

Autecology of *Kentropyx calcarata* (Squamata: Teiidae) in a Remnant of Atlantic Forest in Eastern South America

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ABSTRACT.—*Kentropyx calcarata* is a widely foraging teiid lizard species that inhabits forest environments east of the Andes in South America. We studied the ecology of a *K. calcarata* population in a remnant of Atlantic Forest in Brazil and evaluated lizards' body temperatures, stomach content, activity time, body measurements, and reproduction stage. We tested whether: 1) body temperature was influenced by substrate or air temperatures, 2) diet composition varied according to age and sex, and 3) there was sexual dimorphism in body size and bauplan (morphology). Lizards were more active during the hottest hours of the day, commonly in the litter or fallen logs. Body temperatures were influenced more by substrate temperatures than by air temperatures. Diet was composed mainly of arthropods, with Orthoptera and Araneae as the most important categories (numerically and volumetrically). Diet composition was similar between sexes, but varied ontogenetically as an effect of body size, with juveniles eating smaller prey than adults. Females were larger than males and there was difference in bauplan between sexes. We found reproductive males and females throughout the year. *Kentropyx calcarata* is ecologically similar to other species within the genus and the family, suggesting great importance of the evolutionary history for the ecology of this species.

RESUMEN.—*Kentropyx calcarata* es una lagarto teiido ampliamente forrajero que habita en ambientes forestales al este de los Andes en América del Sur. Estudiamos la ecología de una población de *K. calcarata* en un remanente de Mata Atlántica en Brasil y evaluamos la temperatura, el contenido del estómago, la actividad, las medidas corporales, y la etapa de reproducción de los lagartos. Testamos si: i) la temperatura corporal fue influenciada por la temperatura del sustrato o del aire, ii) la composición de la dieta varió según la edad y el sexo, y iii) hubo dimorfismo sexual en el tamaño y bauplan. Los lagartos fueron más activos durante las horas más calurosas del día, comúnmente en la hojarasca o troncos caídos. Las temperaturas corporales fueron más influenciadas por las temperaturas del sustrato que las temperaturas del aire. La dieta fue compuesta principalmente por artrópodos, siendo Orthoptera y Araneae las categorías más importantes (numéricamente y volumétricamente). La composición de la dieta fue similar entre los sexos, pero varió ontogenéticamente, con los juveniles consumiendo presas menores que los adultos, como un efecto del tamaño. Las hembras fueron más grandes que los machos y hubo dimorfismo sexual en bauplan. Machos y hembras reproductores fueron encontrados durante todo el año. Hembras reproductoras también fueron encontradas en todos los meses del año. *Kentropyx calcarata* es ecológicamente similar a otras especies dentro del género y la familia, lo que sugiere una gran importancia de la historia evolutiva en la ecología de esta especie.

Natural history studies constitute an important foundation for the development of advanced research on evolutionary, behavioral, phylogenetic, and environmental sciences (McCallum and McCallum, 2006). They result in the accumulation of factual information that can be used in several contexts, as theory and methods change, to formulate and test meaningful hypotheses (Vitt, 2013). Examining ecological traits such as activity time, microhabitat use, diet, reproduction, and morphology in species is relevant for a better understanding of the evolution of clades and the forces that shape the ecology of populations. Research on the natural history of lizards has a particular value because they are considered to be model organisms of medium complexity (Carothers et al., 1996) and therefore can provide useful information to theoretical ecology and effective management practices for the conservation of species (Bury, 2006).

Autecological patterns are varied in lizards and are influenced by evolutionary history and the environment (Mesquita et al., 2016). Temperature and seasonality are the most important environmental factors that affect reproduction (Fitch, 1985; Roff, 2002). A common pattern in species inhabiting seasonal climates is the reproductive period concentrated in a single season (Colli, 1991; Wiederhecker et al., 2002; Mesquita

and Colli, 2003a), whereas lizards inhabiting less seasonal environments, such as tropical rain forests, are expected to have prolonged or continuous reproduction (Colli, 1991; Vitt, 1991; Vitt et al., 1995). Reproductive behavior can influence lizard size and bauplan (morphology) because males and females are exposed to different selective pressures (Anderson and Vitt, 1990). Alternatively, sexual dimorphism may arise from ecological differences between sexes (Cox et al., 2003). Minimum size for maturity can also be influenced by temperature and diet because temperature affects digestive efficiency and may promote different rates of growth in lizards (Zhang and Ji, 2004). On the other hand, environmental differences often fail to explain all the variation in lizards' ecology (Werneck et al., 2009; Garda et al., 2012), and some patterns may be highly influenced by phylogenetic conservatism (Vitt and Pianka, 2005; Mesquita and Colli, 2010; Mesquita et al., 2016). Therefore, detailed studies on ecological aspects of organisms from different habitats and taxonomic lineages can contribute to the identification of mechanisms that shape life-history patterns.

Studies on ecology of tropical Teiidae are numerous, mainly on the widespread genera *Cnemidophorus* (now including *Ameivula* and *Aspidoscelis*) (Vitt et al., 1993; Menezes et al., 2000, 2004; Mesquita and Colli, 2003a) and *Ameiva* (Hillman, 1969; Vitt, 1982; Vitt and Colli, 1994); however, knowledge gaps persist for species with restricted distributions. *Kentropyx calcarata* is a teiid lizard species distributed east of the Andes,

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DOI: 10.1670/17-184

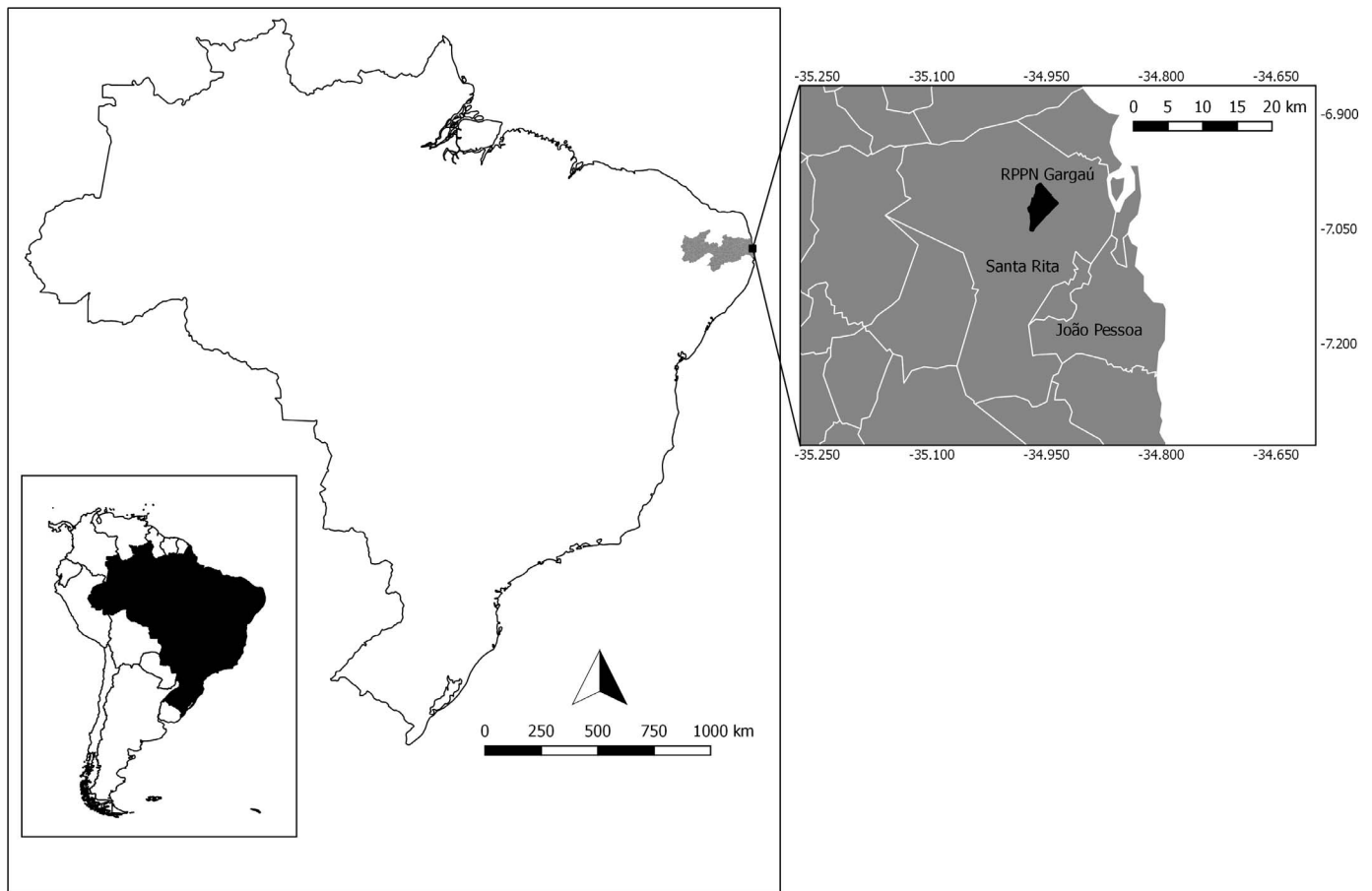


FIG. 1. Location of the private Conservation Unit "Reserva Particular do Patrimônio Natural" Gargaú, in the state of Paraíba, Brazil, municipality of Santa Rita.

occurring mainly in clearings, streams, and forest edges of the Amazon and Atlantic Forests, although they can also be found in certain forest regions of the Cerrado (Avila-Pires et al., 2012). In this paper, we describe the ecology of a population of *K. calcarata* in a remnant of Atlantic Forest. We examined morphology, reproduction, diet composition, microhabitat use, and thermal ecology. We tested these hypotheses: 1) body temperature was influenced by temperatures of substrate and air (Magnusson, 1993); 2) diet composition in the population varied according to age (Paulissen, 1987) and sex (Preest, 1994); and 3) there was sexual dimorphism (Anderson and Vitt, 1990) in body size and bauplan. To better understand the ecology of *K. calcarata* in Atlantic Forest, we also tested additional hypotheses related to sexual dimorphism in head size and use of microhabitat, seasonality in diet, and length of the reproductive period of *K. calcarata*.

MATERIALS AND METHODS

Study Site.—We conducted fieldwork on a private conservation unit: the "Reserva Particular do Patrimônio Natural" (Gargaú; 34°57'25"W, 7°00'44"S; datum WGS 84), property of Japungu Agroindustrial S/A, located in Santa Rita municipality, Paraíba State, Brazil (Fig. 1). The unit covers 1,058.6 ha and the region is warm and wet, with rains concentrated in the winter. Climate is classified as Aw/As in Köppen climate classification. Mean annual temperature is 25°C and mean annual rainfall is 1,597.9 mm, with February to July being the rainiest months. We carried

out monthly 8-day (7 nights) expeditions from September 2016 to August 2017.

Active searches were performed every day by two observers for 3 h. Time of day of these searches varied from 0800 to 1600 h (when sunlight starts to fade at the locality). We used a total of 98 buckets as pitfall traps. Of those, 48 were 20-L buckets arranged in 12 Y-shaped arrays (one bucket in the center and three at the extremities) in which the buckets were 5 m apart from each other and connected by 50-cm-high plastic canvas fences. The other 50 buckets were 60 L and were arranged as a single line and separated from each other by 50-cm-high zinc fences of 5-m length, forming a line of approximately 250 m. This arrangement occurred for logistic reasons only and did not affect the results of the present study, because the goals do not include inventory or spatial distribution of organisms in the area. Buckets were open for 7 nights/mo and were monitored daily.

Activity and Microhabitat.—We collected lizards during active searches and recorded the date, time, microhabitat, and activity of the animal when first sighted and after approached by the observer. Active searches were performed in forested areas with closed canopy and occasional clearings. We considered the following microhabitat categories: litter, fallen log, bush or tangle, ground under vegetation, tree limb, exposed soil, and tree root. To verify intersexual differences on microhabitat use, we used a contingency table containing the obtained frequency of use of each microhabitat category (columns) by each sex (rows) and compared the distribution of our data against a chi-squared

distribution. Lizards were captured by stunning with rubber bands. We euthanized all animals with 10% lidocaine injections, preserved them in 10% formalin, and stored them in 70% ethanol. Collecting and preserving methods followed the pertinent regulations and guidelines listed on the permit. All specimens were deposited in Coleção Herpetológica da Universidade Federal da Paraíba.

Thermal Ecology.—Using a Miller & Weber[®] thermometer (model T3400), we measured the cloacal temperature of 64 lizards that were actively captured, and also the environmental (substrate, air at 5 cm, and air at 1 m) temperatures of the place where each lizard was first observed. To assess the relationship of cloacal temperatures with each one of the environmental temperatures, we performed a stepwise linear regression (Tabachnick and Fidell, 1996). The relationships between substrate and air temperatures at 5 cm and between substrate and air temperatures at 1 m were assessed using simple regressions.

Morphometry.—We measured the snout-vent length (SVL), body and head width and height (at the broadest and highest points), head length (from the tip of the snout to the rear of the tympanum), and fore- and hind limb lengths of 233 adult specimens using a digital caliper (Mitutoyo[™] 500-196-30; Mitutoyo, Inc, Takatsu-ku, Japan). We estimated the tail length of specimens with a broken tail using multiple imputation by chained equations using the R package ‘mice’ (Van Buuren and Groothuis-Oudshoorn, 2011), which is a powerful tool for imputation of missing data (Penone et al., 2014).

We defined each lizard’s body size as an isometric variable (Rohlf and Bookstein, 1987) using an isometric eigenvector (following Mesquita et al., 2015). We performed an analysis of variance to assess body size difference between sexes. To remove the effects of body size on each variable, we used Burnaby’s method (Burnaby, 1966) after log₁₀ transformation of all variables, resulting in a matrix with size-adjusted variables. We evaluated the relative importance of variables for sexual dimorphism by single-term addition model selection (Chamber and Hastie, 1992). We tested the full model against a constant-only model and added the significant term that presented the lowest Akaike information criterion (AIC) value to the null model, generating a new model to which the term with the lowest AIC value in this new model was added; we repeated this procedure until no significant terms remained outside the model. To investigate sexual dimorphism in head shape, we performed an analysis of covariance (ANCOVA) with adjusted head measures (length, width, and height) as dependent variables and sex as the independent variable.

Diet.—We analyzed the stomach contents of 105 specimens of *K. calcarata* under a stereoscopic microscope and identified prey items to the level of order, whenever possible. We measured the length and width of all prey items with a digital caliper, except for those that were too fragmented. We estimated prey volume as an ellipsoid, as shown below, where *w* is prey width and *l* is prey length:

$$V = \frac{4}{3} \pi \left(\frac{w}{2}\right)^2 \left(\frac{l}{2}\right)$$

We calculated the frequency (*F*), the numeric (*N*), and volumetric (*V*) percentages and the importance index of each prey category on the basis of both individual and pooled stomachs (total number of stomachs containing a given prey category divided by the number of stomachs analyzed). The

importance index on the basis of individual stomachs is defined by (*N%* + *V%*)/2 and the importance index on the basis of pooled stomachs is defined by (*F%* + *N%* + *V%*)/3. We estimated the niche breadth on the basis of both individual and pooled stomachs using the inverse of Simpson’s diversity index (*S*) (Simpson, 1949):

$$S = \frac{1}{\sum_{i=1}^n P_i^2}$$

where *P* is the proportion (numeric or volumetric) of prey category *i* and *n* is the total number of categories. This provides a value of niche breadth that varies from 1 (specialist) to *n* (generalist) and that takes into account the frequency that a certain item is ingested, and not only the total number of prey categories in the individual or population.

To test for ontogenetic diet shifts we performed a linear regression using the maximum prey volume ingested by each lizard as the dependent variable and the isometric head size (calculated using the same method applied for body size) as the independent variable and also an ANCOVA with the same variables and the SVL as covariate. Diet overlap between sexes (*n* = 103) and seasons (*n* = 105) was calculated using the niche overlap equation (Pianka, 1973):

$$O_{ab} = \frac{\sum P_{ai}P_{bi}}{\sqrt{(P_{ai}^O)(P_{bi}^O)}}$$

where *P* represents numeric or volumetric proportions of prey category *i* for each category (*a* or *b*) of sex (male/female) or season (dry/rainy). Diet overlap was calculated both for numeric and volumetric proportions using the R package ‘spaa’ (Zhang, 2013).

To assess intersexual differences in prey number and volume, we performed an ANCOVA with individual niche breadth as the dependent variable, sex as the independent variable, and SVL as covariate.

Reproduction.—We sexed lizards by direct observation of the gonads. Using a digital caliper, we measured the length and width of the testes of all male individuals (*n* = 129) and we calculated testes volume as an ellipsoid. For histological analysis, testes were fixed in Bouin’s fixative, dehydrated in ascending alcohol concentrations, cleared in xylene, infiltrated, and embedded in paraffin. Next, we cut the samples into four sections of 3 μm with a microtome and stained sections with hematoxylin and eosin. We analyzed and photographed the sections under an optical microscope equipped with an Olympus DP25 (Olympic Scientific Solutions, Waltham, Massachusetts, USA). From each section, we measured the diameter of 10 transversally oriented tubules at the same section of seminiferous tubule and when lumen was present, the germinative epithelium height was obtained using ImageJ software version 1.45 (National Institutes of Health, Bethesda, Maryland, USA). We classified testes according to spermatogenic activity following Vieira et al. (2001). We recognized the following spermatogenic activities (Fig. 2): stage I—seminiferous tubules without lumen, containing cells at different stages of differentiation (spermatocytes, spermatids, spermatozoa); stage II—spermatocytes in the margins of opened lumen of the seminiferous tubules; stage III—spermatids in the luminal margin; stage IV—spermatozoa in the lumen; stage V—no connection between the epithelium of the seminiferous

TABLE 1. Morphometric variables of female and male lizards of *Kentropyx calcarata*. Values represent mean \pm SE of isometric body size and shape (size-free variables).

	Raw measures (mm)		Size-free variables	
	Females (<i>n</i> = 104)	Males (<i>n</i> = 129)	Females (<i>n</i> = 104)	Males (<i>n</i> = 129)
Body size ^a	4.04 \pm 0.04	3.82 \pm 0.04		
SVL ^a	67.6 \pm 1.98	56.12 \pm 1.78	0.46 \pm 0.002	0.45 \pm 0.002
Tail length ^a	137.81 \pm 4.86	120.74 \pm 4.23	0.76 \pm 0.007	0.78 \pm 0.004
Body width ^a	14.71 \pm 0.62	11.16 \pm 0.42	-0.22 \pm 0.007	-0.26 \pm 0.004
Body height	8.47 \pm 0.37	7.07 \pm 0.29	-0.46 \pm 0.008	-0.47 \pm 0.008
Head width ^a	9.69 \pm 0.23	8.6 \pm 0.24	-0.37 \pm 0.004	-0.36 \pm 0.004
Head height ^a	7.67 \pm 0.21	6.84 \pm 0.24	-0.48 \pm 0.003	-0.47 \pm 0.003
Head length	16.72 \pm 0.43	14.65 \pm 0.45	-0.14 \pm 0.004	-0.13 \pm 0.004
Forelimb length	28.1 \pm 0.81	24.02 \pm 0.72	0.08 \pm 0.006	0.08 \pm 0.004
Hind limb length	54.95 \pm 1.52	46.56 \pm 1.43	0.37 \pm 0.003	0.37 \pm 0.003

^a Variables that are discriminant between sexes (selected in the final model of the discriminant analysis). SVL = snout-vent length.

RESULTS

Activity and Microhabitat.—Lizards were captured from 0900 to 1300 h and 80.3% of all captures were made from 1000 to 1200 h, when air and substrate temperatures reached values around 38°C. Of 66 *K. calcarata* actively observed and captured, 53% were foraging on the substrate when first sighted, whereas the remaining were stationary. After approach by the observer, 74.24% of the lizards fled, usually hiding in bushes. When approached by the observer at the water’s edge, individuals tended to dive, showing ability to swim fast and for distances >2 m.

Approximately half (51.52%; *n* = 34) of the lizards were first sighted on litter and 31.82% (*n* = 21) on fallen logs. Other microhabitats used included bush or tangle (6.06%; *n* = 4), ground under vegetation (4.55%, *n* = 3), African palm tree leaves (3.03%, *n* = 2), exposed soil (1.52%, *n* = 1), and tree roots (1.52%, *n* = 1). Two individuals captured on palm tree leaves were first sighted at heights of ~1 m. Microhabitat use did not differ between sexes ($\chi^2 = 0.30$, *df* = 6, *P* = 0.32). Another adult, not included in these results, was seen climbing a tree trunk at heights >2 m and could not be captured or sexed.

Thermal Ecology.—Cloacal temperatures of *K. calcarata* specimens varied from 27.2 to 39.8°C (34.4°C \pm 0.36°C). Substrate temperatures varied from 26.1 to 38.2°C (30.6°C \pm 0.38°C). Air temperatures at 5 cm above the substrate varied from 25.9 to 38.2°C (29.7°C \pm 0.32°C), and air temperatures at 1 m above the substrate varied from 26 to 38.1°C (29.5°C \pm 0.32°C). Body temperatures were more strongly associated with substrate temperatures ($R^2 = 0.25$, $F_{2,61} = 19.93$, *P* < 0.001, coefficient = 0.54 \pm 0.122 SE), but also significantly associated with temperatures of the air at 5 cm ($R^2 = 0.19$, $F_{2,61} = 14.99$, *P* < 0.001, coefficient = 0.49 \pm 0.126) and 1 m ($R^2 = 0.19$, $F_{2,61} = 14.52$, *P* < 0.001, coefficient = 0.49 \pm 0.129). Substrate temperatures were significantly associated with air temperatures to 5 cm ($R^2 = 0.67$, $F_{1,62} = 130.65$, *P* < 0.001, coefficient = 0.822 \pm 0.07) and 1 m ($R^2 = 0.63$, $F_{1,62} = 107.68$, *P* < 0.001, coefficient = 0.8 \pm 0.08).

Morphometry.—Minimum and maximum SVL of female lizards were 35.11 mm and 100.35 mm, respectively (67.60 \pm 1.98 mm). Minimum and maximum SVL of males were 34.0 mm and 104.01 mm, respectively (56.12 \pm 1.78 mm). Females had larger bodies than males ($F_{1,231} = 15.1$, *P* < 0.001) and there was also dimorphism in bauplan ($\chi^2 = 63.79$, *df* = 8, *P* < 0.001). The shape variables that were most relevant for the discrimination of sexes were body and head width, SVL, tail length, and head height (Table 1). Although females were larger, males had significantly

larger heads when adjusted for the effect of body size (ANCOVA $F_{1,231} = 15.37$, *P* < 0.01).

Diet.—The diet of *K. calcarata* was composed mainly of arthropods; occasional ingestion of plants, Gastropoda, and vertebrates was also observed (Appendix 1). The most important items were Araneae and Orthoptera, which represented, respectively, 36.41% and 25.00% of all items. Volumetrically, Orthoptera was the most important food item (38.77%), followed by Araneae (27.90%) (Appendix 1). Mean niche breadth for numeric proportions was 3.5 and 1.6 \pm 0.08 for pooled and individual stomachs, respectively. Mean niche breadth for volumetric proportions was 4.15 and 1.39 \pm 0.06 for pooled and individual stomachs, respectively.

Diet niche overlap between sexes was near unity, both for prey number (0.96) and prey volume (0.91). We did not detect a significant difference between sexes for prey number (ANCOVA $F_{1,101} = 0.1489$, *P* = 0.70; males = 1.631 \pm 0.11; females = 1.571 \pm 0.11) or volume (ANCOVA $F_{1,101} = 0.879$, *P* = 0.351; males = 1.451 \pm 0.09; females = 1.337 \pm 0.08), indicating that males and females ingest similar amounts of prey. *Kentropyx calcarata* increased the size (volume) of ingested prey ontogenetically ($R^2 = 0.153$; $F_{1,103} = 18.6$; *P* < 0.01; coefficient = 0.39 \pm 105.47) as an effect of body size (ANCOVA $F_{1,103} = 4.296$, *P* = 0.37). Diet overlap between seasons was high (0.96) for numeric proportions, but much lower (0.50) for volumetric proportions. Araneae and Orthoptera represented a high percentage of stomach content, both numerically and volumetrically (Table 2).

Reproduction.—The smallest reproductive male of *K. calcarata* had a SVL of 56.81 mm. All five stages of spermatogenic activity were recognized and most of the individuals were in stage IV throughout the year (Fig. 3), therefore containing spermatozoa in the lumen and presenting high volume of the testes (Table 3). The smallest reproductive female had a SVL of 64.7 mm. We found reproductive females year round and specimens containing eggs in the oviduct in 6 mo of the year (Fig. 4). Three females simultaneously contained eggs and developed vitellogenic follicles (Fig. 4), indicating production of more than one clutch during the same reproductive season. Average clutch size was 5.65 \pm 0.24 (range 5–9) and average egg volume was 360.93 \pm 10.95 mm³. Adult males and females showed continuous reproductive cycles and recruitment occurred throughout the year (Fig. 5).

DISCUSSION

Studies on the natural history of individual species provide data necessary to test hypotheses about habitat use, prey

TABLE 2. Numeric (N) and volumetric (V) proportion of each category of prey present in the diet of *Kentropyx calcarata* from Atlantic Forest in dry and rainy seasons.

Prey category	Dry season		Rainy season	
	N%	V%	N%	V%
Araneae	47.40	15.30	50.89	44.56
Orthoptera	26.01	57.25	14.29	14.35
Plant	4.05	0.40	4.46	8.57
Hemiptera	4.05	1.59	1.79	1.08
Insect larvae	3.47	3.70	6.25	1.84
Blattaria	3.47	10.69	3.57	3.02
Hymenoptera	2.89	3.15	5.36	0.81
Scorpiones	1.73	1.59	3.57	2.42
Gastropoda	1.16	0.18	5.36	0.56
Arthropoda	1.16	1.08	1.79	4.03
Mantodea	1.16	1.82	—	—
Diptera	1.16	0.21	—	—
Squamata	0.58	1.69	—	—
Myriapoda	0.58	1.13	—	—
Lepidoptera	0.58	0.20	0.89	16.28
Insect egg	0.58	<0.01%	—	—
Coleoptera	—	—	0.89	2.01
Anura	—	—	0.89	0.45

acquisition, thermal ecology, bauplan variation, and life histories. Our analyses demonstrate that even though both air and substrate influence body temperatures of *K. calcarata*, substrate temperatures appear to have the greatest effect (hypothesis 1). As in many other species (Costa et al., 2008), diet varies with lizard size (primarily in size of individual prey) but does not appear to vary between sexes (hypothesis 2). Sexual dimorphism exists in both body size and bauplan (hypothesis 3).

Similar to other teiid lizards, *K. calcarata* gains heat by basking in sun. Because of the structural complexity of tropical forests, access to direct sunlight is often limited to treefalls or other clearings, stream edges, and edges of disturbed areas. High activity levels of teiid lizards in general (Vitt, 1991; Vitt and Colli, 1994; Vitt et al., 1995, 2001; Mesquita and Colli, 2003b) suggest that maintaining relatively high body temperatures while active is important for all teiids. Consequently, the thermal ecology of *K. calcarata* in Atlantic Forest should be similar to that of other tropical teiids, which appears to be the case. Although body temperatures of *K. calcarata* are slightly below those of teiids inhabiting open habitats (e.g., deserts of

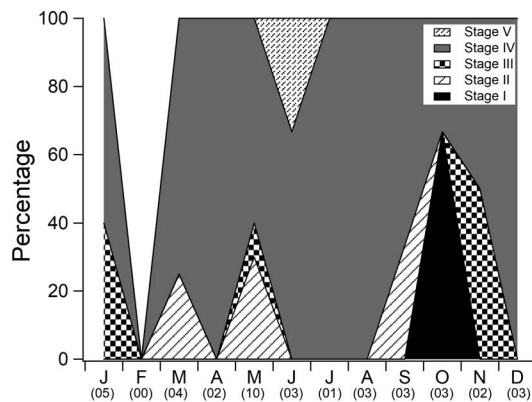


FIG. 3. Percentage of male *Kentropyx calcarata* according to stages of spermatogenic activity throughout the months of the year. Letters on horizontal axis represent months of the year and sample sizes are indicated in parentheses.

TABLE 3. Testes parameters according to stage of spermatogenic activity. DST = diameter of seminiferous tubule (mm), GEH = germinative epithelium height (mm), and V = testis volume (mm³).

Stages	n	Parameters	Average	Minimum	Maximum
I	2	DST	0.275	0.18	0.34
		GEH	0.072	0	0.258
		V	92.62	64.35	120.91
II	5	DST	0.14	0.05	0.22
		GEH	0.035	0	0.09
		V	22.07	9.7	41.8
III	4	DST	0.15	0.11	0.21
		GEH	0.04	0	0.07
		V	39.31	29.62	48.8
IV	27	DST	0.26	0.11	0.42
		GEH	0.067	0	0.146
		V	112.75	0.12	189.16
V	1	DST	0.24	0.18	0.28
		GEH	0.037	0	0.073
		V	63.6	63.6	63.6

North and South America, Caatinga, Cerrado), they are still above those of lizards in other families, regardless of habitat. Consequently, much of the thermal ecology of *K. calcarata* likely can be attributed to a thermal shift that occurred early in the evolutionary history of teiids.

Kentropyx calcarata eats a variety of invertebrates and occasional vertebrates, with spiders and orthopterans dominating the diet. High consumption of spiders, crickets, roaches, and occasional vertebrates is characteristic of the diet of most medium-sized teiids, including several species of *Kentropyx* (Martins, 1991; Vitt, 1991; Vitt et al., 1995, 2001). Lack of a difference in diets between sexes is not surprising, considering that foraging by both sexes occurs primarily on the ground. Some of the most common insects (ants) are uncommon in the diet of teiid lizards, and that appears to be the case for *K. calcarata* as well. Ontogenetic differences in diet appear to simply reflect the effect of lizard body size on size of individual prey taken.

Observed sexual differences in body size and bauplan (especially head size and shape) are similar to those reported for other teiid lizards. The slightly larger bodies of females likely reflect the effect of reproductive investment on female body size considering that larger females produce more eggs (fecundity

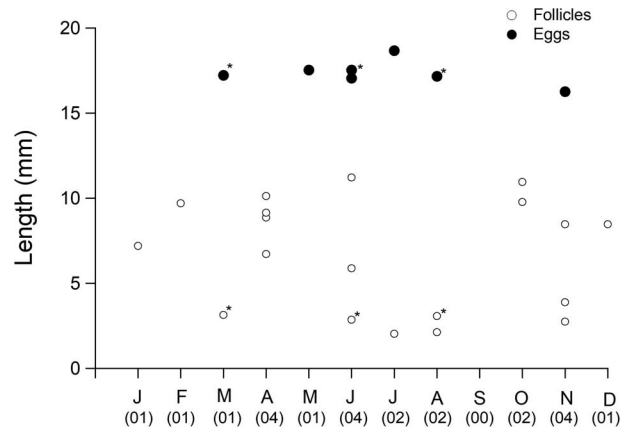


FIG. 4. Monthly distribution of the largest follicle and egg lengths in females of *Kentropyx calcarata* in an Atlantic Forest fragment. Letters on horizontal axis represent months of the year and sample sizes are indicated in parentheses. *, follicles and eggs registered in the same female in a given month.

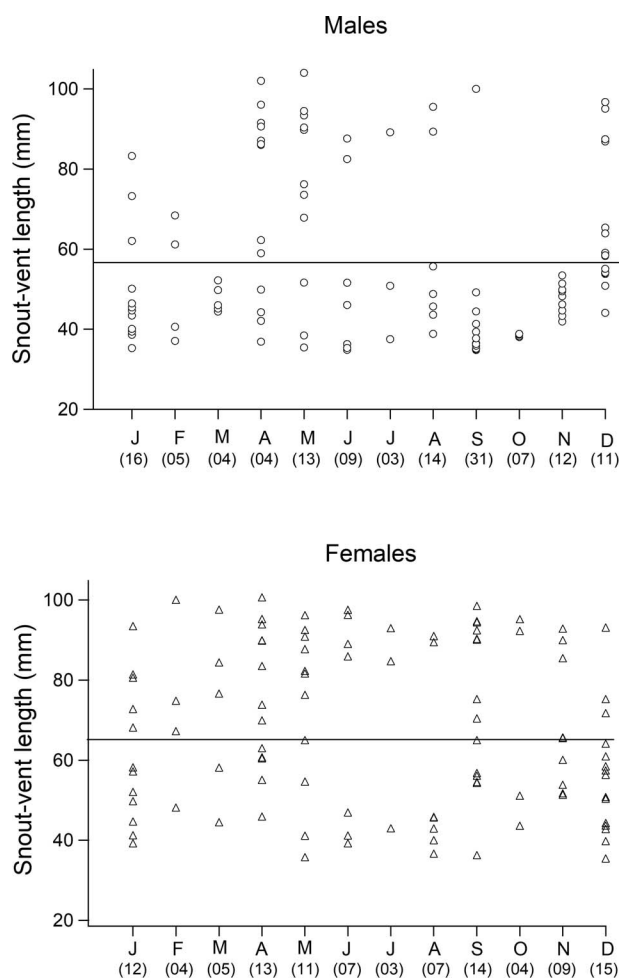


FIG. 5. Monthly distribution of male and female individuals of *Kentropyx calcarata* from Atlantic Forest according to snout-vent length (SVL). Letters on horizontal axis represent months of the year and sample sizes are indicated in parentheses. Horizontal lines represent minimum SVL at maturity.

advantage hypothesis) (Tinkle et al., 1970; Vitt, 1986). Relatively larger heads of males likely arise from sexual selection associated with male–male aggressive interactions in which males with relatively larger heads have greater reproductive success (Anderson and Vitt, 1990).

A few additional points are worth mentioning. First, we provide another example of a teiid lizard living in tropical forest that reproduces continually. In the Amazon rain forest, there are records of reproductive individuals in rainy and dry seasons for *K. calcarata* (Vitt, 1991), *K. pelviceps* (Vitt et al., 1995), and *K. altamazonica* (Serrano Rojas et al., 2016). In rain forests, where rainfall is more uniformly distributed throughout the year, compared with other Neotropical environments, the opportunity to reproduce continuously, laying several clutches per year, exists (Fitch, 1982; Mesquita and Colli, 2010). Temperate-zone teiid lizards, such as those in the genus *Aspidoscelis*, are highly seasonal, both in activity and reproduction (Manríquez-Morán et al., 2005; Ramírez-Bautista et al., 2009), indicating that winter is a primary limiting factor for teiid lizards. Nevertheless, given that many tropical teiids have continuous reproduction, it would be interesting to determine whether temperate-zone teiids are capable of continuous reproduction in the absence of winter. If they are, then the evolution of aseasonal reproduction occurred early in the evolutionary history of teiids. We now

know that there was early divergence of life-history traits among lizard lineages (Mesquita et al., 2016). Finally, even though our data are consistent with the hypothesis that tropical forests offer the opportunity to reproduce continually (Mesquita and Colli, 2010), we cannot conclude that all tropical forest species in general should reproduce continually. Two studies, one in Brazil (Vitt, 1992) and the other in Australia (James and Shine, 1988) in which all species in their tropical habitats were simultaneously studied, suggest otherwise.

In this study, we provided information on life-history traits from *K. calcarata* from the Atlantic Forest and we showed that the body temperature in this species is high and influenced by substrate temperature, that the species is sexually dimorphic in size, and that diet varies with lizard size. *Kentropyx calcarata* shows ecological characteristics that are similar to other studied species of the genus and the teiid family, suggesting great importance of evolutionary history in shaping the ecology of *K. calcarata*.

Acknowledgments.—We thank everyone who helped with the fieldwork, especially the employees at Reserva Particular do Patrimônio Natural Gargaú. F. Maia., L. Q. R. Oliveira, A. Normande, J. Ferro, and J. O. S. Carmo helped with the preparation of the histological material. We are grateful to G. H. C. Viera for orientations regarding testis analyses and suggestions that improved the manuscript. LDF and AAMT thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior for a research fellowship, and DOM thanks Conselho Nacional de Pesquisa e Desenvolvimento for the productivity research grant. This work was authorized by Permit SISBIO No. 54148-1 and all applicable protocols concerning animal care were followed.

LITERATURE CITED

ALMEIDA-SANTOS, S. M., H. B. BRAZ, L. C. SANTOS, L. R. SUEIRO, V. A. BARROS, C. A. ROJAS, AND K. N. KASPEROVICZUS. 2014. Biologia reprodutiva de serpentes: recomendações para a coleta e análise de dados. *Herpetologia Brasileira* 3:14–24.

ANDERSON, R. A., AND L. J. VITT. 1990. Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. *Oecologia* 84:145–157.

AVILA-PIRES, T. C. S., D. G. MULCAHY, F. P. WERNECK, AND J. W. SITES. 2012. Phylogeography of the teiid lizard *Kentropyx calcarata* and the sphaerodactylid *Gonatodes humeralis* (Reptilia: Squamata): testing a geological scenario for the lower Amazon-Tocantins basins, Amazonia, Brazil. *Herpetologica* 68:272–287.

BURNABY, T. P. 1966. Growth-invariant discriminant functions and generalized distances. *Biometrics* 22:96–110.

BURY, B. R. 2006. Natural history, field ecology, conservation biology and wildlife management: time to connect the dots. *Herpetological Conservation and Biology* 1:56–61.

CAROTHERS, J. H., F. M. JAKSIC, AND P. A. MARQUET. 1996. A model for species distributions along a gradient: lizards as study systems. *Revista Chilena de Historia Natural* 69:301–307.

CHAMBER, J. M., AND T. J. HASTIE. 1992. *Statistical Models in S*. Wadsworth & Brooks/Cole Advanced Books & Software, USA.

COLLI, G. R. 1991. Reproductive ecology of *Ameiva ameiva* (Sauria, Teiidae) in the Cerrado of central Brazil. *Copeia* 1991:1002–1012.

COSTA, G. C., L. J. VITT, E. C. PIANKA, D. O. MESQUITA, AND G. C. COLLI. 2008. Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards. *Global Ecology and Biogeography* 17:670–677.

COX, R. M., S. L. SKELLY, AND H. B. JOHN-ALDER. 2003. A comparative test of adaptive hypothesis for sexual size dimorphism in lizards. *Evolution* 57:1653–1669.

FITCH, H. S. 1982. Reproductive cycles in tropical reptiles. *Occasional Papers of the Natural History Museum, University of Kansas* 96:1–53.

- FITCH, H. S. 1985. Variation in clutch and litter size in New World reptiles. *Miscellaneous Publications of the Natural History Museum, University of Kansas* 52:1–247.
- GARDA, A. A., G. C. COSTA, F. G. R. FRANÇA, L. G. GIUGLIANO, G. S. LEITE, D. O. MESQUITA, C. NOGUEIRA, L. TAVARES-BASTOS, M. M. VASCONCELLOS, G. H. C. VIEIRA, ET AL. 2012. Reproduction, body size, and diet of *Polychrus acutirostris* (Squamata: Polychrotidae) in two contrasting environments in Brazil. *Journal of Herpetology* 46:2–8.
- HILLMAN, P. E. 1969. Habitat specificity in three sympatric species of *Ameiva* (Reptilia: Teiidae). *Ecology* 50:476–481.
- JAMES, C., AND R. SHINE. 1988. Life-history strategies of Australian lizards: a comparison between the tropics and the temperate zone. *Oecologia* 75:307–316.
- MAGNUSSON, W. E. 1993. Body temperatures of field-active Amazonian Savanna lizards. *Journal of Herpetology* 27:53–58.
- MANRÍQUEZ-MORÁN, N. L., M. V. CRUZ, AND F. R. M. CRUZ. 2005. Reproductive biology of the parthenogenetic lizard, *Aspidocelis cozumela*. *Herpetologica* 61:435–439.
- MARTINS, M. 1991. The lizards of Balbina, Central Amazonia, Brazil: a qualitative analysis of resource utilization. *Studies on Neotropical Fauna and Environment* 26:179–190.
- MCCALLUM, M. L., AND J. L. MCCALLUM. 2006. Publication trends in natural history and field studies in herpetology. *Herpetological Conservation and Biology* 1:62–67.
- MENEZES, V. A. D., C. F. D. ROCHA, AND G. F. DUTRA. 2000. Termorregulação no lagarto partenogenético *Cnemidophorus nativo* (Teiidae) em uma área de Restinga do Nordeste do Brasil. *Revista de Etologia* 2:103–109.
- MENEZES, V. A., C. F. ROCHA, AND G. F. DUTRA. 2004. Reproductive ecology of the parthenogenetic whiptail lizard *Cnemidophorus nativo* in a Brazilian restinga habitat. *Journal of Herpetology* 38:280–282.
- MESQUITA, D. O., AND G. R. COLLI. 2003a. The ecology of *Cnemidophorus ocellifer* (Squamata, Teiidae) in a Neotropical savanna. *Journal of Herpetology* 37:498–509.
- MESQUITA, D. O., AND G. R. COLLI. 2003b. Geographical variation in the ecology of populations of some Brazilian species of *Cnemidophorus* (Squamata, Teiidae). *Copeia* 2003:285–298.
- MESQUITA, D. O., AND G. R. COLLI. 2010. Life history patterns in tropical South American lizards. Pp. 45–71 in O. H. Gallegos, F. R. M. de la Cruz and J. F. M. Sánchez (eds.), *Reproducción en Reptiles: Morfología, Ecología y Evolución*, Universidad Autónoma del Estado de México. México.
- MESQUITA, D. O., G. C. COSTA, A. S. FIGUEIREDO, F. G. R. FRANÇA, A. A. GARDA, A. H. B. SOARES, L. TAVARES-BASTOS, M. V. VASCONCELLOS, G. H. C. VIEIRA, L. J. VITT, ET AL. 2015. The autecology of *Anolis brasiliensis* (Squamata, Dactyloidae) in a Neotropical savanna. *Herpetological Journal* 25:233–244.
- MESQUITA, D. O., G. C. COSTA, G. R. COLLI, T. B. COSTA, D. B. SHEPARD, L. J. VITT, AND E. R. PIANKA. 2016. Life-history patterns of lizards of the world. *American Naturalist* 187:681–705.
- PAULISSEN, M. A. 1987. Optimal foraging and intraspecific diet differences in the lizard *Cnemidophorus sexlineatus*. *Oecologia* 71:439–446.
- PENONE, C., A. D. DAVIDSON, K. T. SHOEMAKER, M. DI MARCO, C. RONDININI, T. M. BROOKS, B. E. YOUNG, C. H. GRAHAM, G. C. COSTA, AND R. FRECKLETON. 2014. Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods in Ecology and Evolution* 5:961–970.
- PIANKA, E. R. 1973. Structure of lizard communities. *Annual Review of Ecology, Evolution, and Systematics* 4:53–74.
- PREEST, M. R. 1994. Sexual size dimorphism and feeding energetics in *Anolis carolinensis*: why do females take smaller prey than males? *Journal of Herpetology* 28:292–298.
- RAMÍREZ-BAUTISTA, A., G. R. SMITH, AND X. HERNÁNDEZ-IBARRA. 2009. Reproduction and sexual dimorphism in the whiptail lizard *Aspidocelis gularis* (Squamata: Teiidae) in Guadalcázar, San Luis Potosí, Mexico. *Southwestern Naturalist* 54:453–460.
- ROFF, D. A. 2002. *Life History Evolution*. Sinauer Associates, USA.
- ROHLE, F. J., AND F. L. BOOKSTEIN. 1987. A comment on shearing as a method for “size correction”. *Systematic Zoology* 36:356–367.
- SERRANO ROJAS, S. J., J. VILLACAMPA, AND A. WHITWORTH. 2016. Notes on the reproduction of *Kentropyx altamazonica* (Squamata: Teiidae) and *Imantodes lentiferus* (Serpentes: Dipsadidae) from southeast Peru. *Phyllomedusa* 15:69.
- SIMPSON, E. H. 1949. Measurement of diversity. *Nature* 163:688.
- TABACHNICK, B. G., AND L. S. FIDELL. 1996. *Using Multivariate Statistics*. Harper Collins Publishers, USA.
- TINKLE, D. W., H. M. WILBUR, AND S. G. TILLEY. 1970. Evolutionary strategies in lizard reproduction. *Evolution* 24:55–74.
- VAN BUUREN, S., AND K. GROOTHUIS-OUUDSHOORN. 2011. mice: multivariate imputation by chained equations in R. *Journal of Statistical Software* 45:1–67.
- VIEIRA, G. H. C., H. C. WIEDERHECKER, G. C. COLLI, AND S. N. BÃO. 2001. Spermiogenesis and testicular cycle of the lizard *Tropidurus torquatus* (Squamata, Tropiduridae) in the Cerrado of Central Brazil. *Amphibia-Reptilia* 22:217–233.
- VITT, L. J. 1982. Reproductive tactics of *Ameiva ameiva* (Lacertilia: Teiidae) in a seasonally fluctuating tropical habitat. *Canadian Journal of Zoology* 60:3113–3120.
- VITT, L. J. 1986. Reproductive tactics of sympatric gekkonid lizards with a comment on the evolutionary and ecological consequences of invariant clutch size. *Copeia* 1986:773–786.
- VITT, L. J. 1991. Ecology and life history of the wide-foraging lizard *Kentropyx calcarata* (Teiidae) in Amazonian Brazil. *Canadian Journal of Zoology* 69:2791–2799.
- VITT, L. J. 1992. Diversity of reproductive strategies among Brazilian lizards and snakes: the significance of lineage and adaptation. Pp. 135–149 in W. Hamlett (ed.), *Reproductive Biology of South American Vertebrates*. Springer-Verlag, USA.
- VITT, L. J. 2013. Walking the natural-history trail. *Herpetologica* 69:105–117.
- VITT, L. J., AND G. R. COLLI. 1994. Geographical ecology of a neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. *Canadian Journal of Zoology* 72:1986–2008.
- VITT, L. J., AND E. R. PIANKA. 2005. Deep history impacts present-day ecology and biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* 102:7877–7881.
- VITT, L. J., P. A. ZANI, J. P. CALDWELL, AND R. D. DURTSCHKE. 1993. Ecology of the whiptail lizard *Cnemidophorus deppii* on a tropical beach. *Canadian Journal of Zoology* 71:2391–2400.
- VITT, L. J., P. A. ZANI, J. P. CALDWELL, AND E. O. CARRILLO. 1995. Ecology of the lizard *Kentropyx pelviceps* (Sauria: Teiidae) in lowland rain forest of Ecuador. *Canadian Journal of Zoology* 73:691–703.
- VITT, L. J., S. S. SARTORIUS, T. C. S. AVILA-PIRES, AND M. C. ESPÓSITO. 2001. Life at the river's edge: ecology of *Kentropyx altamazonica* in Brazilian Amazonia. *Canadian Journal of Zoology* 79:1855–1865.
- WERNECK, F. P., L. G. GIUGLIANO, R. G. COLLEVATTI, AND G. R. COLLI. 2009. Phylogeny, biogeography and evolution of clutch size in South American lizards of the genus *Kentropyx* (Squamata: Teiidae). *Molecular Ecology* 18:262–278.
- WIEDERHECKER, H. C., A. C. S. PINTO, AND G. C. COLLI. 2002. Reproductive ecology of *Tropidurus torquatus* (Squamata: Tropiduridae) in the highly seasonal Cerrado biome of central Brazil. *Journal of Herpetology* 36:82–91.
- ZHANG, J. 2013. spaa: SPECies Association Analysis. R package version 0.2.1.
- ZHANG, Y. P., AND X. JI. 2004. The thermal dependence of food assimilation and locomotor performance in southern grass lizards, *Takydromus sexlineatus* (Lacertidae). *Journal of Thermal Biology* 29:45–53.

Accepted: 6 March 2019.

Published online: 13 September 2019.

APPENDIX 1. Diet composition of a *Kentropyx calcarata* population from Atlantic Forest ($n = 105$). N = prey number, V = prey volume in mm^3 , F = number of stomachs containing prey item, IIS = importance index based on individual stomachs, IPS = importance index based on pooled stomachs. Percentages were calculated on the basis of the total frequency, number, or volume.

	Pooled stomachs							Individual stomachs				
	F	$F\%$	N	$N\%$	V	$V\%$	IPS	$N \pm SE$	$V \pm SE$	$N\% \pm SE$	$V\% \pm SE$	IIS
Araneae	67	36.41	134	47.86	7,713.42	27.90	37.39	1.28 ± 0.13	73.46 ± 13.56	44.16 ± 3.45	39 ± 3.69	41.58
Orthoptera	46	25	61	21.79	10,717.6	38.77	28.52	0.58 ± 0.1	102.07 ± 35.53	22.66 ± 4.22	28.78 ± 5.05	25.72
Insect larvae	11	5.98	13	4.64	802.15	2.90	4.51	0.12 ± 0.11	7.64 ± 9.15	4.96 ± 5.07	5.74 ± 5.58	5.35
Plant	7	3.80	12	4.29	1,084.6	3.92	4	0.11 ± 0.15	10.33 ± 23.97	5.84 ± 6.63	5.14 ± 6.22	5.49
Hymenoptera	9	4.89	11	3.93	592.84	2.14	3.65	0.1 ± 0.12	5.65 ± 10.52	5.53 ± 6.35	5.04 ± 6.28	5.29
Blattaria	9	4.89	10	3.57	2,041	7.38	5.28	0.1 ± 0.11	19.44 ± 30.91	3.81 ± 4.57	3.89 ± 4.85	3.85
Hemiptera	9	4.89	9	3.21	379.16	1.37	3.16	0.09 ± 0.1	3.61 ± 5.93	2.47 ± 2.9	2.56 ± 3.29	2.52
Gastropoda	6	3.26	8	2.86	95.27	0.34	2.15	0.08 ± 0.13	0.91 ± 1.43	3.12 ± 5.33	2.06 ± 4.86	2.59
Scorpiones	7	3.80	7	2.50	538.48	1.95	2.75	0.07 ± 0.1	5.13 ± 9.17	3.07 ± 5.62	2.74 ± 5.51	2.91
Arthropoda	4	2.17	4	1.43	650.26	2.35	1.98	0.04 ± 0.1	6.19 ± 22.96	1.43 ± 3.81	1.34 ± 4.82	1.38
Lepidoptera	2	1.09	2	0.71	1,971.73	7.13	2.98	0.02 ± 0.1	18.78 ± 133.88	1.27 ± 7.25	1.61 ± 8.34	1.44
Diptera	1	0.54	2	0.71	33.32	0.12	0.46	0.02 ± 0.14	0.32 ± 2.3	0.38 ± 2.77	0.2 ± 1.48	0.29
Mantodea	1	0.54	2	0.71	287	1.04	0.77	0.02 ± 0.14	2.73 ± 19.81	0.48 ± 3.45	0.46 ± 3.30	0.47
Anura	1	0.54	1	0.36	53.45	0.19	0.36	0.01 ± 0.1	0.51 ± 5.22	0.14 ± 1.39	0.05 ± 0.53	0.09
Coleoptera	1	0.54	1	0.36	239.76	0.87	0.59	0.01 ± 0.1	2.28 ± 23.4	0.16 ± 1.63	0.54 ± 5.5	0.35
Insect Egg	1	0.54	1	0.36	1.46	0.01	0.3	0.01 ± 0.1	0.01 ± 0.14	0.1 ± 0.98	0 ± 0.02	0.05
Myriapoda	1	0.54	1	0.36	177.96	0.64	0.51	0.01 ± 0.1	1.69 ± 17.37	0.19 ± 1.95	0.42 ± 4.3	0.31
Squamata	1	0.54	1	0.36	266	0.96	0.62	0.01 ± 0.1	2.53 ± 25.96	0.24 ± 2.44	0.42 ± 4.32	0.33
Total	184	100	280	100	27,645.46	100						