Reproduction of *Psammodromus algirus* in coastal sandy areas of NE Spain

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Abstract. The variation in the reproductive cycle of three populations of the lizard *Psammodromus algirus* living in coastal sandy areas of NE Spain was analyzed. In contrast with those in continental climates, they showed evidence of reproductive stress: the reproductive season began sooner and was longer. Moreover, body size was smaller and sexual size dimorphism did not arise. Only the end of the breeding period was relatively constant. Nevertheless, these different reproductive traits seem to follow a common trend. In general, no important reproductive differences were found among the three coastal areas. Females laying two clutches have been detected in one locality. Clutch size was correlated with female size. The high phenological plasticity of this species is associated with its wide ecological niche.

Resumen. Se analiza la variación en el ciclo reproductor de tres poblaciones de *Psammodromus algirus* que viven en arenales costeros del NE ibérico. En contraste con lo que ocurre en climas continentales, éstas poblaciones muestran evidencia de estrés reproductor: el período reproductor comienza antes y es más prolongado. Además, el tamaño corporal es menor y el dimorfismo sexual en talla no llega a manifestarse. Tan sólo se mantiene constante el final del período reproductor. Las diferentes características reproductoras parecen, no obstante, seguir una tendencia común. En general, no se hallaron diferencias reproductoras importantes entre las tres áreas costeras. Se han detectado dos puestas en hembras de una de las localidades. El tamaño de la puesta se halla correlacionado con la talla de la hembra. La elevada plasticidad fenológica de esta especie se asocia con su amplio nicho ecológico.

Introduction

Psammodromus algirus (Large Psammodromus) is the most common lacertid in many Mediterranean regions of the Iberian Peninsula (Barbadillo, 1987) and is also found in SE France (see Bons, 1989) and NE Africa. This ground-dwelling lizard of medium size can occupy a wide variety of open or semi-open habitats (Barbadillo, 1987), associated with medium-high plant covers, mainly of bushes (Carrascal et al., 1989). Since it lives under very diverse environmental conditions, its life history patterns are feasible to vary

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widely as it has been demonstrated for other euryoic species with wide distribution ranges (see for instance Taylor et al., 1992; Howland, 1992).

General information on the reproduction of this species is available in several studies (Böhme, 1981; Pérez-Mellado, 1981; Bons and Saint-Girons, 1982; Seva, 1982; Escarré and Vericad, 1983; Barbadillo, 1987). Nevertheless, there are only three specific studies dealing with the whole reproductive cycle both in central Spain (Pollo and Pérez-Mellado, 1990; Díaz et al., 1994) and in the south of the Iberian Peninsula (Pérez-Quintero, 1996). In some cases, differences in body size between localities were evident. This study aims to analyze the reproductive cycle and the life history of *P. algirus* in a Mediterranean coastal climate of NE Iberia and to verify whether local variation among populations monitored in similar habitats occurs.

Material and methods

Three localities, all of them coastal sandy areas of NE Spain, were prospected (fig. 1). These were Aiguamolls de l'Empordà (U.T.M. grids 31TEG1075/0975/0974), Torredembarra (31TCF6857) and the Ebro Delta (31TCF1810). The climate can be defined as littoral Mediterranean with warm temperatures, irregular precipitations in autumn and spring and a dry period in summer. Some climatological data are: Aiguamolls, mean annual temperature 14.9°C (thermal amplitude 15.9°C), annual rainfall 572.6 mm; Torredembarra, 15.8°C (13.7°C), 475.9 mm; Ebro Delta 16.6°C (15.5°C), 548.6 mm (30 years

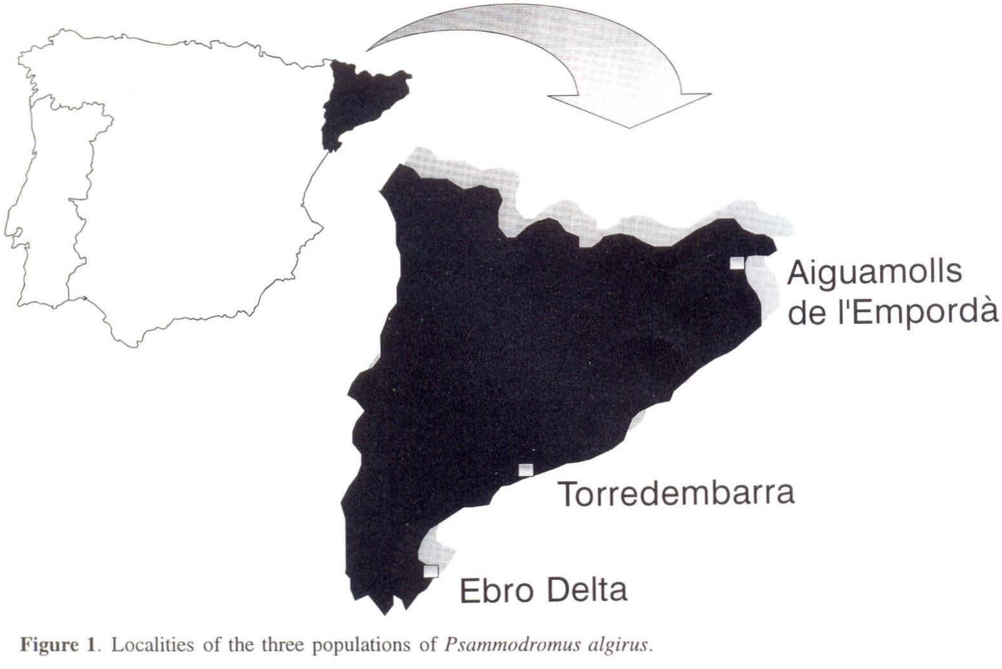


Figure 1. Localities of the three populations of *Psammodromus algirus*.

means, Panareda and Nuet, 1973). During the years of study, 1986 and 1987, climatological parameters remained very similar (data from Figueres, Tarragona and Roquetes observatories, respectively). Aiguamolls is the coldest area with the shortest dry period. Vegetation was composed of psammophile and halophile plants (see Farràs and Casasayas, 1989; Perdigó and Papió, 1985; Curcó, 1990, respectively, for a complete phytosociological description). Other lacertids living in these areas were *Podarcis hispanica* (in Aiguamolls and Torredembarra) and *Acanthodactylus erythrurus* (in Torredembarra and Ebro Delta).

However, *P. algirus* was the dominant species in all cases. In general, *P. algirus* reaches sexual maturity within the first year of age in the Ebro Delta as deduced from marking-recapture and the sizes of lizards observed throughout the year combined with skeletochronological data (Carretero, 1993; Carretero and Llorente, 1994; Marí et al., 1996). However, only a proportion of the individuals do so in Torredembarra and almost none of them in Aiguamolls (Carretero, 1993). The adult lizards undergo a winter diapause period from October (Aiguamolls) or November (Torredembarra and Ebro Delta) to February. However, immature specimens can be seen, even in the middle of winter, on sunny days.

During 1986 and 1987, active lizards were monthly and uniformly sampled in the three localities throughout the annual activity period and sacrificed using chloroform. The three samplings of each month were performed within a period of one week maximum. The snout-vent length (SVL) of each lizard was measured and its secondary sexual features (see Carretero, 1996) were registered. After dissection, animals with active gonads in the reproductive period were considered adults and the minimum sizes were determined for each sex. Outside the reproductive period, only those lizards with SVL larger than these minima were included in the adult class. Consequently, the numbers of adults captured were 30/33 in Aiguamolls de l'Empordà, 29/31 in Torredembarra and 32/30 in Ebro Delta (males/females, respectively).

Several variables of sexual significance were measured in the specimens. In males, both testes were weighed and their length and width were measured. The diameter of both epididymis was also measured. In females, both ovaries were weighed and the condition of the oviducts was observed. Ovarian follicles and oviductal eggs were counted and measured. The total weight of the fat bodies was registered in both sexes. A caliper (0.05 mm precision) was used for the linear measurements. Weights were immediately measured after capture and dissection with a digital balance (0.0001 g precision).

Regression residuals between all variables and SVL (both log-transformed) were calculated to standardize those variables to the animal size as seen in figs 2 and 3. A two-way ANCOVA with month and site as factors and SVL (log-transformed) as covariate was performed for each variable (log-transformed) in order to test its seasonal and geographic variation.

Finally, some field observations, the distribution of size classes in the field throughout the year and some making-recapture data were considered in the study of phenology.

Results

Table 1 shows the SVL values of the adult lizards captured in each locality. No evidence of sexual dimorphism in body size was found in any population. However, animals from Aiguamolls de l'Empordà were larger than those from Torredembarra and Ebro Delta considering both sexes separately; seasonal size variation was not significant (two way ANOVA males, site factor $F = 7.15$, 2, 62 df., $P = 3 \times 10^{-5}$, month factor $F = 0.76$, 7, 62 df., $P = 0.62$, n.s., interaction $F = 1.13$, 14, 62 df., $P = 0.33$, n.s.; two way ANOVA females, site factor $F = 7.31$, 2, 70 df., $P = 0.0013$, month factor $F = 0.88$, 5, 70 df., $P = 0.49$, n.s., interaction $F = 1.29$, 10, 70 df., $P = 0.25$, n.s.; Scheffé's post hoc tests $P < 0.01$ for both sexes).

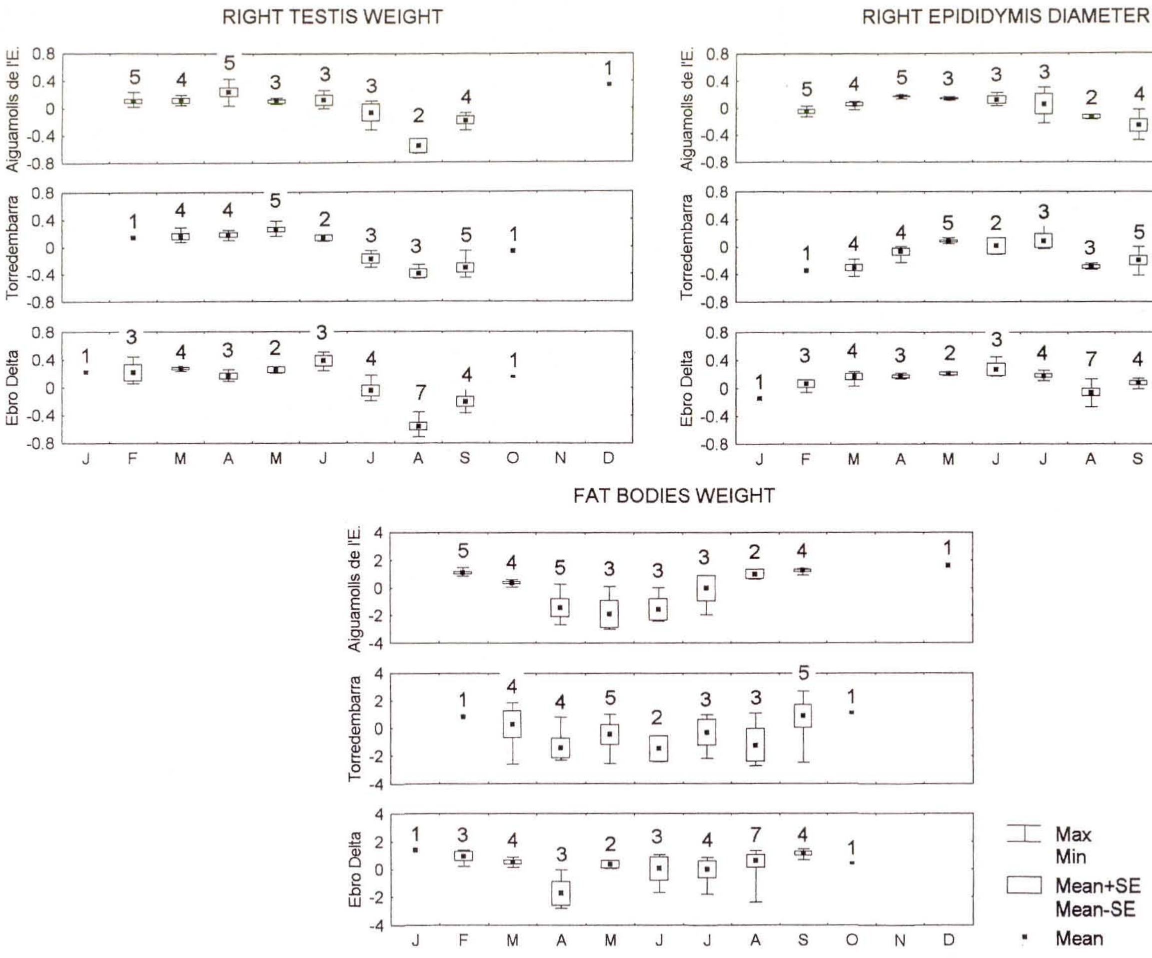
On the evidence of the analysis of the internal organs as well as the field observations, the reproductive period lasted from March-April to July. During this period animals with active, well-developed gonads were found and adult male and female couples were observed in the field.

In males (fig. 2), the testis weight showed a high degree of seasonal (not interpopulational) variation (two way ANCOVA, site factor n.s., month factor $F = 43.90$, 7, 61 df., $P < 10^{-6}$, interaction n.s.). The size of the testis was already large at the end of the winter when adults emerged from their wintering burrows (no inactive lizards were analyzed). The high values continued until the last months of the breeding season. After that, a strong regression of the testis was observed in July-August in all cases, but with lower slope than the rest in Torredembarra (Scheffé's post hoc tests $P < 0.01$). It was followed by a fast recovery until the start of the next cycle. No significant differences were found between left and right testes in any locality (t tests for paired data).

Table 1. Snout-vent length (SVL) values in mm of *Psammodromus algirus* in the three localities studied. n = sample, $\bar{x}$ = mean; s = standard deviation, CV = coefficient of variation.

Locality/Sex	n	$\bar{x}$	s	CV	lim (95%)	Range
Aiguamolls						
adult males	30	65.39	4.73	7.24	±1.69	55.65-74.55
adult females	33	66.48	5.82	8.75	±1.98	58.55-81.00
Torredembarra						
adult males	29	61.80	3.93	6.35	±1.43	55.50-70.35
adult females	31	60.56	4.55	7.51	±1.60	55.05-73.90
Ebro Delta						
adult males	32	63.39	4.61	7.27	±1.60	52.15-72.15
adult females	30	61.15	4.26	6.97	±1.53	53.20-68.65

Figure 2. Annual variation of the weight of the testis, the epididymis diameter and the weight of the fat bodies in the *Psammodromus algirus* males from the three localities studied. Abscises show the regression residuals between each variable and the SVL (both log-transformed). Numbers indicate the sample size.


RIGHT TESTIS WEIGHT
RIGHT EPIDIDYMIS DIAMETER
FAT BODIES WEIGHT
Aiguamolls de l'E.
Torredembarra
Ebro Delta
0.8
0.4
0
-0.4
-0.8
4
2
0
-2
-4
J F M A M J J A S O N D
Max
Min
Mean+SE
Mean-SE
Mean

In contrast to the testis, the epididymis (fig. 2) did not appear well-developed outside the breeding season, reaching maximum diameter in the middle of this period; significant interpopulational variation was detected (two way ANCOVA, site factor $F = 29.46$, 2, 61 df., $P < 10^{-6}$, month factor $F = 10.27$, 7, 61 df., $P < 10^{-6}$, interaction $F = 2.07$, 14, 61 df., $P = 0.026$). In March, the epididymis was less developed in the Torredembarra population than in the other sites (Scheffé's post hoc tests $P < 0.01$).

Conversely, the lowest values in the fat bodies weight cycle (fig. 2) appeared in the reproductive season and the highest ones at the end of the cycle (autumn) and the beginning of the next one (late winter) (two way ANCOVA, site factor n.s., month factor $F = 4.74$, 7, 61 df., $P = 0.0002$, interaction n.s., Scheffé's post hoc tests $P < 0.01$). This cycle was not exactly inverse to the testicular one since no correlation between testis and fat bodies weights was observed in any case.

In the females, the plots of the ovary weight (fig. 3) show only one maximum in May-June in Aiguamolls whereas two maxima in May and July appeared in the Torredembarra population. In the Ebro Delta, the second one was not evident. However, only significant seasonal but not interpopulational variation was detected (two way ANCOVA, site factor n.s., month factor $F = 11.94$, 2, 69 df., $P < 10^{-6}$, interaction n.s., Scheffé's post hoc tests $P < 0.01$). No significant evidence of laterality was found between both ovaries in any population (t tests for paired data).

Unlike the males, the cycle of fat bodies in the females was inverse to that of the gonads. A significant negative correlation between the monthly mean weights of the ovaries and the fat bodies was found in Aiguamolls ($R_{\text{Pearson}} = -0.75$, 8 df., $P < 0.03$). Seasonal (not interpopulational) variation was detected (two way ANCOVA, site factor n.s., month factor $F = 8.84$, 5, 69 df., $P = 0.00002$, interaction n.s., Scheffé's post hoc tests $P < 0.01$). Moreover, females showed more fat reserves outside the reproductive period and a more marked fat cycle than males (three way ANCOVA, sex factor $F = 8.78$, 1, 116 df., $P = 0.003$; site factor n.s.; month factor $F = 8.70$, 5, 116 df., $P < 10^{-6}$, sex × month interaction $F = 3.32$, 5, 116 df., $P = 0.007$; rest of interactions n.s.). Some of the females even lacked fat bodies during some months of spring (fig. 3).

The minimum diameter of the vitellogenic follicles was 2 mm (maximum 8.9 mm) and their shape was spherical. The greater the diameter of the follicles, the wider the oviducts, which appeared strongly developed. Those months when vitellogenic follicles and oviductal eggs appeared are represented in fig. 4. Table 2 shows the values of clutch size as calculated from both sources of information. Since no significant differences in clutch size were detected neither between follicles and eggs nor among populations (two way ANCOVA on log-transformed data using SVL as covariate) data were pooled for the subsequent analysis. Egg size did not show significant variation among localities either.

A significant correlation between the body size of the female and the size of her clutch was detected pooling together the three populations ($R_{\text{Spearman}} = 0.38$, 38 df., $P < 0.01$; fig. 5). However, after separating the three samples, this significant correlation remained only in Aiguamolls de l'Empordà ($R_{\text{Spearman}} = 0.61$, 13 df., $P < 0.01$).

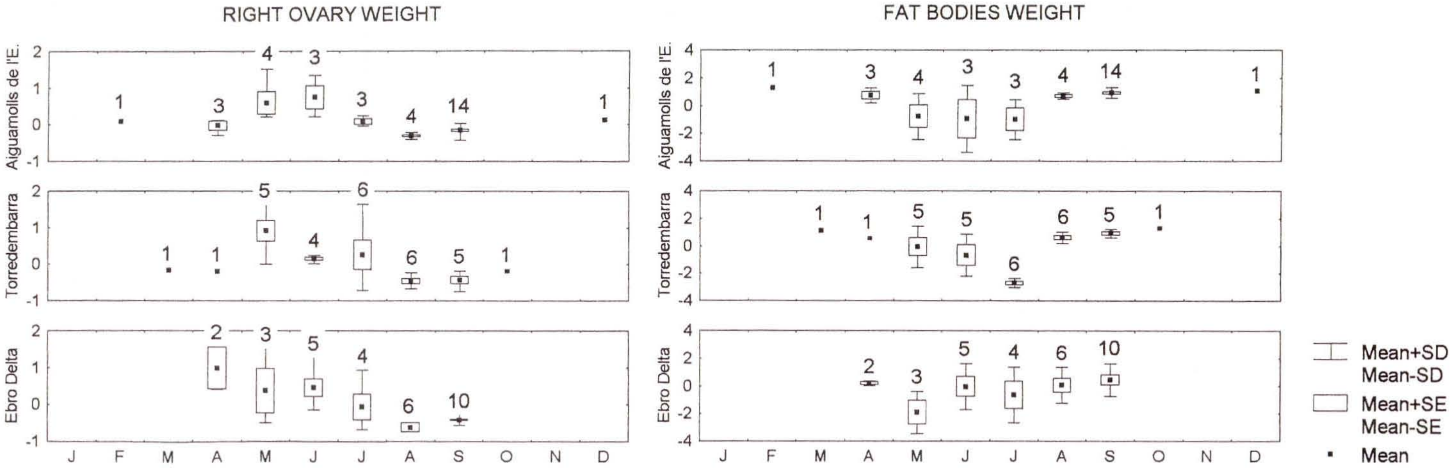


Figure 3. Annual variation of the ovary and the fat bodies weights in the *Psammodromus algirus* females from the three localities studied. Abscises show the regression residuals between each variable and the SVL (both log-transformed). Numbers indicate the sample size.

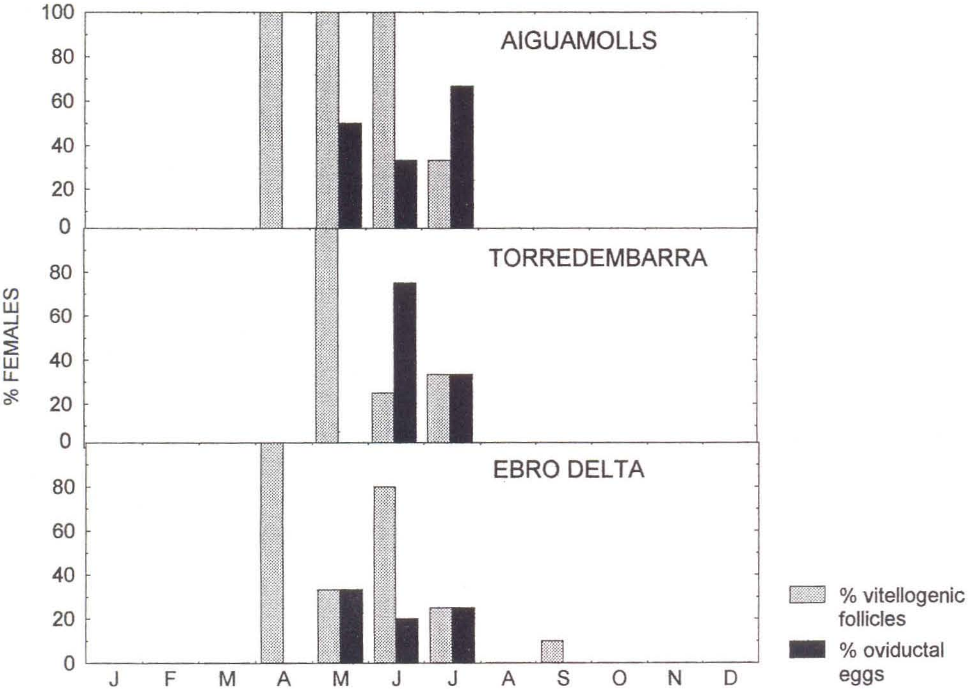


Figure 4. Percentage of females with vitellogenic follicles and oviductal eggs throughout the year in the three *Psammodromus algirus* populations.

Table 2. Clutch size (as calculated from vitellogenic follicles, oviductal eggs or both) in the *Psammodromus algirus* females from the three localities studied. n = number of females, $\bar{x}$ = mean; s = standard deviation, CV = coefficient of variation.

Locality/Source	n	$\bar{x}$	s	CV	lim (95%)	Range
Aiguamolls						
vitellogenic follicles	9	3.77	1.09	28.91	±0.71	2-5
oviductal eggs	6	5.50	1.97	35.76	±1.57	4-8
both combined	15	4.46	1.68	37.67	±0.85	2-8
Torredembarra						
vitellogenic follicles	7	4.00	0.81	20.25	±0.60	2-5
oviductal eggs	5	5.00	2.34	46.80	±2.05	3-9
both combined	12	4.23	1.69	39.95	±0.92	2-9
Ebro Delta						
vitellogenic follicles	9	3.77	0.66	17.51	±0.43	3-5
oviductal eggs	3	3.33	0.57	17.12	±0.65	3-4
both combined	12	3.66	0.65	17.76	±0.37	3-5

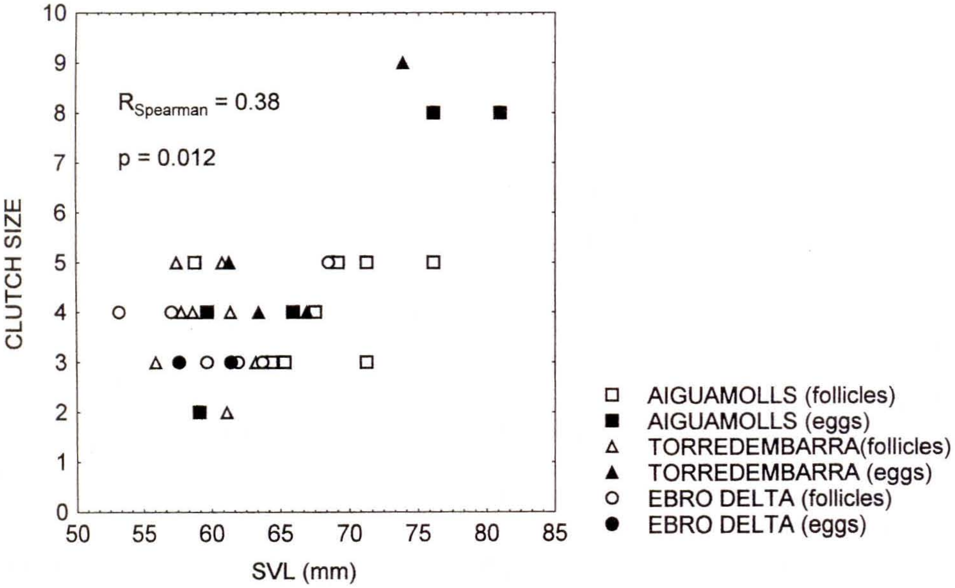


Figure 5. Relationships between the female size (SVL) and clutch size (all populations combined). Correlation coefficient is significant.

The first new-born animals were observed at the end of August, but many of them were found later, especially in Aiguamolls, where they could be seen until October. The SVL of the smallest animal was 25 mm.

Discussion

The coastal Mediterranean climate plays a determinant role in the phenological patterns exhibited by the *Psammodromus algirus* populations analyzed here. Other populations have been studied previously in Central Spain (see Mellado and Martínez, 1974; Pérez-Mellado, 1981; Barbadillo, 1987; Pollo and Pérez-Mellado, 1990; Díaz et al., 1994), the Mediterranean coast (Seva 1982; Escarré and Vericad, 1983; Barbadillo, 1987; Pollo and Pérez-Mellado, 1990; Pérez-Quintero, 1996) and northern Africa (Bons and Saint-Girons, 1982). The reproductive season is longer in the coastal localities than in the other ones but the end of reproduction is relatively simultaneous in all cases observed. In the continental populations, the hot summer often promotes aestivation in post-reproductive lizards, preventing them from being observed and captured (Pollo and Pérez-Mellado, 1990, but see also Díaz et al., 1994). However, in general, no important reproductive variation was detected at the geographic scale level analyzed here.

Considering first the testicular cycle, the increase of the testis begins earlier and the variation is less marked in the coastal localities with low thermal amplitude than in central Spain but the regression is almost simultaneous in all cases (see previous references). So, a more temperate climate promotes longer and less marked testicular cycles as reported of other Lacertidae (Braña et al., 1990; Carretero and Llorente, 1991). It has been pointed out (Joly and Saint-Girons, 1975; Angelini et al., 1976) that spermatogenesis in Lacertidae is temperature-dependent but its interruption is endogenous, hence, very constant.

The pattern seen in the epididymis, which is well developed only during the breeding period, has also been recorded (Saint-Girons and Duguy, 1970; Braña et al., 1990; Carretero and Llorente, 1991). It is noteworthy that a slight increase occurs already in autumn in the most southern locality (see similar patterns for other Mediterranean species in Hraoui-Bloquet and Bloquet, 1988; Castilla and Bauwens, 1990).

Psammodromus algirus males display the most common cycle in saurians from temperate regions with spermatogenesis of mixed type in autumn and spring (Saint-Girons, 1963, 1984; Fitch, 1970; Bons and Saint-Girons, 1982; Marion, 1982; Braña, 1983; Carretero and Llorente, 1991). The increase in testis size at the end of winter corresponds to the development of the seminiferous tubules in the spermiogenic phase, just before the breeding season, when temperatures are still low. During this season, the dilation of the epididymis is due to the production of a great amount of mature spermatozoa. In this sense, it is interesting to remark the retardation of this process in Torredembarra while the testis is already well-developed (as in the other localities). Afterwards, in mid-summer, the epididymis no longer contains spermatozoa, the cells of the testis being mainly spermatogonia and primary spermatocytes. Finally, a new spermatogenesis occurs in autumn (Angelini et al., 1979; Bons and Saint-Girons, 1982) when a new development of the seminiferous tubules takes place, increasing again the testis size (and sometimes the diameter of the epididymis, see Angelini et al., 1979).

In females, the increase in ovary size during the reproductive period is due to vitellogenesis and egg production. The dispersion of ovarian size in these months should be attributed to the asynchrony among individuals with different conditions (vitellogenic follicles in different stages) and prevents the detection of eventual differences. Nevertheless, the first females showing vitellogenesis belong to the Ebro Delta population. The end of the reproductive period is again very synchronic in all cases. As in the testicular cycle, the factors controlling the process are environmental (beginning of vitellogenesis and the sharpness of the variation) as well as endogenous (ovarian regression, see Botte, 1976; Angelini et al., 1976; Carretero and Llorente, 1991).

The pattern of ovary variation, as well as the simultaneous presence of oviductal eggs and vitellogenic follicles in six females (three in Aiguamolls, one in Torredembarra and two in Ebro Delta), indicated the possibility of two clutches in the same individual. This event became confirmed in Torredembarra since two marked females were captured twice carrying oviductal eggs (detected by palpation) in different campaigns. It is not unreasonable to suppose that this event occurs in the other localities. A second clutch has been already described, generally for some populations of *P. algirus* living on the southern coast (Böhme, 1981; Seva, 1982; Barbadillo, 1987), but only one clutch has been reported for continental populations (Barbadillo, 1987; Pollo and Pérez-Mellado, 1990). Nevertheless, in all cases the detection (or refuse) of iteroparity is difficult with the available data.

Pregnancy is estimated to last 30-40 days (from first copulations to first clutches). The incubation time, calculated as the period between first clutches (May) and first hatchlings (late August), lasts approximately 3 months (Barbadillo, 1987; but see also Pollo and Pérez-Mellado, 1990). The incubation time of the later clutches is likely to be shorter because of the higher incubation temperature (Kjaergaard, 1982; Bosch, 1986; Heulin et al., 1991). This effect as well as the asynchrony of female reproduction could make the distribution of the birth dates to be continuous.

With regard to fat bodies, they have been demonstrated to be an important fraction of the energetic reserve which can be rapidly mobilized for reproduction (Derikson, 1976). In temperate climates, the fat is stored in autumn and consumed in the breeding period (Braña, 1983). The *P. algirus* adults do not consume their reserves during the winter diapause (case 1, see figs 2 and 3). The same result has been observed in some populations or species with full winter activity which replace (and/or increase) the fat consumed by the food eaten (case 2, see Carretero and Llorente, 1991, for *Psammodromus hispanicus*). However, this does not happen in adult lizards with a small degree of winter activity (case 3, Saint-Girons and Duguy, 1970; Hraoui-Bloquet and Bloquet, 1988; Llorente, 1988), which reduce their fat bodies during winter. So, whereas in the first two cases, the populations under colder winters show a delay in the beginning of reproduction, in the latter case, the reverse happens. Thus, the effect of climate on the reproductive cycle depends on the species' requirements (Braña et al., 1990).

Males start activity first after the diapause (pers. obs.) consuming their fat reserves before the females. This has been attributed to the high pre-reproductive and reproductive activity associated with searching for females, copulations and social interactions. The increase in testis and epididymis sizes is not too expensive energetically since there is no negative correlation between these parameters and the weight of the fat bodies (Derikson, 1976; Braña, 1983). On the other hand, the role of the fat bodies in the females is to support energetically the vitellogenesis corresponding to the first clutch, which occurs in a period of scarcity (Hahn and Tinkle, 1965; Braña, 1983; Braña et al., 1992), hence the negative correlation between fat bodies and ovaries. If a second clutch is laid, then it does not depend on fat bodies but on the food eaten in the period of abundance (Etheridge et al., 1986) and reserves do not re-increase until the end of the clutch period.

In comparison with the inland populations, those in coastal areas with reduced diapause tend to reach sexual maturity earlier excluding or minimizing the subadult phase and attain smaller body sizes. Consequently, overall body size differences have been found among some of them but sexual dimorphism in body size only arises in the populations with the largest animals (Mellado and Martínez, 1974) as reported for other lizard species (see Griffith, 1991; Stamps, 1993). A demographic and skeletochronological study is now in progress in order to analyze what are the causes of such variation (see preliminary results in Marí et al., 1996; see also Dunham and Miles, 1985; Stamps, 1993).

The number of eggs and clutches are the main factors modulating reproductive effort (see Fitch, 1970; Tinkle et al., 1970; Braña, 1983). The correlation between clutch and female sizes is commonly found in Mediterranean Lacertidae but the sample size as well as the range width of the variables should be taken into account, since it is easier to detect correlation in large species laying many eggs (Carretero and Llorente, 1991). This seems to be the case since a significant correlation was only found in the population of the largest size. This high reproductive plasticity within a common general pattern is one of the factors allowing this euryoic species to occupy a wide geographical range, living under different environmental conditions (Barbadillo, 1987).

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