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Habitat use, daily activity periods, and thermal ecology of *Ameiva ameiva* (Squamata: Teiidae) in a caatinga area of northeastern Brazil

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Abstract

Habitat use, daily activity periods, and thermal ecology of *Ameiva ameiva* (Squamata: Teiidae) in a caatinga area of northeastern Brazil. We studied the use of spatial, temporal, and thermal resources by the Neotropical lizard *Ameiva ameiva* during rainy and dry seasons in a caatinga (xerophilous open forests) environment in northeastern Brazil. Lizards used the vegetation habitats and microhabitats in the ground, but never were seen in the rocky habitat. Adults usually used the arboreal-shrubby habitat, whereas juveniles were sighted more often in the shrubby-herbaceous habitat. Ontogenetic differences in spatial use seem to be linked to different thermal needs between age groups owing to differences in body size. Body temperatures were significantly higher in juveniles than in adults. Most teiid species have elevated body temperatures, usually above 37ºC, and are active during the hottest times of day, as was observed for *A. ameiva* in this study. Seasonality influenced habitat use and daily activity periods of adults, but not body temperatures. We verified annual fluctuations in adult abundance, with a decline of active lizards in the dry season; this phenomenon may be related to aestivation and/or increased mortality rate during the driest months.

Keywords: abundance, body size, ontogeny, seasonality, thermoregulation.

Resumo

Uso do hábitat, períodos diários de atividade e ecologia térmica de *Ameiva ameiva* (Squamata: Teiidae) em uma área de caatinga do nordeste do Brasil. Estudamos o uso dos recursos espaciais, temporais e térmicos pelo lagarto neotropical *Ameiva ameiva* durante as estações seca e chuvosa em um ambiente de caatinga do nordeste do Brasil. Os lagartos utilizaram os hábitats e micro-hábitats de vegetação baixa, mas nunca foram observados no hábitat rochoso. Os adultos

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utilizaram usualmente o hábitat arbóreo-arbustivo, enquanto os juvenis foram observados mais frequentemente no hábitat arbustivo-herbáceo. Diferenças ontogenéticas no uso do espaço parecem estar relacionadas a diferentes necessidades térmicas entre as classes de idade devido a diferenças de tamanho corporal. As temperaturas corporais dos juvenis foram significativamente maiores que as dos adultos. A maioria das espécies de Teiidae possui temperaturas corporais elevadas, usualmente acima de 37ºC, e atividade concentrada nas horas mais quentes do dia, como observado em *A. ameiva* neste estudo. A sazonalidade influenciou o uso do hábitat e os períodos diários de atividade dos adultos, mas não influenciou as temperaturas corporais. Verificamos flutuações anuais na abundância de indivíduos adultos, com um declínio de lagartos ativos na estação seca; esse fenômeno pode estar relacionado à estivação e/ou ao aumento da taxa de mortalidade durante os meses mais secos.

Palavras-chave: abundância, ontogenia, tamanho corporal, sazonalidade, termorregulação.

Introduction

Body size is a fundamental trait that varies over different orders of magnitude among organisms within biological communities, with important implications for metabolism, physiology, and ecological aspects of individuals (Vitt 2000, Brown *et al*. 2004, Woodward *et al*. 2005, Costa *et al*. 2008). Within a lizard population, differences in body sizes of juveniles and adults may influence the ways in which the lizards use space, their diet, thermoregulation, competition, their predators, and home ranges (Vitt 2000). Seasonal variations in a number of extrinsic factors such as rainfall, availability of food resources, and environmental temperatures also produce variations in ecological aspects, such as space use, body temperatures, and daily activity periods, especially in seasonal ecosystems (Pianka 1986, Zaluar and Rocha 2000, Angert *et al*. 2002, Ribeiro *et al*. 2009).

The teiid lizard *Ameiva ameiva* (Linnaeus, 1758) has one of the largest geographic distributions among New World lizards, occurring from southern Mexico, through Central America and most of South America (Pianka and Vitt 2003). In Brazil, this lizard inhabits several different ecosystems, making it a conspicuous member of most lizard assemblages (Vitt and Colli 1994). It is a mid-sized lizard (snout–vent length up to 190 mm) that actively forages, moving about constantly in search of prey (Vitt and Colli 1994). The use of spatial and temporal resources, and thermal ecology of *A. ameiva* have been investigated in autoecological (Vitt and Colli 1994, Cruz-Neto and Gordo 1996, Sartorius *et al*. 1999, Zaluar and Rocha 2000), as well as in community ecological studies (Heatwole 1966, Duellman 1978, Vitt 1995, Mesquita *et al*. 2006a, b). These studies have shown that the species inhabits both open and forested habitats, has a relatively short daily activity period that usually is concentrated in the late morning and early afternoon, and maintains elevated body temperatures when active, usually above 37ºC. Few studies (Zaluar and Rocha 2000) have investigated the influence of seasonality and ontogeny on the life history traits of *A. ameiva*. In addition, the only published ecological study conducted with this species in the Brazilian caatinga is a result of fieldwork carried out in the 1970s in the state of Pernambuco by Vitt (1995), who did not report ontogenetic and seasonal variations in the ecology of *A. ameiva* because he was focusing more broadly on the lizard community structure.

We studied the ecology of *Ameiva ameiva* in the semiarid caatinga, an ecosystem with markedly seasonal rainfall. Our objectives were to: (1) evaluate habitat and microhabitat use by adults and juveniles; (2) identify lizard daily activity periods and relative abundance between rainy and dry seasons; and (3) investigate the existence of seasonal and ontogenetic variations in body temperatures and the influence of local environmental temperatures in determining body temperatures in lizards. We hypothesized that seasonality and ontogeny would influence life history traits of *A. ameiva* in the caatinga.

Materials and Methods

Study Site

The study was conducted at the Ecological Station of the Seridó (ESEC Seridó, 06º34'36.2" S, 37º15'20.7" W; datum: WGS84; altitude: 192 m), which encompasses a caatinga area of 1166.38 ha located in the municipality of Serra Negra do Norte, state of Rio Grande do Norte, Brazil (Figure 1). The climate is semiarid, hot and dry (Ab'Sáber 1974), with rainfall usually ranging between 500 and 700 mm/year. Mean annual temperatures vary from 28–30ºC, and maximum temperatures exceed 40°C on some days of the year, whereas the minimum ranges between 17ºC and 20ºC. Relative humidity varies between 30 and 50% in the dry season and between 80 and 90% in the rainy season (Nimer 1972). The vegetation of ESEC Seridó is arboreal-bushy hyperxerophilous; the ground is covered with herbaceous vegetation in the rainy season, which is greatly reduced in the dry season (Varela-Freire 2002). During the 1-yr period during which this study was conducted, the total rainfall was 782.3 mm. The rainy season included the month of June 2009, and between January and May 2010, whereas the dry season was from July–December 2009. Mean monthly rainfall during the dry and rainy seasons was 21.2 mm and 109.5 mm, respectively.

We categorized local habitats in our study site as: (1) *open habitat,* characterized by areas with only herbaceous vegetation and a small number of dispersed bushes; (2) *shrubby-herbaceous habitat,* characterized by areas covered predominantly by shrubs and interspersed with small areas of herbaceous cover; (3) *arboreal-shrubby habitat,* characterized by tree-covered areas interspersed with bushes, forming canopies in some areas of dense tree growth; and (4) *rocky habitat,* characterized by areas of rocky outcrops.

Field Work and Data Analysis

Fieldwork consisted of monthly excursions for three consecutive days between June 2009 and May 2010. To analyze activity periods and space use, we observed the lizards between 0800 and 1700 h, along trails that crossed the different habitat types in the study site. We walked continuously along the observational trails in a haphazard way (i.e., no time, speed or direction constraints), a technique maximizing the amount of information collected on the highest possible number of teiid lizards (Vitt and Colli 1994). For each individual observed, we recorded time, habitat and microhabitat type, and age class (adult or juvenile). The classification of lizards into adult or juveniles was based on a combination of the individual's size (adults having a snout–vent length [SVL] > 100 mm; Vitt 1995) and skin coloration (adults lacking the black lateral band from head to thighs that occurs in juveniles; Figure 2). Sampling times in the dry and rainy seasons were similar to allow a comparative seasonal approach with respect to the relative abundance of active individuals. We determined seasonal and ontogenetic differences in daily activity periods and space use by the Kolmogorov-Smirnov two-group test (Siegel 1975). Pearson's correlation (Zar 1999) was applied to test the relationship between the number of lizards observed per sampling hour each month and the monthly rainfall in the study site.

To analyze thermal ecology, we captured a number of lizards with 4.5-mm caliber air rifles (Urko®). At the moment of capture, we measured the following temperatures with a temperature sensor (Instrutherm® model S-02K) coupled to a digital thermohygrometer (accurate to 0.1ºC; Instrutherm® model HTR-300): body (cloacal), substrate, and air at 5 cm and 1.5 m above the substrate. The only lizards included in the analyses were those for which the body temperature was

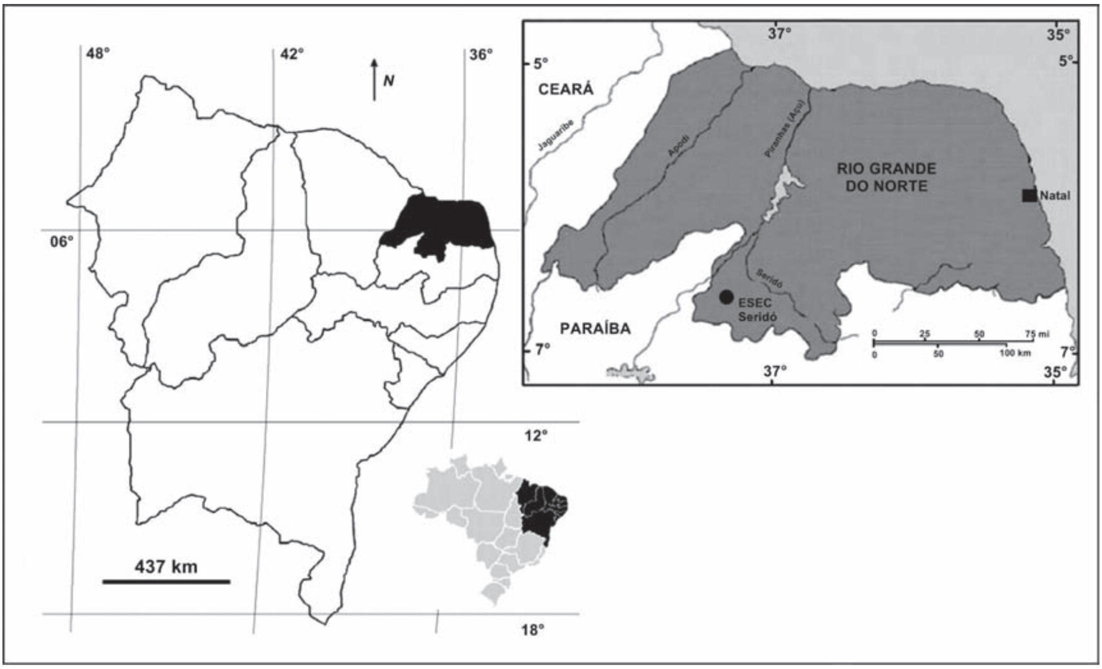

Figure 1. Geographic location of the Ecological Station of the Seridó (black dot = ESEC Seridó) in the southwest portion of the state of Rio Grande do Norte, Brazil.

obtained within 30 s of their capture. The body size of each lizard captured was recorded, and the specimens were deposited in the Herpetological Collection of the Department of Botany, Ecology and Zoology (CHBEZ) of the Universidade Federal do Rio Grande do Norte (UFRN).

Mean body temperatures of active *Ameiva ameiva* were determined by calculating the average of all cloacal temperatures recorded. Simple linear regressions were performed to test the relationship between body temperatures, and substrate and air temperatures. Analysis of variance (ANOVA) was conducted to evaluate the existence of body temperature differences between adults and juveniles. Analysis of covariance (ANCOVA) was used to assess differences between body temperatures of adults and juveniles, with substrate and air temperatures as covariates to remove the effect of environmental temperatures. The same analysis was used to determine seasonal differences in body temperatures with SVL as the covariate to eliminate the body-size bias in the sample among the seasons.

All statistical tests were performed using SPSS 16.0 software for Windows, with a significance level of 5% to reject the null hypotheses. Before performing parametric tests, all variables were tested for normality and homoscedasticity of variances, and met the requirements of parametric in all cases (Shapiro-Wilk's test, $p > 0.05$; Levene's test, $p > 0.05$). Descriptive statistics are represented as mean ± standard deviation (SD).

Results

Space Use

Of the four habitats recognized in the study site, lizards used the open, shrubby-herbaceous and arboreal-shrubby habitats, but none was

Figure 2. Adult male (**A**) and juvenile (**B**) *Ameiva ameiva* in the caatinga of the state of Rio Grande do Norte, Brazil. Note the black lateral band from head to thighs that occurs in juveniles but not in adults.

observed in the rocky habitat (Figure 3). Adults and juveniles differed in habitat use (D_{max} = 0.218, df = 2, p = 0.005), with adults using the arboreal-shrubby habitat more and juveniles using more the shrubby-herbaceous habitat (Figure 3). The main microhabitats used by both age classes were herbaceous vegetation and under shrubs (Figure 3). We found no differences in microhabitat use between adults and juveniles (D_{max} = 0.147, df = 2, p = 0.095). Habitat use

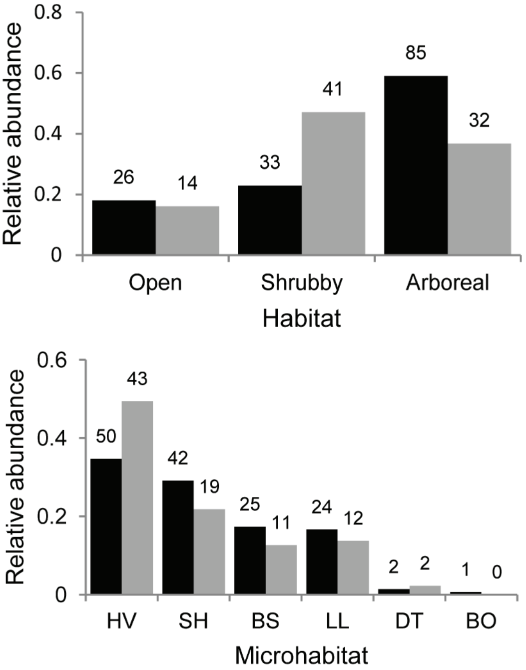

Figure 3. Relative distribution of adults (black bars) and juveniles (gray bars) by Habitat and Microhabitat at ESEC Seridó, Rio Grande do Norte, Brazil, from June 2009–May 2010. The numbers above the bars indicate the absolute abundance. Only habitats/microhabitats with occurrence of *Ameiva ameiva* are showed. Microhabitats: (HV) among herbaceous vegetation, (SH) under shrubs, (BS) bare sand, (LL) in leaf litter, (DT) on decomposing tree trunks, and (BO) on boulders.

differed between rainy and dry seasons for adults (D_{max} = 0.307, df = 2, p = 0.012), but not for juveniles (D_{max} = 0.114, df = 2, p = 0.623). We found no seasonal differences in microhabitat use for adults (D_{max} = 0.154, df = 2, p = 0.312) or juveniles (D_{max} = 0.237, df = 2, p = 0.102).

Activity Periods

Total fieldwork in the dry and rainy seasons was 194 and 171 hours, respectively. The daily activity periods of adults and juveniles during both seasons were concentrated between 0900 and 1500 h, corresponding to the hottest times of the day (Figure 4). During the dry season, we observed an average of 0.46 individuals of *Ameiva ameiva* per hour (0.24 juveniles/h and 0.22 adults/h). In the rainy season, we observed 1.17 individuals/hour (1.04 adults/h and 0.12 juveniles/h).

The activity period of the adult population was significantly different between seasons (D_{max} = 0.292, df = 2, p = 0.002). Peak activity occurred between 1200 and 1500 h in both seasons, but the activity period in the rainy season was slightly more extensive, with a considerable increase in the number of active lizards after 1000 h, whereas in the dry season, the number of active lizards increased only after 1100 h. The number of active adults was much greater during the rainy months (Figures 4A, 5); the number of lizards observed in the field decreased substantially in the dry season, and in the driest months (October–December), only one adult was observed (Figure 5). The highest daily activity peak for juveniles in the dry season occurred between late morning and early afternoon (1100 and 1500 h), whereas the activity period was reduced in the rainy season, with no individuals observed after 1400 h; however, activity periods did not differ significantly between seasons (D_{max} = 0.255, df = 2, p = 0.141). In contrast to adults, juvenile abundance was greater in the dry season (Figures 4B, 5). Activity periods did not differ between adults and juveniles, in either the dry (D_{max} = 0.233, df = 2, p = 0.087) or rainy season (D_{max} = 0.195, df = 2, p = 0.223).

A significant positive correlation was recorded between the number of adults sighted per hour in each month and monthly rainfall in the study site (r_p = 0.579, p = 0.048); however, there was no association between monthly rainfall and the number of juveniles observed per hour each month (r_p = -0.451, p = 0.141).

Thermal Ecology

Body temperatures of active lizards ranged from 32.5–41.0ºC (38.3 ± 1.8ºC, n = 22).

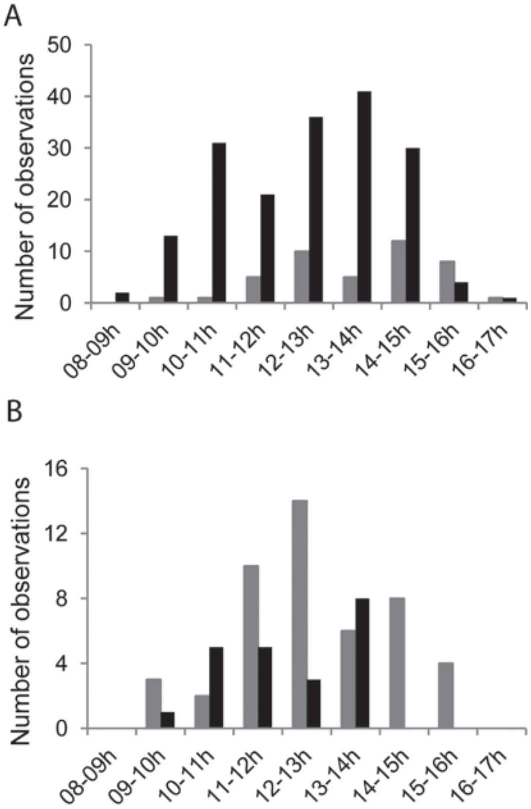

Figure 4. Daily activity periods of adults (**A**) and juveniles (**B**) of *Ameiva ameiva*, in the dry (gray bars) and rainy season (black bars), at ESEC Seridó, Rio Grande do Norte, Brazil, from June 2009–May 2010. In A: *n* = 43 (dry) and 179 (rainy); B: *n* = 47 (dry) and 22 (rainy).

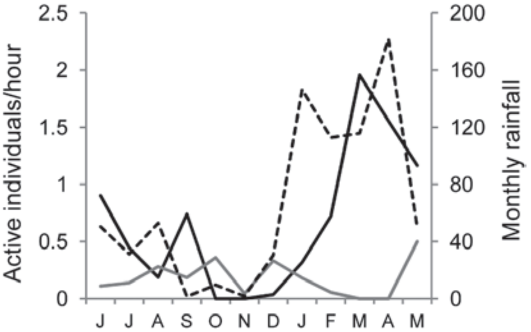

Figure 5. Number of active adult (black line) and juvenile (gray line) *Ameiva ameiva* observed per sampling hour between June 2009 and May 2010, at ESEC Seridó, Rio Grande do Norte, Brazil. The dashed line indicates monthly rainfall (mm) in the study site.

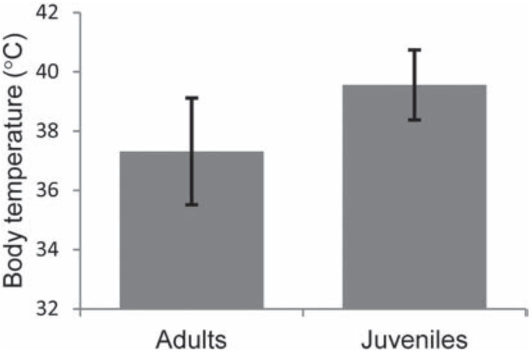

Figure 6. Mean body temperatures of adult (*n* = 12) and juvenile (*n* = 10) *Ameiva ameiva* at ESEC Seridó, Rio Grande do Norte, Brazil. Black lines indicate the standard deviation.

Substrate temperatures where lizards were collected varied from 22.5–46.0ºC (34.0 ± 5.0ºC), air temperatures at 5 cm above the ground from 22.7–42.0ºC (32.1 ± 4.2ºC), and at 1.5 m above the ground from 23.2–37.8ºC (31.4 ± 3.3ºC). We found significant positive associations between body temperatures and substrate temperatures ($r^2 = 0.244$, $F_{1,20} = 6.438$, $p = 0.020$), air temperatures 5 cm above the ground ($r^2 = 0.252$, $F_{1,20} = 6.752$, $p = 0.017$), and at a height of 1.5 m ($r^2 = 0.235$, $F_{1,20} = 6.150$, $p = 0.022$).

The mean body temperature of juveniles (39.5 ± 1.1ºC, range: 37.9–41.0, $n = 10$) was significantly higher than that of adults (37.3 ± 1.8ºC, range: 32.5–39.6, $n = 12$; $F_{1,20} = 11.376$, $p = 0.003$; Figure 6). Moreover, even when the effect of environmental temperatures was removed, the difference between juveniles and adults was significant (ANCOVA, $F_{4,17} = 5.834$, $p = 0.027$), showing that juveniles reached higher body temperatures than adults, irrespective of air and substrate temperatures. The mean body temperature of lizards in the dry season (39.1 ± 1.3°C, range: 36.9–41.0, $n = 13$) was higher than in the rainy season (37.1 ± 2.0°C, range: 32.5–39.6, $n = 9$), but this difference was not significant with the effect of body size removed (ANCOVA, $F_{2,19} = 3.173$, $p = 0.091$).

Discussion

Ameiva ameiva is strictly a ground lizard that is not found on vegetation perches or rocky outcrops at ESEC Seridó. This species typically is found in open areas within its vast geographical distribution (e.g., cerrados, Amazonian savannas, coastal restingas, semiarid caatingas), because these contain suitable basking sites to meet their thermal requirements (Zaluar and Rocha 2000). Furthermore, *A. ameiva* is one of the few teiid lizards that also inhabits forested areas with continuous canopy, such as the Amazonian rainforest (Vitt and Colli 1994, Sartorius *et al.* 1999). However, in forested areas, it is restricted to microenvironments that offer opportunities for sunning for extended periods during the day, such as on riverbanks and natural clearings (Sartorius *et al.* 1999). In addition, some studies have demonstrated that *A. ameiva* increases in abundance in areas that undergo deforestation and substitution by agricultural lands (Heatwole 1966, Duellman 1978). Therefore, it is one of the few lizard species that seems to benefit from changes in landscape caused by human activities (Vitt and Colli 1994).

We found seasonal differences in habitat use only for adult *Ameiva ameiva*, apparently due to a more equal utilization of habitats in the dry season. Nevertheless, we found no seasonal differences in microhabitat use for either adults or juveniles. In a restinga of southeastern Brazil, Zaluar and Rocha (2000) found no seasonal differences in spatial use. In the restinga, *A. ameiva* uses primarily the center of bushes for thermoregulation and foraging, and rarely is found on bare sand (Zaluar and Rocha 2000).

We verified that there are significant differences in the distributions of adults and juveniles in habitats. Adult lizards frequented the arboreal-shrubby habitat, an area with more vegetation cover, whereas juveniles were sighted more often in the shrubby-herbaceous habitat. This distinction may result from different thermal requirements in response to different body sizes. As the lizards grow, the surface/volume ratio is modified, resulting in changes in heating and cooling rates. As demonstrated experimentally by Sartorius *et al.* (1999), heating and cooling times on a gradient between 33 and 40°C were positively correlated with lizard body mass in an Amazonian population of *Ameiva ameiva*. Some studies have shown that small-bodied lizards tend to have a thermoregulatory advantage in sunny areas owing to the lower heat retention rate resulting from a high surface/volume ratio. Conversely, greater heat retention and thermal inertia of large-bodied lizards allows them to forage in shaded areas, unlike small-bodied lizards, which lose heat more rapidly (Hillman 1969, Asplund 1974). These studies suggest that lizards can change in terms of thermal needs as they grow and, as a consequence, experience changes in habitat use. This trend was evidenced for *Ameiva leptophrys* in Costa Rica, where adults and juveniles segregated in habitat use as a function of different thermal needs (Hillman 1969). Another hypothesis for the ontogenetic habitat segregation would be the avoidance of intraspecific competition for food between the age classes (e.g., Freeman and Stouder 1989, Davey *et al.* 2005). Adult *A. ameiva* consume larger prey than do juveniles, but also continue to feed on small prey (Sales *et al.* 2011). Thus, the age classes may compete for food resources. The plausibility of this hypothesis does not exclude the hypothesis of different thermal needs—i.e., both factors may affect habitat segregation.

As demonstrated by Pianka (1986), many sympatric lizard species share spatial resources, such that larger species use microhabitats with more vegetation cover than do smaller species. This tendency was observed, for example, in *Ameiva ameiva* and *Cnemidophorus littoralis* in a restinga of southeastern Brazil, where the former forages primarily in the center of bushes, while the latter forages on the edges (Zaluar and Rocha 2000, Teixeira-Filho *et al*. 2003). This tendency also seems to characterize *A. ameiva* and *Cnemidophorus ocellifer* in the ESEC Seridó (Sales, pers. obs.), as well as adult and juvenile *A. ameiva*, albeit with less intensity. Moreover, most adults observed in the open habitat were basking, not foraging. Thus, adult *A. ameiva* seem to use more open areas primarily for thermoregulation, restricting foraging to shadier areas with greater vegetation cover, in contrast to juveniles, which also forage in more open areas. The differences we found between juvenile and adult *A. ameiva* in habitat use and in body temperatures seem to be linked.

Body temperature of active *Ameiva ameiva* at the ESEC Seridó was similar to the mean temperatures recorded for other populations of this species studied in different ecosystems (Table 1). Despite the fact that the caatinga has a semiarid climate and the least canopy coverage of any habitat occupied by *A. ameiva*, the mean body temperatures of *A. ameiva* in the caatinga lie within the range of 37–40°C reported for all previously studied populations (Table 1). This similarity in temperatures among populations living in different habitats reveals conservation of body temperature during activity for this species. Some studies show that the body temperatures of lizards are more related to phylogenetic history than to ecological factors, suggesting that different populations of the same species or genus tend to have similar temperatures despite occurring in different types of environments (e.g., Bogert 1949, Andrews 1998, Menezes and Rocha 2011). The maintenance of elevated body temperatures during activity is a trend found in teiid lizards, as evidenced in other *Ameiva* species (e.g., Hillman 1969), and lizards of the genera *Cnemidophorus* (e.g., Menezes *et al*. 2000, Hatano *et al*. 2001, Mesquita and Colli 2003) and *Kentropyx* (e.g., Vitt 1991). These lizards maintain high body temperatures to sustain their elevated activity levels behaviorally, by alternating between areas of sun and shade, and sometimes stopping to bask when their body temperatures start to decline. The constant movement of *A. ameiva* seems to confirm the fact that different environmental temperatures explain only a small portion of the variation in lizard body temperatures.

The relatively short activity period of *Ameiva ameiva* restricted to the hottest times of day (between 0900 and 1500) is another trend found in teiid lizards (Rocha *et al*. 2009). The activity period observed for adults was longer during the

Table 1. Mean body temperatures of eleven *Ameiva ameiva* populations of different ecosystems in Brazil.

Ecosystem	Mean body temperature (°C)	Reference
Amazonian rainforest	38.8	Vitt and Colli 1994
	37.5	Sartorius *et al*. 1999
Amazonian savannas	38.9	Vitt and Colli 1994
	38.6	Vitt and Colli 1994
	37.0	Vitt and Carvalho 1995
	38.9	Mesquita *et al*. 2006b
Caatinga	39.4	Vitt 1995
	38.3	This study
Cerrado	37.7	Vitt and Colli 1994
	38.8	Mesquita *et al*. 2006a
Restingas (Atlantic rainforest)	37.8	Zaluar and Rocha 2000

rainy season, and this may be related to seasonal variations in environmental temperatures, as suggested by Zaluar and Rocha (2000) in a study of another population of *A. ameiva*, and Ribeiro *et al*. (2009) for a population of *Tropidurus torquatus* in southeastern Brazil.

The decline in the abundance of active adult lizards in the dry season seems to be related to rainfall seasonality, as demonstrated by the positive correlations between monthly rainfall and number of individuals observed per hour each month. Adult lizards were most abundant at the peak of the rainy season, whereas abundance in the dry season declined to the point that almost no adults were sighted in the three driest months, only juveniles. This pattern does not seem to have occurred as a result of a methodological flaw, given that the same phenomenon was observed in the dry season of 2008, the year before this study was conducted (Sales, pers. obs.). One explanation would be the aestivation of most individuals owing to low food supply in the environment; another possibility would be the increased mortality rate of older individuals during these months. Vitt (1991) reported a similar phenomenon for *Kentropyx calcarata* in the Amazonian rainforest, where he observed a fall in adult abundance during the dry season and attributed this finding to annual variations in population turnover. Magnusson (1987) also reported a similar trend for the teiid *Cnemidophorus lemniscatus* in an Amazonian savanna in northern Brazil, and suggested that the species might be annual. Likewise, we suggest that *A. ameiva* may be an annual species at the ESEC Seridó, with turnover of the population each year.

We conclude that the seasonality of the caatinga and lizard ontogeny influence some aspects of the ecology of *Ameiva ameiva*. Adults and juveniles differed to some extent in spatial use and body temperatures, apparently owing to different thermal demands as a consequence of differences in body size. Seasonality influenced spatial use and daily activity periods of adults, but not body temperatures of lizards. Finally, the reason for the massive decline in adult lizard abundance during the dry season may be related to aestivation caused by diminished abundance of food resources and/or an increase in adult mortality rate in this period.

Acknowledgments

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