

Reproductive cycles in Mediterranean lacertids: plasticity and constraints

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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

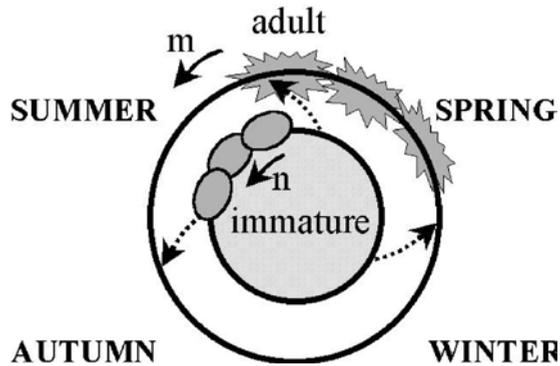


Fig. 1. Schematic representation of the life cycle in a Mediterranean lacertid. Stars: copulation period; ellipses: clutch period; dashed arrows: attainment of sexual maturity; n: number of cycles in immature stage; m: number of cycles in adult stage.

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, Arribas 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

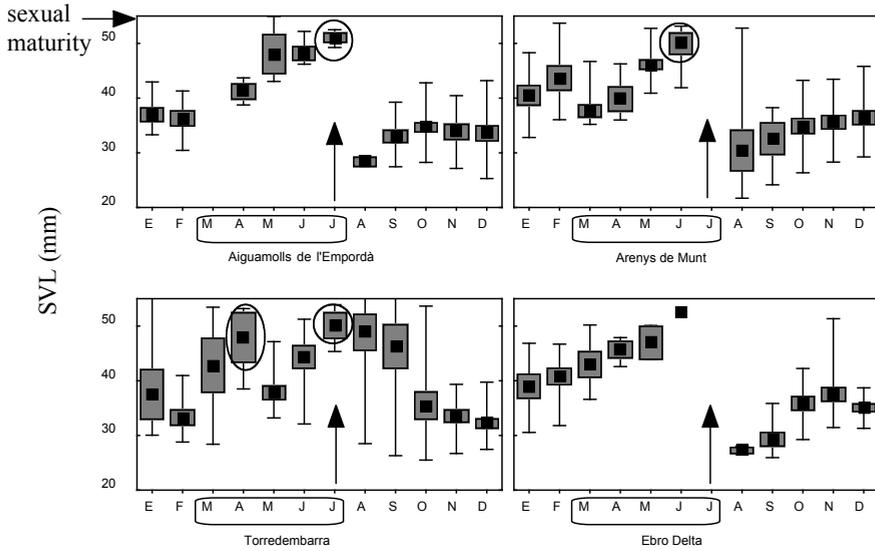


Fig. 2. Variation of the life history of the lacertid *Psammodromus algirus* between four coastal populations in NE Iberian (from north to south) studied during the same period. Distribution of immatures randomly sampled throughout the year: in the northernmost population (A. Empordà) no immatures reached sexual maturity within the first calendar year but all of them did in the southernmost one (Ebro Delta); the other two populations were intermediate, Torredembarra being especially asynchronous. Hatchlings started appearing in August. Rectangles: reproductive season; arrows: end of the reproduction. Box: mean \pm SE; whisker: mean \pm SD.

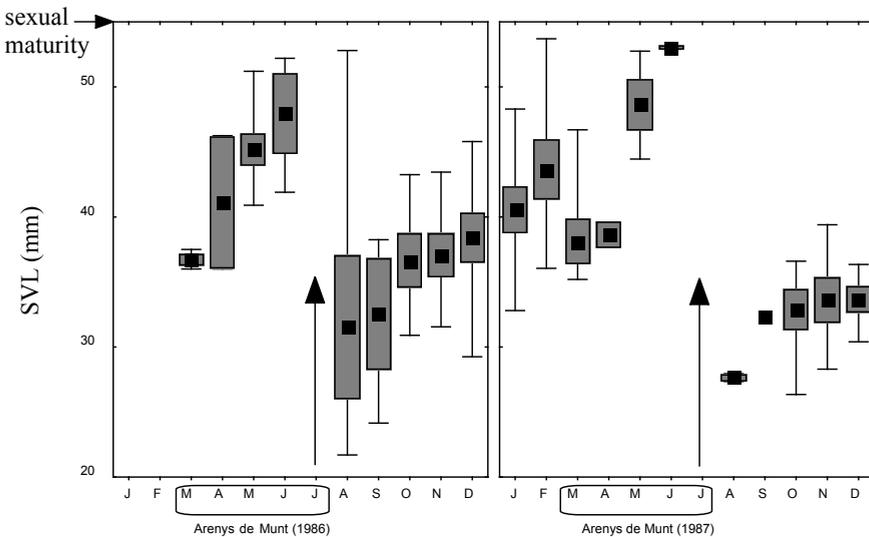


Fig. 3. Variation of the life history of the lacertid *Psammodromus algirus* between two consecutive years in the same locality. Distribution of immatures randomly sampled throughout the year: whereas only a part of the individuals attained sexual maturity before the end of the breeding season in 1986 (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 \pm SE; whisker: mean \pm 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

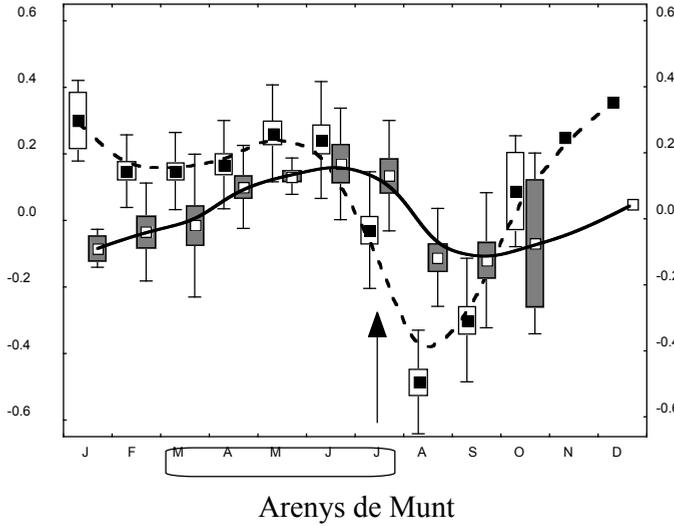


Fig. 4. Seasonal variation of testis (closed squares) and epididymis (open squares) sizes in the lacertid *Psammodromus algirus* from a coastal Mediterranean locality. The sizes of both organs have been standardised to the lizard size using regression residuals of log-transformed variables. Lines have been fitted by least-squares. Rectangles: reproductive season; arrows: end of the reproduction. Box: mean \pm SE; whisker: mean \pm SD.

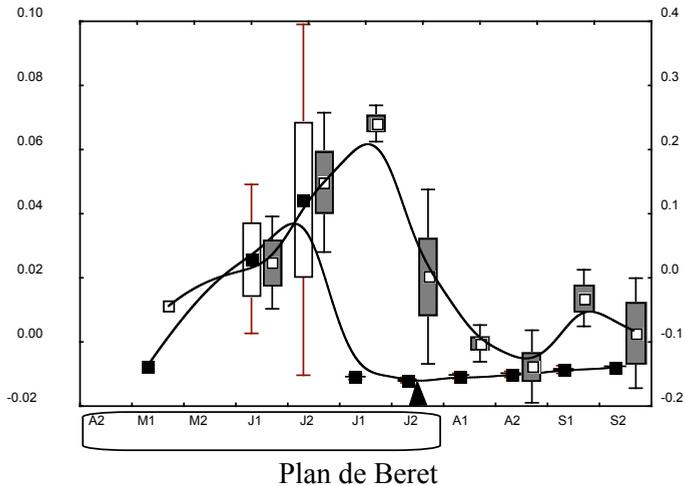


Fig. 5. Seasonal variation in 15-days periods of ovary (closed squares) and oviduct (open squares) sizes in the lacertid *Lacerta (Zootoca) vivipara* from the western Pyrenees. The sizes of both organs have been standardised to the lizard size using regression residuals of log-transformed variables.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

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 spermatogenic 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 vitellogenic 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)

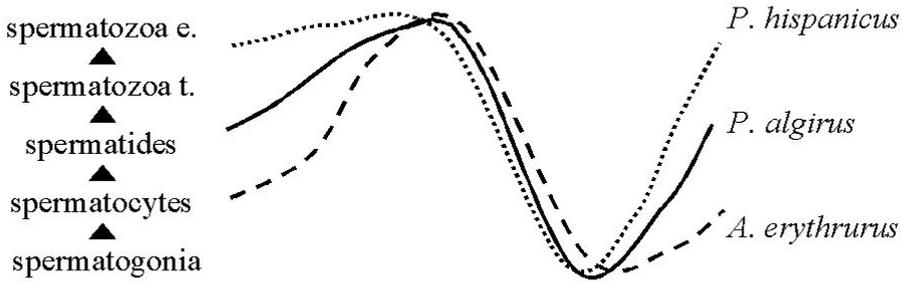


Fig. 6. Schematisation of the spermatogenic cycles in three species of Mediterranean lacertids from coastal areas of NW Iberia (data taken from Carretero & Llorente 1991, 1995, 1997).

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

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

(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; Laloï *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 asynchronous 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

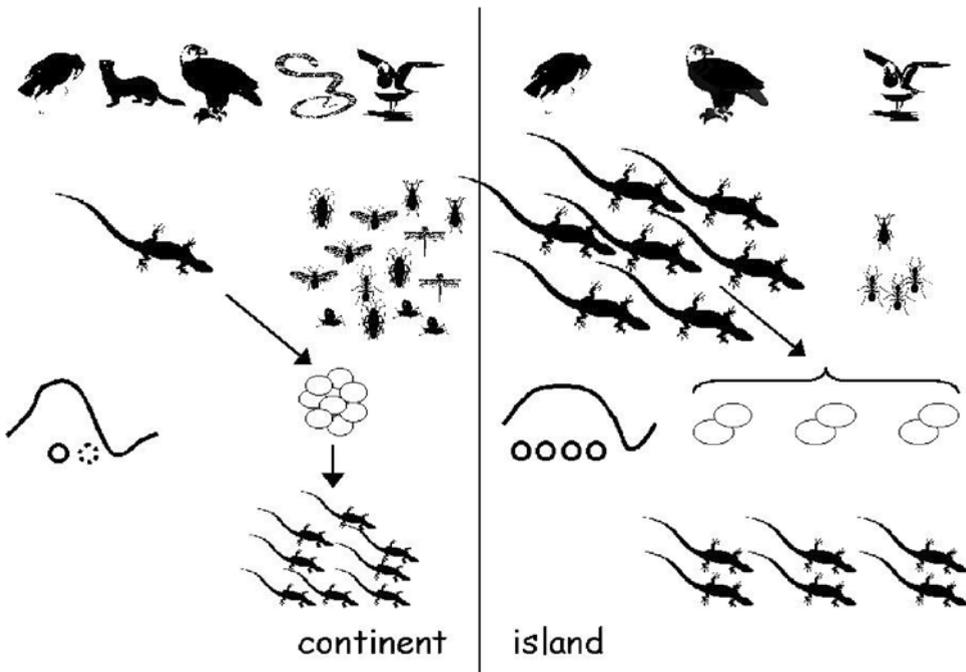


Fig. 7. Diagram of the reproductive strategy of insular lacertids. In islands, lizards have fewer terrestrial predators, attain high densities but face high intraspecific competition and low arthropod availability. Consequently, reproductive period is enlarged, males prolonging sperm production (lines) 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 plesiomorphic 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.

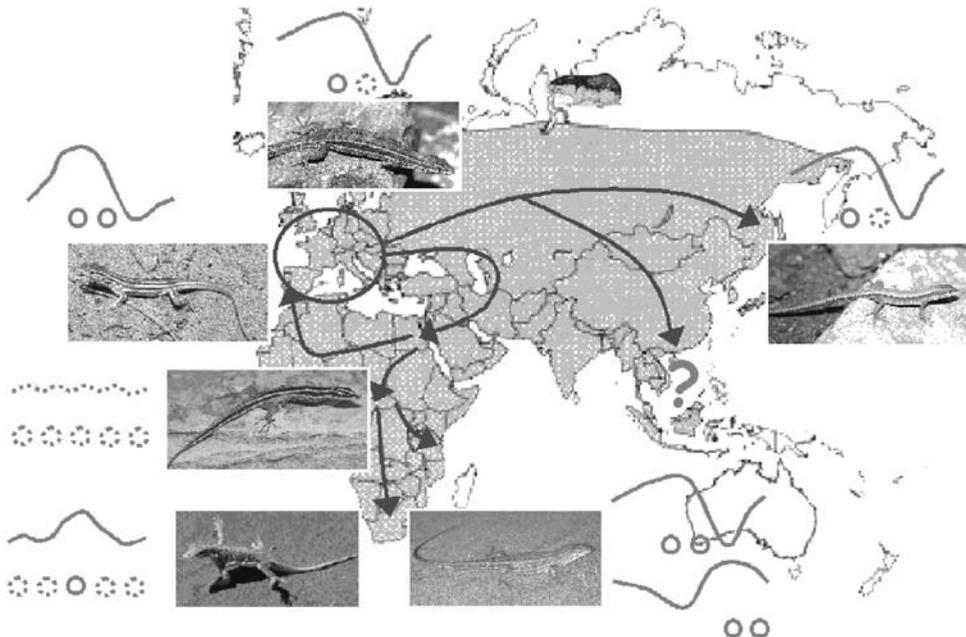


Fig. 8. Tentative scheme of the evolution of the reproductive cycles in lacertids according to the biogeography of this family. Sperm production (lines) and clutches (circles) are represented as in Figs 6 and 7.

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REFERENCES

- Adamopoulou C. & Valakos E.D. 2000. Small Clutch Size in a Mediterranean Endemic Lizard (*Podarcis milensis*). *Copeia* 2000: 610-614.
- Adolph S.C. & Porter W.P. 1993. Temperature, activity, and lizard life histories. *The American Naturalist* 142 (2): 273-295.
- Amat F. 1997. Biología reproductora de una población pirenaica del lagarto ágil *Lacerta agilis* (Lacertidae: Reptilia). Graduate Thesis, University of Barcelona.
- Amat F., Llorente G.A. & Carretero M.A. 2000. Reproductive cycle of *Lacerta agilis* in its southeastern boundary. *Amphibia-Reptilia* 21: 463-476.
- Angelini F., Brizzi R. & Barone C. 1979. The annual spermatogenic cycle of *Podarcis sicula campestris* De Betta (Reptilia Lacertidae). I The spermatogenic cycle in nature. *Monitore zoologico italiano (N.S.)* 13: 279-301.
- Angelini F., Picariello O. & Botte V. 1976. Influence of photoperiod and temperature on the testicular activity of the lizard, *Lacerta sicula sicula* Raf. *Bolletino di Zoologia* 43: 111-113.
- Argüello J.A. 1990. Biología reproductiva de *Lacerta monticola* en una población de la Cordillera Cantábrica. *Graellsia* 46: 253-261.
- Arnold E.N. 1989. Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology. *Bulletin of the British Museum Natural History (Zoology)* 55 (2): 209-257.
- Arribas O.J. 2004. Characteristics of the reproductive biology of *Iberolacerta aurelioi* (Arribas, 1994). *Herpetozoa* 17: 3-18.

- Bauwens D. 1999. Life-history variation in lacertid lizards. *Natura Croatica* 8: 239-252.
- Bauwens D. & Díaz-Uriarte R. 1997. Covariation of life-history traits in lacertid lizards: a comparative study. *The American Naturalist* 149: 91-111.
- Bauwens D. & Verheyen R.F. 1987. Variation of reproductive traits in a population of the lizard *Lacerta vivipara*. *Holarctic Ecology* 10: 120-127.
- Bejakovic D., Aleksic I., Crnobrnja-Isailovic J., Dzukic G. & Kalezic M.L. 1996a. Female reproductive traits in the Common Wall lizard (*Podarcis muralis*) from the Skadar Lake region, Montenegro. *Revista Española de Herpetología* 10: 91-96 (23-28).
- Bejakovic D., Aleksic I., Crnobrnja-Isailovic J., Dzukic G. & Kalezic M. 1996b. Reproductive cycle and clutch size in female sharp-snouted rock lizards, *Lacerta oxycephala*. *Amphibia-Reptilia* 17: 73-77.
- Bejakovic D., Aleksic I., Tarasjev A., Crnobrnja-Isailovic J., Dzukic G. & Kalezic M. 1996c. Life-history variation in a community of lacertid lizards from the lake Skadar region (Montenegro). *Herpetological Journal* 6: 125-132.
- Bons N. 1969. Le cycle sexuel du male chez *Acanthodactylus erythrurus* Dum. & Bibr. (Sauria, Lacertidae). *Bulletin de la Société des Sciences Naturelles et Physiques du Maroc* 49: 161-167.
- Bons N. 1972. Variations histophysiologiques du tractus genital femelle du lézard *Acanthodactylus erythrurus* au cours du cycle annuel. *Bulletin de la Société des Sciences Naturelles et Physiques du Maroc* 52: 59-111.
- Bons J. & Saint-Girons H. 1982. Le cycle sexuel des reptiles au Maroc et ses rapports avec la répartition géographique et le climat. *Bulletin de la Société zoologique de France* 107 (1): 71-86.
- in den Bosch H. 1994. First record of noting plugs in lizards. *Amphibia-Reptilia* 15: 89-93.
- Botte V., Angelini F., Picariello O. & Molino R. 1976. The regulation of the reproductive cycle of the female lizard *Lacerta sicula sicula* Raf. *Monitore zoologico italiano (N.S.)* 10: 119-133.
- Braña F. 1983. La reproducción en los saurios de Asturias (Reptilia; Squamata): ciclos gonadales, fecundidad y modalidades reproductoras. *Revista de Biología de la Universidad de Oviedo* 1: 29-50.
- Braña F. 1986. Ciclo reproductor y oviparismo de *Lacerta vivipara* en la Cordillera Cantábrica. *Revista Española de Herpetología* 1: 273-292.
- Braña F., Arrayago M.J., Bea A. & Barahona A. 1990. Ciclo reproductor y cuerpos grasos en los machos de *Lacerta monticola cantabrica*. Comparación entre dos poblaciones situadas a diferente altitud. *Amphibia-Reptilia* 11: 41-52.
- Braña F., Bea A. & Arrayago M.J. 1991. Egg retention in Lacertid lizards: relationships with reproductive ecology and the evolution of viviparity. *Herpetologica* 47: 218-226.

- Braña F., González F. & Barahona A. 1992. Relationship between ovarian and fat body weights during vitellogenesis for three species of lacertid lizards. *Journal of Herpetology* 26: 515-518.
- Branch B. 1998. *Field Guide to the Snakes and Other Reptiles of Southern Africa*. Third Ed. Struik, Cape Town.
- Broadley D.G. 1967. The life cycles of two sympatric species of *Ichnotropis* (Sauria: Lacertidae). *Zoologica Africana* 3: 1-2.
- Busack S.D. & Klostermann L.L. 1987. Reproduction in a Spanish population of *Acanthodactylus erythrurus*. *Annals of Carnegie Museum* 56: 97-102.
- Carretero M.A. 1992. Reintroduction of *Psammodromus hispanicus* in a coastal sand area of NE Spain, pp. 107-113. In: Korsos Z. & Kiss I. (eds). *Proceedings of the Sixth Ordinary General Meeting SEH Budapest*.
- Carretero M.A. 2004. From set menu to *à la carte*. Linking issues in trophic ecology of Mediterranean lacertids. *Italian Journal of Zoology* 74 (Suppl. 2): 121-133.
- Carretero M.A. & Llorente G.A. 1991. Reproducción de *Psammodromus hispanicus* en un arenal costero del nordeste ibérico. *Amphibia-Reptilia* 12 (4): 395-408.
- Carretero M.A. & Llorente G.A. 1993. Morfometría en una comunidad de lacértidos mediterráneos, y su relación con la ecología. *Historia Animalium* 2: 77-79.
- Carretero M.A. & Llorente G.A. 1995. Reproduction of *Acanthodactylus erythrurus* in its Northern boundary. *Russian Journal of Herpetology* 2 (1): 10-17.
- Carretero M.A. & Llorente G.A. 1997. Reproduction of *Psammodromus algirus* in coastal sandy areas of NE Spain. *Amphibia-Reptilia* 18: 369-382.
- Carretero M.A., Llorente G.A., Santos X. & Montori A. 1995. Características reproductoras de una población introducida de *Podarcis pityusensis*. *Revista Española de Herpetología* 9: 93-102.
- Carretero M.A. & Mateos J. 2002. Características reproductoras de *Psammodromus algirus* en un bosque termomediterráneo: una pieza más para el rompecabezas. Abstract book. VII Congreso Luso-Español, XI Congreso Español de Herpetología. Évora (Portugal).
- Carretero M.A., Ribeiro R., Barbosa D., Sá-Sousa P. & Harris D.J. 2006. Spermatogenesis in two Iberian *Podarcis* lizards: Relationships with male traits. *Animal Biology* 56 (1): 1-12.
- Carretero M.A., Roig J.M. & Llorente G.A. 2005. Variation in preferred body temperature in an oviparous population of *Lacerta (Zootoca) vivipara*. *Herpetological Journal* 15 (1): 51-55.
- Castanet J. & Báez M. 1988. Data on Age and Longevity in *Gallotia galloti* (Sauria, Lacertidae) Assessed by Skeletochronology. *Herpetological Journal* 1: 218-222.
- Castanet J. & Báez M. 1991. Adaptation and evolution in *Gallotia* lizards from the Canary Islands: age, growth, maturity and longevity. *Amphibia-Reptilia* 12: 81-102.

- Castilla A.M., Barbadillo L.J. & Bauwens D. 1992. Annual variation in reproductive traits in the lizard *Acanthodactylus erythrurus*. *Canadian Journal of Zoology* 70: 395-402.
- Castilla A.M. & Bauwens D. 1989. Reproductive characteristics of the lacertid lizard *Lacerta lepida*. *Amphibia-Reptilia* 10: 445-452.
- Castilla A.M. & Bauwens D. 2000a. Reproductive Characteristics of the Lacertid Lizard *Podarcis atrata*. *Copeia* 2000: 748-756.
- Castilla A.M. & Bauwens D. 2000b. Reproductive Characteristics of the Island Lacertid Lizard *Podarcis lilfordi*. *Journal of Herpetology* 34: 390-396.
- Castilla A.M. & Dunlap P. 2001. Rate of Infanticide by Adults in a Natural Population of the Insular Lizard, *Podarcis hispanica atrata*, p. 132. In: Vicente L. & Crespo E.G. (eds). *Mediterranean Basin Lacertid Lizards. A Biological Approach*. ICN, Lisboa.
- Derikson W.K. 1976. Lipid storage and utilization in reptiles. *American Zoologist* 16: 711-726.
- Díaz J.A., Pérez-Tris J., Tellería J.L., Carbonell R. & Santos T. 2005. Reproductive Investment of a Lacertid Lizard in Fragmented Habitat. *Conservation Biology*. 19: 1578-1585.
- Elbing K. 2001. *Die Smaragdeidechsen: zwei (un)gleiche Schwestern*. Bochum, Laurenti Verlag.
- Elvira B. & Vigal C.R. 1985. Further data on the reproduction of *Lacerta monticola cyreni* (Sauria, Lacertidae) in Central Spain. *Amphibia-Reptilia* 6: 173-179.
- Estes R. 1983. The fossil record and early distribution of lizards, pp 265-398. In: Rhodin A.G.J. & Miyata K. (eds). *Advances in Herpetology and Evolutionary Biology*. Cambridge, Massachusetts, Museum of Comparative Zoology.
- Etheridge K., Wit L.C., Sellers J.C. & Trauth S.E. 1986. Seasonal changes in reproductive condition and energy stores in *Cnemidophorus sexlineatus*. *Journal of Herpetology* 20: 554-559.
- Fitch H.S. 1970. *Reproductive Cycles of Lizards and Snakes*. Lawrence, The University of Kansas Museum of Natural History.
- Galán P. 1996a. Reproductive and fat body cycles of the lacertid lizard *Podarcis bocagei*. *Herpetological Journal* 6: 20-25.
- Galán P. 1996b. Sexual maturity in a population of the lacertid lizard *Podarcis bocagei*. *Herpetological Journal* 6: 87-93.
- Galán P. 1997. Reproductive ecology of the lacertid lizard *Podarcis bocagei*. *Ecography* 20: 197-209.
- Galán P. 2003. Reproductive Characteristics of an insular Population of the Lizard *Podarcis hispanica* from Northwest Spain (Cies Islands, Galicia). *Copeia* 2003: 657-665.

- Galán P. & Arribas O.J. 2005. Reproductive characteristics of the Pyrenean high-mountain lizards: *Iberolacerta aranica* (Arribas, 1993). *I. aurelioi* (Arribas, 1994) and *I. bonnali* (Lantz, 1927). *Animal Biology* 55 (2): 163-190
- Galán P. & Vicente L. 2003. Reproductive characteristics of the insular lacertid *Teira dugesii*. *Herpetological Journal* 13: 149-154.
- Gavaud J. 1991. Role of cryophase temperature and thermophase duration in thermoperiodic regulation of testicular cycle in the lizard *Lacerta vivipara*. *Journal of Experimental Zoology* 260: 239-246.
- Goldberg S.R. & Robinson M.D. 1979. Reproduction in two Namib Desert lacertid lizards (*Aporosaurus anchietae* and *Meroles cuneirostris*). *Herpetologica* 35 (2): 169-175.
- Gullberg A., Olsson M. & Tegelström H. 1997. Male mating success, reproductive success and multiple paternity in a natural population of sand lizards: behavioural and molecular genetics data. *Molecular Ecology* 6: 105-112.
- Harris D.J., Arnold E.N. & Thomas R.H. 1998. Relationships of the lacertid lizards (Reptilia: Lacertidae) estimated from mitochondrial DNA sequences and morphology. *Proceedings of the Royal Society of London (B)* 265: 1939-1948.
- Harris D.J., Batista V. & Carretero M.A. 2004. Assessment of genetic diversity within *Acanthodactylus erythrurus* (Reptilia: Lacertidae) in Morocco and the Iberian Peninsula using mitochondrial DNA sequence data. *Amphibia-Reptilia* 25 (2): 227-232.
- Heulin B., Oseneegg K. & Lebouvier M. 1991. Timing of embryonic development and birth dates in oviparous and viviparous strains of *Lacerta vivipara* using the predictions of an evolutionary hypothesis. *Acta-Oecologica* 12 (5): 517-528.
- Heulin B., Oseneegg K. & Michael D. 1994. Survie et incubation des oeufs dans deux populations ovipaires de *Lacerta vivipara*. *Amphibia-Reptilia* 15: 199-219.
- Huang W.S. 1998. Reproductive Cycles of the Grass Lizard, *Takydromus hsuehshanesis*, with Comments on Reproductive Patterns of Lizards from Central High Elevation Area of Taiwan. *Copeia* 1998 (4): 866-873.
- Hraoui-Bloquet S. 1985. Le cycle sexuel des mâles chez *Lacerta laevis* dans les montagnes du Liban. *Amphibia-Reptilia* 6: 217-227.
- Hraoui-Bloquet S. 1987. Le cycle sexuel des femelles chez *Lacerta laevis* Gray 1838 dans la montagne du Liban. *Amphibia-Reptilia* 8: 143-152.
- Hraoui-Bloquet S. & Bloquet G. 1988. Le cycle sexuel des mâles chez *Lacerta laevis* sur la côte du Liban et comparaison avec les lézards de montagne. *Amphibia-Reptilia* 9: 185-195.
- James C. & Shine R. 1985. The seasonal timing of reproduction: a tropical-temperate comparison in Australian lizards. *Oecologia (Berlin)* 67: 464-474.
- Ji X., Zhou W., Zhang X. & Gu H. 1998 Sexual dimorphism and reproduction in the grass lizard *Takydromus septentrionalis*. *Russian Journal of Herpetology* 5 (1): 44-48.

- Joly J. & Saint-Girons H. 1975. Influence de la température sur la vitesse de la spermatogenèse, la durée de l'activité spermatogénétique et l'évolution des caractères secondaires du lézard des murailles, *Lacerta muralis* L. (Reptilia, Lacertidae). Archives d'Anatomie microscopique 6 (4): 317-336.
- Laloi D., Richard M., Lecomte J., Massot M. & Clobert J. 2004. Multiple paternity in clutches of common lizard *Lacerta vivipara*: data from microsatellite markers. Molecular Ecology 13: 719-723.
- Llorente C. 1988. Contribución al conocimiento de la biología de una población de lagartija común (*Podarcis hispanica* Steindachner, 1870). Graduate Thesis, University of Barcelona.
- Marco A. & Pérez-Mellado V. 1998. Influence of Clutch Date on Egg and Hatchling Sizes in the Annual Clutch of *Lacerta schreiberi* (Sauria, Lacertidae). Copeia 1998 (1): 145-150.
- Marco A., Pérez-Mellado V. & Gil-Costa M.J. 1994. Reproductive strategy in a montane population of the lizard *Lacerta schreiberi* (Sauria: Lacertidae). Herpetological Journal 4: 49-55.
- Mateo J.A. & Castanet J. 1994. Reproductive strategies in three Spanish populations of ocellated lizards, *Lacerta lepida* (Sauria, Lacertidae). Acta Oecologica 15 (2): 215-229.
- Méndez de la Cruz F.R., Guillette L.J. Jr. & Villagran-Santa Cruz M.N. 1993. Differential atresia of ovarian follicles and its effect on the clutch size of two populations of the viviparous lizard *Sceloporus mucronatus*. Functional Ecology 7: 535-540.
- Moreira P.L. & Birkhead T.R. 2004a. Copulatory plug displacement and prologued copulation in the Iberian rock lizard (*Lacerta monticola*). Behavioral Ecology and Sociobiology 56: 290-297.
- Moreira P.L. & Birkhead T.R. 2004b. Copulatory plugs in the Iberian Rock Lizard do not prevent insemination by rival males. Functional Ecology 17: 796-802.
- Myers N., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A.B. & Kent J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853-858.
- Nkosi W.T., Heideman N.J.L. & Van Wyk J.H. 2004. Reproduction and Sexual Size Dimorphism in the lacertid Lizard *Pedioplanis burchelli* (Sauria: Lacertidae) in South Africa. Journal of Herpetology 38: 473-480.
- Nuland G.J. van & Strijbosch H. 1981. Annual Rhythmics of *Lacerta vivipara* Jacquin and *Lacerta agilis agilis* L. (Sauria, Lacertidae) in the Netherlands. Amphibia-Reptilia 2: 83-95.
- Olsson M., Gullberg A. & Tegelström H. 1996. Mate guarding in male sand lizards. Behaviour 133: 367-386.
- Olsson M., Gullberg A. & Tegelström H. 1997a. Sperm competition in the sand lizard, *Lacerta agilis*. Animal Behaviour 48: 193-200.

- Olsson M., Gullberg A., Tegelström H., Madsen T. & Shine R. 1994a. Promiscuous lizards: Females have more viable young. *Nature* 369: 528.
- Olsson M. & Madsen T. 1996. Cost of mating with infertile males selects for late emergence in female sand lizard (*Lacerta agilis* L.). *Copeia* 1996: 462-464.
- Olsson M., Madsen T. & Shine R. 1997b. Is sperm really so cheap? Costs of reproduction in male adders, *Vipera berus*. *Proceedings of the Royal Society of London, (B)* 264: 455-459.
- Olsson M., Madsen T., Shine R., Gullberg A. & Tegelström H. 1994b. Rewards of "promiscuity". *Nature* 372: 230.
- Olsson M. & Shine R. 1996. Does reproductive success increase with age or with size in the species with indeterminate growth? A case study using sand lizards (*Lacerta agilis*). *Oecologia* 105: 175-178.
- Olsson M. & Shine R. 1997. The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): why early clutches are better. *Journal of Evolutionary Biology* 10: 369-381.
- Olsson M. & Shine R. 2002. Growth to death in lizards. *Evolution* 56: 1867-1870.
- Pascual J.A. & Pérez-Mellado V. 1989. Datos sobre la reproducción y el crecimiento de *Psammotromus hispanicus* Fitzinger, 1826 en un medio adhesionado de la España Central. *Doñana, Acta Vertebrata* 16 (1): 45-55.
- Perera A. 2005. Autoecología de *Lacerta perspicillata*: efectos de la insularidad en un lacértido continental. PhD thesis, University of Salamanca.
- Perera A. & Pérez-Mellado V. 2002. Ausencia de plasticidad fenotípica en las estrategias reproductoras de la lagartija balear, *Podarcis lilfordi* (Squamata, Lacertidae). *Revista de Menorca* 86: 159-171.
- 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.
- Pérez-Mellado V., Valakos E.D., Guerrero F. & Gil-Costa M.J. 1993. Ecological similarity of lacertid lizards in the Mediterranean region. The case of *Ophisops elegans* and *Psammotromus hispanicus*, pp. 231-242. In: Valakos E.D., Böhme W., Pérez-Mellado V. & Maragou P. (eds). *Lacertids of the Mediterranean Region. A Biological approach*. Athens, Hellenic Zoological Society.
- Perry G. & Dmi'el R. 1994. Reproductive and population biology of the fringe-toed lizard, *Acanthodactylus scutellatus*, in Israel. *Journal of Arid Environments* 27: 257-263.
- Pollo C.J. & Pérez-Mellado V. 1990. Biología reproductora de tres especies mediterráneas de Lacertidae. *Mediterránea (Biología)* 12: 149-160.
- Roig J.M., Carretero M.A. & Llorente G.A. 2000. Reproductive cycle in a Pyrenean oviparous population of the common lizard (*Zootoca vivipara*). *Netherlands Journal of Zoology* 50 (1): 15-27.

- Roitberg E. & Smirina E. 2004. Geographic variation in sexual size dimorphism in the sand lizard, *Lacerta agilis*, p. 37. In: Corti C. & Lo Cascio P. (eds). Fifth International Symposium on the Lacertids, Lipari, Aeolian Islands, Sicily, Italy, 7-11 May 2004, Abstracts. Firenze, Firenze University Press.
- Rúa M. & Galán P. 2003. Reproductive characteristics of a lowland population of an alpine lizard: *Lacerta monticola* (Squamata, Lacertidae) in north-west Spain. *Animal Biology* 53: 347-366.
- Salvador A. 1987. Actividad del lagarto verdinegro (*Lacerta schreiberi*) (Sauria: Lacertidae). *Mediterránea (Biología)* 9: 41-56.
- Saint-Girons H. 1963. Spermatogenèse et évolution cyclique des caractères sexuels secondaires chez les Squamata. *Annales des Sciences Naturelles (Zoologie, 12^a Ser.)* 5: 461-476.
- Saint-Girons H. 1984. Les cycles sexuels des lézards mâles et leurs rapports avec le climat et les cycles reproducteur des femelles. *Annales des Sciences Naturelles (Zoologie)* 6: 221-243.
- Saint-Girons H. & Duguay R. 1970. Le cycle sexuel de *Lacerta muralis* L. en plaine et en montagne. *Bulletin du Muséum National d'Histoire Naturelle* 42: 609-625.
- Saint-Girons H. & Saint-Girons M.C. 1956. Cycle d'activité et thermorégulation chez les reptiles (Lézards et Serpents). *Vie et Milieu* 7: 133-226.
- Saint-Girons M.C. 1976. Relations interspécifiques et cycle d'activité chez *Lacerta viridis* et *Lacerta agilis* (Sauria, Lacertidae). *Vie et Milieu* 26 (1): 115-132.
- Santos X. & Llorente G.A. 2001. Seasonal variation in reproductive traits of the oviparous water snake, *Natrix maura*, in the Ebro Delta of Northeastern Spain. *Journal of Herpetology* 35: 653-660.
- Schleich H.H., Kästle W. & Kabisch K. 1996. Amphibians and reptiles of North Africa. Koenigstein, Koeltz.
- Seva E. 1982. Taxocenosis de lacértidos en un arenal costero alicantino. Ph.D. Thesis, University of Alicante.
- Shine R. 1983. Reptilian viviparity in cold climates: testing the assumptions of an evolutionary hypothesis. *Oecologia* 57: 397-408.
- Sinervo B. 1990. The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* 44: 279-294.
- Spawls S., Howell K., Drewes R. & Ashe J. 2002. A field guide to the reptiles of Eastern Africa. Academic Press, London.
- Stephens P.R. & Wiens J.J. 2003. Explaining Species Richness from Continents to Communities: The Time-for-Speciation Effect in Emydid Turtles. *The American Naturalist* 161 (1): 112-128.

- Szczerbak N.N. 2000. Guide to the reptiles of the Eastern Palearctic. Krieger, Melbourne, Florida.
- Telford S.R. 1997. The ecology of a symbiotic community. Volume 1: Population biology of the Japanese lizard *Takydromus tachydromoides* (Schlegel) (Lacertidae). Krieger, Melbourne, Florida.
- Tosini G., Bertollucci C. & Foa A. 2001. The circadian system of reptiles: a multioscillatory and multiphotoreceptive system. *Physiology and Behaviour* 72: 461-471.
- Uller T. & Olsson M. 2005. Multiple copulations in natural populations of lizards: evidence for the fertility assurance hypothesis. *Behaviour* 142: 45-56.