

## AUTECOLOGY OF THE GECKO *HEMIDACTYLUS AGRIUS* IN A PROTECTED AREA OF THE BRAZILIAN SEMIARID CAATINGA

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**Abstract.**—We studied the autecology of the gecko *Hemidactylus agrius* at the Seridó Ecological Station (ESEC Seridó), a protected area of the Brazilian Caatinga, northeastern Brazil. Monthly, we inspected a sampling area composed of five transects of 200 m from August 2012 to August 2013. We recorded active lizards only during the night, predominantly in areas with rocky outcrops, where lizards used all available microhabitats equitably. Adult females ( $n = 25$ ) were significantly larger than adult males ( $n = 18$ ) in body size, but males had relatively longer and wider heads than females. The diet was composed mainly by insect larvae, termites, and spiders, and showed variations between dry and wet times, both qualitatively and quantitatively. We found no intersexual differences in diet, but ontogenetic differences were evident, chiefly in prey size. The body size of lizards was positively associated with maximum prey size, but not with minimum prey size. Rainfall seasonality did not play a determining role in habitat/microhabitat use and lizard abundance but influenced diet composition.

**Key Words.**—cannibalism; diet; Gekkonidae; habitat use; lizards; seasonality; sexual dimorphism; Squamata

### INTRODUCTION

In tropical habitats, which have more stability in temperature and photoperiod than temperate habitats, seasonality in rainfall stands out as the most important extrinsic factor affecting the ecology of lizards (Miranda and Andrade 2003; Sales and Freire 2015). Among tropical habitats in South America, the Caatinga is a well-recognized ecological region of about 912,000 km<sup>2</sup> in semiarid northeastern Brazil. It is the largest and most continuous expanse of Seasonally Dry Tropical Forest and Woodland biome in the world (Queiroz et al. 2017). Like other semiarid regions, the Caatinga has an extended dry period in which rainfall is scarce, and most of the vegetation is deciduous (Velloso et al. 2002). Ecological studies with lizards from the Caatinga have identified apparent effects of rainfall seasonality in abundance of active individuals (Sales et al. 2011a), diet composition (Kolodiu et al. 2009; Sales et al. 2011b), foraging behavior (Ribeiro and Freire 2011; Sales and Freire 2015), thermoregulatory behavior (Ribeiro and Freire 2010; Sales and Freire 2019), and reproductive cycles (Ribeiro et al. 2012).

*Hemidactylus* is one of the most species-rich genera of the family Gekkonidae, currently with 164 described species (Uetz P., P. Freed, and J. Hošek. 2020. The Reptile Database. Available at <http://www.reptiledatabase.org>. [Accessed 23 October 2020]), and is widely distributed around the world, from tropical rainforests to arid areas

(Vanzolini 1968; Carranza and Arnold 2006; Bansal and Karanth 2010). Most *Hemidactylus* species, however, have a small geographic range (Carranza and Arnold 2006). Among the few species with broad geographic distribution, the Moreau's Tropical House Gecko (*Hemidactylus mabouia*) is native to Africa, but has been introduced throughout the New World (Vanzolini et al. 1980; Carranza and Arnold 2006; Rödder et al. 2008; Rocha et al. 2011). Besides the exotic *H. mabouia*, three native species are known to occur in Brazil, the Amaral's Brazilian Gecko (*H. brasiliensis*), the Antilles Leaf-toed Gecko (*H. palaichthus*), and the Country Leaf-toed Gecko (*H. agrius*; Fig. 1). The first is widely distributed in different Brazilian ecosystems (Rodrigues 2003), the second occurs only in the Amazon region (Ribeiro-Júnior 2015), and the third species seems to have a relictual distribution in the Caatinga region, northeastern Brazil (Vanzolini 1978; Rodrigues 1986, 2003), with a single occurrence record in Cerrado (Andrade et al. 2004).

Most knowledge on *Hemidactylus* lizards are from cosmopolitan species, such as the South Asian House Gecko (*H. frenatus*; McKay et al. 2009; Cameron et al. 2013), *H. mabouia* (Bonfiglio et al. 2006; Rocha and Anjos 2007; Iturriaga and Marrero 2013), and the Mediterranean House Gecko (*H. turcicus*; Williams and McBrayer 2007). Advances in the study of native *Hemidactylus* species with narrow distribution ranges in South America are still needed (Passos et al. 2015).



FIGURE 1. (A) An adult Country Leaf-toed Gecko (*Hemidactylus agrius*) from Seridó Ecological Station, Rio Grande do Norte state, northeastern Brazil. (B) General view of a rocky outcrop; the main habitat used by *H. agrius* in the study site. (Photographed by Maria Jaqueline Monte de Andrade).

For *H. agrius* in the Brazilian Caatinga, there are some published information on diet (Passos et al. 2015), habitat and activity periods (Andrade et al. 2013), occurrence of communal nesting (Bezerra et al. 2011), endoparasites (Anjos et al. 2011), sexual dimorphism (Passos et al. 2015), and morphometry of hatchlings (Passos and Borges-Nojosa 2011).

The Seridó Ecological Station (ESEC Seridó), a protected area of the Caatinga, is within a region of high environmental suitability for the invasion of the alien species *Hemidactylus mabouia* (Rödder et al. 2008), which has extended its range in Brazil and is commonly found in anthropic and perianthropic environments, but has also become established in natural habitats of different Brazilian ecosystems (Vanzolini et al. 1980; Rocha et al. 2011). Recent studies on the lizard assemblage of ESEC Seridó, however, revealed a relatively common occurrence of *H. agrius* and absence of the native *H. brasiliensis* and the exotic *H. mabouia* (Andrade et al. 2013; Caldas et al. 2016). The invasion of *H. mabouia* in the New World has resulted in negative impacts on populations of other native geckos (Carranza

and Arnold 2006).

The current occurrence of only *H. agrius* in this protected area and the future possibility of eventual invasion by *H. mabouia*, highlights the relevance of a study on the autecology of *H. agrius*, without the presence of congeneric competitors. Unfortunately, previous studies on the ecology of *H. agrius* (Anjos et al. 2011; Bezerra et al. 2011; Passos and Borges-Nojosa 2011; Passos et al. 2015) did not comment on whether sympatric congeneric species occurred in the study sites. In our study, we collected data to answer the following questions: (1) Is there sexual dimorphism in the population? (2) Is *H. agrius* a specialist or generalist in the use of habitats and microhabitats at ESEC Seridó? (3) Which types of prey compose the diet of *H. agrius*? (4) Are there sexual and ontogenetic variations in the diet composition? (5) Does temporal differences in rainfall influence lizard abundance and resource use by the population?

#### MATERIALS AND METHODS

**Study area.**—The Seridó Ecological Station (ESEC Seridó; central point: 06°34'36.2"S, 37°15'20.7"W; datum: WGS84; elevation = 192 m) comprises about 1,165 ha and is located in the municipality of Serra Negra do Norte, Rio Grande do Norte state, Brazil (Fig. 2). The climate is semiarid, hot, and dry (Bsw in Köppen classification) and the average temperature ranges from 28°–30° C; relative humidity ranges from 30–50% 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); however, our study period (August 2012 to August 2013) involved an unusual dry year, where annual rainfall reached only about 300 mm (Fig. 3). In our study, we based the dry and wet periods on the monthly precipitation and on the general appearance of the vegetation. Thus, the wet period corresponded to the months of March, April, and May 2013, when levels of rainfall were above 40 mm (Fig. 3) and the vegetation was green with a dense herbaceous stratum. The dry period covered the months of August 2012 to January 2013 and June to August 2013, which had the lowest levels of rainfall (Fig. 3) and a remarkable dry vegetation, with most trees and shrubs without green leaves, and a reduced herbaceous stratum.

**Methodological procedures.**—We inspected ESEC Seridó before for choosing and delimitating the most appropriate sampling areas based on areas with different

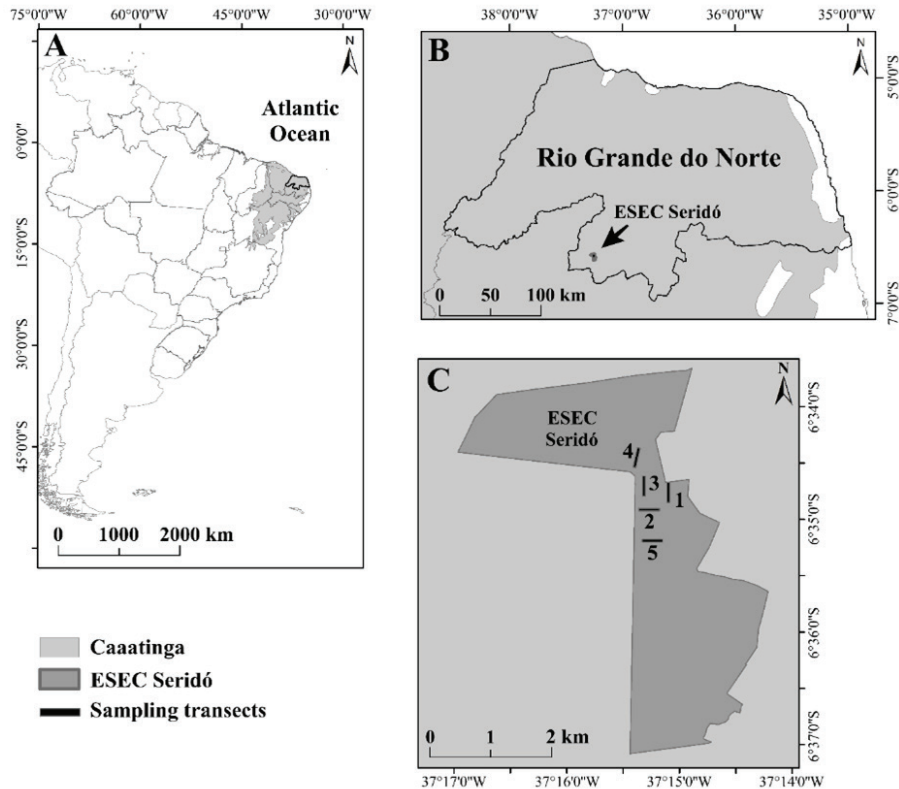


FIGURE 2. (A, B) Geographic localization of Seridó Ecological Station in Rio Grande do Norte state, northeastern Brazil. (C) Map of the study area showing the spatial distribution of sampling transects used in this study.

vegetation types, rocky outcrops, and anthropic areas, which constitute habitats for different species of *Hemidactylus*. According to these criteria, we selected five sampling areas, including the different habitats (Fig. 4). In each of these five sampling areas, we demarcated a transect of 200 m, with a minimum distance of 300 m from the starting point of the next transect (Fig. 2).

We made monthly excursions throughout wet and dry periods from August 2012 to August 2013, except in September 2012, February 2013, and July 2013 due to logistic issues. During each excursion, two collectors actively searched over the five delimited transects for three consecutive days, in nighttime and daytime periods. We searched from 1800–0000 on the first day, 0830–1100 and 1400–1730 the second day, and 0000 to 0500 the third day. Along the transects, we made incursions 10 m to the right and 10 m to the left to increase the sampling area per habitat types, which corresponds to each physiognomy. Thus, the total sampling area reached about 20,000 m<sup>2</sup> (2 ha). We identified seven habitats in the sampling area (Fig. 4): (1) Anthropogenic areas (AA): areas with the presence of human-made structures; (2) Arboreal-Shrubby Vegetation (ASV): areas predominantly composed of interspersed trees and shrubs; (3) Dense Shrubby Vegetation (DSV): areas with predominance of shrubs spaced < 1 m apart; (4)

Sparse Shrubby Vegetation (SSV): areas with shrubby vegetation spaced > 1 m apart, interspersed with herbaceous vegetation; (5) Herbaceous Vegetation in Open Area (HVOA): areas only covered by herbaceous vegetation; (6) Rocky Outcrops (RO): areas with predominantly fixed and loose rocks outcropping from soil surface interspersing the vegetation (Fig. 1); and (7) Rocky Formation (RF): areas of predominantly

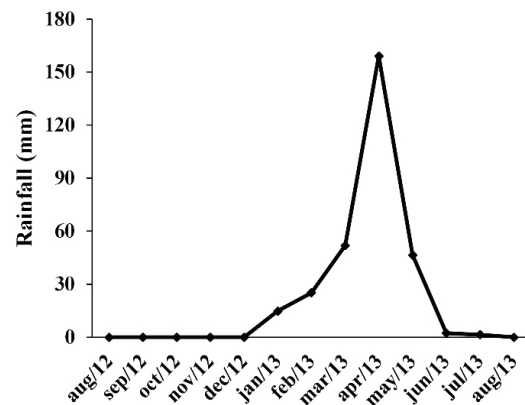
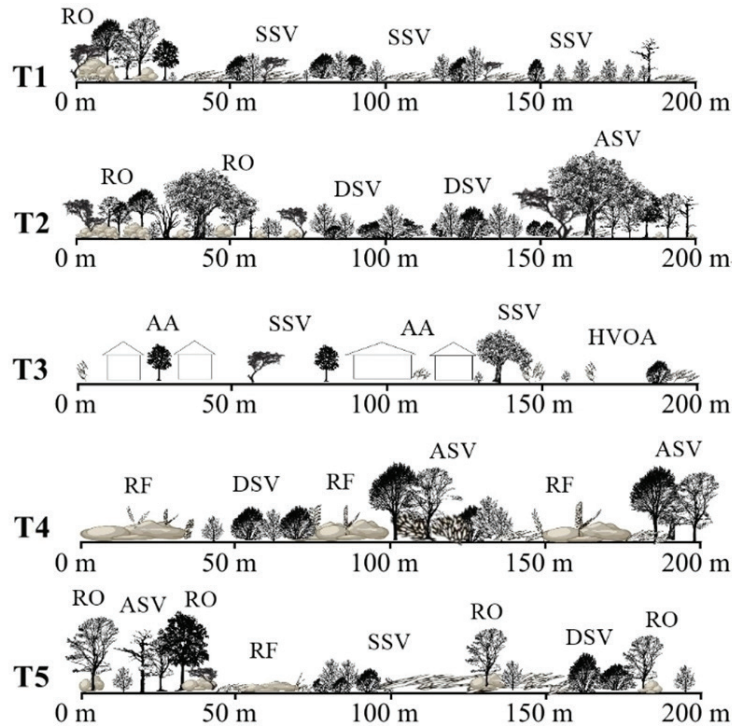


FIGURE 3. Total monthly rainfall (mm) recorded for Seridó Ecological Station, northeastern Brazil, from August 2012 to August 2013. (Taken from Empresa de Pesquisa Agropecuária do Rio Grande do Norte, EMPARN. <http://www.emparn.rn.gov.br/>).





**FIGURE 4.** Representative scheme showing the distribution of habitat categories along the five sampling transects (T1-T5) delimited in the Seridó Ecological Station, northeastern Brazil, from August 2012 to August 2013. Abbreviations are AA = Anthropogenic area, ASV = Arboreal-Shrubby Vegetation, DSV = Dense Shrubby Vegetation, SSV = Sparse Shrubby Vegetation, HVOA = Herbaceous Vegetation in Open Area, RO = Rocky Outcrops, and RF = Rocky Formation.

long stretches of rock that outcrop at the soil surface forming rocky pavements with absence of vegetation. Throughout these habitats, we identified a total of seven microhabitats: (1) Boulder (BO): rock with approximate spherical form, loose in the soil surface, with up to 1 m diameter; (2) Surface of Decomposing Trunk or Branch (DTB); (3) Base of Tree or Shrub (BTS); (4) Soil with Leaf Litter (SLL); (5) Human-made Structure (MS): houses or other human construction; (6) Inside Termite Nest (ITN); and (7) Soil with Herbaceous Vegetation (SHV).

For each *H. agrius* specimen registered in the field, we recorded time of observation and habitat/microhabitat where the lizard was first sighted. We successfully collected most individuals we found, but a few lizards escaped capture. In these cases, we noted the microhabitat patch, and we did not search this area again during the current field excursion to avoid counting the same individual twice. With the use of a digital caliper (0.01 mm precision), we took the following measurements of all animals collected prior to fixation: (1) snout-vent length (SVL), (2) head length (HL), (3) head width (HW), and (4) Jaw Length (JL). Then, we examined and dissected the lizards to identify the sex and to remove the stomachs. We determined the sex of lizards by direct examination of gonads. We estimated size at maturity for females based on the smallest

individual containing vitellogenic follicles or oviductal eggs and, for males, based on the smallest individual bearing enlarged testes and convoluted epididymis (Vitt 1983). We considered lizards with SVL below the size at maturity as juveniles. We fixed all captured specimens with 10% formalin, then preserved specimens in 70% ethanol, which we deposited at the Herpetological Collection of Universidade Federal do Rio Grande do Norte (voucher numbers: UFRN-CH 4023 to 4084).

We examined the stomach contents using a stereomicroscope to identify the ingested food items, usually to the level of Order. We measured the length and width of each prey item with using millimeter-ruled graph paper, and we estimated the volume by the formula for a prolate spheroid (Dunham 1983):

$$V = 4/3\pi (\text{length}/2) \times (\text{width}/2)^2$$

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. We also 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 summing the occurrence, numeric, and volumetric percentages and dividing by three (e.g., Mesquita and Colli 2003). For each individual

**TABLE 1.** Summary of morphometric characters (in millimeters) of adult males, adult females, and juveniles Country Leaf-toed Gecko (*Hemidactylus agrius*) at the Seridó Ecological Station, Rio Grande do Norte state, northeastern Brazil.

Variables	Males (n = 18)	Females (n = 25)	Juveniles (n = 19)
snout-vent length	44.9 ± 3.4 (40.3–50.5)	47.4 ± 3.1 (40.0–52.3)	31.6 ± 5.3 (22.0–37.7)
head length	12.9 ± 1.0 (11.5–14.7)	13.2 ± 0.9 (11.4–14.8)	9.5 ± 1.2 (7.0–10.9)
head width	9.0 ± 0.8 (7.9–10.5)	8.9 ± 0.6 (7.6–9.9)	6.4 ± 0.9 (4.9–7.7)
jaw length	8.4 ± 0.6 (7.1–9.3)	8.6 ± 0.7 (6.9–9.8)	6.3 ± 1.0 (4.5–7.7)

we calculated prey size (maximum, minimum, and mean prey volume). We excluded lizards that ingested fewer than two prey items from prey-size analyses due to incompatibility of estimating both maximum and minimum prey sizes (e.g., Sales et al. 2012).

**Statistical analysis.**—We calculated the niche breadths for space (number of individuals registered in each habitat and microhabitat category), time (number of individuals registered in each hourly interval) and food dimensions (values of importance index for each prey category) by using the Levins' Standardized Index (Krebs 1999):

$$B_L = (B - 1)/(N - 1)$$

with  $N$  as the number of categories and  $B$  as the Reciprocal Simpson Index. We calculated niche overlaps between adult males, adult females, and juveniles by using the Overlap Index ( $O_{jk}$ ) proposed by Pianka (1973), which is widely used in herpetological studies (e.g., Vitt 1995; Andrade et al. 2013).

We tested all variables for normality and homoscedasticity and only used parametric tests if assumptions were met. We tested for differences in SVL between adult males and females with a Student's  $t$ -test (Zar 1999). To evaluate the existence of sexual differences regarding the other morphometric measures (HL, HW and JL), we performed covariance analyses (ANCOVA) using SVL as the covariate (Zar 1999). To assess sexual, ontogenetic, and precipitation period differences in prey size (mean, minimum and maximum prey volume), number of food items ingested, and total stomach volume (total volume of prey inside the stomach) of each lizard, we used the Mann-Whitney U test (Zar 1999). We investigated the occurrence of precipitation period differences in diet composition with the Kolmogorov-Smirnov Two-group test (Siegel 1956), using the ratios of volume and importance index of each prey category during each season. We used this same test to investigate precipitation period differences in habitat/microhabitat use and activity patterns. We tested the relationship between body size of lizards (SVL) and prey size through simple linear regressions, with all variables log10-transformed to meet the requirements of normality. We made statistical

decisions at a significance level of 0.05 using IBM SPSS Statistic 20 software (IBM Corp., Armonk, New York, USA). We give descriptive statistics as mean ± 1 standard deviation.

## RESULTS

We made a total sampling effort of 92.25 h in the 7 mo of the dry period (77 h during the night and 15.25 h during the day) and 47.25 h in the 3 mo of the wet period (33 h during the night and 14.25 h during the day). We made 76 records of *H. agrius* in the field and collected 62 specimens (25 females, 18 males, and 19 juveniles). Relativizing by sampling effort (nocturnal hours only), in the dry period we made one record every 1.4 h (56 records, 45 lizards collected), while in the wet period we had one record for every 1.65 h of effort (20 records, 17 lizards collected).

The average SVL of adult females was significantly higher than that of adult males ( $t = -2.605$ ,  $df = 41$ ,  $P = 0.013$ ; Table 1). The sexes did not differ in jaw length ( $F_{1,40} = 0.722$ ,  $P = 0.401$ ), but head length ( $F_{1,40} = 7.428$ ,  $P = 0.009$ ) and head width ( $F_{1,40} = 20.00$ ,  $P < 0.001$ ) were significantly larger in adult males when the effect of SVL was removed (Fig. 5). We observed tail regeneration in 31 of 59 individuals (52.5%).

*Hemidactylus agrius* used five of the seven habitats in the study area (Table 2). We recorded most lizards (69.7%) in the Rocky Outcrop habitat, followed by the Arboreal-Shrubby habitat (15.7%) and Dense Shrubby Vegetation (10.5%; Table 2). The habitat niche breadth was narrow, both in dry ( $B_L = 0.30$ ) and wet periods ( $B_L = 0.33$ ). The distribution of lizards by habitats was similar between precipitation periods ( $D_{max} = 0.050$ ,  $P > 0.050$ ). The overlap in the use of habitats among males, females, and juveniles was almost complete ( $\phi_{MxF} = 0.984$ ,  $\phi_{MxJ} = 0.980$ ,  $\phi_{FxJ} = 0.976$ ).

We registered *H. agrius* in all seven recognized microhabitats (Table 2), of which the most used were Surface of Decomposing Trunk or Branch (40%), Boulder (36%), and Base of Tree or Shrub (12%; Table 2). The microhabitat niche breadth in the dry period ( $B_L = 0.54$ ) was broader than in the wet period ( $B_L = 0.32$ ); however, the distribution of lizards by microhabitats did not differ significantly between periods ( $D_{max} = 0.346$ ,  $P > 0.05$ ). Similar to habitat use, the overlap in the use

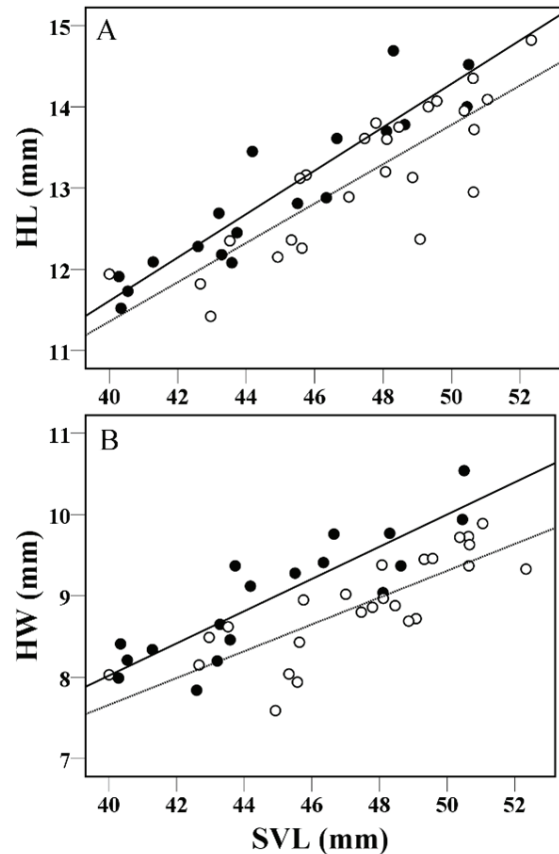
**TABLE 2.** Number of Country Leaf-toed Geckos (*Hemidactylus agrius*) recorded in each habitat and microhabitat categories used during dry and wet periods at the Seridó Ecological Station, Rio Grande do Norte state, northeastern Brazil, from August 2012 to August 2013.

	Dry period	Wet period	Total (%)
<b>Habitats</b>			
Rocky outcrop	39	14	53 (69.7)
Arboreal-shrubby vegetation	9	3	12 (15.7)
Dense shrubby vegetation	6	2	8 (10.5)
Anthropic area	2	--	2 (2.6)
Open herbaceous vegetation	--	1	1 (1.3)
Sparse shrubby vegetation	--	--	--
Rocky formation	--	--	--
<b>Microhabitats</b>			
Boulder	17	13	30 (39.5)
Decomposing trunk or branch	22	4	26 (34.2)
Base of tree or shrub	10	1	11 (14.5)
Soil with leaf litter	4	1	5 (6.5)
Human-made structure	2	--	2 (2.6)
Inside termite nest	1	--	1 (1.3)
Soil with herbaceous vegetation	--	1	1 (1.3)

of microhabitats among males, females and juveniles was almost complete ( $\emptyset_{MxF} = 0.951$ ,  $\emptyset_{MxJ} = 0.978$ ,  $\emptyset_{FxJ} = 0.947$ ).

Of the 76 records of *H. agrius* that we recorded, 75 (99.6%) occurred during the night, from 1800 to 0500 (Fig. 6). The only specimen recorded during the day was inactive. In dry times, we verified two apparent peaks of activity, the first one between 1800 and 2000, and the second between 0000 and 0300 (Fig. 6). In the wet period, records of active individuals were more evenly distributed along the night, with a single apparent peak between 2200 and 2300 (Fig. 6); however, the distribution of lizards by sampling hours did not differ significantly between precipitation periods ( $D_{\max} = 0.160$ ,  $P > 0.05$ ). The time niche breadth was broader in the wet period ( $B_L = 0.95$ ) than in the dry period ( $B_L = 0.76$ ).

The diet of *H. agrius* was mainly composed of arthropods (Table 3). Considering the total sample, the main prey categories in the diet, based on the Importance index, were insect larvae, Isoptera, and Araneae (Table 3). These three prey categories were the most frequently observed and the most important in number (Table 3). In terms of volume, Araneae, insect larvae, and Lepidoptera were the most important (Table 3). Besides arthropods, we also registered plant material (1% of total volume), and one vertebrate in the diet of *H. agrius*: a conspecific juvenile in the stomach of an adult female (42.6 mm SVL), characterizing a case of



**FIGURE 5.** Relationship between (A) snout-vent length (SVL) and head length (HL) and (B) SVL and head width (HW) of the Country Leaf-toed Gecko (*Hemidactylus agrius*) from Seridó Ecological Station, Rio Grande do Norte state, northeastern Brazil. Black circles represent males ( $r^2 = 0.86$ ,  $HL = 0.267SVL + 0.919$ ;  $r^2 = 0.77$ ,  $HW = 0.198SVL + 0.100$ ) and white circles represent females ( $r^2 = 0.70$ ,  $HL = 0.242SVL + 1.674$ ;  $r^2 = 0.65$ ,  $HW = 0.165SVL + 1.069$ ).

cannibalism. Seven (11.3%) of the 62 specimens we examined had empty stomachs, six of them we collected in the dry period.

During dry times ( $n = 45$ ), the prey categories with highest Importance index were insect larvae, Araneae, and Orthoptera, while when wet ( $n = 17$ ), Isoptera, insect larvae, and Lepidoptera were the most important (Table 3). The dietary niche breadth was narrower when wet ( $B_H = 5.6$ ) when compared to sampling when dry ( $B_H = 7.5$ ). The diet composition differed significantly between periods when we considered both the volumetric proportions of each prey category ( $D_{\max} = 0.258$ ,  $P < 0.050$ ) and the Importance index ( $D_{\max} = 0.314$ ,  $P < 0.010$ ). With respect to prey size, there are no significant differences between precipitation periods (minimum prey volume,  $U = 112.0$ ,  $P = 0.600$ ; maximum prey volume,  $U = 120.0$ ,  $P = 0.822$ ; mean prey volume,  $U = 101.0$ ,  $P = 0.349$ ). The number of prey items ingested, however, was significantly higher in the wet period ( $U = 113.0$ ,  $P = 0.012$ ), despite total

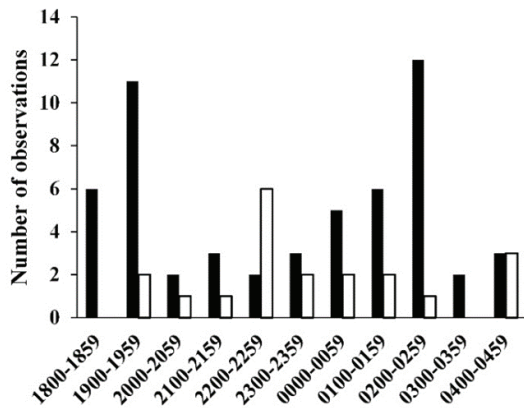


FIGURE 6. Hourly activity from 1800–0500 based on the number of Country Leaf-toed Geckos (*Hemidactylus agrius*) observed at ESEC Seridó, northeastern Brazil, during two dry (black bars) and one wet (white bars) periods, from August 2012 to August 2013.

stomach volume being similar between precipitation periods ( $U = 212.0$ ,  $P = 0.120$ ).

The diet of adult males ( $n = 18$ ) and females ( $n = 25$ ) of *H. agrius* was similar in relation to all variables analyzed (minimum prey volume:  $U = 67.5$ ,  $P = 0.568$ ; mean prey volume:  $U = 55.0$ ,  $P = 0.211$ ; maximum prey volume:  $U = 60.0$ ,  $P = 0.328$ ; numbers of prey items ingested:  $U = 130.0$ ,  $P = 0.457$ ; total stomach volume:  $U = 164.0$ ,  $P = 0.67$ ). On the other hand, adults and juveniles differed in maximum prey volume ( $U = 48.5$ ,  $P = 0.030$ ), mean prey volume ( $U = 38.0$ ,  $P = 0.009$ ), minimum prey volume ( $U = 42.5$ ,  $P = 0.016$ ), and total stomach volume ( $U = 150.0$ ,  $P = 0.004$ ), with higher values in adults. Adults and juveniles did not differ significantly in number of prey items ingested ( $U = -162.5$ ,  $P = 0.432$ ). The body size of lizards (SVL) was positively correlated with maximum prey volume ( $r^2 = 0.141$ ,  $F_{1,31} = 5.079$ ,  $P = 0.031$ ) and mean prey volume ( $r^2 = 0.187$ ,  $F_{1,31} = 7.118$ ,  $P = 0.012$ ), but not with minimum prey volume ( $F_{1,31} = 2.917$ ,  $P = 0.098$ ).

## DISCUSSION

In this study, we registered a similar relative number of individuals *Hemidactylus agrius* during dry and wet times. Variations in abundance of geckos based on precipitation periods may be related to mating activity (Tanaka and Nishihira 1987), but geckos in the Caatinga tend to reproduce year-round as a consequence of rainfall unpredictability (Vitt 1986; Alcantara et al. 2019). The sexual dimorphism in body size in *H. agrius* from ESEC Seridó, with females having larger SVL than males, differs from the pattern observed for this species in another Caatinga site, where males and females did not differ in SVL (Passos et al. 2015). The most common patterns in *Hemidactylus* species are absence

of intersexual differences in body size (Williams and McBrayer 2007; Iturriaga and Marrero 2013; Passos et al. 2015), or males being larger than females (Galina-Tessaro et al. 1999; Xu and Ji 2007; Díaz et al. 2012). Larger size in female lizards are attributable to fecundity selection favoring larger females (Xu and Ji 2007), but unlike many other lizards, female gekkonids do not increase clutch size by increasing body size (Vitt 1986). Nevertheless, the larger female size in *H. agrius* might possibly be associated with selection historically favoring females capable of producing slightly larger eggs (Vitt 1986), a hypothesis that still needs to be tested in *H. agrius*. We also cannot disregard the possibility of a greater number of older females than males in our sample producing the false impression of larger body size in females. On the other hand, the sexual dimorphism in head size, with *H. agrius* males having relatively larger and longer heads may be a result of sexual selection (Cooper and Vitt 1989; Anderson and Vitt 1990). This dimorphic morphological feature has also been recorded in other *Hemidactylus* species, such as *H. turcicus* in Texas, USA (Johnson et al. 2005), and the Oriental Leaf-toed Gecko (*H. bowringii*) in China (Xu and Ji 2007).

Regarding habitat use, *H. agrius* predominantly inhabits areas with rocky outcrops at ESEC Seridó. This habitat has a wide variety of microhabitats, providing shelter against high temperatures because crevices in rocks usually show a pattern of gradual microclimatic variation (Novaes-Silva and Araújo 2008). Additionally, the rocky outcrop habitat also includes trees and bushes that surround the rocks, presenting, in this way, other important sites widely used by *H. agrius* when inactive, such as trunk barks of trees and fallen trunks (Passos et al. 2015). Furthermore, rock crevices supply other important needs for sedentary lizards; for facilitating detection and access to certain types of prey (Kun et al. 2010) and enabling shelter against predators (Smith and Ballinger 2001; Ventura et al. 2017).

The nocturnal activity of *H. agrius* is similar to that found for the sympatric geckos *Phyllopezus pollicaris* (Brazilian Gecko) and *P. periosus* (Paraíba Gecko) at ESEC Seridó (Andrade et al. 2013), and is in accordance to what is described for species of the genus *Hemidactylus* (Rocha and Rodrigues 2005; Rocha and Anjos 2007). The activity profiles with a tendency to bimodality in dry times and unimodality in wet times might be related to thermoregulation and deserves further investigation. Daily bimodal activity is common among some diurnal heliothermic lizards, which decrease the activity in the hottest hours of the day (Caicedo-Portilla et al. 2010; Ribeiro and Freire 2010; Andrade et al. 2013). It is possible, however, that the temperature is not a determining factor in the activity profile of *H. agrius* at ESEC Seridó, as suggested for *H.*



**TABLE 3.** Diet composition based on the frequency, number, and volume (mm<sup>3</sup>) of prey items found in the stomachs of Country Leaf-toed Geckos (*Hemidactylus agrius*) during two dry and one wet periods at the Seridó Ecological Station, Rio Grande do Norte state, northeastern Brazil, from August 2012 to August 2013. Abbreviations are F = frequency of occurrence, N = number, V = volume, I = Importance index, and UAR = unidentified arthropod remains.

Prey category	Dry period (n = 45)				Wet period (n = 17)				Total sample (n = 62)			
	F (%)	N (%)	V (%)	I	F (%)	N (%)	V (%)	I	F (%)	N (%)	V (%)	I
Acari	1 (1.2)	1 (1.1)	3.5 (0.1)	0.8	—	—	—	—	1 (0.8)	1 (0.4)	3.5 (0.1)	0.4
Araneae	12 (15.1)	14 (15.3)	768.8 (31.8)	20.8	2 (6.1)	2 (1.5)	45.7 (3.6)	3.7	14 (12.5)	16 (7.3)	814.6 (22.1)	14.0
Blattaria	2 (2.5)	2 (2.1)	74.1 (3)	2.6	—	—	—	—	2 (1.7)	2 (0.9)	74.1 (2)	1.5
Coleoptera	5 (6.3)	5 (5.4)	51.9 (2.1)	4.6	1 (3)	1 (0.7)	32.9 (2.6)	2.1	6 (5.3)	6 (2.7)	84.9 (2.3)	3.4
Dermaptera	2 (2.5)	3 (3.2)	14.6 (0.6)	2.1	—	—	—	—	2 (1.7)	3 (1.3)	14.6 (0.3)	1.1
Diplopoda	—	—	—	—	2 (6.1)	2 (1.5)	28.2 (2.2)	3.2	2 (1.7)	2 (0.9)	28.2 (0.7)	1.1
Diptera	—	—	—	—	1 (3)	1 (0.7)	0.6 (0.1)	1.2	1 (0.8)	1 (0.4)	0.6 (0.01)	0.4
Homoptera	1 (1.2)	1 (1.1)	127.1 (5.2)	2.5	—	—	—	—	1 (0.8)	1 (0.4)	127.1 (3.4)	1.6
Hymenoptera	2 (2.5)	5 (5.4)	1.8 (0.07)	2.7	—	—	—	—	2 (1.7)	5 (2.2)	1.8 (0.05)	1.3
Insect Larvae	18 (22.7)	37 (40.6)	318.6 (13.2)	25.5	9 (27.2)	17 (13.3)	262 (20.7)	20.4	27 (24.1)	54 (24.7)	580.7 (15.8)	21.5
Isoptera	1 (1.2)	2 (2.1)	3.7 (0.1)	1.2	6 (18.1)	97 (76.3)	217.2 (17.2)	37.2	7 (6.25)	99 (45.4)	221 (6)	19.2
Lepidoptera	3 (3.7)	4 (4.3)	37.7 (1.5)	3.2	2 (6.1)	4 (3.1)	354.5 (28.1)	12.4	5 (4.4)	8 (3.6)	392.2 (10.6)	6.2
Orthoptera	6 (7.5)	8 (8.7)	360.9 (14.9)	10.4	—	—	—	—	6 (5.3)	8 (3.6)	360.9 (9.8)	6.2
Pseudoscorpiones	2 (2.5)	3 (3.2)	7 (0.2)	2	—	—	—	—	2 (1.7)	3 (1.3)	7 (0.2)	1.1
Thysanura	4 (5.0)	5 (5.4)	69.9 (2.9)	4.4	1 (3)	3 (2.3)	55.2 (4.3)	3.2	5 (4.4)	8 (3.6)	125.2 (3.4)	3.8
Plant material	4 (5)	—	4.8 (0.2)	—	2 (6.1)	—	35.2 (2.7)	—	6 (5.3)	—	40 (1.1)	—
Vertebrata (Lizard)	1 (1.2)	1 (1.1)	316.6 (13.1)	5.1	—	—	—	—	1 (0.8)	1 (0.4)	316.6 (8.6)	3.3
UAR	15 (18.9)	—	251.2 (10.4)	—	7 (21.2)	—	228 (18.1)	—	22 (19.6)	—	479.2 (13)	—

*turcicus* (Paulissen and Buchaman 1991).

Like other species of gekkonids (Perry and Brandeis 1992; Hibbitts et al. 2005), *H. agrius* showed a generalist diet, with predominance of insects with clumped distribution and low mobility (larvae, non-winged termites), and also nocturnal arthropods with high mobility (spiders, moths, crickets, winged termites). The diet composition of *H. agrius* at ESEC Seridó was similar to the one recorded for *H. brasiliensis* elsewhere in the Caatinga (Rocha and Rodrigues 2005; Menezes et al. 2013), and was also similar to another population of *H. agrius* in the Caatinga, except for the predominant consumption of orthopterans in that study (Passos et al. 2015). With respect to *H. mabouia*, it is important to stress that although this species is considered highly generalist, the same types of prey predominant in *H. agrius* diet are predominant in the diet of *H. mabouia* (Vitt 1995; Rocha and Anjos 2007;

Iturriaga and Marrero 2013). One possible explanation for the high consumption of both sedentary and active prey is that *H. agrius* may have a fluctuating foraging mode, sometimes behaving as an active forager and sometimes as a sit-and-wait predator, as observed for others geckos (Werner et al. 1997; Aowphol et al. 2006). The difference in the diet composition of *H. agrius* from dry and wet times was possibly due to the prevalence of opportunistic predation of termites and moths during the wet period. Additionally, the case of cannibalism recorded in *H. agrius* also suggests an opportunistic predatory behavior for this species, similar to *H. mabouia*, which also occasionally preys upon conspecifics (Bonfiglio et al. 2006; Costa-Campos and Furtado 2013). Several studies have reported cannibalism in lizards (Germano and Williams 1994; Bonke et al. 2011; Díaz et al. 2012), and these events are commonly associated with intraspecific aggression,



accidental feeding, and opportunism (Jenssen et al. 1989; Siqueira and Rocha 2008).

The absence of sexual differences in the diet of *H. agrius* is in accordance with studies conducted with *H. mabouia* (Bonfiglio et al. 2006; Rocha and Anjos 2007). On the other hand, we verified significant ontogenetic differences in prey size, with adults consuming larger prey, thus corroborating previous studies with others gekkonids (Perry and Brandeis 1992; Rocha and Anjos 2007). The absence of relationship of lizard body size with minimum prey size indicates that, although adults add larger prey to their diet, they continue to consume small prey, a pattern observed in several lizard species (Costa et al. 2008; Sales et al. 2011).

We conclude that *Hemidactylus agrius* is a strictly nocturnal species, inhabiting predominantly areas with rock outcrops at ESEC Seridó, where it uses all available microhabitats, mainly boulders, decomposing trunks and bases of trees and shrubs. Its diet is composed mainly by insect larvae, termites (both winged and non-winged forms) and spiders, and do not vary among sexes, but changes ontogenetically, chiefly in prey size. Rainfall differences among sampling periods did not play a determining role in habitat/microhabitat use and lizard abundance but influenced diet composition. Finally, additional studies would be useful to compare our data with areas where *H. agrius* occurs in sympatry with the native *H. brasiliensis* and/or the exotic and invasive *H. mabouia*.

**Acknowledgments.**—We thank the staff of Seridó Ecological Station for local logistics. This study was supported by research grants from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) to MJMA and RFDS, and from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) to EMXF. The permit for collecting the lizards was granted by the Instituto Chico Mendes de Conservação da Biodiversidade /Sisbio (Permit #36189-1).

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