

Reproductive cycle of male wall lizard, *Podarcis vaucheri* (Reptilia: Sauria: Lacertidae), in Djurdjura, Northern Algeria

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Received: 15 February 2017; returned for review: 5 April 2017; accepted 4 September 2017.

The reproductive cycle of male wall lizard *Podarcis vaucheri* (Boulenger, 1905) living in Djurdjura Mountain, was analyzed from April until October 2014. Its seasonal mixed-type cycle was characterized by three phases: sexual activity, quiescence and recrudescence. After the emergence of lizards from hibernation, an intense sexual activity was observed in spring (April, May, and June), at which the testicular weight and seminiferous tubules diameter reached their maximal values. At this period, spermiogenesis was also maximal and the spermiation allowed the release of a large quantity of spermatozoa in both the seminiferous tubules and epididymis lumen. In July, a short sexual resting period followed, during which the testes mass and seminiferous tubules diameter decreased. Spermatogonia and some primary spermatocytes were observed against the wall of seminiferous tubules. The recrudescence period (August, September and October) was characterized by a progressive increase of the testis weight and seminiferous tubules diameter. Spermatocytogenesis began in August, and spermiogenesis occurred in September and October, before the diapause period. However, the presence of spermatozooids was not signaled in the epididymis lumen. Field observations and microscopic evidence of testis showed that both sexes reproduced synchronously during spring and early summer.

Key words: Algeria; Djurdjura; Lizard; *Podarcis vaucheri*; reproductive cycle; spermatogenesis.

Reproduction imposes high-energy requirements, illustrated by a large diversity in terms of resource acquisition and allocation strategies (JÖNSSON, 1997). Seasonal breeding represents a valuable strategy in order to use this energy economically, but the reproductive timing becomes one of the most critical issues in the lizard's biology (JAMES & SHINE, 1985). For that, the reproduction occurs when the environment is the most favorable to offspring survival and when parents can physiologically sustain reproduction with the lowest cost (WHITTIER & CREWS, 1987; PIANKA & VITT, 2003).

Timing of reproductive activity is

widely variable in lizards (MANRÍQUEZ-MORÁN *et al.*, 2005; CARRETERO, 2006; VILLAGRÁN-SANTA CRUZ *et al.*, 2009; GRIBBINS, 2011): in temperate-zones, breeding takes place in spring and early summer, with the reproductive season being longer in coastal than in continental populations (CARRETERO & LLORENTE, 1995,1997; GALÁN, 1997; CARRETERO *et al.*, 2006a, AL-AMRI *et al.*, 2012), while in cold and high-altitude environments, mating occurs later in the season and lizards exhibit a short breeding period (SAINT-GIRONS & DUGUY, 1970; HRAOUI-BLOQUET, 1985; HRAOUI-BLOQUET & BLOQUET, 1988; BRAÑA *et al.*, 1990; OLSSON & SHINE, 1999; ROIG *et al.*, 2000; ARRIBAS & GALÁN, 2005). Further, in desert environments reproduction can be postponed as well as anticipated compared to temperate zones (HAMMOUCHE & GERNIGON-SPYCHALOWICZ, 1996; HAMMOUCHE *et al.*, 2007; GOLDBERG, 2013), and can continue until autumn (GOLDBERG, 2013). Lastly, it is in tropical areas that lizards exhibit the highest variability of reproductive patterns, ranging from continuous to seasonal reproduction (FITCH, 1970; JAMES & SHINE, 1985; JENSSEN & NUNEZ, 1994; PRANKA & VITT, 2003; HUANG, 2010; MÉNDEZ-DE LA CRUZ *et al.*, 2013).

Besides the environmental conditions, several studies showed reproductive cycles to be influenced also by the interaction between endogenous and exogenous factors (LICHT *et al.*, 1969; LICHT, 1972; ANGELINI *et al.*, 1976; LOFTS, 1978; MARION, 1982; JENSSEN & NUNEZ, 1994; CARRETERO, 2006). On one hand, indeed, the gonadal and hormonal activity can be considered the main endogenous mechanisms controlling reproductive cycles (DÍAZ *et al.*, 1994;

IKEUCHI, 2004). Being partly predetermined (ANGELINI *et al.*, 1976), it is also expected that these mechanism are subject to some kind of phylogenetic constrains (DUNHAM & MILES, 1985; CARRETERO, 2006), which can limit the observed environmental and geographic variability. On the other hand, the relationships between reproductive cycles and environmental variables suggest that the endogenous mechanisms can plastically respond to climatic components, such as temperature (LICHT, 1971,1973; ALDRIDGE, 1975; ANGELINI *et al.*, 1976; MARION, 1982; FLEMMING, 1993; CARRETERO, 2006; ABU-ZINADAH, 2008), precipitation (JENSSEN & NUNEZ, 1994), photoperiod (LICHT, 1971,1973; DUNHAM & MILES, 1985; FLEMMING, 1993; CARRETERO, 2006), or other environmental features, like food availability (LOFTS, 1978; MARION, 1982; COLLI *et al.*, 2003; DOMÍNGUEZ *et al.*, 2010).

The seasonal testicular cycle in lizards was described in several species (AL-AMRI *et al.*, 2013). Specifically, for temperate regions three spermatogenic cycles were described: i) the vernal or prenuptial type, where spermatogenesis occurs during spring, immediately before or even during breeding (LICHT *et al.*, 1969; SAINT-GIRONS, 1982; CARRETERO, 2006); ii) the postnuptial type, where spermatogenesis is held during summer of the previous year (SAINT-GIRONS, 1982; CARRETERO, 2006; HRAOUI-BLOQUET *et al.*, 2007); iii) an finally the mixed type, where spermatogenesis begins at the end of summer and is interrupted in winter (LICHT *et al.*, 1969; SAINT-GIRONS, 1982; CARRETERO, 2006). However, SAINT-GIRONS (1982) recognized two sub-types of this cycle. The first sub-type corresponds to the classical definition, with

spermiogenesis extending until spring of the following season. While in the second sub-type, there are two periods of spermiogenesis, spermatozoa are already produced in autumn of the previous season and continues in spring after hibernation. Whatever the cycle, in most cases spermatogenesis is synchronized with vitellogenesis and ovulation in females (PIANKA & VITT, 2003; CARRETERO, 2006).

Lizards of the genus *Podarcis* (WAGLER 1830) represent a group that has evolved and diversified in the Mediterranean Basin (ARNOLD *et al.*, 2007). An exemplary case is that of the *Podarcis hispanicus* complex, which is among the most studied European reptiles, and is characterized by a high genetic diversity (KALIONTZOPOULOU *et al.*, 2011). The inclusion of genetic sequences from North African specimens has allowed the separation of *P. vaucheri* from the *hispanicus* complex, and elevating it to the species rank (OLIVERIO *et al.*, 2000; BUSACK *et al.*, 2005). In addition, morphological and phylogenetic studies of Iberian and North African populations (OLIVERIO *et al.*, 2000; BUSACK *et al.*, 2005; PINHO *et al.*, 2006,2007; LARBES *et al.*, 2007; LIMA *et al.*, 2009; RENOULT *et al.*, 2010; KALIONTZOPOULOU *et al.*, 2011,2012) have shown the occurrence of several evolutionary lineages suggesting that *Podarcis vaucheri* can be considered a species complex. Furthermore, very few information is available, especially on the ecology and physiology of this species. Notably, even if some previous studies have provided data on trophic ecology (CARRETERO *et al.*, 2006b; MAMOU *et al.*, 2016), thermal biology (VERÍSSIMO & CARRETERO, 2009), and parasitology (CARRETERO *et al.*, 2011; DAMAS-

MOREIRA *et al.*, 2014), none of them has focused on describing the reproductive cycle of this variable species.

The aim of the present work was to describe the spermatogenic cycle of male wall lizards *Podarcis vaucheri* based on the histological analysis of testis, in order to provide some preliminary information about its reproductive strategy.

MATERIAL AND METHODS

Site of study

Tala Guilef is located in the western part of the northern slope of the Djurdjura Mountain (Djurdjura National Park), Kabylie, Algeria. It is located approximately 140 km southeast of Algiers and 45 km south west of Tizi Ouzou (36°39' N, 4°01' E). The region is characterized by a mountain climate influenced by the Mediterranean Sea, and belongs to the humid climate scene (HAMDINE *et al.*, 1993).

The specimens were collected in a rocky environment particularly attractive for this species, characterized by the presence of stones and rocks from the Haïzer massif and bushy vegetation including: *Crataegus monogyna*, *Crataegus laciniata*, *Rubus ulmifolius*, *Rosa canina*, *Rosa sicula*, *Prunus prostrata* and *Berberis hispanica*. In grass stratum, we essentially found: *Anthemis kabilica*, *Artemisia absintium*, *Astragalus armatus*, *Eryngium tricuspedatum*, *Euphorbia luteola* and *Ferula communis*.

Data analysis

Adult males of *P. vaucheri* were collected monthly (between the tenth and the twenty-fifth day of each month; three individuals/month), from April until October 2014. The snout-vent length (SVL) of each

individual was measured using a digital caliper (± 0.01 mm). After dissection, the left testes were removed, weighted with a digital balance (± 0.0001 g), and fixed with buffered formalin for 24 hours, and then preserved in ethanol 70°. The tissues were dehydrated in a graded series of ethanol, cleared in butanol prior to be infiltrated and embedded in paraffin. 5 μ m sections were stained with hematoxylin-eosin, following standard histological protocols.

Spermatogenic activity was assessed qualitatively by determining the various stages of germ cells. The presence of spermatozoa and secretions in the epididymis lumen were also noted. For a quantitative characterization of testis activity, three measures were taken: the (i) number and (ii) diameter of seminiferous tubes, and (iii) epididymis epithelium thickness. These measures were repeated on three randomly selected testis sections for each individual (Table S1).

Sections of each testis were examined and photographed using a Nikon Eclipse E400 light microscope, equipped with a Nikon digital DXM1200 camera coupled with a picture analyzer Nis-Element BR 3.1(Lucia software).

For the data analysis, the mean value of each histological parameter among the three sections of each individual was considered. All parameters were Log transformed, and comparisons between the different measurements were performed with ANCOVA, using the logarithm of SVL as a covariate. Further, to investigate the influence of body size in the gonadal development, we used a Pearson correlation between SVL and testis weight.

RESULTS

Mean snout-vent length (SVL) of lizards was 54.73 ± 0.50 mm, ranging between 50.85 and 58.74 mm. A positive correlation was found between testicular weight and body size (SVL) ($r = 0.44$, $P = 0.047$). The weight of testis varied significantly throughout the months (ANCOVA $F_{(6,13)} = 44.51$, $P < 0.0001$), and the spermatogenesis cycle of *P. vaucheri* might be divided into three main phases (Fig. 1): i) the phase of sexual activity (April, May, June), which was characterized by the highest weight; a short period of regression and a sexual quiescence (July), during which the testis weight decreased; a recrudescence phase (August, September, October), where the testicular weight started to increase (August), reaching its maximum in October, just before the period of hibernation (November – March).

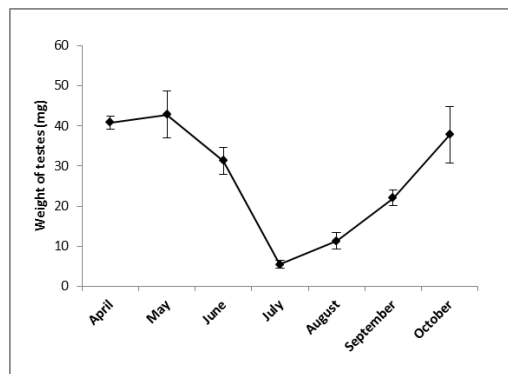


Figure 1: Monthly variation of mean weight testes in *P. vaucheri*.

The average number of seminiferous tubules by section oscillated between 45 and 55 (Fig. 2A), and did not vary along the season ($F_{(6,13)} = 0.6$, $P = 0.726$). On the contrary, the mean diameter of the semi-

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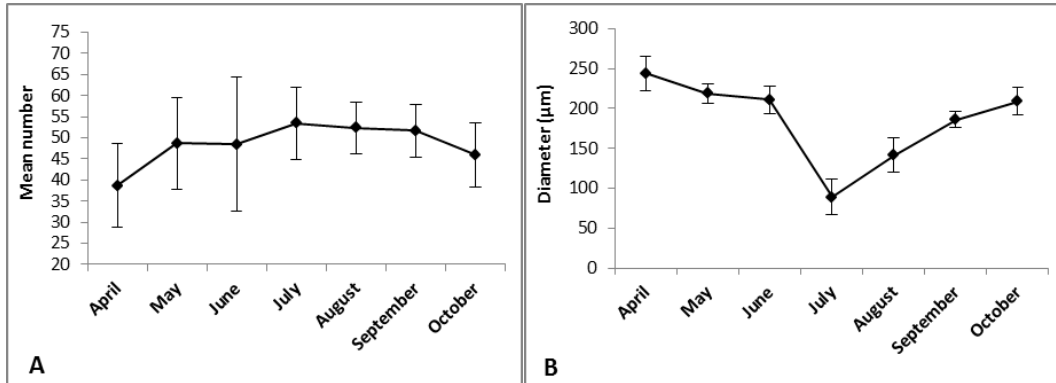


Figure 2: Monthly variation of the (A) mean number and (B) the diameter of the seminiferous tubules in *P. vaucheri*.

niferous tubules showed a clear monthly variation ($F_{(6,13)} = 9.18, P = 0.005$; Fig. 2B), peaking during the breeding season (April-June). The sexual resting period was characterized by a maximal regression of the seminiferous tubules diameter with an absence of lumen. During the period of recrudescence this parameter increased progressively again, with the lumen remaining absent in August (Fig. 4E). The evolution of the diameter of seminiferous tubules corresponded to the resumption of testicular activity interrupted in November by the temperature decrease, and followed by the beginning of hibernation.

The thickness of the epididymis epithelium showed a significant monthly variations ($F_{(6,13)} = 32.23, P < 0.001$; Fig. 3). During the phase of sexual activity this parameter was at maximum, while a sudden reduction of the height was observed in July, persisting until October.

The examination of histological sections revealed some variations of the different categories of germinal cells during the reproductive cycle (Fig. 4). After

the emergence of lizards in spring (sexual activity), the spermiogenesis was maximal and persisted until June, so, all sperm cells categories were observed (Fig. 4A), with a decrease of spermatocytes number. The spermiation allowed the release of a large quantity of spermatozoa in the lumen of the seminiferous tubules and epididymis. Moreover, the morpho-functional characteristics of the epididymis have changed; the epithelial cells became secreting and take a prismatic shape (Fig. 4B).

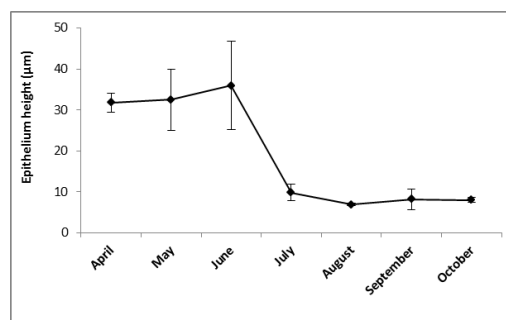


Figure 3: Monthly variation of the epididymis epithelium height in *P. vaucheri*.

In July, at sexual rest, the seminiferous

tubules contained spermatogonia and some primary spermatocytes (Fig. 4C). In August, at the beginning of the recrudescence period, the seminiferous tubules showed a lot of primary and secondary spermatocytes, and some young spermatids (Fig. 4E). In September and October spermiogenesis occurred, and a large number of spermatid and spermatozoa were found in the seminiferous tubules lumen (Fig. 4G).

In spite of an active spermiogenesis in autumn accompanied with the presence of mature spermatozooids in the lumen of the seminiferous tubules, the epididymis lumen remained empty (Fig. 4H).

DISCUSSION

The spermatogenic cycle of *Podarcis vaucheri* is of the "mixed-type", in agreement with what is the dominant pattern in temperate lizards (LICHT *et al.*, 1969; SAINT-GIRONS, 1982; CARRETERO, 2006), especially those belonging to the genera *Lacerta* s.l. and *Podarcis* (SAINT-GIRONS & DUGUY, 1970; ANGELINI *et al.*, 1979; HRAOUI-BLOQUET, 1985; HRAOUI-BLOQUET & BLOQUET, 1988; BRAÑA *et al.*, 1990; CASTILLA & BAUWENS, 1990; GALÁN, 1996; AMAT *et al.*, 2000; ROIG *et al.*, 2000; CARRETERO *et al.*, 2006a). Males of *P. vaucheri* exhibited an intense sexual activity in April after the hibernation phase, followed by an interruption of the spermatogenesis in June. Then, a short sexual resting phase was observed during the hot period of the year, specifically in July and at the beginning of August. This period was characterized by the maximal decrease of the morphological characters, with a disappearance of the lumen in the seminiferous tubes, and only the presence

of spermatogonia. Testicular recrudescence started early in late summer (in August) and some young spermatids were already observable. Testis weight increased progressively until the onset of hibernation; and that is accompanied with a development of the seminiferous tubules corresponding to the spermatogenic activity. These observations are in agreement with those of mountains populations, such as *Phoenicolacerta laevis* (Mahrouka-Sannine Mount in Lebanon; HRAOUI-BLOQUET, 1985; HRAOUI-BLOQUET & BLOQUET, 1988), *P. muralis* (Orédon Biologic Station of High Pyrenees in France; SAINT-GIRONS & DUGUY, 1970), and *Iberolacerta monticola* (high and low altitudes in Asturias in northern Spain; BRAÑA *et al.*, 1990). However, a very early stop of the spermatogenesis was reported at the end of May in *Phoenicolacerta laevis* (HRAOUI-BLOQUET, 1985; HRAOUI-BLOQUET & BLOQUET, 1988), which is not the case in *P. vaucheri*.

In addition to the obvious spring testicular activity, another active spermiogenesis was also found in September and October. Finally, this defines two periods of spermiogenesis, corresponding to the second sub-type of the mixed cycle (SAINT-GIRONS, 1982). Similar results were already observed in several Mediterranean lacertids such as *Podarcis muralis* (SAINT-GIRONS & DUGUY, 1970), *Podarcis siculus campestris* (ANGELINI *et al.*, 1979), *Zootoca vivipara* (ROIG *et al.*, 2000), *Podarcis bocagei* (CARRETERO *et al.*, 2006a), *Iberolacerta monticola cantabrica* (BRAÑA *et al.*, 1990), *Phoenicolacerta kulzeri* (RIZK & NASSAR, 2015) and *Phoenicolacerta laevis* (HRAOUI-BLOQUET, 1985; HRAOUI-BLOQUET & BLOQUET, 1988).

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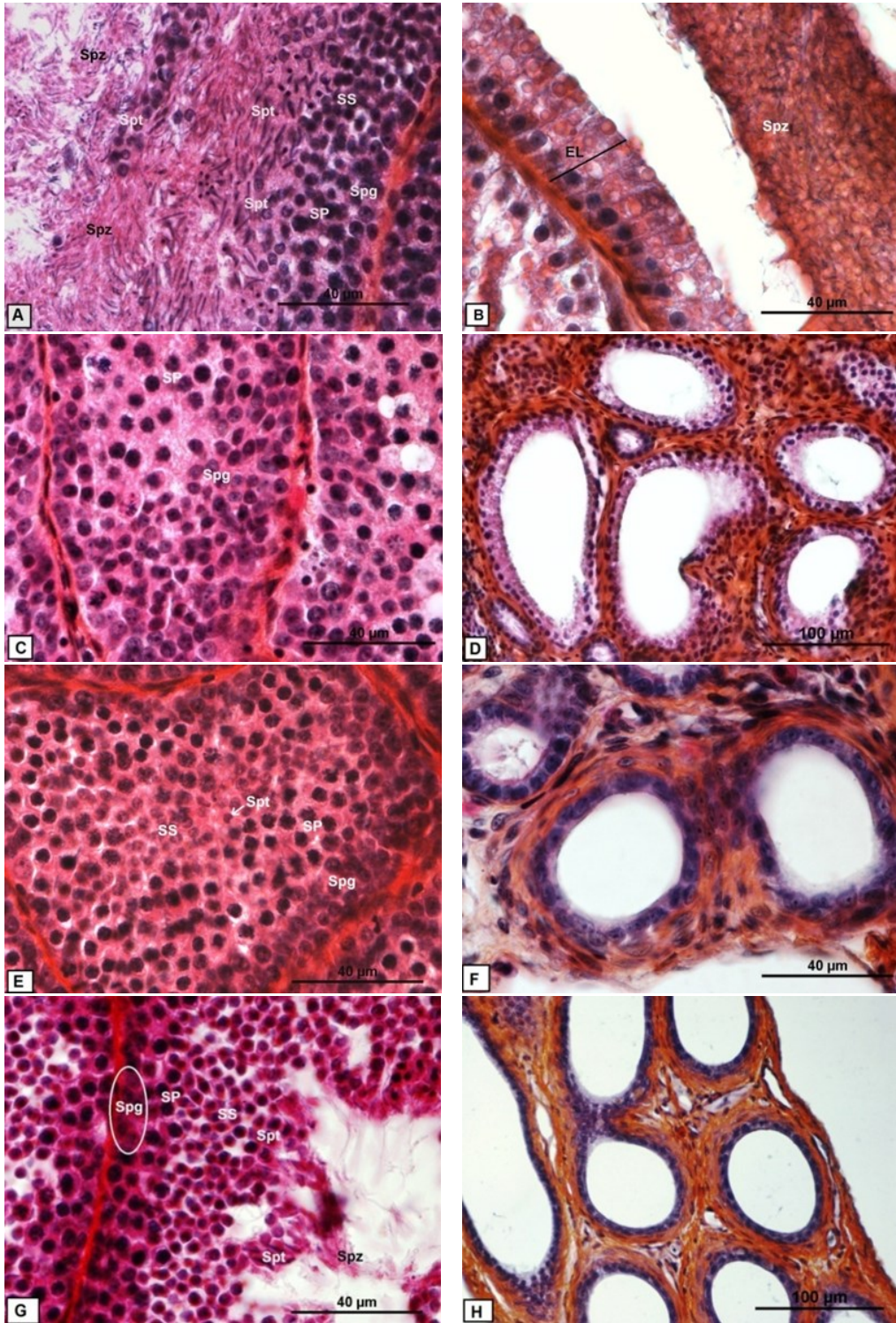


Figure 4: Testis and epididymis histological sections during the reproductive cycle of *P. vaucheri*. **A and B:** Sexual activity phase (April, May, June). **A:** Seminiferous tubules contained all cell categories. Spermatogonia (Spg), primary spermatocytes (SP), secondary spermatocyte (SS), spermatid (Spt) and spermatozoa (Spz). **B:** Observation of spermatozoa in the epididymis lumen. Epithelium layer (EL); **C and D:** Sexual rest phase (July). **C:** Seminiferous tubules with only spermatogonia (Spg) and some primary spermatocytes (SP). **D:** Empty epididymis lumen; **E and F:** Early recrudescence phase (August). **E:** Seminiferous tubules at the beginning of spermatocytogenesis. **F:** Empty epididymis lumen; **G and H:** Autumnal spermiogenesis (September and October). **G:** All cell categories were observed in the seminiferous tubules. **H:** Epididymis lumen remains empty.

This autumnal spermiogenesis has been interpreted as an abortive spermatogenesis (ANGELINI *et al.*, 1979), or as a potential second reproductive season (CARRETERO, 2006).

In addition, no follow-up was possible during winter because of the local climate characterizing the Tala Guilef sector. Snowing time remained from November until March in this region (HAMDINE *et al.*, 1993), reducing the period of lizards' activity to seven months, and thus influencing the reproductive cycle. Wall lizard *Podarcis vaucheri* from Djurdjura did not exhibit any sperm storage in the epididymis during hibernation. Even though spermatozoa were already present in autumn, these remained in the testes. Hence, males can be regarded as unfertile during this period (ANGELINI *et al.*, 1979; ROIG *et al.*, 2000; CARRETERO *et al.*, 2006a; RIZK & NASSAR, 2015). They became fertile in spring only when spermatozoa migrated to the epididymis. Moreover, during the phase of sexual activity, a hypertrophy of the epididymis resulted in an increase of epithelium height and accumulation of secretory granules in its lumen. These various substances secreted by the epithelial cells seem to perform a significant role in the spermatozoa maturation (FERREIRA *et al.*,

2009; AL-AMRI *et al.*, 2013). However, the epididymis cycle of *P. vaucheri* was similar to that of *Podarcis bocagei* (GALÁN, 1996), *P. muralis* (SAINT-GIRONS & DUGUY, 1970), *Iberolacerta monticola* (BRAÑA *et al.*, 1990), *Acanthodactylus erythrurus* (CARRETERO & LLORENTE, 1995), *Psammodromus algirus* (CARRETERO & LLORENTE, 1997), and seems different from that of *Timon lepidus* (CASTILLA & BAUWENS, 1990) and *Phoenicolacerta laevis* (HRAOUI-BLOQUET, 1985; HRAOUI-BLOQUET & BLOQUET, 1988), where the secondary sexual characters are well developed in both autumn and spring. RIZK & NASSAR (2015) reported also this post-hibernation activity in *Phoenicolacerta kulzeri*, with the presence of spermatozoa and secretory granules in the epididymis only in spring. However, the occurrence of spermatozoa in the testes and epididymis in spring and autumn was reported in *Lilolaemus* species from Patagonian, Argentina (MEDINA & IBARGÜENGOYTÍA, 2010).

Both the histological analysis of testes and field observations showed the reproduction period lasting three months, from April to June. In the field, several male-female pairs were seen in copulation positions, females with recent copulation scars were found, and those captured in June were pregnant (*pers. obs.*). This led to

think that spermatogenesis and oogenesis are synchronous, and that mating really lead to fertilization. If so, the cycle of reproduction of *P. vaucheri* would belong to the associated type, which is common in temperate climate (HRAOUI-BLOQUET, 1985; HRAOUI-BLOQUET & BLOQUET, 1988; AMAT *et al.*, 2000; ROIG *et al.*, 2000; CARRETERO *et al.*, 2006a). According to the definition of Whittier & Crews (1987), in the associated reproductive pattern, male mating behavior coincides with the time of the year at which gonads are enlarged and actively producing gametes, while in the dissociated reproductive pattern, spermatogenesis occurred before mating and consequently the gametes are stored until the mating period (e.g. in epididymis or spermato-phores).

In conclusion, data presented here allowed us to shed light on some of the adaptive strategies used by the wall lizard *Podarcis vaucheri* in Djurdjura Mountain. Our results showed that timing of spermatogenesis reflect the "Mediterraneity" of the reproductive strategy of this species with an adaptive response to altitudinal conditions. An early interruption of the spermatogenic activity, a short sexual rest and an early resumption of spermatogenic activity represent adaptations allowing compensating both the long hibernation period and the late emergence in spring (SAINT-GIRONS & DUGUY, 1970). However, comparative studies between the different evolutionary lineages will be necessary to assess the geographical variations in their reproductive characteristics.

Acknowledgements

We are grateful to the anonymous re-

viewers for their comments on the earlier version of the manuscript. Also, we sincerely thank Mr Meribai Y. Director of the Djurdjura national park for permission. We are especially grateful to Moussa and Mohand for their unfailing support during our fieldwork. Animal handling followed humane treatment, and was in agreement with current laws of Algeria. We are also sincerely grateful to Dr. Merzouk Mamou for his help and to enable us to carry out the first steps of this work in Laboratory of analytical chemistry, Tizi Ouzou University.

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