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SEXUAL MATURITY IN A POPULATION OF THE LACERTID LIZARD *PODARCIS BOCAGEI*

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The attainment of sexual maturity by males and females of the lacertid lizard *Podarcis bocagei* was studied in a population from NW Spain (La Coruña province). Two methods were used. The first method involved capture, marking and recapture of marked hatchlings in a study plot. The second method examined the development of sexual organs through dissection of lizard samples from the same locality. Sexual maturity was attained at a minimum size (females: 44-45 mm; males: 46-51 mm snout-vent length), not a minimum age. Some individual and seasonal variation was observed in this minimum size, which decreased as the reproductive season progressed. Slightly fewer than half of the individuals from a given cohort (50.0%-44.4% in males and 47.1%-44.4% in females, from samples of 1989 and 1990 cohorts respectively) attained the minimum size and reproduced towards the end of the next reproductive period (at 11-12 months of age). The mature yearling individuals were those that hatched from the first clutches of the preceding year, most of them in July. By their second autumn, all specimens from the previous year's cohort had exceeded the sexual maturity-threshold size.

INTRODUCTION

Age and size at sexual maturity are important traits in the life history of an organism. Both can exercise a marked influence on the demographic strategies of squamate reptile populations (Tinkle *et al.*, 1970; Dunham *et al.*, 1988). There are two general strategies of maturation in squamate reptiles: "early" versus "late" maturity. Each of these strategies presumably reflects natural selection favouring successful genotypes under certain environmental conditions (James, 1991). Early maturity may increase life-time reproductive success if there is no reduction in future reproductive output as a result. Late maturity may be more successful if the delay is compensated by larger clutch sizes (as a result of larger body size), or enhanced survival rates (Cole, 1954; Tinkle *et al.*, 1970).

As the rate of growth of reptiles is highly variable, sexual maturity is linked more closely to stage of development or size rather than to age (e.g. Spellerberg, 1982). Among the suborder Lacertilia, sexual maturity is often reached after one or two years, despite considerable variation between species. According to data derived from articles listed in the reviews of Andrews (1982), Dunham *et al.* (1988) and Shine & Schwarzkopf (1992), age at maturity in lizards ranges between 0.65 and 2 yr (data from 28 species or populations), with only two exceptions: *Xantusia vigilis* (3 yr) and *Cyclura carinata* (6.5 yr). In the family Lacertidae, small species also attain sexual maturity between one and two years of age (e.g. Bauwens & Verheyen, 1987; Hraoui-Bloquet, 1987; Barbault & Mou, 1988; Carretero & Llorente, 1991). Nevertheless, larger species attain maturity at an age of 2-4 yr (e.g. Strijbosch, 1988; Castilla & Bauwens, 1989; Marco & Pérez-Mellado, 1989; Saint Girons *et al.*, 1989).

Reptiles, like most other vertebrates and invertebrates, begin reproducing before they attain their maximum body size. In lizards and snakes, body size at maturation is a relatively constant proportion of maximum size, with a ratio of size at maturity to maximum adult body size generally ranging between 0.50 and 0.90, and an overall mean of 0.71 (Shine & Charnov, 1992). According to Tinkle *et al.* (1970) and Dunham *et al.* (1988), lizards maturing at later age also mature at a larger size, remain larger throughout life, and produce more eggs per clutch than do lizards maturing at an earlier age.

As pointed out by these latter authors, there are two complementary approaches for establishing sexual maturity in reptiles. The first relies upon the recognition of secondary sexual characters or behaviour patterns appearing after sexual maturity. The second relies upon dissection and direct observation of mature gonads or gametes. In this paper, both methods are used to establish size and age of sexual maturity in both sexes of a population of the lacertid lizard *Podarcis bocagei*. The aim was to provide quantitative data on body size and age at sexual maturity in this species, and to describe between-individual and seasonal variation in size and age at maturity.

MATERIAL AND METHODS

NATURAL HISTORY

Bocage's wall lizard, *P. bocagei* (Seoane, 1884), is an endemic species with a restricted distribution in the north-west and west Iberian Peninsula. It is a small, diurnal, insectivorous lizard of the family Lacertidae. Species of this family are abundant and widespread in the Old World; nevertheless, few accounts of their life histories have been published.

Data obtained during 1989-1991, principally on the basis of mark-recapture experiments but also from laboratory hatching studies (Galán, 1994), show that mating takes place between the end of March and July. The results of this study indicated that during the laying period (from May to July) 8.5% of reproductive females produced three clutches, 52.1% two clutches and 39.4% one clutch. In general, single clutches were produced by small females. Only a small proportion of large females produced three clutches. Mean clutch size was 4.12 eggs (range 2-7). Both clutch size and egg volume increased with maternal SVL. There was no significant between-year variation in clutch size, breeding females' SVL, egg weight or relative clutch mass. Hatching success (as estimated in 1989, 1990 and 1991 from natural nests at the study site) was high, ranging from 83% in 1991 to 91% in 1989.

Dimorphism occurs in this species. The males are bigger than females on average (adult males SVL, 46-65 mm and adult females SVL, 44-63 mm in the population studied) and colour patterns are present during the reproductive period. Adult males show a bright green dorsum whereas females (with few exceptions) have a brown dorsum, like immature lizards (Galán, 1986, 1995; Galán & Fernández-Arias, 1993). The annual activity season of *P. bocagei* from north-western Spain is long. Active individuals can be observed all months of the year; nevertheless, during the winter season (November to January) activity was reduced to basking in the vicinity of winter retreats. The pattern of growth of individuals from the studied population is described by the von Bertalanffy equation (Galán, 1994).

STUDY AREA AND AGEING TECHNIQUES

Lizards were studied in a 45 x 60 m plot located in San Vicente de Vigo (45°18' N-8° 20' W; UTM 29T NH5687; 90 m elevation), Carral (province of La Coruña, north-western Spain). The study area was of the wet-oceanic climatic type, characteristic of the coastal areas of the north-western Iberian Peninsula. Average annual rainfall is 1200 mm and average annual sunshine is about 2000 h. Annual temperature oscillation is small, about 10°C between the coldest month (January, mean temperature: 8°C) and the hottest month (July, mean temperature: 18°). For more details of the study area, see Galán (1994).

Data were gathered during a population study conducted in September 1989-October 1991. Lizards in the study plot were captured by hand, marked individually by toe-clipping, and released after recording identity, sex, reproductive condition, snout-to-vent length (SVL, to nearest 0.1 mm), tail length, and weight (to nearest 0.1 g, on a Pesola® dynamometer).

Age at maturity was investigated by reference to records of juveniles born and marked in 1989 and 1990, and recaptured during 1990 and 1991 respectively. Although a large number of hatchlings were marked (128 in 1989 and 153 in 1990), only 27 (17 females and 10 males) were recaptured between April and July of 1990, and again only 27 (18 females and 9 males) between April and July of 1991. The causes of this low recapture rate (mainly high mortality and dispersal of young age classes) have been discussed elsewere (Galán, 1994).

Hatching occurred between July and September. Hatchlings have a SVL of 22 to 26 mm (Galán, 1994). Hatchlings of these body sizes collected and marked during July had obviously been born in that month. To determine the time of hatching of hatchlings marked in August and September, the ventral navel scar was examined with a x10 lens. If the navel scar was still open, these individuals had an age of less than 7-10 days (Galán, unpublished data). Average growth rates of hatchlings during their first activity season (from July to September) were 0.186 and 0.142 mm/day, in males and females respectively (Galán, 1994).

Acquisition of sexual maturity by individuals of a population of this species was studied mainly through external signals shown by live animals. Following Tinkle & Ballinger (1972), age at maturity is defined here as age at first breeding rather than age at which mature size is attained. Sexual maturity in the field was assessed in females by noting the presence of enlarged vitellogenic follicles or oviductal eggs, both identified by ventral palpation (pregnant females show a marked distension of the body), or the presence of a mating scar (all mated females that were subsequently recaptured proved to be gravid).

In males it is more difficult to determine minimum age and size at maturity, since they show less evident external signals of sexual activity (e.g. Dunham *et al.*, 1988; James, 1991). Furthermore, both secondary sexual characters and testicular volume decrease towards the end of the breeding season. Sexual maturity was assessed in view of the presence of secondary sexual characters (e.g. bright green dorsum, presence of an enlarged tail base, presence of enlarged femoral pores).

In addition, five males and five females were dissected in each month of the reproductive season to examine their sexual organs and to establish their maturity (total 40 lizards). These lizards were collected from close to the study plot (within 50-500 m of its border), and showed the same size range and external characteristics as those marked in the plot. For each dissected 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; stage of follicular development (non-vitellogenic, vitellogenic, luteal) and presence of oviductal eggs. In the text, mean values are cited ± standard error of the mean.

RESULTS

FEMALES

Body size (SVL) distributions of females of *Podarcis bocagei* collected during each month of the 1991 reproductive season are show in Fig. 1. Several adult females that still had not begun reproduction in April were considered non-reproductive. Nevertheless, recapture records show that virtually all females that were mature in the previous year showed signs of reproductive activity in May.

The minimal size at which sexual maturity is attained appears to decrease from the beginning to the end of the mating season. In April, the smallest female found to be gravid by ventral palpation had a SVL of 52 mm; in May, the smallest SVL was 49 mm and in June and July, 44 mm. On the other hand, some females of 50-53 mm SVL did not show signs of sexual activity in May; in June, maximal size of non-reproductive females was 50 mm SVL and in July this maximal size was 45 mm. Thus, the size at sexual maturity in females is 49-53 mm SVL in May, 44-50 mm in June and 44-45 mm in July. The smallest female known to be mature had SVL of 44 mm. Nevertheless, one female, collected about 1.5 km from the study plot, had SVL of 41.7 mm and bore three oviductal eggs; this is the only reproductively mature female of less than 44 mm SVL that I have ever seen (Galán, 1986, and unpublished data).

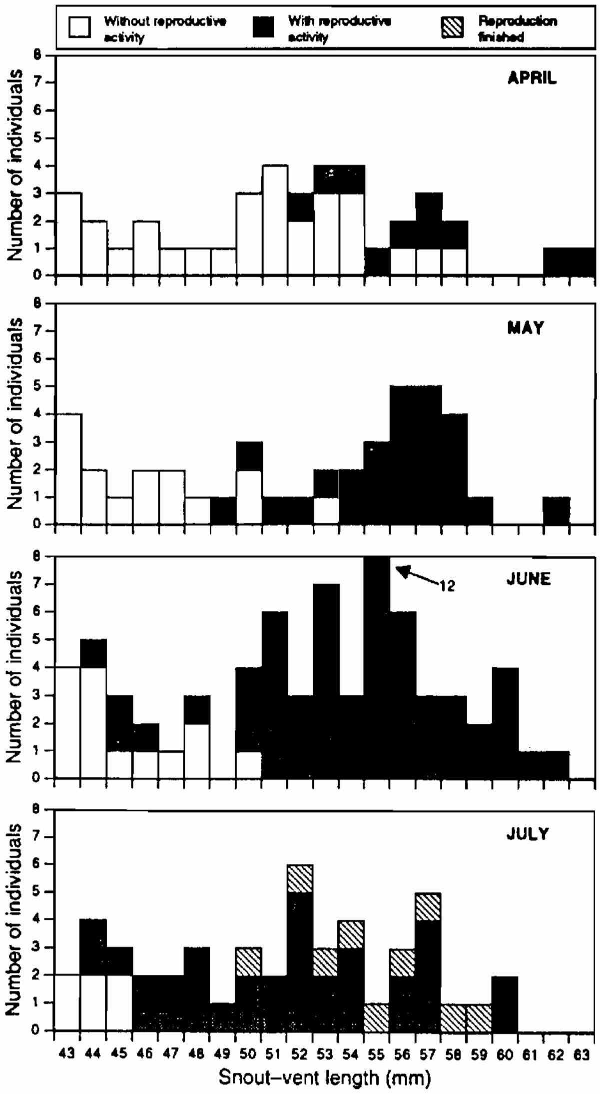

FIG. 1. Body size distribution of female *Podarcis bocagei* collected during each month of the 1991 reproductive season (April to July). These individuals were classified according to whether they showed signs of reproductive activity or not. Signs of reproductive activity were the presence of recent mating scars, or enlarged vitellogenic follicles or oviductal eggs (both noted by ventral palpation).

Body size (SVL) of reproductive females varies significantly between months during the mating season (ANOVA, $F = 7.41$; df = 3, 126; $P < 0.001$). *A posteriori* Scheffé test revealed significant differences ($P < 0.01$) between April-July ($F = 4.45$) and between May-July ($F = 5.24$).

Samples of dissected females during each month of the reproductive season show the same minimal body size at maturity as do the records obtained from live specimens (May: 49 mm SVL; June and July: 44 mm).

In females, slightly less than half of the marked individuals of each cohort can reach sexual maturity and reproduce at the age of 11-12 months (Table 1). The 52.9% (1990) or 55.6% (1991) of females remain as subadults until the next breeding season.

Recapture records also show that the individuals that attained the minimum size of sexual maturity before the end of the mating season, and hence participated in reproduction, were born in the first clutch of the previous year (laid in May and hatched in July). In females from the 1989 cohort, individuals that had been born in July had 35.6-40.5 mm SVL (average: 37.5 ± 0.66 mm; SD = 1.72; $n = 7$) in autumn 1989, and all lizards of this sample reproduced the following year, in 1990. In contrast, the recaptured individuals of the same cohort that had not attained maturity in 1990 had a smaller body size during au-

TABLE 1. Frequencies of lizards of both sexes from the 1989 and 1990 cohorts that attained sexual maturity in each month of the breeding season during their second activity season (one year old). Dates obtained from recapture records in the study plot during 1990 and 1991.

1990:	April	May	June	July	Total (Jun-Jul)	*n*
Males	0	0	20.0	30.0	50.0	10
Females	0	0	17.7	29.4	47.1	17
1991:						
Males	0	0	11.1	33.3	44.4	9
Females	0	0	16.7	27.8	44.4	18

TABLE 2. Minimal body size and sizes of sex organs of male animals with secondary sexual characters (green dorsal colouration) and clear internal sexual maturity signs (high development and capillarization of testis and epididymis) during every month of the breeding season.

Month	Minimal body size (SVL)	Testicular length	Testicular volume	Epididymis width
April	50.5	4.60	22.84	1.25
May	47.6	3.85	15.52	1.00
June	45.8	4.28	14.00	0.90
July	48.9	3.55	5.69	0.75

tumn 1989: 28.9-35.5 mm SVL (average: 32.8 ± 1.22 mm; SD = 2.98; *n* = 6). These last females came from clutches hatched in the second half of August or September.

MALES

Dissection indicated that minimum size at maturity of males (as of females) decreased between April and June of 1990. Nevertheless, in July a strong reduction was observed in both testis and epididymis sizes in all males examined. During this last month, all dissected male lizards smaller than 48 mm SVL were clearly immature (Table 2).

The body size distribution of live males with and without secondary sexual characters collected from the study plot in the 1991 breeding season also show that the minimum body size at maturity of males, like that of females, decreased during the breeding season, from 48 mm (SVL) in May, through 47 mm in June to 46 mm in July. Body size of males that were immature or without reproductive activity likewise decreased from May to June (Fig. 2).

These estimates of minimum size at maturity of males agree closely with estimates based on dissection. The bright green colouration of the dorsal region can thus be considered a reliable external sign of sexual maturity in males of this species, almost throughout the breeding season. On the basis of estimates obtained by both methods, it is considered that the size at which males attain sexual maturity ranges between 46 and 51 mm SVL.

This body size range varies between months. So, in May the variation ranges between 48 mm and 55 mm, in June between 47 and 50 mm, and in July between 46 and 51 mm. In contrast to females, differences were not significant (ANOVA: $F = 1.26$; df = 3, 110; $P = 0.29$).

The number of recaptures of yearling males marked as hatchlings was lower than that of females. Nevertheless, a similar pattern in age at maturity was observed in both sexes (Table 1). Approximately half the male cohort attained sexual maturity during its second active season. As for females, recapture records show that yearling males that attain sexual maturity at 11-12 months come from the first clutches of the previous breeding season, laid in May and hatched in July. Yearling male lizards, recaptured as mature adults before the end of the 1990 breeding season, had a SVL between 37.3 mm and 40.5 mm (average 38.7 ± 0.61; SD = 1.37; *n* = 5) during the previous autumn (October and November 1989). In contrast, males of this cohort that did not attain maturity before the end of the 1990 breeding season had smaller SVL during the preceding autumn (ranged 26.9-37.0 mm; average: 32.2 ± 1.73; SD = 3.88; *n* = 5). Recapture records show that these latter males came from clutches hatched in mid-August and September.

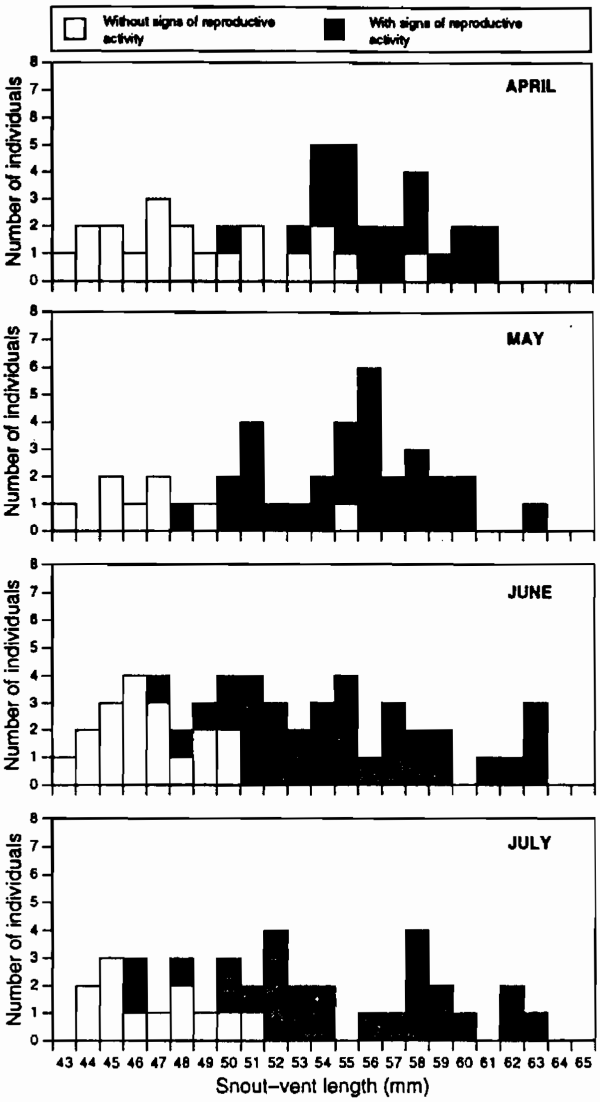

FIG. 2. Body size distribution of male *P. bocagei* collected during each month of the 1991 reproductive season. Signs of reproductive activity were a bright green dorsal colouration and courtship behaviour.

DISCUSSION

Both sexes of the *Podarcis bocagei* population reached sexual maturity after 11-12 months, at least in the earliest hatchlings (early July until mid-August). This age is attained in mid-June or July. They then begin reproduction immediately (in the case of females, see below). For hatchlings born in mid-August to mid-

September, sexually mature size would be reached in late summer or autumn of their second activity season, an inappropriate time for reproduction. Their first breeding would be in the subsequent spring (third activity season). So these belong in the class categorized as "delayed maturing" (Tinkle, 1969). This pattern has been described in several lizard species (e.g. Tinkle & Ballinger, 1972; Dunham *et al.*, 1988) and is a frequent event in small Mediterranean lacertids (e.g., Henle, 1988; Carretero, 1993). In contrast, in bigger lacertid species, sexual maturity is always later, with differences between the sexes (e.g. Castilla, 1989; Marco & Pérez-Mellado, 1990; Marco, 1994).

Sexual maturity in *Podarcis bocagei* is related to the attainment of a minimal body size and not a minimal age, as in other lacertids (Heulin, 1985; Bauwens & Verheyen, 1987). Differences in age at maturity between individuals of the same cohort may be a direct consequence of the long hatching season (July to September). On the other hand, particular events (such as diseases or injury) delay growth (Galán, 1994) and may also cause differences in age at maturity.

High variability (both among individuals and within-season) was also observed in the minimal body size at which sexual maturity is attained by females. Over the reproductive season, minimum size at maturity decreases significantly. The widest among-individual range was that observed in July 1990 (41-45 mm), although 41 mm appears to be exceptionally small. In many other populations of *Podarcis bocagei* from north-western Spain, adult females smaller than 44 mm SVL have not been recorded (Galán, 1986 and unpublished data). Many other authors have described a high variability in the size and age at sexual maturity in female lizards, but this variability is between different populations of the same species (e.g., Bauwens *et al.*, 1986) or between different years within the same population (e.g., Bauwens & Verheyen, 1987). In the study population, variability occurs within the same population and year.

Individual differences in minimal body size at maturity within the same period can be related to differences in the amount of lipid stores between young females. These fat bodies are necessary for vitellogenesis and egg development (e.g. Braña *et al.*, 1992 for northern Spain *P. bocagei* populations). Thus, female lizards that have not obtained enough lipid for egg production at the end of the reproductive season (in July), cannot reproduce even though they have attained the minimal body size for maturity.

It is important to point out that the young females that mature sufficiently early in the breeding season to produce one clutch grow more slowly during the second half of the summer than the other females of the same age that did not reproduce. This may be due to the high energy expenditure involved in the egg production for yearling females. At the end of the activity season, the body size of yearling mature females may be smaller than that of females that did not reproduce. For example, of two yearling female lizards of approximately the same body size during July, the female that did not reproduce (45.6 mm in July) attained 53.8 mm SVL in the following autumn (November), whereas the female that laid three eggs (45.8 mm) attained 51.5 mm SVL in the same time.

During autumn, female *P. bocagei* classified as adults on the basis of size are, in fact, two classes: adult females that produced eggs and adult females that did not. The same pattern was observed by Andrews (1989) in a population of the tropical lizard *Anolis limifrons* and he gave this observation particular importance. In studies of lizard population dynamics, a large proportion of immature females can be considered to be mature and producing eggs if the sole criterion is body size during pre- and postreproductive seasons. In this population, during the autumn and following spring, several females that had not laid eggs in the previous breeding season had a larger body size than females of the same cohort that had reproduced and laid eggs in that period. In females that had not reproduced, energy was allocated only in growth and in this way they attained a larger body size than females that diverted a proportion of their energy to egg production (see also Andrews, 1979, 1989).

One clear result, despite often wide variation in size at maturity, is that males matured at a larger SVL than females: 46-51 mm versus 44-45 mm. Nevertheless, both sexes matured at the same age, between one and two years and also with a similar proportion between these two ages in each sex: slightly fewer than half of each cohort. As in the case of females, differences in age at maturity can be related to the hatching period and, consequently, to the amount of time for growth between different individuals.

It is interesting to point out that the attainment of sexual maturity in yearling males does not necessarily imply that they participate in reproduction that year, as in the case of adult yearling females. In young females, all individuals that attain sexual maturity before the end of the mating season are mated and produce eggs (Galán, 1994). Direct field observation shows that smaller adult males with recent attainment of sexual maturity (clear presence of secondary sexual characters, but small size), are unable to win in contests with larger males. In all encounters between a yearling adult male and a two or more year-old male observed in the field ($n = 17$), young males showed submissive behaviour (tail lashing and "Treteln" displays) and flight. So, recently matured males can have access to females and mate only in the absence of the full adult males. Consequently most of them probably do not mate until their third activity season.

Shine & Charnov (1992) observed that, in lizards and snakes, body size at maturity is a relatively constant proportion of maximum size. The mean ratio of size at maturity to maximum body size in the lizard species studied by these authors was 0.74. In the population of *P. bocagei* studied here, maximum adult body size (SVL) is 65 mm in males and 63 mm in females. Thus, the ratios obtained were 0.71-0.78 in males, and 0.70-0.71 in females. All of these values are very close to the overall mean given by Shine & Charnov (1992).

Maintenance of a high variability in age and, to a certain extent, body size at maturity, presumably reflects an adaptation to unpredictable environments, as observed in the studied *Podarcis bocagei* population. This lizard population lives in a place with pronounced slopes and uncovered excavated land (a gravel pit and surrounding areas) which was rapidly recolonized by opportunistic vegetation (Galán, 1994). Excavation for gravel creates new derelict uncovered areas, which again suffer the process of plant recolonization. In these environments, as in others such as urban areas, the edges of cultivated areas, trenches, etc. (all of them typical small lacertid lizard habitats, see Arnold, 1987) may favour the maintenance of high variability in the life-history strategies for facing different selection pressures.

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