

REPRODUCTION OF *Acanthodactylus erythrurus* IN ITS NORTHERN BOUNDARY

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Variation in the reproductive cycle of two populations of *Acanthodactylus erythrurus* living in coastal sandy areas of the NE extreme of its range was analyzed. This species exhibits strong influence of historical factors in its reproductive traits: vernal spermatogenic cycle, short incubation, K-selection, and high egg size variation. The populations studied are more similar to others from the Mediterranean coast than to those from Central Spain. In comparison with the latter, reproductive season is longer, adult sizes are smaller and sexual dimorphism is reduced. A second clutch can be laid when the reproductive season is long enough. Nevertheless, phenology in this species is less variable than in other Mediterranean Lacertidae. Since no evidence of suboptimal conditions was found in any population, it is concluded that factors other than reproductive ones may have restricted the range of this species in NE Spain.

Key words: reproduction, historical constraints, Lacertidae, *Acanthodactylus erythrurus*

The genus *Acanthodactylus* (Reptilia: Lacertidae) is broadly distributed in the Middle East and North-Africa, from India to Mauritania. Nevertheless, only one species, *A. erythrurus*, reaches Southern Europe. The Fringe-toed Lizard lives in Morocco, North Algeria and the Iberian Peninsula, except the Northern third (Salvador 1981; Barbadillo 1987). In NE Spain, the species reaches its northern limits with some isolated populations, mainly associated with coastal sandy areas. This ground-dwelling lizard of medium size occupies open areas with a semi-arid Mediterranean climate, typically with eroded (but not necessarily sandy) soils (Barbadillo 1987).

Several studies have reported information on the reproduction of this species in Central (Pérez-Mellado 1981; Barbadillo 1987; Barbadillo et al. 1987; Pollo and Pérez-Mellado 1990; Castilla et al. 1992) and Southern Spain (Seva 1982; Escarré and Vericad 1983; Busack and Klosterman 1987) and in Morocco (Bons 1962, 1963, 1965, 1968, 1969, 1972 and 1973; Bons and Saint-Girons 1982). The aims of this study are to analyze the reproductive cycle of populations of *A. erythrurus* in two coastal localities which represent the NE boundary of this species and to compare their reproductive traits with to those of populations under less extreme conditions.

MATERIALS AND METHODS

The study sites were two coastal sandy areas (Fig. 1) in good condition of conservation: Torredembarra (U.T.M. 31TCF6857) and Ebro Delta (31TCF1810). The climate in both cases is littoral Mediterranean characterized by warm temperatures, irregular precipitation in autumn and spring and a dry period in summer. However, Torredembarra is colder and drier than Ebro Delta (Torredembarra: mean annual temperature 15.8°C, annual rainfall 475 mm; Ebro Delta: 16.6°C, 548 mm, respectively) (Panareda and Nuet 1973). During the years of study, 1986 and 1987, climatological parameters remained similar (data from Tarragona and Roquetes observatories, both close to Torredembarra and Ebro Delta respectively). Vegetation was composed of prammophile and halophile plants (see Perdigó and Papió 1985, and also Curcó 1990, for a complete phytosociological description).

Other lacertids living in these areas were *Psammodromus algirus* (in both localities) and *Podarcis hispanica* (only in Torredembarra). *P. algirus* was always the dominant species being twice (Ebro Delta) or three times (Torredembarra) more abundant than *A. erythrurus*. *P. hispanica* was only a marginal species in Torredembarra (Carretero and Llorente in press).

A. erythrurus reaches sexual maturity in the first or second year of age, depending on the individual, in both localities (Carretero and Llorente in press; unpubl. data). The lizards undergo a winter diapause,

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Fig. 1. General distribution and localities of the two populations of *Acanthodactylus erythrurus*.

which is shorter in immature animals than in adults, and in Ebro Delta than in Torredembarra.

During 1986 and 1987, active lizards were captured in the two localities, by means of monthly sampling throughout the annual activity period and sacrificed using chloroform. Their snout-vent lengths (SVL) were measured and their secondary sexual features were registered. After dissection, animals with developed gonads captured 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. The sample of adults captured was 20/14 in Torredembarra and 25/20 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 measured with a digital balance (10^{-4} g precision). The volumes of testes, vitellogenic follicles and oviductal eggs were calculated, supposing them to be ellipsoidal, by using the formula:

$$V = \frac{4}{3} \pi \frac{a}{2} \left(\frac{b}{2}\right)^2,$$

where a and b are length and width, respectively.

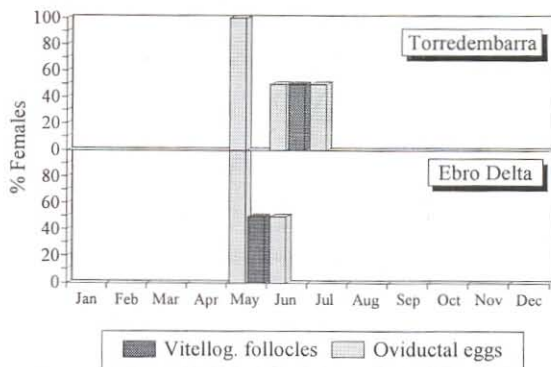


Fig. 2. Annual variation of the testis weight, the epididymis diameter and the weight of the fat bodies in the *Acanthodactylus erythrurus* males from the two localities studied (means and standard deviations).

Two types of gonadosomatic indices (see Carretero and Llorente 1991) were used to standardize the variables to the animal size (represented by the SVL) (Figs. 2 and 3). Moreover, field observations were also considered in the study of phenology.

RESULTS

The SVL values were $x = 66.67$ mm (range 55.30 – 76.05) for adult males and $x = 64.35$ mm (56.40 – 70.75) for adult females in Torredembarra. In the Ebro Delta, they were $x = 69.23$ mm (56.60 – 77.65) and $x = 66.83$ mm (56.40 – 71.25), respectively. Although males seemed slightly larger than females and individuals from Torredembarra seemed smaller than those from Ebro Delta, no significant differences were found in either case.

On the evidence of the analysis of the internal organs and the field observations, the reproductive period lasted from April to July. During this period animals with active, well-developed gonads were found and male-female couples were seen in the field. Females with recent copulation scars were also observed. In Ebro Delta, the sample at the beginning of the season was clearly insufficient.

In males, the testis weight showed a high degree of seasonal variation (Fig. 2) and the volume (not represented) exhibited a similar pattern in the two localities. The size of the testis increased from the emergence from their hibernation burrows (no inactive lizards were analyzed) until the middle of the reproductive season (April – May). These high values were also noted in June and, in some cases, in July. A strong regression of the testis was then observed in

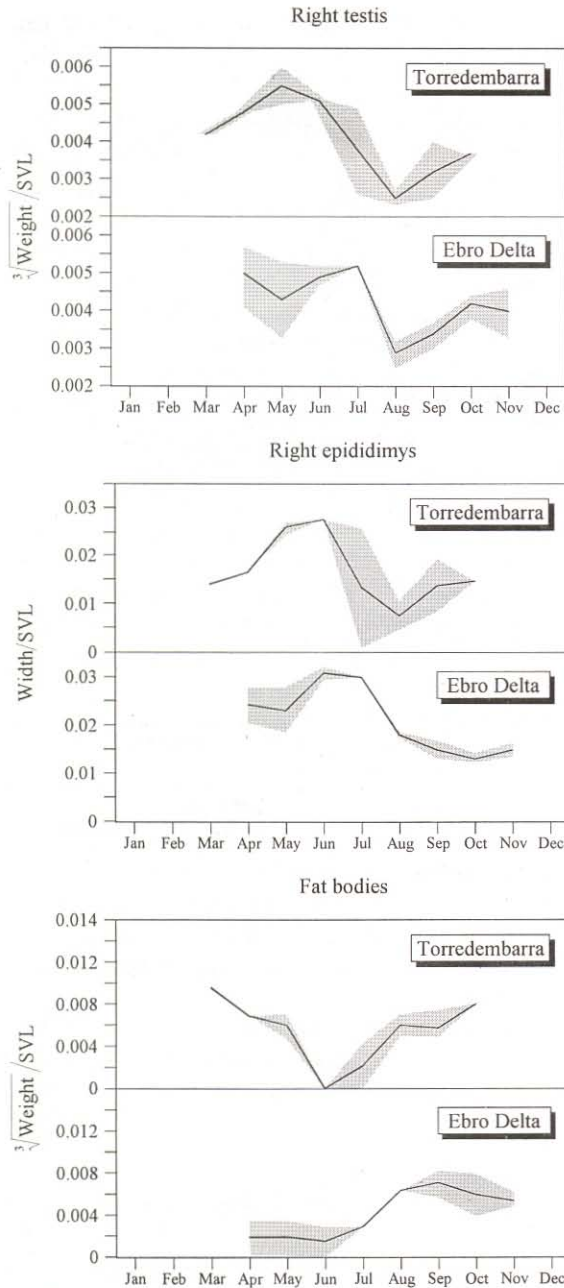


Fig. 3. Annual variation of the ovary and the fat bodies weights in the *Acanthodactylus erythrurus* females from the two localities studied (means and standard deviations). Shaded is the area of standard deviation (the same in Figs. 3 and 4).

August (in July in some individuals). Afterwards, testis size began to increase again before the diapause period. No significant differences were found between left and right testes in any locality (Student's *t*-test). The epididymis (Fig. 2) followed a parallel

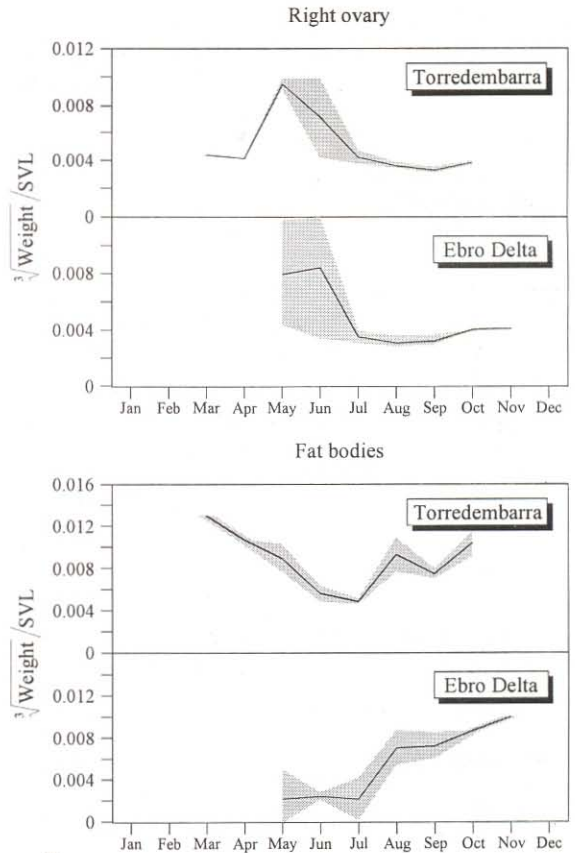


Fig. 4. Percentage of females with vitellogenic follicles and oviductal eggs throughout the year in the two *Acanthodactylus erythrurus* populations.

pattern of variation, being well-developed only during the breeding season and reaching maximum diameter in the middle of this period. A certain delay in the regression was observed in Ebro Delta.

In the cycle of the fat bodies (Fig. 2), the lowest values appeared during the reproductive season and the higher ones were reached at the beginning of autumn and maintained until the next breeding season. The fat body cycle was not exactly inverse to the testicular cycle, since no correlation between testis and fat body weights was observed in any case.

In the females, the weight of the ovary also showed a clear seasonal variation (Fig. 3). Only one peak was observed in May (Torredembarra) or May – June (Ebro Delta). No significant evidence of laterality was found in the ovaries in any population (Student's *t*-test). No correlation was detected between ovaries and fat bodies in any population. Females showed more fat reserves outside the reproduc-

tive period (approximately double) and a more marked fat cycle than the males. Some of the females from the Ebro Delta even lacked fat bodies in some months of spring (Fig. 3).

The minimum diameter of the vitellogenic follicles was 3 mm and their shape was spherical. The greater the diameter of the follicles, the wider the oviducts, which appeared strongly developed. The eggs gradually became elongated, adapting their shape to the walls of the oviduct. Those months when vitellogenic follicles and oviductal eggs appeared are represented in Fig. 4. Tables 1 and 2 show the sizes of follicles and eggs respectively and Table 3 shows the values of clutch size as calculated from both sources of information. No significant differences among localities were detected either in the clutch size (Kruskal – Wallis tests) or in the egg size (ANOVA tests). No correlation between the body size of the female and the size of the clutch or the eggs was found in any case.

The first hatchlings were observed in the middle of August in both populations. The minimum SVL measured was 30 mm.

DISCUSSION

Despite the northern geographical situation of the two localities studied, it should be borne in mind that both are under the influence of the warm Mediterranean climate. Thus, it is not surprising that the results are more similar to those obtained in more southern localities, even in Morocco (Bons 1962, 1963, 1965, 1968, 1969, 1972, 1973; Bons and Saint-Girons 1982; Seva 1982; Escarré and Vericad 1983; Busack

and Klosterman 1987) than in the populations from Central Spain (Pérez-Mellado 1981; Barbadillo 1987; Barbadillo et al. 1987; Pollo and Pérez-Mellado 1990; Castilla et al. 1992), which are more similar in latitude. So, the reproductive season is longer in the coastal and southern localities than in the continental areas but this season ends at approximately the same time in all areas. Furthermore, the cycle of *A. erythrurus* is one of the shortest and the most marked of the Mediterranean Lacertidae.

In the male, the increase in testis size begins earlier (one month) and the variation is less marked than in the inland localities but it is very similar to that found in warmer areas (see references above). Differences have even been observed within the same population between cold and warm years (Castilla et al. 1992). Testicular regression is practically simultaneous in all cases. Spermatogenesis is considered to be a temperature-dependent process but its interruption has an endogenous origin (Joly and Saint-Girons

TABLE 2. Biometry of the Oviductal Eggs in the *Acanthodactylus erythrurus* Females from the Two Localities Studied (linear measures in mm and volumes in mm³)

Locality (N)	X	S	CV ± lim (95%)	Range
Torredembarra (3)				
length	14.61	2.26	15.51 ± 2.56	12.10 – 16.50
width	10.25	2.29	22.40 ± 2.59	8.85 – 12.90
volume	841.57	434.00	51.57 ± 491.12	496.20 – 1328.73
Ebro Delta (4)				
length	13.57	0.58	4.34 ± 0.57	13.00 – 14.20
width	8.53	0.36	4.26 ± 0.35	8.05 – 8.90
volume	518.72	49.84	9.60 ± 8.84	473.31 – 588.92

TABLE 3. Clutch Size (as calculated from vitellogenic follicles, oviductal eggs or both) in the *Acanthodactylus erythrurus* Females from the Two Localities Studied

Locality/source	N	X	S	CV ± lim (95%)	Range
Torredembarra					
vitellogenic follicles	5	4.40	0.89	20.23 ± 0.78	3 – 5
oviductal eggs	1	3.00	–	–	–
both combined	6	4.00	1.09	27.25 ± 0.87	3 – 5
Ebro Delta					
vitellogenic follicles	3	3.66	0.57	15.57 ± 0.65	3 – 4
oviductal eggs	1	4.00	–	–	–
both combined	4	3.75	0.50	13.33 ± 0.49	3 – 4

TABLE 1. Biometry of the Vitellogenic Follicles in the *Acanthodactylus erythrurus* Females from the Two Localities Studied (linear measures in mm and volumes in mm³)

Locality (N)	X	S	CV ± lim (95%)	Range
Torredembarra (21)				
length	4.37	1.49	34.08 ± 0.64	2.05 – 6.35
width	3.75	1.52	40.47 ± 0.65	1.50 – 5.60
volume	45.20	35.93	79.48 ± 5.37	2.88 – 104.26
Ebro Delta (9)				
length	7.12	2.85	40.05 ± 1.86	2.05 – 9.15
width	6.23	2.45	39.41 ± 1.60	2.00 – 9.05
volume	193.51	124.98	63.60 ± 1.65	4.29 – 390.23

Note. N) number of females, X) mean; S) standard deviation, CV) coefficient of variation. The same in Tables 2 and 3.

1975; Angelini et al. 1976). So, a warm climate promotes longer and less marked testicular cycles (Braña et al. 1990; Carretero and Llorente 1991; see also Carretero and Llorente submitted, for the case of *Psammotromus algirus* in the same localities). When aestivation takes place, most individuals may remain inactive, then being their testis re-increase hidden (see Pollo and Pérez-Mellado 1990; Castilla et al. 1992). It can be observed in the population from the Ebro Delta. The epididymis is well developed only during the breeding period as in other Lacertidae (Saint-Girons and Duguy 1970; Braña et al. 1990; Carretero and Llorente 1991, submitted). It should be pointed out that a previous small increase was observed in Torredembarra. This was not observed neither in the Ebro Delta nor in any other population studied.

Males show a vernal spermatogenetic cycle (Saint-Girons 1963, 1984; Fitch 1970; Bons and Saint-Girons 1982) in contrast to other Iberian Lacertidae, which show the mixed type (Castilla et al. 1992). Testicular recrudescence occurs mainly after the diapause, reaching the maximum in the middle of the breeding season, when temperatures relatively high. During this season, the dilation of the epididymis is due to the production of a great amount of mature spermatozoa. Afterwards, in mid-summer, the epididymis no longer contains spermatozoa. A second spermatogenesis may take place in autumn (Bons 1969; but see Busack and Klosterman 1987). Historical reasons have been suggested to explain this cycle in relation to the desert conditions in the origin of the genus (Arnold 1989; Castilla et al. 1992).

The increase in ovary weight in the female, is due to vitellogenesis and egg production during the reproductive period. The high dispersion observed in these months may be attributed to the asynchrony between individuals in different conditions (vitellogenic follicles in different stages, atresic follicles, etc.). The general pattern of variation seems to indicate that vitellogenesis may start earlier in the Ebro Delta than in Torredembarra but there is a lack of data in the beginning of the breeding season in this locality to confirm this opinion. However, the end of the reproductive period is synchronic. The factors controlling gonad variation seem again to be environmental (the temperature for the beginning of vitellogenesis and the sharpness of the variation) as well as endogenous (ovarian regression, see Botte et al. 1976; Carretero and Llorente 1991, submitted).

The simultaneous presence of oviductal eggs and vitellogenic follicles indicated the possibility of two clutches in one female from the Ebro Delta, but no marking-recapture data were recorded. Iteroparity in this species has been observed in some cases (Bons 1962; Barbadillo 1987; Seva 1982; Castilla et al. 1992) but not in others (Busack and Klosterman 1987; Pollo and Pérez-Mellado 1990; Castilla et al. 1992). In general, a second (or even a third) clutch seem to occur in the warmer climates or in the warmer years in the same locality (Castilla et al. 1992). If breeding begins early, larger females may lay their clutches earlier than smaller ones (Etheridge et al. 1986), thus been able to lay a second (or third) clutch (Bons 1962; Seva 1982).

Gestation, calculated as the period from first copulations to first clutches, has been estimated to last 20 days (see also Seva 1982; Pollo and Pérez-Mellado 1990). The incubation time, calculated as the period between first clutches (May) and first newborn animals (mid August), lasts 2.5 months, approximately (see Pollo and Pérez-Mellado 1990). This estimation coincides with the results obtained in captivity, under seminatural conditions: 70 – 75 days in SE Spain (Seva 1982) and 73 – 78 days in Central Spain (Castilla et al. 1992). As pointed out by Carretero and Llorente (1991), the shortening of the incubation time of the later clutches could concentrate the dates of birth more than expected, because of their higher incubation temperatures (Kjaergaard 1982; Heulin et al. 1991; Sinervo 1990).

In reptiles, the fat bodies represent an important fraction of the energy reserves, which can rapidly be mobilized for reproduction or other needs (Derikson 1976). In temperate climates, these reserves are stored in autumn and consumed during the breeding period (Braña 1983). The consumption of lipids during diapause is almost null (Figs. 2 and 3; Castilla et al. 1992) and most of the reserves are used for reproduction. This is common in lizards with a full diapause period such as *A. erythrurus* (Carretero and Llorente submitted). So, the populations living in colder areas exhibit a delay at the beginning of the reproduction because they remain inactive for longer period.

Males consume their fat reserves before the females (Figs. 2 and 3). This has been attributed to the high pre-reproductive and reproductive activity associated to the search of females, copulations, etc. (Braña 1983; Derikson 1976). The increase in reproductive tissues and sperm production do not seem to

be too expensive energetically since there is no negative correlation between the testis or the epididymis sizes and the weight of the fat bodies (Braña 1983; Derikson 1976). In the females, the fat bodies are mobilized later, in the first vitellogenesis, which occurs already in a period of scarcity (Hahn and Tinkle 1965; Braña 1983; Braña et al. 1992). In the case of second or third clutches, females do not depend on fat bodies but on the food eaten during the second half of the reproductive season when food is more abundant (Etheridge et al. 1986). Fat reserves do not recover until the end of the clutch period.

There are three traits which characterize the oviposition of *A. erythrurus* in comparison with other Mediterranean Lacertidae of similar size: 1) eggs are larger, 2) variation in egg size is wider, and 3) clutch size is smaller than other species (Pollo and Pérez-Mellado 1990; Castilla et al. 1992). The mean size of the eggs found here are not different from other populations of the same species (Seva 1982; Escarré and Vericad 1983; Pollo and Pérez-Mellado 1990; Castilla et al. 1992) but they are double those of the similar-sized *Psammodromus algirus* in the same localities (see results in Carretero and Llorente in litt.). Conversely, the clutch size is smaller in *A. erythrurus* than in *P. algirus*. Moreover, variations in the egg volume can be as much as 100% in the same population of *A. erythrurus* (see results; Pollo and Pérez-Mellado 1990; Castilla et al. 1992).

In consequence, this species can be considered more K-selected than other Mediterranean Lacertidae, mainly modulating its reproductive effort by means of the variation in egg size (Steward 1979; Frankenberg and Werner 1992). Since the slope of the clutch size – female size regression is low in these cases (Castilla et al. 1992), a significant association has not probably been detected because of the small sample and the reduced clutch size. Larger females lay their eggs earlier (Seva 1982). These eggs are also larger and produce larger juveniles with higher survival possibilities (Sinervo 1990). This effect could be partially compensated in smaller females, because smaller eggs have shorter incubation times and juveniles appear earlier (Sinervo 1990). Obviously, the size of the females restricts the size of their eggs. Nevertheless, the shape is also important. The robust trunk of the *Acanthodactylus* species, which lack sexual dimorphism in the number of presacral vertebrae (Arnold 1989, 1993) could be an adaptation (or an exaptation) in this respect. Thus, the egg size would be less restricted but, at the same time, the egg num-

ber would be more limited than in slender species because the eggs are arranged linearly in the oviduct.

A second way of modulation is the number of clutches (Fitch 1970; Tinkle et al. 1970). In any circumstance when the reproductive season is lengthened (warm years, coastal Mediterranean climate, southern range, large females) there is a tendency to increase clutch frequency (Seva 1982; Castilla et al. 1992; Carretero and Llorente in litt.) since opportunities to allocate more energy into eggs increase.

In comparison with those from Central Spain (see references at the begging of the discussion), the small body sizes found, not only here but also in other coastal localities, as well as an early sexual maturity in all areas, indicate reproductive stress (Begon et al. 1986) in these populations. Usually, strong differences in body size between sexes can arise allometrically only in the largest lizards (Griffith 1991; Stamps 1993), coastal populations then being less dimorphic than inland ones. Moreover, the coastal populations should have higher annual fecundity and shorter longevity than them (Dunham and Miles 1985; Stamps 1993).

In conclusion, *Acanthodactylus erythrurus* exhibits its strong influence of historical factors in its reproductive traits. The vernal spermatogenic cycle, the short incubation period, the tendency to K-selection, and the modulation of the reproductive effort through egg size variation are plesiomorphic features in this genus, and they probably evolved under stable, arid conditions (Castilla et al. 1992; Frankenberg and Werner 1992; Arnold 1993). The colonization of the Iberian Peninsula by *A. erythrurus* is geologically recent (7.5 – 5 mybp) in comparison with the age of the genus (20 mybp) (Böhme and Corti 1993), and these traits are evolutionarily conservative and remain. On the other hand, the clutch frequency modulation represents a response to unpredictable variations of the Mediterranean ecosystems (Henry 1977). No evidence of suboptimal conditions has been detected here (see for instance, Strijbosch et al. 1980), those populations from Central Spain being apparently more ecologically restricted. Some dubious citations report this species in some coastal sites to the north of its present range during the second half of this century (Vives-Balmaña 1978; Filella and Pascó 1984; Fretey 1987; see also Llorente et al. in press, for some criticisms). This could lead us to presume a recent extinction of these isolated populations, probably by human modification of the habitat structure (see Rocha and

Bergallo 1992; personal observations). Nevertheless, further research is needed in this respect.

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