Reproductive cycle of the sand lizard (*Lacerta agilis*) in its southwestern range

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Abstract. The reproductive cycle of *Lacerta agilis* was studied in the Pyrenees at the southwestern boundary of the species range. The activity period is short (about 4.5 months). Males attain sexual maturity at smaller sizes than females and show mixed type spermatogenesis and spring spermiogenesis. Vitellogenesis in females is rapid (45 days for the whole population) with a long period of oviductal retention. Clutches are laid at the beginning of summer. During the reproductive period males mobilise reserves during the mating activities. Females deplete more fat reserves but later in the season than males and they are at their lowest after egg production. In both sexes, energy resources are mobilised from the fat bodies and also from the liver and the proximal part of the tail. Clutch size increases with female size but also depends on other factors. The short activity period does not appear to affect the reproductive cycle of this species. The gonad cycles and clutch traits do not show substantial differences from other European populations, perhaps with the exception of slight variation in the timing of reproductive events and, to a lesser extent, clutch frequency. This evidence strongly suggests that the limited southwestern range of *Lacerta agilis* is not due to environmental constraints but to very recent colonization.

Introduction

Life history traits such as the reproductive cycle and output, the age and size at sexual maturity often exhibit both spatial and temporal inter- and intraspecific variation in lizards (Tinkle et al., 1970; Shine and Schwarzkopf, 1992; Tinkle et al., 1993; Bauwens and Díaz-Uriarte, 1997).

The sand lizard (*Lacerta agilis*) is a medium-sized lacertid found in the Eurosiberian region. Several aspects of its reproductive biology have already been studied intensively but, surprisingly, only indirect references about its reproductive cycle are available (Kehl and Combescot, 1955; Rykena, 1988a, b; Strijbosch, 1988; Olsson, 1993, 1994; Olsson and Madsen, 1996; Olsson and Shine, 1996, 1997a, b; Olsson and Silverin, 1997; Olsson et al., 1996a, b, 1997).

The Pyrenees constitute the southwestern boundary of the wide range of this species (Llorente et al., 1997; Gasc et al., 1997). It has been postulated (Yablokov et al., 1980) that the present range of *L. agilis* in Europe is recent. Consequently, the small Iberian distribution may be the result of recent colonization. In fact, this species is absent from many favourable habitats in central and western Pyrenees probably due to recent colonization (Llorente et al., 1997). If true, reproductive traits of the Pyrenean sand lizards should be similar to other populations in its central range. Otherwise, if substantial differences appear they could be due to suboptimal abiotic conditions limiting the species range as reported for other lacertid lizards (Saint-Girons, 1984; Strijbosch, 1988).

In order to test between these hypotheses, this study aimed a) to describe the cycles of gonads and organs containing lipid reserves in both sexes; b) to look for relationships between female reproductive traits and body size c) to compare the results of this study to those conducted in other European populations.

Material and methods

The study was carried out on a population of *L. agilis* living at 1600 m in the Sierra del Cadí, Eastern Pyrenees (UTM 31T DG18) at the southwestern boundary of the distribution range between May 1994 and October 1996. This population occupies subalpine meadows surrounded by *Pinus uncinata* forest. The study area comprised approximately 200 ha. The dominant vegetation consists of *Juniperus communis*, *Buxus sempervirens*, *Rosa canina* and *Cirsium* sp. The climate is temperate-cold-continental, typical of the high central mountains of the Pyrenees (Capel-Molina, 1981; fig. 1).

When possible, 4 adult lizards (2 males and 2 females) were collected every 15 days throughout the whole period of annual activity (from May to September), resulting in a total of 83 lizards (41 males and 42 females); these were sacrificed humanely for further analyses. This rate of collection was unlikely to have had an adverse effect on the population of sand lizards in a meadow of this size.

The following variables were recorded, where possible, for each lizard: total body mass, liver mass, fat bodies mass, snout-vent length (SVL), carcass mass, and the height and width of the tail base (at the level of the 7th scale verticil). In males, the masses of the testes and epididymis were measured. In females, the ovary was weighed and the oocytes and eggs were counted and measured. The number of vitellogenic follicles was also recorded. Unless stated otherwise, data on the right organs were used. SVL was measured with callipers (± 0.01 mm) and the other linear measurements were recorded with an ocular micrometer eyepiece (± 0.01 mm). Mass was recorded with a digital balance (± 0.0001 g). For some variables, only a subsample of the lizards could be analysed due to logistic constraints.

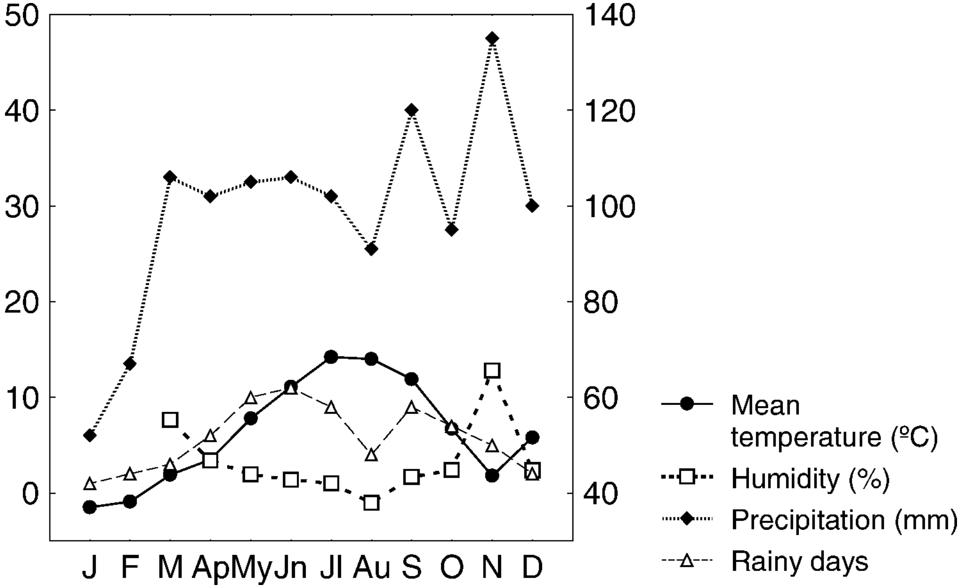

Figure 1. Annual variation of some climatic parameters in the study site. Left axis: mean temperature, humidity index (mean precipitation/mean evapotranspiration) and number of rainy days. Right axis: precipitation.

Egg volumes were obtained by approximating the volume of the ellipsoid, $V = 4/3 * \pi * (a/2) * (b/2)^2$, where a is length, b is the width. The tail base section was calculated as $S = \pi ab$ where a is the height and b is the width.

Cytological preparations of testes and epididymis using the Diff-Quick technique (Durfort, 1978) were analysed in order to observe germinal cells. The different cell types were identified and counted in 10 microscope fields at 400× for each male.

Furthermore, 15 gravid females were collected for obtaining clutches in terraria and weighed daily in order to assess female mass immediately before egg deposition. The eggs were measured in the same way as oviductal ones. After egg-laying, females were released into their natural habitat. Reproductive effort was calculated as clutch size divided by SVL of the female and relative clutch mass was clutch mass divided by female mass before oviposition excluding clutch mass (RCM).

All variables were log-transformed and tested for normality. Since no interannual differences were detected, samples were pooled for analysing variation in 15-day intervals by means of ANCOVA, using the logarithm of SVL as a covariate. ANCOVA was used only when assumptions (homocedasticity and parallelism) were attained.

Finally, field observations on pregnancy, copulation scars and evidence of parturition in females as well as nuptial coloration and mate guarding in males were recorded. Sampling was intensified in the beginning of the season for detecting such reproductive traits (4 days per each 15-days period in May).

Results

Sexual dimorphism and maturity

The SVL of the smallest male with spermatozoa in testes and epididymis was 61.5 mm, whereas the smallest gravid female measured 70.5 mm. Females were significantly larger than males (mean ± standard error, sample; males 77.70 ± 0.63, $n = 41$; females $85.74 \pm 0.80, n = 70; t = 8, 30, d.f.\ 81, P < 0.0001$). Males were heavier for their length than females (carcass mass standardized by SVL; ANCOVA, $F_{1,16} = 26.05$, $P < 0.002$); no seasonal differences were detected for this trait.

Phenology

In males, the reproductive period (mating) began by the first week of May and finished in mid-June (data from 1996, fig. 2). During this period, males exhibited typical nuptial coloration and increased their exploratory activities.

Females left winter burrows one week after males and mate-guarding was immediately detected. Females carrying oviductal eggs were observed from mid-May to the second week of July, which marked the end of their reproductive period. The first clutch was observed in mid-June (direct observation of a female laying eggs) and hatchlings appeared in the second half of August. The activity period was over at the end of September.

Reproductive cycles

Males. Significant seasonal variation of the relative testis mass was detected (ANCOVA, $F_{7,32} = 7.88$, $P < 0.0001$; fig. 3). The testes reached a maximum size in mid-May, decreased rapidly to a minimum in the second half of June and before beginning to increase again at the end of the activity period.

Figure 4 shows the seasonal variation of the different germinal cells in testis. Spermatogonia and spermatocytes were observed throughout all year whereas spermatids and spermatozoa were absent immediately after the reproductive period.

The standardised mass of the epididymis also showed significant seasonal variation (ANCOVA $F_{7,24} = 9.00$, $P < 0.001$, fig. 3). Similar results were obtained for the width

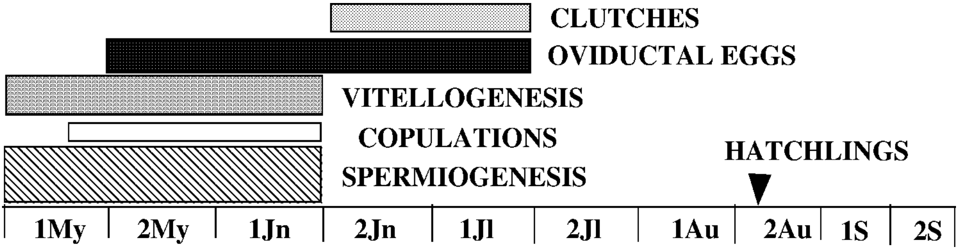

Figure 2. Phenology of the main reproductive events of the Pyrenean population of *Lacerta agilis*.

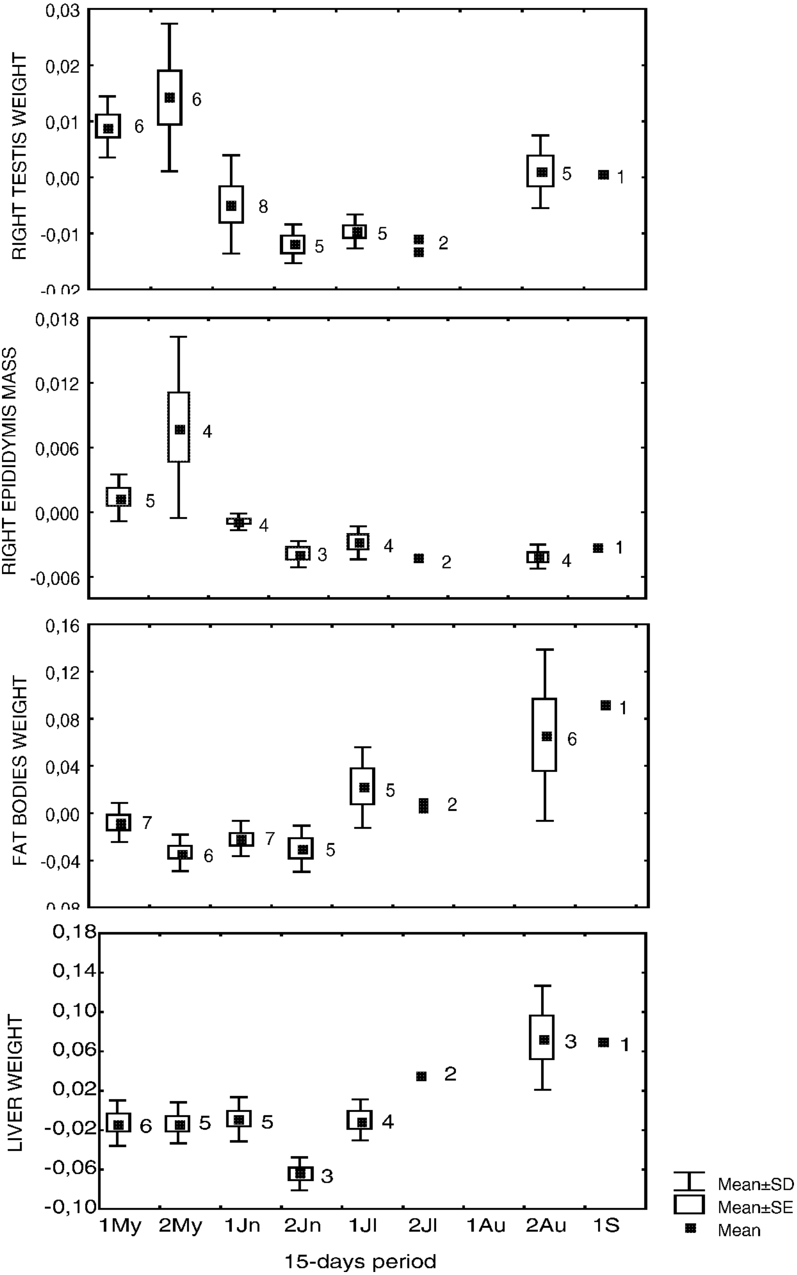

Figure 3. Seasonal variation of the testes, epididymis, fat bodies and liver in the Pyrenean *Lacerta agilis* males. Abscises show the regression residuals between each variable and the SVL (both log-transformed). SD: standard deviation, SE: standard error. Numbers indicate sample size.

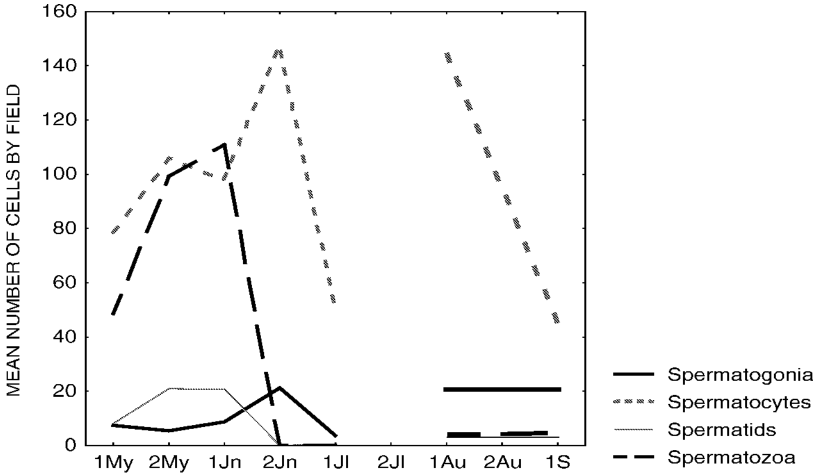

Figure 4. Seasonal variation of the different types of sexual cells in testis.

of the epididymis (ANCOVA $F_{7,24} = 4.98$, $P = 0.001$). High values were only observed from the beginning of May, decreasing abruptly in the second half of May (Scheffé post hoc test, $P < 0.01$). During the rest of the year, the values were low (fig. 3). Spermatids and spermatozoa were detected in both testes and epididymis from the first week of May to the first week of June.

Females. The highest relative ovary mass coincided with the vitellogenic period lasting from the first half of May to the first half of June (fig. 5). Large oocytes (see below) were only detected during that period. Significant differences were detected when comparing relative ovary masses inside and outside of this period (ANCOVA $F_{2,36} = 9.44$, $P = 0.005$). The variance of the ovary mass was larger during vitellogenesis than during the rest of the period (Levene's test $F_{1,37} = 8.38$, $P = 0.004$).

In May and the first half of June, two groups of follicles could be distinguished: those larger than 2.5 mm diameter (minimum size for vitellogenesis) and those smaller than 1.5 mm. Restricting the analysis to those females with vitellogenic follicles, female size was larger in the second half of May than in the first half of June (89.77 ± 3.08, $n = 4$ and 77.73 ± 3.55, $n = 3$, respectively; ANOVA, $F_{1,5} = 8.89$, $P = 0.03$); but no other size differences were found. Those small females in vitellogenesis at the end of the season were found simultaneously with large females carrying oviductal eggs. No atretic follicles were found in any case.

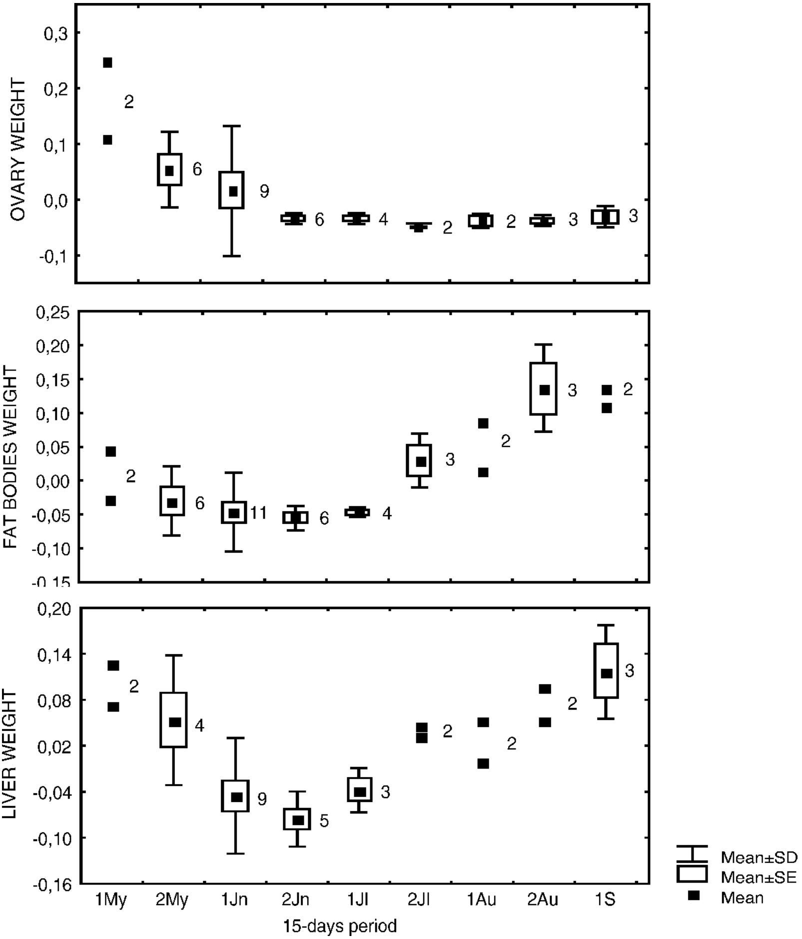

Figure 5. Seasonal variation of the ovary, fat bodies and liver in the Pyrenean *Lacerta agilis* females. Abscises show the regression residuals between each variable and the SVL (both log-transformed). SD: standard deviation, SE: standard error. Numbers indicate sample size.

Cycles of liver, fat body mass and tail base section

Males. Seasonal variation of fat bodies mass was detected (ANCOVA, $F_{7,32} = 7.72$, $P < 0.001$, fig. 3). Minimum levels were found from the second half of May to the second half of June. Afterwards, progressive recovery was observed and the highest values were attained at the end of the activity cycle (Scheffé post hoc tests, $P < 0.01$); these values were higher than those at the beginning of spring (fig. 3).

The tail base section varied seasonally (ANCOVA, $F_{7,25} = 2.58$, $P = 0.03$) following a similar pattern to fat bodies (ANCOVA, $F_{7,32} = 7,12$, $P < 0.01$). The mass of the liver also changed in the same way but with minimum in the second half of June (ANCOVA,

$F_{7,23} = 10.09$, $P < 0.001$, Scheffé post hoc tests, $P < 0.05$, fig. 3). In contrast, the carcass mass remained constant throughout the year (ANCOVA, $F_{2,8} = 1.419$, $P = 0.43$).

Females. The relative mass of fat bodies in females also showed seasonal variation (ANCOVA, $F_{8,31} = 13.30$, $P < 0.001$, fig. 5) which was more marked and delayed compared to that of males. Minimum values were found in the second half of June. The highest values were observed in late summer, similar to males. These values were higher than those after the winter diapause (fig. 5). The same pattern was observed for the liver mass (fig. 5) and tail base section (ANCOVAs, $F_{8,25} = 6.23$, $P = 0.001$; $F_{8,22} = 2.97$, $P = 0.01$, respectively). The only difference was that liver mass was similar at the end and at the beginning of the activity period. No seasonal differences in carcass mass were observed (ANCOVA, $F_{7,10} = 0.16$, $P = 0.97$). No correlation between the SVL and the fat bodies mass (means of 15 days periods) during the reproductive season was detected in either males or females.

The mass of fat bodies was significantly correlated with the mass of the liver (males, $r = 0.63$, $P < 0.001$, $n = 32$, females, $r = 0.67$, $P < 0.001$, $n = 31$) and the tail base section (males, $r = 0.580$, $P < 0.001$, $n = 34$, females, $r = 0.83$, $P < 0.001$, $n = 31$). However, it should be taken into account that liver and tail base were correlated with SVL. Therefore, partial correlations were used to exclude the effect of size when correlating these two variables. Results indicated the persistence of the significant correlation between liver and tail base (males, $r = 0.494$, $P < 0.0001$, $n = 27$, females, $r = 0.780$, $P < 0.0001$, $n = 21$).

Clutch traits

No differences were found between the number of vitellogenic follicles, oviductal eggs and eggs laid, with respect to female size (ANCOVA, $F_{2,33} = 0.94$, $P = 0.9$, $n = 38$). Hence, these data were pooled for estimating clutch size (mean 9.13 ± 0.45, median 9). A significant correlation between clutch and female size was found ($r = 0.75$, $P < 0.001$, $n = 37$). The descriptive statistics of the main clutch parameters are shown in table 1. Mean egg and clutch mass were higher in eggs laid in terraria than in those found in the oviduct of dissected females (ANCOVA, $F_{1,24} = 14.27$, $P = 0.003$, $F_{1,24} = 5.53$, $P = 0.02$, respectively). Moreover, mean egg mass was not correlated with either SVL or clutch size when considering separately oviductal eggs and clutches in terraria (oviductal eggs: $r = 0.07$, $P = 0.81$; clutches: $r = 0.35$, $P = 0.27$).

Discussion

Dimorphism and sexual maturity

As other large lacertids which are phylogenetically related with *Lacerta agilis*, such as *Lacerta schreiberi* (Marco et al., 1994) or *Lacerta bilineata* (Amann et al., 1997;

Table 1. Descriptive statistics of the main oological parameters of the Pyrenean population of *Lacerta agilis*. $s_{\bar{x}}$: standard error, CV: coefficient of variation.

Variable	*n*	Mean	Range	$s_{\bar{x}}$	CV
Clutch size (vitellogenic follicles)	9	8.88	4-15	1.033	34.87
Clutch size (oviductal eggs)	15	9.13	4-14	0.638	27.09
Clutch size (clutches)	14	9.28	5-15	0.814	32.85
Clutch size (total)	38	9.13	4-15	0.449	30.35
SVL reproductive females (mm)	38	85.05	70.9-98.8	1.074	7.88
Clutch volume (oviductal eggs) (mm^3)	15	4057.4	6294.7-1381.5	340.4	12.49
Clutch volume (clutches) (mm^3)	13	4100.8	5715.7-1686.2	354.3	14.19
Egg volume (oviductal eggs) (mm^3)	15	453.4	568.87-333.1	16.6	31.15
Egg volume (clutches) (mm^3)	13	481.3	758.6-339.0	32.2	24.12
Total mass of oviductal eggs (g)	15	4.172	1.021-6.016	0.322	29.91
Mean mass of oviductal eggs (g)	15	0.447	0.255-0.592	0.023	19.69
Total clutch mass (g)	13	5.163	2.279-7.383	0.455	31.77
Mean egg mass (g)	13	0.599	0.455-0.853	0.0331	19.69
Reproductive effort	38	0.106	0.056-0.157	0.0044	25.42
Relative clutch mass (RCM)	11	0.53	0.201-0.733	0.0457	29.86

Barbadillo, 1987), females of Pyrenean population have a size dimorphism favourable. Furthermore, the high robustness of males compared to females in Pyrenean population has also been observed to occur for most European lacertids.

Phenology

The Pyrenean populations of *Lacerta agilis* are found in environments which apparently offer low availability of suitable temperatures and limit the activity period of this medium-sized species (Amat et al., 1998). Nevertheless, other European populations are probably under similar conditions. In comparison with populations studied in Britain (Jackson, 1978), Sweden (Olsson and Madsen, 1996) and Germany (Glandt, 1993), the beginning of the annual activity is delayed (10-60 days). Environmental temperatures between this study site and the others should be considered for explaining these results. Nevertheless, Pyrenean lizards were not active in October when the thermal conditions were still favourable. This suggests that although this activity period is short, it is long enough to complete the reproductive cycle.

The appearance of males earlier in the season than females from winter burrows has previously been detected in *L. agilis* (Van Nuland and Strijbosch, 1981; Olsson and Madsen, 1996) and in other lacertidae (Castilla et al., 1992; Roig et al., 1996). Both sociobiological (Olsson and Madsen, 1996) and physiological (Gavaud, 1991) explanations have been suggested for this behaviour.

The copulation period seems to be more concentrated in the Pyrenean than Swedish populations (Olsson, 1994). However, all females found during the reproductive period had copulation scars. This suggests that all adult females of the population are participating in reproduction.

In the population, the period of oviductal retention is long (about 45 days, approximately), probably due to ovulation asynchrony among females. In contrast, the period for egg-laying is short (20-25 days). Early clutches probably allow early hatching and high hatchling survival in a limited thermal environment (Olsson and Shine, 1997a).

Reproductive cycles

Males. The Pyrenean populations of *Lacerta agilis* exhibit shorter cycles of testes and epididymis than other Iberian lacertids studied (Braña, 1983; Castilla, 1989; Galán-Regalado, 1994; Carretero and Llorente, 1995; Roig et al., 1996; Rubio de Lucas, 1996). Spermatogenesis is of a mixed type (sensu Saint-Girons, 1984) and spermiogenesis occurs in spring time. The period of spermiogenesis coincides with the observations of copulation marks on females and mate-guarding behaviour by males.

Females. Vitellogenesis also occurs in spring and it is very short. Results suggest than small females tend to start vitellogenensis later in the season. This has been observed in other sand lizard populations (Olsson and Shine, 1996) and results in a short vitellogenic period for the smallest females. Large females can invest more energy (coming from feeding) in vitellogenesis and less in growth than small females, since growth rates decrease with age (Olsson and Shine, 1996). In contrast, small females deflect more energy for growth and, since clutch size is related to body size, this maximises lifetime fecundity (Shine and Schwarzkopf, 1992).

The short vitellogenic period, the minimum adult size which is similar to other populations of *L. agilis* and the lack of atresia in vitellogenic follicles (e.g. Méndez de la Cruz et al., 1993) provide evidence that the reproductive cycle is completed by females without difficulties despite the short activity period.

Cycles of liver, fat bodies and tail base

The high levels of activity by males during the reproductive season has been associated with home-range recognition and searching for females (Ortega and Barbault, 1986). Consequently, the fat stores of males decrease not only because these activities are energy-consuming but also because time for feeding is probably restricted. This is consistent with the low levels of energy storage (fat bodies and liver) during spring by *L. agilis* in our study. Nevertheless, fat consumption during winter diapause should not be discarded since it has been observed in *Zootoca vivipara* (Avery, 1970). Sperm production and testes enlargement early in the season could be energetically costly (e.g. in *Vipera berus*, Olsson et al., 1997).

Consumption of fat reserves by females is delayed and more intense than in males due to the high energetic requirements of vitellogenesis and oviposition. The energetic investment in clutches by females depends on energetic input from both current availability (diet during early spring) and stored lipidic reserves from the previous season. This varies among females due to the different opportunities for biomass ingestion depending on microhabitat, status, level of activity, productivity of habitat and opportunities for thermoregulation. However, the absence of correlation between body size and energy storage during the reproductive period suggests that all females are able to store energy after oviposition irrespective of size.

Fat reserves increase markedly throughout summer in both sexes after reproductive activity is complete (figures 3 and 5). This may be explained by the high arthropod abundance in late summer as well as the favourable thermal conditions for feeding and activity (pers. obs.; see also Avery, 1978; Van Damme et al., 1991) and, the reproductive activity is also finished. In both sexes, there is some evidence of fat consumption during winter diapause, as reported for other species (Avery, 1970). However, activity at the beginning of spring prior to the first field sampling should not be overlooked.

Clutch traits

The short period of annual activity allows females to lay only one clutch per season. A second clutch in this species has only rarely been detected under more favourable conditions (Jensen, 1981; Strijbosch, 1988). In fact, no limitations of clutch frequency have been detected in captivity (Rykena, 1988b). Nevertheless, a single annual clutch is still observed in populations experiencing more extreme environmental conditions such as those observed in some sites in Romania and other northern latitudes. However, in the population, females may be gravid until August (Fuhn and Vancea, 1961).

Clutch size is similar to that found in Swedish populations of this species (Olsson and Shine, 1997b) but considerably higher than in the populations in the Netherlands (mean 4.9 to 6.7; Strijbosch, 1988). Although this parameter is mainly determined by body size in our study, there is still a high portion of variability which is not explained by this variable in the population studied. This suggests that clutch size could be influenced by variables independent from body size such as food assimilation (sand lizards in terraria increase fecundity in relation to size, Olsson and Shine, 1997b), thermal availability, home range size, diseases or parasites.

Conclusions

To sum up, *Lacerta agilis* does not show outstanding changes in its reproductive pattern in comparison with the other European populations examined, perhaps with minor variation in the timing of reproductive events and, to a smaller extent, clutch frequency. This evidence strongly suggests that the limited southwestern range of *Lacerta agilis* is not due to environmental constraints but to very recent colonization of the area (100000-150000 years in eastern Europe, Yablokov et al., 1986, and probably more recently in the Pyrenees, Llorente et al., 1997). Furthermore, although the wide distribution of this species reveals considerable plasticity for occupying different habitats, it is absent from other areas of similar environmental characteristics, some of which are close to the present range. This is the case of the Central Pyrenees (Aragon) where the sand lizard is absent although no barrier existed with the area studied, at least until recently.

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