Reproductive cycles in Mediterranean lacertids: plasticity and constraints

Miguel Angel Carretero

CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, 4485-661 Vairão (Portugal); e-mail: carretero@mail.icav.up.pt

Reproductive timing is one of the most critical issues for lacertids inhabiting temperate regions where favourable conditions are restricted seasonally. Cycles of gonads and associated lipid reserves represent the manifestation of this discontinuous reproductive mode. Although lacertids seem to use both temperature and photoperiod to adjust their reproductive clocks to the environmental conditions, these cues seem to act at different stages of the cycle. Within species, interindividual, interpopulational and interannual variation have been documented. Thermal seasonality, changing between sites and years, determines not only the length of the reproductive season but also the intensity of variation for several reproductive parameters. Except in those species/populations with extremely short reproductive activity, lacertids are rather asynchronous, large adults starting reproduction later than small ones. In contrast, the end of the breeding period is less variable and probably associated with photoperiod.

Prior to all these factors, lipid storage of excess energy is a necessary condition for beginning reproduction. Lipids peak in late summer or early autumn, are not depleted in winter and are consumed during the reproductive season. Males spend reserves earlier than females in the activities related with breeding and recover them soon after since mixed-type spermatogenesis distributes energy costs along a prolonged period. Only spermiogenesis is highly variable in time depending on the species/population although previous classifications based on it are simplistic. Females mainly behave as capital breeders investing lipids in developing a first (or unique) clutch but may act as income breeders for the subsequent clutches if any. The degree of iteroparity depends on the same factors but just within the species limits. Some of the patterns observed are, nevertheless, uncorrelated with abiotic environment and may reflect other pressures. Theoretically, any influence able to provoke food shortage would delay reproduction independently of climate conditions. In some cases, traits could be historical, deriving from pressures acting in the past. Long egg retention and viviparity are strong constraints since they prolong single reproductive events preventing its repetition even when environmental conditions would allow it. Moreover, thermophile species evolved under mild conditions are unable to start reproduction when and where other more cold-adapted species do. On the other hand, insular lacertids enlarge the reproductive period in comparison with their continental equivalents living under similar
climate regimes but with different demographic pressures. Finally, a biogeographic scenario for the evolution of reproductive cycles in the whole family is proposed.

Keywords: reproduction, phenology, spermatogenesis, vitellogenesis, fat bodies, viviparity, insularity, Lacertidae.

INTRODUCTION

Lacertids are among the most genuine Mediterranean vertebrates since the whole group originated around this area (Estes 1983, Arnold 1989) and radiated and diversified there tracking its complex geological history (Harris et al. 1998, Carretero 2004), extensively contributing for it to be considered a biodiversity hotspot at the global level (Myers et al. 2000). Since the Mediterranean Basin falls within the temperate region, seasonal restriction of favourable conditions for ectotherms, more or less intensified throughout the geological changes and climatic cycles, has undoubtedly modelled the evolution of lacertids since the beginning and still plays a prominent role on the lineages inhabiting this area. Under such environmental constraints, reproductive timing becomes one of the most critical issues in the lizard’s biology (James & Shine 1985). Life cycles as well as the cyclical variations of gonads and associated lipidic reserves represent the expression of this discontinuous reproductive mode. Whereas life history traits in lacertids have been extensively reviewed (Bauwens & Díaz-Uriarte 1997, Bauwens 1999), no comprehensive general approach is available on how such biological events are allocated in time. This is the aim of this review.

LIFE CYCLES

Regarding their life cycles, Mediterranean lacertids are conservative. Despite the number of phylogenetically diverse lineages present in this region (Harris et al. 1998) no strong variation of patterns is found. Cycles work on an annual basis (Fig. 1), breeding season taking place in spring-early summer, clutches in late spring-early summer and hatchling in summer-early autumn. Lacertids become sexually mature when attaining a minimum body size rather than an age (Marco et al. 1994, Galán 1996b, Olsson & Shine 1997, Bauwens 1999). Depending on the species and the
Reproductive cycles in Mediterranean lacertids

population, sexual maturity can be attained either during the first calendar year or one to several years later, then passing through a subadult stage (Carretero & Llorente 1993) simultaneously present with adults and juveniles. Such distinction is not irrelevant since the lack of autumnal reproduction prevents the existence of intermediate patterns. In fact, if the minimum size is not attained in a given season, individuals do not incorporate to the adult stage but continue growing and attain bigger adult sizes the following one (Carretero & Llorente 1997). At an intraspecific level, variation in the age of sexual maturity between sexes (Amat et al. 2000, Olsson & Shine 1997, Galán & Arribas 2005), populations (Bauwens & Verheyen 1987, Fig. 2) and years (Bauwens & Verheyen 1987, Heulin et al. 1994, Fig. 3) has been described. Usually, mild conditions tend to promote fast growth and early reproduction. This effect can be responsible for the adult size differences found between populations of the same species facing different climatic conditions (sensu Adolph & Porter 1993), especially for those undergoing deep winter diapause and may even contribute with other factors to sexual size dimorphism (Carretero & Mateos 2002, Roitberg & Smirina 2004).

In those species with a subadult stage, the number of years involved may vary between one, being the most common in small-sized species (Galán 1996b), to three-four in the large green lizards (Mateo & Castanet 1994, Elbing 2001). Nevertheless, some small species inhabiting mountains or northern habitats delay several years before attaining sexual maturity (Bauwens & Verheyen 1987, Arríbas 2004, Galán & Arribas 2005) although it could be argued that the effective life (i.e. in activity) is not very different from lizards under less extreme conditions (Carretero & Mateos 2002). Sexual maturity and total longevity tend to be correlated at population and species level. As an exception, giant *Gallotia* species from the Canary Islands start reproduction relatively early but their growth does not decrease with sexual maturity and continues for a long period (Castanet & Báez 1988, 1991) resulting in a high maximum

![Fig. 1. Schematic representation of the life cycle in a Mediterranean lacertid. Stars: copulation period; ellipses: clutch period; dashed arrows: attainment of sexual maturity; n: number of cycles in immature stage; m: number of cycles in adult stage.](image-url)
Fig. 2. Variation of the life history of the lacertid *Psammodromus algirus* between four coastal populations in NE Iberian (from north to south) studied during the same period. Distribution of immatures randomly sampled throughout the year: in the northernmost population (A. Empordà) no immatures reached sexual maturity within the first calendar year but all of then did in the southernmost one (Ebro Delta); the other two populations were intermediate, Torredembarra being especially asynchronic. Hatchlings started appearing in August. Rectangles: reproductive season; arrows: end of the reproduction. Box: mean ± SE; whisker: mean ± SD.

Fig. 3. Variation of the life history of the lacertid *Psammodromus algirus* between two consecutive years in the same locality. Distribution of immatures randomly sampled throughout the year: whereas only a part of the individuals attained sexual maturity before the end of the breeding season in 1986 (see increased variance in August), most of them had already reached the minimum size in June 1987. Rectangles: reproductive season; arrows: end of the reproduction. Box: mean ± SE; whisker: mean ± SD.
longevity with considerable size variation within adults. On the opposite extreme, the small-sized *Psammodromus hispanicus* may reach minimum adult size in less than three months and most individuals only breed during one season, all within less than one year of life span (Pascual & Pérez-Mellado 1989, Carretero & Llorente 1991, Carretero 1992). Members of other dwarf genera as *Ophisops* and *Mesalina* from N Africa, Levant and Asia Minor probably display similar patterns (Pérez-Mellado et al. 1993, Schleich et al. 1996). Olsson & Shine (2002) have experimentally evidenced negative relationships between the rates of early growth and late survivorship for one skink species and this may also be the case in lacertids.

**Gonad cycles: variability and regulation**

Male and female cycles in lacertids are linked, which seems rather obvious but is not the rule in many other squamates (Fitch 1970). That means that neither sperm needs to wait for ovarian follicles to mature nor these become “frozen” waiting for spermiogenesis. In fact, no long-term sperm storage have been demonstrated in the whole family. Conversely, although copulatory plugs have been described (in den Bosch 1994), their effectiveness is limited (Moreira & Birkhead 2004a, b) and males mainly rely on mate guarding to ensure their reproductive success (Olsson et al. 1996, 1997a, b; Gullberg et al. 1997).

At a macroscopic level, male cycle consists of seasonal changes in the size of the sexual organs (Fig. 4). Essentially, testis suffers a strong decrease after the reproductive period and keeps its size throughout the rest of the year whereas epididymis enlarges in the reproductive period (or immediately before) and remains small out of it. Such changes are related, although not completely, with the seasonal variation in the abundance of the different sexual cells (see spermatogenesis section). In contrast, female cycle displays changes, affecting ovary and oviduct, exclusively concentrated in the reproductive period (Fig. 5).

Although lacertids seem to use both temperature and photoperiod to adjust their reproductive clocks to the environmental conditions, these cues seem to act at different stages of the cycle. Thus, experimental research has demonstrated that the spermatogenesis is thermodependent (Joly & Saint-Girons 1975; Angelini et al. 1976, 1979), the beginning of the reproductive activity thermally controlled in both sexes. In contrast, the end of the reproduction remains similar under different thermal regimes probably adjusted with the photoperiod and endogenous clocks (Angelini et al. 1976, Botte et al. 1976, Tosini et al. 2001). The environmental and internal set points for such events are expected not only to change between species (Saint-Girons & Saint-Girons 1956, Saint-Girons & Duguy 1970) but also to carry substantial phylogenetic inertia according to
Fig. 4. Seasonal variation of testis (closed squares) and epididymis (open squares) sizes in the lacertid *Psammodromus algirus* from a coastal Mediterranean locality. The sizes of both organs have been standardised to the lizard size using regression residuals of log-transformed variables. Lines have been fitted by least-squares. Rectangles: reproductive season; arrows: end of the reproduction. Box: mean ± SE; whisker: mean ± SD.

Fig. 5. Seasonal variation in 15-days periods of ovary (closed squares) and oviduct (open squares) sizes in the lacertid *Lacerta (Zootoca) vivipara* from the western Pyrenees. The sizes of both organs have been standardised to the lizard size using regression residuals of log-transformed variables. Lines have been fitted by least-squares. Rectangles: reproductive season; arrows: end of the reproduction. Box: mean ± SE; whisker: mean ± SD (from Roig et al. 2000, modified).
Reproductive cycles in Mediterranean lacertids

the past environmental conditions in the areas of origin of each group, which probably parallel preferred temperatures (see Carretero et al. 2005 and references therein). This means that groups evolved under mild conditions and recently colonising more extreme environments should display a more restricted reproductive period than those originated in such restrictive environments (Perez-Mellado 1982, Busack & Klostermann 1987, Pollo & Perez-Mellado 1990, Castilla et al. 1992, Carretero & Llorente 1995).

Within species, interindividual (Seva 1982, Braña 1986, Bauwens & Veheyen 1987, Marco et al. 1994, Castilla & Bauwens 1989, Carretero & Llorente 1997, Galán 1997, Olsson & Madsen 1996, Olsson & Shine 1996), interpopulational (Hraoui-Bloquet 1985, 1987; Hraoui-Bloquet & Bloquet 1988; Braña et al. 1990; Carretero & Llorente 1997) and interannual (Castilla et al. 1992, Carretero & Mateos 2002) variation in reproductive events have been documented. Thermal seasonality, changing according to locations and years, determines not only the length of the reproductive season but also the intensity of variation for several reproductive parameters (Gavaud 1991). The beginning of the reproductive season is usually more variable than the end, reproduction in warmer years or sites starting earlier (see previous references). Except in those species/populations with extremely short reproductive activity (Elvira & Vigal 1985, Argüello 1990, Carretero & Llorente 1995, Amat et al. 2000, Roig et al. 2000, Arribas 2004, Galán & Arribas 2005) lacertids are rather asynchronous, larger adults and specially females starting reproduction earlier than small ones (Olsson & Shine 1997, Galán 1997, Marco & Pérez-Mellado 1998). In contrast, the end of the breeding period does not show much variation and is probably associated with photoperiod. Nevertheless, the final part of the reproduction may be truncated when harsh summer conditions promote aestivation (Hraoui-Bloquet & Bloquet 1988, Pollo & Perez-Mellado 1990).

Spermatogenetic cycles

In males, the variation of cell types parallels macroscopic changes observed in the testis but just during the reproductive season (Roig et al. 2000, Carretero et al. 2006) whereas the rest of the year the abundance and proportion of the different cell types change without affecting the organ size.

Classic literature classifies reptile spermatogenetic cycles according to the stage in which sexual cells become after the reproductive period (Saint-Girons 1963, 1984). Lacertids do not produce spermatozoa immediately after the breeding season (postnuptial spermatogenesis) as found in many snakes and tortoises (Bons & Saint-Girons 1982) but delay this process along a variable period, thus distributing the energetic costs associated (Olsson et al. 1997, Roig et al. 2000). Instead, two other types of spermatogenesis occur in Mediterranean lacertids: spermatogonia may rapidly develop into spermatocytes and
spermatides immediately after breeding and then the maturation to spermatozoa extends until the following season (mixed type) or the whole maturation from spermatogonia to spermatozoa is concentrated immediately before or even during breeding (prenuptial or vernal type). In theory, most mesic species (*Psammodromus, Podarcis, Lacerta s.l.*) fall within the first category whereas only those with desert affinities (*Acanthodactylus, Mesalina*) belong to the second (Bons & Saint-Girons 1982). Nevertheless, such dichotomy constitutes a simplification since the final part of the spermatogenesis (the spermiogenesis) is highly variable in time within species. For instance, some individuals of species ascribed to the mixed type are able to produce spermatozoa already in autumn (*Lacerta vivipara, Roig et al. 2000; Podarcis sicula, Angelini et al. 1979; P. bocagei, Carretero et al. 2006*). Whether this autumnal spermiogenesis is just abortive (Angelini et al. 1979) or represents a potential second reproductive season remains speculative (see below). Furthermore, advanced states of sexual cells are even found in autumn for typically prenuptial species (i.e. *Acanthodactylus erythrurus*, Bons 1969).

Whatever the case, even if spermatozoa have already been produced in testis, males become fertile only when these pass to the epididymis which is revealed externally by the enlargement of this organ (Roig et al. 2000, Carretero et al. 2006). Among the Mediterranean lacertids the anticipation of this enlargement to the breeding season is variable (Fig. 6) but is specially marked in some species inhabiting warm, mesic habitats (*Psammodromus hispanicus, Carretero & Llorente 1991; Lacerta laevis, Hraoui-Bloquet & Bloquet 1988 and Lacerta lepida, Castilla & Bauwens 2000a, b*). In those species undergoing a marked winter diapause, males usually emerge earlier than females (Saint-Girons 1976, Nuland & Strijbosch 1981, Salvador 1987) and this phase takes place when females are still inactive (Olsson & Madsen 1996, Roig et al. 2000, Carretero et al. 2006). It is considered that, in fact, females are avoiding copulation with these functionally infertile males at the beginning of the season (Olsson & Madsen 1996).

**Vitellogenesis**

In comparison, the female cycle is relatively simple with all events restricted to the reproductive period. Ovary increases in size due to the maturation of vitello-gevic follicles at the beginning of the reproductive season. After fecundation, eggs develop inside the oviducts which have previously increased their diameter and change their histology to receive them (Bons 1972, Roig et al. 2000). Minimum diameters of vitellogenic follicles (2-3 mm) have been described for different species (Carretero & Llorente 1991, 1995, 1997; Roig et al. 2000). Clutch and egg size usually correlate with body size and depend on population and species (see below) but follicle and egg numbers are equivalent in all cases (see previous references)
which suggest that atresia may be rare in lacertids (but not in other groups, see Méndez de la Cruz et al. 1993). Egg retention inside the female changes not only with the reproductive modality (oviparous/viviparous, Heulin et al. 1991) but also between different oviparous species (Braña et al. 1991, Galán & Arribas 2005) and maybe between populations.

**Cycles of lipidic reserves**

Prior to climatic factors, lipid storage of excess energy is a necessary condition for beginning reproduction in reptiles (Derikson 1976). Such lipids are stored in abdominal fat bodies in lacertids (Fitch 1970) but other compartments such as the tail, liver and carcass may also be involved (Roig et al. 2000). Such reserves describe an annual cycle inverse to the gonadal: lipids peak in late summer or early autumn, are not depleted in winter and are consumed during the reproductive season (Braña 1983; Braña et al. 1990, 1992; Carretero & Llorente 1991, 1995, 1997; Amat et al. 2000; Roig et al. 2000). Nevertheless, male and female cycles differ in level, intensity and timing of this cycle. Males store less reserves and spend them earlier than females in the activities related with breeding (mate searching and guarding, agonistic interactions, copulation) and recover them soon after because sperm production extends along several months (see spermatogenesis). As a result, the cycles of gonads and reserves are uncorrelated in males.

In contrast, ovarian and lipidic cycles are strongly adjusted. Females mainly behave as capital breeders directly investing lipids stored in the previous season developing the first (or unique) clutch (Derikson 1976, Etheridge et al. 1986). In the iteroparous lacertids, this does not apply to the subsequent clutches since after the first egg laying females lack or almost lack fat bodies (Braña 1983; Braña et al. 1992; Galán 1996a; Carretero & Llorente 1991, 1997). This finding suggests that they apparently behave

---

**Fig. 6.** Schematisation of the spermatogenetic cycles in three species of Mediterranean lacertids from coastal areas of NW Iberia (data taken from Carretero & Llorente 1991, 1995, 1997).
as income breeders investing the matter and energy provided by the prey ingested during the breeding season. As in the case of gonadal cycles, the degree of iteroparity (clutch frequency, % females involved) also depends on the “window chance” provided by temperature, photoperiod and food availability but just within the species limits.

**OTHER FACTORS?**

Some of the patterns observed are, nevertheless, uncorrelated with abiotic environment and may reflect other pressures. Theoretically, any influence able to provoke food shortage would delay reproduction independently of climate conditions. Carretero & Llorente (1997) detected a delay in the reproduction of *Psammodromus algirus* in comparison with other localities with similar temperature and photoperiod associated with low spring rainfall and arthropod availability (see Santos & Llorente 2001 for a similar case in snakes). Habitat fragmentation also reduced the clutch size and mass in this species (Díaz *et al.* 2005) but these authors do not provide evidence if that takes place via follicular atresia (Méndez de la Cruz *et al.* 1993). Similarly, Amat (1997) in a path analysis of factors determining the clutch traits in a Pyrenean population of *Lacerta agilis* concludes that, whereas egg number is controlled by female size, her body condition is reflected on egg size. Furthermore at present, the only studies specifically testing for competitive influences in reproductive cycle Carretero *et al.* (2006) produced negative results.

**HISTORICAL CONSTRAINTS**

Some reproductive traits are not environmentally mediated but historical, deriving from pressures acting in the past. Viviparity and, in general, egg retention (evolved in extreme cold environments, Shine 1983) represent strong constraints for reproductive timing since they prolong single reproductive events preventing its repetition even when environmental conditions would allow it. This affects mainly females since viviparous species (Heulin *et al.* 1991) and those with long egg retention (Roig *et al.* 2000, Arribas 2004, Galán & Arribas 2005) are not iteroparous. The same applies to large-sized species which are more constrained thermically than small ones (Bauwens 1999). Paradoxically, the thermophile species evolved under mild conditions but living in colder environments also face similar problems because they are more selective when starting reproduction (see before). In all cases, males are also affected since opportunities for fecundating monoestrous females are then more restricted in time.
Reproductive cycles in Mediterranean lacertids (Roig et al. 2000, Carretero et al. 2006) although female promiscuity and multiparental clutches seem to be the rule in such cases (Olsson et al. 1994a, b; Laloi et al. 2004; Uller & Olsson 2005).

Another example of historical influences on reproductive timing is constituted by those lacertids evolving under insular conditions, essentially, low predation, high density and intraspecific competition and unpredictable prey availability (Fig. 7). In order to face such pressures, insular lacertids enlarge the reproductive period in comparison with their continental equivalents living under similar climate regimes (Carretero et al. 1995; Adamopoulou & Valakos 2000; Castilla & Bauwens 2000a, b; Perera & Pérez-Mellado 2002; Galán 2003; Galán & Vicente 2003). This strategy assures the exploitation of scarce resources available since the body condition of lizards of both sexes may be extremely variable throughout the year without following a clear cycle (Carretero et al. 2005). Thus, male spermiogenesis is probably forced to track an extremely irregular and asynchronic vitellogenesis in females; it could be even predicted strong sperm competition based on amount and not in mate guarding Why? Putting the eggs in several clutches would be a way to provide suitable conditions for at least

---

**Fig. 7.** Diagram of the reproductive strategy of insular lacertids. In islands, lizards have fewer terrestrial predators, attain high densities but face high intraspecific competition and low arthropod availability. Consequently, reproductive period is enlarged, males prolonging sperm production (lines) and females laying clutches (circles) of few, large eggs.
a part of the progeny and making them large would increase the survival possibilities of juveniles (Sinervo 1990) to face intraspecific aggression and cannibalism which are more common in dense island populations (Castilla & Dunlap 2001).

Such traits are shared by lacertids belonging to lineages with a long evolution in insularity (see previous references) and do not display much variation either between islands (Perera & Pérez-Mellado 2002) or when island species are introduced in the continent (Carretero et al. 1995). On the other hand, they do not appear in lacertids recently colonising islands which are more similar to continental forms (Bejakovic 1996a, c; Rúa & Galán 2003). Such conservativeness has also been evidenced for trophic ecology and provides additional support for the time-for-evolution hypothesis (Stephens & Wiens 2003, Carretero 2004).

One last example are lacertids with strong anatomical constraints, namely, those adapted to a strongly saxicolous life. In such cases, crevice dwelling limits not only the shape but also the number of eggs and such species usually lay elongated eggs in small, numerous clutches along a considerable period (Bejakovic et al. 1996b, Perera 2005), much as insular species do.

**An evolutionary perspective**

Lacertid early evolution took place in the Western Palearctic (Estes 1983, Arnold 1989) where the most based branches of the family are still restricted (Harris et al. 1998). This suggest that reproductive cycles with “mixed-type” tendency in spermatogenesis and facultative iteroparity appeared as adaptations to temperate climate and can be considered plaeosiomorphic within the whole family (Fig. 8). As commented previously, the autumnal spermatogenesis and even vitellogenesis (Carretero & Llorente 1997) could represent the remains of a second reproductive season in the past under subtropical climates perhaps during the Miocene but more evidence on this should be provided.

In the context of conservativeness of lizard cycles (James & Shine 1985), adaptations to insularity and mountains or cold environments would just constitute derivations from such a primitive cycle. The same cycle has also been conserved in the lineages colonising central Asia and Far East living under temperate regimes (Telford 1997, Huang 1998, Ji et al. 1998, Szczerbak 2000). However, when the more advance members of the armatured clade colonised Africa (Arnold 1989) they had to face desertic and equatorial conditions of the Ethiopian region where temperature and photoperiod may be uninformative about environmental resources. Desert and savannah species in North Africa and the Middle East have probably shifted spermatogenesis to the breeding period (Perry & Dmi’el 1994, Schleich
et al. 1996) but tend to rely more on precipitation as an environmental cue for starting reproduction. Some members of the clade, namely *Acanthodactylus*, have secondarily recolonized Europe in the late Miocene (Harris et al. 2004) and still conserve this reproductive pattern (see previous references). However, equatorial species completely lost the seasonality in reproduction and display a continuous spermatogenesis, vitellogenesis and egg-laying solely constrained by food availability (Spawls et al. 2002, Fig. 8). Although temperate climate is also present in southern Africa where some species display patterns similar to those in Western Palearctic (Goldberg & Robinson 1979, Nkosi et al. 2004), it seems that crossing the equator has “released” some secondary temperate species from their phylogenetic constraints and more diversity is found. The aseasonal iteroparity of *Aporosaura achietae* from Namibia (Goldberg & Robinson 1979) and the inverse, autumnal cycle of *Ichnotropis capensis* from Botswana (Broadley 1967, Branch 1998, Fig. 8) can be interpreted in this sense. The subtropical members of the Asian genus *Takydromus* would be equally interesting to be investigated.

Fig. 8. Tentative scheme of the evolution of the reproductive cycles in lacertids according to the biogeography of this family. Sperm production (lines) and clutches (circles) are represented as in Figs 6 and 7.
Acknowledgements

Thanks are due to F. Amat (El Prat de Llobregat), D. Barbosa (Porto-València), P. Galán (A. Coruña), A. Kaliontzopoulou (Vairão-Barcelona-Irakleio), D.J. Harris (Vairão), C. Llorente (Vilanova i La Geltrú), G.A. Llorente (Barcelona), J. Mateos (Barcelona), A. Montori (Barcelona), A. Perera (Burgos), V. Pérez-Mellado (Salamanca), R. Ribeiro (Vairão), J.M. Roig (Catelldefels) and X. Santos (Granada-Barcelona) for their assistance and comments. I am also grateful to C. Corti and P. Lo Cascio for their kind invitation to give a plenary talk in the 5th International Symposium on the Lacertids of the Mediterranean Basin and to all the participants for the creative ambient generated. The elaboration of this review was supported by the projects POCTI/BSE/45664/2002 and POCTI/BIA-BDE/55865/2004 as well as by the post-doctoral grant SFRH/BPD/3596/2000, all from Fundação para a Ciência e a Tecnologia, FCT (Portugal).

References


Pérez-Mellado V. 1982. Algunos datos sobre la reproducción de dos especies de Lacertidae (Sauria, Reptilia) en el Sistema Central. Boletín de la Real Sociedad Española de Historia Natural (Biología) 80: 165-173.
Reproductive cycles in Mediterranean lacertids


