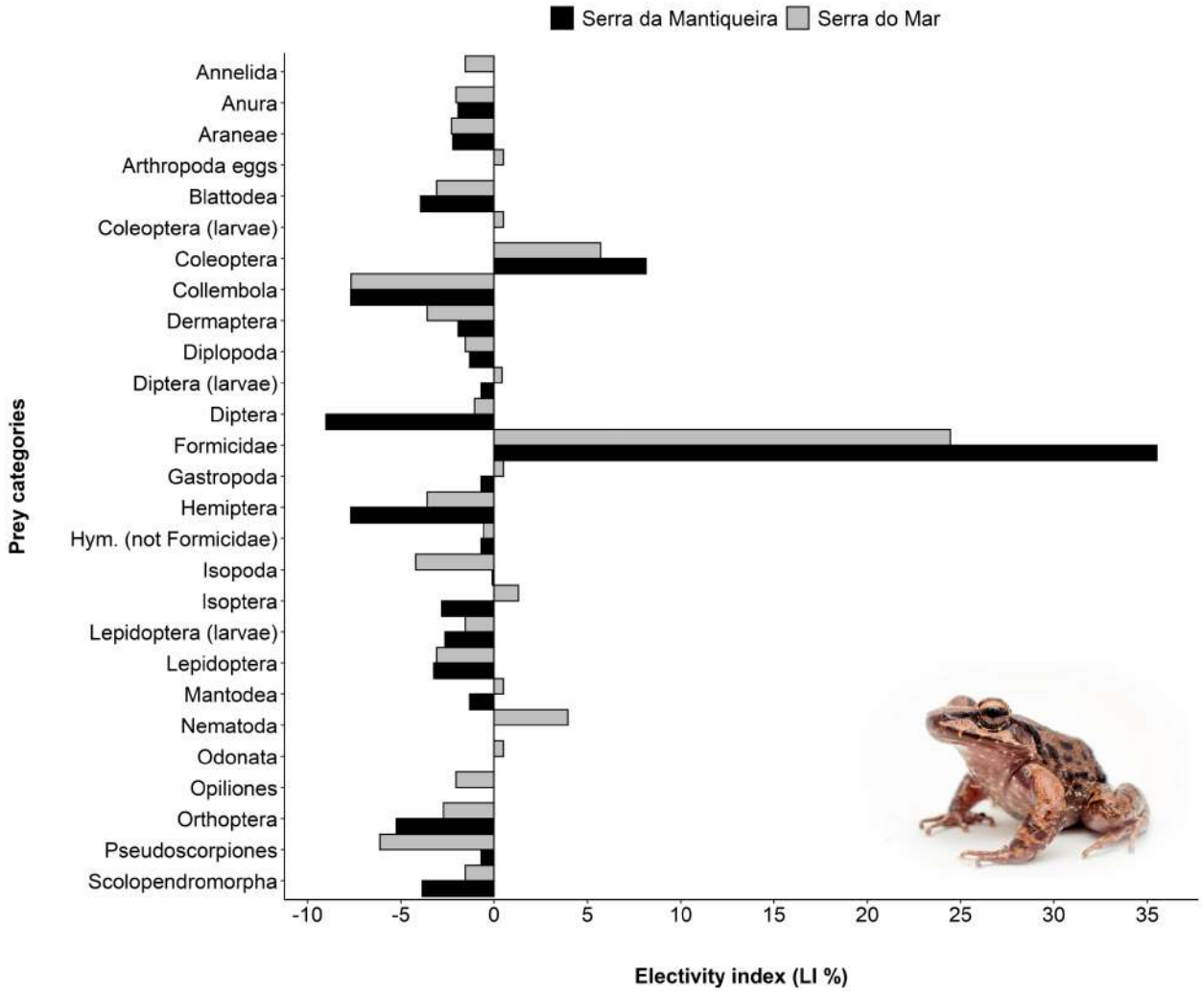

FIGURE 3 Electivity index (LI%) of *Thoropa miliaris* in Serra da Mantiqueira and Serra do Mar, south-eastern, Brazil. Hym., Hymenoptera. For details, see (Strauss, 1979). Photo of *T. miliaris* by Carlos H. O. Nogueira.

DISCUSSION

Populations of *T. miliaris* from Serra do Mar and Serra da Mantiqueira consume ants in a greater volume, frequency and abundance than any other prey category. Through the selective index analysis, we determined that *T. miliaris* actively selects ants as their primary prey rather than simply consuming them because of their high availability in the environment. This interpretation of the feeding strategy in *T. miliaris* contradicts previous notions that the species has a generalist/opportunistic habit (Pertel

et al., 2010; Siqueira et al., 2006). Although ants are often unpalatable and challenging for several predators to metabolize (Hirai & Matsui, 2000), the myrmecophagous behaviour grants *T. miliaris* access to an abundant and underexplored food source (Clarke, 1974). Myrmecophagy has been observed in many anuran families, such as Bufonidae, Dendrobatidae and Microhylidae (Darst et al., 2005; Isacch & Barg, 2002; Mebs et al., 2018; Toft, 1981) and appears to be widespread in Cycloramphidae as well (Brasileiro et al., 2010; Maia-Carneiro et al., 2012; Silva & Ouvernay, 2012; Weber et al., 2011).

The diet of *T. miliaris* is not influenced by location. Individuals of this frog species selectively forage for ants regardless of the environment, even though the Serra do Mar offers a greater variety of prey categories. Studies comparing the diets of anuran populations in different localities have shown that specialist species tend to maintain their preferences for a specific prey category, regardless of their habitat (e.g. Mageski et al., 2019 – for *Phyllodytes luteolus*). In contrast, generalist species exhibit variations in their diet as the environment changes, which is likely due to differences in prey availability across their habitats (García-Padrón & Quevedo, 2022; Santana et al., 2019). The greater availability of prey categories in Serra do Mar might be attributed to a more humid climate, as coastal environments generally have higher primary productivity due to increased photosynthetic rates and organic matter transport (Knoppers et al., 2009; Nixon et al., 1986).

Although *T. miliaris* is typically found on humid rocks, which are constantly wetted by streams or waterfalls (Feio et al., 2006; Giaretta & Facure, 2004), we observed that foraging sites, mainly ravines surrounded by rocks, are slightly different from reproductive sites (humid rocks). Anurans' degree of specialization in ants is related to their foraging mode, with active foragers being better adapted to capture small, gregarious and locally abundant prey, such as ants (Toft, 1985). In contrast, 'sit-and-wait' predators consume larger, more nutritious prey, such as beetles, and expend less energy actively foraging (Blanco-Torres et al., 2020; Toft, 1981).

Populations of *T. miliaris* mainly consumed ants from the genera *Odontomachus* (in Serra da Mantiqueira) and *Solenopsis* (in Serra do Mar). These genera do not nest in rocky habitats and usually forage on the leaf litter (Baccaro et al., 2015; Ehmer & Hölldobler, 1995; Raimundo et al., 2009), supporting our hypothesis that *T. miliaris* leaves the reproductive sites to actively seek their prey. Almost all prey categories we collected in the environment were consumed by *T. miliaris* (although many prey types were consumed in low frequency), suggesting *T. miliaris* has a broad trophic niche (Amundsen et al., 1996), which can be explained by the optimal foraging theory. According to this theory, the energy and nutrients obtained from an available resource at a given moment are greater than the energy spent in searching for a preferred resource (Chaves & Alves, 2010). Investing energy in preying upon large items, such as some Coleoptera, can result in an economy of time and energy, as the energetic assimilation of this type of prey can be higher than that of various small and abundant prey (Costa et al., 2016). While the availability of Isoptera was nearly equal in both mountain ranges, termites were more important in the diet of *T. miliaris* in the Serra do Mar, particularly in the Reserva Ecológica de Guapiaçu, where they were highly abundant. However, the frequency of termites was low in stomachs of *T. miliaris* specimens from Serra do Mar. Although this study did not focus on determining individual or population specialization, this result, interpreted by the diagram proposed by Amundsen et al. (1996), suggests that the high consumption of termites, even with low availability, may indicate a specialization of this

population. This is similar to what was observed for *Pithecopus nordestinus* in a study by Oliveira et al. (2019).

Our study investigated several aspects of the diet of *T. miliaris*, including both prey composition and availability. Contrary to our expectations, we found that *T. miliaris* does not exhibit a generalist diet or opportunistic feeding behaviour, as described for most anurans. Furthermore, we observed little variation in its diet across populations. Interestingly, two other species of Cycloramphidae (*Thoropa taophora* and *Cycloramphus brasiliensis*) appear to have a preference for consuming ants (Brasileiro et al., 2010; Maia-Carneiro et al., 2012). This may suggest that selective myrmecophagy (ant specialization) (Toft, 1981) is an ancestral trait in the family. However, the diet of the other 34 species of Cycloramphidae remains unknown, and only the prey availability for *T. miliaris* was addressed. Further research on the trophic ecology of other Cycloramphidae species is necessary to gain a more complete understanding of diet evolution in this family of neotropical anurans and its natural history.

AUTHOR CONTRIBUTIONS

Henrique J. Oliveira: Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); project administration (equal); writing – original draft (equal). **Marcella D. Aperibense:** Data curation (equal); investigation (equal); methodology (equal). **André Yves:** Investigation (equal); methodology (equal); writing – review and editing (equal). **Rafaela R. Machado:** Data curation (equal); investigation (equal); methodology (equal). **Diego J. Santana:** Conceptualization (equal); formal analysis (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); validation (equal); writing – review and editing (equal). **Henrique C. Costa:** Conceptualization (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); validation (equal); writing – review and editing (equal).

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DATA AVAILABILITY STATEMENT

Additional supporting information may/can be found online in the supporting information tab for this article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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