Foraging behavior and diet composition of the gecko *Phyllopezus periosus* (Squamata: Phyllodactylidae) in the Brazilian semiarid Caatinga

Cristiane Nikely Silva Palmeira[1,3], Ubiratan Gonçalves[2,3], Raul Fernandes Dantas Sales[1,4], Eliza Maria Xavier Freire[1,4]

[1]Programa de Pós-graduação em Desenvolvimento e Meio Ambiente, Centro de Biociências, Universidade Federal do Rio Grande do Norte, 59078900, Natal, RN, Brasil.

[2]Laboratório de Biologia Integrativa, Universidade Federal de Alagoas, 57072-970, Maceió, AL, Brasil.

[3]Museu de História Natural da Universidade Federal de Alagoas, 57010-060, Maceió, AL, Brasil.

[4]Departamento de Botânica e Zoologia, Laboratório de Herpetologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte – UFRN. CEP 59078900, Natal, RN, Brasil.

ABSTRACT

In this study, we provide new data about the foraging behavior and feeding ecology of *Phyllopezus periosus*, a large-sized gecko endemic from the semiarid Caatinga, northeastern Brazil, looking to answer the following questions: (1) how is the foraging mode of *P. periosus*? (2) Which types of prey compose its diet? (3) Are lizards selective in diet? (4) Is prey size correlated with lizard body size? The fieldwork consisted of two ten-day excursions during the dry season in the Seridó Ecological Station, state of Rio Grande do Norte. We registered foraging behavior with a voice recorder and determined movement patterns of each focal lizard. For dietary data, we used stomach flushing to obtain consumed prey items. Prey availability was estimated with sets of pitfall traps placed in the surroundings of rocky outcrops where lizards occur. Our results indicate that *P. periosus* is a typical sit-and-wait forager, spending most of the time immobile (proportion time moving: 1.7 ± 1.9%, number of moves per minute: 0.4 ± 0.3) and performing mainly head moves and postural adjustments. The diet was massively composed of beetles, present in 48.4% of stomachs, representing 44.4% of total prey items and 63.5% of total volume. Lizards consumed beetles in a proportion slightly higher than their proportional availability in the environment, suggesting some preference for this prey category. Males and females presented similar body sizes and did not differ in diet composition. Body size was correlated with maximum prey size, but not with minimum prey size, suggesting that lizards in this population add larger prey items to the diet while growing, but at the same time continue consuming smaller ones. In addition, records of predation upon sympatric lizards and tree sap foraging evidence that *P. periosus* has opportunistic feeding habits.

Key Words: Electivity; Gekkota; Prey size; Saurophagy; Sit-and-wait foraging.

Introduction

Lizard diets are influenced by both intrinsic and extrinsic factors (Pianka, 1986). In seasonal environments, lizards often switch food based on availability, and diets tend to be more generalized when food is scarce (Pianka, 1970; Dunham, 1981; Carne and Measey, 2013; Sales and Freire, 2015). Besides extrinsic factors, foraging behavior, body size, sex, and ontogeny are important intrinsic factors that might influence lizard diets (Huey and Pianka, 1981; Perry, 1996; Vitt, 2000; Sales *et al.,* 2012). Moreover, lizards of some squamate clades, such as Gekkota (geckos and flap-footed lizards), have a developed

chemosensory system that allow discrimination of prey (Cooper, 1995), hence their diets may not include all range of available prey because individuals are able to avoid less profitable or potentially toxic items (Vitt and Pianka, 2005; Lisboa *et al.*, 2012).

The methods of food acquisition in lizards have been historically classified dichotomically as active (or wide) and sit-and-wait (or ambush) foraging (Pianka, 1966; Schoener, 1971). Active foragers move through the habitat searching for prey by sight and by frequently tongue-flicking to collect chemical cues, whereas sit-and-wait foragers usually remain immobile while scanning visually for approaching prey (Huey and Pianka, 1981). From the classic study of Pianka *et al.* (1979), which diffused quantitative parameters to describe foraging (proportion time moving – PTM; moves per minute – MPM), a continuum of foraging strategies have been identified in lizards, from highly sedentary ambushers that remain most of the time immobile to extreme active foragers that spend more than 80% of time moving while searching for prey (Perry, 1999; 2007).

Most geckos are considered sit-and-waits foragers, presenting low levels of PTM and MPM (Cooper *et al.,* 1999; Perry, 1999; Werner and Chou, 2002). However, a fluctuating foraging mode was identified in some species, characterized by relatively long periods of sedentary behavior, alternating with short bouts of very high activity (Werner *et al.,* 1997; 2006; Perry, 1999). This strategy presumably enables these nocturnal visual predators to ambush mobile prey while immobile, without wasting locomotor energy, and occasionally to actively search for sedentary prey, thereby increasing feeding opportunities (Werner *et al.,* 1997).

Phyllopezus periosus Rodrigues, 1986 (Fig. 1) is one of the largest Brazilian geckos (snout-vent length up to 126 mm; Passos *et al.,* 2013), endemic from the oriental portion of the Caatinga region, northeastern Brazil, from Ceará to Sergipe states (Passos *et al.,* 2013; Mesquita *et al.,* 2017). Information on the ecology of this species includes data on thermal ecology, daily activity and microhabitat use (Andrade *et al.,* 2013; Passos *et al.,* 2013; Ragner *et al.,* 2014), parasite infection (Almeida *et al.,* 2008), reproduction (Lima *et al.,* 2011), and some anecdotal observations about diet (Andrade *et al.*, 2016). *Phyllopezus periosus* has nocturnal activity and shows a fidelity for areas with rocky outcrops in the Caatinga, where it stays on rocky surfaces and climbs trees in the vicinity (Andrade *et al.,* 2013; Passos *et al.,* 2013).

In this study, we provide new data about the foraging behavior and feeding ecology of *P. periosus*, looking to answer the following questions: (1) how is the foraging mode of *P. periosus*? (2) Which types of prey compose its diet? (3) Is *P. periosus* selective in diet or does it capture all available prey in the environment? (4) Is prey size correlated with lizard body size? Our initial hypothesis and predictions were: (1) *P. periosus* behaves as a typical sit-and-wait forager, hence low values of PTM and MPM would be detected in the focal observations; (2) *P. periosus* presents a generalist diet directly associated to prey availability, hence a wide range of prey categories would be found in the stomach contents, and a significant correlation would exist between diet composition and prey availability in the environment; (3) lizards undergo an ontogenetic shift in the size of prey because larger lizards are able to capture larger prey while juveniles are gape limited, hence maximum prey size would to be correlated with lizard size; and (4) due to generalist feeding habits, larger lizards tend to capture all available prey regardless of their sizes, hence minimum prey size would not be correlated with lizard size.

Materials and methods

Study site

The Seridó Ecological Station (ESEC Seridó; central point: 06°34'36.2"S, 37°15'20.7"W, datum: WGS84, altitude: 192 m) comprises about 1165 hectares and is located in the municipality of Serra Negra do Norte, Rio Grande do Norte state, northeastern Brazil. The climate is semiarid, hot and dry (Bswh in Köppen classification) and the average temperature ranges from 28° C to 30° C; relative humidity ranges from 30 to 50% during dry months and from 50 to 70% in the rainy season (Varela-Freire, 2002). The ESEC Seridó is located at the "Depressão Sertaneja Setentrional" ecoregion of the Caatinga, and rainfall irregularity is a major feature of this ecoregion, as there is a quite pronounced water deficit for most of the year; the average annual precipitation ranges from 500 to 800 mm (Velloso *et al.,* 2002).

Fieldwork and morphometry

The fieldwork consisted of two ten-day excursions during the dry season in the study site, one in July 2015 and the other in October 2015. During each excursion, we dedicated a total of eight days for collecting dietary data, conducted by two collectors
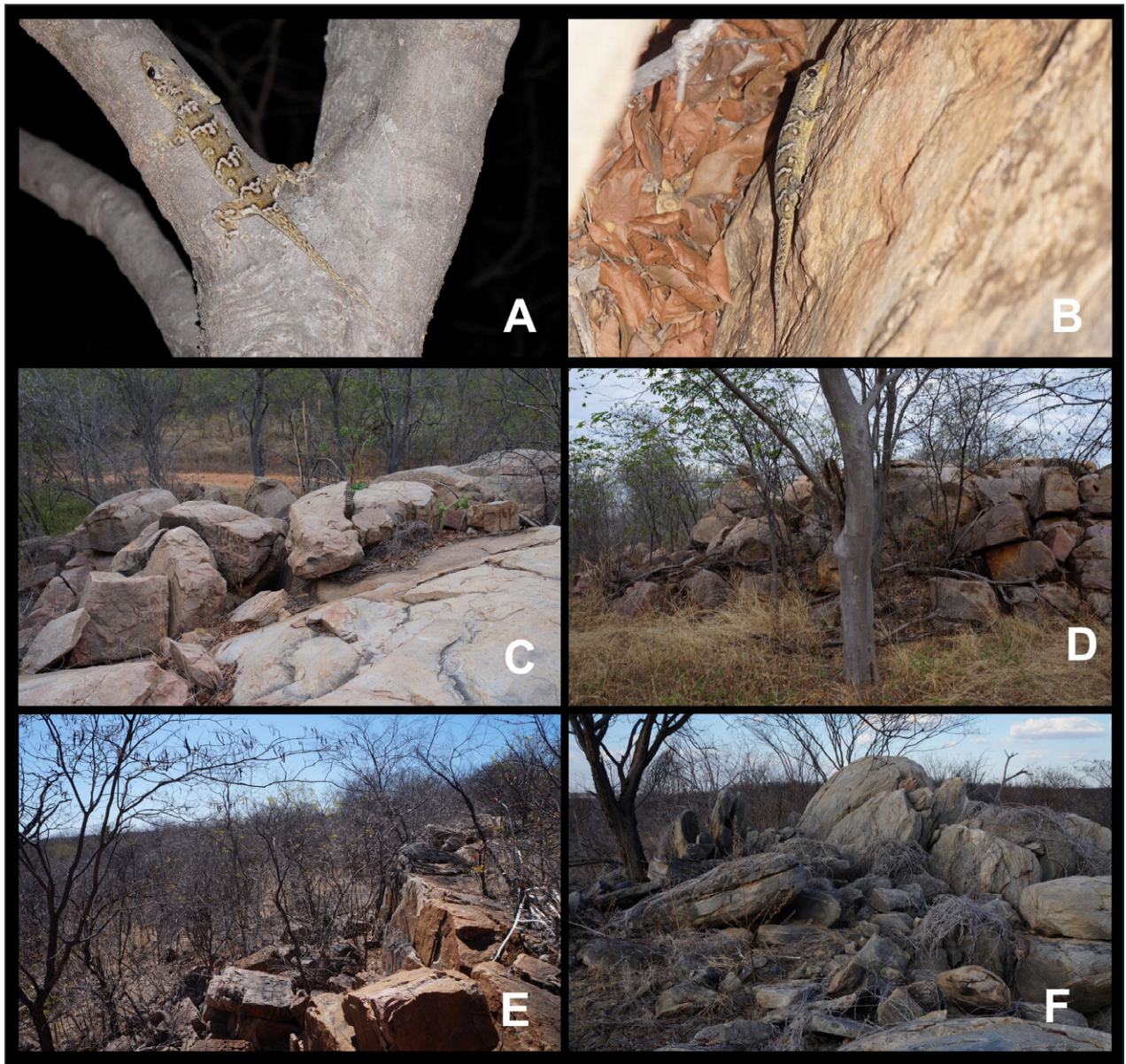
Figure 1. Adult individuals of *Phyllopezus periosus* recorded (A) perched on a tree close to a rocky outcrop and (B) on a boulder of a rocky outcrop, in Seridó Ecological Station, Rio Grande do Norte state, northeastern Brazil. (C-F) General view of rocky outcrops with crevices and shrubs and trees nearby, the habitat of *P. periosus* in the study site. (Photographed by Cristiane Palmeira).

at the same time (CNSP and UG), and two days for collecting behavioral data, conducted by a single observer (CNSP) in an exclusive observational area with 265 square meters (i.e. not surveyed for capturing lizards), hence different lizards were used for evaluation of diet composition and foraging behavior to avoid influence of capture on lizard behavior. The greater sampling effort spent to collect dietary data is justified by the fact that *Phyllopezus periosus* is difficult to capture manually, due to the facility of the lizards to shelter in refuges inside rock crevices.

To locate lizards in the field, we performed haphazard active searches, walking slowly through areas with rocky outcrops and arboreal-shrubby vegetation previously identified, where *P. periosus* occurs (Fig. 1). We alternated sampling times from 1700 to 0000 on one day, from 0000 to 0600 on the second day, and so on, covering the entire nighttime, which corresponds to the activity period of *P. periosus* (Andrade *et al.*, 2013). The sampling effort during the two field campaigns totaled 104 hours for gathering dietary data, and 26 hours for gathering behavioral data. We changed locations every 60 minutes of sampling effort to increase the chances

of locating different lizards.

We recorded foraging behavior without marking the lizards before or after focal observations. Thus, to avoid pseudo-replication, we noted with a GPS device the location where each focal lizard was and did not survey it again (Perry, 2007). To collect dietary data, we captured the lizards by hand and took them alive to the research facilities of ESEC Seridó. Then, with the aid of a digital caliper (0.01 mm precision), we took the following measurements: snout-vent length (SVL), from the tip of the snout to the anterior end of cloaca; head length (HL), from the posterior margin of the tympanum to the tip of the snout; head width (HW) at the widest point of the skull; head height (HH) at the maximum height of the skull; and jaw length (JL), from the tip of the snout to the labial commissure. We determined the sex of the animals by injecting a small amount of mineral water with a disposable syringe at the base of the tail near the cloaca; with this procedure, the hemipenis was everted in males. The classification of individuals into adult and juvenile categories was done according to Rodrigues (1986), considering juveniles those individuals with higher number of well-defined dorsal stripes and SVL < 70 mm, and adults those lizards with gold-yellow belly and SVL > 70 mm. We marked the captured lizards with a non-toxic ink to avoid pseudo-replication and released them and in their respective capture locations.

Foraging behavior

To register foraging behavior, when a lizard was located, the observer stopped moving and waited 5 min with the head flashlight on (355 lumens = 1649.74 lux) but not directed to the lizard to reduce the effect of human disturbance. After this habituation time, the observation period was started, with the observer remaining static and always keeping a minimum distance of 3 m from the animal. The flashlight was not aimed at the lizard, but laterally so that the periphery of the beam of light was sufficient to visualize it. If the lizard showed some indication of disturbance by human presence (e.g., increased head bobbing, flee the foraging spot at high speed), the observation was discontinued. Some of the locomotion of the individuals was towards the observer, hence presumably the observer did not affect them (Werner *et al.,* 1997). Only adults were sampled, and since we did not collect focal lizards (observational areas were different from areas used for dietary data), we could not determine their sex.

We observed only individuals that showed any sign of foraging behavior, such as changing the direction of the head, tongue-flicking the substrate, turning the whole body to another direction, slowly crawling, and/or "micromoves", which are quick moves of a few seconds, followed by immobility (Werner *et al.,* 1997).

Whenever possible, each lizard was observed for up to 15 min (Perry, 2007); however, observations of ≥ 5 min were included in our sample. We classified the focal animal as either "immobile" or "moving" based on its behavior. Lizards were considered immobile when their behavior did not result in displacement (postural changes, movements of head, limbs or tail, turning the body to another direction), whereas lizards exhibiting translational movements (displacement to a new location; e.g., walks, races, jumps), were considered moving. We noted the beginning and the end of each movement performed by the focal animal using an audio recorder. We adopted the methodology used by Werner *et al.* (1997) and Sales and Freire (2015) in the observations, defining a movement as an outbreak of locomotion separated from others through pauses of >1 sec. That is, when a moving animal stopped, the observer counted one second mentally before considering the movement as finished and defined the focal animal in the "immobile" category. The duration of each movement was calculated by summing the time between the beginning and the end of lizard mobility provided in the audio recordings. After completing the analysis of recordings, we calculated PTM and MPM for each focal lizard.

Diet composition

To obtain stomach contents of captured lizards, we used the stomach-flushing method described by Solé *et al.* (2005), with some adaptations. The flushing was done without any anaesthetizing and with careful handling of the animals. Lizards were held in the midbody, with the forelimbs and head supported by the fingers of the same hand. With the other hand, the mouth was opened with the help of a spatula, and a plastic probe was carefully inserted until just after the esophagus. Then mineral water was flushed into the stomach using a syringe of 20 mL for juveniles and of 60 mL for adults. When the water started to return through the mouth, the lizard was positioned vertically with the mouth down and its abdominal region was massaged to stimulate regurgitation of stomach contents, which were collected in an empty

plastic container. This procedure was repeated three times in each lizard to increase the chances of collecting the entire stomach contents. All retrieved food items were labeled and preserved in 70% ethanol. We kept stomach-flushed lizards under observation for 10 hours for survival control after the technique (Legler and Sullivan, 1979).

Stomach contents were spread in petri dishes and examined using a stereomicroscope to identify the ingested food items usually to the taxonomic level of order (Sales and Freire, 2015). Ants (Formicidae) were treated as an exclusive prey category in the order Hymenoptera. Vertebrates (lizards) were identified to the level of species by comparing prey items with voucher specimens of the Herpetology Collection of Rio Grande do Norte Federal University (UFRN-CH). We measured the length and width of each prey item with the help of millimeter-ruled graph paper, and the volume was estimated by the formula for a prolate spheroid: $V = 4/3 \, (length/2)(width/2)^2$ (Dunham, 1983). We determined the frequency of occurrence of each prey category as the number of stomachs containing the prey category *i*, divided by the total number of stomachs. Also, we calculated the numeric and volumetric percentages of each prey category for the pooled stomachs. We calculated the importance index (*I*) for each prey category by the formula: (frequency of occurrence + numerical percentage + volumetric percentage)/3 (Mesquita and Colli, 2003). This index was calculated for males, females, juveniles, and the total sample.

To evaluate prey availability, we placed 12 pitfall traps made up of 500 mL plastic pots (three sets of four pots) buried at ground level, placed about four to five meters away from each other, surrounding the rocky outcrops. Each pitfall remained open during four days in each field excursion, in daytime and nighttime periods. The pitfalls contained 150 mL of 93° ethanol to preserve individuals; 50 g of salt (sodium chloride) to prevent the biological material from disintegrating in the solution; 25 mL of neutral detergent to break the surface tension of the water; and 225 mL of water to mix all the mentioned ingredients (Costa TB, pers. communication). We identified the collected material to the level of order to compare with stomach contents.

For each lizard, we calculated maximum and minimum prey size by considering the items with the largest and smallest volumes in each stomach, respectively. Lizards that ingested fewer than two prey items were excluded from prey-size analyses due to incompatibility of estimating both maximum and minimum prey sizes (Sales *et al.*, 2012).

Statistical analyses

We tested for differences in body size (SVL) between males and females using a Student's t-test. To assess sexual differences in head dimensions (HL, HW, HH, JL), we performed analyses of covariance (ANCOVA), with SVL as the covariate. The degree of qualitative similarity in the diet of adult males and females was examined with the Pianka's Overlap Index – O_{jk} (Pianka, 1973), in which values range from 0 (no similarity) to 1 (complete similarity). The Mann-Whitney U test was applied to verify the existence of sexual differences in diet for the number of food items ingested and the volumetric sum of all prey items inside the stomach. The electivity of prey was calculated using the Ivlev's electivity index (Krebs, 1999): $IEI = (ri – ni)/(ri + ni)$, where *ri* is the percentage of prey category *i* in diet, and *ni* is the percentage of prey category *i* in environment. The values of this index range from -1 to +1, with values near +1 indicating preference, values near -1 indicating rejection, and values near 0 indicating consumption in the same proportion of the environment. We used Spearman's correlation to verify the relationship between diet composition and prey availability, using the number of prey items of each category. Linear regressions were performed to test the relationship between lizard size (SVL, HL, HW, HH, JL) and prey size (maximum and minimum prey volume), with all variables $\log_{10}$-transformed to meet the requirements of normality. All statistical analyses were performed using SPSS Statistics 20.0 software for Windows, with α set at 0.05. Before performing all the parametric tests, all variables were tested for normality and homoscedasticity of variances. Throughout the text, the descriptive statistics are represented as a mean ± standard deviation (SD).

Results

Morphometry

We collected 45 specimens of *Phyllopezus periosus*, 18 adult males, 20 adult females and seven juveniles. The mean SVL did not differ between sexes (males: 103.0 ± 12.2 mm, females: 101.2 ± 17.3 mm; t = 0.360, df = 34.1, p = 0.721). HL (males: 25.6 ± 2.4 mm, females: 25.7 ± 3.4 mm; $F_{1,35}$ = 2.098, p = 0.156), JL (males: 17.9 ± 2.3 mm, females: 17.9 ± 2.3 mm; $F_{1,35}$ = 1.939, p = 0.173), and HW (males: 18.3

± 1.8 mm, females: 17.9 ± 2.4 mm; $F_{1,35}$ = 0.325, p = 0.572) were also similar between sexes, but HH was significantly higher in males (males: 11.3 ± 1.6 mm, females: 10.4 ± 1.9 mm; ANCOVA, $F_{1,35}$ = 7.160, p = 0.011).

Foraging behavior
We recorded foraging behavior of 21 adult individuals of *P. periosus*. Total observation time reached 208 min and averaged 10.0 ± 2.0 min (range: 5.9 – 13.0 min) for each individual. Twelve focal lizards (57.1%) were in rock crevices, six lizards (28.6%) were above exposed rocks, and three lizards (14.3%) were on "catingueira" trees (*Cenostigma pyramidale*) in the vicinity of rocky outcrops, perched 2.5 to 4 meters from the ground. Focal lizards usually tongue-flicked the substrate and slowly moved the head sideways or upwards (at an angle of 90°) while immobile, presumably looking for prey by using both visual and chemical cues. They spent most of the time immobile, performing only directional moves with the head or body (i.e. turning the body to another direction). Translational moves were brief and resulted in displacement for short distances (some centimeters). When moving, lizards made jumps (possibly trying to capture some prey), slowly crawled the substrate or made "micromoves". Average PTM was 1.7 ± 1.9% (range: 0–6.5%), and average MPM was 0.4 ± 0.3 (range: 0–1.03). Although the recorded jumps were possibly prey capture attempts, we did not record successful prey capture episodes (i.e. lizard chewing after the capture attempt). Nonetheless, one lizard perched on a "catingueira" was observed feeding on the sap of the tree, moving its tongue slowly to obtain the sap released by a natural crack in the tree bark.

Diet composition
After the stomach-flushing procedure, only six lizards (three females and three males; 13.3% of total sample) did not regurgitate prey items, indicating that they had empty stomachs. Plus, eight individuals (four females and four juveniles; 17.8% of total sample) contained stomach contents in an advanced degree of digestion, making it impossible to identify any food item. In the other lizards (15 males, 13 females and three juveniles), we identified a total of 90 food items distributed in 16 prey categories, mostly arthropods (Table 1). The main prey category consumed by *P. periosus* was Coleoptera, present in 48.4 % of stomachs, representing 44.4% of total prey

items, 63.5% of total volume, and with a notably higher importance index compared to other prey categories (*I* = 52.1). Besides invertebrates (arthropods and mollusks) and some plant matter, we also identified two vertebrates in the stomach contents of *P. periosus*: the leaf-toed gecko *Hemidactylus agrius* (several body parts in high degree of digestion, evidencing consumption of the entire lizard) and the lava lizard *Tropidurus semitaeniatus* (only the tail, suggesting partial consumption).

Coleoptera was the predominant prey category in the diet of adult males (N = 15) and adult females (N = 13; Table 1). Both sexes ingested 11 different prey categories, and dietary niche overlap was high, both based on numerical (O_{jk} = 0.705) and in volumetric percentages (O_{jk} = 0.914). The number of prey items ingested (males: median = 4 items, females: median = 3 items; Mann-Whitney U = 84.5, p = 0.555) and the volumetric sum of all prey items inside the stomach (males: median = 125.6 mm³; females: median: 287.1 mm³; Mann-Whitney U = 84.0, p = 0.555) were also statistically similar between sexes. Juveniles (N = 3) presented a quite different diet composition, with consumption of only four prey categories, mainly Blattodea and Pseudoscorpiones (Table 1), but the small sample size does not allow major comparisons with adults.

The most registered taxa in the environment were Formicidae (41.8%), Coleoptera (20.2%), Collembola (9.2%), Diptera (8.6%), Blattodea (6.8%) and Acari (5.1%). The comparison between the diet composition of *P. periosus* and prey availability (Table 2) suggests that Coleoptera was slightly elected (IEI = 0.37) and Formicidae was avoided (IEI = -0.58). Moreover, some prey categories proportionally less consumed by *P. periosus*, such as Scorpiones, Phasmatodea, Mantodea, Gastropoda, Lepidoptera larvae and Vertebrata, showed positive values of electivity (Table 2). Diet composition and prey availability in the environment were not significantly correlated (r_s = 0.352, p = 0.071).

The body size of lizards showed a positive association with maximum prey volume (R^2 = 0.247, $F_{1,22}$ = 7.219, p = 0.013, y = 2.72x + 3.41; Fig. 2), but not with minimum prey volume (R^2 = 0.042, $F_{1,22}$ = 0.964, p = 0.337; Fig. 2). Head and mouth dimensions (HL, HW, HH, JL) also showed positive associations with maximum prey volume (R^2 values from 0.188 to 0.328, p-values < 0.05), but not with minimum prey volume (R^2 values from 0.012 to 0.056, p-values > 0.05).

Table 1. Diet composition of *Phyllopezus periosus* at the Seridó Ecological Station, Rio Grande do Norte, Brazil. F = frequency of occurrence, N = number, V = volume (mm3), I = importance index (T = total sample – N = 31; M = adult males – N = 15; F = adult females – N = 13; J = juveniles – N = 3). "—" indicates no individuals of that prey category were found.

Prey category	F (%)	N (%)	V (%)	IT	IM	IF	IJ
Acari	3 (9.7)	3 (3.3)	0.5 (<0.1)	4.3	6.1	3.4	—
Araneae	3 (9.7)	3 (3.3)	42.7 (0.5)	4.5	6.4	3.5	—
Blattodea	2 (6.5)	6 (6.7)	139.1 (1.7)	4.9	3.8	—	47.7
Coleoptera	15 (48.4)	40 (44.4)	5236.4 (63.5)	52.1	46.1	65.8	—
Formicidae	8 (25.8)	10 (11.1)	183.4 (2.2)	13.0	12.6	16.4	—
Gastropoda	1 (3.2)	1 (1.1)	659.4 (8.0)	4.1	—	8.6	—
Hemiptera	1 (3.2)	1 (1.1)	68.2 (0.8)	1.7	—	3.9	—
Lepidoptera (larvae)	2 (6.5)	3 (3.3)	193.8 (2.4)	4.0	4.8	4.1	—
Mantodea	1 (3.2)	1 (1.1)	26.7 (0.3)	1.6	—	3.6	—
Plant material	3 (9.7)	5 (5.5)	85.4 (1.0)	5.4	11.6	—	—
Orthoptera	5 (16.1)	5 (5.5)	157.6 (1.9)	7.9	13.4	3.6	—
Phasmatodea	1 (3.2)	1 (1.1)	613.9 (7.4)	3.9	8.3	—	—
Pseudoscorpiones	3 (9.7)	3 (3.3)	0.9 (<0.1)	4.3	—	—	43.6
Scorpiones	2 (6.5)	2 (2.2)	103.9 (1.3)	3.3	—	3.9	27.0
Thysanura	4 (12.9)	4 (4.4)	68.4 (0.8)	6.1	6.5	3.5	14.9
Vertebrata (lizards)	2 (6.5)	2 (2.2)	475.7 (5.8)	4.8	10.2	—	—
U.A.R.	6 (19.4)	—	188.1 (2.3)	—	—	—	—

Table 2. Diet composition of *Phyllopezus periosus* at the Seridó Ecological Station, Rio Grande do Norte, Brazil. F = frequency of occurrence, N = number, V = volume (mm3), I = importance index (T = total sample – N = 31; M = adult males – N = 15; F = adult females – N = 13; J = juveniles – N = 3). "—" indicates no individuals of that prey category were found.

Taxon	Diet (%)	Environment (%)	IEI
Acari	3 (3.3)	141 (5.1)	-0.21
Araneae	3 (3.3)	62 (2.2)	0.20
Blattodea	6 (6.7)	189 (6.8)	-0.01
Chilopoda	—	1 (<0.1)	-1
Coleoptera	40 (44.4)	559 (20.2)	0.37
Coleoptera (larvae)	—	2 (<0.1)	-1
Collembola	—	254 (9.2)	-1
Diplopoda	—	1 (<0.1)	-1
Diptera	—	237 (8.6)	-1
Embioptera	—	1 (<0.1)	-1
Hymenoptera Formicidae	10 (11.1)	1156 (41.8)	-0.58
Hymenoptera Chalcidoidea	—	48 (1.7)	-1
Isoptera	—	5 (0.2)	-1
Gastropoda	1 (1.1)	—	1
Hemiptera	1 (1.1)	25 (0.9)	0.10
Isopoda	—	4 (0.1)	-1
Lepidoptera (larvae)	3 (3.3)	2 (<0.1)	0.96
Mantodea	1 (1.1)	—	1
Plant material	5 (5.5)	6 (0.2)	0.93
Orthoptera	5 (5.5)	27 (1.0)	0.69

Phasmatodea	1 (1.1)	—	1.0
Pseudoscorpiones	3 (3.3)	16 (0.6)	0.69
Psocoptera	—	1 (<0.1)	-1
Scorpiones	2 (2.2)	—	1
Thysanura	4 (4.4)	17 (0.6)	0.76
Trichoptera	—	9 (0.3)	-1
Vertebrata (lizards)	2 (2.2)	—	1

Discussion

Our behavioral observations indicate that *Phyllopezus periosus* spends most of the time immobile while foraging (low PTM and MPM values), performing mainly head moves and postural adjustments. Hence, our results suggest a sit-and-wait foraging mode for *P. periosus*, and do not support a fluctuating foraging mode in this species, as suggested for some geckos, characterized by relatively long periods of sedentary behavior, alternating with short bouts of high activity (Werner *et al.,* 1997; 2004). Moreover, a widely accepted correlate of foraging mode is that sit-and-wait foragers will tend to eat larger, more active prey, whereas active foragers will tend to eat sedentary or spatially unpredictable prey (Huey and Pianka, 1981; Perry and Pianka, 1997). The diet composition of *P. periosus*, with predominance of beetles, which are mobile and evasive prey, is also a good indirect evidence of sit-and-wait foraging mode in this lizard.

Werner *et al.* (1997), based on movement pattern data, considered geckos as a group of mixed strategists, using a combination of sit-and-wait and active-foraging tactics. Bauer (2007), based on personal qualitative field observations of approximately 250 species of gekkotans, also argued for a fluctuating foraging behavior among some nocturnal geckos. Moreover, Werner *et al.* (1997; 2004) demonstrated that extending the focal observation period for geckos to 30 min reveals significant variation in movement patterns and, in some cases, suggests active-foraging behavior that would have been missed by observations of short duration. In our study, we did not found evidence of short bouts of high activity in any of focal lizards, but since we adopted a shorter duration of observations, ranging from 6 to 13 min, we do not discard the possibility of occasional episodes of more active foraging behavior in *P. periosus*. This saxicolous nocturnal gecko forages not only on rocks, but also climbs trees near rocky outcrops, so it is possible that these lizards, which are able to use both visual and olfactory cues (Cooper, 1995), may exploit serially different ambush sites, becoming more active when searching for these sites (Bauer, 2007).

Bauer (2007) conducted a literature review of studies on foraging modes of gekkotans and verified that only 9% of species and 44% of genera were investigated. However, most studies that characterized foraging mode of geckos used qualitative anecdotal field observations and/or indirect evidence such as diet composition to categorize species as sit-and-wait or active foragers. In fact, characterization of foraging mode in geckos based on movement pattern data (PTM, MPM or both) is restricted to approximately twenty species (Cooper *et al.,* 1999; Werner *et al.,* 1997; 2004; 2006; Perry, 1999; 2007; Werner and Chou, 2002; Hibbits *et al.,* 2005; Bauer, 2007; Murray *et al.,* 2015), which represents only 1% of gekkotan diversity. To our knowledge, this is the first quantitative study about foraging behavior of a gecko of the family Phyllodactylidae.

The diet of *P. periosus* at ESEC Seridó was predominantly composed of beetles (Coleoptera). Predominant consumption of Coleoptera also occurred, for instance, in the phyllodactylid geckos *Phyllopezus pollicaris* in western Brazil (Albuquerque *et al.,* 2013), *Phyllopezus maranjonensis*, *Phyllodactylus delsolari* and *Phyllodactylus reissii* in northern Peru (Aurich *et al.,* 2011), and *Homonota fasciata* in northwestern Argentina (Cocilio *et al.,* 2016). Although with much less importance, other prey categories were consumed by *P. periosus,* such as Formicidae, Orthoptera, Thysanura, Blattodea, Vertebrata (lizards), plant matter, among others. Moreover, the predation of the lizards *Hemidactylus agrius* and *Tropidurus semitaeniatus* reveals opportunistic feeding behavior in *P. periosus*. These two lizard species share the same habitats (rocky outcrops) and microhabi-
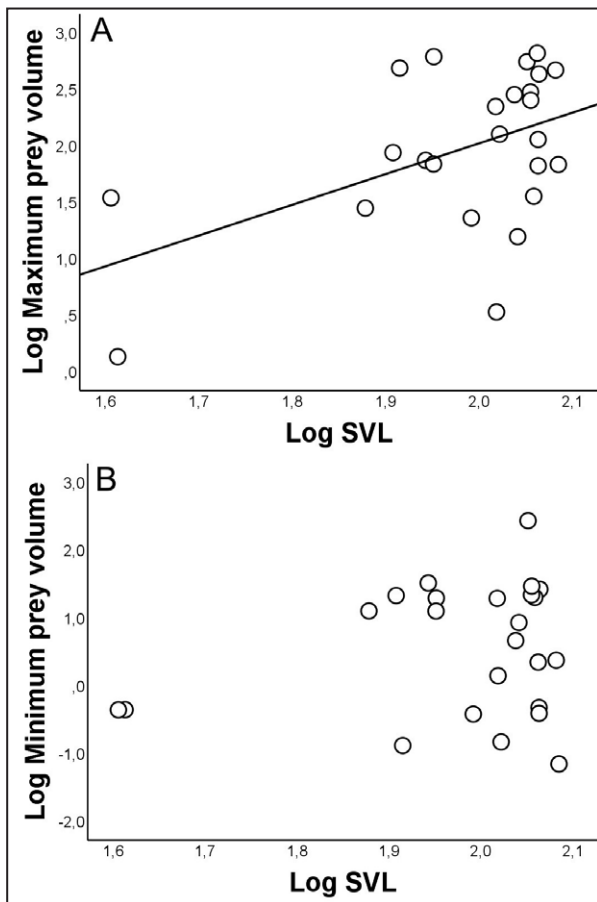
Figure 2. Relationship between snout-vent length – SVL (mm) and prey size (mm3) in *Phyllopezus periosus* at the Seridó Ecological Station, Rio Grande do Norte, Brazil. (A) SVL against maximum prey volume (y = 2.72x + 3.41, p < 0.05), (B) SVL against minimum prey volume (p > 0.05).

tats (rock crevices) with *P. periosus*, so it is likely that occasional encounters between them often result in predation attempts. Saurophagy has been reported for several geckos around the world, including cases of cannibalism (e.g. Bonfiglio *et al.,* 2006; Daza *et al.,* 2009; Blanco *et al.,* 2012). Additionally, it is worth mentioning the consumption of plant matter by *P. periosus*, including some seeds and sap of trees. Besides the consumption of the sap of *Cenostigma pyramidale* ("catingueira") recorded during focal observations, we also casually recorded an individual of *P. periosus* consuming the sap of a "anjico-branco" tree (*Anadenanthera colubrina*; CNSP, pers. Obs.). Besides these two new records of tree sap foraging, Andrade *et al.* (2016) recorded in three different occasions individuals of *P. periosus* eating the sap of the "baraúna" tree, *Schinopsis brasiliensis*.

Males and females of *P. periosus* consumed similar prey types and ingested a similar amount of

food items. Sexual differences in diet composition are usually attributable to sexual dimorphism in body and head dimensions that allows a differential consumption of prey between sexes, with the larger sex having the potential to consume larger prey (Schoener, 1967; Preest, 1994). Therefore, the occurrence of dietary differences between sexes in *P. periosus* was not expected, since there were no sexual differences in body size (SVL) and most of head dimensions (HL, HW, JL). Similarly, Rocha and Anjos (2007) did not find sexual differences in the diet of the House gecko *Hemidactylus mabouia*, which also shows no sexual dimorphism in body size, in an outcrop rocky area of southeastern Brazil.

The absence of relationship between the diet composition of *P. periosus* and prey availability in the environment suggests that lizards are, at least to some degree, selective about what they eat, rather than capturing all available prey items. This assumption is supported by the values of the Ivlev's Electivity Index, which indicated preferences for some prey categories and rejection of others. Lizards consumed beetles in a proportion slightly higher than their proportional availability in the environment, suggesting some degree of preference for this prey category. Moreover, some prey categories proportionally less consumed by *P. periosus*, such as Scorpiones, Phasmatodea, Mantodea, Gastropoda, Lepidoptera larvae and Vertebrata, showed positive values of electivity because they were scarce in the environment. On the other hand, the electivity index showed that ants (Formicidae) were avoided, as they were the predominant prey in the environment, but relatively little consumed by *P. periosus*. Gekkotans have a developed nasal chemosensory (Cooper, 1995) and are possibly able to detect and discriminate prey by chemical cues. Therefore, rejection of Formicidae may be associated with chemosensory avoidance, since many ants produce chemical defenses that may be noxious for predators (Vitt and Pianka, 2005).

The consequences of body size on feeding ecology have been studied in diverse taxonomic groups. In some cases, predators exclude smaller prey items from the diet as they grow and add larger items, in such a way that both minimum and maximum prey sizes increase at similar rates (e.g., Costa *et al.,* 2008; Costa, 2009; Sales *et al.,* 2012). In other cases, the predator adds larger items to its diet as it grows but continues to eat small prey; a positive relationship between predator body size and maximum prey size occurs, but minimum prey size remains constant

or increases with a much slighter slope (e.g., Scharf *et al.,* 2000; Sales *et al.,* 2011). Finally, the predator may not add larger items to its diet as it grows; in this case, minimum and maximum prey sizes are not correlated with body size (dietary specialists, e.g., Vitt *et al.,* 1997; Colli *et al.,* 2003). Our results support the second scenario for *P. periosus*, as body and head size were positively correlated with maximum prey size, but not with minimum prey size. Despite adding larger prey to their diet, larger lizards continue to consume small prey consistently, leaving minimum prey size constant. A skewness of available prey sizes, with predominance of smaller ones, is a possible explanation for this maintenance of consumption of small prey by larger individuals of *P. periosus.* A similar pattern of predator-prey size relationships was found in the sympatric teiid lizard *Ameiva ameiva* in the same study site (Sales *et al.,* 2011).

Conclusion

We conclude that *Phyllopezus periosus* is a sit-and-wait forager that consumes predominantly beetles at ESEC Seridó. Data indicates that these lizards are selective in food use and avoid some prey types with high abundance in the environment. In addition, predation of sympatric lizards and tree sap foraging are evidence of opportunistic feeding habits by *P. periosus.* Males and females have similar body sizes and do not differ in diet composition. Finally, the positive association between lizard body size and maximum prey size, but absence of relationship with minimum prey size suggests that lizards in this population experience an ontogenetic change in the diet, adding larger prey items while growing, but at the same time still continue consuming smaller ones.

Declaration of interest statement

There are no conflicts of interest that may affect the content, results or conclusions of the article.

Literature cited

Albuquerque, NR; Costa-Urquiza, AS; Soares, MP; Alves, LS & Urquiza MVS. 2013. Diet of two sit-and-wait lizards, *Phyllopezus pollicaris* (Spix, 1825) (Phyllodactylidae) and *Hemidactylus mabouia* (Moreau de Jonnès, 1818) (Gekkonidae) in a perianthropic area of Mato Grosso do Sul, western Brazil. *Biota Neotropica* 13(4): 376-381.

Almeida, WO; Santana, GG; Vieira, WS; Wanderley, IC; Freire, EMX & Vasconcelos A. 2008. Pentastomid, *Raillietiella mottae* Almeida, Freire and Lopes, 2008, infecting lizards in an area of caatinga, northeast, Brazil. *Brazilian Journal of Biology* 68: 427-431.

Andrade, MJM; Sales, RFD & Freire, EMX. 2013. Ecology and diversity of a lizard community in the semiarid region of Brazil. *Biota Neotropica* 13: 199-209.

Andrade, MJM; Carvalho, GAB; Kolodiuk, MF; Jorge, JS & Freire, EMX. 2016. *Phyllopezus periosus* (Paraiba Gecko). Tree sap foraging. *Herpetological Review* 47: 672-673.

Aurich, J; Koch, C & Böhme, W. 2011. Ecology of a gecko assemblage (Phyllodactylidae: Squamata) from northern Peru. *North-Western Journal Of Zoology* 7(2): 310-317.

Bauer, G. 2007. The foraging biology of the Gekkota: life in the middle: 371-404. *In*: Reilly, SM; McBrayer, LD & Miles, DB (eds.), Lizard ecology: The evolutionary consequences of foraging mode. Cambridge, UK: Cambridge University Press.

Blanco, G; Acosta, JC; Piaggio, L; Nieva, R; Victorica, A & Castillo, G. 2012. Saurofagia y canibalismo en dos especies de lagartos del centro-oeste de Argentina. *Cuadernos de Herpetología* 26(2): 91-93.

Bonfiglio, F; Lucchesi, BR & Cappellari, LH. 2006. Diet of *Hemidactylus mabouia* (Sauria, Gekkonidae) in urban area of southern Brazil. *Biociências* 14: 107-11.

Carne, L & Measey, J. 2013. Chameleons on the cruise: seasonal differences in prey choice of two dwarf chameleons. *Herpetological Journal* 23: 221-227.

Cocilio, RAN; Blanco, GM & Acosta, JC. 2016. Effects of season, sex and age on the diet of *Homonota fasciata* (Squamata, Phyllodactylidae) from Monte region of Argentina. *Iheringia Série Zoologia* 106: 1-5.

Colli, GR.; Mesquita, DO; Rodrigues, PVV & Kitayama, K. 2003. Ecology of the gecko *Gymnodactylus geckoides amarali* in a Neotropical Savanna. *Journal of Herpetology* 37: 694-706.

Cooper, WEJr. 1995. Prey chemical discrimination and foraging mode in gekkonoid lizards. *Herpetological Monographs* 9: 120–129.

Cooper, WEJr; Whiting, MJ; Van Wyk, JH & Mouton, PFN. 1999. Movement- and attack-based indices of foraging mode and ambush foraging in some gekkonid and agamine lizards from southern Africa. *Amphibia-Reptilia* 20: 391–399.

Costa, GC. 2009. Predator size, prey size, and dietary niche breadth relationships in marine predators. *Ecology* 90: 2014-2019.

Costa, GC; Vitt, LJ; Pianka, ER; Mesquita, DO & Colli, GR. 2008. Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards. *Global Ecology and Biogeography* 17: 670-677.

Daza, JD; Herrera, A; Thomas, R & Claudio, HJ. 2009. Are you what you eat? A geometric morphometric analysis of gekkotan skull shape. *Biological Journal of the Linnean Society* 97: 677–707.

Dunham, AE. 1981. Populations in a fluctuating environment:

the comparative population ecology of the iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus*. *Miscellaneous Publications of Museum of Zoology* 158: 1–62.

Dunham, AE. 1983. Realized niche overlap, resource abundance, and intensity of interspecific competition: 261-280. *In*: Huey, RB; Pianka, ER & Schoener, TW. (eds.), Lizard Ecology: Studies of a Model Organism. Cambridge: Harvard University Press.

Hibbitts, TJ; Pianka, ER; Huey, RB & Whiting, MJ. 2005. Ecology of the Common Barking Gecko (*Ptenopus garrulus*) in southern Africa. *Journal of Herpetology* 39(3): 509-515.

Huey, RB & Pianka, ER. 1981. Ecological consequences of foraging mode. *Ecology* 62: 991-999.

Krebs, CJ. 1999. Ecological Methodology. Addison Wesley Longman. California. 620p.

Legler, JM & Sullivan, LJ. 1979. The Application Of Stomach-Flushing To Lizards And Anurans. *Herpetologica* 35(2): 107-110.

Lima, DC; Passos, DC & Borges-Nojosa, DM. 2011. Communal nests of *Phyllopezus periosus*, an endemic gecko of the caatinga of northeastern Brazil. *Salamandra* 47: 227-228.

Lisboa, CMCA; Sales, RFD & Freire, EMX. 2012. Feeding ecology of the pygmy gecko *Coleodactylus natalensis* (Squamata: Sphaerodactylidae) in the Brazilian Atlantic Forest. Zoologia 29(4): 293-299.

Mesquita, DO & Colli GR. 2003. The Ecology of *Cnemidophorus ocellifer* (Squamata, Teiidae) in a neotropical savanna. *Journal of Herpetology* 37: 498-509.

Mesquita, DO; Costa, GC; Garda, AA & Delfim, FR. 2017. Species composition, biogeography, and conservation of the Caatinga lizards: 151-180. *In*: Silva, J; Leal, I & Tabarelli, M. (eds.), Caatinga. Springer, Cham.

Murray, IW; Fuller, A; Lease, HM; Mitchell, D; Wolf, BO & Hetem, RS. 2015. Low field metabolic rates for geckos of the genus *Rhoptropus* may not be surprising. *Journal of Arid Environments* 113: 35-42.

Passos, DC; Zanchi, D & Rocha, CFD. 2013. Basking in shadows and climbing in the darkness: microhabitat use, daily activity and thermal ecology of the gecko *Phyllopezus periosus*, Rodrigues, 1986. *Herpetozoa* 25(3/4): 171-174.

Perry, G. 1996. The evolution of sexual dimorphism in the lizard *Anolis polylepis* (Iguania): evidence from intraspecific variation in foraging behavior and diet. *Canadian Journal of Zoology* 74: 1238-1245.

Perry, G. 1999. The evolution of search modes: ecological versus phylogenetic perspectives. *American Naturalist* 153: 99-109.

Perry, G. 2007. Movement patterns in lizards: measurement, modality, and behavioral correlates: 13-48. *In*: Reilly, SM; McBrayer, LD & Miles, DB. (eds.). Lizard ecology: The evolutionary consequences of foraging mode. UK: Cambridge University Press. Cambridge.

Perry, G & Pianka, ER. 1997. Animal foraging: past, present and future. *Trends in Ecology and Evolution* 12: 360–364.

Pianka, ER. 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology* 47: 1055-1059.

Pianka, ER. 1970. Comparative autoecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. *Ecology* 51: 703-720.

Pianka, ER. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4: 53-74.

Pianka, ER. 1986. Ecology and natural history of desert lizards. Princeton University Press. Princeton. 208 p.

Pianka, ER; Huey, RB & Lawler, LR. 1979. Niche segregation in desert lizards: 67-115. *In*: Horn, JD; Mitchell, RD & Stains, GR. (eds.), Analysis of ecological systems. USA: Ohio State University Press. Columbus.

Preest, MR. 1994. Sexual size dimorphism and feeding energetics in *Anolis carolinensis*: why do females take smaller prey than males? *Journal of Herpetology* 28: 292-294.

Ragner, P; França, F; França, R & Silva, G. 2014. História natural do lagarto *Phyllopezus periosus* (Squamata: Phyllodactylidae) em um ambiente semi-árido no nordeste do Brasil. *Revista Biociências* 20: 5-12.

Rocha, CFD & Anjos, LA. 2007. Feeding ecology of a nocturnal invasive alien lizard species, *Hemidactylus mabouia* Moreau de Jonnès, 1818 (Gekkonidae), living in an outcrop rocky area in southeastern Brazil. *Brazilian Journal of Biology* 67: 485-491.

Rodrigues, MT. 1986. Uma nova espécie do gênero *Phyllopezus* de Cabaceiras: Paraíba: Brasil; com comentários sobre a fauna de lagartos da área (Sauria Gekkonidae). *Papéis avulsos de Zoologia* 36(20): 237-250.

Sales, RFD & Freire, EMX. 2015. Diet and foraging behavior of *Ameivula ocellifera* (Squamata: Teiidae) in the Brazilian semiarid Caatinga. *Journal of Herpetology* 49: 579-585.

Sales, RFD; Ribeiro, LB & Freire, EMX. 2011. Feeding ecology of *Ameiva ameiva* (Squamata: Teiidae) in a caatinga area of northeastern Brazil. *Herpetological Journal* 21: 199-207.

Sales, RFD; Ribeiro, LB; Jorge, JJ & Freixe, EMX. 2012. Feeding habits and predator-prey size relationships in the whiptail lizard *Cnemidophorus ocellifer* (Teiidae) in the semiarid region of Brazil. *South American Journal of Herpetology* 7: 149-156.

Scharf, FS; Juanes, F & Rountree, RA. 2000. Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic niche breadth. *Marine Ecology Progress Series* 208: 229-248.

Schoener, TW. 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* 155: 474-477.

Schoener, TW. 1971. Theory on feeding strategies. *Annual Review of Ecology and Systematics* 2: 369-404.

Solé, M; Beckmann, O; Pelz, B; Kwet, A & Engels, W. 2005. Stomach-flushing for diet analysis in anurans: an improved protocol evaluated in a case study in Araucaria forests, southern Brazil. *Studies on Neotropical Fauna and Environment* 40(1): 23-28.

Varela-Freire, AA. 2002. A Caatinga Hiperxerófila do Seridó: a sua Caracterização e Estratégias para sua Conservação. Academia de Ciências do Estado de São Paulo. São Paulo.

Velloso, AL; Sampaio, EVSB & Pareyn, FGC. 2002. Ecorregiões: propostas para o bioma Caatinga. Instituto de Conservação Ambiental, Recife.

Vitt, LJ. 2000. Ecological consequences of body size in neonatal and small-bodied lizards in the neotropics. *Herpetological Monographs* 14: 388-400.

Vitt, LJ & Pianka, ER. 2005. Deep history impacts present day ecology and biodiversity. *Proceedings of the National Academy of Sciences* 102: 7877-7881.

Vitt, LJ; Zani, PA & Avila-Pires, TCS. 1997. Ecology of the arboreal tropidurid lizard *Tropidurus* (= *Plica*) *umbra* in the Amazon region. *Canadian Journal of Zoology* 75: 1876-1882.

Werner, YL & Chou, LM. 2002. Observations on the ecology and foraging mode of the arrhythmic equatorial gecko

Cnemaspis kendallii in Singapore (Sauria: Gekkoninae). *Raffles Bull. Zool.* 50: 185–96.

Werner, YL; Okada, S; Ota, H; Perry, G & Tokunaga, S. 1997. Varied and Fluctuating Foraging Modes in Nocturnal Lizards of the Family Gekkonidae). *Asiatic Herpetological Research* 7: 153-165.

Werner, YL; Takahashi, H; Yasukawa, Y & Ota, H. 2004. The varied foraging mode of the subtropical eublepharid gecko *Goniurosaurus kuroiwae orientalis*. *Journal of Natural History* 38: 119–34.

Werner, YL; Takahashi, H; Yasukawa, Y & Ota, H. 2006. Factors affecting foraging behaviour as seen in a nocturnal ground lizard, *Goniurosaurus kuroiwae kuroiwae*. *Journal of Natural History* 40(7–8): 439–459.