

Reproductive biology of a whiptail lizard (Teiidae: *Ameivula*) in the Brazilian Caatinga

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Abstract. This study provides ecological and behavioural data on the reproduction of the whiptail lizard *Ameivula ocellifera* in the Caatinga biome, northeastern Brazil. Our fieldwork consisted of monthly trips for three consecutive days, from January 2009 through June 2010. Incidental observations of reproductive behaviour were recorded in 2012, during a study on foraging behaviour. We found sexual dimorphism in maximum body size and head dimensions, with higher values in males. Clutch size averaged 2.41 ± 0.78 (range: 1–4) and was not correlated with female body size. Egg volume averaged $589.26 \pm 77.27 \text{ mm}^3$, egg mass averaged $0.594 \pm 0.126 \text{ g}$, and relative clutch mass averaged 0.156 ± 0.053 . Twelve of the 29 females in reproductive condition contained vitellogenic follicles and oviductal eggs or corpora lutea simultaneously. We registered reproductive females both in the rainy and dry seasons, and the proportion of reproductive females was significantly correlated with monthly rainfall, but not with air temperature. Average testis volume did not differ annually, and there were no significant relationships of testis volume with rainfall and air temperature. We registered a set of behavioural expressions of *A. ocellifera* related to courtship and mating; cloacal rubbing is among the most evident behavioural expressions involved in courtship, and males accompanying receptive females occurs before and after copulation. We conclude that *A. ocellifera* has a prolonged reproductive period in the Caatinga, is apparently continuous, but exhibits seasonal variations in reproductive activity. Rainfall unpredictability in the study area may be the major factor for the prolonged reproductive cycle. Most females produce series of clutches of two eggs each. The reproductive behaviour of *A. ocellifera* is very similar to North American whiptails, most likely reflecting a common phylogenetic origin among this lineage of lizards.

Key words. Behaviour, cloacal rubbing, clutch size, mate guarding, reproductive cycles, sexual dimorphism.

Introduction

A diversity of reproductive strategies occur among squamates (FITCH 1970, 1982, TINKLE et al. 1970, VITT & CALDWELL 2009). In the family Teiidae, the reproductive cycles of species from temperate regions are markedly seasonal and related to climatic fluctuations between winter and summer, mainly in temperature and photoperiod (PIANKA 1970, VITT & BREITENBACH 1993, MANRÍQUEZ-MORAN et al. 2005, REZENDE-PINTO et al. 2009). On the other hand, tropical teiids exhibit more diversified times of reproduction, ranging from continuous (e.g., SMITH 1968, VITT 1982, 1983, MOJICA et al. 2003) to seasonal (e.g., MAGNUSON 1987, COLLI 1991, MESQUITA & COLLI 2003, ZALDÍVAR-RAE et al. 2008). Seasonal cycles in teiids are commonly related to rainfall (e.g., MAGNUSON 1987, COLLI 1991, RAMÍREZ-BAUTISTA et al. 2000), temperature (e.g., RAMÍREZ-BAUTISTA & PARDO-DE LA ROSA 2002), and photoperiod (e.g., CENSKY 1995a, ZALDÍVAR-RAE et al. 2008). There are also studies that have not found associations between reproductive cycles and environmental variables (e.g., SIMMONS 1975, ZANCHI-SILVA et al. 2014).

Reproductive cycles may vary geographically within a species or genus, and such variation is associated with environmental differences within the geographic distribution of the species. In the teiid *Ameiva ameiva* (LINNAEUS, 1758), for instance, rainfall predictability was proposed as the main factor driving the length of its reproductive cycle (COLLI 1991, VITT & COLLI 1994). According to these authors, reproduction in *A. ameiva* is seasonal in environments that exhibit distinct and predictable seasonality (Cerrado and Amazonian savannas), and continuous in environments where rainfall is abundant all year round (Amazonian rainforest) or seasonal but highly unpredictable (Caatinga).

Whiptails are small-bodied teiid lizards (less than 100 mm in snout–vent length), typical of open habitats throughout the Americas, and are currently distributed over six genera (*Ameivula*, *Aspidoscelis*, *Aurivela*, *Cnemidophorus*, *Contomastix*, and *Glaucomastix*; GOICOECHEA et al. 2016). The genus *Ameivula* (sensu HARVEY et al. 2012; formerly the *Cnemidophorus ocellifer* species complex) is distributed from northeastern Brazil to northern Argentina (ARIAS et al. 2011a, b). With the exception of *A. ocellifera*

(SPIX, 1825), the other species of the genus were described in recent years (e.g., COLLI et al. 2003, 2009, ARIAS et al. 2011a, b, 2014a, b), most of them previously mistaken for *A. ocellifera*. *Ameivula* lizards inhabit open habitats with sandy soils and high temperatures, in the Caatinga (VITT 1983, SALES et al. 2012), Cerrado (VITT 1991a, MESQUITA & COLLI 2003), “campos rupestres” (MENEZES et al. 2011), “restingas” (DIAS & ROCHA 2007, MENEZES & ROCHA 2011, 2014), and in the Chaco (CRUZ 1996, CABRERA 2012).

Ameivula females produce small clutches of between one and five eggs, and clutch size is usually correlated with female body size, with larger females producing larger clutches (MESQUITA & COLLI 2003, MENEZES & ROCHA 2014). In *A. mumbuca* (COLLI et al., 2003) and *A. jalapensis* (COLLI, GIUGLIANO, MESQUITA & FRANÇA, 2009) from the Cerrado, however, clutch size is fixed at one egg (COLLI et al. 2003, 2009). Regarding the reproductive cycles of *Ameivula* populations, the hypothesis of rainfall predictability (COLLI 1991, VITT & COLLI 1994) has received support in some studies. MESQUITA & COLLI (2003) reported a seasonal reproductive cycle for *Ameivula* in the Cerrado, where rainfall is seasonal and predictable, and VITT (1983) reported continuous reproduction for an *A. ocellifera* population in the Caatinga, where rainfall is seasonal but highly unpredictable. On the other hand, ZANCHI-SILVA et al. (2014) reported continuous reproduction for a coastal *A. ocellifera* population in Ceará state, northeastern Brazil, despite the predictable rainfall seasonality in the study area.

With respect to reproductive behaviour, teiid lizards have proven to be difficult to study in the wild with respect to social interactions because of their active mode of foraging, which tends to lead to enlarged home ranges (CENSKY 1995b), and strong wariness, which is linked to their foraging mode and predator escape strategy (VITT & PRICE 1982). Thus, studies reporting social interactions in teiids are often based on incidental observations (VITT 1983, COSTA et al. 2010, 2013, RIBEIRO et al. 2011), and the few studies that investigated social interactions quantitatively were conducted in insular populations (CENSKY 1995b, 1997, BAIRD et al. 2003, ZALDÍVAR-RAE & DRUMMOND 2007, ANCONA et al. 2010), where the lizards often occur at elevated densities and so facilitate observations by investigators. For mainland species, especially *Ameivula*, little is known about courtship and mating behaviour.

This study provides ecological and behavioural data on the reproduction of an *A. ocellifera* population from the Caatinga biome, northeastern Brazil. We looked for answers to the following questions: 1) What is the average clutch size in this population? 2) Is clutch size influenced by female body size? 3) Is reproduction continuous or seasonal? And 4) Is the reproductive cycle related to environmental variables (rainfall and temperature)? We compare the reproductive traits of *A. ocellifera* with data available in the literature for other *Ameivula* populations. With respect to reproductive behaviour, we describe the behavioural repertoire of courtship and mating, based on incidental observations of lizards interacting in the wild.

Material and methods

Study area

The Ecological Station of the Seridó (ESEC Seridó, 06°34'36.2" S, 37°15'20.7" W, datum: WGS84, altitude: 192 m) comprises a Caatinga area of 1,166.38 hectares, and is located in the municipality of Serra Negra do Norte, Rio Grande do Norte state, Brazil. The climate is semiarid, hot, and dry (AB'SÁBER 1974), with a rainy season that predominates between March and May, and rainfall usually reaching between 500 and 800 mm/year. However, there is a high unpredictability in rainfall distribution, with high annual variation. The average annual temperatures vary from 28°C to 30°C; the degree of relative humidity oscillates around 30–50% during the dry season, reaching 80–90% in the rainy season (NIMER 1972). The vegetation of the ESEC Seridó is arboreal-bushy and hyperxerophilous (VARELA-FREIRE 2002).

Lizard sampling

Our fieldwork consisted of monthly trips for three consecutive days, from January 2009 through June 2010. During this period, from 08:00 h to 17:00 h, we walked trails that covered all the types of vegetation of the ESEC Seridó in order to sample the different habitats and microhabitats used by the species. Along these trails, some lizards were secured with 4.5 mm air rifles (Urko®). Killing of animals was conducted in accordance with current legislation.

Incidental observations on reproductive behaviour were recorded in March 2012, during a study of the foraging behaviour of the population (SALES & FREIRE 2015). On two different occasions during the observation of lizards' foraging behaviour, one of us (RFDS) witnessed episodes of reproductive behaviour. Thereafter, the individuals were monitored for a description of their behavioural repertoire. All behavioural observations were recorded verbally with a voice recorder, and photos and videos were taken with a digital camera (Sony Cyber-shot DSC-H50).

Laboratory procedures

In the lab, prior to fixation, the euthanised lizards were measured (SVL, snout–vent length; HL, head length from the posterior margin of the tympanum to the tip of the snout; HW, head width at the widest point of the skull) with the aid of a digital calliper (to the nearest of 0.01 mm), and weighed (in grams) with Pesola® precision scales (to the nearest 0.1 g). They were then dissected for examining their gonads. Females were inspected for the presence of vitellogenic follicles, oviductal eggs, and corpora lutea. Enlarged follicles with yellow coloration were considered as vitellogenic. Eggs, when present, were measured (length and width) with a digital calliper, and then weighed on an

analytical scale (to the nearest 0.001 g). Egg volume (in mm^3) was estimated by the prolate spheroid formula: $V = 4/3\pi (\text{length}/2) \times (\text{width}/2)^2$ (DUNHAM 1983). In four of the eleven females carrying eggs, egg mass ($N = 8$) could not be quantified due to logistic difficulties in the field. To estimate the mass of these eggs, we performed a regression analysis between egg volume and egg mass, using the eggs with available mass data ($N = 15$). We found a strong significant relationship between egg volume and mass ($r^2 = 0.582$, $F_{1,13} = 18.12$, $p = 0.0012$); thus, based on the straight line ($y = 0.0014x - 0.2160$), we predicted the mass of the remaining eggs. In males, the right testis was measured with a digital calliper, and the volume was calculated by the prolate spheroid formula.

Clutch size was estimated by counting the number of vitellogenic follicles or eggs in the oviducts (VITT 1983). The simultaneous occurrence of vitellogenic follicles and oviductal eggs or of vitellogenic follicles and corpora lutea was considered evidence of a production of multiple clutches per reproductive season (VITT & COLLI 1994). Relative clutch mass (RCM) was calculated as clutch mass (oviductal eggs) divided by female total mass (body mass + clutch mass).

Statistical analyses

We tested our data for normality using the Shapiro-Wilk test, and for homogeneity of variances using Levene's F test. When necessary, we log-transformed the data to meet the requirements of parametry. In cases where the assumptions of parametric tests were not met, even after data transformation, we used the corresponding non-parametric tests. We performed statistical analyses in IBM SPSS Statistics 19.0, with the significance level set at 0.05. Throughout the text, the descriptive statistics are presented as a mean \pm standard deviation (SD). In all analyses of annual variation on reproductive features, we grouped the lizards into periods of two consecutive months (i.e., January–February, March–April, etc.).

We tested for differences in body size (SVL) between males and females using a Student's t-test. To assess sexual differences in head length (HL) and width (HW), we performed analyses of covariance (ANCOVA), with SVL as the covariate. The effect of female SVL on clutch size was evaluated using the Spearman rank correlation. We evaluated annual variations in testis volume through a Kruskal-Wallis test, using the regression residuals of SVL against testis volume. The influence of rainfall (Fig. 1; source: Climatological Station of ESEC Seridó) and mean monthly temperatures (maximum and minimum, Fig. 1; source: Instituto Nacional de Meteorologia – INMET) on the frequency of reproductive females in each two-month period was evaluated by means of a Spearman's correlation (r_s). The influence of these same environmental variables on male testis volume (median of each two-month period) was evaluated by a Pearson's correlation (r).

Results

Reproductive biology

We collected a total of 58 males and 42 females between January 2009 and June 2010. The average SVL of males (66.83 ± 10.77 mm, range: 45.55–91.14) and females (63.04 ± 9.75 mm, range: 41.60–77.72) did not differ significantly ($t = 1.806$, $df = 98$, $p = 0.074$). Head dimensions (HL, HW), however, were significantly greater in males (ANCOVA, HL: $F_{1,97} = 32.903$, $p < 0.001$; HW: $F_{1,97} = 57.422$, $p < 0.001$). The smallest male containing enlarged testes (23.55 mm^3) and convoluted epididymides measured 52.9 mm SVL, and the smallest female carrying vitellogenic follicles and/or eggs measured 58.1 mm SVL. These were considered the minimum sizes at sexual maturity in the studied population. The smallest individual in the sample was a hatchling measuring 32.5 mm SVL.

Based on counts of vitellogenic follicles and oviductal eggs, clutch size averaged 2.41 ± 0.78 (range: 1–4, mode: 2, $N = 29$), and was not significantly correlated with female SVL ($r_s = 0.347$, $p = 0.065$; Fig. 2). Clutch size was 2.45 ± 0.86 (range: 1–4, mode: 2, $N = 22$) based on vitellogenic follicle counts, and 2.36 ± 0.51 (range: 2–3, mode: 2, $N = 11$) based on oviductal egg counts. Similarly, there was no significant correlation with female SVL in both cases ($p > 0.05$).

Of a total of 33 adult females in the sample, 29 were in reproductive condition (i.e., containing vitellogenic follicles, oviductal eggs, or fresh corpora lutea). Egg volume averaged $589.26 \pm 77.27 \text{ mm}^3$ ($N = 23$), ranging from 429.86 to 714.64 mm^3 . Egg mass averaged 0.594 ± 0.126 g ($N = 23$), ranging from 0.374 to 0.785 g. Relative clutch mass was 0.156 ± 0.053 ($N = 10$), ranging from 0.094 to 0.245. Twelve of the 29 females in reproductive condition contained vitellogenic follicles and oviductal eggs ($N = 4$) or vitellogenic follicles and corpora lutea ($N = 8$) simultaneously. These females with multiple clutches were registered in most analysed months (Fig. 3).

We collected females in reproductive condition in most months (Fig. 3). Only in November–December 2009 we

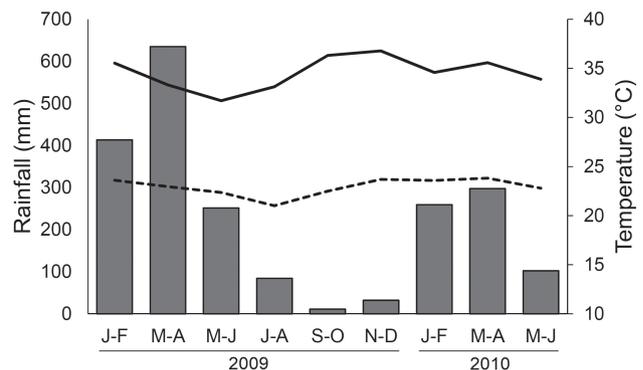


Figure 1. Rainfall (bars) and average maximum (solid line) and minimum (dotted line) temperatures at the Ecological Station of the Seridó, northeastern Brazil, from January 2009 to June 2010.

did not register reproductive females, but in this period, we collected only one adult female, not allowing robust conclusions about the reproductive condition of females during these two months. The proportion of reproductive females in each two-month period was significantly correlated with rainfall ($r_s = 0.693$, $p = 0.038$), but neither with mean maximum temperature ($r_s = -0.554$, $p = 0.121$), nor with mean minimum temperature ($r_s = -0.099$, $p = 0.799$).

With respect to males, there were no significant differences between the months in testis volume (SVL-adjusted) during the studied period (Kruskal-Wallis, $H = 8.695$, $df = 7$, $p = 0.275$; Fig. 4). In addition, there were no significant

relationships of testis volume in each two-month period (median, SVL-adjusted) with rainfall ($r = 0.604$, $p = 0.113$), mean maximum temperature ($r = -0.416$, $p = 0.304$), and mean minimum temperature ($r = -0.330$, $p = 0.424$).

Reproductive behaviour

The first observation began at 11:25 h on 31 March 2012, when a male and a female were recorded foraging together. Every time the female moved, the male followed her, reducing the distance between the two. The female exhibited normal foraging behaviour, moving continuously, tongue-flicking the substrate, turning over the leaf litter with the snout, and sometimes digging with the fore limbs. The male also foraged, but on several occasions he stood motionless with the head up, in a typical position of alert. The female accepted the male's proximity, never showing signs of discomfort. During the observation period, the male established physical contact with the female several times, covering his hind limbs and base of the tail region, sometimes tongue-flicking the female's back, but there was no attempt at copulation. The observation lasted 19 minutes in total until the pair entered dense underbrush, and we could not continue to observe them. A video recording of the observation (8 minutes) is available at <https://youtu.be/US9ZRcfA548>.

The second observation was made about 40 minutes after the first. At 12:25 h, an adult male emerged from his burrow and approached the burrow of a female, about 2 m from his own burrow. Immediately, the male began performing vibratory movements involving the posterior trunk region, pelvis, hind limbs, and base of the tail (cloacal rubbing behaviour). A few seconds later, the male began to dig open the burrow entrance with his fore limbs. In the following minutes, he entered and exited the burrow, continued to dig in its entrance area, and only stopped oc-

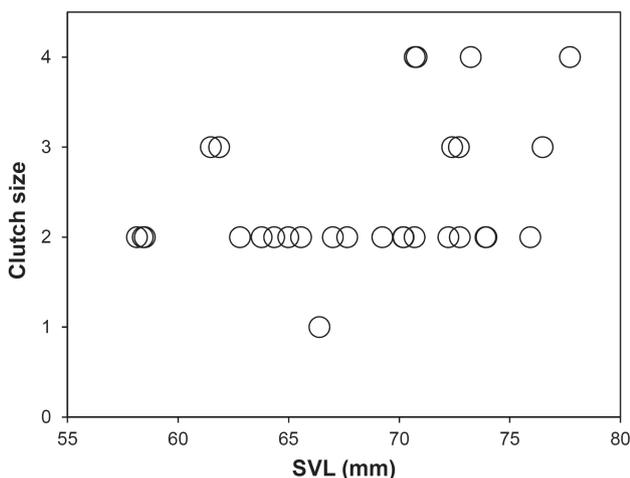


Figure 2. Relationship between clutch size and snout-vent length (SVL) in *Ameivula ocellifera* at the Ecological Station of the Seridó, northeastern Brazil.

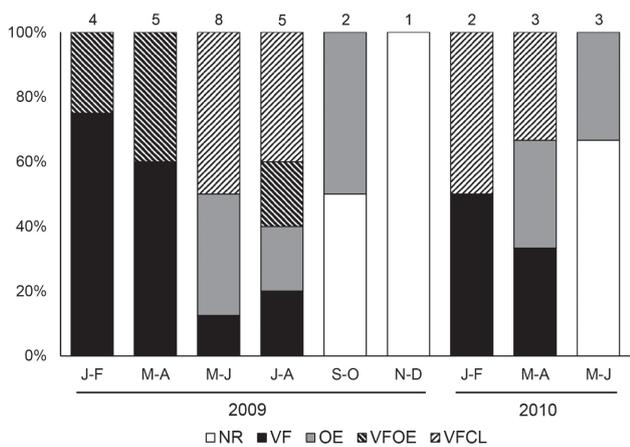


Figure 3. Monthly frequencies of reproductive activity of females of *Ameivula ocellifera* from January 2009 through June 2010 at the Ecological Station of the Seridó, northeastern Brazil. NR – non-reproductive females; VF – presence of vitellogenic follicles; OE – presence of oviductal eggs; VFOE – simultaneous presence of vitellogenic follicles and oviductal eggs; VFCL – simultaneous presence of vitellogenic follicles and corpora lutea. Numbers above each bar indicate sample sizes.

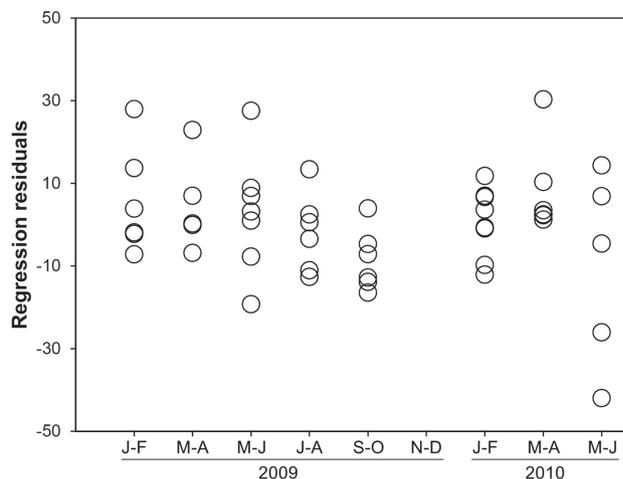


Figure 4. Monthly variation in SVL-independent testis volume of *Ameivula ocellifera* males at the Ecological Station of the Seridó, northeastern Brazil, from January 2009 through June 2010.

asionally to perform more cloacal rubbing again. Sometimes the lizard moved forward by 10–15 cm, then reversed to his original position; these movements appeared to depict a figure of eight. The male performed cloacal rubbing several times, sometimes with the body in the leaf litter, producing noise by displacing the dry leaves and branches, sometimes with the posterior region of the body in the burrow, and sometimes with the body in the burrow's entrance, making circular movements around it. The female appeared at the burrow's entrance three times, and on the first and third occasions, the male grabbed her by the neck with his mouth, but she was able to free herself and went back into the burrow. At 13:12 h, 47 minutes from the beginning of the observation, the male entered the female's burrow, and remained inside for 8 minutes. After that, he left the burrow and returned to perform cloacal rubbing and dig in the burrow's entrance area. Another 25 minutes later, he finally returned to his burrow and remained there for 26 minutes. At 14:10 h, the male came out of his burrow and moved again to the female's burrow, remaining in the entrance for 10 minutes, digging and performing cloacal rubbing. During this period, another male approached the burrow's entrance, but the resident male chased him off. At 14:20 h, the female finally came out of the burrow and began foraging in the vicinity, with the male following her closely and tongue-flicking her back. About 5 minutes later, at 14:26 h, the male mounted the female and assumed the posture of copulation, placing a holding bite on her pelvic region and assuming a highly arched posture across her back. Copulation lasted only 48 seconds before the male released the female, who then quickly ran off and entered a bush. The male remained motionless a few seconds, and then resumed foraging. After this, the animals were lost to sight and we could not continue the observation. The observation lasted 125 minutes in total. A video recording of the observation (11 minutes) is available at <https://youtu.be/tyUHgJqgwIk>.

Discussion

We verified sexual dimorphism in *Ameivula ocellifera* from ESEC Seridó and found that males reach larger body sizes (maximum SVL) and have larger head dimensions than females. Sexual dimorphism is widespread in most investigated species of the family Teiidae (e.g., ANDERSON & VITT 1990, VITT 1991b, CENSKY 1995b, SALES et al. 2011a), and sexual selection is thought to be the main cause for the evolution of this feature in teiids (ANDERSON & VITT 1990). Larger males generally win aggressive intrasexual interactions and gain access to a larger number of females by fending off smaller males and receiving greater acceptance by females (CENSKY 1995b, 1997, LEWIS et al. 2000).

The minimum sizes at maturity of the studied *A. ocellifera* population (males: 52.9 mm; females: 58.1 mm) are in accordance with the ones reported by VITT (1983) for *A. ocellifera* from Exu, Pernambuco state, about 330 km

distant from the ESEC Seridó (males: 55 mm; females: 56 mm). However, we suggest that some *A. ocellifera* females from the ESEC Seridó might reach sexual maturity at smaller sizes. The female involved in the first behavioural observation, for instance, seemed to have a SVL around 50 mm, since she had not yet taken on the greenish coloration typical of adult lizards. This female presumably had reached sexual maturity, since teiid males will pursue only receptive females (CENSKY 1995b, 1997).

Contrary to our expectation, we did not find a significant relationship between clutch size and female SVL in *A. ocellifera*. The main cause for this result was that most females (65.5%) produced clutches of two eggs, independently of size (Fig. 2). Similar to our results, CRUZ (1996) did not find a significant relationship between clutch size and female SVL in an *Ameivula* population from Argentina. On the other hand, the studies of VITT (1983), ZANCHI-SILVA et al. (2014) and MESQUITA & COLLI (2003) found positive relationships between clutch size and SVL. We cannot discard the possible influence of body size on clutch size in *A. ocellifera* from the ESEC Seridó, since clutches of 4 eggs were produced only by females with an SVL > 70 mm (Fig. 2).

The frequency of females with multiple clutches (43.4%) was relatively high when compared with other studies. ZANCHI-SILVA et al. (2014) found only 5.6% of females carrying vitellogenic follicles and eggs/corpora lutea simultaneously in a coastal *A. ocellifera* population, and MESQUITA & COLLI (2003) did not find *A. ocellifera* females with both vitellogenic follicles and eggs/corpora lutea in the Cerrado, indicating that, if multiple clutches are produced during the reproductive season, they are relatively separated in time.

Relative clutch mass of *A. ocellifera* from the ESEC Seridó averaged 0.156, a value relatively lower than that reported by VITT (1983) from another Caatinga population (RCM = 0.207). Average RCMs of studied *Ameivula* populations range between 0.1 and 0.22 (see MENEZES & ROCHA 2014), which are very similar values compared to those from North American whiptails (VITT & PRICE 1982).

Our results suggest that *A. ocellifera* has a prolonged reproductive period in the Caatinga of the ESEC Seridó, since we registered reproductive females both in the rainy and dry seasons. However, in the driest months of the year (October–December), we registered a drastic reduction of active individuals in the field, and this phenomenon renders it difficult to capture adult lizards for reproductive analysis (only one adult female could be collected in this period). A similar trend was noted in the teiid *Ameiva ameiva* in the same study area during the same period (SALES et al. 2011b). Accordingly, we suggest that the reproductive cycle of *A. ocellifera* may be continuous, but it is clearly reduced in intensity during the peak of the dry season in the ESEC Seridó. The absence of monthly differences in mean testis volume indicates that the reproductive cycle of males mirror that of females. Similar to our results, the reproductive cycle of coastal *A. ocellifera* from Ceará state was

continuous, but with seasonal variations in the proportion of reproductive females and a peak of reproduction during the rainy season (ZANCHI-SILVA et al. 2011). On the other hand, VITT (1983) found a continuous reproductive cycle in *A. ocellifera* from Exu, Pernambuco state, which was apparently not linked to rainfall.

We registered a set of behavioural expressions of *A. ocellifera* that are related to courtship and mating, including cloacal rubbing, copulation, and female accompaniment. This same behavioural repertoire was identified in another *A. ocellifera* population from the Caatinga, distant only by 75 km from the ESEC Seridó (RIBEIRO et al. 2011). Cloacal rubbing is a most conspicuous behaviour involved in courtship, and accompaniment of receptive females occurs before and after copulation.

Cloacal rubbing is also known from a North American whiptail, *Aspidoscelis sexlineata* (LINNAEUS, 1766), and was suggested as an auto-exciting mechanism performed by the male when he becomes aware of the proximity or presence of a female (CARPENTER 1962). Furthermore, RIBEIRO et al. (2011) suggested that this behaviour may also play a role in male–female communication through a combination of signals, including tactile (substrate vibration), auditory (sound produced by displacement of leaves and sand), visual (the male passes over the burrow opening so that the female is able to see him), and chemical (by means of femoral pores) cues.

The series of postures performed by the male during copulation seems to be a pattern in whiptail lizards, since they were also observed in another species (e.g., CREWS 1987). The moment when the male inserts a hemipenis into the female's cloaca and transfers his neck-bite hold to the female's pelvic region, assuming a ring-shaped posture ("doughnut posture"; CREWS 1987), characterizes the ejaculation phase. Ejaculation lasted only 48 seconds in *A. ocellifera* from the ESEC Seridó, similar to the copulation event recorded by RIBEIRO et al. (2011) that lasted 65 seconds.

Female-accompaniment behaviour is interpreted as mate guarding in teiids because the male companion will drive away any other males that attempt to approach the female, reducing the likelihood of extra-pair copulation by the female (CENSKY 1995b; ZALDÍVAR-RAE & DRUMMOND 2007). Males guard females only during their receptive peri-ovulatory period, which lasts from one to five days (CENSKY 1995b, ZALDÍVAR-RAE & DRUMMOND 2007). The tongue-flicks performed by the male on the female's back is probably a mechanism to assess her reproductive status (RIBEIRO et al. 2011). ANCONA et al. (2010) showed that mate guarding is costly for males in the North American whiptail *Aspidoscelis costata* (COPE, 1878), because it entails a reduction in energy intake (the male stays more alert and forages less during accompaniment) and increased expenditure on aggression (male–male antagonistic encounters). Female-accompaniment behaviour seems to be a widespread strategy among teiids (ZALDÍVAR-RAE et al. 2008). However, it is known to occur only in a few species of the genera *Aspidoscelis* to date (ANDERSON & VITT 1990,

ZALDÍVAR-RAE & DRUMMOND 2007, ANCONA et al. 2010), *Pholidoscelis* (CENSKY 1995b), and *Ameivula* (RIBEIRO et al. 2011, this study). Future studies will likely record this behaviour from other teiid species, too.

We conclude that *Ameivula ocellifera* has a prolonged reproductive period in the ESEC Seridó, where it appears to be continuous, but with seasonal variations in reproductive activity. The significant influence of rainfall may be related to prey availability, and/or availability of suitable microhabitats for oviposition, considering that the soil is more suited for egg incubation in the rainy season, as suggested by MAGNUSON (1987). Nevertheless, the rainfall unpredictability of the Caatinga may be the driving factor for a prolonged reproductive cycle, resulting in an asynchronous period of reproduction of females. Most females produce series of clutches of two eggs each, which may be a strategy to increase the reproductive output without compromising predator evasion. Finally, the expressions of reproductive behaviour by *A. ocellifera* are very similar to those reported for North American whiptails, most likely reflecting a common phylogenetic origin in this lineage of lizards.

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