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TAIL SHEDDING IN ISLAND LIZARDS [LACERTIDAE, REPTILIA]: DECLINE OF ANTIPREDATOR DEFENSES IN RELAXED PREDATION ENVIRONMENTS

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The ability of an animal to shed its tail is a widespread antipredator strategy among lizards. The degree of expression of this defense is expected to be shaped by prevailing environmental conditions including local predation pressure. We test these hypotheses by comparing several aspects of caudal autotomy in 15 Mediterranean lizard taxa existing across a swath of mainland and island localities that differ in the number and identity of predator species present. Autotomic ease varied substantially among the study populations, in a pattern that is best explained by the presence of vipers. Neither insularity nor the presence of other types of predators explain the observed autotomy rates. Final concentration of accumulated tail muscle lactate and duration of movement of a shed tail, two traits that were previously thought to relate to predation pressure, are in general not shaped by either predator diversity or insularity. Under conditions of relaxed predation selection, an uncoupling of different aspects of caudal autotomy exists, with some elements (ease of autotomy) declining faster than others (duration of movement, lactate concentration). We compared rates of shed tails in the field against rates of laboratory autotomies conducted under standardized conditions and found very high correlation values ($r > 0.96$). This suggests that field autotomy rates, rather than being a metric of predatory attacks, merely reflect the innate predisposition of a taxon to shed its tail.

KEY WORDS: **Evolutionary physiology, insularity, predation, tail autotomy.**

Caudal autotomy, the self-induced breakage of an animal's tail, is considered a close-range, last line antipredator mechanism used when other more low-cost tactics, such as escape or crypsis, become ineffective (Bellairs and Bryant 1985; Arnold 1988). The ability to shed their tail is widespread among lizards, suggesting that this is an ancestral trait in the group (Arnold 1984). Ease of autotomy varies substantially between lizard families; although some groups (e.g., agamids, varanids) have little or no ability to shed their tail, even when it is grasped directly and subjected to great forces (Arnold 1984; McConnachie and Whiting 2003), others appear to be able to do so easily, even in the absence of substantial contact with a predator (Arnold 1984). The shed, and sometimes conspicuously colored, tail thrashes vigorously drawing predator attention away from the escaping lizard (Vitt et al. 1977; Daniels et al. 1986). If grasped by the predator, its violent movements increase handling time, thus providing additional opportunity to escape (Dial and Fitzpatrick 1983; Medel et al. 1988). The high numbers of autotomized tails—but not lizards—found in predator stomachs (Pianka 1969; Arnold 1988), as well as field observations (Haacke 2005) and staged predation encounters (Congdon et al. 1974; Dial and Fitzpatrick, 1981), all indicate that this is a highly effective antipredator strategy.

Caudal autotomy does, however, also carry a series of important and potentially lifelong costs. Although overall cost apparently varies between different taxa (Chapple and Swain 2004; Lin and Ji 2005), a number of studies have demonstrated that autotomy impairs locomotor capacity (Punzo 1982; Brown et al. 1995; Martin and Avery 1998; Chapple and Swain 2002a; Lin et al. 2006), decreases reproductive output (Dial and Fitzpatrick 1981; Vitt and Cooper 1986; Wilson and Booth 1998), lowers social status (Fox and Rostker 1982; Schall et al. 1989; Fox et al. 1990; Salvador et al. 1995), and impacts activity levels (Formanowicz et al. 1990; Martin and Salvador 1995), as well as growth rates (Smith 1996; Niewiarowski et al. 1997). Individuals of species that accumulate energetic reserves in the form of caudal fat experience reduced viability upon loss of their tails (Ballinger and Tinkle 1979; Vitt and Cooper 1986; Fox and McCoy 2000). Finally, tailless individuals are more vulnerable to subsequent predation events (Dial and Fitzpatrick 1984; Wilson 1992; Downes and Shine 2001), in part because regenerated tails may not autotomize as effectively as intact ones (Arnold 1988).

Because tail loss is costly and may be triggered accidentally during nonpredation events (Vitt et al. 1977; Matuschka and Bannert 1987), ease of autotomy in each species should reflect the relative importance of benefits gained versus costs incurred. In particular, it is expected that the degree of expression of this strategy should be related to the local predation environment (Downes and Adams 2001). It has thus been suggested that the reduced rates of autotomy observed in island lizards can be attributed to relaxed predation pressures generally prevailing in insular ecosystems (Curio 1976; Arnold 1984; 1988, Blazquez et al. 1997; Pérez-Mellado et al. 1997; Cooper et al. 2004). For example, populations of *Podarcis* lizards found on small islets in the Balearics have lower rates of autotomy than lizards on larger islands or the mainland (Pérez-Mellado et al. 1997; Cooper et al. 2004). Nevertheless, it is not clear whether it is changes in predator communities or some other characteristic of the island environment that is responsible for these changes in the expression of antipredator strategy (Brodie et al. 2002). For example, it is possible that lack of gene flow and resulting drift (which can limit adaptive evolution) underlie the decline of antipredator defenses in small, isolated island populations. Alternatively, unpredictability of food resources in island environments may decrease tail-shedding predisposition as a means to preserve valuable caudal fat deposits (Ballinger and Tinkle 1979; Vitt and Cooper 1986; Fox and McCoy 2000). Here we compare a diversity of island and mainland taxa in regard to their predisposition to autotomize their tails. Because all taxa originated in a predator-rich mainland environment this study provides the opportunity to examine how predator defenses are lost under different degrees of predation relaxation.

Because individual predator species differ greatly in their specialization and hunting efficiency and ultimately in their impact on the prey population, an index like total predator diversity is only a relatively rough metric of true predation pressure (Medel et al. 1988). For example, it is possible that a single common specialized predator species is more important than a group of other, nonspecialized or rare predators. Thus, beyond total predator diversity, we also investigate separately the two main subcategories of predators: aerial raptors and saurophagous snakes. Because of differences in their hunting strategy, abundance, and dietary preferences, these are likely to have very different impacts on lizard populations. Lastly, we also test the hypothesis that the presence of viperid snakes influences lizard tail-shedding ability. Vipers in the Mediterranean in general, and the Aegean region in particular, are considered to have the most severe impact on lizard populations both because of their high density and dietary specialization (Saint Girons 1980; Bea et al. 1992; Luiselli 1996; Santos et al. 2007).

Rates of autotomized tails observed in field populations reflect a combination of factors, including the taxon-specific facility for autotomy, and composition of sympatric predator communities. Field autotomy rates have been used as an index of predation pressure (Pianka 1970; Turner et al. 1982). However, other authors have criticized this use, largely because predator efficiency has been shown to complicate this relationship (Medel et al. 1988; Schoener 1979). Hence, lizard populations exposed to highly efficient predators may actually have lower rates of autotomized tails than others exposed to inefficient predators. Looking beyond predation alone, sex ratio, density, and type of aggressive social interactions in a population can confound the interpretation of field autotomy rates. Similarly, because the probability of a tail having been autotomized increases over an animal's lifetime, the overall fraction of shed tails observed in the field can be biased by the average age of the individuals in the population. For example the existence of very high predation levels can result in a young lizard population with comparatively low levels of autotomy. Although the ecological significance of autotomy rates has been debated extensively (Schoener 1979; Schall and Pianka 1980), the issue remains unresolved and has never been tested in a rigorous manner. Performing standardized predation simulation trials that induce autotomy under controlled laboratory conditions can help circumvent many of these potential problems (Quattrini 1952; Fox et al. 1994; Pérez-Mellado et al. 1997). Here we use this experimental approach to elucidate the relative importance of exogenous versus endogenous factors in shaping field autotomy rates.

Caudal autotomy constitutes a complex antipredator strategy that consists of at least two functionally distinct quantifiable components: ease of autotomy and duration of movement of the shed tail. Because longer and more vigorous tail movements increase handling time by predators (Dial and Fitzpatrick 1983), this defense feature is likely to be particularly well developed in high-predation environments (Cooper et al. 2004). Observing that anaerobically powered tail thrashing ceases when muscle lactate exceeds certain concentrations, Dial and Fitzpatrick (1983) argued that species that use autotomy as a principal defense mechanism should also tolerate higher lactate levels before tail thrashing comes to a standstill. Consequently, it would be expected that selection will drive lizard populations that are subject to heavier predation pressure to not only exhibit longer movement times but to also evolve tolerance of higher final lactate levels in shed, exhausted tails.

Here we take advantage of the pronounced differences in the composition of sympatric predator communities for 15 lacertid lizard taxa existing on the mainland versus Pleistocene or pre-Pleistocene island sites, to examine the erosion of antipredator mechanisms under relaxed predation selection pressure. The use of a substantial number of taxa and the combination of conventional and phylogenetically informed statistical analyses permit a more comprehensive investigation of the diverse physiological components of caudal autotomy.

This study has four principal aims. First, to determine whether rates of tails shed in the field reflect differences in intrinsic autotomic predisposition, or whether they are primarily shaped by external factors like predation. Second, to test if various aspects of autotomy (ease of shedding, duration of thrashing, final lactate concentrations) differ between taxa that have evolved in mainland, as opposed to Pleistocene or pre-Pleistocene island settings. Third, to test the hypotheses that predation pressure affects these aspects, and if so, whether certain types of predators (e.g., vipers) are more important. Fourth, to evaluate the relationships between the above-mentioned aspects of autotomy to determine if they evolve in tandem or whether they are functionally independent.

Materials and Methods

SPECIES USED AND STUDY SITES

We investigate rates of tail autotomy for 15 lacertid taxa (assigned to 11 species in 5 genera) that exist across a wide range of habitats in the Aegean Sea region (NE Mediterranean Basin, see Table 1, Fig. 1.). All taxa are small generalist arthropod predators, similar in external morphology and body size (55–70 mm SVL; 8–12 g mass; Valakos et al. 2007).

Collecting sites fall into three categories: (1) *Mainland areas*—[M]. These were located on a variety of locations on the southern Balkan Peninsula (Fig. 1). (2) *Pleistocene islands*—[P]. These near-shore islands (Andros, Ikaria) were last connected to a continental landmass 0.2–1 million years ago and are today isolated by relatively narrow water straits ($<$18 km wide). (3) *Pre-Pleistocene islands*—[PP]. This group includes Crete [CR] (Levka Ori site) and the surrounding islets (Dia [DI], Chryssi [CH], Dragonada [DR]), as well as Milos and Skyros islands. All of these islands have been isolated for more than 2 million years from the mainland, with Crete and its satellites probably last connected during the Messinian Salinity Crisis 5.4 million years ago (Creutzburg 1963; Meulenkamp 1985; Dermitzakis 1990).

Lizards were collected by noosing them during the non-reproductive period (October 1998, 1999, 2000) and in accordance with Greek National Law (Presidential Decree 67/81). For each individual collected, we recorded sex, size, and condition of the tail (intact or previously shed, irrespective of amount of regeneration). To obtain a relative index of predation pressure in the field, we calculated for each population (with the exceptions of *Algyroides moreoticus*, *A. nigropunctatus*, *Ophisops elegans*, and *Anatololacerta oertzeni*) the percentage of individuals that were encountered in the field that did not have intact tails (Pafilis 2003).

To reduce variability and the effects of developmental plasticity, only adult male individuals with intact tails were used in the laboratory experiments and physiological assays. Captured lizards were transferred to the laboratory facilities of the Biology Department at the University of Athens and allowed to acclimatize for a period of four weeks before the initiation of the experiment. Handling of lizards was minimized to reduce habituation, which has the potential to affect tail-shedding behavior (Arnold 1984). All animals were housed in couples in vitreous terraria (20 × 25 × 15 cm) at a constant temperature of 25°C and a controlled photoperiod (12 h light: 12 h dark; fluorescent tube lighting). One incandescent heat lamp (60 W) in each terrarium provided 8 h of light per day. Lizards were fed three times weekly with mealworms dusted with supplementary vitamins and had access to water ad libitum. Food was withheld from all animals for the 48 h preceding the experimental predation simulation.

FIELD PREDATION ACROSS STUDY SITES

Lizard predators in the study region fall into three broad categories: (1) mammalian mesopredators (foxes, *Vulpes vulpes*, and golden jackals, *Canis aureus*; [note that feral cats, which can be effective lizard predators (Garcia-Marquez et al. 1999), were never

Table 1. **Species, numbers, and geographic origin of the animals used in the laboratory autotomy tests (map localities given in Fig. 1). Bracketed code denotes type of locality (insularity): [M], Mainland; [P], Pleistocene island; [PP], Pre-Pleistocene island. The last two columns give the main lizard predators (species codes at the end of the table) of each site, as well as supporting references.**

Species	Sample size	Locality	Predators	References
Algyroides moreoticus	10	Libovissi, C. Peloponnese [M]	Snakes: 1, 2, 6, 7, 9, 10, 11 Birds: 1, 3, 5, 7, 8, 9, 10 Mammals: 1, 2	Chondropoulos 1989; Handrinos and Akriotis 1997
A. nigropunctatus	9	Ziros lake, Ipeiros [M]	Snakes: 1, 2, 3, 5, 6, 7, 9, 11 Birds: 1, 3, 4, 5, 7, 8, 9, 10 Mammals: 1, 2	Chondropoulos 1989; Handrinos and Akriotis 1997
Hellenolacerta graeca	23	Taygetos near Kardamyli, S. Peloponnese [M]	Snakes: 1, 2, 6, 7, 9, 10, 11 Birds: 1, 3, 5, 7, 8, 9, 10 Mammals: 1, 2	Kinzelbach 1969; Chondropoulos 1989; Handrinos and Akriotis 1997
Anatololacerta oertzeni	10	Nas, Ikaria Id., E. Aegean [P]	Snakes: 5, 12 Birds: 1, 2, 5, 6, 7, 9, 10	Broggi 2001; Magioris 1986; Handrinos and Akriotis 1997; Watson 1964
Ophisops elegans	11	Ranti Forest, Ikaria Id., E. Aegean [P]	Snakes: 5, 12 Birds: 1, 2, 5, 6, 7, 9, 10	Broggi 2001; Magioris 1986; Handrinos and Akriotis 1997; Watson 1964
Podarcis gaigeae	41	Skyros Id, C. Aegean [PP]	Snakes: 1, 2, 10 Birds: 1, 5, 6, 7, 9, 10	Cattaneo 1998; Handrinos and Akriotis 1997; Watson 1964
P. erhardii mykonensis (AN)	30	Andros Island, N. Cyclades [P]	Snakes: 1, 2, 5, 10, 11 Birds: 1, 3, 5, 6, 7, 9, 10	Blamire 1988; Broggi 1996; Dimaki et al. 1999; Magioris 1995; Pasquali 1986; Handrinos and Akriotis 1997
P. erhardii leucaorii (CR)	12	Lefka Ori Mtns., W. Crete [PP]	Snakes: 6, 10 Birds: 1, 5, 7, 10	Cheylan 1973; Coghlan 1996; Ferlini 1992; Hafemann 1967; Robel 2000; Handrinos and Akriotis 1997; Chondropoulos 1989
P. erhardii shiebeli (DI)	26	Dia Islet, N. Crete [PP]	Snakes: 6 Birds: 1, 5, 6	Stepanek 1936; Chondropoulos 1989; Cheylan 1973; Coghlan 1996; Ferlini 1992; Hafemann 1967; Robel 2000
P. erhardii werneriana (CH)	14	Chryssi Islet, SE. Crete [PP]	Snakes: 10 Birds: 5, 6, 10	Chondropoulos 1989; Cheylan 1973; Coghlan 1996; Ferlini 1992; Hafemann 1967; Robel 2000
P. erhardii rechingeri (DR)	11	Dragonada Islet, NE. Crete [PP]	Snakes: 6 Birds: 5, 6, 10	Chondropoulos 1989; Cheylan 1973; Coghlan 1966; Ferlini 1992; Hafemann 1967; Robel 2000
P. milensis	21	Milos Island, SE. Cyclades [PP]	Snakes: 2, 10, 13 Birds: 1, 6, 7, 9, 10	Adamopoulou et al. 1997; Broggi 2000; Bruno and Maugeri 1990; Dimaki et al. 1999; Gruber 1989
P. muralis	17	Mainalo, C. Peloponnese [M]	Snakes: 1, 2, 6, 7, 9, 10, 11 Birds: 1, 3, 5, 7, 8, 9, 10 Mammals: 1, 2	Chondropoulos 1989; Handrinos and Akriotis 1997
P. peloponnesiacus	34	Kardamyli, S. Peloponnese [M]	Snakes: 1, 2, 6, 7, 9, 10, 11 Birds: 1, 3, 5, 7, 8, 9, 10 Mammals: 1, 2	Kinzelbach 1969; Chondropoulos 1989; Handrinos and Akriotis 1997
P. tauricus	15	Kastoria, Macedonia [M]	Snakes: 1, 2, 3, 5, 7, 11 Birds: 1, 3, 4, 5, 7, 8, 9, 10 Mammals: 2	Chondropoulos 1989; Handrinos and Akriotis 1997

Snakes: (1) *Zamenis situlus*; (2) *Elaphe quatuorlineata*; (3) *Zamenis longissimus*; (4) *Dolichophis jugularis*; (5) *Dolichophis caspius*; (6) *Hemorrhois gemonensis*; (7) *Platyceps najadum*; (8) *Natrix natrix*; (9) *Malpolon monspessulanus*; (10) *Telescopus fallax*; (11) *Vipera ammodytes*; (12) *Montivipera xanthina*; (13) *Macrovipera schweizeri*.

Birds: (1) *Buteo buteo*; (2) *Buteo rufinus*; (3) *Circaetus gallicus*; (4) *Circus aeruginosus*; (5) *Falco tinnunculus*; (6) *Falco eleonorae*; (7) *Athene noctua*; (8) *Lanius collurio*; (9) *Lanius senator*; (10)-*Corvus* sp.

Mammals: (1) *Canis aureus*; (2) *Vulpes vulpes*.

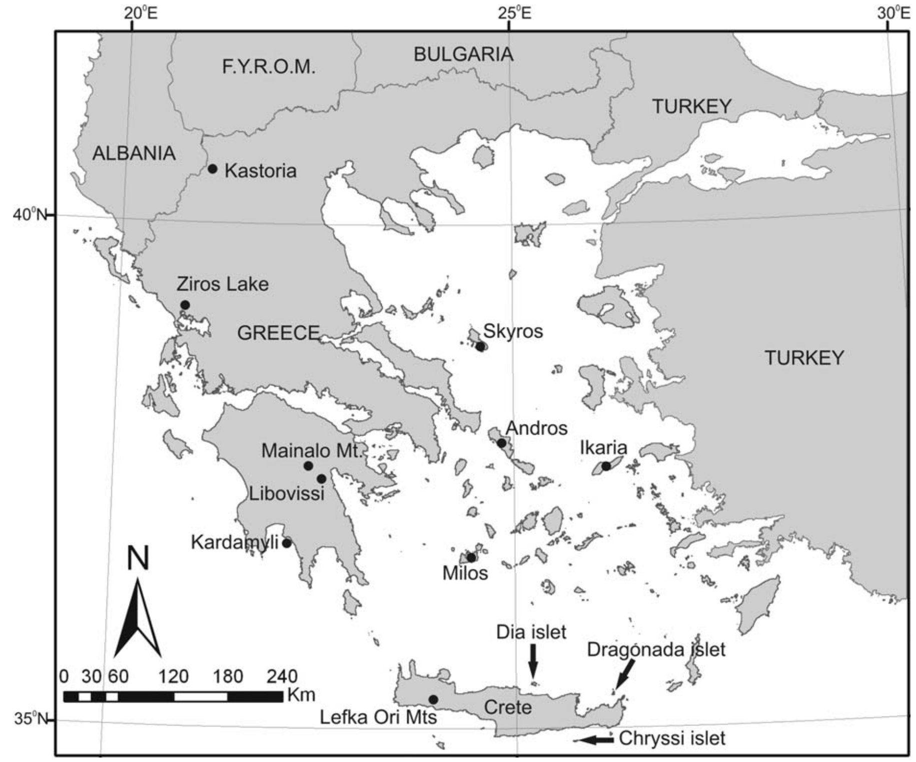

Figure 1. Map of the collecting sites in the Aegean Sea region (Greece, NE Mediterranean Basin).

observed on any of the study sites]); (2) aerial raptors (small to medium-sized raptors but also corvids and shrikes); and (3) saurophagous snakes. Whereas the last category is comprised mostly of constrictors that visually locate their prey before chasing it down, it also includes three allopatric species of highly toxic vipers that rely on crypsis and envenomation to kill their prey. Because of their divergent hunting strategy and possible ecological importance (vipers are both common in Aegean ecosystems and feed heavily on lizards, also see Novak et al. 2008) we also evaluated viper predation separately.

For each study site, we used as an index of predation the number of regularly existing predator taxa (Pérez-Mellado et al. 1997; Cooper et al. 2004). Predator communities were assessed by combining data from published literature reviews with field surveys of the actual sites (see Table 1 for predator identities and corresponding references).

The currently observed patterns of predator diversity appear to be stable and to have existed in similar form throughout much of the Pleistocene, as there is little evidence in the paleontological record suggesting that saurophagous predator communities were different in the past on the islands (Sondaar et al. 1986; Szyndlar 1991). Furthermore insularity of the study sites, the main factor influencing number of predators in each study area, has not changed since the youngest study islands (Andros, Ikaria) became isolated more than 200,000 years ago (Beerli 1994).

PREDATION SIMULATION—POSTAUTOTOMY TAIL MOVEMENT

We quantified each taxon's intrinsic predisposition for caudal autotomy using the laboratory technique proposed by Pérez-Mellado et al. (1997). Because body temperature has the potential to impact caudal autotomy (Daniels 1984) we allowed all animals to thermoregulate freely just prior to the beginning of the experiment. Each lizard was allowed to attain its preferred body temperature by placing it in a long glass box (1 m × 20 cm × 25 cm) providing a broad gradient of thermal conditions. The range of temperatures (17–55°C) was achieved by placing two incandescent heating lamps (100 and 60 W) in one end and two ice bags on the other end of the terrarium (Van Damme et al. 1986).

Individual lizards were placed on a cork substrate so they could maintain full traction during the predation simulation (Pérez-Mellado et al. 1997). To simulate the bite of a predator, we grasped the tail of each lizard with a pair of calipers at a point 20 mm behind the cloaca. To standardize pressure, the calipers were closed to half the original diameter of the tail and pressure was maintained for 15 sec. If autotomy occurred during this period, we recorded the duration of movement of the shed, thrashing tail from the moment of autotomy to complete cessation of movement using a digital timekeeper; then the exhausted tail was placed immediately in liquid N_2. Laboratory autotomy rates for each population were expressed as the fraction of lizards that shed their tails during this standardized procedure.

To investigate the relationship between rates of field autotomy (fraction of nonintact tails encountered in the field), and laboratory predation simulations, we calculated the relative difference between field and laboratory autotomy rates (RD_{FLAR}) using the following formula:

$$RD_{\mathrm{FLAR}} = [(\text{laboratory rates} - \text{field rates})/\text{field rates}] \times 100$$

Hence this variable reflects the percent degree to which laboratory autotomy rates, which are forced, are elevated above incidental field rates that are subject to the confounding effects of age and social interactions in addition to the actual occurrence of failed predation encounters.

LACTATE ESTIMATION

To determine lactate accumulation we sampled exhausted autotomized tails in a carefully standardized fashion. Collected tails tended to have the same size as they autotomized generally at the predetermined position in which the calipers were placed; furthermore, external variation was minimized by only using tails from males that were handled in exactly the same fashion (see previous section). We placed a whole frozen, autotomized tail onto a specially designed aluminum chilling disc (diameter 15 cm, thickness 5 cm) and dissected out muscle tissue from bones and scales. The disc was resting on a vertical aluminum shaft (diameter 5 cm, height 30 cm) that was immersed in liquid N_2 to conduct heat away from the sample.

Tail muscle tissue (approximately 150 mg) was homogenized in 10% w/v ice-cold perchloric acid at 1:3 in a cold pestle placed on ice. The homogenate was subsequently centrifuged for 10 min at 4°C and 5000 rpm. The supernatants were neutralized with 0.5 M Tris/0.5 M KOH and then centrifuged again at 4°C and 10,000 rpm for 10 min. The pellet that formed was discarded; we used the supernatant to estimate total lactate concentration (for details see Hohorst 1965). We expressed lactate concentration as milligrams lactate per milligram tail tissue.

STATISTICAL ANALYSES

Single variable analyses

All variables were checked for deviations from normality; nonparametric tests were used where necessary (Zar 1984). One-way analysis of variance (ANOVA) tests were used to evaluate the effects of type of locality (insularity) or viper presence on various aspects of tail autotomy. All tests were two-tailed ($a = 0.05$). Statistical analyses were conducted using SPSS-16.0 (SPSS Inc. 2007).

Model formulation

Following the initial description of the simple relationships of caudal-autotomy traits to individual environmental characteristics, we tested the simultaneous effects of multiple independent variables on different metrics of caudal autotomy, by using a formal model-selection approach (Burnham and Anderson 1998). In particular, we were interested in testing whether laboratory autotomy rates and RD_{FLAR} values were determined by a combination of various types of predators, as well as type of locality (insularity). For field autotomy rates, which in addition to the aforementioned external factors may also be determined by the intrinsic facility for autotomy, laboratory rates—which reflect this intrinsic facility—were also included in the pool of candidate variables.

Our model selection strategy was to compare single variable models for support received from the data, and then to add variables until the gain in likelihood associated with the added variable was nonsignificant. There has long been debate over how large a gain in likelihood is sufficient for the contemplation of a model with an additional free parameter (Jeffreys 1961; Royall 1997; Edwards 2002; Hitchcock and Sober 2004). We have chosen the traditional and somewhat conservative criterion of the likelihood-ratio test, which is based on the fact that twice the difference of the log-likelihoods of models differing by one parameter is approximately distributed as χ^2 with one degree of freedom (Azzalini 1996). Thus if a two variable model did not provide significant improvement over the one-variable model, then the search for more complex models was discontinued and the simpler model was used (Table 4A,B,C).

Phylogenetic analyses

Conventional statistical tests used in comparative studies have a tendency to be subject to inflated Type I errors (Garland Jr. et al. 1993; Brashares et al. 2000). We therefore repeated the above analyses by taking into account the evolutionary nonindependencies between the study populations. To that end, we constructed a phylogenetic tree using recently available molecular data (Fig. 2). Details of tree construction and topology justifications are provided in Appendix 1. We imported this tree into a statistical program (Phenotypic Diversity Analysis Program [PDAP], version 6.0, Garland et al. 2002) to repeat the conventional ANOVA in a phylogenetically informed fashion (see Van Damme 1999, Brashares et al. 2000). We used the Phenotypic Diversity Simulation (PDSIMUL) module to generate 10^3 simulations of the studied straits evolving along the known lizard phylogeny. For each of the 10^3 sets of simulated tip values we calculated the F-value using the Phenotypic Diversity Analysis of Variance (PDANOVA) module. We computed the 95th percentile of the distribution of these 103 F-values and compared the corresponding F-values obtained from conventional ANOVAs against these distributions.

For each of the caudal-autotomy traits investigated (see Table 3), we also calculated independent contrasts using Felsenstein's (1985) approach in the Phenotypic Diversity Tree (PDTREE) module of PDAP (Garland et al. 2002). These contrasts, corrected for the expected variance of phenotypic change, were then used to calculate correlation coefficients between the traits of interest.

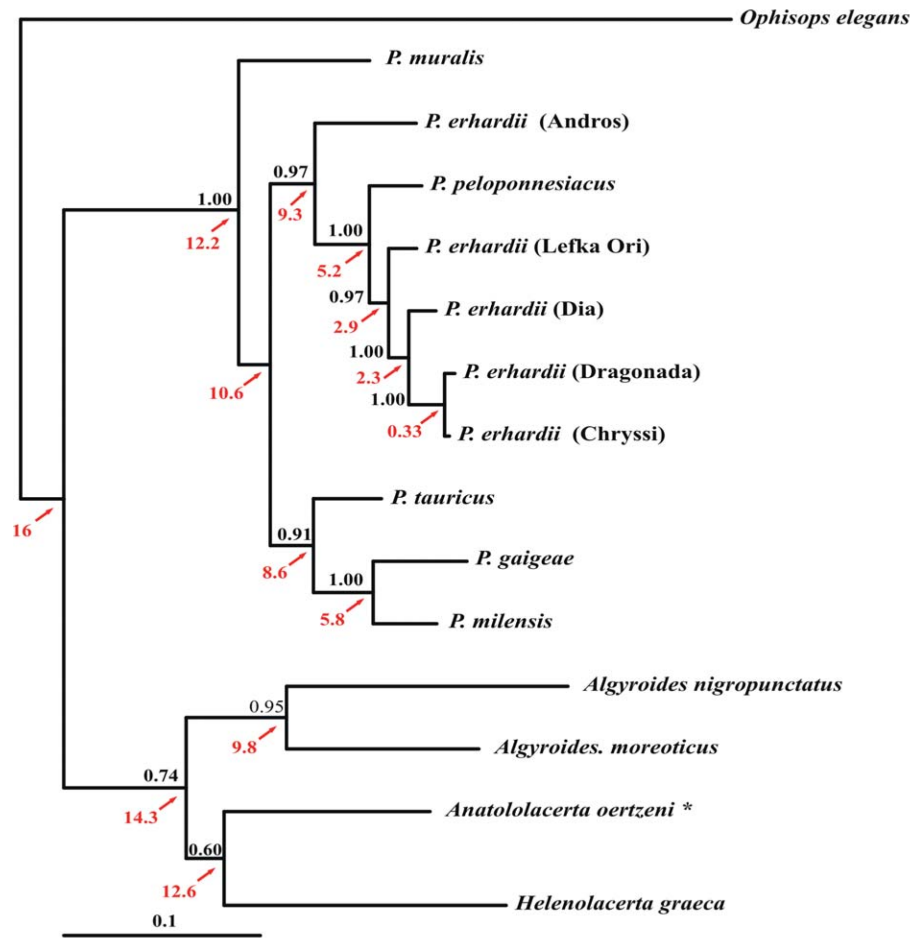

Figure 2. Phylogenetic tree used in the calculations of independent contrasts analyses. Phylogenetic analyses of maximum likelihood (ML) and Bayesian inference (BI) produced trees with the same topology—the BI tree is presented here. Numbers on branches are posterior probabilities of BI. Ages at nodes (red arrows) are given in million of years (see Appendix for details). Molecular data for *Anatololacerta oertzeni* were unavailable in GenBank and position on tree is based on its sister taxon *A. danfordi* (Eiselt and Schmidtler 1986). Note that *P. erhardii* is currently a paraphyletic taxon.

We also repeated in a phylogenetic context the previous search for complex models that incorporate multiple variables. Some of these variables reflect biological characters that can evolve over time (e.g., ease of autotomy), whereas others are for variables that are by definition not subject to evolutionary change (e.g., predator numbers, insularity). Data points in a variable of the latter category are not inherited along a phylogenetic tree and are thus equally independent from each other. As a result, they can be viewed as being located on the tips of one large polytomy (also called a "star" phylogeny) (see Purvis and Garland 1993; Foufopoulos and Ives 1999). While the collapse of a known n-tipped phylogenetic tree, by setting all internal branch lengths to 0, creates such a polytomy, this procedure also preserves the internal topology of the tree and allows for the computation of $n - 1$ independent contrasts for a noninherited variable (see Felsenstein 1985; Purvis and Garland 1993). These contrasts can then be incorporated into the analysis of regular independent contrasts calculated from genetically based variables (Wolf et al. 1998). However, because the independent contrasts method employs regression through the origin, we fitted models that did not include a constant (Garland et al. 1992). We then used the same likelihood-based model selection approach as described above to select the model with the strongest support.

Results

LEVELS OF PREDATION

Number of saurophagous predator species varies greatly between sites with a maximum at Ziros Lake where 18 taxa of possible lizard predators exist (eight snakes including one viper, eight birds, and two mammals), to a minimum on the small islands offshore Crete with a total of only four species of possible predators (one snake, three birds, and no vipers) (Table 1). Type of sampling locality (mainland vs. Pleistocene vs. pre-Pleistocene island) was a significant predictor of number of snake ($K = 10.89$, 2 df, $P < 0.004$ Kruskal–Wallis), avian ($K = 11.615$, 2 df, $P < 0.003$

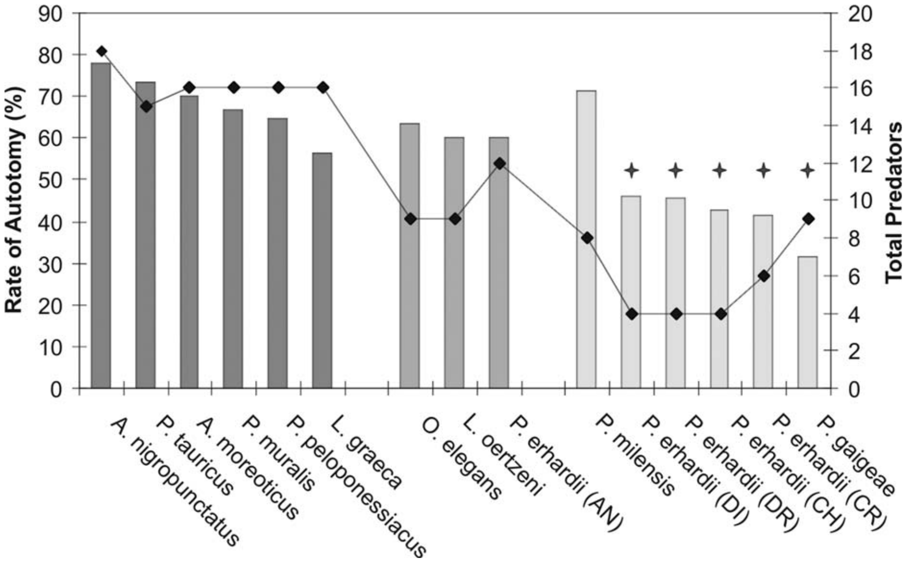

Figure 3. Rates of laboratory autotomy (bars) versus total number of sympatric predators and type of location. Species are grouped into mainland (dark bars), Pleistocene (intermediate gray) and pre-Pleistocene island (light gray) groups and are arranged by decreasing autotomy rates within each cluster. Black diamonds and line represent corresponding numbers of total predators (see Table 1 for species identities). Stars denote viper-free islands.

Kruskal–Wallis), and total predators ($K = 12.14$, 2 df, $P < 0.002$ Kruskal–Wallis), with a general monotonic decrease in total predator diversity from mainland (16.17 ± 0.983) to Pleistocene islands (10 ± 1.73), and then to pre-Pleistocene islands (5.83 ± 2.23) (predator number means ± SD, Fig. 3). Although all mainland and Pleistocene island sites harbored one viper species (either *Vipera ammodytes* or *Montivipera xanthina*), pre-Pleistocene islands were viper-free with the exception of Milos, which has its own endemic species (*Macrovipera schweizeri*).

RATES OF AUTOTOMY—LABORATORY

Laboratory rates of autotomy varied broadly between different populations examined (mean = 58.1% ± 3.51%, range: 31.7–77.8%, $n = 15$). Rates varied according to type of locality—mainland vs. Pleistocene vs. pre-Pleistocene island—(one-way ANOVA, $F_{2,12} = 7.44$, $P = 0.008$), with mainland populations having significantly higher autotomy rates than pre-Pleistocene islands (post hoc Tukey test, $P = 0.006$) but not Pleistocene islands (post hoc Tukey test, $P = 0.13$). These rates also differed according to the presence of vipers both in conventional (one-way ANOVA, $F_{1,13} = 49.31$, $P \ll 0.05$; rates on islands with vipers: 66.40% ± 6.71%, islands without vipers: 41.58% ± 5.82% [Mean ± SD]) and in phylogenetic analyses (where the 95% of the simulation-yielded F-values was 9.19, thus $P < 0.05$). Rates of laboratory autotomy increased significantly with rising snake, avian and total predator diversity both with and without the inclusion of phylogenetic relationships (but only in a marginally nonsignificant trend with avian predator diversity in the phylogenetic analysis) (Table 3). Nonetheless, a comprehensive search for a more complex model whether corrected for phylogenetic relationships or not, resulted in a simple model that included only presence of vipers in addition to the constant ($R^2 = 0.791$, beta = 24.82, $P < 0.001$, $n = 15$) (Table 4A, Figs. 3, 4).

RATES OF AUTOTOMY—FIELD

The percentage of lizards encountered in the field with previously autotomized tails varied substantially between different

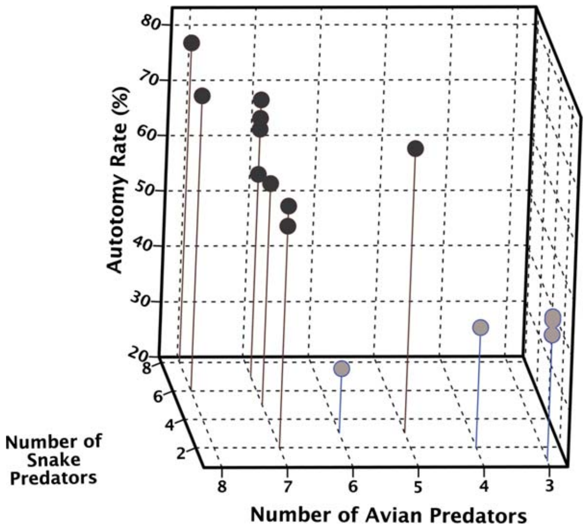

Figure 4. Laboratory autotomy rates versus numbers of avian and snake predators. Black circles represent populations on islands with, and gray circles islands without vipers. Note that several taxa have the same numbers of snake and avian predators resulting in a common projection onto the XY plane.

populations (mean = 49.55% ± 4.07%, range: 28–68.1%, $n = 11$). Rates of tail damage observed in the field and laboratory autotomy rates were highly correlated ($r = 0.969$, $P < 0.001$, $n = 11$). When one outlier (*P. e. rechingeri* [Dragonada], Stud. residual >2.5) was removed, this relationship became even stronger ($r = 0.995$, $P < 0.001$, $n = 10$). Taking the phylogenetic relationships of the taxa into account produced similar results ($r = 0.715$, $P < 0.005$; $r = 0.793$, $P < 0.002$ with and without the outlier, respectively). We then tested for the relative contributions of endogenous (evolved predisposition for autotomy which is directly measured by laboratory autotomy trials) versus exogenous factors (e.g., diversity of coexisting predator communities) to field rates. Although presence of vipers was strongly related to field autotomy rates (indep. samples *t*-test, $t = 5.009$, 9 df, $P < 0.001$, $n = 11$) when considered alone, none of the exogenous factors were significant when the endogenous factor (laboratory autotomy rate) was included, and the best model, whether corrected for phylogenetic nonindependences or not, contained only laboratory autotomy rate as the sole explanatory variable ($R^2 = 0.938$, beta = 0.951, $P < 0.001$, $n = 11$, Table 4B).

Relative differences between field and laboratory autotomy rates (RD_{FLAR}) although overall small, varied distinctly across the taxa examined ($x = 11.17\% \pm 2.54\%$, Range: −8.92% to +25.1%, $n = 11$). *P. e. rechingeri* [Dragonada] constituted a statistical outlier (Stud. residual > 2.3), and was removed from subsequent analyses. There was no relationship between type of locality (insularity) and RD_{FLAR} values (one-way ANOVA, $F_{2,7} = 2.457$, $P > 0.05$). These results also held up when phylogenetic relationships were considered in the analysis (95% boundary for simulated F-values was 6.336, and thus $P > 0.05$). However, RD_{FLAR} values were significantly lower in locations were vipers were present suggesting that these constitute a particularly important component of predation (indep. samples *t*-test, $t = 3.67$, df = 8, $P = 0.006$). RD_{FLAR} values were also negatively correlated with both snake and bird diversity and there was a marginally nonsignificant negative trend to total predator diversity (Table 3). These results, however, were nonsignificant when corrected for the presence of underlying phylogenetic relationships (Table 3). When multiple-variable models were considered the model with the highest likelihood, both with and without phylogenetic correction, contained viper presence as the only significant variable in addition to the constant ($R^2 = 0.627$, beta = −0.8394, $P = 0.002$, $n = 11$, Table 4C), thus further underscoring the importance of vipers as the main selection agent for the evolution of tail-shedding behavior.

POSTAUTOTOMY LACTATE LEVELS

Lactate concentrations of exhausted tails for all species examined are given in Table 2. No statistically significant differences were detected in total lactate concentrations in exhausted tails among the examined taxa (ANOVA $F_{14,144} = 0.733$; $P > 0.05$). Average lactate values also did not differ between taxa inhabiting different types of sampling localities (mainland vs. Pleistocene vs. pre-Pleistocene islands) ($F_{2,12} = 1.827$, $P = 0.21$). This pattern remained unchanged when the phylogenetic relationships of the species were considered in the analyses (95% simulation

Table 2. **Comparative caudal autotomy data for the 15 lacertid taxa in this study. Second column gives percentages of previously broken tails observed in wild populations, and associated sample sizes. RD_{FLAR} represents the relative difference between laboratory and field rates in percent. Time of postautotomy tail movement (in minutes) and lactate concentrations in exhausted tails (expressed in milligrams lactate per milligram tissue).**

Species	Damaged tails, %, (*N*)	RD_{FLAR} %	Time mean±SD; *N*; (range)	Lactate mean±SD; *N*; (range)
Algyroides moreoticus	–	–	5.21±2.38; 7; (2.12–9.55)	1.95±0.23; 7; (1.56–2.28)
A. nigropunctatus	–	–	5.3±2.39; 7; (2.53–9.55)	2.15±0.48; 7; (1.45–2.9)
Hellenolacerta graeca	51.1 (47)	10.61	6.11±2.67; 13; (2–12.23)	1.74±0.42; 13; (1–2.65)
Anatololacerta oertzeni	–	–	5.56±2.79; 6; (2.07–9.45)	1.65±0.36; 6; (1.18–2.18)
Ophisops elegans	–	–	4.97±1.96; 7; (2.55–6.33)	1.73±0.45; 7; (1.06–2.36)
Podarcis gaigeae	28.0 (57)	13.21	5.74±2.22; 13; (2.18–10.12)	1.71±0.34;13; (1.13–2.36)
P. erhardii (AN)	54.5 (66)	10.09	6.1±3.18; 18; (1.28–14.23)	1.9±0.42; 18; (1.23–2.83)
P. erhardii (CR)	33.3 (18)	25.11	5.53±2.81; 5; (2.22–9.25)	1.8±0.43; 5; (1.32–2.5)
P. erhardii (DI)	39.5 (43)	16.84	6.17±3.13; 12; (1.35–11.57)	1.82±0.4; 12; (1.24–2.46)
P. erhardii (CH)	36.4 (22)	17.72	4.57±2.1; 6; (2.14–8.31)	1.68±0.48; 6; (1.18–2.6)
P. erhardii (DR)	50.0 (22)	−8.92	5.21±2.5; 5; (1.57–8.4)	1.73±0.48; 5; (1.27–2.55)
P. milensis	65.0 (60)	9.88	6.44±3.2; 15; (3.15–13.22)	1.78±0.33; 15; (1.23–2.55)
P. muralis	62.2 (45)	7.19	6.18±3.73; 12; (2.26–14.21)	1.8±0.43; 12; (1.14–2.53)
P. peloponnesiacus	57.0 (79)	13.51	6.52±2.99; 22; (1.28–13.43)	1.81±0.38; 22; (1.08–2.84)
P. tauricus	68.1 (47)	7.68	5.53±2.58; 11; (2.28–10.04)	1.79±0.37; 11; (1.25–2.56)

Table 3. Spearman correlation matrix of various physiological parameters related to autotomy and different metrics of predator diversity. Top number in each cell denotes correlation coefficient, bottom associated P-value (based on uncorrected comparison-wise probabilities [Sokal and Rohlf 1969]). Cells above the diagonal include conventional statistics, and below the diagonal phylogeny independent contrasts. Missing cells cannot be calculated meaningfully in a phylogenetically informed context. Statistically significant relationships are given in bold.

Trait	Rate of autotomy	RD_{FLAR}[1]	Movement time (min)	Lactate	No. snake predators	No. avian predators	Total predators
Rate of autotomy	...	**−0.782**	.147	0.494	**0.660**	**0.733**	**0.652**
		0.008	0.602	0.061	**0.007**	**0.002**	**0.008**
RD_{FLAR}[1]	**−0.716**	...	−0.347	−0.061	**−0.636**	**−0.721**	−0.615
	$P<0.01$		0.327	0.868	**0.048**	**0.019**	0.058
Movement time (min)	0.270	0.149	...	0.237	0.325	0.056	0.230
	$P>0.05$	$P>0.05$		0.396	0.237	0.843	0.410
Lactate	0.463	0.04	0.206	...	**0.565**	0.347	0.501
	$P>0.05$	$P>0.05$	$P>0.05$		**0.028**	0.205	0.057
No. snake predators	**0.501**	−0.364	0.335	0.409	...	**0.797**	**0.971**
	$P<0.02$	$P>0.05$	$P>0.05$	$P>0.05$		**0.001**	**0.001**
No. avian predators	0.427	0.295	0.145	0.253	–	...	**0.875**
	$0.1>P>0.05$	$P>0.05$	$P>0.05$	$P>0.05$			**0.001**
Total predators	**0.508**	−0.353	0.085	0.053	–	–	...
	$P<0.02$	$P>0.05$	$P>0.05$	$P>0.05$			

[1] RD_{FLAR} correlations presented without a statistical outlier (Dragonada Isl.)

boundary = 7.05, so $P > 0.05$). Similarly, presence of vipers was not associated with differences in lactate levels in exhausted tails both in regular ($F_{1,13} = 1.519$, $P = 0.24$), and phylogenetically informed analyses (95% boundary = 8.21, $P > 0.05$). We found final lactate concentrations to be significantly related to snake diversity but neither to avian nor total predator diversity (Table 3).

DURATION OF POSTAUTOTOMY TAIL MOVEMENT

Mean duration of the tail movement until exhaustion, ranged between 4 and 7 min (Table 2). We found no statistically significant differences in tail movement times among the species examined ($F_{14,144} = 0.978$; $P > 0.05$). There were also no differences in mean duration of tail movement between populations existing in different types of sampling locality with or without consideration of phylogenetic relationships (conventional $F_{2,12} = 0.255$, $P = 0.78$; and with a 95% simulation boundary = 6.53, phylogenetic $P > 0.05$). Similarly, we did not detect any statistical differences in duration of average tail movement between populations that co-existed with vipers and others that did not: (conventional: $F_{1,13} = 2.75$, $P = 0.28$; for a 95% simulation boundary = 8.39, thus $P > 0.05$).

Discussion

In this study, we investigate the decline of antipredator behaviors under conditions of relaxed predation in a number of mainland and island lizard populations existing in the eastern Mediterranean basin. Using a combination of conventional and phylogenetic approaches, we demonstrate that field and laboratory caudal-autotomy rates are highly correlated, and both are shaped by the presence of predators. However, among all predator categories only the presence of vipers is significantly related to the maintenance of strong autotomic ability. Other factors such as differences in social interactions can potentially shape caudal-autotomy rates as well. In addition, it is possible that variation in the ability to store lipids in the tail, a trait that can vary between mainland and island lizard taxa, may also influence ease of tail-shedding (Chapple and Swain 2002b). However, we found no variation among our study taxa neither in type of social system, nor in the amount of lipids stored in the tail (see also Pafilis et al. 2005) suggesting that these factors are likely unimportant in our study system. Clearly more study is needed on this particular subject. Lastly, insularity, when considered independent from predation, appears to be statistically unimportant; instead, the main factor shaping ease of caudal autotomy is predation pressure by vipers.

PREDATION RATES

Predator species diversity, varied substantially between the locations investigated. Both Pleistocene and pre-Pleistocene island sites had lower predator diversities than mainland sites; this drop was especially pronounced for snakes, which are poor over-water dispersers. Pre-Pleistocene island predator communities were

Table 4. Log likelihoods of tested phylogenetic and nonphylogenetic models for: (A) laboratory autotomy rates; (B) field autotomy rates; and (C) RD_{FLAR} values. Larger value signifies a better model. Phylogenetic regressions do not include a constant (see Garland et al. 1992). One-variable models are first compared against the constant-only model (or against each other in the case of phylogenetic regressions). Two-variable models include the single variable that gave the highest likelihood one-variable model, as well as the other indicated variable, and are then compared against the best one-variable model. An asterisk indicates the model had a significantly higher likelihood ($\chi^2>3.841$) when compared to the best simpler model. The log likelihood of the preferred model is boldfaced. For example, for the laboratory autotomy rate analysis (A) the best model (constant + viper) was chosen because it was the best of those one-variable models that were significant improvements over the constant-only model, whereas at the same time none of the two-variable models performed significantly better.

		Conventional statistics		Phylogenetic statistics	
	Constant only	One variable	Two variable	One variable	Two variable
A. Dependent variable: laboratory autotomy rate	−59.935				
Vipers		**−48.180***		**66.53**	
Snakes		−55.452*	−48.026	58.670	66.592
Birds		−54.930*	−47.672	57.631	67.023
Total predators		−54.635*	−48.154	58.217	66.664
Insularity		−54.114*	−48.085	58.224	66.573
B. Dependent variable: field autotomy rate	−43.730				
Intrinsic ability (lab autotomy rate)		**−28.407***		**56.77**	
Vipers		−36.404*	−28.241	40.425	57.896
Snakes		−41.052	−28.285	36.48	57.376
Birds		−41.520	−28.311	36.002	57.959
Total predators		−41.180	−28.303	36.335	57.507
Insularity		−40.798	−28.392	36.664	57.368
C. Dependent variable: RD_{FLAR}	−30.660				
Vipers		**−25.724***		**47.05**	
Snakes		−27.480	−25.715	45.76	47.127
Birds		−26.546*	−25.204	45.815	47.058
Total predators		−27.265	−25.644	45.876	47.088

further impoverished relative to Pleistocene islands, with only a handful of resident predator taxa (typically one or two species of nonviperid snakes, a corvid and two species of small raptors) existing there. Reduced presence of predators in Aegean island environments is furthermore reflected in the high lizard population densities on many small islands but also by the relatively fearless behavior of animals in some of these populations (Gruber 1986). Because the present island lizard populations all originated in a predator-rich mainland environment, they can help evaluate how various antipredator defenses are being lost following removal of various aspects of predation.

RELATIVE IMPORTANCE OF VIPERS VERSUS OTHER PREDATOR TAXA

Although caudal-autotomy rates are correlated to the number of both snake predators and avian raptors, by far the most important determining factor appears to be the presence of vipers. This is perhaps best illustrated by the lizard sister taxa *Podarcis gaigeae* and *P. milensis*; although the first species lives on the viper-free Skyros cluster, the second one coexists on the Milos cluster with the endemic viper *M. schweizeri*, the young of which are documented lizard hunters (Adamopoulou et al. 1997). Whereas *P. gaigeae* has the lowest autotomy rate (28%) of all species examined here, *P. milensis* has the highest (71%) among island species and the third highest overall [Table 2, Figs. 3, 4]. In the final model predicting degree of caudal autotomy, as selected both in a conventional and a phylogenetic framework, only presence of vipers is significant whereas all other predator categories or even island characteristics are not. The disproportionate importance of viperid predators is best explained by the frequency and the peculiarities of viper attacks. Vipers are rather common on the study islands (Van Wingerde 1986; Nilson et al. 1999) and, especially as juveniles, attack frequently lizards (Adamopoulou et al. 1997). During predation attempts by nonvenomous predators, tail shedding becomes mostly important in the relatively few cases when a lizard's tail has been firmly grasped by a predator. In contrast, for viper attacks, in which even a glancing tail strike can deliver a lethal venom dose, rapid caudal autotomy can be a crucial survival mechanism preventing toxins from reaching vital organs.

Populations isolated on islands experience reduced interpopulation gene flow and are also generally genetically impoverished (Seddon and Baverstock 1999). As a result, they may differ in a variety of important physiological and life history traits often summarized under the term "island syndrome" (Adler and Levins 1994; Lindstrom et al. 2004; Whiteman et al. 2006; Pafilis et al. 2007). We tested the hypothesis that insularity shapes antipredator defenses, and although we find that island taxa, especially those from the pre-Pleistocene island group, have lost much of their tendency to shed their tail, this appears to be less attributable to insularity per se but is rather the result of substantially impoverished predator communities in island ecosystems. Other factors, such as amount of fat reserves stored in the tail or variation in intraspecific interactions also appear to not be important in determining tail autotomy strategies in our lizard populations. In a previous study (Pafilis et al. 2005) we found that there is no variation in amount of lipids stored in the tail between mainland and island lizards suggesting that caudal fat reserves do not matter in our system. We also did not witness any unusual patterns in the intensity or nature of social interactions on our study islands. If indeed intraspecific aggression and concomitant predation on tails were to be elevated in high-density, predator-poor islands, then we would actually expect the opposite pattern of what we documented. Thus, in summary, beyond its effect in shaping predator communities, there is no evidence that insularity alone results in changes in autotomic facility in lizards.

RELATIONSHIP BETWEEN FIELD AND LABORATORY METHODS

Frequency of caudal autotomy in a natural lizard population represents the interaction of at least two different elements: an endogenous one, thus the intrinsic ability of an individual to shed its tail, and an exogenous one, that is, the nature of the predation and social environment that triggers the tail-shedding. By comparing forced laboratory autotomies, which reflect only intrinsic ability, with field autotomy rates, which represent both elements, we can evaluate the relative contribution of each element in shaping field rates. The very high correlation ($r > 0.96$; [$r > 0.99$ without the outlier]) between field and laboratory autotomy rates, strongly suggests that fraction of autotomized tails in the field is essentially exclusively determined by the intrinsic ability of a taxon to shed its tail rather than variation in environmental opportunities to do so. However, because this intrinsic ease of autotomy in a population has evolved in response to the presence of at least some predator species (see previous section), predation pressure is not linked directly to field rates through variation in attacks triggering caudal autotomy, but rather indirectly via past selection for elevated ease of tail shedding (Fig. 5).

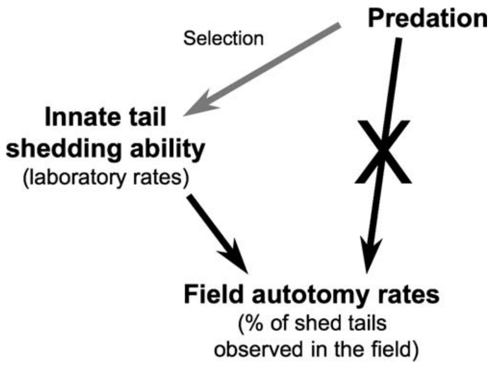

Figure 5. Functional relationships between predation and the caudal-autotomy rates observed in the field. Field autotomy rates are highly correlated to the intrinsic ability to shed the tail as measured by standard laboratory challenges, and not to sympatric predator diversity. Instead, selection by predators and especially vipers has lead to marked evolved differences in the ease of intrinsic autotomic ability between different lizard populations. As a result, predation is not the direct cause of the autotomized tails encountered in the field but rather an indirect driver that has shaped a taxon-specific ease of autotomy via past selection.

We further investigated the nature and the differences between field and laboratory rates by calculating the relative percent difference (RD_{FLAR}) between the two. Although these differences and the corresponding RD_{FLAR} values were—with the exception of one outlier—fairly small (Table 2), we detected a clear negative relationship between RD_{FLAR} values and various predator diversity metrics. Thus, the higher the predator diversity that a lizard population is exposed to, the more field autotomy rates resemble values observed during the forced autotomy conditions of the lab. This in turn suggests that although the large majority of the interpopulation variability in field autotomy rates can be attributed to evolved differences in autotomic predisposition, there is also a weak but clear signal of direct predation pressure on RD_{FLAR} values.

LACTATE LEVELS AND DURATION OF TAIL MOVEMENT

Duration of tail movement is considered to be an important component of the caudal-autotomy defense strategy (Dial and Fitzpatrick 1983). Although we had previously hypothesized that lizards existing in areas with diverse predator communities would have tails that would thrash longer, as this would provide more time for escape, we failed to find any evidence to support this thesis (Pafilis et al. 2005). Here we examine this relationship again using a larger sample of species, and come largely to the same conclusion. This suggests first that—in lacertids at least—longer duration of movement does not appear to convey a significant advantage to an escaping lizard. Second, the relatively limited variation in mean thrashing times among the taxa investigated, may also suggest that duration of movement is an evolutionary conservative trait that does not respond to relaxed selection (Pafilis et al. 2005). A possible explanation for this may be that this trait is tied to other aspects of locomotory performance such as sprint speed that remain functionally important for social interactions (Husak and Fox 2006), even in the face of relaxed predation.

Our analyses reveal a significant positive relationship between final lactate concentrations in tails that have ceased thrashing and snake but not avian or total predator diversity. Two possible mechanisms may underlie this relationship. First, tolerance of higher lactate concentrations after autotomy could allow for longer periods of tail thrashing which in turn may permit lizard escape during snake attacks. However, the equivocal relationship between duration of movement and any metric of predator diversity (see previous paragraph, Table 3), as well as the lack of a strong correlation between final lactate concentrations and movement times (Table 3) provide at most weak supporting evidence for these causal relationships.

Alternatively, it is possible that high final lactate concentrations in exhausted tail muscles are simply reflective of a general tolerance of high lactate levels in the rest of the lizard muscles. In turn, such high lactate tolerance appears to be associated with increased locomotory performance (Bennett and Licht 1972; Hailey et al. 1987), an important trait in environments with high-predation pressure (Van Damme et al. 1998; Miles et al. 2001; Miles 2004). Hence high lactate concentrations in exhausted tail muscles may merely be the byproduct of a generally elevated anaerobic running capacity rather than an adaptive trait related specifically to caudal autotomy. Seen in this light, the long tail movement times documented by Dial and Fitzpatrick (1983) in taxa living under high predation pressure, may not have been functionally important per se, but rather were a side effect of selection for high sprinting speeds that have been shown to be adaptive in high-predation environments (Vervust et al. 2007).

Caudal autotomy is a complex antipredator strategy that combines at least two different interdependent defenses to facilitate escape from predators. Our data suggest that under relaxed predation conditions, an uncoupling of the two components exists. Ease of autotomy, the more expensive defense becomes down regulated, whereas duration of thrashing remains unchanged, either because it is less costly, or because the underlying physiological pathways are conservative.

From a practical perspective, these results indicate that field autotomy rates constitute an excellent metric of the intrinsic ease of autotomy and need not be substituted with logistically challenging laboratory experiments. However, if the aim is to obtain a metric of field predation pressure, both field and laboratory autotomy rates are required, and RD_{FLAR} values will need to be calculated, as only they are reflective of field predation attacks on lizards. Lastly our results suggest that, for lacertids at least, movement times or muscle metabolites in exhausted tails do not respond to differences in predator selection pressure and are in this regard uninformative for comparative analyses of antipredator responses.

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LITERATURE CITED

Adamopoulou, C., E. D. Valakos, and A. Legakis. 1997. Notes on the diet and reproduction of the Cyclades blunt-nosed viper *Macrovipera schweizeri* (Werner, 1935). Herpetozoa 10:173–175.

Adler, G. H., and R. Levins. 1994. The island syndrome in rodent populations. Q. Rev. Biol. 69:473–490.

Akaike, H. 1974. New look at statistical-model identification. IEEE T. Automat. Contr. 19:716–723.

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

———. 1988. Caudal autotomy as a defense. Pp. 236–273 *in* C. Gans and R. B. Huey, eds. Biology of the reptilia, Vol. 16. Alan Liss, New York, NY.

Arnold, E. N., O. Arribas, and S. Carranza. 2007. Systematics of the Palaearctic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. Zootaxa 1430:3–86.

Azzalini, A. 1996. Statistical inference based on the likelihood. Chapman and Hall, New York, NY.

Ballinger, R. E., and D. W. Tinkle. 1979. On the cost of tail regeneration to body growth in lizards. J. Herpetol. 13:374–375.

Bea, A., F. Brana, J. P. Baron, and H. Saint-Girons. 1992. Régimes et cycles alimentaires des vipères Européenes (Reptilia: Viperidae). Ann. Biol. 31:25–4.

Beerli, P. 1994. Genetic isolation and calibration of an average protein clock in western Palearctic waterfrogs of the Aegean region. Ph.D. diss. University of Zurich, Switzerland.

Bellairs, D. A., and S. V. Bryant. 1985. Autotomy and regeneration in reptiles. Pp. 301–410 *in* C. Gans and F. Billet, eds. Biology of the reptilia, Vol. 15. John Wiley and Sons, New York, NY.

Bennett, A. F., and P. Licht. 1972. Anaerobic metabolism during activity in lizards. J. Comp. Physiol. 81:277–288.

Blamire, D. 1988. Notes on the birds seen in Evia and Andros. Nature (Athens) 40:63–64.

Blazquez, M. C., R. Rodriguez-Estrella, and M. Delibes. 1997. Escape behavior and predation risk of mainland and island spiny-tailed iguanas (*Ctenosaura hemilopha*). Ethology 103:990–998.

Brashares, J., T. Garland, Jr., and P. Arcese. 2000. The ecology, behavior, and phylogeny of the African antelope. Behav. Ecol. 11: 452–463.

Brodie, E. D., Jr., B. J. Ridenhour, and E. D. Brodie, III. 2002. The evolutionary response of predators to dangerous prey: hotspots and coldspots in the geographic mosaic of coevolution between garter snakes and newts. Evolution 56:2067–2082.

Broggi, M. F. 1996. Wetlands on the island of Andros, their amphibians and hydrophilous reptiles. Herpetozoa 8:135–144.

———. 2000. Herpetological notes on the islands of Milos and Sifnos (Cyclades, Greece). Herpetozoa 13:89–93.

———. 2001. Notes on the herpetofauna of the Aegean island of Ikaria (Greece). Herpetozoa 14:9–14.

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

Bruno S., and S. Maugeri. 1990. Serpenti d'Italia e d'Europa. Editoriale Giorgio Mondatori, Milan, Italy.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and multimodel inference: a practical information theoretical approach, 2nd ed. Springer, New York, NY.

Carranza, S., E. N. Arnold, and F. Amat. 2004. DNA phylogeny of *Lacerta* (*Iberolacerta*) and other lacertine lizards (Reptilia: Lacertidae): did competition cause long-term mountain restriction? Syst. Biodivers. 2:57–77.

Cattaneo, A. 1998. Gli anfibi e i rettili delle isole greche di Skyros, Skopelos e Alonissos (Sporadi settentrionali). Att. Soc. Ital. Sci. Nat. 139:127–149.

Chapple, D. G., and R. Swain. 2002a. Effect of caudal autotomy on locomotor performance in a viviparous skink, *Niveoscincus metallicus*. Func. Ecol. 16:817–825.

———. 2002b. Distribution of energy reserves in a viviparous skink: does tail autotomy involve the loss of lipid stores? Aust. Ecol. 27:565–572.

———. 2004. Inter-populational variation in the cost of autotomy in the metallic skink (*Niveoscincus metallicus*). J. Zool. 264:411–418.

Cheylan, G. 1973. Voyage ornithologique en Crete. L'Oiseau 43:330–339.

Chondropoulos, B. P. 1989. A checklist of the Greek reptiles. II. The snakes. Herpetozoa 2:3–36.

Coghlan, S. 1996. A birdwatching guide to crete. Arlequin Publications, Essex, UK.

Congdon J. D., L. J. Vitt, and W. W. King. 1974. Geckos: adaptive significance and energetics of tail autotomy. Science 184:1379–1380.

Cooper, W. E., V. Pérez-Mellado, and L. J. Vitt. 2004. Ease and effectiveness of costly autotomy vary with predation intensity among lizard populations. J. Zool. 262:243–255.

Creutzburg, N. 1963. Paleogeographic evolution of Crete from the Miocene till our days. [in Greek]. Cretan Ann. 15/16:336–342.

Curio, E. 1976. The ethology of predation. Springer-Verlag, Berlin.

Daniels, C. B. 1984. The importance of caudal lipid in the gecko *Phyllodactylus marmoratus*. Herpetologica 40:337–344.

Daniels, C. B., S. P. Flaherty, and M. P. Simbotwe. 1986. Tail size and effectiveness of autotomy in a lizard. J. Herpetol. 20:93–96.

Dermitzakis, D. M. 1990. Paleogeography, geodynamic processes and event stratigraphy during the Late Cenozoic of the Aegean area. International symposium on biogeographical aspects of insularity, Roma 1987. Accad. Naz. Lincei 85:263–288.

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

———. 1983. Lizard tail autotomy: Function and energetics of postautotomy tail movement in *Scincella lateralis*. Science 219:391–393.

———. 1984. Predator escape success in tailed versus tailless *Scincella lateralis* (Sauria: Scincidae). Anim. Behav. 32:301–302.

Dimaki, M., J. Ioannides, and A. Dimitropoulos. 1999. Ornithological observations from some Cyclades islands (Aegean Sea, Greece). Ann. Mus. Gulandris 10:185–199.

Downes, S., and M. Adams. 2001. Geographic variation in antisnake tactics: the evolution of scent-mediated behavior in a lizard. Evolution 55:605–615.

Downes, S., and R. Shine. 2001. Why does tail loss increase a lizard's later changes of being consumed by snake predators? Ecology 82:1293–1303.

Eiselt, J., and Schmidtler, J. F. 1986. Der *Lacerta danfordi*-Komplex. Spixiana, Munich 9:289–328.

Edwards, A. W. F. 2002. Occam's bonus. Pp. 128–132 *in* A. Zellner, H. Keuzenkamp, and M. McLeer, eds. Simplicity, inference, and modelling. Cambridge University Press, Cambridge.

Felsenstein, J. 1981. Evolutionary trees from DNA sequences: a maximum likelihood approach. J. Mol. Evol. 17:368–376.

——— 1985. Phylogenies and the comparative method. Am. Nat. 125:1–15.

Ferlini, F. 1992. Osservazioni ornitologische nelle isole di Creta e Santorini (Grecia). Uccelli d'Italia 17:61–64.

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

Foufopoulos, J., and A. R. Ives. 1999. Reptile extinctions on land-bridge islands: life history attributes and vulnerability to extinction. Am. Nat. 153:1–25.

Fox, S. F., and J. K. McCoy. 2000. The effect of tail loss on survival, growth, reproduction, and sex ratio of offspring in the lizard *Uta stansburiana* in the field. Oecologia 122:327–334.

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

Fox, S. F., N. A. Heger, and L. S. Delay. 1990. Social cost of tail loss in *Uta stansburiana*: lizard tail as status signaling badges. Anim. Behav. 39:549–554.

Fox, S. F., S. Perea-Fox, and R. Castro-Franco. 1994. Development of the tail autotomy adaptation in lizards under disparate levels of predation at high and low elevations in Mexico. Southwest. Nat. 39:311–322.

Garcia-Marquez, M., A. Caetano, I. Bello, L. P. Lopez-Jurado, and J. A. Mateo. 1999. Ecology of the feral cat in the thermophilic ecosystem of El Hierro (Canary Islands, Spain), and its impact on the giant lizard *Gallotia simonyi* [in Spanish]. Monografias de Herpetologia 4:207–222.

Garland, T. J., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Syst. Biol. 41:18–32.

Garland, T., Jr., A. W. Dickerman, C. M. Janis, and J. A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. Syst. Biol. 42:265–292.

Garland, T., Jr., P. E. Midford, J. A. Jones, A. W. Dickerman, and R. Diaz-Uriarte. 2002. PDAP: phenotypic diversity analysis programs version 6.0.

Gruber, U. 1986. *Podarcis erhardii* (Bedriaga, 1876)—Ägäische Mauereidechse. Pp. 25–49 *in* W. Böhme, ed. Handbuch der reptilien und amphibien Europas, Echsen (Sauria) II. AULA-Verlag, Wiesbaden, Germany.

———. 1989. Die schlangen Europas. Franckh'sche Verlagshandlung, Stuttgart, Germany.

Haacke, W. D. 2005. Constricting behaviour in an Australian elapid: a personal experience. Sauria 27:19–22.

Hafemann, D. 1967. Beobachtungen zum Frühjahrs-Vogelzug auf Kreta. Bonn. Zool. Beitr. 18:221–233.

Hailey, A., C. Gaitanaki, and N. S. Loumbourdis. 1987. Metabolic recovery from exhaustive activity by a small lizard. Comp. Bioch. Physiol. A 38:683–689.

Handrinos, G., and T. Akriotis. 1997. Birds of Greece. C. Helm and C. Black, eds. Christopher Helm Publishers Ltd, London.

Harris, D. J., E. N. Arnold, and R. H. Thomas. 1998. Relationships of lacertid lizards (Reptilia: Lacertidae) estimated from mitochondrial DNA sequences and morphology. Proc. Roy. Soc. Lond. 265:939–1948.

———. 1999. A phylogeny of the European lizard genus *Algyroides* Bibron and Bory 1833 based on DNA sequence, with comments on the evolution of the group. J. Zool. 249:49–60.

Hitchcock, C., and E. Sober. 2004. Prediction versus accommodation and the risk of overfitting. Brit. J. Philos. Sci. 55:1–34.

Hohorst, H. J. 1965. L- (+) lactate determination with lactate dehydrogonase and DNP. Pp. 266–270 *in* H. U. Bergmeyer, ed. Methods of enzymatic analysis. Academic Press, New York.

Husak, J. F., and S. F. Fox. 2006. Field use of maximal sprint speed by collared lizards (*Crotaphytus collaris*): compensation and sexual selection. Evolution 60:1888–1895.

Jeffreys, H. 1961. Theory of probability, 3rd ed. Oxford University Press, Oxford, U.K.

Kinzelbach, R. 1969. Ornithologische Beobachtungen von dem Peloponnes (Griechenland). Bonn. Zool. Beitr. 20:175–181.

Lin, Z. H., and X. Ji. 2005. Partial tail loss has no severe effects on energy stores and locomotor performance in a lacertid lizard, *Takydromus septentrionalis*. J. Comp. Phys. B. 175:567–573.

Lin, Z. H., J. F. Qu, and X. Ji. 2006. Energetic and locomotor costs of tail loss in the Chinese skink, *Eumeces chinensis*. Comp. Biochem. Phys. A 143:508–513.

Lindström, K., J. Foufopoulos, H. Pärn, and M. Wikelski 2004. Immunological investments reflect parasite abundance in island populations of Darwin's finches. Proc. R. Soc. Lond. Ser. B 1574:1513–1519.

Luiselli, L. 1996. Food habits of an alpine population of the Sand Viper (*Vipera ammodytes*). J. Herpetol. 30:92–94.

Magioris, S. 1986. Observations on the avifauna of Ikaria island, East Aegean, Greece. Rapp. Comm. Int. Mer. Medit. 30:102.

———. 1995. The avifauna of Cyclades, Greece: a general overview. Biol. Gal. Hell. 22:115–121.

Martin, J., and R. A. Avery. 1998. Effects of tail loss on the movement patterns of the lizard, *Psammodromus algirus*. Func. Ecol. 12:794–802.

Martin, J., and A. Salvador. 1995. Effects of tail loss on activity patterns of rock lizards, *Lacerta monticola*. Copeia 1995:984–988.

Matuschka, F. R., and B. Bannert. 1987. Cannibalism and autotomy as predator-prey relationship for monoxenous Sarcosporidia. Parasitol. Res. 74:88–93.

Mayer, W., and O. Arribas. 2003. Phylogenetic relationships of the European lacertid genera *Archaeolacerta* and *Iberolacerta* and their relationships to some other 'Archaeolacertae' (*sensu lato*) from the Near East, derived from mitochondrial DNA sequences. J. Zool. Syst. Evol. Res. 41:157–161.

McConnachie S., and M. J. Whiting. 2003. Costs associated with tail autotomy in an ambush foraging lizard, *Cordylus melanotus melanotus*. Afr. Zool. 38:57–65.

Medel, R. G., J. E. Jiminez, S. F. Fox, and F. M. Jaksic. 1988. Experimental evidence that high-population frequencies of lizard tail autotomy indicates inefficient predation. Oikos 53:321–324.

Meulenkamp, J. E. 1985. Aspects of the Late Cenozoic evolution of the Aegean region. Pp. 307–321 *in* D. J. Stanley and F. C. Wezel, eds. Geological evolution of the Mediterranean Basin. Springer, New York.

Miles, D. B. 2004. The race goes to the swift: fitness consequences of variation in sprint performance in juvenile lizards. Evol. Ecol. Res. 6:63–75.

Miles, D. B., H. L. Snell, and H. M. Snell. 2001. Intrapopulation variation in endurance of Galapagos lava lizards (*Microlophus albemarlensis*): evidence for an interaction between natural and sexual selection. Evol. Ecol. Res. 3:795–804.

Niewiarowski, P. H., J. D. Congdon, A. M. Dunham, L. J. Vitt, and D. W. Tinkle. 1997. Tales of lizard tails: effects of tail autotomy on subsequent survival and growth rates of free-ranging hatchling *Uta stansburiana*. Can. J. Zool. 75:542–548.

Nilson, G., C. Andrén, J. Ioannidis, and M. Dimaki. 1999. Ecology and conservation of the Milos viper, *Macrovipera schweizeri* (Werner, 1935). Amphib. Reptil. 20:355–375.

Nowak, E. M., T. C. Theimer, and G. W. Schuett. 2008. Functional and numerical responses of predators: where do vipers fit in the traditional paradigms? Bio. Rev. 83:601–620.

Pafilis, P. 2003. Adaptations of lacertids based on their thermal biology, metabolic rate and phylogenetic history. Ph.D. diss. University of Athens, Greece.

Pafilis, P., E. D. Valakos, and J. Foufopoulos. 2005. Comparative postautotomy tail activity in six Mediterranean lacertid species. Physiol. Biochem. Zool. 78:828–838.

Pafilis, P., J. Foufopoulos, J., N. Poulakakis, N., P. Lymberakis, and E. D. Valakos, E. D. 2007. Digestive performance in five Mediterranean lizard species: effects of temperature and insularity. J. Comp. Physiol. B 177:49–60.

Pasquali, R. 1986. Osservazioni ornitologische nelle isole Cicladi. Uccelli d'Italia 11:115–118.

Pavlicev, M., and W. Mayer. 2006. Multiple copies of coding as well as pseudogene c-mos sequence exist in three lacertid species. J. Exp. Zool. B 306:539–550.

Pérez-Mellado, V., C. Corti, and P. Lo Cascio. 1997. Tail autotomy and extinction in Mediterranean lizards. A preliminary study of continental and insular populations. J. Zool. 243:553–541.

Pianka, E. R. 1969. Notes on the biology of *Varanus caudolineatus* and *Varanus gilleni*. West. Aust. Nat. 11:76–82.

———. 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. Ecology 51:703–720.

Posada, D., and K. A. Crandall. 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14:817–818.

Poulakakis, N., P. Lymberakis, A. Antoniou, D. Chalkia, E. Zouros, M. Mylonas, and E. D. Valakos. 2003. Molecular phylogeny and biogeography of the wall-lizard *Podarcis erhardii* (Squamata: Lacertidae). Mol. Phyl. Evol. 28:38–46.

Poulakakis, N., P. Lymberakis, E. D. Valakos, P. Pafilis, E. Zouros, and M. Mylonas. 2005a. Phylogeography of Balkan wall lizard (*Podarcis taurica*) and its relatives inferred from mitochondrial DNA sequences. Mol. Ecol. 14:2433–2443.

Poulakakis, N., P. Lymberakis, E. D. Valakos, E. Zouros, and M. Mylonas. 2005b. Phylogenetic relationships and biogeography of Balkan *Podarcis* species by Bayesian and maximum likelihood analyses of mitochondrial DNA sequences. Mol. Phylog. Evol. 37:845–857.

Punzo, F. 1982. Tail autotomy and running speed in the lizards *Cophosaurus texanus* and *Uma notata*. J. Herpetol. 16:329–339.

Purvis A., and T. Garland. 1993. Polytomies in comparative analyses of continuous characters. System. Biol. 42:569–575.

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*). Arc. Zool. Ital. 37:131–170.

Robel, D. 2000. Vogelbeobachtungen im April 1995 auf Ost-Kreta. Brutvogel 5:13–21.

Rodriguez, F., J. L. Oliver, A. Marin, and J. R. Medina. 1990. The general stochastic-model of nucleotide substitution. J. Theor. Biol. 142:485–501.

Ronquist, F., and J. P. Huelsenbeck. 2003. Mr. Bayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574.

Royall, R. 1997. Statistical evidence: a likelihood paradigm. Chapman & Hall, New York, NY.

Saint Girons, H. 1980. Modifications sélectives du régime des Vipères (Reptilia: Viperidae) lors de la croissance. Amphib. Reptil. 1:127–136.

Salvador, A., J. Martin, and P. Lopez. 1995. Tail loss reduces home range size and access to females in male lizards (*Psammodromus algirus*). Behav. Ecol. 6:382–387.

Sanderson, M. J. 1997. A nonparametric approach to estimating divergence times in the absence of rate constancy. Mol. Biol. Evol. 14:1218–1231.

———. 2003. r8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. Bioinformatics 19:301–302.

Santos, X., G. A. Llorente, J. M. Pleguezelos, J. C. Brtio, S. Fahd, and X. Parellada. 2007. Variation in the diet of the Lataste‘s viper *Vipera latastei* in the Iberian Peninsula: seasonal, sexual and size-related effects. Anim. Biol. 57:49–61.

Schall, J. J., and E. R. Pianka. 1980. Evolution of escape behavior diversity. Am. Nat. 115, 551–566.

Schall, J. J., C. R. Bromwich, Y. L. Werner, and J. Mildedge. 1989. Clubbed regenerated tails in *Agama agama* and their possible use in social interactions. J. Herpetol. 23:305–307.

Schoener, T. W. 1979. Inferring the properties of predation and other injury-producing agents from injury frequencies. Ecology 60:1110–1115.

Seddon J. M., and P. R. Baverstock 1999. Variation on islands: major histocompatibility complex (MHC) polymorphism in populations of the Australian bush rat. Mol. Ecol. 8:2071–2079.

Smith, G. R. 1996. Tail loss in the stripped plateau lizard, *Sceleporus virgatus*. J. Herpetol. 30:552–555.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W.H Freeman, San Francisco, CA.

Sondaar, P. Y., J. de Vos, and M. D. Dermitzakis. 1986. Late Cenozoic faunal evolution and palaeogeography of the South Aegean island arc. Mod. Geol. 10:249–259.

Stepanek, O. 1936. Kreta a nastin jeja obrat lovey fauny. Veda Prirodni 18:53–58.

Sullivan, J., Z. Abdo, P. Joyce, and D. L. Swofford. 2005. Evaluating the performance of a successive-approximations approach to parameter optimization in maximum-likelihood phylogeny estimation. Mol. Biol. Evol. 22:1386–1392.

Swofford, D. L. 2002. PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland, MA.

Swofford, D. L., G. J. Olsen, P. J. Waddel, and D. M. Hillis. 1996. Phylogenetic inference. Pp. 407–514 *in* D. M. Hillis, C. Moritz, and B. K. Mable, eds. Molecular systematics. Sinauer, Sunderland, MA.

Szyndlar, Z. 1991. A review of Neogene and Quaternary snakes of central and eastern Europe. I. Scolecophidia, Boidae, Colubrinae. Estud. Geol. 47:103–126.

Turner, F. B., P. A. Medica, R. I. Jennrich, and B. G. Maza. 1982. Frequencies of broken tails among *Uta stansburiana* in southern Nevada and a test of the predation hypothesis. Copeia 1982:835–840.

Valakos E. D., P. Pafilis, K. Sotiropoulos, P. Lymberakis, P. Maragou, and J. Foufopoulos. 2007. The amphibians and reptiles of Greece. Edition Chimaira. Frankfurt a.M., Germany.

Van Damme, R., D. Bauwens, and R. F. Verheyen. 1986. Selected body temperatures in the lizard *Lacerta vivipara*: variation within and between populations. J. Therm. Biol. 11:219–222.

Van Damme, R., P. Aerts, and B. Vanhooydonck. 1998. Variation in morphology, gait characteristics and speed of locomotion in two populations of lizards. Biol. J. Linn. Soc. 63:409–427.

Van Wingerde, J. 1986. The distribution of *Vipera xanthina* (Gray, 1849) on the East Aegean Islands and in Thrace. Litt. Serp. 6:131–139.

Vervust, B., I. Grbac, and R. Van Damme. 2007. Differences in morphology, performance and behaviour between recently diverged populations of *Podarcis sicula* mirror differences in predation pressure. Oikos 116:1343–1352.

Vitt, L. J., and W. E. Cooper. 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.

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

Watson, G. E. 1964. Ecology and evolution of passerine birds on the islands of the Aegean Sea. Ph.D. thesis. Yale University, New Haven, CT.

Whiteman, N. K., K. D. Matson, J. L. Bollmer, and P. G. Parker. 2006. Disease ecology in the Galapagos hawk (*Buteo galapagoensis*): host genetic diversity, parasite load and natural antibodies. Proc. R. Soc. Lond., B, Biol. Sci. 273:797–804.

Wilson, R. S. 1992. Tail injuries increase the risk of mortality in free-ranging lizards (*Uta stansburiana*). Oecologia 92:145–152.

Wilson, R. S., and D. T. Booth. 1998. Effect of tail loss on reproductive output and its ecological significance in the skink *Eulamprus quoyii*. J. Herpetol. 32:128–131.

Wolf, M. C., T. Garland, and B. Griffith. 1998. Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts. Biol. Conserv. 86:243–255.

Zar, J. H. 1984. Biostatistical analysis. Prentice Hall, NJ.

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Appendix

TREE CONSTRUCTION AND JUSTIFICATION

We constructed the phylogenetic tree of the populations investigated in this study by using available molecular data. Lacertid sequences for 16S rRNA and cytochrome *b* (cyt *b*) from several studies were combined into a single data matrix. In particular, 10 combined sequences (16S and cyt *b*, respectively) of *Podarcis* spp. [*P. gaigeae*: AY768739 and AY768775, *P. milensis*: AY768741 and AY768777, *P. taurica*: AY768721 and AY768757, *P. erhardii*: AY896152 and AF486211, AY896148 and AF486212, AY896162 and AF486206, AY896169 and AF486219, AY896242 and AY896115, *P. muralis*: AY896180 and AF486233, and *P. peloponnesiaca*: AY896177 and AY896121 (Poulakakis et al. 2003, 2005a,b)], 1 specimen of *Algyroides nigropunctatus* [AF019650 (Harris et al. 1999) for 16S, not available for cyt *b*], 1 specimen of *A. moreoticus* [AF019649 (Harris et al. 1999) for 16S, not available for cyt *b*], 2 specimens of *Lacerta (Hellenolacerta) graeca* [AF440617 (Mayer and Arribas 2003) and AF080273 (Harris et al. 1998) for 16S and AF080272 (Harris et al. 1998) for cyt *b*], 1 specimen of *Lacerta* (*Anatololacerta*) *danfordi* [AF080324 (Harris et al. 1998) for 16S and DQ461765 (Pavlicev and Mayer 2006) for cyt *b*] and 1 specimen of *Ophisops elegans* [AF112293 (Harris unpublished data) for 16S and EU081642 (Kyriazi et al. under review)] were retrieved from GenBank and used in this phylogenetic analysis.

Phylogenetic inference analyses were conducted using maximum likelihood (ML) (Felsenstein 1981) and Bayesian inference (BI) approaches. The model used for the ML analyses [general time reversible, GTR; (Rodriguez et al. 1990) + gamma (G)] was selected using Modeltest version 3.7 (Posada and Crandall 1998) under the Akaike Information Criterion (AIC) (Akaike 1974), whereas BI was performed under mixed models (the data were partitioned by gene), and full parameter estimation was performed during tree search for each gene. Heuristic ML searches were performed in Phylogenetic Analyses Using Parsimony (PAUP*) (version 4.0b10) (Swofford 2002) with 10 replicates of random sequence addition and Tree-Bisection-Reconnection (TBR) branch swapping using the search strategy of successive-approximations (Swofford et al. 1996; Sullivan et al. 2005).

BI analysis was performed in MrBayes version 3.1 (Ronquist and Huelsenbeck 2003), with four runs and four chains for each run for 10^7 generations and the current tree saved every 100 generations. A 50% majority rule consensus tree was produced from the posterior distribution of trees, and the posterior probabilities calculated as the percentage of samples recovering any particular clade, with posterior probabilities $\geq$ 95% indicating significant support. Two further independent Bayesian analyses were run so that global likelihood scores, individual parameter values, topology, and nodal support could be compared to check for local optima.

Maximum likelihood analysis under the GTR+G model resulted in a topology with $ln\mathrm{L} = -4702.2282$. Bayesian inference under the GTR+G model for *cyt b* and GTR+I+G model for *16S* produced a topology with mean $ln\mathrm{L} = -4319.122$. The $-ln\mathrm{L}$ stabilized after approximately 10^6 generations and the first 10^4 trees (10% "burn-in," chain had not become stationary) were discarded as a conservative measure to avoid the possibility of including random, sub-optimal trees. Identical topologies were recovered for each of the four runs with the full dataset. The 50% majority-rule consensus tree of the 9×10^4 trees remaining after burn-in are presented in Figure 2. The divergence times on the tree of Figure 2 were estimated using the nonparametric rate smoothing (NPRS) analysis with the recommended Powell algorithm as implemented in the software r8s (version 1.7.1 for Mac) (Sanderson 1997; 2003), which relaxes the assumption of a molecular clock. As a calibration point, we used the divergence of *P. erhardii* of Crete from *P. peloponnesiacus* at 5.2 million years ago (Poulakakis et al. 2003, 2005b), and have set the maximum age of the Lacertinae lineage at 16 million years ago (Carranza et al. 2004; Arnold et al. 2007).