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LIFE-HISTORY VARIATION IN A COMMUNITY OF LACERTID LIZARDS FROM THE LAKE SKADAR REGION (MONTENEGRO)

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We compared life-history attributes of *Algyroides nigropunctatus*, *Lacerta oxycephala*, *Podarcis melisellensis* and *Podarcis muralis* populations in the Lake Skadar region (mainland and islands). These lacertids are moderately sized with differing morphology (flattened vs. cylindrical). They have similar duration of egg incubation, size at onset of sexual maturity, size of hatchlings, and rate of juvenile growth. Clutch size is variable between populations and species: *P. muralis* produced larger clutches than the other species, especially *A. nigropunctatus* and *L. oxycephala*. A significant difference in egg size was apparent at the population level only. Smaller clutch size and elongated eggs were associated with a flattened body in *L. oxycephala*. A canonical discriminant analysis of reproductive variables showed that species similarities in ecological characteristics reflect phylogenetic relationships.

INTRODUCTION

Components of an organism's life history (reproductive characteristics, behaviour, longevity, growth rate, etc.) may be viewed as co-adapted traits that in concert produce the best strategy for survival in a particular environment (e.g. Stearns, 1976). Most studies on life-histories of lizards show large interspecific differences and considerable intraspecific temporal and geographic variations of the traits (reviewed in Dunham *et al.*, 1988). These variations have been attributed primarily to the local environment (e.g. Tinkle and Dunham, 1986; Abts, 1987). However, foraging mode, phylogenetic inertia and morphological constraints (body size and shape) were also evoked as factors potentially influencing variation of life-history traits (e.g. Vitt & Congdon, 1978; Vitt, 1981; Vitt & Price, 1982). In order to obtain empirical data essential to discern the relative importance of all these determinants for the evolution of life-history traits in lizards, simultaneous studies on a set of syntopic populations of species differing in the degree of their phylogenetic relatedness, ecological traits and morphology, are apparently needed (Vitt, 1986; Tinkle & Dunham, 1986; Henle, 1990). Studies on life-history traits of lacertids (Lacertidae) in comparison with other lizard families are still scarce (see Dunham *et al.*, 1988). This is particularly true for the Balkan lacertids (*Podarcis* spp., *Lacerta* spp., *Algyroides* spp., *Ophisops* spp.). Also, almost all previous studies of these lizard populations have been conducted in locations lacking diverse lizard communities. Out of 19 species that can be encountered throughout the Balkans, nine species compose the lacertid lizard community of the Lake Skadar region (Crnobrnja-Isailovic & Dzukic, 1995). In this report we compare the life-history attributes of four sympatric (in some cases syntopic) species, both in a coastal area and on islands in Lake Skadar. In addition to differences in the genetic background and meaning of the species, these lacertids also differ in morphology, distribution and ecological traits.

MATERIALS AND METHODS

SPECIES STUDIED

The species studied here represent the closest genera within Old-World lacertids, with affinities as follows: (*Podarcis-Lacerta*) (*Algyroides*) (Arnold, 1989). The Dalmatian *Algyroides*, *Algyroides nigropunctatus*, ranges along the coastal region of the Adriatic and Ionian seas, from Italian and Slovenian karst regions to the Akarnanien region (Greece), including some northern Adriatic islands. There are a few significant range penetrations inland. This species is usually encountered in degraded scrub, bushes between fields and rocky cliff areas, usually near water. The sharp-snouted rock lizard, *Lacerta oxycephala*, is a steno-endemic Balkan species, restricted in its range to a narrow zone along the Adriatic coast, from the river Krka to the northwestern part of Albania. *L. oxycephala* differs distinctly in morphology from all other lacertids by having a flattened body, with a very pointed snout. In an ecological sense, this species is peculiar among the Balkan's lacertids because it is the most specialist petricole, inhabiting mostly sunny cliff faces, rock-pavements, stone piles and screes. The Dalmatian wall lizard, *Podarcis melisellensis*, is a polymorphic species, with a considerable abundance in diverse habitats, but it is mainly encountered in densely vegetated places. It ranges from Monfalcone (Italy) to Skadar (Albania) along the coastal zone of the Dinaric Alps, extending inland in Lika, Hercegovina, Montenegro and Albania (Tiedemann & Henle, 1986). The common wall lizard, *Podarcis muralis*, has a wide geographic distribution (central and southern Europe), with immense geographic variation in morphology and habitat characteristics (Gruschwitz & Bohme, 1986). Thus, this lizard is thought to be more opportunistic with regard to microhabitat preference than its relatives.

HABITAT AND SPECIES COMPOSITION

Lake Skadar is the largest of the Balkan lakes. The lake is located in a karst terrain in the outer part of the south-eastern Dinaric Alps. Mountains rise steeply from the lake's south-western shore along which an archipelago of about forty large and small islands exists. Vegetation of this part, including the islands, is characterized by maquis and guarigue. Scattered xeromorphic trees are separated by patches of dry grass and herbs. Larger islands usually have a water's-edge rocky zone with scattered trees only, and a central grassy zone with bushy vegetation. The northern and north-eastern shores are flat, providing an extensive semi-littoral zone. This formerly inundated terrain with recent alluvial deposits is now mostly under cultivated soil, with fragments of common oak forests. The climate of the region is characterized by a large amount of precipitation and high summer temperatures (Lasca *et al.*, 1981). The shore region of the lake has two distinct zones with respect to lizard distribution, but on the islands there are species in various combinations of allotopic and syntopic occurrence (Crnobrnja-Isailovic & Dzukic, 1995). *P. muralis* and *L. oxycephala* appear to be the most common species, probably due to their better colonizing abilities. They are the only species with allotopical distributions. *L. oxycephala* occurs as the only lizard on 19, and *P. muralis* on 10, of the 40 islands. These islands are the most densely populated (up to one individual per 2 m^2, unpublished data.). When species are syntopic, spatial partitioning occurs; in such cases they generally follow their prefered habitats. Thus, *P. melisellensis* is mostly encountered in vegetated areas, *P. muralis* and *L. oxycephala* incline to shoreline rocky zones, while *A. nigropunctatus* show habitat preferences between these two groups. Data on morphological traits relevant to this study came from the complete lizard samples taken from the overall Lake Skadar region. Specimens included in the analysis of life-history traits were collected from the following six localities. Bistrica is located on the northern lowland bank. Lizards were collected there from the grassy sides of railroad tracks and nearby road (Podgorica-Bar). *P. melisellensis* shares this habitat with *P. muralis*. Malo Starcevo is a small island (0.9 ha) with dense populations of *P. muralis* only. Beska Velja is one of the biggest islands (15.9 ha), with *L. oxycephala* as the only lizard species. The island Malo Besko (1.7 ha) is characterized by a dense tree vegetation and grassy patches with boulders of various sizes, inhabited by a relatively robust population of *P. melisellensis*. In nearby waters, mainly on rocks, many *P. muralis* individuals can be encountered. Mali Moracnik is a moderate-size island (0.7 ha), with a sparse tree vegetation and grassy fields among large stony patches. Here the large *P. melisellensis* population inhabits grassy areas syntopically with *L. oxycephala*. A few individuals of *P. muralis* were noticed on this island as well. Bisage is an island of 2.8 ha, with *P. melisellensis* and *A. nigropunctatus* as the lizard inhabitants.

DATA COLLECTION AND STATISTICAL ANALYSES

Details about field and laboratory methods (body and egg measurements, egg-laying process, egg incubation period, hatchlings raised), including data on clutch and egg size, size at sexual maturity for females of *L. oxycephala*, *P. melisellensis* and *P. muralis*, can be found in our previous papers on reproductive characteristics of the lacertids from the Lake Skadar region (Aleksic & Tucic, 1994; Bejakovic *et al.*, 1995, 1996). Snout-vent length (SVL) was taken as a measure of overall size. Head dimensions (length, height, width), relative to SVL, expressed the body shape. The length of hind limb relative to SVL was considered as a morphological indicator of mobility capacities of the lizard species (see Pianka, 1986). Egg volume (V) was taken as the overall measure of size of eggs laid. RCM values were calculated as the ratio of clutch mass to body mass after egg laying (see Shine, 1980) and were used as a measure of reproductive investment per clutch. The size of the smallest female with enlarged vitellogenic follicles was considered the minimum size at maturity.

Female reproductive characteristics were studied on a number of individuals, except for *A. nigropunctatus* where only ten sexually matured females were available, of which three laid eggs. Nevertheless, we included this species in this study, though we were aware that the paucity of sample size precluded well-supported conclusions.

Statistics were calculated with SAS package (SAS Institute, 1989). Mean values and standard errors of life-history traits were weighted for population sizes. SVL, egg volume and clutch size were logarithmically transformed. Life-history traits (estimated on females) were analysed with populations nested within species. For each species, one-way ANOVA's were also performed. Pair-wise comparisons between species and populations were done by Scheffe test which controls an experimental type I error. Morphological traits were

TABLE 1.Comparison of male and female morphology among lacertid species from the Lake Skadar region. HL (head length), HW (head width), HH (head height), HLL (hind limb length) are presented as a proportion of snout-vent length (SVL). Means (±S.E.) and sample sizes (*n*) are given. ANOVA for HL,HW, HH and HLL was performed on residuals from regression on SVL.

Species	*n*	SVL	HL/SVL	HW/SVL	HH/SWL	HLL/SVL
A. nigropunctatus						
Males	27	61.27±1.06	0.26±0.00	0.16±0.00	0.10±0.00	0.56±0.01
Females	10	56.71±1.30	0.23±0.00	0.14±0.00	0.08±0.00	0.51±0.01
L. oxycephala						
Males	292	63.01±0.32	0.27±0.00	0.16±0.00	0.09±0.00	0.59±0.00
Females	196	61.21±0.37	0.25±0.00	0.14±0.00	0.08±0.00	0.55±0.00
P. meliselensis						
Males	92	59.76±1.20	0.24±0.00	0.14±0.00	0.10±0.00	0.54±0.00
Females	77	59.70±0.80	0.21±0.00	0.12±0.00	0.09±0.00	0.48±0.00
P. muralis						
Males	396	70.74±0.35	0.26±0.00	0.15±0.00	0.12±0.00	0.57±0.00
Females	367	67.93±0.32	0.22±0.00	0.13±0.00	0.09±0.00	0.52±0.00
Significance levels from ANOVA						
Sex		0.0003	0.0001	0.0001	0.0001	0.0001
Species		0.0039	0.0002	0.0079	0.0005	0.0080
Locality (Species)		0.2183	0.0011	0.0961	0.1331	0.0554
Sex x species		0.0001	0.0001	0.0001	0.0001	0.0001
Sex x locality (species)		0.0136	0.0001	0.0001	0.0001	0.0027

estimated on both males and females and analysed by partial hierarchical ANOVA on residuals from regression of each trait on SVL (both logarithmically transformed). Sex and species were considered as fixed main factors and populations as random factors nested within species. Effect of sex was tested over error mean square (MS), effect of species over population MS, and sex x species interaction over sex x population interaction. Growth rates were estimated by regressing juvenile length on months. Comparison of growth rates was done by analysis of covariance (ANCOVA). Month x species interaction (measure of slope's heterogeneity) was tested over month x female interaction. Since product-moment correlations estimated on population means were insignificant due to the small number of populations, correlations between life-history traits were estimated on the whole sample. As we dealt here with structured data sets, a canonical discriminant analysis, which maximized variation between groups, was used for joint analysis of reproductive traits instead of a principal component analysis (James & McCulloch 1990). We turned to populations as groups rather than species because of the small number of species used in this study.

RESULTS

MORPHOLOGY

Significant differences in SVL were found among species (*P. muralis* vs. *P. melisellensis* and *L. oxycephala*), and between sexes (males are larger than females; Table 1). Males and females of all species differ significantly in head dimensions relative to body size (SVL), males having larger heads (Table 1). Species differ in head height (*L. oxycephala* vs. *Podarcis* species). Head dimensions correlated with the size of prey items (length and width) are considerably different between species. Relative head length discriminates long-headed *L. oxycephala* and *A. nigropunctatus* vs. *Podarcis* species. Differences in the relative head width are less apparent; only *L. oxycephala* has a significantly wider head than *P. melisellensis*. Males of all species have statistically longer hindlimbs (relative to SVL) than females (Table 1), which indicates their higher locomotor capabilities. For one morphological trait, locality effect (within species) is statistically highly significant.

Egg shape also varies between the species. *L. oxycephala* has the most elongated eggs (width/length:

TABLE 2. Comparison of reproductive traits among lacertid species from Skadar Lake region. Mean values (±S.E.) and significance levels from nested ANOVA's are given. Species (populations) that share the same letter do not differ significantly. *n*-sample size.

Species	Population	Female SVL (mm)	Number of eggs per female	Egg volume (mm^3)	RCM
A. nigropunctatus	Bisage	57.84	3.33 AB	360.64	0.29
	n=3	±2.94	±0.33	30.08	±0.08
L. oxycephala		62.76	3.40 A	272.38	0.22
		±0.27	±0.10	±38.45	±0.02
	Beska	62.49	3.50	310.83 a	0.24
	n=10	±0.62	±0.27	±16.09	±0.01
	Mali Moracnik	63.03	3.30	233.94 b	0.20
	n=30	±0.40	±0.11	±10.00	±0.01
P between populations		0.4838	0.6323	0.0024	0.0672
P. melisellensis		62.91	4.05 AB	257.02	0.22
		±2.52	±0.43	±23.78	±0.01
	Mali Moracnik	63.38 a	4.90 a	217.12 a	0.23
	n=20	±0.67	±0.26	±15.50	±0.02
	Mala Beska	67.02 a	3.60 b	299.38 b	0.21
	n=10	±0.88	±0.16	±15.18	±0.02
	Bistrica	58.33 c	3.64 b	254.56 ab	0.23
	n=14	±0.84	±0.25	±22.19	±0.02
P between populations		0.0001	0.0007	0.0285	0.7836
P. muralis		70.71	5.51B	266.89	0.24
		±2.76	±0.49	±39.56	±0.02
	M. Starcevo	74.59 a	4.60	206.67 ab	0.20
	n=5	±1.03	±0.24	±54.53	±0.01
	Mala Beska	72.18 a	5.67	341.44 a	0.25
	n=18	±0.97	±0.41	±19.66	±0.02
	Bistrica	65.36 b	6.26	252.56 b	0.26
	n=19	±0.82	±0.42	±7.99	±0.01
P between populations		0.0001	0.1642	0.0010	0.3340
P between species		0.2031	0.0711	0.7867	0.5080

0.51±*0.01),* followed by *P. melisellensis* (0.53±0.01), *P. muralis* (0.57±0.04) and *A. nigropunctatus* (0.59±0.02) with the most rounded eggs. Differences among species appeared non-significant (P=0.260), but differences withing species (interpopulation variability) were significant (P<0.05).

LIFE-HISTORY TRAITS

Size of "laid-egg" females did not differ between species, but there was significant variation in interpopulation comparisons in *P. melisellensis* and *P. muralis* (Table 2). Females mature at minimum SVL of 51.0 mm (*P. melisellensis*), 53.3 mm (*A. nigropunctatus*), 53.3 mm (*L. oxycephala*) and 55.0 mm (*P. muralis*). Thus, females at the onset of reproductive life have already reached more than 80% of the average laid-egg female sizes in all species studied. (For the sake of comparison, most female squamates grow between 15 and 30% after maturation; Andrews, 1982.) *P. muralis* produced the largest clutches and *A. nigropunctatus* the smallest clutches (Table 2). The clutch size of *P. muralis* and *L. oxycephala* were statistically different, though overall interspecies differences in clutch sizes were not. A significant intraspecies difference in clutch size was found only in *P. melisellensis*. The number of females in clutch size classes showed quite different distribution patterns, where *P. muralis* was distinguished by the largest variation in clutch size (Fig. 1). Egg size did not differ significantly among species, but there were remarkable differences within species (Table 2). The measure of the reproductive investment per clutch, RCM, was nearly uniform for the Skadar Lake lacertids ranging

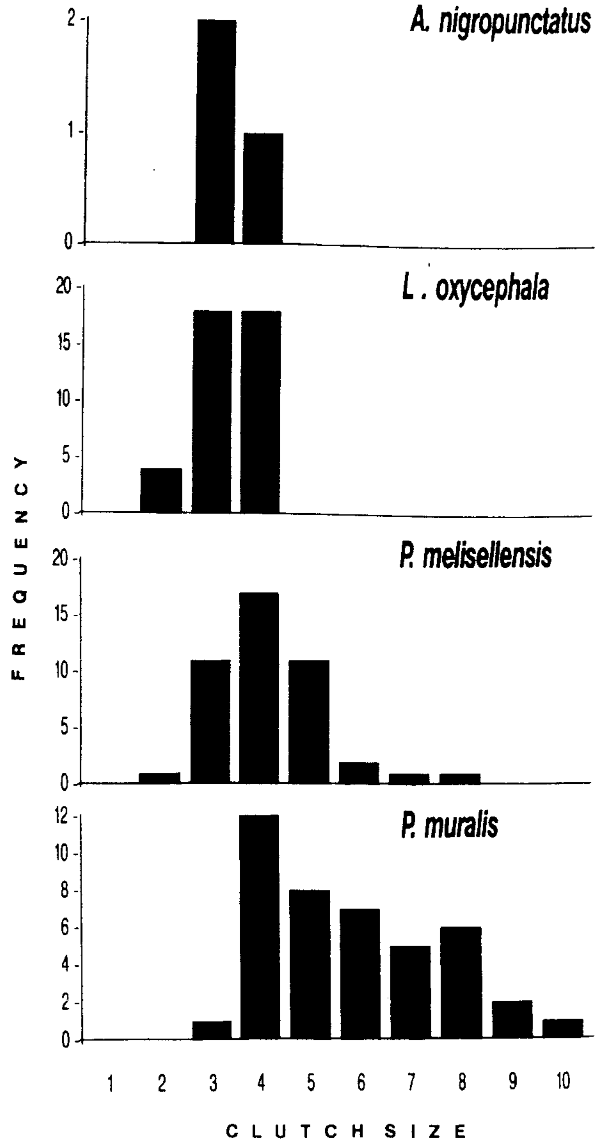

FIG. 1. Clutch size distribution in four lacertid species from Skadar lake region.

from 0.29 in *A. nigropunctatus* to 0.22 in *L. oxycephala* and *P. melisellensis*. Time to hatching and size of hatchlings were studied in three populations of *P. melisellensis*, and in one population of *P. muralis* (Malo Starcevo) and *L. oxycephala* (Beska). Minimum and maximum time necessary for newborns to hatch from eggs in incubators were found in *P. melisellensis* and ranged from 33.4±2.8 days (Bistrica) to 38.0±0.4 (Mali Moracnik). The smallest newborns were those of *P. melisellensis* (Bistrica, 65.5±3.3 mm) and the biggest those of *P. muralis* (Malo Starcevo, 71.2±3.0 mm).

We found no significant differences between species for these life history traits, nor between populations of *P. melisellensis*. The somewhat faster juvenile growth rate of *P. muralis* (Malo Starcevo population) compared to *L. oxycephala* (Beska) was insignificant, too (ANCOVA, P=0.124).

TABLE 3. Between population canonical structure from canonical discriminant analysis performed on reproductive traits measured in four lizard species from Skadar Lake region.

	CAN 1	CAN 2
Number of eggs per female	0.911	-0.400
Egg volume	0.551	0.800
RCM	0.685	0.015
Eigenvalue	1.5317	0.4979
Proportion	0.7256	0.2359
Cumulative	0.7256	0.9615
P	0.0001	0.0001

CORRELATION BETWEEN LIFE-HISTORY TRAITS

As expected, RCM was significantly correlated with the number of eggs per brood, and with the volume of eggs (r=0.471, P<0.001, and r=0.593, P< 0.001, respectively). The body size (SVL values) also was significantly correlated with these variables of reproductive potential (r=0.424, P<0.0001, r=0.288, P<0.01; respectively), as was found in most reptiles (Fitch, 1970; Dunham *et al.*, 1988). There was no relationship between the number of eggs and the size of hatchlings (r=-0.24, P=0.439), or between RCM and the size of hatchlings (r=-0.167, P=0.585). It is possible that small sample size precluded confirming such relationships. Egg shape (width/length ratio) was significantly positively correlated with the number of eggs per female, egg volume and RCM (r = 0.47, 0.35 and 0.39, respectively), and significantly negatively correlated with total length of hatchling (r=-0.70). Therefore, more round egg shape associates with larger brood, bigger egg size and, concomitantly, higher reproductive investment (RCM), while newborn lizards are bigger when they hatch from more elongated eggs.

MULTIVARIATE COMPARISONS

Reproductive variables were estimated for populations of *P. muralis*, *P. melisellensis* and *L. oxycephala*, and for one population of *A. nigropunctatus*. A canonical discriminant analysis was performed on this data set. CAN1 axis took 72.6% of variation in the original variables while 23.6% of that variation could be described by CAN2 axis (Table 3). CAN1 described a positive relationship among all three variables, while the egg number was negatively correlated with CAN2 axis and, at the same time, contrasted strongly with the egg volume. Species were mostly separated by the egg number on CAN1 axis and by the egg volume on CAN2 axis. In the CAN1 and CAN2 scatter diagram, populations separated well by their species designations (Fig. 2). Species were differently distributed along the first axis. *P. muralis* populations had positive values of CAN1 axis, while the populations of *L. oxycephala* and *A. nigropunctatus*

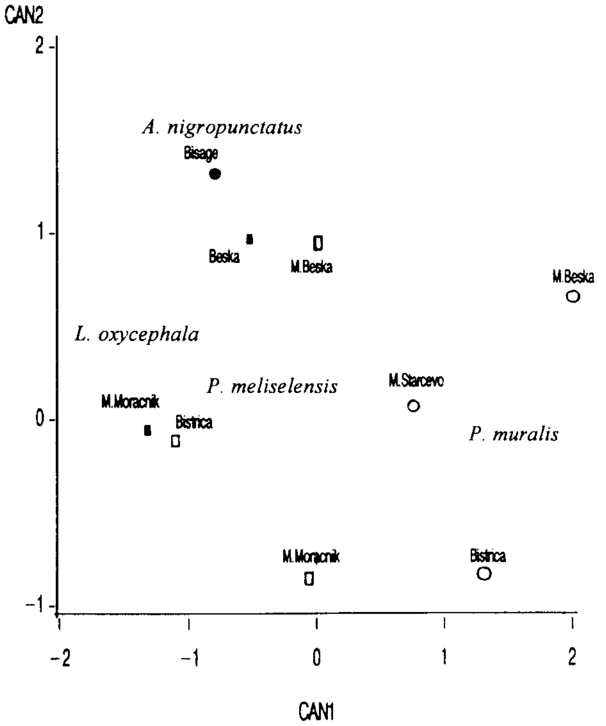

FIG. 2. Mean population scores on first two cannonical axes for four lacertid species from Skadar lake region. *Algyroides nigropunctatus*-solid circles; *Lacerta oxycephala*-solid squares; *Podarcis melisellensis*-empty squares; *Podarcis muralis* - empty circles.

had the most negative values along this axis reflecting their tendency for the most dissimilar clutch size. *P. melisellensis* populations took the middle position between these species. Two pairs of closely associated *L. oxycephala* and *P. melisellensis* populations (Mali Moracnik - Bistrica, Beska - Malo Besko) emerged due to close similarities in the egg size and the egg volume. Syntopic populations (Mali Moracnik - *P. melisellensis* and *L. oxycephala*; Bistrica - *P. muralis* and *P. melisellensis*; Malo Besko - *P. muralis* and *P. melisellensis*) differed considerably in their position indicating species-specific effect on reproductive characteristics, rather than site effect.

DISCUSSION

The following discussion is centered around the main question in this paper: How do these variations in life-history traits correlate with the species body shape, phylogenetic relatedness, distribution areas and ecological demands? Individuals of *L. oxycephala*, and to a lesser extent of *A. nigropunctatus*, are dorsoventrally flattened, showing striking dissimilarities to streamlined morphology of *Podarcis* species. Such a morphology is adaptive as it allows individuals to seek refuge in narrow crevices when disturbed or inactive. Cylindrical body morphology, on the other hand, enhances locomotor capabilities in more open, usually vegetated habitats. Predator pressures on surface-active lizards (e.g. when basking) in the Skadar Lake region are presumably similar. However, potential predators of these species once they are within crevices may be quite different. Their known predators in the Skadar Lake region include snakes (*Malpolon monspessulanus*, *Coluber laurenti*, *Natrix tessellata*), some birds (e.g. *Ardea purpurea*, *Larus* spp.) and rats (*Rattus rattus*). Because of the cylindrical morphology of snakes, they are not capable of predating lizards once they are in a rock crevice: the flattened morphology decreases the vulnerability to predation. Thus one may expect lower predator pressure on *L. oxycephala* and *A. nigropunctatus* than on those *Podarcis* species studied and, concomitantly, their higher lifetime reproductive success. Concomitant reproductive adaptations, associated with the effect of habitat selection on flattened morphology, usually include a reduced clutch size and more elongated eggs compared to other relatives (Vitt, 1981; 1993). The consequence is that non-reproductive females are as flat as females carrying eggs. In *L. oxycephala*, and in *A. nigropunctatus* to a lesser extent, reproductive adaptations that appear to be consequences of the exclusive use of rock outcrops are just as noted above. However, reduced clutch size in this species was not associated with reduced clutch volume, as was found in some flat lizards (Vitt, 1981). Also, contrary to other lizards in which morphological adaptations associated with the use of crevices in rocks for predator escape constrain RCM value (Vitt, 1981), the reproductive investment per clutch of *L. oxycephala* and *A. nigropunctatus* is about the same as in other lacertids from the Skadar Lake region.

Analyses made to date have suggested that phylogenetic relationships account for a large proportion of the variation observed in life-history variables of squamata (e.g. Dunham & Miles, 1985). This seems to be proven in our study as well. When reproductive characteristics, which determinate the coevolutionary framework for other life-history features (see Stearns, 1976; 1977) are compared, populations of *P. muralis* and *P. melisellensis* appeared to be closer to each other than populations of other the two species (*L. oxycephala* and *A. nigropunctatus*). The most common species (*P. muralis* and *L. oxycephala*) are on the opposite sides in reproductive traits similarity. Both tactics seem to work well in the Skadar Lake lizard community. Apparently, species level effects here are superseded by genus level effects as proposed by Stearns (1984) for the squamate reptiles.

Species distribution patterns in CAN1 and CAN2 reproductive-dependent space correspond to their general ecological relatedness. Both *A. nigropunctatus* and *L. oxycephala* are highly specialized with respect to their habitat choice. Contrary, *P. muralis* is more generalist with regard to microhabitat preference. It seems that *P.*

melisellensis is probably, in this respect, somewhere between these two groups. As stated above, intraspecific variations in reproductive traits are apparent, but well within species multivariate framework. Such variation is due to adaptations to specific environmental conditions and plasticity in characteristics that reflect immediate responses to proximate conditions. In this respect insular populations, at least those of *P. muralis* and *P. melisellensis* species, differ from continental populations in body size and clutch size. Island lizards are larger than conspecifics on the nearby continental area. It seems that lizards on islands, under high intraspecific competition (islands in Skadar Lake have much denser populations than the mainland; unpublished data), allocate more energy to somatic growth than to reproduction. In contrast, the life-history strategy of the continental populations could be to invest more in the number of offspring than in growth.

In conclusion, our analysis substantiates the claim that much of the pattern of covariation in life-history data can be explained by lineage-specific effects, either constrained by or coadapted with morphological differences, even if phylogenetically close taxa are compared.

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REFERENCES

Abts, M. L. (1987). Environment and variation in life history traits of the Chuckwalla, *Sauromalus obesus*. *Ecol. Monogr.* **57**, 215-232.

Aleksic, I., Tucic N. (1994). Changes in the comparisons of phenotypic variance and covariance among traits during ontogeny in the sharp-snouted rock lizard (*Lacerta oxycephala*). *Amphibia-Reptilia* **15**, 47-61.

Andrews, R. M. (1982). Patterns of growth in reptiles. In: *Biology of Reptilia.* C. Gans & F.H. Pough (eds.), **13**, pp. 273-320. Academic Press, New York.

Arnold, E. N. (1989). Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology. *Bull. Br. Mus. nat. Hist. (Zool.)* **55**, 209-257.

Bejakovic, D., Kalezic, M. L., Aleksic, I., Dzukic, G., & Crnobrnja, J. (1995). Female reproductive cycle and clutch traits in the Dalmatian wall lizard (*Podarcis melisellensis*). *Folia Zoologica* **44**, 371-380.

Bejakovic, D., Aleksic, I., Crnobrnja-Isailovic, J., Dzukic, G. & Kalezic, M. L. (1995). Reproductive cycle and clutch size in female sharp-snouted rock lizard, *Lacerta oxycephala*. *Amphibia-Reptilia* (in press).

Bejakovic, D., Aleksic, I., Crnobrnja-Isailovic, J., Dzukic, G. & Kalezic, M. L. (1996). Female reproductive traits in the common wall lizard (*Podarcis muralis*) from the Skadar lake region, Montenegro. *Revista Espanola de Herpetologia* in press.

Crnobrnja-Isailovic, J. & Dzukic, G. (1995). First report about conservation status of herpetofauna in the Skadar Lake region (Montenegro): current situation and perspectives. In: *Scientia Herpetologica.* Llorente et al. (eds.), pp.373-380. Barcelona.

Dunham, A. E. & Miles, D. B. (1985). Patterns of covariation in life history traits of squamate reptiles: the effects of size and phylogeny reconsidered. *Am. Nat.* **126**, 231-257.

Dunham, A. E., Miles, D. B. & Reznik, D. N. (1988). Life history patterns in squamate reptiles. In: *Biology of Reptilia.* C. Gans & R.B. Huey (eds.), **16**, pp. 441-522. Alan R. Liss, Inc., New York.

Gruschwitz, M. & Bohme, W. (1986). *Podarcis muralis* (Laurenti, 1768) - Mauereidechse. In: *Handbuch der Reptilien und Amphibien Europas.* Band 2/II. W. Bohme (ed.), pp. 155-208. Aula-Verlag, Wiesbaden.

Fitch, H. S. (1970). Reproductive cycles in lizards and snakes. *Univ. Kansas Publ. Mus. Nat. Hist.* **13**, 85-288.

Henle, K. (1990). Population ecology and life history of three terrestrial geckos in arid Australia. *Copeia* **3**:759-781.

James, F. C. & McCulloch, C. E. (1990). Multivariate analysis in ecology and systematics: Panacea or Pandora's box? *Ann. Rev. Ecol. Syst.* **21**, 129-166

Lasca, N., Radulovic, V., Ristic, R. & Cherkauer, D. (1981). Geology, hydrology, climate and bathymetry of Lake Skadar. In: *The Biota and Limnology of Lake Skadar.* G. S. Karaman & A. M. Beeton (eds.), pp. 17-38. Institut za bioloska i medicinska istrazivanja, Titograd, Smithsonian Institution, Washington.

Pianka, E. R. (1986). Ecology and Natural History of Desert Lizards. Princeton University Press, Princeton.

SAS Institute (1989). SAS/STAT User's Guide, version 6. Forth Edition.

Shine, R. (1980). "Cost" of reproduction in reptiles. *Oecologia (Berl.)* **46**, 92-100.

Stearns, S. C. (1976). Life history tactics: a review of ideas. *Q. Rev. Biol.* **51**, 3-47.

Stearns, S. C. (1977). The evolution of life history traits. *Ann. Rev. Ecol. Syst.* **8**, 145-171.

Stearns, S. C. (1984). The effects of size and phylogeny on patterns of covariation in the life-history traits of lizards and snakes. *Am. Nat.* **123**, 56-72.

Tiedemann, F. & Henle, K. (1986). *Podarcis melisellensis* (Braun, 1877) -Adriatische-Mauereideschse, Karstlaufer. In: *Handbuch der Reptilien und Amphibien Europas.* W. Bohme (ed.), pp. 111-141. Aula-Verlag, Wiesbaden.

Tinkle, D. W. & Dunham, A. E. (1986). Comparative life histories of two syntopic sceloporine lizards. *Copeia* **1986**, 1-18.

Vitt, L. J. (1981). Lizard reproduction: habitat specificity and constraints on relative clutch mass. *Am. Nat.* **117**, 506-514.

Vitt, L. J. (1986). Reproductive tactics of sympatric gekkonid lizards with comment on the evolutionary and ecological consequences of invariant clutch size. *Copeia* **1986**, 773-786.

Vitt, L. J. (1993). Diversity of reproductive strategies among Brazilian lizards and snakes: The significance of lineage and adaptation. In: *Reproductive Biology of South American Vertebrates*. W. C. Hamlett (ed.), pp. 135-149. Springer-Verlag.

Vitt, L. J. & Congdon, J. D. (1978). Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *Am. Nat.* **112**, 595-608.

Vitt, L. J. & Price, H. J. (1982). Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica* 38, 237-255.

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