Comparative Postautotomy Tail Activity in Six Mediterranean Lacertid Lizard Species

Panayiotis Pafilis[1]
Efstratios D. Valakos[1,*]
Johannes Foufopoulos[2]
[1]Section of Human and Animal Physiology, Department of Biology, University of Athens, Panepistimioupolis, Ilissia 157-84, Greece; [2]School of Natural Resources and Environment, 440 Church Street, University of Michigan, Ann Arbor, Michigan 48109-1041

Accepted 1/26/2005; Electronically Published 6/28/2005

ABSTRACT

Tail autotomy, the self-induced tail separation from the body, is a common and effective antipredator mechanism in lizards. In this study, we examine the muscle energetics of tail shedding in six lacertid lizard species (*Podarcis erhardii*, *Podarcis peloponnesiaca*, *Podarcis muralis*, *Podarcis gaigeae*, *Podarcis milensis*, and *Lacerta graeca*) from the northeast Mediterranean region. Very long periods of postautotomy tail movement were demonstrated for all species (range = 6–8 min), and differences among species were not statistically significant. Postautotomy tail movement, powered by anaerobic muscle activity, resulted in a strong increase in lactate concentrations and a concomitant depletion of muscle glycogen of exhausted tails relative to resting tails. No significant differences were found in either lactate or glycogen concentrations among the species examined. Duration of movement was negatively correlated with final lactate concentrations. The lack of differentiation in postautotomy energetic physiology in this group of species that have evolved under very different predation environments indicates that postautotomy muscle metabolism involves an overall conservative suite of characters.

Introduction

Tail autotomy, the self-induced tail separation from the body, is widespread among lizards (Bellairs and Bryant 1985; Arnold 1988; Fox and McCoy 2000). The vigorous movements of the detached tail are believed to aid escaping by diverting the predator's attention away from the lizard's body (Vitt et al. 1977; Dial and Fitzpatrick 1984). In addition, tail movement increases handling time as the predator attempts to consume it, further facilitating the lizard's escape (Daniels 1981; Medel et al. 1988).

Caudal autotomy is considered a primitive trait in lizards, but this mechanism has been retained only in evolutionary time when its benefits exceed its costs (Arnold 1988; Perez-Mellado et al. 1997). Because many lizards store substantial amounts of lipids in their tails, tail loss can reduce survival during unfavorable periods of the year (Avery 1974; Daniels 1984; Vitt and Cooper 1986). Moreover, intact tails play a significant role in locomotion in many lizards, especially for climbing species (Ballinger et al. 1979; Punzo 1982). Tails can also be important in courtship and territorial use and behavior (Fox et al. 1990; Martin and Salvador 1993*a*, 1993*b*, 1993*c*, 1997; Salvador et al. 1995, 1996). In many lizard species, tailless individuals lose social status (Fox and Rostker 1982; Schall et al. 1989; Martin and Salvador 1995; Salvador et al. 1995; but see Kaiser and Mushinsky 1994). Finally, lizards without tails are more susceptible to subsequent predator attacks (Congdon et al. 1974). In summary, the significant costs associated with tail shedding make caudal autotomy an expensive escape strategy and raise interesting questions about the environmental circumstances under which this strategy is beneficial to the animal.

The capacity for autotomy is often correlated with ecological parameters such as habitat preference or predator-prey interactions (Vitt et al. 1977; Dial and Fitzpatrick 1981). Differences among species in the ease of tail autotomy also appear to be related to differences in levels of predation pressure (Fox et al. 1994; Perez-Mellado et al. 1997). For example, Perez-Mellado et al. (1997) demonstrated that lacertid species from the Mediterranean mainland shed their tail more easily than insular taxa experiencing reduced predation pressure.

In most taxa, the shed tail thrashes around strongly for the first 1 or 2 min after autotomy, effectively distracting predators from the escaping lizard (Clark 1971). Past studies (Congdon et al. 1974; Dial and Fitzpatrick 1983) have shown that vigor and duration of tail thrashing not only influence the attention the predator pays to the tail but also increase handling time, hence facilitating the lizard's escape. Given the potential significance of tail thrashing duration to the survival of the lizard, it is reasonable to expect that this trait, together with its underlying metabolic processes, will be influenced by general ecological circumstances such as predation pressure.

Because blood supply to the tail muscles ceases after autot-

* E-mail: evalakos@biol.uoa.gr.

Physiological and Biochemical Zoology 78(5):828–838. 2005. 1522-2152/2005/7805-3170$15.00

Table 1: Species identities, numbers used, geographic origin, and known predator species (including supporting references) of the lizards included in this study

Species	Sample Size Male/Female	Localities	Predators	References
Lacerta graeca	18/14	Stymfalia Lake, Peloponnese, Greece	Snakes: 1, 2, 3, 4, 5, 6, 7 Birds: 1, 2, 3, 5, 6, 7, 8 Mammals: 1, 2	Chondropoulos 1989, 1996; Mayer et al. 1990; Maragou 1995; Handrinos and Akriotis 1997
Podarcis peloponnesiaca	33/37	Stymfalia Lake, Peloponnese, Greece	Snakes: 1, 2, 3, 4, 5, 6, 7 Birds: 1, 2, 3, 5, 6, 7, 8 Mammals: 1, 2	Chondropoulos 1989, 1996; Mayer et al. 1990; Maragou 1995; Handrinos and Akriotis 1997
Podarcis erhardii	30/20	Crete Island and surrounding islets, Greece	Snakes: 2, 6 Birds: 2, 3, 5, 6	Stepanek 1936; Chondropoulos 1989; Handrinos and Akriotis 1997
Podarcis gaigeae	11/9	Skyros Island, Greece	Snakes: 3, 4, 6, 7 Birds: 2, 3, 4, 5	Handrinos and Akriotis 1997; Cattaneo 1998
Podarcis milensis	22/19	Milos Island, Greece	Snakes: 3, 6, 8 Birds: 2, 4, 5, 7	Chondropoulos 1989; Adamopoulou et al. 1997; Handrinos and Akriotis 1997; Dimakis et al. 1999; Broggi 2000
Podarcis muralis	19/20	Mt. Mainalo, Peloponnese, Greece	Snakes: 1, 2, 3, 4, 5, 6, 7 Birds: 1, 2, 3, 5, 6, 7, 8 Mammals: 1, 2	Chondropoulos 1989, 1996; Mayer et al. 1990; Maragou 1995; Handrinos and Akriotis 1997

Note. Predator species identities are as follows: snakes: 1 = *Coluber najadum*, 2 = *Coluber gemonensis*, 3 = *Elaphe quatorlineata*, 4 = *Elaphe situla*, 5 = *Malpolon monspessulanus*, 6 = *Telescopus fallax*, 7 = *Vipera ammodytes*, 8 = *Macrovipera schweizeri*; birds: 1 = *Circaetus gallicus*, 2 = *Buteo buteo*, 3 = *Falco tinnunculus*, 4 = *Falco eleonorae*, 5 = *Tyto alba*, 6 = *Corvus corax*, 7 = *Corvus corone*, 8 = *Lanius collurio*; mammals: 1 = *Vulpes vulpes*, 2 = *Canis aureus*.

omy, any later tail movement can be supported only through anaerobic metabolism (Dial and Fitzpatrick 1983), which results in the production of lactic acid. Indeed, according to Dial and Fitzpatrick (1983), for those species that use tail autotomy as a principal escape tactic, tail lactate concentrations after thrashing ends rise to significantly higher levels than in intact tails even after an exhaustive escape trial. Unfortunately, with the exception of that of Meyer et al. (2002), no recent work has been carried out on lactate production in autotomized tails, whereas many researchers have worked on anaerobic metabolism in the whole body (e.g., Bennett and Licht 1972; Hailey et al. 1987; Gleeson and Dalessio 1989; Gleeson 1996).

Glycogen is the main substrate for muscle anaerobiosis and supplies the greatest quantity of ATP used by the muscles in postautotomy movement (Gleeson 1982, 1996). During glycolysis (the breakdown of carbohydrate into lactic acid under anaerobic conditions), glycogen is oxidized incompletely into lactate (Schmidt-Nielsen 1997). Thus, estimating the initial and final levels of both metabolites is the first crucial step in understanding the physiology of tail movement. Because lactate dehydrogenase (LDH) is the key anaerobic enzyme in the interconversion of lactate and pyruvate (Wolfe et al. 1988), dissimilarities in the total levels of LDH "may underlie differences in thrashing duration and activity" (Meyer et al. 2002, p. 83). Hence, in addition to glycogen and lactate levels, we compare LDH activity among all species included in this study. As mentioned above, many lizards also use their tail for energy storage. To elucidate underlying differences in energy storage and tail tissue composition that could affect duration of postautotomy movement, we also conducted a total lipid and protein content analysis.

In their original study, Dial and Fitzpatrick (1983) did not examine any relationships between various physiological variables (such as lactate production) and duration of movement in shed tails. Furthermore, they focused their experiments on only two lizard species from different families (*Scincidae* and *Iguanidae*). No information exists about variation in the physiology of tail autotomy within a single family.

In this study, we focus on a group of small lizards in the genera *Podarcis* and *Lacerta* (*Archaeolacerta*) that are widespread in Mediterranean ecosystems. In mainland ecosystems at least, these diurnal, terrestrial insectivores are subject to heavy predation pressure and have evolved rapid escape and tail-shedding behaviors. While mainland lizards are exposed to diverse communities of reptilian, avian, and mammalian predators, most of the islands in the Aegean are too small and too isolated to support significant predator populations (Chondropoulos 1989, 1996; Mayer et al. 1990; Maragou 1995; Handrinos and Akriotis 1997; Cattaneo 1998; see also Table 1). This sets the stage for an interesting comparison in tail energetics between congeneric taxa that have evolved under very different predation regimes.

The first aim of this study is to present new information on several physiological variables associated with muscle function and tail autotomy in six species of Mediterranean lacertid lizards. Second, we examine associations between duration of thrashing and levels of several physiological metabolites involved in tail muscle energetics (e.g., resting and exhausted levels of lactate and glycogen) using both a traditional statistical approach and phylogenetically corrected statistical analyses. Last, we compare variation in postautotomy tail activity among species occurring in the same general region but experiencing different predation pressures (Pafilis 2003) to evaluate the selective influence of environmental circumstances on the evolution of these traits.

Material and Methods

Species

We conducted this study on six species of lacertid lizards found in the northeast quadrant of the Mediterranean Basin (for collecting locations, see Table 1). Five of the species belong to the genus *Podarcis* while the last, *Lacerta graeca* (Bedriaga), belongs to the *Archaeolacerta* sister lineage. *Podarcis milensis* (Bedriaga) and *Podarcis gaigeae* (Werner) are small-bodied (snout-vent length [SVL] about 65 mm) Aegean Sea island endemics, restricted to the Milos and Skyros island groups, respectively. *Podarcis erhardii* (Bedriaga) is of similar size (SVL about 70 mm), though this species has a wider distribution on the southern Balkan Peninsula, many central Aegean islands, and Crete. *Podarcis muralis* (Laurenti), another similar-sized lizard (SVL 70 mm) has a broader distribution on the Balkan Peninsula as well as central and western Europe. *Podarcis peloponnesiaca* (Bibron & Bory) and *L. graeca* (SVL 75–85 mm) are narrow-range endemics of the Peloponnese Peninsula (southern Greece). The two species prefer different microhabitats (open flat ground vs. rock surfaces) within their broadly overlapping ranges.

All of the animals were collected in the wild during the nonreproductive period (October–November 1998, 1999) and in accordance with Greek National Law (Presidential Decree 67/81). They were subsequently held at the laboratory facilities of the biology department at the University of Athens. Animals were housed in couples in vitreous terraria (20 cm × 25 cm × 15 cm) on a substrate of sand; bricks and stones were provided as hiding places. The lizards were held at 25°C under a controlled photoperiod (12L : 12D) using fluorescent lights for a period of at least 4 wk before the experiments took place to allow adjustment to conditions in captivity. Additional incandescent lamps (60 W) allowed animals to thermoregulate behaviorally for 8 h/d. Animals had access to water ad lib. and were fed every other day with mealworms (*Tenebrio* sp.), with the exception of not receiving food for the last 2 d before an experiment.

Predation Simulation

Immediately before the start of an experiment, we allowed each animal to attain its preferred body temperature by placing it into a terrarium (1 m × 20 cm × 25 cm) outfitted to provide a range of thermal environments. A broad temperature gradient ranging from 17° to 55°C was achieved by placing two incandescent heating lamps (100 and 60 W) at one end and two ice bags at the other of the terrarium (for similar setup, see also Van Damme et al. 1986).

To simulate predation, we adopted a technique proposed by Perez-Mellado et al. (1997) that closely resembles a predator's attack. Lizards were placed in a terrarium covered with a rough cork mat, which allowed them to maintain good traction. To simulate the bite of a predator, we used a pair of calipers to grasp the tail at a distance of 20 mm from the cloaca. The use of calipers is an excellent technique to reduce pressure variation and standardize experimental conditions. If a lizard broke free, autotomy always took place just anterior to the point of contact with the calipers. Each trial lasted maximally 15 s. If at that point the tail was not shed, the animal was returned to its terrarium, and the procedure was repeated the next day. Once a tail was shed, we measured the time from the moment of autotomy to cessation of movement (determined as the moment at which all visible activity came to a complete stop for 10 s). These samples were termed "exhausted tails." In an alternative treatment group, we manually removed the tails using forceps at the same distance from the cloaca. This procedure, which resulted in the tail being shed rapidly (within 1–2 s), was used to determine baseline concentrations of lactate and other components at time zero (these are termed from now on "resting tails"'). To preserve physiological metabolites, exhausted tails were placed into liquid N_2 after the cessation of all movement whereas resting tails were placed into liquid N_2 immediately after separation from the body.

Tissue Lactate Determination

To determine lactate levels in tail muscle tissue, we placed the frozen tail fragment on an aluminum disk (diameter = 15 cm, thickness = 5 cm), which, in turn, was resting on a vertical aluminum shaft (diameter = 5 cm, height = 30 cm). By placing the lower end of the shaft in liquid N_2, heat was conducted away from the round table and the sample, therefore keeping the tail frozen during this stage of manipulation. Muscle tissue was separated from scales and bones using scissors and was stored at −80°C.

Muscle tissue (approximately 150 mg) was then homogenized (1 : 3 w/v) with 10% ice-cold perchloric acid in a cold pestle on ice. The homogenate was centrifuged at 4°C and 5,000 *g* for 10 min. The supernatant was then neutralized with 0.5 M Tris/0.5 M KOH and subsequently centrifuged at 4°C and 10,000 *g* for 10 min. The pellet was discarded, and the super-

natant was used for the estimation of total lactate concentration according to the method described by Hohorst (1965). Lactate concentration was expressed as milligrams lactate per grams tissue and milligrams lactate per milligrams protein.

Tissue Glycogen Determination

For glycogen determination, we followed the indirect method of Seifter et al. (1950) against a glucose standard after modifying the homogenization procedure. Specifically, tail muscle tissue was minced, and the pieces were boiled for 20 min in the presence of 30% KOH. Measurements were read at 620 nm using a spectrophotometer (Novaspec II, Pharmacia Biotech).

Tissue Lipid Determination

Extraction of total lipids was performed by homogenizing muscle tissue (30–40 mg) with 1.5 mL of a mixture containing two volumes of chloroform and one volume of absolute methanol. The homogenate was then centrifuged at 4°C and 3,000 *g* for 10 min. The pellet was used for protein analysis (see below), and the supernatant was used for the determination of total lipid concentration, using an appropriate kit (Chromatest) according to the method described by Alexis et al. (1985). A mixture of olive and corn oil (2 : 1 v/v) was used as the standard.

Tissue Protein Determination

Determination of total protein levels was performed using the Biuret method. Briefly, the pellet of centrifugation obtained from the lipid analysis (see above) was dissolved with 0.5 mL of 0.1 N NaOH and incubated at 37°C for 30 min with occasional vortexing. We diluted 50 μL of the sample with 950 μL of H_20 and added 4 mL of the Biuret reagent. The mixture was incubated for 30 min at room temperature, and the absorbance was read at 550 nm using a spectrophotometer (Novaspec II, Pharmacia Biotech). Bovine serum albumin (0.5 mg/mL–10 mg/mL) was used as a standard.

Tissue LDH Activity Determination

We measured LDH activity following the method of Kornberg (1955). We homogenized 0.1–0.15 g of a tissue sample in proportion 1 : 10 using a special solution (0.1 M Tris/HCl pH 7.5, 1 mM EDTA). The homogenate was centrifuged at 4°C and 12,000 *g* for 1 min. We then prepared a reaction mixture (3 mL) containing 0.1 M Tris/HCl pH 7.3, NADH 0.1% (w/v), 0.15 M pyruvate acid, 6 mM KCN, and double-distilled water. The reaction was initiated with the addition of 50 μL of the tissue homogenate; we then measured the decrease in absorption at 340 nm, in relation to time.

Statistical Analysis

We used one-way and two-way ANOVAs to simultaneously test for species, treatment (autotomy), and interaction effects on the physiological traits under consideration. An initial analysis of all physiological variables revealed a near universal lack of difference between the sexes. For all subsequent analyses, data from male and female lizards were analyzed together. Relationships between the different variables were examined using Pearson correlations. Statistical analysis followed that of Zar (1984).

Phylogenetic Analysis

Because conventional statistical methods frequently produce high Type I errors (Garland et al. 1993; Brashares et al. 2000), we repeated the correlation analyses between duration of movement and levels of lactate and glycogen by taking the phylogenetic relationships between the species into account. To do so, we first reconstructed the phylogenetic tree of the species used in this study based on previously published data (Fig. 1). Tree topology and branch length estimations were based on a combination of molecular and morphological data (Mayer and Tiedemann 1980, 1981; Lutz and Mayer 1985; Mayer 1986; Harris et al. 1998; Harris and Arnold 1999; Chondropoulos et al. 2000; Oliverio et al. 2000; Poulakakis et al. 2003). Divergence times for *P. erhardii* and *P. milensis* were calibrated using geological information on the isolation of the Crete and the Milos island groups, respectively (Hsü et al. 1977; Dermitzakis and

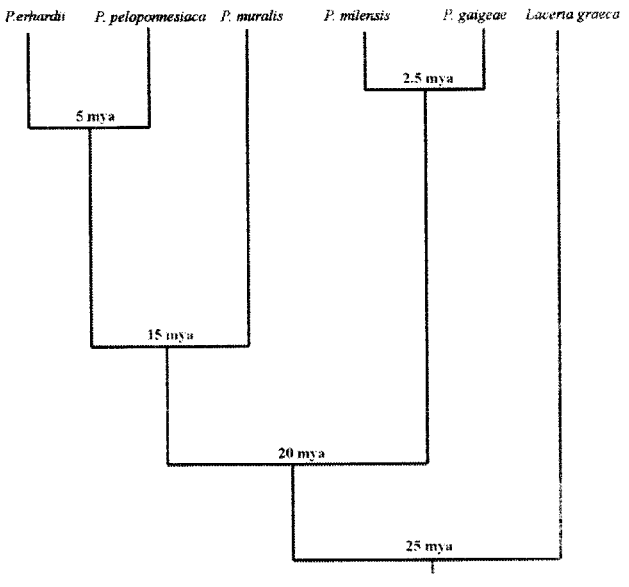

Figure 1. Hypothesized phylogenetic tree of the species used in this study. Tree topology is based on morphological and molecular data. Some divergence times (numbers at nodes given in millions of years ago [mya]) are calibrated using geological events.

Papanikolaou 1981). Justifications of tree topology and times of divergence are available upon request from the authors.

To control for phylogenetic nonindependencies, we calculated for each variable a set of standardized independent contrasts (Felsenstein 1985; Harvey and Pagel 1991) using the PDAP software (ver. 6.0; Garland et al. 2002; for methodological details, see Martins and Garland 1991; Garland et al. 1992, 1993; Bauwens and Diaz-Uriarte 1997). These programs calculate standardized contrasts for two continuous variables under examination and produce diagnostic screens that allow for evaluation of test assumption violations (Garland et al. 1993; Brashares et al. 2000). The final sets of independent contrasts were then analyzed using regression through the origin (for justification of this, see Grafen 1989; Garland et al. 1992).

Results

Postautotomy Tail Movement

Mean duration of the tail movement ranged between 6 and 8 min (range of all times = 2–15 min; Fig. 2). We detected no statistically significant differences in tail movement times among the species examined (ANOVA: $F_{5,153} = 0.96$, $P > 0.05$).

Lactate Accumulation

Lactate concentrations of resting and exhausted tails for all species examined are given in Table 2. As expected, we observed a strong increase in lactate concentrations in exhausted relative to resting tails (two-way ANOVA: $F_{1,172} = 109.23$, $P < 0.001$) but did not detect any statistically significant differences among the six species ($F_{5,172} = 0.26$, $P > 0.05$); the interaction term was also not significant ($F_{5,172} = 0.28$, $P > 0.05$). Very similar results were obtained when lactate accumulations were expressed in milligrams lactate per milligrams protein (Table 2; two-way ANOVA: species effect: $F_{5,130} = 0.19$, $P > 0.05$; treatment effect: $F_{1,130} = 63.9$, $P < 0.001$; interaction between the two factors: $F_{5,130} = 0.33$, $P > 0.05$).

Glycogen Depletion and LDH Activity

Glycogen concentrations in all species examined were significantly higher in resting than in exhausted tails (two-way ANOVA: $F_{1,131} = 109.23$, $P < 0.001$); no differences were detected between species (two-way ANOVA: $F_{5,131} = 0.703$, $P > 0.05$; interaction between treatment and species: $F_{5,131} = 0.32$, $P > 0.05$). LDH activity values for all six species are given in Figure 3. No statistically significant differences in LDH activity were detected among the species examined (ANOVA: $F_{5,62} = 0.06$, $P > 0.05$).

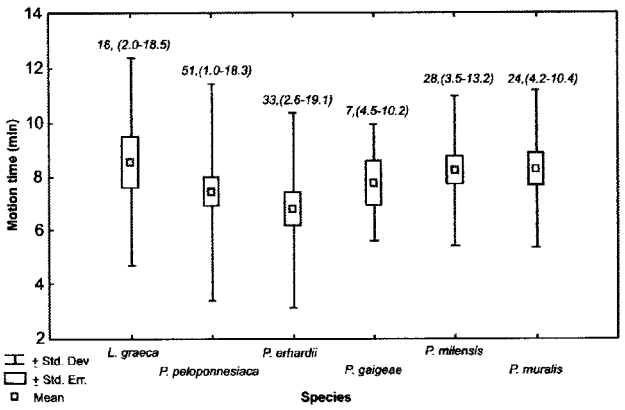

Figure 2. Mean duration of movement until exhaustion (min) in the autotomized tails of the six lacertid lizard species examined. Numbers above the bars represent the number of lizards; numbers in parentheses represent the range of duration for each species.

Lipid Concentration

Concentrations of total lipids in tail tissue before and after autotomy are given in Table 3. We failed to detect any significant differences in lipids either between resting and exhausted tails (two-way ANOVA: $F_{1,129} = 0.35$, $P > 0.05$) or between species (two-way ANOVA: $F_{5,129} = 1.04$, $P > 0.05$; interaction: $F_{5,129} = 0.94$, $P > 0.05$).

Protein Concentration

Protein concentrations in resting and exhausted tails for all examined species are provided in Table 3. We did not find any significant differences in protein concentrations either between resting and exhausted tails (two-way ANOVA: $F_{1,130} = 1{,}463$, $P > 0.05$) or between species ($F_{5,130} = 1.38$, $P > 0.05$; interaction: $F_{5,130} = 0.96$, $P > 0.05$).

Interspecies Relations

Despite the absence of statistically significant differences among species, correlation analyses between physiological variables constitute an important method to help elucidate the functional relationships between muscle metabolites. Pairwise correlations between selected physiological variables (time of movement, resting and exhausted lactate, resting and exhausted glycogen) for the six species examined are given in Table 4. The analysis was conducted twice, once using traditional statistical tests on the original, untransformed values and once among the independent contrasts of these traits (five contrasts based on six taxa). Both analyses produce the same results and point to a statistically significant negative relationship between resting lactate and resting glycogen ($r = -0.883$, $P < 0.05$ and $r = -0.924$, $P < 0.05$, respectively). Both tests also reveal a statistically significant negative relationship between mean final lac-

Table 2: Lactate concentrations (mg lactate/g fresh tissue and mg lactate/mg protein) in resting and exhausted tails in the six species examined

	Tissue (mg/g)				Protein (mg/mg)			
	Resting Tails		Exhausted Tails		Resting Tails		Exhausted Tails	
Species	Mean ± SD (Range)	*N*	Mean ± SD (Range)	*N*	Mean ± SD (Range)	*N*	Mean ± SD (Range)	*N*
Lacerta graeca	.78 ± .06 (.72–.86)	4	1.47 ± .21 (1.18–1.93)	16	.027 ± .004 (.0023–.036)	4	.050 ± .011 (.036–.074)	14
Podarcis peloponnesiaca	.75 ± .07 (.68–.85)	5	1.62 ± .33 (.92–2.58)	51	.028 ± .004 (.025–.034)	5	.056 ± .013 (.035–.083)	31
Podarcis erhardii	.76 ± .11 (.59–.85)	5	1.68 ± .38 (1.10–2.60)	33	.025 ± .005 (.020–.031)	5	.057 ± .017 (.033–.094)	23
Podarcis gaigeae	.82 ± .07 (.77–.82)	2	1.52 ± .26 (1.10–1.83)	7	.030 ± .005 (.027–.034)	2	.049 ± .007 (.037–.060)	6
Podarcis milensis	.72 ± .03 (.70–.75)	4	1.51 ± .27 (1.10–2.23)	28	.029 ± .004 (.025–.033)	4	.052 ± .010 (.040–.085)	22
Podarcis muralis	.75 ± .06 (.67–.83)	5	1.54 ± .28 (1.18–2.23)	24	.028 ± .006 (.025–.035)	5	.056 ± .013 (.040–.084)	21

Note. All pairwise comparisons in lactate levels between resting and exhausted tails are statistically significant. *N* = number of individuals in each test.

tate and mean time of tail movement ($r = -0.891$, $P < 0.05$ and $r = -0.86$, $P < 0.05$, respectively).

Discussion

Tail autotomy is considered an important antipredator mechanism in lacertid lizards (Arnold 1984; Perez-Mellado et al. 1997). Dial and Fitzpatrick (1984) first suggested that the high anaerobic capacity of autotomized lizard tails is an adaptation to predation because it allows for prolonged tail thrashing. Long-lasting tail activity has been shown to be particularly effective in diverting a predator's attention away from the lizard body and in increasing a predator's handling time necessary for tail ingestion (Dial and Fitzpatrick 1983). We found average tail thrashing duration to be similar to the times required for intact lizard bodies to reach exhaustion (e.g., 4.9 min for *Podarcis erhardii* in Hailey et al. 1987; see also Bennet and Licht 1972) but markedly longer than the duration of thrashing for autotomized tails reported from many other species of lizards. Specifically, average durations of tail movement for all taxa analyzed here are substantially longer than analogous times in *Eumeces fasciatus* (0.8 min), *Eumeces laticeps* (0.95 min), and *Holbrookia garnotii* (1.7 min; Vitt and Cooper 1986; Lochetto 1998) and closer but still exceeding those of *Hemidactylus mabouia* (5.2 min; Meyer et al. 2002) and *Scincella lateralis* (approximately 5 min; Dial and Fitzpatrick 1983). Moreover, the six lacertid species examined here appear to have average times of tail movement considerably longer than analogous times given in the only other study on lacertid lizard autotomy published to date (Perez-Mellado et al. 1997). These differences stem most likely from small sample sizes in previous studies, as well as differences in methodology (e.g., differences in criteria in when tail movement was considered to have ceased).

Glycogen is the primary substrate for muscle anaerobiosis (Gleeson 1982), and tail movement is mainly fuelled by glycogen metabolism (Bennett and Licht 1972; Gleeson 1982; Meyer et al. 2002). During anaerobic glycolysis occurring in tail muscles, glycogen converts into lactate and provides the energy required for muscle activity (Shah and Hiradhar 1974). In resting tail muscles, glycogen was found at levels similar to those in whole-body muscles (average resting tail glycogen = 7.5 vs. 8.2 mg/g in *Podarcis* hind limb muscle; Hailey et al. 1987). Anaerobic glycolysis converted most of that glycogen

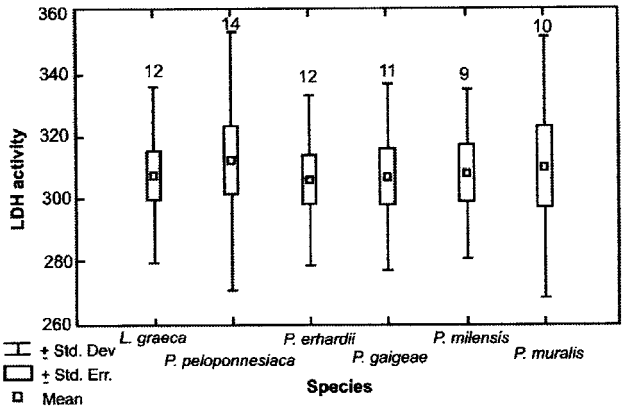

Figure 3. Lactate dehydrogenase (LDH) activity (μmol/min/g) measured in the tails of the six lizard species examined. Numbers above the bars represent the number of lizards used in each measurement.

Table 3: Glycogen, lipid, and protein concentrations (mg/g tissue) in resting and exhausted tails for the six species examined

	Glycogen				Lipid				Protein			
	Resting Tails		Exhausted Tails		Resting Tails		Exhausted Tails		Resting Tails		Exhausted Tails	
Species	Mean ± SD (Range)	*N*	Mean ± SD (Range)	*N*	Mean ± SD (Range)	*N*	Mean ± SD (Range)	*N*	Mean ± SD (Range)	*N*	Mean ± SD (Range)	*N*
Lacerta graeca	7.46 ± .30 (7.032–7.68)	4	2.15 ± .31 (1.90–3.10)[a]	14	169.46 ± 17.3 (145.20–186.23)	4	174.99 ± 48.4 (101.55–247.11)	14	29.83 ± 3.24 (25.58–33.24)	4	30.25 ± 3.22 (22.85–33.33)	14
Podarcis peloponnesiaca	7.59 ± .27 (7.22–7.85)	5	2.55 ± .65 (1.20–3.65)[a]	31	164.14 ± 48.7 (122.50–245.65)	5	166.67 ± 45 (98.50–286.23)	7	26.91 ± 2.11 (25.24–30.18)	5	29.31 ± 3.03 (22.34–34.34)	31
Podarcis erhardii	7.45 ± .25 (7.24–7.86)	5	2.29 ± .42 (1.76–3.44)[a]	24	198.92 ± 39.3 (145.70–244.33)	5	156.86 ± 41.7 (78.65–268.48)	24	31.10 ± 2.52 (27.79–34.44)	5	29.14 ± 3.61 (22.51–35.97)	23
Podarcis gaigeae	7.41 ± .63 (7.36–7.45)	2	2.21 ± .38 (1.85–2.68)[a]	6	130.90 ± 4.9 (127.4–134.4)	2	138.07 ± 22.4 (121.60–157.23)	6	26.77 ± 1.92 (25.41–28.13)	2	30.10 ± 2.47 (25.11–35.98)	6
Podarcis milensis	7.64 ± .15 (7.43–7.78)	4	2.29 ± .42 (1.85–3.42)[a]	22	126.72 ± 35.49 (97.50–174.70)	4	145.36 ± 17.4 (117.23–186.5)	22	24.72 ± 3.5 (22.34–29.84)	4	28.17 ± 2.69 (24.21–32.57)	22
Podarcis muralis	7.50 ± .21 (7.32–7.82)	5	2.33 ± .48 (1.87–2.88)[a]	21	145.48 ± 19.84 (117.56–165.24)	5	143.29 ± 20.6 (99.23–175.20)	21	26.77 ± 2.72 (23.71–30.52)	5	28.10 ± 2.25 (22.34–32.06)	21

Note. N = number of individuals. Mean is shown as milligrams/gram tissue.

[a] Statistically significant differences between resting and exhausted tails ($P < 0.05$).

into lactate so that glycogen levels in exhausted tails were much lower than in rested tails. After cessation of movement, tail glycogen levels had decreased to levels comparable to those in exhausted body tissues (average for the six species analyzed here = 2.303 vs. 3 mg/g for postexercise hind limb muscle; Hailey et al. 1987). Despite such similarities between autotomized tail and whole-body muscles in both pre- and postexercise glycogen levels, there appear to be significant differences in glycogen metabolism between the two systems. For example, the Cori cycle removes accumulated lactate in the liver (Brooks et al. 1973; Gaesser and Brooks 1980) while gluconeogenesis has been observed in whole-body muscles (Gleeson and Dalessio 1989); neither of these processes occurs in a severed tail.

Average lactate concentrations in shed tails after cessation of movement had increased approximately twofold over average baseline levels in resting tails for all species examined here. Although average lactate accumulations in exhausted tails reported here were comparable to those in *Anolis carolinensis* (1.64 mg/g tissue), they were lower than those in *S. lateralis* (2.71 mg/g tissue; Dial and Fitzpatrick 1983) or *H. mabouia* (2.25 mg/g tissue; Meyer et al. 2002). The divergence in these values is probably the result of among-species differences in the proportion of the tail composed of contractile versus noncontractile tissue. Indeed, once lactate concentrations were expressed as milligrams lactate per milligrams protein, we obtain very similar results as those reported for *H. mabouia* (Meyer et al. 2002).

Average lactate concentrations for exhausted tails reported here are very similar to exhausted whole-body values published elsewhere (e.g., see Table 1 in Bennett and Licht 1972). Nonetheless, the only study to examine whole-body lactate accumulation values in exhausted lacertids (Hailey et al. 1987) found significantly higher levels in *Podarcis taurica* and *P. erhardii* (2.28 and 2.17 mg/g tissue, respectively), thus suggesting that tolerance for metabolic lactate may be higher in the lizard body.

The fact that independent of the duration of movement, levels of accumulated lactate do not rise above 2–2.71 mg/g tissue (based on our results and related literature) while LDH activity is similar to those of previous studies (Meyer et al. 2002) indicates that the rate of lactate formation is slower in tail muscles. Although other rate-regulating enzymes such as phosphofructokinase (Bennett 1972) may be responsible for these patterns, their role in determining anaerobic capacity in autotomized lizard tails remains unknown (Meyer et al. 2002). Similarly, the accumulation of other anaerobic end products has not been widely studied, though some of them have been detected in certain lizard (Bennett 1982) and sea turtle taxa (Hochachka 1973). Further studies of the energetics of post-autotomy tail movement are needed in order to clarify the exact metabolic pathways involved in tail motion.

In summary, in comparing exhausted and resting tails, we detected differences in the levels of lactate and glycogen, with final levels of the first dropping and the second rising in relation to resting tissue. Interestingly, however, we did not find any pre- and postexercise differences in protein and lipid concentrations, suggesting that these are not involved in the short-term energetic metabolism associated with autotomy. This is not surprising, however, considering that the metabolism of

Table 4: Pairwise correlations between physiological variables for the six species examined before and after statistically removing the effects of phylogenetic nonindependencies

Traits	Time	Resting Lactate	Exhausted Lactate	Resting Glycogen	Exhausted Glycogen
Time	…*	−.116	−.883*	.495	.389
Resting lactate	−.05	…*	−.141	−.891*	−.45
Exhausted lactate	−.924*	−.19	…*	−.273	−.149
Resting glycogen	.163	−.86*	−.47	…*	.703
Exhausted glycogen	−.41	−.47	.576	.583	…*

Note. Elements above the diagonal are conventional between-species Pearson correlations of the original variables; elements below the diagonal are correlations based on independent contrasts obtained from the phylogenetic tree given in Figure 1.

* $P < 0.05$.

lipids and proteins is a time-consuming process that mainly takes place in whole-body tissues.

Comparing physiological traits among species despite the absence of significant interspecies differences can not only reveal interesting statistical patterns but also point to potentially important physiological relationships. A between-species correlation analysis of the physiological variables associated with autotomy reveals a strong negative relationship between duration of tail thrashing and final lactate concentrations. This lends support to the notion that accumulation of lactic acid may be at least partially responsible for termination of movement in the autotomized lizard tail. We also detect a statistically significant negative relationship between resting glycogen and resting lactate concentrations among species; this too underscores the biochemical relationship between these two variables and is likely the result of species-specific shifts along a continuum in muscle physiology.

Perhaps the most surprising result of this study is how little variation exists in several important physiological muscle metabolites among the species examined here. This is evidenced by both Figures 2 and 3, as well as from the lack of significance in among-species ANOVA comparisons. Reconstructed phylogenetic trees based on morphological and immunological data indicate that the species included in this study have been separated for up to 25 million years (Lutz and Mayer 1985). During that period, they have evolved at least partially in very different habitats under divergent environmental constraints. *Lacerta graeca*, *Podarcis muralis*, and *Podarcis peloponnesiaca* evolved in mainland ecosystems together with diverse communities of mammalian, avian, and reptilian predators and under high predation pressures. In contrast, *P. erhardii* and *Podarcis gaigeae* have been isolated since the Pleistocene on Aegean islands that today harbor only impoverished predator communities. *Podarcis milensis*, finally, although an island taxon, shares its habitat with the blunt-nosed viper (*Macrovipera schweizeri*), another Milos endemic and a demonstrated lizard predator (Adamopoulou et al. 1997).

A review of the published literature suggests that Aegean predator communities today, and likely in the past as well, are more diverse on mainland study sites than on island study sites (Table 1). Several mainland species of reptilian hunters (e.g., *Malpolon monspessulanus*, *Vipera ammodytes*), avian raptors (*Circaetus gallicus*, *Lanius collurio*), and mammalian mesopredators (*Vulpes vulpes*, *Canis aureus*), all of which regularly consume lizards, are absent from the islands. Similar conclusions of relaxed predation pressure on islands have been reported from other regions of the world (Curio 1976; Arnold 1984, 1988; Stone et al. 1994; Blazquez et al. 1997; Perez-Mellado et al. 1997; Cooper et al. 2004). Lack of predators is considered to be responsible for the evolution of fearlessness in island endemics, as well as for the significant population declines these species experience following the introduction of exotic predators.

Beyond the demonstrated reduced diversity of predator species on islands, ecological factors suggest that island ecosystems may also have lower densities of predator populations. Indeed, because of reduced average rainfall, as well as a concomitant productivity drop in arid Aegean island ecosystems (Handrinos and Akriotis 1997), it is reasonable to expect that predator densities are also lower on the islands than in wetter and more productive mainland habitats. Although predation pressure is probably the most important driver of capacity for caudal autotomy, other factors may also influence the ability of a species to shed its tail. Specifically, for insular Mediterranean ecosystems, which are characterized by limited food availability over long periods of time (Fuentes 1984; Brown and Perez-Mellado 1994) and where many species of lizards may store substantial amounts of lipids in their tails (Avery 1974; Vitt and Cooper 1986; Wilson 1992), the energetic cost of caudal autotomy can be particularly severe. Consequently, tail shedding may be a relatively more expensive strategy for island taxa than for mainland taxa (although our inability to detect a difference in tail lipid concentrations between mainland and island taxa would not support this idea).

In conclusion, both diversity and densities of patent lizard predators vary greatly between the regions studied. Because vigor and duration of thrashing have been shown to effectively distract predators and increase handling time (Daniels 1981; Medel et al. 1988), one would expect lizard populations evolving under higher predation pressures to exhibit not only longer tail thrashing times but also corresponding changes in underlying physiological muscle characteristics. Instead, we find that the six species examined here show remarkably little variation in concentrations of several physiological traits (LDH, glycogen, lactate, lipids, and protein) associated with the energetics of movement in the autotomized tail. This suggests that in contrast to ease of autotomy (Perez-Mellado et al. 1997; Cooper et al. 2004), the physiological pathways underlying muscle movement in a shed tail appear to be very conservative and not apt to rapid evolutionary change. One possible explanation for this is that the same metabolic processes that underlie thrashing of a shed tail are also responsible for muscle performance during burst locomotion. Hence, any selection on the lizard population driven by varying tail thrashing performances will also affect other crucial aspects of muscle-based performance such as sprint speed. As a result, physiologic pathways may already be optimized and are not likely to respond to further selection.

Acknowledgments

This study was supported by grants from the PENED (Research Capacity Support Program) 99 project of the General Secretariat of Research, Greek Ministry of Development (ED231), and the Program for Modern Greek at the University of Michigan. We would like to thank T. Garland for insightful comments regarding the phylogenetic analysis of the data as well as three anonymous reviewers. J. Howard read the final version of the manuscript. We would also like to thank P. Lymberakis for his assistance in the field. All experimental procedures were in full compliance with Greek national legislation on the scientific use and protection of wildlife.

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.

Alexis M., E. Papaparaskeva-Papoutsoglou, and V. Theochari. 1985. Formulation of practical diets for rainbow trout (*Salmo gardneri*) made by partial or complete substitution of fish meal by poultry by-products. Aquaculture 50:61–73.

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. 235–273 in C. Gans and R.B. Huey, eds. Biology of the Reptilia. Vol. 16. Ecology B: Defense and Life History. Liss, New York.

Avery R.A. 1974. Storage lipids in the lizard *Lacerta vivipara*: a quantitative study. J Zool (Lond) 173:419–425.

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

Bauwens D. and R. Diaz-Uriarte. 1997. Covariation of life-history traits in lacertid lizards: a comparative study. Am Nat 149:91–111.

Bellairs D.A. and S.V. Bryant. 1985. Autotomy and regeneration in reptiles. Pp. 301–410 in B.C. Gans and F. Billet, eds. Biology of the Reptilia. Vol. 15. Development. Wiley, New York.

Bennett A.F. 1972. A comparison of activities of metabolic enzymes in lizards and rats. Comp Biochem Physiol 42B:637–647.

———. 1982. The energetics of reptilian activity. Pp. 155–199 in B.C. Gans and F.H. Pough, eds. Biology of Reptilia. Vol. 12. Physiology. Academic Press, New York.

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

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.

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

Brooks G., K. Brauner, and R.G. Cassens. 1973. Glycogen synthesis and metabolism of lactic acid after exercise. Am J Physiol 224:1162–1166.

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

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

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

———. 1996. Further information on the herpetofauna of the Lake Stimfalia, NE Peloponnisos, Greece. Newsl Hell Zool Soc 28:3–4.

Chondropoulos B.P., S. Fraguedakis, N. Tsekoura, G. Tryfonopoulos, P. Pafilis, and E.D. Valakos. 2000. Contribution to the study of the genetic variability and taxonomic relationships among five lizard species of the family *Lacertidae* from Greece. Belg J Zool 130:37–41.

Clark D.R. 1971. The strategy of tail autotomy in the ground skink *Lygosoma laterale*. J Exp Zool 176:295–302.

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. Perez-Mellado, and L.J. Vitt. 2004. Ease and effectiveness of costly autotomy vary with predation intensity among lizard populations. J Zool (Lond) 262:243–255.

Curio E. 1976. The Ethology of Predation. Springer, Berlin.

Daniels C.B. 1981. The Role of Caudal Lipid in the Adaptive Strategy of Tail Autotomy in the Gekkonid *Phyllodactylus marmoratus* (Gray, 1844). BS thesis. University of Adelaide.

———. 1984. The importance of caudal lipids in the gecko *Phyllodactylus marmoratus*. Herpetologica 40:337–344.

Dermitzakis M. and D. Papanikolaou. 1981. Paleogeography and geodynamics of the Aegean region during the Neogene. Seventh International Congress on Mediterranean Neogene, Athens. Annu Geol Pays Helleniques 30:245–289.

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.

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

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

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. 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., 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.

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

Fuentes J.A. 1984. Evolution of lizard niches in Mediterranean habitats. Pp. 417–444 in F. Di Castri, D.W. Goodall, and R. Specht, eds. Mediterranean Type Shrublands: Ecosystems of the World. Vol. 11. Elsevier, Amsterdam.

Gaesser G.A. and G.A. Brooks. 1980. Glycogen repletion following continuous and intermittent exercise to exhaustion. J Appl Physiol 49:722–728.

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.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., P.E. Midford, J.A. Jones, A.W. Dickerman, and R. Diaz-Uriarte. 2002. PDAP: Phenotypic diversity analysis programs. Version 6.0. Available at http://www.biology.ucr.edu/people/faculty/Garland/PDAP.html.

Gleeson T.T. 1982. Lactate and glycogen metabolism during and after exercise in the lizard *Sceloporus occidentalis*. J Comp Physiol 146:79–84.

———. 1996. Post-exercise lactate metabolism: a comparative review of sites, pathways, and regulation. Annu Rev Physiol 58:565–581.

Gleeson T.T. and P.M. Dalessio. 1989. Lactate and glycogen metabolism in the lizard *Dipsosaurus dorsalis* following exhaustive exercise. J Exp Biol 144:377–393.

Grafen A. 1989. The phylogenetic regression. Philos Trans R Soc Lond B Biol Sci 326:119–157.

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

Handrinos G. and T. Akriotis. 1997. Birds of Greece. Helm & Black, London.

Harris D.J. and E.N. Arnold. 1999. Relationships of wall lizards *Podarcis* (Reptilia: Lacertidae) based on mitochondrial DNA sequences. Copeia 1999:749–754.

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 R Soc Lond B Biol Sci 265:1939–1948.

Harvey P.H. and M.D. Pagel. 1991. The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford.

Hochachka P.W. 1973. Multiple end products of anaerobiosis in the green turtle *Chelonia mydas mydas*. Physiologist 16: 373–386.

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

Hsü K.J., L. Montadert, D. Bernoulli, M.B. Cita, A. Erickson, R.E. Garrison, R.B. Kidd, F. Melieres, C. Müller, and R. Wright. 1977. History of the Mediterranean salinity crisis. Nature 267:399–403.

Kaiser B.W. and H.R. Mushinsky. 1994. Tail loss and dominance in captive, adult male *Anolis sagrei*. J Herpetol 28:342–346.

Kornberg A. 1955. Lactic dehydrogenase of muscle. Pp. 705–707 in S.P. Colowick and N.O. Kaplan, eds. Methods of Enzymology. Vol. 1. Academic Press, New York.

Lochetto S. 1998. Autotomy and Predator Distraction in Lizards: Is a Regenerated Tail as Effective as the Original? Undergraduate honors thesis. University of Miami.

Lutz D. and W. Mayer. 1985. Albumin evolution and its phylogenetic and taxonomic implications in several lcertid lizards. Amphib-Reptilia 6:53–61.

Maragou P. 1995. The herpetofauna of Stimfalia Lake, Peloponnisos. Newsl Hell Zool Soc 26:1.

Martin J. and A. Salvador. 1993*a*. Tail loss consequences on habitat use by the Iberian rock lizard, *Lacerta monticola*. Oikos 65:328–333.

———. 1993*b*. Tail loss reduces mating success in the Iberian rock-lizard. Behav Ecol Sociobiol 32:185–189.

———. 1993*c*. Thermoregulatory behaviour of rock lizards in response to tail loss. Behaviour 124:123–136.

———. 1995. Effects of tail loss on activity patterns of rock lizards, *Lacerta monticola*. Copeia 1995:984–988.

———. 1997. Effects of tail loss on the time-budgets, movements, and spacing patterns of Iberian rock lizards, *Lacerta monticola*. Herpetologica 53:117–125.

Martins E.P. and T. Garland Jr. 1991. Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. Evolution 45:534–557.

Mayer W. 1986. Proteinelectrophoretic investigations in *Podarcis erhardii* and *Podarcis peloponnesiaca* (Lacertidae, Sauria). Biol Gallo-Hell 12:459–462.

Mayer W., K. Richter, and W. Kammel. 1990. Kartierung der Herpetofauna des Beckens von Feneos (Griechenland: Nord-Peloponnes). Herpetozoa 2:87–106.

Mayer W. and F. Tiedemann. 1980. Elektrophoretische Untersuchungen an europaeischen Arten der Gattungen *Lacerta* und *Podarcis*. I. Die *Podarcis*-Formen der griechischen Inseln Milos und Skiros. Sonderdr Z Zool Syst Evol 18:147–152.

———. 1981. Elektrophoretische Untersuchungen an europaeischen Arten der Gattungen *Lacerta* und *Podarcis*. II. Zur systematischen Stellung der Eidechsen auf der Insel Piperi (Noerdliche Sporaden, Griechenland). Zool Anz 207:143–150.

Medel R.G., J.E. Jimenez, 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.

Meyer V., M.R. Preest, and S.M. Lochetto. 2002. Physiology of original and regenerated lizard tails. Herpetologica 58:75–86.

Oliverio M., M.A. Bologna, and P. Mariottini. 2000. Molecular biogeography of the Mediterranean lizards *Podarcis* Wagler, 1830 and *Teira* Gray, 1838 (Reptilia, Lacertidae). J Biogeogr 27:1403–1420.

Pafilis P. 2003. Adaptations of Lacertids Based on Their Thermal Biology, Metabolic Rate and Phylogenetic History. PhD thesis. University of Athens. (In Greek with English summary.)

Perez-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 (Lond) 243:553–541.

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

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

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.

Salvador A., J. Martin, P. Lopez, and J. Veiga. 1996. Long-term effect of tail loss on home-range size and access to females in male lizards (*Psammodromus algirus*). Copeia 1996:208–209.

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.

Schmidt-Nielsen K. 1997. Animal Physiology, Adaptation and Environment. 5th ed. Cambridge University Press, Cambridge.

Seifter U., S. Dayton, B. Novic, and E. Muntwyler. 1950. The estimation of glycogen with anthrone reagent. Arch Biochem 24:191–200.

Shah R.V. and P.K. Hiradhar. 1974. Studies on glycogen, glycogen synthetase and respiratory quotient in the normal and regenerating tail of the house lizard, *Hemidactylus flaviviridus*. Neth J Zool 24:1–9.

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

Stone P.A., H.L. Snell, and H.M. Snell. 1994. Behavioral diversity as biological diversity: introduced cats and lava lizard wariness. Conserv Biol 8:569–573.

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.

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

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

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

Wolfe R.R., F. Jahoor, and H. Miyoshi. 1988. Evaluation of the isotopic equilibration between lactate and pyruvate. Am J Physiol 254:E532–E535.

Zar J.H. 1984. Biostatistical Analysis. 2nd ed. Prentice Hall, Englewood Cliffs, NJ.