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Ecology of the Balkan Wall Lizard, *Podarcis taurica ionica* (Sauria: Lacertidae) from Greece

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***Podarcis taurica ionica* is the dominant lizard species on most Ionian islands and is abundant in the western Greek mainland. Population densities range between 82 and 365 lizards/ha. The species occupies primarily habitats with low vegetation and is characterized by a high degree of seasonal color adaptation to its environment as well as by poor climbing ability in comparison with other Wall Lizards of the Balkans.**

Daily activity is bimodal during the largest part of the annual activity period. Many individuals (27.78–57.14%) show broken tails but both interpopulation and intersexual differences of injury frequencies are not significant. Hibernation usually lasts from early Nov. to late Feb. or early March. Most copulations are observed from early April to early May. Females with oviductal and/or large ovarian eggs are present mainly from mid April to mid July, but the peak of gestation occurs from mid May to mid June. Normally there are two clutches per season. The first oviposition occurs from mid May to early June and the second one from mid June to mid July. Hatching usually takes place from mid July or early Aug. to early Sept., after an incubation period of about 8–9 weeks. Sex ratio is usually near 1:1, and observed deviations are not significant. Reproductive maturity in females is attained at an approximate snout–vent length (SVL) of 52–56 mm, which corresponds to an age of 18–20 months. Clutch size ranges from 2 to 10 eggs (usually from 3 to 5 eggs), and is significantly larger in mainland populations. There is a positive correlation between SVL and clutch size in most populations studied. Oviductal egg size and mass differ significantly among the populations examined but are not correlated to SVL. The ratio of egg to body mass differs significantly among some of the studied populations, but there are no differences of relative clutch mass (RCM).

THE Balkan wall lizard *Podarcis taurica* is distributed in Hungary, the largest part of the Balkan Peninsula, Crimea (in the Black Sea coasts of USSR) and a few localities on the coasts of NW Asia Minor. It is believed that this lizard originated in the S Russian steppes and then dispersed westwards (Cyren, 1941). Three subspecies are known all over the species range (Fuhn and Vancea, 1961) and all of them live in Greece as well (Ondrias, 1968). *P. taurica ionica* is found in the west part of the Greek mainland and Ionian islands (all large ones except Lefkada) and in Albania.

The Old World lizard genera *Podarcis* and *Lacerta* (Lacertidae) are considered to be ecologically equivalent to the New World genus *Cnemidophorus* (Teiidae) (Stamps, 1977). Various aspects of life history of *P. t. taurica* are known from previous works (Schreiber, 1912; Lantz and Cyren, 1948; Kabisch and Engelmann, 1970; Cruce and Leonte, 1973; Cruce, 1977) but none of them concerns Greek material. To our knowledge, studies concerning the biology and ecology of *P. t. ionica* are absent up to now. Since 1977 we have been studying the biology, ecology and taxonomy of this lizard. As we noted in a previous work (Chondropoulos and Lykakis, 1978) *P. t. ionica* is the dominant species among lizards of the Ionian Islands.

In this paper we present data on population density, tail-break frequency, sex ratio, and habitat type, as well as on diurnal and seasonal activity patterns. We also give information for age at maturity, number of clutches per season, clutch size, egg size, egg size relative to female size and relative clutch mass. The importance of these reproductive variables in interpreting species and population adaptations of various lizards is well known (Tinkle, 1969; Tinkle et al., 1970; Vitt, 1977). However, relatively little information is available on intraspecific variation of these variables in Old World lizards.

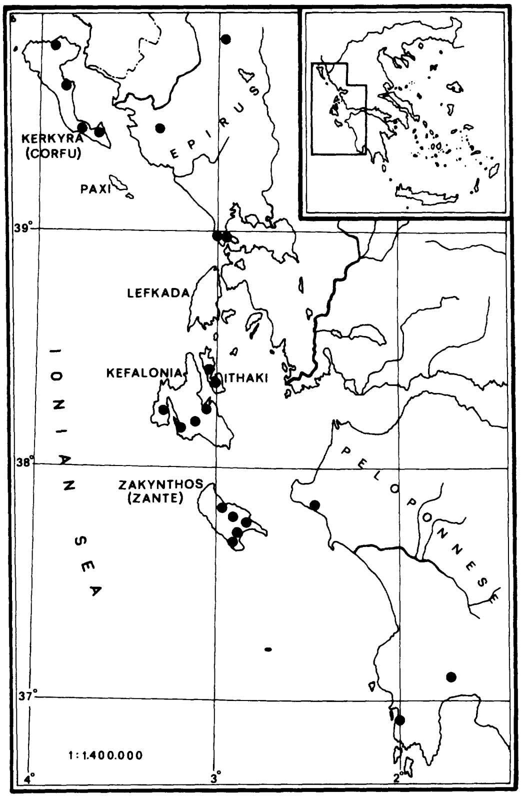

Fig. 1. Map showing the collection sites of *Podarcis taurica ionica* within each study area.

METHODS AND STUDY AREAS

The data are based on 308 specimens which were collected and preserved and an additional 130 individuals that were observed but not collected. Field work was performed from March to Nov. of 1977–1979 at collection sites shown in Fig. 1. The material came mostly from lowland populations (altitudes ≤100 m), and only a few individuals from Epirus belonged to a montane population. The animals were kept alive in the laboratory for short periods before preservation.

For each lizard snout–vent length (SVL) and total body mass were measured. All females were examined for tail condition, sex and reproductive condition. For each gravid female the total number of oviductal and/or large ovarian eggs (diameter ≥3 mm) was counted, and the dimensions and mass of each oviductal egg were measured. Linear measurements were taken to the nearest 0.1 mm; body and egg mass to the nearest 0.1 and 0.001 g, respectively. In females which did not bear oviductal eggs, we searched for external and/or internal marks of recent oviposition, i.e., loose skin on flanks, widened oviducts, and corpora lutea on ovaries. The estimation of clutch size was made separately for oviductal, large ovarian and both types of eggs. Relative clutch mass (RCM) was expressed as the ratio of oviductal clutch mass to the total body mass (Vitt and Congdon, 1978).

Population density was estimated by making transects through the habitat, recording distances covered with a leg pedometer. The effective width of the transects was about 5 m. The total number of lizards observed on a study site was divided by the total surface of the site (i.e., meters walked multiplied by the width of the transect) and the result was expressed as number of lizards per hectare (Pianka, 1970). These density estimations as well as observations on diurnal activity pattern were performed during the peak activity period (mid April–late June).

RESULTS AND DISCUSSION

Habitat and adaptations.—The lizard *P. t. ionica* lives mainly in open lowland areas with short grass-forb-shrub vegetation. We identified the following dominant plant taxa: *Inula* sp., *Calendula* sp., *Chrysanthemum* sp., *Daucus carota*, *Euphorbia* sp. and *Trifolium* sp. This lizard also lives in olive groves, cultivated areas, gardens, as well as in road sides, brambles and fences. Sometimes we found it on stream banks or sandy places near the sea shore having halophytic vegetation. In general, any place with a little vegetation even in habitated sites could be suitable for this lizard. Similar biotopes are referred by other authors for *P. t. taurica* (Kabisch and Engelmann, 1970). Montane populations of *P. t. ionica* occur in Epirus and Peloponnese. In comparison to other wall lizards of the Balkan Peninsula (e.g., *Podarcis erhardii, Podarcis peloponnesiaca, Podarcis melisellensis* and *Podarcis muralis*) *P. taurica* is more closely associated with low vegetation and its climbing ability is considerably reduced (Klemmer, 1975; Arnold et al., 1978). Our observations on *P. t. ionica* confirm these ecological associations.

This lizard shows a high degree of seasonal color match with its environment. All individuals of each population possess the same color, although the color changes from season to season. The basic dorsal color is bright grass-green in spring and early summer and becomes dark

TABLE 1. POPULATION DENSITIES OF *Podarcis taurica ionica.* Estimations are based on the total number of lizards which were caught or observed during the period of maximum daily and seasonal activity.

Study area	Number of samples	Total number of lizards	Mean density (range) in lizards/ha
Zakynthos	4	98	222.25 (180.82–365.27)
Kefalonia	5	60	185.80 (133.18–280.75)
Ithaki	3	31	118.33 (82.10–148.81)
Kerkyra	4	89	247.50 (186.16–356.30)
W. Peloponnese	5	62	205.33 (179.07–252.91)
Epirus	3	34	165.00 (108.42–253.11)

or olive green to brown or olive brown towards the autumn. In general, the green of lizards exists as long as the habitat remains green. This seasonal color change is strongly associated with the character of vegetation. For example, on Ithaki Island where the vegetation is of more xeric character in comparison to other areas studied, the skin color is generally less green and less bright during all seasons. Lantz and Cyren (1948) found similar color adaptation in *P. t. taurica* of Crimea.

Abundance.—Population density of *P. t. ionica* is relatively high and varies from island to island or from one continental area to another (Table 1). Differences among all samples examined are not statistically significant ($F_{5,18} = 1.80, P > 0.1$), but Ithaki Island values are usually smaller. The absence on this island of any particular predation pressure or competition with other lizard species (since no other wall lizard lives there) implies that the low density of the population may be attributed to low productivity due to the xeric character of Ithaki Island. Cruce and Leonte (1973) mentioned a much lower density for a population in Romania, 45.4 animals/ha, and Cruce (1977) reported a value of 100 animals/ha as an average density of another Romanian population. For *Podarcis sicula,* which is an ecologically equivalent species, Verbeek (1972) found that in an island population, density reaches levels up to 400–800 animals/ha. This value is much higher than those of *P. t. ionica,* but in exceptionally favorable microhabitats the population density of this lizard may attain values of even 500 animals/ha.

TABLE 2. DAILY ACTIVITY PATTERN OF *Podarcis taurica ionica.* Numbers of lizards observed during three days in three different study sites.

	Study site and date		
Hour of day	Zakynthos (Vanato) 16-5-79	Kerkyra (Alykes) 22-6-79	W. Peloponnese (Kyllini) 25-5-78
Before 0800	—	—	—
0800–0900	2	1	—
0900–1000	6	9	5
1000–1100	16	18	10
1100–1200	15	18	21
1200–1300	10	10	12
1300–1400	3	5	8
1400–1600	—	—	—
1600–1700	2	5	5
1700–1800	11	14	12
1800–1900	11	10	12
1900–2000	2	5	6
After 2000	—	—	1

Diurnal activity.—*P. t. ionica* shows a clear bimodal daily activity pattern, especially during the period from the middle of April to the end of Sept. (Table 2). Two or more hours after sunrise lizards emerge from their nocturnal shelters. The exact time depends on season, weather conditions and habitat characteristics (orientation, microclimatic conditions, etc.). Each individual selects a convenient basking site (e.g., on ground without vegetation, on small rocks or wood pieces) where it orients itself for maximum absorption of sunlight. This warming-up period lasts for one hour or more depending on the factors mentioned above. Afterwards, lizards begin to search for food, moving through the vegetation. Peak activity occurs at 1000–1200 h. After 1230 h the number of individuals is reduced rather sharply and by 1330 h all animals have disappeared. This retiring period lasts for about two hours, and a second peak of activity occurs at 1700–1830 h. Since the number of animals which can be observed during the afternoon peak is usually smaller than that of the morning one, a number of individuals evidently take food only during the morning activity phase and spend the rest of the day in their refuges. About one hour before sunset all animals disappear. In early spring and late autumn daily activity is confined between late morning and mid-afternoon. Similar daily activity cycles strongly influenced by weather conditions were reported by Avery (1978) for *P. muralis* in Central Italy. In general, many diurnal heliothermic lizards show similar activity patterns which are determined by cli-

TABLE 3. NUMBERS AND PERCENTAGES OF LIZARDS WITH BROKEN AND REGENERATED TAILS.

	Males			Females		
Study area	N	Broken tails	%	N	Broken tails	%
Zakynthos	43	19	44.19	39	15	38.46
Kefalonia	45	22	48.89	35	20	57.14
Ithaki	18	5	27.78	18	6	33.33
Kerkyra	20	11	55.00	31	14	45.16
Island subtotal	126	57	45.24	123	55	44.72
W. Peloponnese	15	6	40.00	15	7	46.37
Epirus	15	6	40.00	14	5	35.71
Mainland subtotal	30	12	40.00	29	12	41.38
Overall total	156	69	44.23	152	67	44.08

mate and weather conditions (Pianka, 1970; Busack, 1976; Mitchell, 1979).

Broken tails.—Like other lacertids *P. t. ionica* exhibits tail autotomy to escape potential predation. A large number of the collected animals were found with broken and regenerated tails (Table 3). Both interpopulational and intersexual differences are not significant (χ^2-test gives in all cases $P > 0.05$), but the Ithaki Island population shows the lowest values. This could be explained by Pianka's hypothesis (1970) according to which tail loss frequency of lizards is correlated directly to predator abundance and indirectly to the primary productivity of the community. Indeed, Ithaki Island is undoubtedly the driest and hence the least productive among study areas. In contrast, Kerkyra Island is the wettest, most productive area and its lizard population shows a high value of tail loss. Other workers suggest that different tail-break frequencies may be attributed to differences in longevity (when species are compared) or community structure (when populations of the same species are compared) (Tinkle and Ballinger, 1972; Vitt et al., 1977). Differences of community structure may affect the nature and intensity of predation, thereby causing different tail-break frequencies among intraspecific populations. Schoener's results (1979) suggest that if predation is the major source of mortality, then the lesser the predation intensity the greater the tail-break frequency. However, our data are insufficient so far to support any of the above hypotheses.

The absence of any significant sexual difference in tail-breaks of *P. t. ionica* may suggest that tail autotomy of this lizard is used by both sexes for escaping predator attacks and are not attributed to intraspecific fights (usually between males). On the other hand, interpopulational homogeneity probably reflects the lack of any considerable environmental differences among study areas. Fig. 2 shows higher tail-break frequencies in larger (hence older) individuals of both sexes. This can be explained by the increased probability of the older individuals to encounter a predator.

Timing of reproduction.—On the average hibernation lasts from early Nov. to late Feb. or early March. It was observed that the length of this period is strongly influenced by climate or weather conditions prevailing in each area during a given year. Thus, it is shorter for populations of SW Peloponnese and longer for montane populations of Epirus, while the differences among all other populations examined are very small. The reproductive period begins near the end of March. Most copulations were observed from early April to early May but some sporadic ones took place until late June. Gravid females with oviductal and/or large ovarian eggs were collected mainly from the middle of April to the middle of July, but the peak of the gestation period occurs from the middle of May to the middle of June (Table 4). In several cases we found gravid females outside of this period and this fact implies that there is no strict synchronization of reproductive cycles for all females of each population. From several females which were caught in spring and laid their eggs in the laboratory it is concluded that gestation lasts 4–6 weeks.

A total of 152 females were examined of which 101 individuals were found carrying oviductal

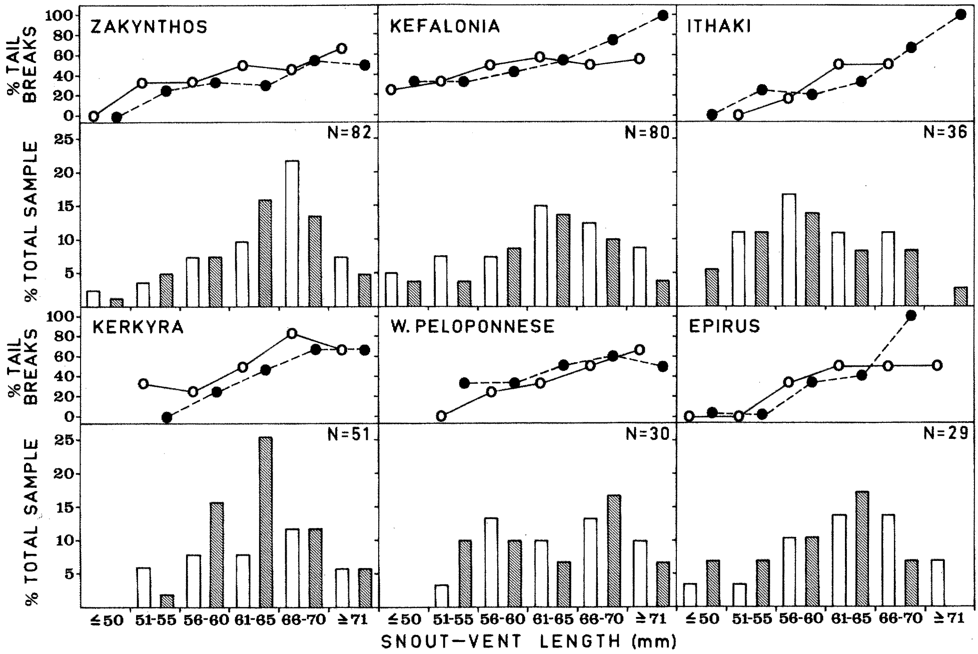

Fig. 2. Composition, sexual dimorphism, and relative tail breaks in the samples of *Podarcis taurica ionica* from all study areas. White circles and columns concern males while dark ones females.

TABLE 4. SEASONAL DISTRIBUTION OF GRAVID FEMALES OF *Podarcis taurica ionica* IN EACH STUDY AREA. Letter exponents characterize data as below: a = total number of females in the sample, b = gravid females as percentage of total number of females in the sample, c = gravid females with oviductal eggs, d = gravid females with large ovarian eggs (in many of them corpora lutea coexist), and e = gravid females with both oviductal and large ovarian eggs. Data indicated by c, d, and e are given as percentages of the number of gravid females.

Study area	Late March	Late April	Mid-late May	Early-mid June	Late June	Mid July	Late July–early August	Early-mid September
Zakynthos		14^{a}, 85.7^{b} 33.3^{c}, 41.7^{d} 25.0^{e}	17^{a}, 94.1^{b} 68.8^{c}, 25.0^{d} 6.2^{e}			5^{a}, 20.0^{b} 100.0^{c}, — —		3^{a}, — —, — —
Kefalonia		7^{a}, 85.7^{b} 33.3^{c}, 50.0^{d} 16.7^{e}		10^{a}, 90.0^{b} 33.3^{c}, 55.6^{d} 11.1^{e}	10^{a} ,60.0^{b} 80.0^{c}, 20.0^{d} —	8^{a}, 25.0^{b} 100.0^{c}, — —		
Ithaki				12^{a}, 83.3^{b} 30.0^{c}, 70.0^{d} —			6^{a}, 16.6^{b} 100.0^{c}, — —	
Kerkyra			18^{a}, 94.4^{b} 47.1^{c}, 47.1^{d} 5.8^{e}		13^{a}, 76.9^{b} 70.0^{c}, 30.0^{d} —			
W. Peloponnese	3^{a}, 100.0^{b} 66.7^{c}, 33.3^{d} —				5^{a}, 40.0^{b} 50.0^{c}, 50.0^{d} —	7^{a}, 14.3^{b} 100.0^{c}, — —		
Epirus			5^{a}, 100.0^{b} 60.0^{c}, 40.0^{d} —					9^{a}, — —, — —

and/or large ovarian eggs, and ten individuals had no eggs but had external and/or internal marks of recent oviposition (loose skin on flanks, widened oviducts and corpora lutea in ovaries). In addition, 33 mature females (SVL $\geq$ 52 mm, see below) possessed neither eggs nor the above marks. The remaining eight individuals were immature (SVL < 50 mm). The seasonal distribution of gravid females caught is shown in Table 4.

In the case of multiple clutches per season (see below) the first egg deposition usually occurs from the middle of May to early June and the second one from the middle of June to the middle of July. In the southern part of the range of *P. t. ionica* the period of oviposition is generally more extensive (see below). For *P. t. taurica* Fuhn and Vancea (1961) and Lantz and Cyren (1948) reported that in Romania and South Crimea, respectively, egg deposition occurs in May.

Hatching and appearance of young usually occurs from mid July or early Aug. to early Sept. This indicates that in lowland areas embryos complete their development in about 8–9 weeks at a mean daily air temperature of 18.3–26.0 C. For montane populations this period is presumably longer. In Romania, hatchlings of *P. t. taurica* appear in Sept. (Fuhn and Vancea, 1961), while in South Crimea in late July or early Aug. (Lantz and Cyren, 1948). The more or less shorter period of egg incubation in Greek populations of *P. t. ionica* may be explained by the warmer climate of Greece in comparison to that of Romania and Crimea.

Such an extensive breeding season which covers most of the annual activity period appears to characterize all Lacertidae inhabiting the temperate zone (Fitch, 1970).

Sex ratios.—With the exception of the Kerkyra Island population, all other populations studied show a sex ratio of 1:1 or slightly deviated toward the males (Table 5). However, all these deviations from the 1:1 ratio are not significant (χ^2-test, $P > 0.05$).

In other works concerning *P. t. taurica* (Cruce, 1977) and *Cnemidophorus* sp. (Pianka, 1970; Schall, 1978) a temporary deviation towards males during the summer was noted which was attributed to cryptic behavior of females until the egg deposition. Deviation towards females during the second half of the activity period was reported for a montane population of *Cnemidophorus tigris multiscutatus* (Goldberg, 1976). Our findings for the lizard *P. t. ionica* differ because the sex ratio was near 1:1 for the majority of populations regardless of the sampling season. The slight deviation towards males may be attributed to a higher activity of males in searching for food.

TABLE 5. SEX RATIOS AMONG POPULATIONS OF *Podarcis taurica ionica*.

Study area	Total number of lizards	Males/females
Zakynthos	82	1.10
Kefalonia	80	1.29
Ithaki	36	1.00
Kerkyra	51	0.65
Island subtotal	249	1.02
W. Peloponnese	30	1.00
Epirus	29	1.07
Mainland subtotal	59	1.03
Overall total	308	1.03

Body size and age at maturity.—Females of *P. t. ionica* are mature at an approximate SVL of 52–56 mm, and according to our crude estimations (SVL measurements of hatchlings, juveniles and adults at different seasons) this length is usually aquired at an age of 18–20 months. The smallest reproductive female had SVL = 52.2 mm and contained two large ovarian eggs. Thus, females are capable of reproduction after their second hibernation. Earlier maturation is probable for animals living in favorable areas and born early in the reproductive period. These animals may reach maturity before their second hibernation. Cruce (1977) found that *P. t. taurica* reaches maturity at an age of 22 months. Among other lacertids *Podarcis muralis* and *Lacerta viridis* in Central France attain maturity at an age of four and three years, respectively (Rollinat, 1897, 1900), *Lacerta vivipara* in Britain at an age of three years (Avery, 1975), while in Romania of three years or more (Fuhn and Vancea, 1961).

When females of *P. t. ionica* reach reproductive maturity their body size is approximately equal to two thirds of the maximum body size of females in each population: it was found that the ratio of minimum gravid female SVL to maximum SVL of females in our study ranges between 0.696 to 0.785.

Number of clutches per season.—Seven females possessed both oviductal and large ovarian eggs

TABLE 6. CLUTCH SIZE STATISTICS. Estimations are based on counts of oviductal and large ovarian eggs, or both. N indicates the number of clutches examined.

	Oviductal eggs		Ovarian eggs		Oviductal and ovarian eggs	
Study area	N	$\bar{x}$ ± SE (range)	N	$\bar{x}$ ± SE (range)	N	$\bar{x}$ ± SE (range)
Zakynthos	20	3.6 ± 0.2 (2–5)	13	3.6 ± 0.6 (2–10)	33	3.6 ± 0.3 (2–10)
Kefalonia	13	3.6 ± 0.3 (2–7)	12	3.5 ± 0.3 (2–5)	25	3.6 ± 0.2 (2–7)
Ithaki	4	3.8 ± 0.3 (3–4)	7	3.9 ± 0.5 (2–6)	11	3.8 ± 0.3 (2–6)
Kerkyra	16	4.3 ± 0.4 (2–8)	12	4.4 ± 0.2 (4–6)	28	4.3 ± 0.2 (2–8)
Island subtotal	53	3.8 ± 0.2 (2–8)	44	3.8 ± 0.2 (2–10)	97	3.8 ± 0.1 (2–10)
W. Peloponnese	4	6.5 ± 1.5 (4–10)	2	4.5 (4–5)	6	5.8 ± 1.0 (4–10)
Epirus	3	4.3 ± 0.7 (3–5)	2	5.0 (4–6)	5	4.6 ± 0.5 (3–6)
Mainland subtotal	7	5.6 ± 0.9 (3–10)	4	4.8 ± 0.5 (4–6)	11	5.3 ± 0.6 (3–10)
Overall total	60	4.0 ± 0.2 (2–10)	48	3.9 ± 0.2 (2–10)	108	4.0 ± 0.1 (2–10)

while 18 possessed both ovarian eggs and corpora lutea, indicating that at least a percentage of females lay more than one clutch per season (Table 4). We suppose that two clutches per season is the rule for most populations of *P. t. ionica.* In SW Peloponnese three clutches per season may be produced. This conclusion comes from the following observation. Three females caught at the end of March in SW Peloponnese were found to be gravid. Two of them carried eight and ten oviductal eggs, respectively, and the third one four very large ovarian eggs. Such early gestation allows enough time for two additional ovipositions during the same reproductive period. In the Epirus montane population one clutch per season is presumably typical. These differences might be explained by different lengths of activity periods which are determined by climatic conditions. McCoy and Hoddenbach (1966) and Pianka (1970) found a comparable geographic variation of clutch number for *Cnemidophorus tigris,* i.e., one clutch in the north and at least two clutches in the south of its range. Multiple clutches have been reported for other lacertids: *Lacerta agilis* lays two clutches (Smith, 1951), *Podarcis muralis* 2–3 clutches (Cooper, 1958; Fuhn and Vancea, 1961) and *Lacerta viridis* 1–2 clutches in nature (Porter, 1972), two clutches in captivity (White, 1957).

For several species of *Cnemidophorus* Porter (1972), Goldberg (1976) and other authors reported two or more clutches per season.

Clutch size.—Analysis of clutch size is based on the number of oviductal and ovarian eggs separately as well as on the number of both types of eggs (Table 6). The three separate estimations of clutch size do not differ significantly (*t*-test, $P > 0.05$), and hereafter for comparisons we use the results of estimations which are based on both types of eggs. On the average each female lays four eggs per clutch, with a range of 2–10 and more frequently 3–5 eggs per clutch (Fig. 3).

Schreiber (1912) found three eggs in the unique female of *P. t. taurica* that he examined. There is a highly significant difference in clutch size among study areas ($F_{5,102} = 3.81, P < 0.005$) because of higher values in continental material. Indeed, the mean island clutch size differs significantly from the continental one ($t = 3.24$, $P < 0.01$), while clutch size differences among island populations are not significant ($F_{3,93} = 2.15$, $P > 0.05$). Clutch size of the SW Peloponnese population is significantly larger than that of other areas (*t*-test, $P < 0.01$). This may be attributed to the large body size of the individuals of this population, a character which is known from an earlier study (Cyren, 1941). In each study area a positive correlation between SVL and clutch size was found. This correlation is significant ($P < 0.05$) in all areas except Kerkyra island and Epirus ($P > 0.1$). The

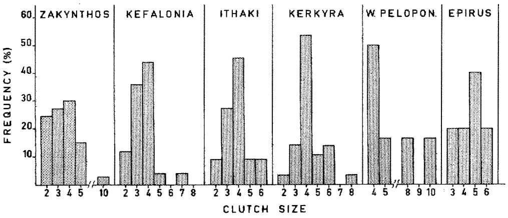

Fig. 3. Clutch size frequency (%) in females of *Podarcis taurica ionica* from each study area.

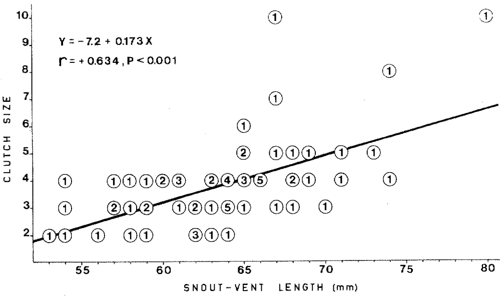

Fig. 4. Correlation of clutch size (number of oviductal or large ovarian eggs) and SVL in females of *Podarcis taurica ionica* from Zakynthos, Kefalonia, Ithaki and W Peloponnese. Circled numbers indicate frequency of females. Regression, correlation coefficient and significance level are given.

SVL-clutch size correlation is illustrated in Fig. 4 in which data of the Zakynthos, Kefalonia, Ithaki and W Peloponnese populations are combined. For island populations, clutch size increases slightly with latitude, but an inverse relation seems to exist for mainland populations. A more detailed study is needed to clarify the correlation of clutch size to latitude in this lizard. Clutch size increases with latitude in *Cnemidophorus tigris* (Fitch, 1970; Pianka, 1970), but in other lizard and snake species the reverse relation is true (Fitch, 1970).

In females with both oviductal and large ovarian eggs we compared the two successive clutch sizes. In four females from the Zakynthos population the average size was 3¼ eggs for the first clutch and 4¼ eggs for the second one. In two females from Kefalonia the respective values were 3 and 3½ eggs. In one female from Kerkyra the corresponding numbers were 4 and 6.

Because of the very limited sample, we cannot suggest any certain difference among clutches of *P. t. ionica*. Comparable differences and other data on reproduction of a number of North American lizards are summarized by Vitt (1977).

Dimensions and mass of oviductal eggs.—Means of length, width and mass of oviductal eggs, as well as means of female SVL and mass for each study area are presented in Table 7. Interpopulational differences for each of these characteristics are statistically significant (F-test, $P < 0.05$). The eggs of Kerkyra island and Epirus populations are larger than those of other areas, but as already mentioned for clutch size, we cannot suggest any certain correlation between egg size and latitude. No significant correlation was found between egg size and SVL ($P > 0.05$) for all study areas. Therefore, we conclude that increase of SVL is associated with an increase of clutch size but not of egg size. The ratio of egg mass to body mass (without clutch) differs significantly between W Peloponnese and all island populations, and between Ithaki and Kerkyra populations (H-test, $P < 0.05$).

Relative clutch mass (RCM).—This life history parameter has been used as a measure of reproductive output. Vitt and Congdon (1978) found that RCM (clutch/body, in mass or calories) is related to strategies of foraging and predator escape, and two classes of lizards are distinguished. Lizards of the first category have compact body, slow movement, cryptic behavior and are "sit-and-wait" foragers (e.g., Agamidae, many Iguanidae). These lizards are characterized by high values of RCM. In contrast, lizards of the second category have elongated, slender body, fast movement and non-cryptic behavior. They forage widely and escape from predators by running (e.g., Teiidae, Scincidae, Lacertidae). On the basis of this distinction, *P. t. ionica* certainly belongs to the second group, but our estimations of RCM (Table 8) yield higher values than those which are given by Vitt and Congdon (1978) for this group. This deviation may be explained if we accept that additional ecological factors influence the reproductive strategy of *P. t. ionica.* A similar constraint on RCM due to the habitat specificity is reported by Vitt (1981) for the iguanid *Platynotus semitaeniatus.* In spite of this RCM deviation, the values of 0.990 g for the mean clutch mass and 74.1 mm for the maximum SVL of adult females classify *P. t. ionica* in the second of the two groups, according to the regression lines given by Andrews and Rand (1974) and Vitt and Congdon (1978). *Cnemidophorus* sp. (Teiidae), *Nucras tesselata* and *Eremias lugubris* (Lacertidae) are classified in the same group.

It is well known that differences in the behavior of lizards or in resource abundance of their habitats influence RCM considerably (Vitt and Congdon, 1978; Schall, 1978; Congdon et al., 1978). The interpopulational differences of RCM in *P. t. ionica* are not significant (H-test, $P > 0.05$) except for one case, i.e., between Ithaki Island and Epirus populations ($P = 0.048$). Difference of RCM values between Kerkyra and Ithaki populations is not significant, although

TABLE 7. ADULT FEMALE BODY AND OVIDUCTAL EGG STATISTICS. Values represent $\bar{x}$ ± SE (range, N). Linear measurements are in mm and masses are in grams. Body mass values concern individuals with intact tails and do not comprise the mass of oviductal eggs.

	Body		Eggs			Egg mass
Study area	SVL	Mass	Length	Width	Mass	Body mass
Zakynthos	63.7 ± 0.8 (53.5–72.5, 38)	3.6 ± 0.2 (2.7–5.6, 23)	12.2 ± 0.1 (10.0–14.1, 71)	6.9 ± 0.1 (5.7–7.8, 71)	0.243 ± 0.003 (0.196–0.329, 71)	0.075 ± 0.004 (0.051–0.107, 12)
Kefalonia	64.8 ± 1.4 (54.0–73.7, 32)	3.6 ± 0.2 (2.5–4.6, 12)	12.2 ± 0.1 (11.0–14.0, 47)	6.8 ± 0.1 (6.3–7.6, 47)	0.247 ± 0.003 (0.211–0.314, 47)	0.077 ± 0.006 (0.055–0.095, 7)
Ithaki	62.4 ± 1.9 (54.3–66.0, 16)	3.6 ± 0.2 (2.7–4.5, 10)	12.2 ± 0.1 (11.6–13.0, 15)	6.7 ± 0.1 (6.3–7.0, 15)	0.233 ± 0.004 (0.198–0.256, 15)	0.060 ± 0.003 (0.057–0.065, 3)
Kerkyra	62.6 ± 0.8 (56.2–69.5, 31)	3.4 ± 0.1 (2.6–4.2, 16)	12.8 ± 0.1 (11.0–13.8, 68)	7.3 ± 0.1 (5.8–8.0, 68)	0.252 ± 0.003 (0.202–0.313, 68)	0.077 ± 0.004 (0.059–0.096, 8)
Island subtotal	63.6 ± 0.9 (53.5–73.7, 117)	3.5 ± 0.1 (2.5–5.6, 61)	12.4 ± 0.1 (10.0–14.1, 201)	7.0 ± 0.0 (5.7–8.0, 201)	0.246 ± 0.002 (0.196–0.329, 201)	0.074 ± 0.003 (0.051–0.107, 30)
W. Pelopon.	66.7 ± 1.1 (53.5–79.5, 15)	5.5 ± 0.3 (3.7–7.1, 8)	12.2 ± 0.1 (11.7–12.6, 26)	7.1 ± 0.1 (6.3–7.7, 26)	0.250 ± 0.002 (0.229–0.284, 26)	0.047 ± 0.006 (0.036–0.055, 3)
Epirus	62.6 ± 1.6 (53.3–69.5, 12)	4.1 ± 0.3 (2.7–5.2, 7)	12.5 ± 0.1 (12.0–13.1, 13)	7.5 ± 0.1 (7.0–7.8, 13)	0.260 ± 0.003 (0.238–0.277, 13)	0.060 ± 0.009 (0.050–0.078, 3)
Mainland subtotal	65.0 ± 1.2 (53.3–79.5, 27)	4.8 ± 0.3 (2.7–7.1, 15)	12.3 ± 0.1 (11.7–13.1, 39)	7.2 ± 0.1 (6.3–7.8, 39)	0.254 ± 0.002 (0.229–0.284, 39)	0.053 ± 0.006 (0.036–0.078, 6)
Overall total	63.9 ± 1.0 (53.3–79.5, 144)	3.8 ± 0.1 (2.5–7.1, 76)	12.4 ± 0.1 (10.0–14.1, 240)	7.0 ± 0.0 (5.7–8.0, 240)	0.247 ± 0.002 (0.196–0.329, 240)	0.071 ± 0.003 (0.036–0.107, 36)

TABLE 8. RELATIVE CLUTCH MASS STATISTICS. Data concern gravid females with intact tails.

Study area	N	$\bar{x}$ ± SE (range)
Zakynthos	12	0.201 ± 0.008 (0.142–0.249)
Kefalonia	7	0.188 ± 0.006 (0.160–0.203)
Ithaki	3	0.179 ± 0.008 (0.164–0.188)
Kerkyra	8	0.227 ± 0.022 (0.105–0.300)
Island subtotal	30	0.203 ± 0.007 (0.105–0.300)
W. Peloponnese	3	0.190 ± 0.017 (0.167–0.224)
Epirus	3	0.198 ± 0.004 (0.191–0.203)
Mainland subtotal	6	0.194 ± 0.008 (0.167–0.224)
Overall total	36	0.201 ± 0.006 (0.105–0.300)

these two areas exhibit obvious habitat differentiation.

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Preferred Temperature of Two Sympatric *Ambystoma* Larvae: A Proximate Factor in Niche Segregation?

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Acute preferred temperatures of both *Ambystoma jeffersonianum* and *Ambystoma maculatum* larvae varied with acclimation temperature (i.e., recent thermal history). The final preferred temperature of *A. jeffersonianum* was 25.2 C and for *A. maculatum*, 34.6 C. There was no significant ($P < 0.05$) difference between acute preferred temperatures at low acclimation temperatures, but preferred temperatures were significantly different when salamander larvae were acclimated to 30 C. It was postulated that temperature may be an important dimension along which the larvae segregate during the late spring and early summer months.

TEMPERATURE is one of the most important environmental parameters governing the metabolism, activity and behavior of aquatic poikilotherms (Fry, 1947; Stauffer, 1980). Much of the behavioral data collected to date have been associated with the effects of thermal discharges on the responses of fishes (Stauffer, 1980). Amphibians do not normally encounter temperatures that threaten their survival (Bogert, 1952; Keen and Schroeder, 1975), with the possible exception of toad embryos (Volpe, 1957), salamander embryos (Anderson, 1968) and some juvenile salamanders (Pough and Wilson, 1970). However, various thermal regimes may influence activities such as digestion rates (Skoczylas, 1970), conversion efficiencies (Brett, 1971) and growth (Licht et al., 1969). Certainly, benefits derived from maintaining a preferred body temperature through behavioral means are constrained by metabolic costs (Lillywhite, 1971).

Compared to those on fish, studies of temperature selection of amphibians are relatively rare. Lillywhite et al. (1973) identified the need to determine the ecological significance of temperature selection in all ectothermal groups, and Brattstrom (1979) reviewed thermal regulation studies of amphibians. In a recent study, Thompson and Gates (1982) noted that breeding pools used solely by *Ambystoma jeffersonianum* tended to have cooler water temperatures than those with *Ambystoma maculatum*, a species with which it is often syntopic. They hypothesized that one of the dimensions along which the two