

Activity, foraging mode and microhabitat use of *Enyalius perditus* (Squamata) in a disturbed Atlantic rainforest in southeastern Brazil

ANDRÉ F. BARRETO-LIMA¹, ÊNIO DE O. PIRES² & BERNADETE M. DE SOUSA²

¹) Universidade de Brasília – Programa Nacional de Pós-Doutorado, Instituto de Biociências, Departamento de Zoologia, Distrito Federal, Brazil. 70.910–900.

²) Programa de Pós-Graduação em Comportamento e Biologia Animal, Universidade Federal de Juiz de Fora, Instituto de Ciências Biológicas, Departamento de Zoologia, Minas Gerais, Brazil. 36.036–900.

Corresponding author: ANDRÉ F. BARRETO-LIMA, email: aflima1@gmail.com

Manuscript received: 2 April 2013

Abstract. We studied the activity, foraging mode and microhabitat use of *Enyalius perditus* in a disturbed reserve of Atlantic Forest in Minas Gerais, Brazil, during 2003 and 2004. We registered behavioural expressions of this species in the field for the first time. We inferred foraging modes based on distance covered, movement rates, and prey consumed by lizards. Activity was evaluated according to gender by frequency of movements per hour. This species exhibited diurnal activity, with all lizards foraging on the leaf litter, and males covered larger distances than females. The leaf litter was the microhabitat used most often by the lizards. At dusk, *E. perditus* used shrubs as “perch dormitories” and refuges. There was no difference in microhabitat use between genders. Although *Enyalius* species can be regarded as “sit-and-wait” foragers, our data showed that *E. perditus* can be an opportunistic forager, preying on leaf litter invertebrates, and moving about as a “cruising forager” in a disturbed forest model. We affirm that *E. perditus* is a “semi-arboreal” species, and this habit could primarily be a pattern conserved in the *Enyalius*’ genus as an anti-predatory adaptation.

Key words. Atlantic forest biome, cruising forager, Leiosaurinae, lizards, perch dormitories, semi-arboreal.

Introduction

Foraging habits are of central importance when interpreting ecological characteristics and life history traits of lizards since it influences various biological aspects (HUEY & PIANKA 1981, HUEY et al. 1983). An ecological premise of the theory of feeding strategies (SCHOENER 1971) classifies foraging mode as an influential factor in the activity pattern of the animal within its habitat (HUEY & PIANKA 1981). Its foraging mode can be inferred from the distance a predator covers for the purpose of foraging within its environment (PIANKA 1986), the types of prey consumed (HUEY & PIANKA 1981), and/or phylogenetic predispositions (COOPER 1995, 2007). Its diet can tell us much about its foraging mode, with larger active types of prey being associated with “sit-and-wait” foragers (‘sw’), while small, inactive, randomly distributed and clumped prey types will typically be associated with active foragers (‘af’) (HUEY & PIANKA 1981, PIANKA 1986, VITT et al. 1996b). Phylogenetic studies showed that frequency of movement and the time spent on foraging can reveal a classic dichotomy between the major taxa of lizards: as *Iguania* and *Gekkota* are more sedentary (‘sw’) with the lowest movement rates/min and percent-

age of time spent on movement for foraging compared to *Scincomorpha* and *Anguimorpha* (‘af’), which have greater movement rates and are more active (PERRY 1999). Recently, this dichotomy was also discovered in *Iguania* (‘sw’) vs. *Scleroglossa* (‘af’) (COOPER 2007), as well as in *Iguania* (‘sw’) vs. *Autharchoglossa* (‘af’) (PERRY 2007). However, for lizard taxonomic groups, the foraging mode seems to be a continuum that is defined by the distribution frequencies of these rates (POUGH et al. 2001). Another pattern characteristic of iguanids appears to be that males have larger distance rates and home ranges than females (ROSE 1982, STAMPS 1983), but then again, the microhabitat can be the principle factor for the ecological distribution of the species rather than food and activity expended on food acquisition (DUELLMAN 1987). As far as the *Enyalius* lizards endemic to Brazilian forests are concerned, this genus was initially regarded as “arboreal” (ETHERIDGE 1969, VANZOLINI 1972, JACKSON 1978, CARVALHO & ARAÚJO 2004, LIMA & SOUSA 2006, SOUSA et al. 2008), but it has not been clear whether *Enyalius* would forage in arboreal habitats, too (ZAMPROGNO et al. 2001), because little is known as yet about the natural history of this genus (VAN SLUYS et al. 2004, LIMA & SOUSA 2006, BARRETO-LIMA 2009). There

was evidence that species of *Enyalius* foraged on the forest floor from some observations of lizards being active on the leaf litter and findings that there are terrestrial arthropods in their diet (VANZOLINI 1972, JACKSON 1978, ÁVILA-PIRES 1995, VITT et al. 1996a, ZAMPROGNO et al. 2001, VAN SLYUS et al. 2004, TEIXEIRA et al. 2005, SOUSA & CRUZ 2008, BARRETO-LIMA 2009, STURARO & SILVA 2010). Although this genus can be regarded as “arboreal to semi-arboreal” (TEIXEIRA et al. 2005, RODRIGUES et al. 2006) or, as has recently been suggested, “semi-arboreal” (STURARO & SILVA 2010, BARRETO-LIMA & SOUSA 2011), we in fact still do not have detailed knowledge of its behavioural ecology from any population of *Enyalius* species.

Enyalius perditus JACKSON, 1978 is endemic to the Atlantic rainforest in the southeastern and south parts of Brazil, but ecological and behavioural data are scarce (LIMA & SOUSA 2006). Until recently, few studies investigated the diet of *E. perditus*, which found that it consumed terrestrial arthropods (SOUSA & CRUZ 2008, BARRETO-LIMA 2009, STURARO & SILVA 2010, BARRETO-LIMA & SOUSA 2011). These lizards can therefore make for an excellent model to answer hypotheses. It was for this reason why we conducted a behavioural study on the foraging habits of this species for the first time, which eventually produced new and interesting ecological data about *E. perditus*. As the optimal foraging theory (‘off’) has been tested mainly in arid environments such as deserts (SCHOENER 1971), *E. perditus* would furthermore be an interesting model system from a tropical rainforest that would permit to test whether the results corroborated the general theory developed in dry areas. According to the ‘off’, Iguania lizards would be expected to be ‘sw’ predators (SCHOENER 1971). *Enyalius* males would therefore also be expected to explore their environment more extensively than females and all members of the genus exhibiting a tendency towards ‘sw’ (see ROSE 1982, STAMPS 1983, PERRY 1999). This study aimed to answer questions as to: 1) the type of foraging employed by this species; 2) the rates of activity of the species as per gender; 3) whether the distances covered differed between the genders; and 4) whether there were differences between the microhabitats used by males and females and which was the microhabitat used most by the species? Our observations revealed new findings on the ecology of *E. perditus* and facilitated some interesting conclusions by comparing our results with the information available on other *Enyalius* species.

Materials and methods

Data collection

The municipal biological reserve Santa Cândida (MBRSC) – (21°45'35" S, 43°20'50" W), Juiz de Fora, Minas Gerais, is a forest remnant containing 113 ha of Atlantic rainforest vegetation. The climate is mesothermic (Cwa-KOEPEN classification) with a mean annual precipitation of 1,547 mm and a mean annual temperature of 19.4°C. From 2003 to 2004, we collected ten adult specimens of *E. perditus* with pitfall

Table 1. Relation of snout–vent length (mm) and mass (g) of adult individuals of *E. perditus* monitored in the field.

Males		Females	
SVL (mm)	Mass (g)	SVL (mm)	Mass (g)
72.0	6.0	80.0	15.3
72.0	6.4	80.0	12.9
69.0	7.0	80.0	10.5
68.0	6.0	93.0	17.0
70.0	6.5	86.0	14.0

traps in the ‘MBRSC’. We identified the sex of the individuals on the basis of the sexual dichromatism in evidence. The snout–vent length (mm) was taken with a manual caliper and mass (g) (scale: 0.1 mm) with a manual Pesola® scale (scale: 0.1 g; Tab. 1). One lizards couple was observed twice times and considered in analyses.

Foraging mode

Since these lizards are quiet and have a cryptic colouration, we marked them with silicone collars and non-toxic paint (red colour) on their backs and limbs to facilitate observations. Afterwards we released each lizard at the site of its original capture. Before the initiation of this research, we monitored two lizards for two consecutive days in order to train and calibrate our observations as to microhabitat use accuracy (these observations were not taken into account for analysis). We monitored each lizard in the field from a distance of 3 m, from 09:00 to 18:00 h, applying the focal animal technique (ALTMANN 1974). If the “observer effect” was noted, recordings were paused for 10 minutes. Using a tape measure, we estimated the distances (m) covered by the lizard under observation. We recorded the daily mean distance (D_{MD}) or total distance covered at the end of each observation period, from the release location to the point where the lizards sheltered and remained motionless. We evaluated the mean covered distance/hour (D_H) per gender, counted the number of movements per hour (M_H), and recorded the period of activity per gender. We consider it a movement when the lizard moved all its limbs from their original position to a new location. We infer the foraging mode from three important factors analysed together: distances, movements, and the type of prey acquired by the lizards.

Activity pattern and microhabitat use

We verified lizard microhabitat use by quantifying the frequencies of contact with shrubs (S_H), trees (T_R), ground without leaves (G_R), dry branches on the ground (B_R), tree roots (R_G), leaf litter (L_L), and dry logs on the ground (L_G). We recorded vegetation parameters such as height and diameter (cm) of plants with a tape measure, when the liz-

ards used them to perch and/or sleep on them. Initially, we performed a normality test to analyse if the distribution was normal (parametric data). Later, we performed a *t*-test to examine if there were sex-related differences in the D_{TD} , and auto re-sampling by bootstrap (1,000 iterations) to analyse if there were differences in microhabitat use. In addition, we performed a principal component analysis (PCA) to identify the microhabitat most used by *E. perditus*. Finally, we performed a MANOVA test to examine if there were differences in the microhabitat use within the genders. We used the software Multiv (PILLAR 2007), and the significance criteria for all tests was $\alpha = 0.05$.

Results

Foraging mode

We collected all data within 12 days (mean = one lizard per day) from 105 h spent on observations in the forest. The morphological data of the lizards observed are shown in Table 1. In general, specimens covered a D_{MD} of 8.6 m/day ($sd \pm 5.37$; range = 3.4–17). These data follow a normal distribution ($p = 0.681$), and the variance among groups did not differ ($p = 0.334$). However, males covered larger distances ($D_{MD} = 11.03$ m; $sd = \pm 3.835$, $r = 6.2-17$, $n = 6$) than females ($D_{MD} = 5.72$ m; $sd = \pm 1.681$, $r = 3.4-7.5$, $n = 5$), being almost twice the distance ($t = 2.858$; $p = 0.019$, $df = 9$; Tab. 2). The mean D_H was around 1 m/h (males = 1.22 m/h, females = 0.63 m/h). The lizards quietly foraged on the litter, with short fast sprints followed by long pauses before they became active once more. Some lizards entered the leaf litter to hunt prey and/or hide (Fig. 1), and we observed Formicidae, Coleoptera, Araneae and Diptera locally. A female lizard consumed opportunistically a Formicidae and a Diptera, while a male lizard, perched on S_H (1.5 m above the ground), spotted an Annelida 2 m away and jumped to the leaf litter to consume it quickly.

Table 2. Student (*t*) test of the daily mean distance (D_{MD}) covered by *Enyalius perditus*, according to gender. Degree of freedom (*df*), number (*n*), probability (*p*), and standard deviation (*sd*).

Gender	n	mean	sd	t	p	df
Males	6	11.0	3.835	2.858	0.019	9
Females	5	5.7	1.681	–	–	–

We observed some lizards that licked dew off the leaf litter. Tongue flicking behaviour was seen a few times, in some situations in which the lizards had moved from their observation points.

Activity pattern and microhabitat use

Lizards were active during the morning and afternoon, showing a unimodal pattern. The mean M_H was 3.34 movements/h. Female activity peaked from 10:00 to 11:00 h and that of males from 14:00 to 15:00 h (Fig. 2). The last peaks of activity (mostly for females) were noted around dusk, between 16:40 to 17:40 h, when the lizards were seeking out shelters to sleep. We recaptured two marked males, originally collected two and three months earlier, 100 and 200 m from their release sites, respectively. All specimens were observed foraging on the litter (Fig. 3), which was also the most used microhabitat (Tab. 3 + 4). There were no differences in microhabitat use between genders (MANOVA: $p = 0.379$; $df = 10$). Four males and four females slept on perches such as coffee seedlings (shrub), on branches with 9.0 cm in mean diameter ($sd = \pm 9.9$; $r = 2.0-16.0$ cm) and 60 cm above the ground ($sd = \pm 41.0$; $r = 15.0-150.0$ cm). In “sleeping position”, the lizards hugged a twig from a leaf on a shrub, being oriented horizontally relative to the ground (Fig. 4). Just four lizards slept on or hidden in the leaf litter layer.



Figure 1. a) *Enyalius perditus* male on the leaf litter foraging. b) *Enyalius perditus* female hiding and foraging in the layer of leaf litter. Both lizards were marked with silicone collars and painted with red colour.

Table 3. Confidence intervals generated by bootstrap auto re-sampling (1,000 iterations). Frequencies of microhabitat used by *Enyalius perditus* (n = 12) with means and confidence intervals (CI) ($\alpha = 0.05$). Shrubs (S_H), branches and tree trunks (T_R), ground without leaves (G_R), dry branches on the ground (B_R), tree roots (Ro), leaf litter (L_L) and dry logs on the ground (L_G).

Micro-habitat	Use frequency		Observed means	CI 95%	
	(n°)	(%)		Min	Max
L_L	297	81.6	0.77	0.64	0.90
S_H	33	9.1	0.09	0.03	0.18
B_R	10	2.7	0.04	0	0.10
L_G	8	2.2	0.04	0.01	0.07
G_R	6	1.6	0.03	0	0.07
T_R	8	2.2	0.02	0	0.06
R_O	2	0.6	0	0	0.01
Total	364	100.0	-	-	-

Table 4. Percentage of describing variables for each axis of ordination (Principal Components Analysis): Leaf litter (L_L), shrubs (S_H), dry branches on the ground (B_R), dry logs on the ground (L_G), ground without leaves (G_R), trees (T_R), and tree roots (R_O).

Micro-habitat	%	Axis1	Axis2	Axis3	Axis4	Axis5
L_L	32.029	1.532	5.535	3.726	1.078	0.124
S_H	1.289	19.862	51.042	1.726	5.488	0.610
B_R	18.198	23.918	0.431	2.519	13.673	29.760
L_G	13.119	22.686	8.616	0.006	39.272	13.006
G_R	20.530	3.537	25.416	0.070	8.788	36.136
T_R	11.532	28.369	6.977	0.651	28.699	20.239
R_O	3.302	0.095	1.981	91.301	3.000	0.124

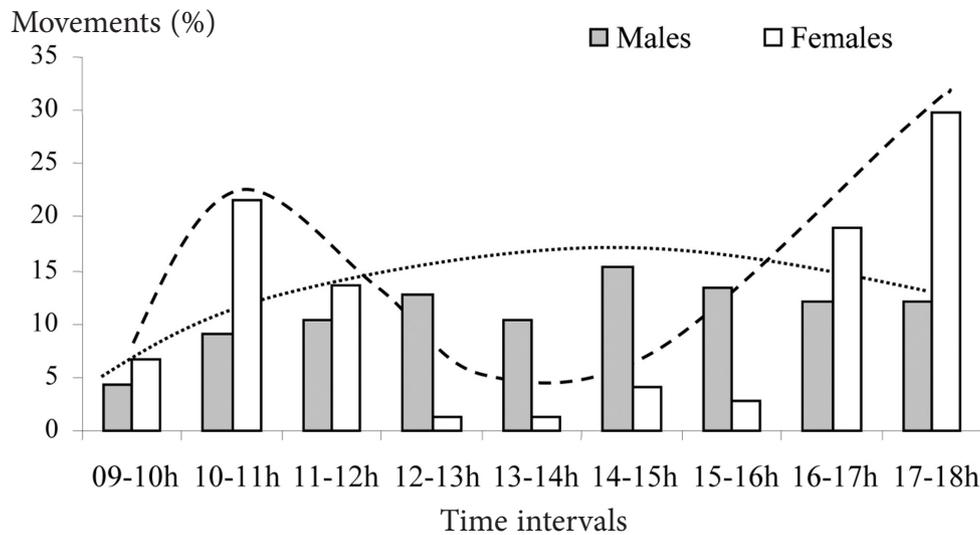


Figure 2. Hourly rates of movement per gender in *Enyalius perditus*.

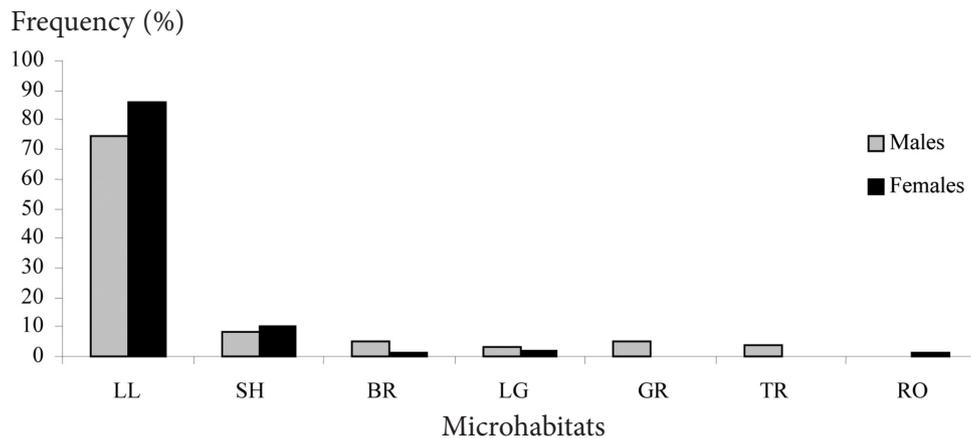


Figure 3. Frequency of microhabitats used by *Enyalius perditus* per gender. LL – leaf litter; SH – shrub; BR – dry branches on the ground; LG – dry logs on the ground; GR – ground; TR – tree; RO – tree roots.

Discussion

Foraging mode

The predators' ability to hunt their prey varies with their biological needs, sensory capabilities, and foraging strategies adopted in a determined environment. Specifically, the foraging mode can depend directly on the density, availability, distribution, activity and mobility of a species' prey, as well as the types of microhabitats existing in its habitat (PIANKA 1986, VAN SLUYS 1995, EIFLER & EIFLER 1999, HEIDEMAN & BATES 1999, PITT & RITCHIE 2002). In the present study, *E. perditus* exploited different types of active prey on the leaf litter at low frequencies of movement, but over relatively large distances and at different points of the forest, and were not necessarily confined to a certain spot as would be expected of a 'sw' forager. In a dietary study involving these and more specimens from the same population in this area it was found that Formicidae, Isoptera, Orthoptera and insect larvae constituted the main prey in a relatively diversified diet of *E. perditus*, suggesting this species to be an opportunistic predator of terrestrial arthropods (BARRETO-LIMA & SOUSA 2011). On the other hand, based on dietary studies in different forests, *E. perditus* females appeared to present themselves as 'sw' foragers and males as 'af' (SOUSA & CRUZ 2008), whereas both genders were regarded as 'af' by STURARO & SILVA (2010). It is known that iguanid lizards tend to be 'sw' foragers due this pattern being observed in their group phylogeny. However, there may be exceptions to this rule (COOPER 1995, 2007, PERRY 1999, 2007, POUGH et al. 1999). *A priori*, the 'sw' foraging species tend to have cryptic colour patterns and show a discrete behaviour with little movement, which explains their occupation density within relatively small

areas (VITT 1990, ROCHA 1999, POUGH et al. 2001, PERRY & GARLAND 2002). However, in the present study, male *E. perditus* explored larger areas than females, with 100 or 200 m in displacement, being long distances for both, small lizards as well as a sedentary ('sw') forager. However, in forests in São Paulo state in general the spatial distribution patterns of both genders of *E. perditus* were similar with regard to the displacement on the ground or above it and in perch heights (LIOU 2008). Moreover, leaf litter specialists are usually active foragers ('af') that use large areas rather than 'sw' predators. However, the singular observation in this study of an Annelida that was observed from a distance of 2 m and actively predated in an opportunistic manner indicates that vision also plays an important role in the discrimination of prey quite beyond the regular striking range of a 'sw' predator (HUEY & PIANKA 1981, POUGH et al. 1999). The infrequently noted tongue-flicking in 'sw'-predators associated with the change of place might serve to recognize surrounding structures; it is known that frequent tongue-flicking is a characteristic of 'af'-predators (COOPER 1995, PERRY 1999). In fact, we observed that *E. perditus* in an anthropized forest exhibits mixed characteristics of an active and sedentary predator, which makes understanding their foraging patterns a difficult. Thus, the species' diet with its active and sedentary prey components that are consumed opportunistically (BARRETO-LIMA & SOUSA 2011) and the relative covered distances together with low movement rates revealed in this study (see HUEY & PIANKA 1981, PERRY 1999, POUGH et al. 1999) plausibly support the idea that *E. perditus* is able to modulate its predation strategies from 'sw' foraging to "cruising forager" in a disturbed forest in response to prey availabilities in the area.

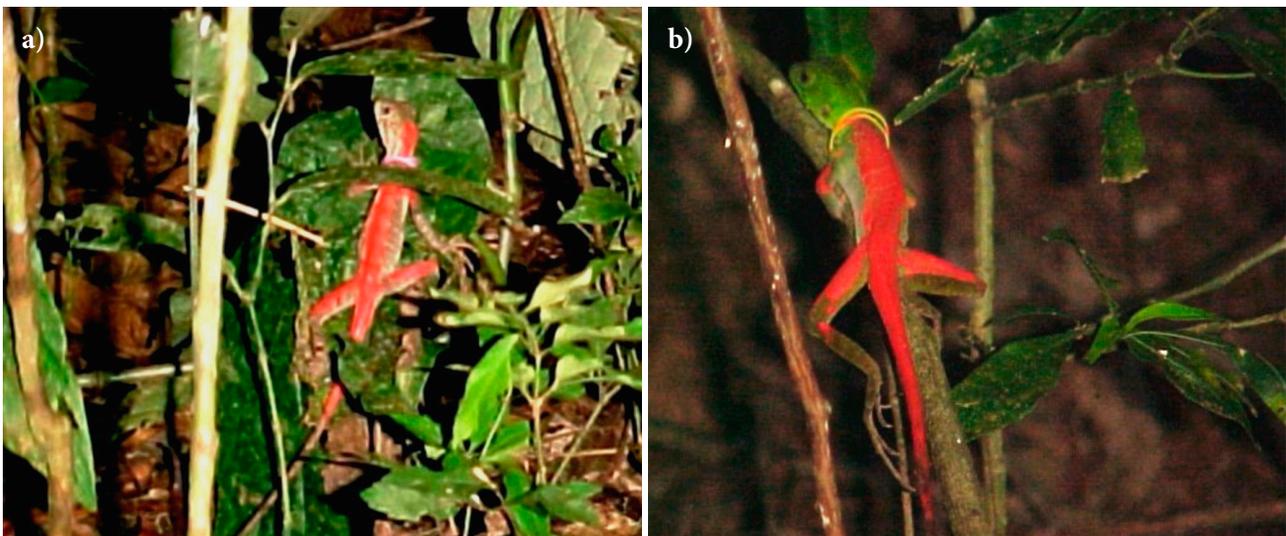


Figure 4. a) *Enyalius perditus* female climbing a shrub to reach a sleeping spot. b) *Enyalius perditus* male in sleeping position on a shrub. Both lizards were marked with silicone collars and painted with red colour.

Activity pattern

The majority of records on *Enyalius* were from diurnal activity, but did not specify if they were active at all times of the day (VAN SLUYS et al. 2004). For the first time, we monitored the activity of this species from the morning to the late hours of afternoon in the forest. It is known the species may reduce its activity or seasonally hibernate during the Brazilian winter (GRANTSAU 1966). We observed that lizards were active during the morning and afternoon, even though with low movements per hour, apparently showing a unimodal pattern. Females were more active in late morning and males more so in the early afternoon hours and at dusk when the last peaks of activity were due to the lizards seeking out shelters for sleeping. It is plausible that sex-specific differences in the diel activity periods could be a strategy to avoid to some extent competition for prey in the same area. In a dietary study involving our and other specimens from the same population in the same area, no differences in diet between the genders were found (BARRETO-LIMA & SOUSA 2011). However, the intersexual trophic similarities found, *a priori* suggested there was no food resource partitioning in the population studied in the 'MBRSC'. The existence of competition for prey within this population might possibly have been masked by the minimising effects of temporal resource partitioning. In general, male lizards move about more than females and frequent more perches per foraging area (SCOTT et al. 1976, VAN SLUYS 1997). Only male lizards were observed far from their original collection sites, in areas where we also found pregnant females and juveniles. We in fact noted that males covered double the distance of females. The differences in area use by gender were also observed in other taxa that have been reported to have territorial and non-territorial groups (PERRY & GARLAND 2002). It is known that territorial males are larger than females (STAMPS 1977) and may have larger home ranges during the reproductive season (VAN SLUYS 1997, ROCHA 1999). In the present study, although male lizards were not significantly larger than females, they explored and covered a greater area than females, maybe for reproduction-related reasons. In many species of iguanids, males cover larger distances and have double the home range of females, which is an important factor during the reproductive season (ROSE 1982, STAMPS 1983). This might indicate that larger distances are also a result of males looking for females during the local reproductive season. Other studies also reported that increased movement was due to intraspecific sexual partner search rather than looking for prey in the environment (VAN SLUYS 1997, ROCHA 1999, PERRY & GARLAND 2002). For females, there is a cost attached to reproduction, with pregnancy reducing their locomotor performance and thus their fitness, favouring their predation and limiting their exploration area (PERRY & GARLAND 2002). In another study, the displacement rate of *E. perditus* males was 11.71 m, while for females it was 11.05 m, i.e., without significant difference by gender (LIOU 2008). In our study,

the displacement rate of *E. perditus* males was in a similar range (11.03 m), but different from females (5.72 m).

Microhabitat use

We collected *E. perditus* just by pitfalls traps, indicating that they move about on the forest floor, as was already suggested by JACKSON (1978). In communities where terrestrial species predominate, most can be collected with pitfalls traps (CECHIN & MARTINS 2000). Despite this, the members of the genus *Enyalius* have traditionally been regarded as arboreal (ETHERIDGE 1969), even though strong evidence emerging from consecutive studies have indicated that these species do utilize and/or forage on the forest ground (VANZOLINI 1972, JACKSON 1978, VITT et al. 1996a, ZAMPROGNO et al. 2001, VAN SLUYS et al. 2004, TEIXEIRA et al. 2005, SOUSA & CRUZ 2008, BARRETO-LIMA 2009, STURARO & SILVA 2010, BARRETO-LIMA & SOUSA 2011). It was only recently that *Enyalius* spp. were reclassified as "arboreal to semi-arboreal" (TEIXEIRA et al. 2005, RODRIGUES et al. 2006) or "semi-arboreal" based on their diet (STURARO & SILVA 2010, BARRETO-LIMA & SOUSA 2011). Following a new and in-depth review of this issue and analysing the available evidence and accounts of many witnesses (Tab. 5), we advocate that *Enyalius* spp. should no longer be regarded as being exclusively "arboreal" or "arboreal to semi-arboreal" since this would totally or partly exclude an important habitat used – the terrestrial portion – and hinder the understanding of the biology of *Enyalius* species. Our observations prove some important facts: 1) it is clear that *Enyalius* species have developed "semi-arboreal" habits, and *E. perditus* can modulate its foraging mode in a disturbed forest to "cruising forager". 2) For the first time, specimens of *Enyalius* were monitored throughout the day and found to be foraging and using leaf litter more than the vertical structure of the forest (in 100% of cases). Excluding *E. bilineatus* that may also occur in open areas near forests, all *Enyalius* taxa have similar perching niches, indicating that their largely allopatric distribution results from the inability of partitioning niches and that differentiation was not driven by adaptation to new foraging niches in the environment of forests (JACKSON 1978). Currently, studies are underway on the potential distribution of this genus to clarify the ecological niches occupied by *Enyalius* species (BARRETO-LIMA et al. in print). 3) We observed both genders of *E. perditus* using the available microhabitats in a similar manner, mostly the leaf litter, without differences being evident between them. 4) In addition, the exploitation of intersexually similar trophic niches observed within the same population supports the previous comment and the reclassification of these lizards as semi-terrestrial, as their main prey is terrestrial leaf litter-dwelling arthropods (BARRETO-LIMA & SOUSA 2011). Moreover, it is known that *E. perditus* perches on shrubs with diameters from 3 to 200 cm and heights from 20 to 600 cm, without differences between the sexes in the height of perches used (LIOU 2008).

Table 5. Dataset of *Enyalius* species in “terrestrial” and “arboreal” habitats according to biome types, including details on the collecting site, diet, and use of perches, with the respective sources. Brazilian biomes: AR – Atlantic rainforest, CA – Caatinga (isolated forest), AF – Amazon Forest, CE – Cerrado (gallery forest).

Species	Type of Biome	On the ground, litter, or collected in pitfalls traps	Terrestrial arthropods in the diet of species	Vegetation used as perches (active or sleeping)	Type of sources
<i>E. bilineatus</i>	AR	x	–	x	JACKSON (1978)
	AR	x	x	x	ZAMPROGNO et al. (2001)
	AR	x	x	x	TEIXEIRA et al. (2005)
	AR	x	x	–	BARRETO-LIMA (2009)
	AR	x	x	x	TEIXEIRA et al. (2005)
<i>E. bibronii</i>	CA	x	–	–	RIBEIRO et al. (2012)
	CA	x	–	x	COLLI (pers. comm.)
	CA	–	–	x	FREIRE (1996)
<i>E. brasiliensis</i>	AR	x	–	x	JACKSON (1978)
	AR	x	x	x	VAN SLUYS et al. (2004)
	AR	–	x	x	TEIXEIRA et al. (2005)
<i>E. catenatus</i>	AR	x	x	x	VANZOLINI (1972, 1974)
	AR	x	–	x	JACKSON (1978)
<i>E. erythrocephalus</i>	CA	x	–	–	RODRIGUES et al. (2006)
<i>E. iheringii</i>	AR	x	–	x	JACKSON (1978)
	AR	x	–	x	SAZIMA & HADDAD (1992)
	AR	x	–	x	BARRETO-LIMA (pers. obs.)
	AR	x	x	x	LIU (2008)
	AR	x	x	x	RAUTENBERG & LAPS (2010)
<i>E. leechii</i>	AF	x	–	x	ÁVILA-PIRES (1995)
	AF	x	x	x	VITT et al. (1996b)
	AF	x	–	–	MACEDO et al. (2008)
	AF	x	–	–	FREITAS et al. (2012)
<i>E. perditus</i>	AR	x	–	x	JACKSON (1978)
	AR	x	–	–	LIMA & SOUSA (2006)
	AR	–	–	x	MALAGOLI (pers. comm.)
	AR	x	x	x	BARRETO-LIMA (pers. obs.)
	AR	x	x	–	SOUSA & CRUZ (2008)
	AR	x	x	x	LIU (2008)
	AR	x	x	–	BARRETO-LIMA (2009)
<i>E. pictus</i>	AR	x	–	–	SANTORO (pers. comm.)
<i>Enyalius</i> sp n.	CE	x	x	x	COLLI, PANTOJA (pers. comm.)
	CE	x	–	–	ZATZ (2002)
	CE	x	–	–	BARRETO-LIMA (pers. obs.)

5) Our study confirms that *E. perditus* uses shrubs mainly as “perch dormitories”. Possibly the shrubs primarily serve as refuges from predators (ZAMPROGNO et al. 2001). The “sleeping position” described here is very similar to the perching behaviour known from *Anolis ventrimaculatus*, with the body lying along the longitudinal axis of the leaf (KATTAN 1984). Many arboreal and semi-arboreal iguanid lizards spend the night sleeping exposed on leaves and

twigs, and this habit has been reported for several species of *Anolis*, *Basiliscus*, *Iguana* and *Polychrus* (KATTAN 1984 and references therein). In another forest reserve in Minas Gerais, *E. perditus* perched in bromeliads, lianas and shrub branches 40 to 150 cm above the ground to sleep at night. In the forest of the Fazenda Castanheiras, on the peninsula of Bororé, São Paulo, *E. perditus* slept in shrubs 80 cm above the ground (MALAGOLI pers. comm. 2005).

As far as congeneric species are concerned, *E. leechii* was seen sleeping on tree branches or trunks 1.5 m above the ground, in the Amazon forest on “terra firme” (VITT et al. 1996a), *E. iheringii* perches on branches (SAZIMA & HADDAD 1992), *E. bilineatus* sleeps on shrubs (ZAMPROGNO et al. 2001), and *Enyalius* sp. n. perches on branches around 1 m above the ground in the Cerrado’s gallery forest (COLLI, pers. comm. 2009). We understand that sleeping on shrub perches a few centimetres or metres above the ground must be a protective adaptive characteristic that is common amongst *Enyalius* species. While the living area must of course provide adequate shelter and thermal conditions, the most important elements are the availability of prey (TRIVERS 1976) and mating sites (STAMPS 1983, PERRY & GARLAND 2002) in the habitat. Regarding foraging mode, *Enyalius* genus may in general be regarded as a ‘sw’ forager according to the ‘oft’, we observed that under the particular conditions of a disturbed forest, *E. perditus* can modulate to “cruising forager”. As expected, males covered larger distances and, consequently, areas than females. We conclude that *E. perditus*, as well as other *Enyalius* species, are truly “semi-arboreal” lizards that often forage on the leaf litter during the day, finish their activities at dusk and then perch on shrubs to sleep protected from predators. It is plausible that the “semi-arboreal” conserved habits of the members of the genus *Enyalius* are primarily a predator-avoidance adaptation, but the entire subject still needs further investigation.

Acknowledgements

This study was part of a master’s thesis within the framework of the Programa de Pós-Graduação em Comportamento e Biologia Animal – UFJF. Our thanks are due to the Course Coordination for assistance, to the Prefeitura Municipal de Juiz de Fora for granting us access to the reserve, and to IBAMA for issuing the collection permit (227/2003). We are grateful to G. R. COLLI (Universidade de Brasília), F. PREZOTO (UFJF), L. C. M. COSTA (Pontifícia Universidade Católica do Paraná), A. ANDRIOLLO (UFJF), E. DAEMON (UFJF), and A. GAINS (University of Texas, Austin – EUA) for reviewing the draft manuscript, to L. S. DUARTE (Universidade Federal do Rio Grande do Sul) for suggestions on the statistical analysis of our data, and to I. NOVELLI, L. RIBEIRO, and G. and L. ALVES (UFJF) for their support during the pilot test in the field before this study commenced. Thanks to CAPES for the financial support (a master’s scholarship to A. F. BARRETO-LIMA, 2003–2005) and to CNPQ (scholarship to B. M. SOUSA).

References

- ALTMANN, J. (1974): Observation study of behaviour: sampling methods. – *Behaviour*, **49**: 227–267.
- ÁVILA-PIRES, T. C. S. (1995): Lizards of Brazilian Amazonia (Reptilia: Squamata). – *Zoologische Verhandelingen, Leiden*, **299**.
- BARRETO-LIMA, A. F. (2009): Gastric suction as an alternative method in studies of lizard diets: tests in two species of *Enyalius* (Squamata). – *Studies on Neotropical Fauna & Environment*, **44**(1): 23–29.
- BARRETO-LIMA, A. F. & B. M. SOUSA (2011): Feeding ecology and sexual dimorphism of *Enyalius perditus* in an Atlantic forest, Brazil. – *Hepetological Bulletin*, **118**: 1–9.
- CARVALHO, A. L. G. & A. F. B. ARAÚJO (2004): Ecologia dos lagartos da Ilha da Marambaia, RJ. – *Revista da Universidade Rural Seropédica, Ciências da Vida. Seropédica, Rio de Janeiro, EDUR, Brazil*, **24**(2): 159–165.
- CECHIN, S. T. Z. & M. MARTINS (2000): Eficiência de armadilhas de queda (pit fall traps) em amostragens de anfíbios e répteis no Brasil. – *Revista Brasileira de Zoologia*, **17**(3): 729–740.
- COOPER, W. E. J. (1995): Foraging mode, prey chemical discrimination, and phylogeny in lizards. – *Animal Behaviour*, **50**(4): 973–985.
- COOPER, W. E. J. (2007): Foraging modes as suites of coadapted movement traits. – *Journal of Zoology*, **272**: 45–56.
- DUELLMAN, W. E. (1987): Lizards in an Amazonian rain forest community: resource utilization and abundance. – *National Geographic Research*, **3**(4): 489–500.
- EIFLER, D. A. & M. A. EIFLER (1999): The influence of prey distribution on the foraging strategy of the lizard *Oligosoma grande* (Reptilia: Scincidae). – *Behavioral Ecology Sociobiology*, **4**: 397–402.
- ETHERIDGE, R. (1969): A review of the iguanid lizard genus *Enyalius*. – *Bulletin British Museum (natural history), Zoology*, **18**(8): 231–260.
- FREIRE, E. M. X. (1996): Estudo ecológico e zoogeográfico sobre a fauna de lagartos (Sauria) das dunas de Natal, Rio Grande do Norte e da restinga de Ponta de Campina, Cabedelo, Paraíba, Brasil. – *Revista Brasileira de Zoologia*, **13**(4): 903–921.
- FREITAS, M. A., D. VERÍSSIMO, S. ALBUQUERQUE & T. O. LIMA (2012): Distribution extension for the lizard *Enyalius leechii* (Boulenger, 1885) (Squamata: Leiosauridae): Third record for the state of Rodônia, Brazil. – *Herpetology Notes*, **5**: 33–34.
- GRANTSAU, R. (1966): *Enyalius catenatus*, das brasilianische “Chamaleon”. – *Aquarien- und Terrarien-Zeitschrift*, **19**(7): 217–219.
- HEIDEMAN, N. J. L. & M. F. BATES (1999): Diet as possible indicator of size-related microhabitat partitioning in *Mabuya striata wahlbergii* (Peter, 1869) (Reptilia: Scincidae). – *African Journal of Ecology*, **37**: 110–112.
- HUEY, R. B. & E. R. PIANKA (1981): Ecological consequences of foraging mode. – *Ecology*, **62**(4): 991–999.
- HUEY, R. B., E. R. PIANKA & T. W. SCHOENER (1983): Lizards ecology: studies of a model organism. – Harvard University Press, Cambridge, Massachusetts, USA.
- JACKSON, J. F. (1978): Differentiation in the genera *Enyalius* and *Strobilurus* (Iguanidae): implications for pleistocene climatic changes in eastern Brazil. – *Arquivos de Zoologia*, **30**(1): 1–79.
- KATTAN, G. (1984): Sleeping perch selection in the lizard *Anolis ventrimaculatus*. – *Biotropica*, **16**(4): 328–329.
- LIMA, A. F. B. & B. M. SOUSA (2006): Court and copulation behaviors of *Enyalius perditus* Jackson, 1978 (Sauria: Leiosauridae) in captivity conditions. – *Revista Brasileira de Zootecias*, **8**(2): 189–194.
- LIU, N. S. (2008): Historia natural de duas espécies simpátricas de *Enyalius* (Squamata, Leiosauridae) na Mata Atlântica do sudeste brasileiro. – Master dissertation, Universidade de São Paulo, São Paulo, Brazil.

- MACEDO, L. C., P. S. BERNADE & A. S. ABE (2008): Lagartos (Squamata: Lacertilia) em áreas de Floresta e de pastagem em Espigão do Oeste, Rondônia, sudoeste da Amazônia, Brasil. – *Biota Neotropical*, **8**(1): 133–139.
- PERRY, G. (1999): The evolution of search modes: ecological versus phylogenetic perspectives. – *American Naturalist*, **153**: 98–109.
- PERRY, G. & T. JR. GARLAND (2002): Lizard home ranges revisited: effects of sex, body size, diet, habitat, and phylogeny. – *Ecology*, **83**(7): 1870–1885.
- PERRY, G. (2007): Movement patterns in lizards: measurement, modality, and behavioral correlates. – pp. 13–48. – in: REILLY, S. M., L. D. MCBRAYER, & D. B. MILES (Eds.): *Lizard Ecology*. – Cambridge University Press.
- PIANKA, E. R. (1986): *Ecology and natural history of desert lizards*. – Princeton University Press, New Jersey, New York, USA.
- PILLAR, V. D. (2007): MULTIV – Multivariate exploratory analysis, randomization testing and bootstrap resampling user's guide v2.5. – Departamento de Ecologia, UFRGS, Porto Alegre, Brazil. Software and manual available at <http://ecoqua.ecologia.ufrgs.br>. Accessed at 2007.
- PITT, W. C. & M. E. RITCHIE (2002): Influence of prey distribution on the functional response of lizard. – *Oikos*, **96**: 157–163.
- POUGH, F. H., J. B. HEISER & W. N. MCFARLAND (1999). *A vida dos vertebrados*. 2ª ed. – Ed. Atheneu, São Paulo, Brazil.
- POUGH, F. H., R. M. ANDREWS, J. E. CADLE, M. L. CRUMP, A. H. SAVITZKY & K. D. WELLS (2001): *Herpetology*. – 2ª ed. Prentice-Hall, Upper Saddle River, New Jersey.
- RAUTENBERG, R. & R. R. LAPS (2010): Natural history of the lizard *Enyalius iheringii* (Squamata, Leiosauridae) in southern Brazilian Atlantic forest. – *Iheringia, Série Zoológica*, **100**(4): 287–290.
- RIBEIRO, S. C., I. J. ROBERTO, D. L. SALES, R. W. ÁVILA & W. O. ALMEIDA (2012): Amphibians and reptiles from the Araripe bioregion, northeastern Brazil. – *Salamandra* **48**(3): 133–146.
- ROCHA, C. F. D. (1999): Home range of the tropidurid lizard *Lio-laemus lutzae*: sexual and body size differences. – *Revista Brasileira de Biologia*, **59**(1): 125–130.
- RODRIGUES, M. T., M. A. DE FREITAS, T. F. S. SILVA & C. E. V. BERTOLLOTO (2006): A new species of lizard of genus *Enyalius* (Squamata, Leiosauridae) from the highlands, Chapada Diamantina, state of Bahia, Brazil, with a key to species. – *Phylomedusa* **5**(1): 11–24.
- ROSE, B. R. (1982): Lizard home ranges: methodology and functions. – *Journal of Herpetology*, **1**(6): 253–269.
- SAZIMA, I. & C. F. B. HADDAD (1992): Répteis da Serra do Japi: notas sobre história natural. – pp. 212–236. – in: MORELLATO L. P. C. (Ed): *História natural da Serra do Japi: ecologia e preservação de uma área florestal no sudeste do Brasil*. – Ed. Unicamp/FAPESP, Campinas, São Paulo, Brazil.
- SCOTT, N. JR, D. E. WILSON, C. JONES & R. M. ANDREWS (1976): The choice of perch dimensions by lizard of the genus *Anolis* (Reptilia, Lacertilia, Iguanidae). – *Journal of Herpetology*, **10**(2): 75–84.
- SCHOENER, T. W. (1971): Theory of feeding strategies. – *Annual Review of Ecology and Systematic*, **2**: 369–404.
- SOUSA, B. M. & C. A. G. CRUZ (2008): Hábitos alimentares de *Enyalius perditus* (Squamata, Leiosauridae) no parque estadual do Ibitipoca, Minas Gerais, Brasil. – *Iheringia, Série Zoológica*, **98**(2): 260–265.
- STAMPS, J. A. (1983): Sexual selection, sexual dimorphism and territoriality in lizards. – in: HUEY R. B., PIANKA E. R. & T. W. SCHOENER (Eds.): *Lizard ecology: studies on a model organism*. – Harvard University Press, Cambridge.
- TEIXEIRA, R. L., K. ROLDI & D. VRCIBRADIC (2005): Ecological comparisons between the sympatric lizards *Enyalius bilineatus* and *Enyalius brasiliensis* (Iguanidae, Leiosaurinae) from an Atlantic rainforest area in southeastern Brazil. – *Journal of Herpetology*, **39**(3): 504–509.
- TRIVERS, R. L. (1976): Sexual selection and resource-acquiring abilities in *Anolis garmani*. – *Evolution*, **30**: 253–269.
- VAN SLUYS, M. (1995): Seasonal variation in prey choice by the lizard *Tropidurus itambere* (Tropiduridae) in southeastern Brazil. – *Ciência e Cultura (Journal of the Brazilian Association for the Advancement of Science)*, **47**(1/2): 61–65.
- VAN SLUYS, M. (1997): Home range of the saxicolous lizard *Tropidurus itambere* in Southeastern Brazil. – *Copeia*, **3**: 623–628.
- VAN SLUYS, M., V. M. FERREIRA & C. F. D. ROCHA (2004): Natural history of the lizard *Enyalius brasiliensis* (Lesson, 1828) (Leiosauridae) from an Atlantic forest of southeastern Brazil. – *Brazilian Journal of Biology*, **64**(2): 353–356.
- VANZOLINI, P. E. (1972): Miscellaneous notes on the ecology for some Brazilian lizards (Sauria). – *Papéis Avulsos de Zoologia*, **26**(80): 83–115.
- VANZOLINI, P. E. (1974): Ecological and geographical distribution of lizards in Pernambuco, northeastern Brasil (Sauria). – *Ibidem*, **28**(4): 61–90.
- VITT, L. J. (1990): The influence of foraging mode and phylogeny on seasonality of tropical lizard reproduction. – *Papéis Avulsos de Zoologia*, **37**(6): 107–123.
- VITT, L. J., T. C. S. ÁVILA-PIRES & P. A. ZANI (1996a): Observations on the ecology of the rare Amazonian lizard, *Enyalius leechii* (Polychrotidae). – *Herpetological Natural History*, **4**(1): 77–82.
- VITT, L. J., P. A. ZANI & J. P. CALDWELL (1996b): Behavioral ecology of *Tropidurus hispidus* on isolated rock outcrops in Amazonia. – *Journal of Tropical Ecology*, **12**: 81–101.
- ZAMPROGNO, C., M. ZAMPROGNO & R. L. TEIXEIRA (2001): Evidence of terrestrial feeding in the arboreal lizards *Enyalius bilineatus* (Sauria, Polychrotidae) of south-eastern Brazil. – *Revista Brasileira de Biologia*, **61**(1): 91–94.
- ZATZ, M. G. (2002): Polimorfismo cromático e sua manutenção em *Enyalius* sp. n. (Squamata: Leiosauridae) no Cerrado do Brasil Central. – Masters Dissertation, Universidade de Brasília, Distrito Federal, Brazil.