REPRODUCTIVE AND FAT BODY CYCLES OF THE LACERTID LIZARD *PODARCIS BOCAGEI*

PEDRO GALÁN

Departamento de Biología Animal, Facultad de Biología,
Universidad de Santiago de Compostela, E-15706 Santiago de Compostela, Spain

This paper presents data on reproductive and fat body cycles of the oviparous lacertid lizard *Podarcis bocagei* in northwest Spain. Testes exhibited their maximal volume during December-March and decreased in size throughout the summer. This pattern agrees with the "mixed type" of spermatogenetic cycle proposed by Saint Girons (1963, 1982). Vitellogenesis started at the end of March or April. Females with oviductal eggs were found from mid-April to mid-July. Oviposition occurs between mid-May and the end of July. Fat bodies of males were smallest during the spring mating period. Female fat body volumes declined during vitellogenesis. No significant decline of lipid stores was detected during the winter period (October-March).

INTRODUCTION

Since the pioneer studies of Tinkle (1969) and Tinkle *et al.* (1970), lizard life histories have received considerable attention. Life history traits can vary within a single population over time (Ballinger, 1977; Dunham, 1978, 1981; Ferguson *et al.*, 1980; Jones *et al.*, 1987; Castilla *et al.*, 1992) as well as among populations of a single species (Tinkle & Ballinger, 1972; Dunham, 1982; Ballinger, 1983; Tinkle & Dunham, 1983). Numerous studies document such temporal variation and spatial differences in life histories among lizards.

Among the components of an organism's life history, reproduction is perhaps the most fundamentally important process (Gillis & Ballinger, 1992). An important indicator of the reproductive biology of a species is the determination of its reproductive cycle (e.g. Fitch, 1970; Ramírez-Pinilla, 1991*a*, 1991*b*; etc.). Reproductive cyclicity has been studied in numerous temperate zone lizards. Nevertheless, the literature on species of the genera *Podarcis* (family Lacertidae) is sparse and restricted to a few species (e.g. Saint Girons & Duguy, 1970; Botte *et al.*, 1976; Braña, 1984; Kwiat & Gist, 1987; Barbault & Mou, 1988; Henle, 1988; Llorente, 1988; García-Fernández, 1990; etc.).

The genus *Podarcis*, with 15 species (Arnold, 1989; see also Böhme, 1986), occupies a wide variety of habitats over its geographic distribution (south Europe and northwest Africa), particularly in the Mediterranean range, in which it shows great ecological versatility (Arnold, 1987). The reproductive biology of *Podarcis bocagei*, an endemic species with a restricted distribution in the Northwest of the Iberian Peninsula, is poorly known (Pérez-Mellado, 1982; Braña, 1983, 1984; Braña *et al.*, 1992; Galán, 1994). The present study provides data on seasonal changes in gross gonadal morphology and fat body sizes of *P. bocagei* collected in a population from NW Spain.

MATERIALS AND METHODS

A total of 73 adult males and 69 adult females of *Podarcis bocagei* were collected in San Vicente de Vigo, Carral (La Coruña province, Spain; 43° 14' N, 8° 17' W; UTM 29T NH5687; 90 m elevation). Lizards were captured by hand at monthly intervals, from January to December 1990.

The study area experiences a characteristics wet oceanic climate, which is common in coastal areas of the northwestern Iberian Peninsula. Average annual rainfall is 1200 mm and average annual sunshine is about 2000 h. Annual temperature oscillation is very small, about 10° C between the coldest month (January, mean temperature: 8°C) and the hottest month (July, mean temperature: 18°C).

For each lizard, the following measurements were taken: SVL (to the nearest 0.1 mm); body mass (0.1 g); longest and shortest axes of the right testis; maximum diameter of the right epithelio-epididymis; diameter of the largest ovarian follicle; length, width and height of the right abdominal fat body; stage of follicular development (non-vitellogenic, vitellogenic, luteal) and presence of oviductal eggs.

An estimate of testicular volume was obtained using the formula for the volume of an ellipsoid ($V = \frac{4}{3}\pi a^2 b$, where $a = \frac{1}{2}$ shortest diameter and $b = \frac{1}{2}$ largest diameter). Although fat bodies vary in shape, their general form was approximated as the longitudinal half of a flat ellipsoid with unequal lengths for the three axes. Accordingly, we calculated an estimate of fat body volume by the formula $V = \frac{2}{3}\pi abc$, where $a = \frac{1}{2}$ length, b $= \frac{1}{2}$ width and $c = \frac{1}{2}$ height (see Castilla & Bauwens, 1990).

Testicular volume, maximum diameter of the epididymis and fat body volume increased significantly with SVL. An index of SVL-adjusted dimensions of each organ was calculated using residuals from the least-squares regression line between organ size and SVL (both variables log-transformed). To assess differences
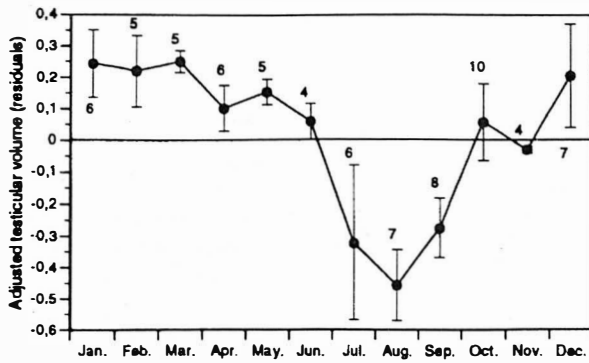
FIG. 1. Monthly changes (mean ±SD and sample size) in SVL-adjusted testicular volume (residuals) of *Podarcis bocagei* throughout 1990.

FIG. 2. Monthly changes (mean ±SD and sample size) in SVL-adjusted maximum diameter of the epididymis (residuals) of *Podarcis bocagei* throughout 1990.

between means a one-way analysis of variance (ANOVA) was used followed by Scheffe's *a posteriori* test. When the data did not meet assumptions of normality, I used a Kruskal-Wallis analysis of variance, followed by Mann-Whitney *U*-tests for comparison among pairs of means.

As part of a demographic study (Galán, 1994), other lizards were marked and recaptured at regular intervals on a 0.27 ha study area adjacent to the sites for collecting specimens for autopsy. Data from this portion of the study were used as corroborative evidence of clutch frequency and timing.

The snout-vent lengths (SVL) of the smallest sexually mature specimens examined in this population were 48.1 mm in males and 45.3 mm in females (Galán, 1994). The mean SVL of male lizards used for this study was 56.1 ± 0.35 mm (range: 50.2-64.5 mm; $n = 73$) and of females was 53.8 ± 0.27 mm (range: 45.9-60.5 mm; $n = 69$).

RESULTS

GONADAL CYCLES

Testicular volume cycle. There were significant differences among months in SVL-adjusted testicular volume (residuals of the regression of testicular volume on male SVL; ANOVA: $F = 25.82$; df = 11, 72; $P< 0.001$; Fig. 1). An *a posteriori* analysis (Scheffe-test) revealed two principal groups in SVL-adjusted testicular volume. The first is July-September (negative residuals) and the second is October-May (without November). A third group was formed by June (not significantly different from October-May) and November (only significantly different from August).

Testicular volume began to increase in September, was maximal in December-March and decreased thereafter (Fig. 1). Minimal volume was in July-August. Increasing testicular volume in autumn appeared to be correlated with decreasing photoperiod and temperature, and increasing rainfall.

Epididymis diameter cycle. Maximum diameter of the epididymis, adjusted for SVL, also exhibited seasonal changes during 1990 (Fig. 2; ANOVA: $F = 19.62$; df = 11, 69; $P < 0.001$). *A posteriori* analysis of
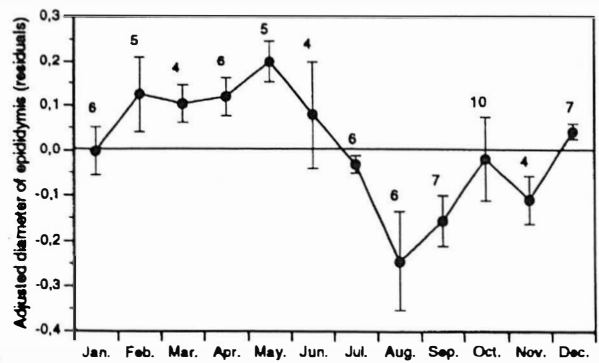
the data by Scheffe-test shows two principal groups of the monthly values: December-June (without January; positive residuals) and August, September and November (highly negative residuals). June and October did not differ significantly from these two groups.

Maximal epididymis diameter was reached in May and diameter began to decrease in June. Minimal diameter was reached in August, at the end of the reproductive season.

Female gonadal cycle. Females with immature ovaries that contained many transparent grey-to-translucent white follicles less than 1.6 mm in diameter were found between August and March. Vitellogenesis began at the end of March (always in bigger females; SVL > 56 mm) and ovarian follicles increased in size to a maximum diameter of about 7.0 mm prior to ovulation (Fig. 3). Ovulations occured in late April (1990) or early May (1991) so that females produced the first clutch before the end of May. The second clutch was deposited in June. In some females, the third clutch was deposited in July. Oviductal eggs were seen on three occasions after mid-July. Most females collected on these dates and all females collected later were postreproductive.

Apparently there was asynchrony among females during the reproductive season. For example, between 1 and 5 June, 1990, three individuals had oviductal eggs whereas four had vitellogenic follicles (about 5.5 mm diameter) and one had just completed oviposition.

Data on clutches shown in Fig. 3 were obtained from females collected in the study area that later laid clutches in terraria. These ovipositions were recorded between May 12 and July 22, 1990.

FAT BODY CYCLES

Male and female abdominal fat body volumes related to SVL showed a clear seasonal cycle (Fig. 4). There were significant differences between months (Kruskal-Wallis: males: $H = 48.25$; $P < 0.001$; females: $H = 45.78$; $P < 0.0001$).

In males, we detected two principal clusters of monthly values (differences not significant in each group, Mann-Whitney *U*-test $P > 0.05$). On the one
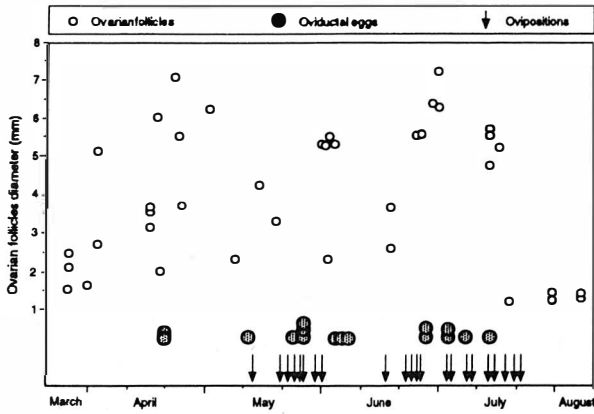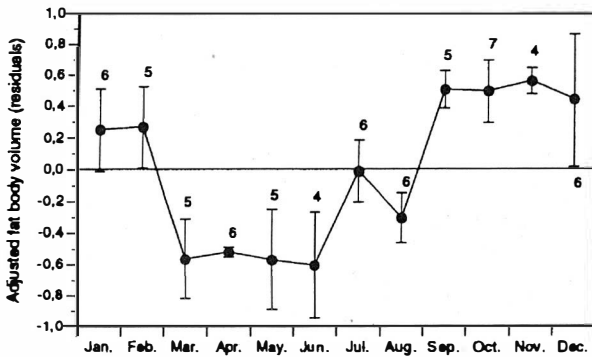
FIG. 3. Gonadal cycle of female *Podarcis bocagei* in the study area during the reproductive season of 1990. Open circles: diameter of the largest ovarian follicle from both ovaries. Shaded circles: oviductal eggs; arrows: oviposition.
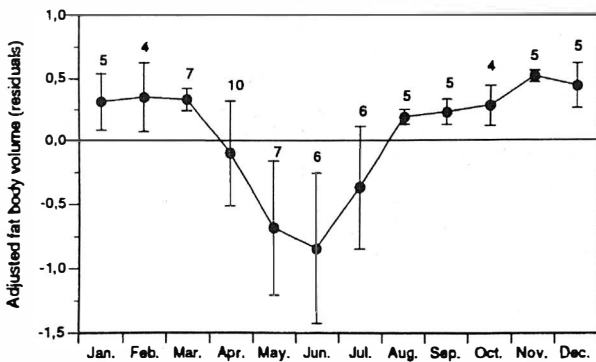

FIG. 4. Monthly changes (mean ±SD and sample size) in SVL-adjusted fat body volume (residuals) on male and female *Podarcis bocagei* throughout 1990.

hand, September to February (positive residuals), and on the other, March to June (negative residuals). July and August do not differ significantly in these two groups. Fat stores of the males decreased rapidly in volume between February and March and were at their lowest levels during March to June.

The fat bodies of females were lightest in June, began to be deposited in July and reached a peak in November. As can be observed in Fig. 3 and 4, there was an inverse relationship between vitellogenesis and fat body lipid deposits in females.

DISCUSSION

The reproductive cycle of *Podarcis bocagei* is similar to that of many other temperate zone lizards. The spermatogenetic cycle is of the "mixed type", in the terminology of Saint Girons (1963, 1982). Testicular recrudescence began in September and proceeded until the onset of hibernation. Testes attained their maximum volume from January-March, decreased in volume during April-July and reached their minimum size during August. All European lacertids studied to date, except *Acanthodactylus erythrurus* from central Spain (see Castilla *et al.*, 1992), exhibit a mixed type reproductive cycle (e.g. Pérez-Mellado, 1982; Bons & Saint Girons, 1982; Pascual-González & Pérez-Mellado, 1989; Castilla & Bauwens, 1990).

The annual epididymis cycle observed in this population is similar to the cycle of this organ shown by *Lacerta monticola cantabrica* in populations from high and low altitudes in Asturias (northern Spain), principally the latter (Braña *et al.*, 1990). Nevertheless, it differs from the other Mediterranean Lacertidae such as *Lacerta laevis* (Hraoui-Bloquet & Bloquet, 1988), *Lacerta lepida* (Castilla, 1989; Castilla & Bauwens, 1990) and *Psammodromus algirus* (Carretero & Llorente, 1991). In these species, the maximum diameter of the epididymis is not attained in spring, as in *Podarcis bocagei*, but in autumn instead, and the organ remains hypertrophied until the end of the mating season. As pointed out by Braña *et al.* (1990), a possible explanation of these differences may be the contrasted environmental characteristics of these populations (Mediterranean versus Atlantic). Mediterranean lizards are exposed to higher maximal temperatures and a greater thermal amplitude than the Northwestern (Atlantic) Iberian lizard populations. These environmental conditions allowed some winter activity and an early beginning of the mating season (Amores *et al.*, 1980; Mellado & Olmedo, 1987; Hraoui-Bloquet, 1987; Hraoui-Bloquet & Bloquet, 1988). Nevertheless, this 'Mediterranean' type of epididymis annual cycle cannot be considered as a general pattern for all Mediterranean Lacertidae (see Angelini *et al.*, 1978).

The female gonadal cycle is also similar to that of other Iberian Lacertidae. Nevertheless, ovarian activity lasts longer in this population of *Podarcis bocagei* than in other Lacertidae which inhabit areas with continental climate or high altitudes (Pérez-Mellado, 1982; Braña, 1983; Busack & Klosterman, 1987; Pascual-González & Pérez-Mellado, 1989; Pollo & Pérez-Mellado, 1990; Braña *et al.*, 1992; Castilla *et al.*, 1992). Vitellogenesis began in late-March or April. The ovarian follicles are translucent and small (maximum about 1.6 mm) in juvenile lizards and in adult females between August and March. Large fe-

males (SVL more than 56 mm) were the first to start vitellogenesis and, consequently, began reproduction earlier than small females. Ovulations occurred from mid-April until mid-July and oviposition from May until late July. A mature female at the onset of reproduction, in April, could produce three clutches by the end of the season in July. (Galán, 1994; see also Braña, 1983). Reproduction ended in July, after which time all females examined were post-reproductive.

This prolonged female reproductive cycle is similar to that of other strictly Mediterranean *Podarcis* species, such as *P. sicula* from south Italy (Botte *et al.*, 1976; Limatola *et al.*, 1989). It is also like the female gonadal cycle of populations of *Lacerta monticola cantabrica* from low altitudes in La Coruña province, the other unique species of small lacertid that inhabits this area (Galán, 1991).

The general model of continuous reproduction throughout the breeding season, with three phases of ovulation and laying, shown by this population, is only valid at the population level. At the individual level, there is high variability. For example, at equal size and age, females with a high level of lipid inguinal storage begin reproduction early and can lay several clutches (Galán, 1994). If there are differences in size between females, the variability in timing, clutch characteristics and clutch frequencies are very high.

There may be a close relation between the temperate environmental conditions of the study area (low temperature oscillation, absence of dry season) and the duration of the reproductive period. Moderate temperatures at the end of winter and in early spring permitted the beginning of the mating season in March and, on the other hand, the absence of a dry summer period permitted oviposition to be prolonged until late-July.

The fat body cycles were closely coupled with the timing of reproductive events in both sexes. As pointed out by Castilla & Bauwens (1990), in estimating fat body volumes, we unrealistically assume that these have uniform and fixed shape. Therefore, these estimates are subject to error that would increase variance within the sampling period. Even so, a fat body cycle emerges which is consistent with those of other temperate zone lizards (Ballinger & Schrank, 1972; Avery, 1974; Derickson, 1976a; Etheridge *et al.*, 1986; Castilla & Bauwens, 1990; Castilla *et al.*, 1992).

Mature females have distinctly larger fat bodies than males and there is a decrease in stores throughout the reproductive season, as happen in many species of lizards from temperate areas (e.g. Derickson, 1976a; Ballinger, 1973; Diller & Wallace, 1984; Braña *et al.*, 1992). The inverse relationship between follicular development and inguinal fat body volume has been demonstrated in other populations of *Podarcis bocagei* from northern Spain (Asturias) by Braña *et al.* (1992). A large fraction of the energy invested in the development of the ovarian follicles come from the lipids stored in the inguinal fat bodies, as in many lizard species (Hahn & Tinkle, 1965; Derickson, 1976b; Guillette & Sullivan, 1985; Vitt & Cooper, 1985) and other reptiles (Congdon & Tinkle, 1982; Diller & Wallace, 1984). Nevertheless, these lipid stores are useful mainly in the first clutch, remaining vestigial during the rest of the breeding season. Thus, energy allocated to vitellogenesis in later clutches seems to be obtained from food consumed during that period (Braña *et al.*, 1992).

The fat body stores of males show an abrupt decrease at the beginning of the reproductive season (March). These stores remain low throughout the mating period. As pointed out by Castilla *et al.* (1992) for another lacertid species, *Acanthodactylus erythrurus*, the abrupt depletion of the males' fat body stores at the beginning of the activity season probably reflects high energy requirements associated with the acquisition and defence of a territory, searching for and guarding a mate, and courtship during this period. This relation is also observed in other lizard species (e. g. Vitt *et al.*, 1978; Ortega & Barbault, 1986; Méndez de la Cruz *et al.*, 1988; Braña *et al.*, 1990).

In both sexes fat body volumes remain high during winter. Therefore, the energy requirements during the winter diapause appear to be only a rather small fraction of the fall lipid stores, as reported in other temperate lizard species (Derickson, 1976a). This pattern can be observed in this population, although they show some winter activity during periods of favourable weather (Galán, 1994).

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