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Tail autotomy and extinction in Mediterranean lizards. A preliminary study of continental and insular populations

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(With 3 figures in the text)

Tail autotomy is one of the main anti-predator mechanisms of lacertid lizards, but it has been predicted that it is only retained in its full capacity when its benefits exceed its costs (Arnold, 1988). To test this hypothesis, ease of tail shedding was examined in a number of continental and insular lacertid lizard populations, each of which showed a different shedding capacity. Tails are shed more easily in those continental and insular populations where there is a greater probability of predation. In insular populations not subjected to strong predation, the tail tends to be retained. The relationship of these findings to insular Mediterranean lizard populations and to the extinction of the Balearic lizard, *Podarcis lilfordi* are discussed.

Introduction

The influence of predators as agents controlling abundance, mortality and population dynamics of their prey is widely recognized (Taylor, 1984). Tail autotomy is considered an important anti-predator mechanism in lacertid lizards because, in this family, it is rarely the result of intraspecific encounters (Arnold, 1988). Caudal autotomy also occurs in many other lizards, as well as some other lepidosaurians, some salamanders and a few rodents (Arnold, 1984, 1988 and references therein).

Ability to autotomize the tail is primitive in lizards and it is postulated that the mechanism is only retained in evolutionary time when its benefits exceed the costs (Arnold, 1988). Loss or reduction of autotomic capacity is frequent among lizards but has not been reported among lacertids. Costs of tail autotomy include those affecting reproduction, i.e. the energy of regeneration that is diverted from growth and reproductive effort (Dial & Fitzpatrick, 1981; Arnold, 1988). The loss of energy stored as fat in the tail and the effects on social status, thermoregulatory capacities and other natural history traits (see Congdon, Vitt & King, 1974; Vitt, Congdon & Dickson, 1977; Ballinger, Nietfeldt & Krupa, 1979; Dial & Fitzpatrick, 1981; Fox & Rostker, 1982; Arnold, 1984; Daniels, Flaherty & Simbotwe, 1986; Martín & Salvador, 1993*a*, *b* and *c*) are other potential costs of the autotomy. The other costs can be summarized (Formanowicz, Brodie & Bradley, 1990) as those derived from the subsequent inability to use the tail as an anti-predator mechanism and the reduction in escape speed (but see Daniels, 1983 and Brown, Taylor & Gist, 1995).

The ease of tail breakage varies widely at different times and in different individuals, ontogenic stages and taxa (Arnold, 1984, 1988 and references therein). Arnold (1988) stressed the importance of both historical and current selective factors influencing tail autotomy. Owing to this variability, we examine

TABLE I

Populations used in the study of tail autotomy

Species	Sample size	Population
Lacerta monticola	15	Circo de Gredos (Avila, Spain)
Psammodromus algirus	6	Linares de Riofrío (Salamanca, Spain)
Podarcis bocagei	24	Nava de Francia (Salamanca, Spain)
Podarcis milensis	10	Milos island (Greece)
Podarcis hispanica 1	20	Nava de Francia (Salamanca, Spain)
Podarcis hispanica 2	11	Benidorm island (Alicante, Spain)
Podarcis lilfordi	20	Nitge
Islets around Menorca	9	Aire
(Spain)	9	Colom
	4	Sargantana
	11	Addaya Gran
	8	Rovells
	8	Rei
Podarcis sicula	4	Stromboli
Aeolian archipelago	6	Llisca Bianca
(Italy)	6	Bottaro
	3	Panarea
Podarcis raffonei	13	Strombolicchio
Podarcis pityusensis	10	Ibiza Island (Spain)

differences in nine species from *Podarcis*, *Lacerta* and *Psammodromus* genera, inhabiting the Iberian Peninsula and some Mediterranean islands. Several species belong to the genus *Podarcis* and are closely related, so that differences encountered may be assumed to have evolved against similar genetic backgrounds.

Material and methods

Nine species of lacertid lizards were investigated. The origins of the populations used are indicated in Table I. The different sizes of the populations, as well as the fact that some are fully protected, meant that samples taken from them could not be equal. All experiments were performed within the body temperature (Tb) range of normally active animals (Pérez-Mellado, In press and pers. obs.). This avoided problems due to the potential thermal sensitivity of autotomic capacity (Quattrini, 1952).

In the past, ease of autotomy has been measured by attaching increasingly heavy weights to the tail (Quattrini, 1952). This is quite unlike what actually happens when a predator grasps a lizard (Arnold, 1984, 1988) and, although it is impossible to mimic such contact fully, a closer approximation to this event seems feasible. We consequently devised a simple procedure which avoided the attachment of weights to the tail. During each trial, a lizard was gently placed on a cork substratum so that its limbs could gain purchase and its tail was then grasped with a digital calliper, to simulate the bite of a predator. In order to apply comparable pressure in each trial, we measured the diameter of the tail at the point of contact and then closed the digital calliper around it until the initial movement was halved; pressure was then maintained for 15 seconds, or less if autotomy occurred.

''Economy of autotomy'' often occurs in lacertid lizards (Arnold, 1988), in that when the tail is autotomized, breakage occurs just anterior to the point of contact with the predator. Hence, in our experimental procedure, we ''bit'' the lizard at 3 points. First, 20 mm from the cloaca (the most ''expensive'', in terms of length lost), the second, if necessary, at 40 mm from the cloaca, and the third, at 60 mm from the cloaca. Thus, we were able to perform 3 different consecutive experiments on the same individual with a supposedly decreasing cost of tail shedding and, conversely, increasing probability of tail breakage.

After autotomy, the tail of lacertids commonly continues to move as in many other lizards (Arnold, 1984, 1988).

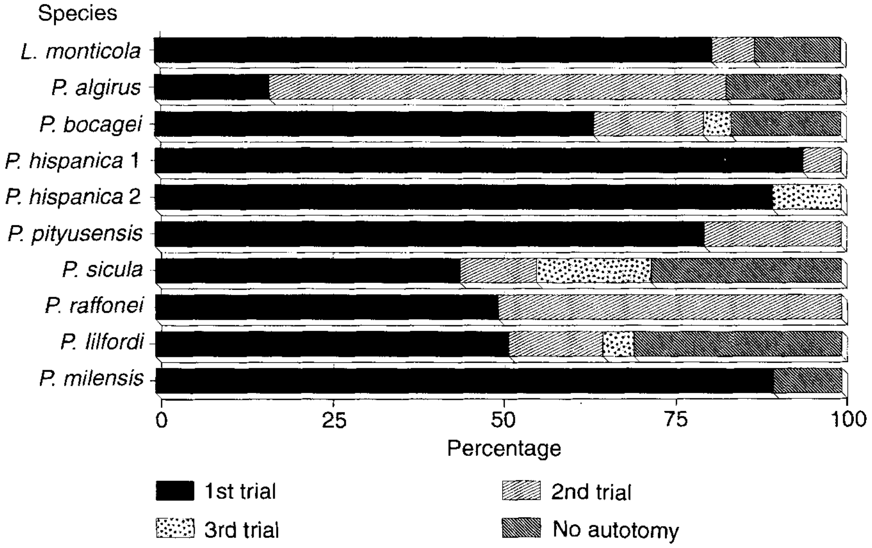

FIG. 1. Percentage of autotomized and non-autotomized individuals in three trials of the nine species under study.

This appears to distract the attention of the predator away from the body (Vitt & Cooper, 1986) and it has been experimentally demonstrated that predators are more attracted by thrashing rather than exhausted and immobile tails (Dial & Fitzpatrick, 1983). Hence, we measured the duration of tail movement after autotomy.

To avoid the effect of potential changes in autotomic capacity during ontogeny (Arnold, 1988), we used only

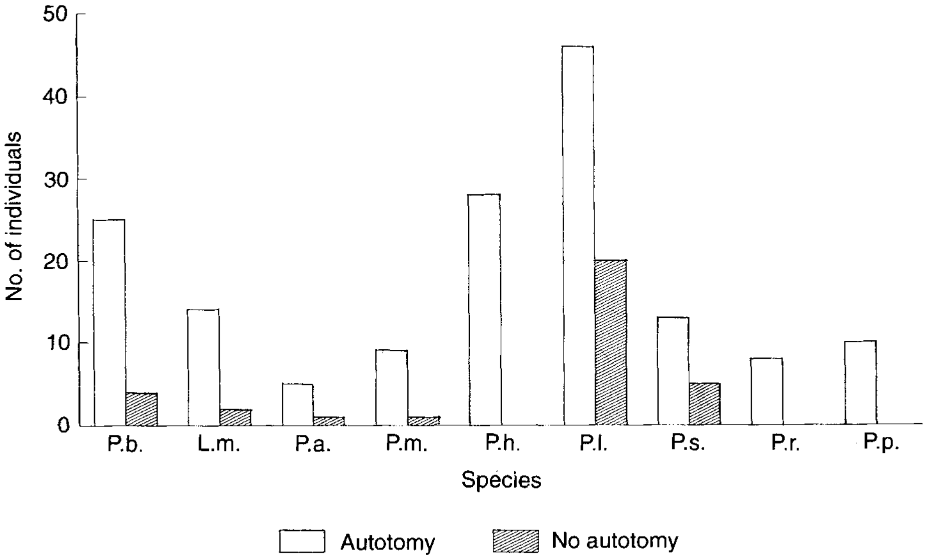

FIG. 2. Proportion of autotomized tails in the nine species under study (P.b.: *Podarcis bocagei*, L.m.: *Lacerta monticola*, P.a.: *Psammodromus algirus*, P.m.: *Podarcis milensis*, P.h.: *Podarcis hispanica*, P.l.: *Podarcis lilfordi*, P.s.: *Podarcis sicula*, P.r.: *Podarcis raffonei*, P.p.: *Podarcis pityusensis*.

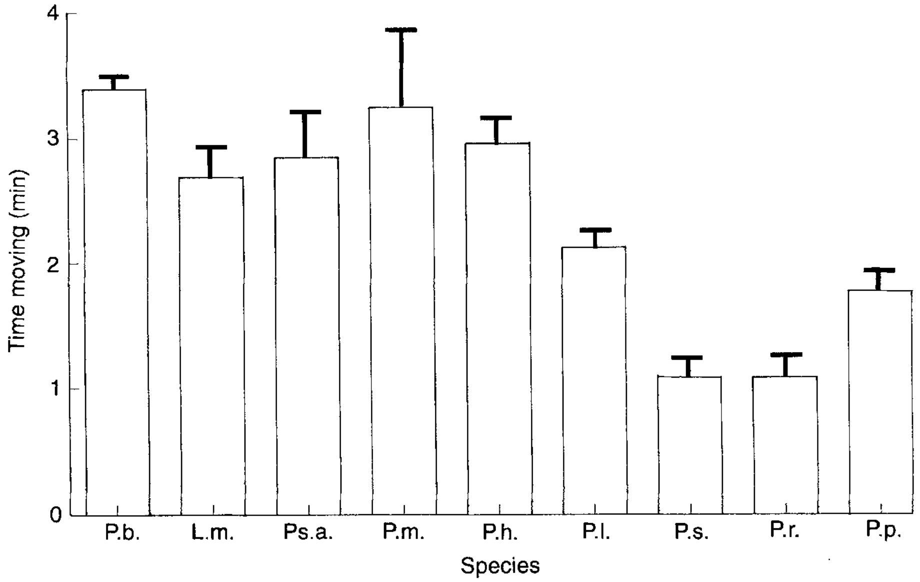

FIG. 3. Average time of tail movement after autotomy in the nine species under study.

adult individuals of each species. Our intention was to use only adult males in order to obviate any sexual effect on tail shedding, but, in some very small populations, it was impossible to obtain an adequate sample of adult males with intact tails.

It might be argued that the experimental procedure was imperfect because some factors present in a real predatory encounter, such as chemical and other sensory clues emanating from the predator, which might have elicited a higher response rate, are absent. However, this does not invalidate the relative value of the experiment as any bias from such causes is likely to be similar for all species involved.

Results

The restricted availability of animals from many of the Balearic Islands (see Table I), precluded an analysis of interpopulation differences. Hence, in analyses between species, the data from *Podarcis lilfordi* populations were pooled. Also pooled into single samples were the data for *Podarcis sicula* and for *Podarcis raffonei* from the Aeolian islands where again no interpopulation analysis was performed, due to the small sample size from some of the islets (Table I).

When all samples are considered, there is a significant difference in the frequency of autotomized tails between species (G-test, $G = 26.34$, $P < 0.05$). However, this significance disappears when *P. lilfordi* ($G = 14.94$, $P > 0.05$) or *Podarcis hispanica* ($G = 14.75$, $P > 0.05$) were excluded from the analysis. Thus, only excluding one of these two species, we obtained a non-significant subset (Sokal & Rohlf, 1981). This result indicates that statistical differences are due to the lowest (*P. lilfordi*) and highest (*P. hispanica*) frequencies of autotomized tails included in the analyses (Figs 1 and 2). Hence, there is no difference in the frequency of autotomized tails between continental species and the insular *Podarcis pityusensis* and *Podarcis milensis*.

The interspecies analysis of tail wiggling duration revealed a shorter duration in the four insular species: *P. lilfordi*, *P. sicula*, *P. raffonei* and *P. pityusensis* than in the continental ones (see Fig. 3, one-way ANOVA of log-transformed data, $F = 13.42$, $P < 0.001$).

The Duncan *a posteriori* test indicated that these four insular species form a homogeneous group, statistically differentiated from *Podarcis milensis* and the continental species: *Lacerta monticola*, *Psammodromus algirus*, *Podarcis bocagei* and *Podarcis hispanica*.

These results are only partially consistent with our prediction of a shorter time in populations with a lower predation pressure but, in any case, show that in situations of higher predation pressure the higher ease of tail autotomy is accompanied by a longer time of tail moving.

Discussion

From our data, it is clear that a reduction in the proportion of autotomized tails was present in *Podarcis lilfordi* from the Menorca islets and, to a lesser extent, in *Podarcis sicula* from the Aeolian Islands. These insular populations are subject to little or no predation pressure. Present day populations of *P. lilfordi* inhabiting the small islets around the main island of Menorca are almost entirely free from terrestrial predators and, until recent times, presumably also from birds, because there are no small birds of prey reported from the fossil record of Menorca (Alcover, Moyá-Solá & Pons-Moyá, 1981; Mayol, 1985; Salvador, 1986; Pérez-Mellado, 1989). This situation was maintained from the end of the Pliocene through the Pleistocene, up to the arrival of humans and, in some cases, to the present day (see below), hence long before the isolation of islets and extinction of lizards inhabiting the main islands of Mallorca and Menorca.

The other Balearic species, *Podarcis pityusensis*, shows a tail-shedding capacity similar to that of the continental species. On Ibiza island it is subject to heavy predation by the genet (30% of whose diet consists of this lizard [Delibes, 1977; Alcover, 1984]) as well as by feral cats and small birds of prey (Pérez-Mellado, pers. obs.). There, *P. pityusensis* has retained its full capacity to shed the tail.

We lack detailed information on populations of *P. sicula* of the Aeolian Islands, but there may be a significant lack of pressure from terrestrial predators here too (Lo Cascio & Pancioli, unpubl. data). In any case, further experiments are necessary to assess the extent of reduction in tail-shedding capacity and potential interpopulational differences. This may be an insular situation where predation pressure is low, and where the tail is particularly important as a counterpoise during locomotion (Arnold, 1984, 1988), so the tail is even more likely to be retained. According to Arnold (1988), maximum speed is substantially reduced after tail breakage in *P. sicula*.

In *P. raffonei*, no reduction of ability to autotomize the tail seems to have taken place, possibly indicating that predation pressure may have been continuous on the populations studied: or else, despite a lack of predation pressure on islets as small as Strombolicchio, due to an isolation time too short to build up a selective retention of tail. The origin of the Aeolian Archipelago dates from the Pleistocene (Capula, 1994 and references therein). Also, there may be an absence of a selective pressure towards tail retention (see below). The population density on Strombolicchio is much lower than in the Balearic islets (Capula, 1994 and Pérez-Mellado *et al.*, pers. obs.) and the isolation of this islet from Stromboli took place in recent times, just prior to the supposed extinction of *P. raffonei* on Stromboli, either as the result of competition with *P. sicula* (Capula, 1994), or through an increase in predation, or both.

Podarcis milensis inhabits the island of Milos where several terrestrial predators, autochthonous or introduced, are present, including the blunt-nosed viper, *Vipera lebetina schweizeri* (see, for example, Grüber, 1989), and where lizards are one of the most important prey items for juvenile individuals (Bruno & Maugeri, 1990). Thus, predation pressure is likely to be similar or even higher than in continental situations.

In continental species, minor differences appeared between the species studied but, generally, all of them fit well the prediction of a full tail shedding capacity, in close connection with the high predation pressure to which they are subject. Predatory species extremely common at locations of capture include such saurophagous specialists as the smooth snake, *Coronella austriaca,* for *Lacerta monticola*, and *Coronella girondica* for *P. hispanica*, *P. bocagei* and *Psammodromus algirus* (Pérez-Mellado, In press and pers. obs.).

Significant differences among species also occurred in the duration of time of movement after autotomy, with shorter times in *P. lilfordi*, *P. sicula*, *P. raffonei* and *P. pityusensis* than in continental species. These results are consistent with the postulated importance of this postautotomic movement in escape from predators (Dial & Fitzpatrick, 1983).

Regarding the facility of autotomy in relation to position of the experimental bite, our results indicated that autotomy occurred during the first trial in more than 75% of cases in some species of easier autotomy such as *Lacerta monticola*, *P. hispanica*, *P. pityusensis* and *P. milensis*. However, other results are difficult to interpret, as in *Psammodromus algirus*, with a higher proportion of autotomized tails during the second trial. It is clear that we need more information to address the ''economy of autotomy''.

The reduction of autotomic capacity is a common phenomenon in several reptiles and amphibians. For example, in gekkonid lizards it is reported as a result of increased importance of the tail during locomotion in ground-dwelling species (Werner, 1968), or in species employing the tail for camouflage (Wellborn, 1933; Cott, 1957, see a revision in Arnold, 1994).

Ducey, Brodie & Baness (1993) report a similar ''relaxed selection'' for tail autotomy in the urodelan amphibian, *Bolitoglossa subpalmata*, from some mountain areas lacking predation pressure by snakes. Also Arnold (1988, and references therein) mentions loss of autotomic capacity, even during ontogeny, in lizards inhabiting small islands with a low or absent predation pressure.

Our preliminary results also agree with some suggestions made by Arnold (1994) regarding the loss of autotomic capacity in lizards. This author pointed out that the balance between costs and benefits of autotomy is at the centre of evolutionary losses of autotomic capacity in several lineages of lizards. At least in these insular populations, the partial reduction of autotomic capacity seems to be linked to a reduction or absence in predation pressure over several thousand years.

Caudal fat deposits are important in many lizard species (Arnold, 1988 and references therein). Thus, the loss of the tail can affect survivorship of individuals during periods of low food availability (Bauwens, 1981; Daniels, 1985). It has been proposed that the reduction of autotomic capacity in some gekkonid lizards is linked to the value of the tail as a fat deposit (Waite, 1929; Holder, 1960).

Small Mediterranean islands are characterized by very low food availability over long periods (see, for example, Brown & Pérez-Mellado, 1994). Hence, there is a strong selective advantage in storing fat in the tail and retaining it in these populations where, indeed, the density of lizards is normally very high (Pérez-Mellado, 1989; Brown *et al.*, 1992; Brown & Pérez-Mellado, 1994). Furthermore, some anecdotal observations indicate that the morphology of the tail in some microinsular populations of *P. lilfordi* changes to a more bottle-like shape, allowing a higher capacity for fat accumulation (Salvador, pers. comm. and Pérez-Mellado, unpubl. data).

The consumption of conspecific tails has been reported in some insular lizards of the Mediterranean basin (see Kammerer, 1926 for *Podarcis melisellensis*; Mertens, 1926 for *Podarcis filfolensis*; Ouboter, 1981 for *Podarcis sicula* or Salvador, 1976 for *Podarcis lilfordi*) and, even if it is an uncommon behaviour among the majority of lacertid lizards (Arnold, 1988), it is considered as a very common phenomenon in *Podarcis lilfordi* (Salvador, 1986). Arnold (1984, 1988) pointed out that individuals of *P*. *lilfordi* living in captivity often pull the tails of other lizards, including conspecifics, a common behaviour among other insular members of the genus *Podarcis* (Pérez-Mellado, unpubl. obs.). The observation of tails from other individuals inside the digestive tracts of lizards is quite common in Balearic populations (Salvador, 1976, 1986 and pers. comm.). Thus, a lizard can enhance both its survival probability and reproductive success (Vitt & Cooper, 1986), using as energy resources other individuals of the same population.

In this scenario, we could expect an increasing tendency towards tail retention, providing that there is an absence of selective pressure for autotomy (i.e. predation) and the presence of a selective pressure against autotomy (the loss of energy resources). We can speculate that this tendency took place on the main islands of Mallorca and Menorca in the Balearics, during the post-Messinian period in which these islands were devoid of small terrestrial predators specialized in the capture of lizards, as well as small diurnal raptors (see, for example, Kotsakis, 1981; Alcover *et al.*, 1981).

During the Holocene, the arrival of Man and the introduction of such exotic predators as *Mustela nivalis*, feral cats and snakes (*Macroprotodon cucullatus* and *Elaphe scalaris* in Menorca) occurred on islands inhabited by lizards partially lacking one of their most important anti-predator devices. Similar effects were recorded following the introduction of small carnivores in the Caribbean Islands (Iverson, 1978) and also in Mauritius, Rèunion and Rodrigues in the Indian Ocean.

Previous explanations about the extinction of *P. lilfordi* in Menorca and Mallorca assumed an unrealistic strong predation effect on these big populations over hundreds of square kilometres (Mertens, 1957; see also Alcover & McMinn, 1994 for a review). It is unlikely that a predator can cause such a complete extinction if current anti-predator mechanisms are still working. Thus, we propose that the extinction of Balearic lizards in Mallorca and Menorca took place because of this high predation intensity and the partial loss of their autotomic capacity.

According to Greene (1988), the importance of birds and mammals, as visually guided predators, in shaping the anti-predator mechanisms of reptiles could be higher than the role of snakes, which rely more on chemical cues to locate prey (see, for example, Burghardt, 1971). However, in the Balearic islands the situation could be different because the evolution of lizard populations took place in the absence of snakes and many other continental predators. Thus, the introduction of even one terrestrial predator could be enough to lead to the extinction of an entire lizard population. In fact, Greene (1988) recognized that many snakes and mammal species feed on the most abundant reptile taxa. Hence, we can imagine the rapid destruction by the newcomers, imported by humans to the Balearic islands during the Holocene, of the abundant and vulnerable lizards.

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REFERENCES

Alcover, J. A. (1984). Über die Nahrung der Ginsterkatze *Genetta genetta* (Linnaeus, 1758) auf den Inseln Mallorca, Ibiza und Cabrera. *Säugetierkd. Mitt.* **31:** 189–195.

Alcover, J. A. & McMinn, M. (1994). Predators of vertebrates on islands. *BioScience* **44**(1): 12–18.

Alcover, J. A., Moyá-Solá, S. & Pons-Moyá, J. (1981). *Les Quimeres del Passat. Els vertebrats fossils del Plio-Quaternari de les Balears i Pitiüses. Monogr. Cient.* **1.** Ciutat de Mallorca: Editorial Moll.

Arnold, E. N. (1984). Evolutionary aspects of tail shedding in lizards and their relatives. *J. Nat. Hist.* **18:** 127–169.

Arnold, E. N. (1988). Caudal autotomy as a defense. In *Biology of the Reptilia* **16**, *Ecology B*: *Defense and life history*: 235–273. Gans, C. & Huey, R. B. (Eds). New York: Alan R. Liss.

Arnold, E. N. (1994). Investigating the evolutionary effects of one feature on another: does muscle spread suppress caudal autotomy in lizards? *J. Zool. (Lond.)* **232:** 505–523.

Ballinger, R. E., Nietfeldt, J. W. & Krupa, J. J. (1979). An experimental analysis of the role of the tail in attaining high running speed in *Cnemidophorus sexlineatus* (Reptilia: Squamata: Lacertilia). *Herpetologica* **35**(2): 114–116.

Bauwens, D. (1981). Survivorship during hibernation in the European Common lizard, *Lacerta vivipara*. *Copeia* **1981:** 741–744.

Brown, R. M., Taylor, D. H. & Gist, D. H. (1995). Effect of caudal autotomy on locomotor performance of wall lizards (*Podarcis muralis*). *J. Herpetol.* **29**(1): 98–105.

Brown, R. P. & Pérez-Mellado, V. (1994). Ecological energetics and food acquisition in dense Menorcan islet populations of the lizard *Podarcis lilfordi*. *Funct. Ecol.* **8:** 427–434.

Brown, R. P., Pérez-Mellado, V., Diego-Rasilla, J., García, J. A., Naranjo, A. & Speakman, J. R. (1992). Individual and population energetics of a lizard on a Mediterranean islet. *Oecologia (Berl.)* **91:** 500–504.

Bruno, S. & Maugeri, S. (1990). *Serpenti d'Italia e d'Europa*. Milano: Giorgio Mondadori & Associati Editore.

Burghardt, G. M. (1971). Chemical-cue preferences of newborn snakes: influence of prenatal maternal experience. *Science (Washington DC)* **171:** 921–923.

Capula, M. (1994). Genetic variation and differentiation in the lizard, *Podarcis wagleriana* (Reptilia: Lacertidae). *Biol. J. Linn. Soc.* **52:** 177–196.

Congdon, J. D, Vitt, L. J & King, W. W. (1974). Geckos: Adaptive significance and energetics of tail autotomy. *Science (Washington DC)* **184:** 1379–1380.

Cott, H. B. (1957). *Adaptative coloration in animals*. London: Methuen.

Daniels, C. B. (1983). Running: an escape strategy enhanced by autotomy. *Herpetologica* **39:** 162–165.

Daniels, C. B. (1985). The effect of tail autotomy on the exercise capacity of the water skink, *Sphenomorphus quoyii*. *Copeia* **1985**(4): 1074–1076.

Daniels, C. B., Flaherty, S. P. & Simbotwe, M. P. (1986). Tail size and effectiveness of autotomy in a lizard. *J. Herpetol.* **20**(1): 93–95.

Delibes, M. (1977). Sobre las ginetas de la Isla de Ibiza (*Genetta genetta isabelae* n. ssp.). *Doñana Acta Vertebr.* **4:** 139–160.

Dial, B. E. & Fitzpatrick, L. C. (1981). The energetic costs of tail autotomy to reproduction in the lizard *Coleonyx brevis* (Sauria: Gekkonidae). *Oecologia (Berl.)* **51:** 310–317.

Dial, B. E. & Fitzpatrick, L. C. (1983). Lizard tail autotomy: function and energetics of postautotomy movement in *Scincella lateralis*. *Science (Washington DC)* **219:** 391–392.

Ducey, P. K., Brodie, E. D. & Baness, E. A. (1993). Salamander tail autotomy and snake predation. Role of antipredator behavior and toxicity for 3 Neotropical *Bolitoglossa* (Caudata, Plethodontidae). *Biotropica* **253:** 344–349.

Formanowicz, D. R., Brodie, E. D. & Bradley, P. J. (1990). Behavioural compensation for tail loss in the ground skink, *Scincella lateralis*. *Anim. Behav.* **40**(4): 782–784.

Fox, S. F. & Rostker, M. A. (1982). Social cost of tail loss in *Uta stansburiana*. *Science (Washington DC)* **218:** 692–693.

Greene, H. W. (1988). Antipredator mechanisms in reptiles. In *Biology of the Reptilia 16, Ecology B: Defense and life history*: 1–152. Gans, C. & Huey, R. B. (Eds). New York: Alan R. Liss.

Grüber, U. (1989). *Die Schlangen Europas und Rund ums Mittelmeer*. Stuttgart: Frackh-Kosmos Verlags-GmbH & Co.

Holder, L. A. (1960). The comparative morphology of the axial skeleton in the Australian Gekkonidae. *J. Linn. Soc. Lond.* **44:** 300–335.

Iverson, J. B. (1978). The impact of feral cats and dogs on populations of the West Indian iguana, *Cyclura carinata*. *Biol. Conserv.* **14:** 63–73.

Kammerer, P. (1926). *Der Artenwandel auf Inseln und seine Ursachen, ermittelt durch vergleich und versuch an den Eidechsen der dalmatinischen Eilande*. Wien und Leipzig.

Kotsakis, T. (1981). Le lucertole (Lacertidae, Squamata) del Pliocene, Pleistocene e Olocene delle Baleari. *Bolletí Soc. Hist. Nat. Balears* **25:** 135–150.

Martín, J. & Salvador, A. (1993*a*). Thermoregulatory behaviour of rock lizards in response to tail loss. *Behaviour* **124**(1–2): 123–136.

Martín, J. & Salvador, A. (1993*b*). Tail loss reduces mating success in the Iberian rock-lizard, *Lacerta monticola*. *Behav. Ecol. Sociobiol.* **32**(3): 185–189.

Martín, J. & Salvador, A. (1993*c*). Tail loss and foraging tactics of the Iberian rock-lizard, *Lacerta monticola*. *Oikos* **66:** 318–324.

Mayol, J. (1985). *Rèptils i Amfibis de les Balears*. Palma de Mallorca: Editorial Moll.

Mertens, R. (1926). Zoologische Ergebnisse einer Reise nach den Pelagischen Inseln und Sizilien. *Senckenb. Biol.* **8**(5/6): 225–259.

Mertens, R. (1957). Mallorca: ein herpetogeographisches Problem. *Zool. Beitr.* **3:** 1–16.

Ouboter, P. E. (1981). The ecology of the island lizard *Podarcis sicula salfii*: correlation of microdistribution with vegetation coverage, thermal environment and food size. *Amphib-Reptilia* **2:** 243–257.

Pérez-Mellado, V. (1989). Estudio ecológico de la lagartija balear *Podarcis lilfordi* (Günther, 1874) en Menorca. *Rev. Menorca* **53:** 455–511.

Pérez-Mellado, V. (In press). Familia Lacertidae. In *Fauna Ibérica. Reptiles.* Madrid: Museo Nacional de Ciencias Naturales. C.S.I.C.

Quattrini, D. (1952). Richerche anatomiche e sperimentali sulla autotomia della coda lucertole. I. Dinamica dell'anatomia e conseguenza nel tegumento (Osservazioni nella *Lacerta sicula sicula* Raf.). *Arch. zool. ital.* **37:** 131–170.

Salvador, A. (1976). *La Alimentación de los reptiles de Cabrera.* Degree thesis, University of Madrid.

Salvador, A. (1986). *Podarcis lilfordi* (GUNTHER, 1874)—Balearen-Eidechse. In *Handbuch der Amphibien und Reptilien Europas* **III** *(Podarcis)*: 83–110. Böhme, W. (Ed.). Wiesbaden: Akademische Verlagschaft.

Sokal, R. R. & Rohlf, R. (1981). *Biometry.* San Francisco: W. H. Freeman & Co.

Taylor, R. J. (1984). *Predation.* New York: Chapman & Hall.

Vitt, L. J., Congdon, J. D. & Dickson, N. A. (1977). Adaptive strategies and energetics of tail autotomy in lizards. *Ecology* **58:** 326–337.

Vitt, L. J. & Cooper, W. E. (1986). Tail loss, tail color, and predator escape in *Eumeces* (Lacertilia, Scincidae): age-specific differences in costs and benefits. *Can. J. Zool.* **64:** 583–592.

Waite, E. R. (1929). *The reptiles and amphibians of South Australia.* Adelaide: British Science Guild (South Australian Branch).

Wellborn, V. (1933). Vergleichende osteologische Untersuchungen an Gekkoniden, Eublephariden und Uroplatiden. *Sitzungsber. Ges. Naturforsch. Freunde Berl. N.F.* **1933:** 126–199.

Werner, Y. L. (1968). Regeneration frequencies in geckoes of two ecological types (Reptilia: Gekkonidae). *Vie Milieu* **19:** 199–222.