

COMPARATIVE DATA ON REPRODUCTION IN *PODARCIS ERHARDII*,
PODARCIS PELOPONNESIACA, AND *PODARCIS TAURICA* (REPTILIA,
SAURIA, LACERTIDAE)

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ABSTRACT

Variation in the reproductive traits of Greek populations of *Podarcis erhardii*, *P. peloponnesiaca*, and *P. taurica* living in similar habitats along the same latitude was examined. Female body size, clutch size, and egg volume were determined. In all three species, clutch size was positively correlated with maternal body size. *P. erhardii* appears to modulate its reproductive effort by means of variation in both egg size and number. On the other hand, egg size in *P. peloponnesiaca* and *P. taurica* has probably been optimized, and an increase in reproductive effort would result in the production of a larger number of eggs.

INTRODUCTION

One of the most important challenges faced by evolutionary ecologists is the study of life history variables (Vitt and Price, 1982) and whether their nature enhances the survival of the species. Reproduction may be considered such a variable. Until recently, most studies of European lacertid lizards have been mainly descriptive and, though informative, are limited to life history theory. Comparative studies allow for the identification of general patterns among lizards that live in similar habitats and, in some cases, also reveal underlying mechanisms that could affect the adaptability of a species (Vitt, 1986). Recently, there has been an increase in the number of comparative studies in reproductive traits (Vitt, 1986; Werner, 1989; Pollo and Pérez-Mellado 1990; Frankenberg and Werner, 1992; Bauwens and Diaz-Uriarte, 1997).

Podarcis erhardii (Bedriaga, 1882), *Podarcis peloponnesiaca* (Bibron and Bory, 1833), and *Podarcis taurica* (Pallas, 1814) are phylogenetically related (Olmo et al., 1993). Also, they are similar in body shape, active searching/foraging mode, arthropod-based diet and thermoregulatory behavior (Chondropoulos and Lykakis, 1983; Valakos, 1990; Maragou, 1997). Furthermore, they can be considered the most abundant lacertids in Greece.

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Our goal was to study some reproductive characteristics of these three species and examine whether their reproductive strategy had remained the same, in spite of differences in their biotopes, or had adapted. Moreover, we provide new data on the reproductive ecology of *P. erhardii* and *P. peloponnesiaca*.

MATERIALS AND METHODS

Podarcus erhardii is distributed in the south of the Balkan peninsula. More specifically, in Greece it is found in the eastern Peloponnisos, most of the remaining Greek mainland, the majority of the Aegean Islands, and in Crete (Gruber, 1997). On the Greek mainland, however, its range is rather discontinuous. It is a highly differentiated polytypic species, especially in the insular ecosystems of the Aegean where it can be found at altitudes up to 1000 m. It typically inhabits dry, often rocky places with low, dense, xerophilous bushy vegetation. It climbs to some extent but not extensively. In *P. erhardii*, the mating season starts in February and reaches its peak during April to mid-May. Large oviductal eggs are present from March to June. The mean clutch size is 2.42 eggs. The incubation period lasts about 40 days and hatchlings appear from mid-June to September (Valakos, 1990).

P. peloponnesiaca is a Greek endemic species confined to Peloponnisos. It is found from sea level to 1600 m asl in a wide variety of habitats, but especially in dry, often broken and stony areas (Bringsøe, 1985, 1986; Buttle, 1987; Sofianidou, 1997). Although *P. peloponnesiaca* is basically a ground dweller, it is frequently seen on stones, low walls, etc., and sometimes climbs, although rather clumsily. Published data on reproduction of this species are limited. First copulations occur in March, and between one and two clutches of 2–4 eggs are produced annually (Maragou, 1997). Incubation period at 28 °C lasts 40 days and the hatchlings emerge from July to the beginning of August (Bringsøe, 1986).

P. taurica shows the broadest range, occurring from Greece north to Hungary and the northern coasts of the Black Sea. In Greece, it is distributed on the mainland and the Ionian islands (Chondropoulos, 1986, 1997). The main habitats of *P. taurica* are typically flat, open areas with low vegetation that receive a lot of sunshine. The species is found at altitudes of 0–2000 m or even higher. It is a ground-dwelling lizard with limited climbing ability, and is usually seen in rural areas, forest clearings, salt flats, gardens, olive groves, country road sides, etc.; it is always clearly associated with vegetated areas. Its reproductive period starts at the end of March with the majority of copulations occurring from mid-April to early May. The first oviductal eggs are present in mid-April and last until mid-July, with the peak from mid-May to mid-June. The mean clutch size is 5.6 eggs. The incubation period in *P. taurica* lasts 4–6 weeks, and the hatchlings emerge from mid-July to early September (Chondropoulos and Lykakis, 1983; Chondropoulos, 1984).

The three examined species are heliothermic lacertids that feed mainly on arthropods and are characterized as thermoregulators. All three species are protected by Directive 92/43/EEC (Annex IV), the International Convention of Bern (Annex II), and, in Greece, by Presidential Decree 67/1981.

The authors collected all material during spring. A total of 81 alcohol-preserved specimens of female lizards was examined: 33 *P. erhardii* from Naxos Isl. (Aegean Islands), 19 *P. peloponnesiaca* from the area of Stymfalia Lake (Peloponnisos), and 29 *P. taurica* from western Peloponnisos and Zakynthos Isl. (Ionian Islands). *P. taurica* and a few *P. peloponnesiaca* specimens were deposited in the Zoological Museum of the University of Patras. *P. erhardii* and the remaining *P. peloponnesiaca* specimens belong to the Herpetological Collection of the Section of Animal and Human Physiology of the University of Athens.

Lacertid eggs are not completely cleidoic and, depending on environmental conditions, their mass and dimensions may change quite rapidly after oviposition (Frankenberg and Werner, 1992), thus affecting the results of comparative studies. Therefore, we exclusively used large oviductal eggs, larger than 8 mm, from already-preserved females (Frankenberg and Werner, 1992). This action is also sound for conservation reasons. All specimens had been uniformly stored in 70% ethanol for periods usually longer than one year. The eggs had not been previously removed from the oviducts.

For each lizard the following data were noted: (a) body length (snout-vent, SVL) taken with a vernier caliper to the nearest 0.1 mm, (b) number and type of eggs in each oviduct, (c) length and width of all oviductal eggs to the nearest 0.01 mm by means of a micrometer scale in the stereoscope objective lens, and (d) date and place of capture.

Minimum SVL at sexual maturity was assessed by the presence of enlarged ovarian follicles (>3 mm in diameter) or oviductal eggs (Vitt, 1983; Castilla et al., 1992).

The volume of each egg was calculated using the equation: $V = 4/3\pi(LW^2/8)$, where V is the egg volume, and L and W are the length and width of the egg, respectively, in mm. The average volume of all shelled eggs measured in a female constituted the characteristic egg volume for that individual. These individual averages were then used to calculate the egg volume for each species (Frankenberg and Werner, 1992). Egg volume is less susceptible than egg mass to the possible distorting effects of fixation and storage in alcohol (Guillete et al., 1988). Moreover, our material was uniformly preserved; therefore, we believe that storage and fixation did not affect the results of intraspecific comparison.

RESULTS

The descriptive statistics of the reproductive characteristics for the species examined are summarized in Table 1. In the case of *P. taurica*, the females from Peloponnisos have different mean clutch size x (t -test $t = 3.9$, $df:27$, $p < 0.05$) than those from the Ionian (in Peloponnisos $x = 5.77 \pm 2.16$, range 4–10, and in the Ionian Islands $x = 3.55 \pm 0.94$, range 2–5).

The smallest *P. peloponnesiaca* female with oviductal eggs had an SVL of 60 mm. This figure is taken as an estimate of the minimum size for sexual maturity. The smallest reproductive females of *P. erhardii* and *P. taurica* had SVLs of 48 mm and 55 mm, respectively.

Analysis of covariance (ANCOVA), with SVL as a covariate to eliminate side effects

Table 1
Descriptive statistics of reproductive parameters for the examined species

Species		N	Mean	Min	Max	SD
<i>Podarcis erhardii</i>	SVL	33	59.11	48	66	4.35
	Clutch size	33	2.64	1	5	1.08
	Egg length	87	8.47	3	18.3	2.26
	Egg width	87	5.99	2.5	10.6	1.62
<i>P. peloponnesiaca</i>	SVL	19	69.58	60	82	4.54
	Clutch size	19	3.52	2	5	0.96
	Egg length	68	9.62	3.28	16.56	3.78
	Egg width	68	7.12	3.8	10	1.61
<i>P. taurica</i>	SVL	29	65.53	55	79.5	5.01
	Clutch size	29	4.24	2	10	1.74
	Egg length	126	12.32	10	14	0.83
	Egg width	126	6.87	5.7	7.9	0.47

N—sample size, SD—standard deviation

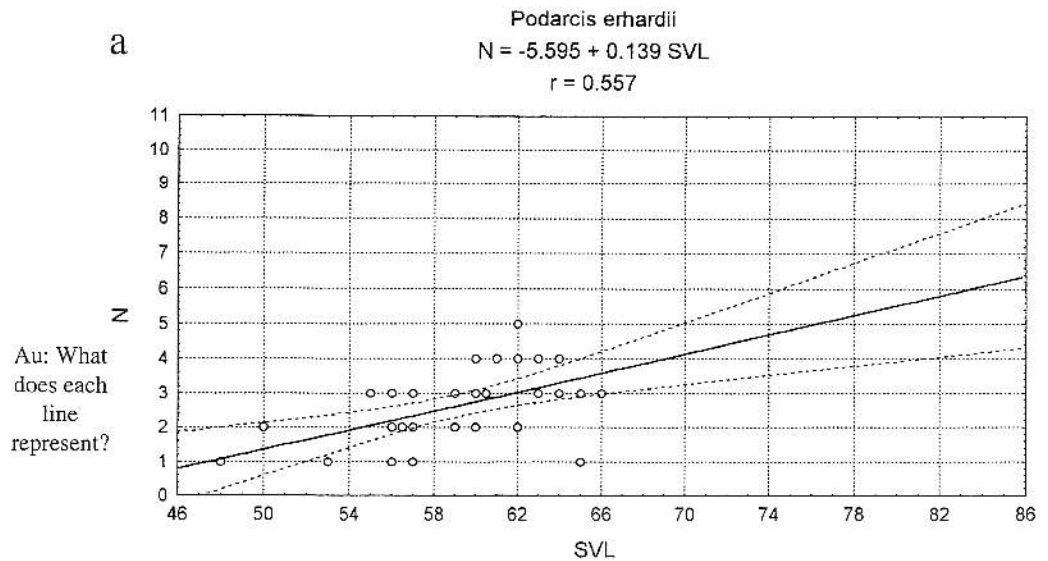


Fig. 1. a–c: Relationship of clutch size (N) to snout–vent length (SVL). (a) *Podarcis erhardii* (Standard error of estimate: 0.914; Intercept: 1.69; Slope: 0.139); (b) *Podarcis peloponnesiaca* (Standard error of estimate: 0.774; Intercept: 2.79; Slope: 0.13); (c) *Podarcis taurica* (Standard error of estimate: 1.533; Intercept: 1.98; Slope: 0.194). Dotted lines: 95% confidence interval.

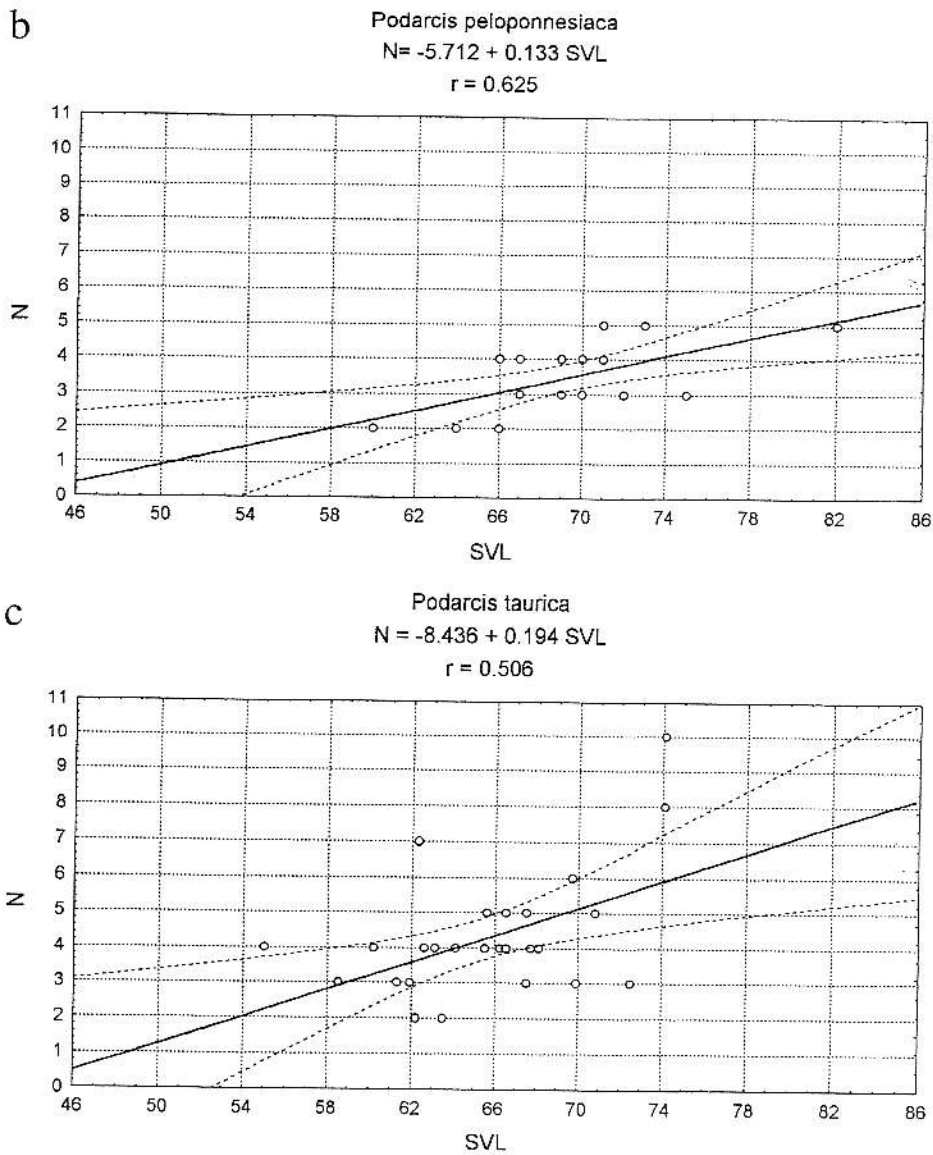


Fig. 1 continued.

from differences in the mean SVL of the three species, was used to determine whether clutch size was related to body size. Clutch size was correlated with SVL instead of body mass because it is a less variable measure of body size than mass and unaffected by storing conditions (Ramirez-Bautista et al., 1995).

Table 2

Partial correlations between reproductive data for the three examined species. The variable in parenthesis is the one held constant

Species	R		
	N-SVL (V)	SVL-V (N)	N-V (SVL)
<i>Podarcis erhardii</i>	0.43*	0.06	0.47*
<i>P. peloponnesiaca</i>	0.78*	0.18	-0.14
<i>P. taurica</i>	0.63*	0.03	-0.09

R—Coefficient of partial correlation; SVL—snout-vent length, N—clutch size, V—egg volume, *—statistically significant correlation ($p < 0.05$); otherwise the correlation is not significant.

The comparison among *P. erhardii*, *P. peloponnesiaca*, and *P. taurica* revealed significant differences in the clutch size [ANCOVA (with SVL as a covariate), $p < 0.05$]. However, post hoc analysis showed that this difference was due to the *P. taurica* sample from the Greek mainland (Tukey's-test, $p < 0.05$).

The three species examined showed significantly positive correlations between clutch size and maternal SVL (Fig. 1). Regression slopes for all species were parallel (ANCOVA, $F_{2,61} = 1.74$, $p > 0.05$).

Mean egg volume for a female's clutch did not increase significantly with SVL. We used ANCOVA, with species as the grouping variable, to determine which of the three variables (SVL, clutch size, egg volume) actually correlated in each species. In *P. peloponnesiaca* and *P. taurica*, no significant partial correlation between egg volume and clutch size or SVL was found. In *P. erhardii*, the partial correlation was significant between egg volume and clutch size but insignificant between egg volume and SVL. The relation between the three variables is presented for each species in Table 2 and suggests two categories of reproductive strategy: (1) in response to increasing body size the number of eggs, but not their volume, increases (e.g., *P. peloponnesiaca* and *P. taurica*); and (2) with increasing maternal size, both the total number and the volume of eggs increase (e.g., *P. erhardii*).

DISCUSSION

Our results regarding smallest SVL at sexual maturity are similar to those reported for *P. erhardii* and *P. taurica* of 50 mm and 52.8 mm, respectively, (Chondropoulos and Lykakis, 1983; Chondropoulos, 1984; Valakos, 1990). Data on this reproductive trait for *P. peloponnesiaca* are presented here for the first time.

Significant differences in the clutch size of different populations of *P. taurica* have been found previously (Chondropoulos and Lykakis, 1983) and have been attributed mainly to respective body size differences. However, our data indicate that clutch volume is independent of changes in population SVL, and the observed difference could be due to variation in climate. Clutch size is a reproductive trait that has been shown to

be correlated with environmental conditions, resource availability, and changes in latitude (Vitt 1983; Taylor et al., 1992; Michaud and Echternacht, 1995).

In the three species examined, clutch size is related to female body size. Since the regression slopes were similar, we suggest that the three species follow the same pattern of maximizing clutch size with SVL, as do most lizards with variable clutches reported so far (Tinkle et al., 1970; Castilla and Bauwens, 1989; Frankenberg and Werner, 1992).

As the available amount of energy for reproduction is limited, increase in offspring size is accompanied by a decrease in clutch size (Bauwens and Diaz-Uriarte, 1997 and references therein), and a balance is normally established between egg number and the general energy expenditure per offspring. Nevertheless, more than one combination of egg number and egg volume can be considered optimal, even within a species (Tinkle et al., 1970; Castilla and Bauwens, 1989; Michaud and Echternacht, 1995). It has been shown that in reptile populations a number of life history characteristics may vary in response to different environmental factors (Ferguson et al., 1990 and references therein). It is interesting to note that variation in reproductive output is due mostly to changes in clutch size and number of clutches per season, and not in egg size and egg volume. (Brockelman, 1975).

Egg volume and SVL did not yield statistically significant correlations in the three species examined. In *P. erhardii*, egg volume was not significantly correlated with SVL, since small females were able to produce large eggs, but it correlated significantly with clutch size, indicating that, as a response to larger body size, animals try to increase both the number and the volume of their eggs. The Mediterranean-type ecosystems in the islands where *P. erhardii* has been mainly differentiated are patchy and characterized by fluctuating, unpredictable conditions, limited resources, and permit a rather long activity period for the species. These environmental factors also influence the diet of *P. erhardii*, which has been shown to differ significantly between the dry summer and the wet winter as a result of distinct variations in available prey (Valakos, 1990). Moreover, *P. erhardii* has a comparatively longer annual and daily activity period than *P. peloponnesiaca*, which is only partially active during winter (Maragou, 1997), and *P. taurica*, which hibernates from early November to late February (Chondropoulos and Lykakis, 1983).

Proportionally larger eggs need a longer incubation period at a given temperature, but result in larger offspring that are both faster (Sinervo, 1990) and able to prey upon a wider variety of prey than smaller ones, making them competitively more likely to survive to maturity (Congdon et al., 1978; Michaud and Echternacht, 1995).

On the other hand, in *P. peloponnesiaca* and *P. taurica*, egg volume is not significantly correlated with both SVL and clutch size; larger females produce more, rather than larger, eggs. It seems that egg size has been optimized by natural selection (Congdon et al., 1978), and an increase in energy expenditure on reproduction, resulting from larger female body size, would result in the production of more eggs of about the same size. This strategy could also be advantageous in terms of predator intensity: if we use the number of individuals with broken or regenerated tails as an index, the percentage in *P. taurica* rises to 43% (Chondropoulos and Lykakis, 1983) whereas in *P. erhardii* it is lower than 10% (Valakos, 1990). Another explanation is related to the

increased incubation period of larger eggs (Sinervo, 1990). This could result in hatchlings that emerge very late in the reproductive period, thus counterbalancing all possible benefits associated with increased egg size (Bauwens and Diaz-Uriarte, 1997). Published data on mating, the appearance of oviductal eggs, and hatchling emergence show that *P. peloponnesiaca* and *P. taurica* have shorter activity and reproductive periods than *P. erhardii*. Finally, both species are found in areas with more predictable climatic conditions, as well as higher humidity (Mauromatis, 1978), where neonates can easily encounter food (e.g., see Karamaouna, 1987) regardless of their size. This prey abundance is depicted in the diet of *P. peloponnesiaca*, which does not differ among the seasons and neither does the percentage of the commonest arthropods in the biotope, which are also the main prey groups. Also, in agreement with the theory that predicts an expansion of the trophic niche in drier and hotter ecosystems, using the Levins index, the maximum niche breadth of *P. taurica* in Zakynthos is 4.72, whereas in *P. erhardii* it varies from 5.55 in the dry season to 6.42 in the wet season (Chondropoulos et al., 1993).

It seems that *P. erhardii* has either not yet established a balance between optimal clutch size and the desirable hatchling size, or has selected an opportunistic approach, in contrast to the other two species. However, further study is necessary to elucidate this aspect of their reproduction.

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