

PAEDOMORPHOSIS AND DIFFERENCES IN LIFE-HISTORY TRAITS OF TWO NEIGHBOURING CRESTED NEWT (*TRITURUS CARNIFEX*) POPULATIONS

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Two neighbouring crested newt populations (Ceklin and Lokanj) from Montenegro differ in several important life-history traits. Females from Ceklin laid significantly larger eggs. Larval size at hatching did not differ between Ceklin and Lokanj, but larvae from larger eggs survived better under laboratory conditions. Newts from Lokanj had a higher overall larval growth rate and a longer larval period. Consequently, they metamorphosed at larger size than Ceklin individuals. They also attained sexual maturity at smaller size than newts from Ceklin. It is shown that male newts with larval morphology may be sexually mature. Individuals from Lokanj population had a more plastic life-history, including facultative paedomorphosis, than individuals from Ceklin population. Out of five ontogenetic stages, juveniles and adult males showed significant interpopulation difference in size-shape trajectories. This might be the consequence of different ontogenetic pathways followed by crested newts from these populations.

INTRODUCTION

The life-history of urodeles is generally characterized by an aquatic larval stage and an adult stage adapted to diverse terrestrial habitats. The transition between these two ecologically distinct phases occurs during the period of metamorphosis. The timing of metamorphosis can influence associated traits such as body size at metamorphosis, one of the most important life-history features in this group (e.g. Smith-Gill & Berven, 1979; Werner, 1986), which potentially may affect adult survival, body size and age at first reproduction, and fecundity. In other words, a direct relationship exists between phenotypic variation generated in the larval stage and adult traits closely associated with fitness (Semlitsch, Scott & Pechmann, 1988). Timing of metamorphosis in urodeles is further complicated if some individuals in the population follow other ontogenetic trajectories, excluding metamorphosis in extreme cases.

The genus *Triturus* is of interest in this respect because some species are facultatively paedomorphic; i.e. some sexually mature individuals are characterized by adult morphology while others reproduce in the larval form. Among these species the alpine newt (*Triturus alpestris*) and the smooth newt (*Triturus vulgaris*) show a high incidence of paedomorphosis, especially in the Balkan area (Dzukic, Kalezic, Tvrtkovic & Djorovic, 1990).

In the crested newt (*Triturus cristatus* superspecies), however, the reproductive strategy of facultative paedomorphosis seems to be very rare. Occasionally 'giant overwintering larvae' have been found, or the in-

cidence of paedomorphosis has been reported but without firm evidence that specimens were sexually mature (for recent reports see Frazer, 1983; Kalezic & Dzukic, 1990; Fasola & Canova, 1992). In the course of our intensive study of the crested newt populations from former Yugoslavia, out of more than 1500 specimens examined (unpubl.), only a few males from a Montenegrin population had well developed gills and were sexually mature.

Variation in life-history traits on a large geographic scale has been the subject of considerable attention in urodeles, but differences on a smaller scale have received little study. This paper compares some of the life-history traits of *Triturus carnifex* in two neighbouring breeding sites in Montenegro. In one of these sites clear evidence of a nontransforming life-history path has been observed. The traits measured in this study included: (1) egg size and embryo survival; (2) larval survival and growth rate; (3) duration of larval stage; (4) time and size at metamorphosis; (5) size at onset of sexual maturation; and (6) characteristics of ontogenetic size-shape trajectories.

MATERIALS AND METHODS

STUDY SITES

Population localities are situated in the Montenegrin part of the Dinaric Alps, a limestone area of exposed karst. The climate is Mediterranean with hot and dry summers and rainy, mild autumns and winters. In spite of very high precipitation (3500 mm yearly on average), highly porous limestone base causes extreme aridity during summer. Such environ-

ment is rarely occupied by the crested newt elsewhere (Kalezic & Dzukic, 1990).

The study populations inhabit water bodies in sinkholes with impermeable bottoms. During summer months the water level in these ponds decreases considerably. Physical characteristics of the newt breeding sites are similar in many respects. The first pond (Ceklin) is a transformed sinkhole, 21 m wide and 56 m long with the maximum depth of about 1.8 m. The other pond, Lokanj, is 16 m wide and 19 m long basin with the maximum depth of about 2 m. The distance between the ponds is about 5 km. Both ponds are rain fed and hence show wide fluctuations of water level, especially Ceklin pond.

FIELD AND LABORATORY PROCEDURES

The crested newt larvae, juveniles and adults from both ponds were collected in September 1991, brought into the laboratory and anaesthetized by immersion in a 2:1000 MS 222 Sandoz solution before being measured. Shortly after measuring, juveniles and adults were put into hibernation in the cold room at 7.5°C.

Characteristics of the Lokanj and Ceklin populations, from oviposition to metamorphosis, were studied under laboratory conditions. Three males and nine females of each population sample were put to breed in separate aquaria in February 1992 to provide eggs and larvae. To exclude possible effects of larval density, food level and aquaria drying regime on life-history pathways (see Semlitsch, 1987), these variables were kept constant. Water in aquaria was continually recycled and filtered. Aquaria with the breeding individuals, and thereafter eggs and larvae, were exposed to natural photoperiod and daily changes in room temperature (10°C - 25°C).

Courtship, insemination, and oviposition occurred during February, March and April. As the first egg appeared, aquaria were checked twice a day, so that no eggs older than 12 hours were measured. Eggs were measured to the nearest 0.01 mm using a dissecting microscope fitted with an ocular micrometer. After measuring, embryos were cultured in aerated tap water until hatching.

Larvae were fed *ad libitum* with a concentrated mixture of zooplankton, phytoplankton and other micro-organisms collected from natural ponds. Total body length (L) was measured at hatching and each subsequent 15 days. From day 60 onward larvae were measured for total length, head width and tail height. The length of the larval period was defined as the number of days from hatching to metamorphosis. Metamorphosis was considered as completed upon loss of the gills and the closure of the gill slits. Body mass was determined by blotting individuals dry and weighing them to the nearest 0.01 g.

The reproductive organs of specimens thought to be sexually mature were examined by dissection. Maturity in females was determined by the presence of enlarged,

yolk-filled ovarian follicles and/or enlarged oviducts. Maturity in males was determined by the presence of enlarged and/or pigmented testes and vasa deferentia.

MORPHOMETRIC VARIABLES

In 461 hatchlings only body length was measured. Three linear measurements were taken from 44 specimens of 60-day old larvae (larvae I), 75 larvae about the time of metamorphosis (larvae II), 133 juveniles, 50 adult females and 39 adult males. Total body length (L) was measured from the snout to the tail tip, head width (Ltc) was taken at the angle of the jaw, and the maximum fin height (Lh) was measured at the base of the tail from dorsal to ventral edges. These three characters were chosen to document a difference in shape between paedomorphs and metamorphs, as suggested by Shaffer (1984) and Harris (1989). Larval measurements were taken under a dissecting microscope fitted with an ocular micrometer. Older larvae, juveniles and adults were measured with dial calipers with 0.1 mm precision.

TESTICULAR HISTOLOGY

A testis, removed from an adult male with well developed gills (Lokanj pond), was embedded in paraffin wax and longitudinal sections 5 µm thick were cut. Sections were stained with Alcian Blue Pas Orange G.

AGE DETERMINATION

Age was estimated by the technique used initially for fish otolith preparation (Mosegaard, Svedang & Taberman 1988). Humeri were removed from individuals, rinsed in water, air-dried, and mounted in thermoplastic resin. The surface of the bone was then ground and polished in aluminosilicate paste to enhance visibility and to achieve maximal contrast and high transparency. The age appeared to be accurately reflected by the number of the growth lines with a precision of ±1 year. The results were checked using the standard skeletochronological technique on the same humerus bones (for detailed description see Francillon, 1979).

STATISTICAL ANALYSIS

Data were examined using various univariate and bivariate analyses, and the multivariate procedure of principal-component analysis (PCA). PCA was used to derive multivariate measures of newts, size and shape (e.g. Bookstein, Chernoff, Elder, Humphries, Smith, & Strauss, 1985). The analysis was performed on the variance-covariance matrix of log-transformed variables L, Ltc and Lh. The use of variance-covariance matrix rather than correlation matrix is recommended when dealing with morphometric data. The original variables were log-transformed in order to meet the assumption of homoscedasticity (Zar, 1974). Ontogenetic trajectories were obtained for each group (larvae I, larvae II, juveniles and adults) by linear regression analysis of PC2 scores (an aspect of shape) on PC1

scores (a general size aspect). Rate of change in shape relative to size was estimated by the slope of the regression lines.

RESULTS

Females from Ceklin laid larger eggs than females from Lokanj. Differences in all corresponding egg measures appeared to be highly significant (Table 1). Muroid capsules in Ceklin eggs were thicker, relative to ova, than those of Lokanj eggs, the difference being highly significant as well.

Eggs from Ceklin, with more yolk and thicker muroid capsules, survived incubation in our laboratory better than those from Lokanj; survival was 0.413 and 0.227, respectively.

Ceklin eggs produced hatchlings with mean total length of 9.90 ± 0.09 mm ($n = 165$), while those of Lokanj were somewhat smaller (9.81 ± 0.07 mm, $n = 296$). The difference was insignificant (t -NOVA, $P > 0.05$). In both cases the range of total length of newly hatched larvae appeared to be the same (7.1 - 14.0 mm; Fig. 1a).

Larval survival was low during the period from 15-45 days after hatching (0.47 for Ceklin and 0.25 for Lokanj larvae). After this critical period, larval survival stabilized at high level (about 0.90) in both groups until metamorphosis. Apparently, larvae from larger eggs (Ceklin) survived better during the first 45 days of larval life than larvae from smaller eggs (Lokanj).

Larval growth, from hatching to metamorphosis, was estimated as the change in mean body length between measuring dates (each 15 days). Linear

Measure		Ceklin $n=124$	Lokanj $n=133$
Ovum	length	2.68 ± 0.02	2.59 ± 0.02
	width	2.49 ± 0.02	2.39 ± 0.02
Total egg	length	5.50 ± 0.04	4.73 ± 0.04
	width	3.40 ± 0.02	3.10 ± 0.03
Ovum/total egg	length	0.49 ± 0.00	0.55 ± 0.00
	width	0.73 ± 0.00	0.78 ± 0.00

TABLE 1. Mean values (\pm SE) of egg size (in mm) and of ovum/total egg ratio for two crested newt populations. n = sample size. All corresponding egg measures between populations are highly significant (ANOVA, $P < 0.001$).

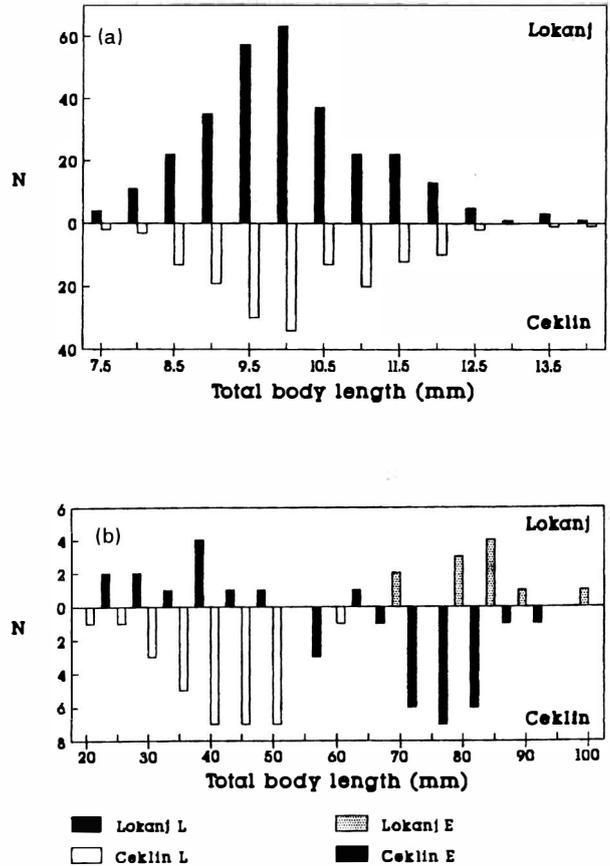


FIG. 1. (a) Distribution of total body length (in mm) of hatchlings from Lokanj and Ceklin populations. n = number of individuals. (b) Distribution of total body length (in mm) of 60-day old larvae (L) and efts (E) from Lokanj and Ceklin populations. n = number of individuals.

regressions of total length on age are presented in Fig. 2. Growth appeared to be faster in larvae from Lokanj; the difference between the two slopes was significant (t -test, $P < 0.01$).

The mean duration of larval development was 176.9 ± 8.2 days (range 122-211; $n = 11$) in the Lokanj sample, and 158.8 ± 6.3 days (range 89-200; $n = 25$) in the Ceklin sample. A non-significant difference between mean time of metamorphosing of Ceklin and Lokanj larvae was found in this study (ANOVA, $P > 0.05$). Probably the number of surviving larvae was insufficient to detect subtle difference in this obviously variable life-history trait.

Total body length at which Ceklin larvae metamorphosed ranged from 52.3 mm to 87.0 mm, with the mean value of 70.39 ± 1.62 , while larvae from Lokanj sample transformed at larger size (range 65.4 - 95.6; mean \pm SE = 79.43 ± 2.39); the difference being highly significant (ANOVA, $P < 0.005$). Putting this in terms of weights, at metamorphosis the crested newt reached 19.7% (Ceklin) and 33.6% (Lokanj) of its mean adult weight.

Sample	<i>n</i>	Body length	Head width	Fin height
<i>Lokanj</i>				
Larvae I	12	36.53 ± 11.57	5.33 ± 1.65	6.23 ± 1.66
Larvae II	35	83.89 ± 3.53	9.19 ± 0.53	8.35 ± 0.83
Juveniles	43	89.67 ± 6.16	8.77 ± 0.53	7.22 ± 0.62
Adults (female)	21	130.81 ± 9.31	12.84 ± 1.13	9.57 ± 1.14
Adults (male)	19	123.89 ± 8.16	12.46 ± 0.96	9.68 ± 1.36
<i>Ceklin</i>				
Larvae I	32	38.80 ± 8.20	5.75 ± 1.23	7.25 ± 1.59
Larvae II	40	64.18 ± 5.50	7.39 ± 0.47	6.74 ± 0.79
Juveniles	90	73.93 ± 5.86	7.34 ± 0.56	5.70 ± 0.70
Adults (female)	29	142.50 ± 12.48	14.00 ± 1.31	11.28 ± 1.80
Adults (male)	20	122.80 ± 10.44	12.49 ± 0.75	10.18 ± 1.14
<i>F values</i>				
Larvae I		0.53	0.84	3.53
Larvae II		330.61***	239.43***	74.10***
Juveniles		203.25***	193.82***	144.08***
Adults (female)		13.07***	10.68**	14.75***
Adults (male)		0.13	0.01	1.53

TABLE 2. Means and standard errors of morphometric characters (in mm) for five forms (*n* = sample size). Differences between two populations were tested by means of ANOVA. ** $P < 0.01$, *** $P < 0.001$.

Sixty-day-old larvae (larvae I) from both populations showed statistically non-significant differences in body size (Table 2). Being longer in larval stage was associated with larger size at metamorphosis: larvae II were much larger in the Lokanj sample for all measured traits. Also, a little overlap in total length of Lokanj and Ceklin efts (Fig. 1b) was even less in postmetamorphic juveniles (Fig. 3).

Frequency distribution of body length of adults is shown in Fig. 3. Adult males from Lokanj and Ceklin were of about the same size and weight (ANOVA, $P > 0.05$ in both cases). Females from Ceklin appeared to be much larger and heavier than those from Lokanj (ANOVA, $P < 0.001$). Morphological differences between sexes were apparent in both populations (Table 2). Adult females were larger than adult males; the difference was more pronounced in the Ceklin sample. Comparing body weights, females and males from the Lokanj population did not differ significantly (ANOVA, $P > 0.05$), in contrast with Ceklin adults (ANOVA, $P < 0.001$).

Out of 40 sampled branchiate males from Lokanj, four specimens had secondary sexual characteristics, including a well developed dorsal crest, a prominent cloaca, and a whitish streak along the side of the tail.

The size of the smallest one ($L = 92.0$ mm, $L_{sv} = 52.9$ mm) was assumed to be the size of the first reproduction of Lokanj males. The testes of this male were lobulated. The largest branchiate male ($L = 116.0$ mm, $L_{sv} = 66.1$ mm) had one-lobe testes. The breeding capability of this male was confirmed by the presence of spermatozoa in the spermatic ductus and ampullae with spermatids (April 1992). The estimated age of this male, 5 years, was in the range shown by breeding males from Ceklin and Lokanj (4-11; $n = 38$; unpubl. data). It is also in concordance with data on the age of sexual maturation in crested newt in France (Francillon-Vieillot, Arntzen & Geraudie, 1990). Sexually mature branchiate females were not found. The size of the smallest mature female from Lokanj ($L = 97.0$ mm, $L_{sv} = 55.9$ mm) was taken to be the size of the first reproduction of this sex.

In the Ceklin population only non-branchiate mature specimens were found; the smallest male had 100 mm body length ($L_{sv} = 67.1$ mm) and female 114 mm ($L_{sv} = 65.6$ mm). These figures were taken to represent the size of the first reproduction in Ceklin. This size happened to be very close to those established for the crested newt (*Triturus cristatus*) from England (Bell, 1979).

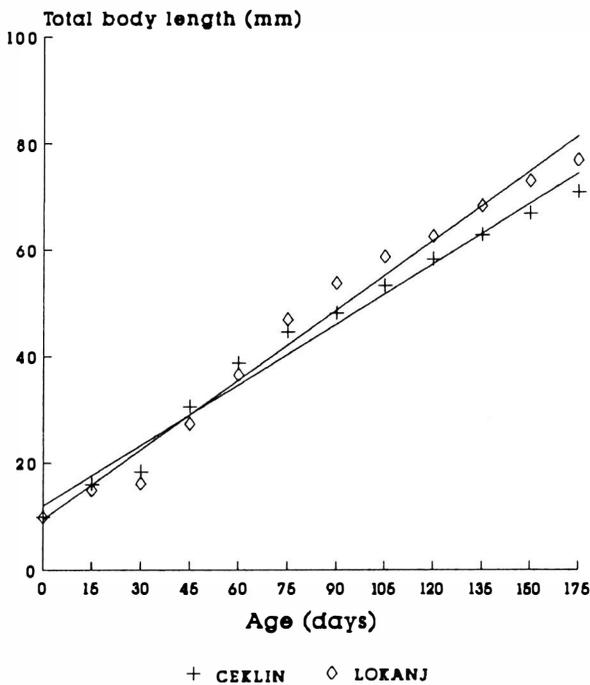


FIG. 2. Regressions of total length on age for larvae from two populations.

Principal component one (PC1) is highly positively correlated with the original morphological variables and it was taken as a latent size variable (in the sense of Bookstein *et al.*, 1985). This component explained almost 90% of the total variation in trivariate sample space (Table 3). Total body length, head width and fin height loaded positively and significantly on the first component in decreasing contributions. Principal com-

	Variance-covariance matrix			Eigenvectors		
	Lsv	Ltc	Lh	PC1	PC2	PC3
Lsv	0.031	0.022	0.014	0.72	-0.51	-0.47
Ltc		0.018	0.013	0.56	0.04	0.83
Lh			0.014	0.40	0.86	-0.32
	Eigenvalues			0.0561	0.0061	0.0004
	Percent of variance			89.58	9.65	0.77

TABLE 3. The PCA of variance-covariance matrix derived from pooled data (larvae I, larvae II, juveniles and adults) of two populations. The variables are the logarithms of body length (L), head width (Ltc) and fin height (Lh).

ponent two (PC2), contrasted original measures with each other. Thus, eigenvector of total body length had negative value, while fin height was positively correlated to PC2. Ltc showed a negligible correlation with PC2. Therefore, PC2 summarizes aspects of newts' shape, explaining about 10% of the remaining variation. PC3 explained a negligible amount of variation (< 1%), and was not considered further.

Means and standard errors of PC1 and PC2 scores for different life stages are presented in Table 4. The ontogenetic trajectories, represented by separate regressions of PC2 on PC1 scores for five corresponding

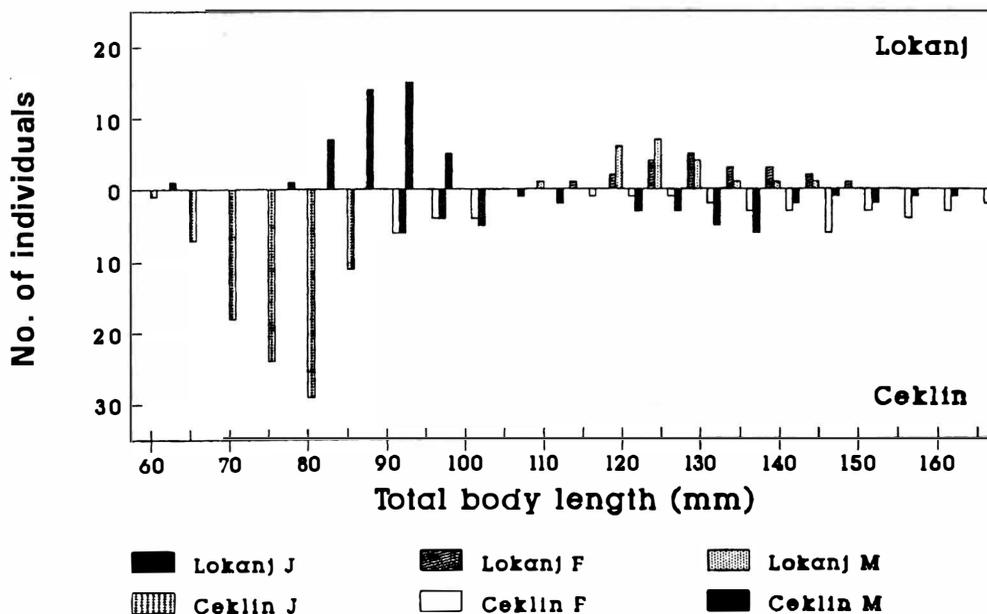


FIG. 3. Distribution of total body length (in mm) of juveniles (J), males (M) and females (F) from two populations.

	<i>Lokanj</i>		<i>Ceklin</i>		<i>t</i>
	PC1	PC2	PC1	PC2	
Larvae 1	1.83±0.22	-0.09±0.05	1.90±0.18	-0.05±0.05	1.37
Larvae 2	2.30±0.04	-0.16±0.03	2.13±0.05	-0.18±0.04	1.53
Juveniles	2.28±0.04	-0.22±0.03	2.14±0.06	-0.28±0.04	2.38**
Females	2.54±0.05	-0.20±0.04	2.62±0.07	-0.16±0.05	0.51
Males	2.52±0.06	-0.18±0.04	2.53±0.06	-0.16±0.03	1.97*

TABLE 4. Means and standard errors of PC1 and PC2 scores. *t*-values obtained from testing for difference between regression coefficients of PC2/PC1 scores between five corresponding forms from two populations. * $P < 0.05$, ** $P < 0.01$.

forms of two populations, estimate changes of shape relative to size. Regression coefficients were compared by means of *t*-test. Adult females appear to be most similar, followed by younger larvae and older larvae, respectively. Juveniles and adult males showed significant interpopulation differences in the ontogeny of size and shape changes.

DISCUSSION

This study deals with differences in life-history traits of two neighbouring populations of the crested newt. Females from Ceklin laid significantly larger eggs (with more yolk for larval development) than those from Lokanj. The size of mucoid capsule is also relevant for the future of the developing embryo; it gives protection from injury and fungal infestation and improves fastening to an object (Duellman & Trueb, 1986).

We found that larvae from larger eggs survived better under laboratory conditions than larvae from smaller eggs. That egg size was related to larval success, was found previously for *Ambystoma talpoideum* (Semlitsch & Gibbons, 1990). However, in contrast with the above study, larval size at hatching did not differ between Ceklin and Lokanj; egg size did not significantly affect body size of larvae at hatching.

Newts from Lokanj had higher overall larval growth rate and a longer larval period; consequently, they transformed at larger size than Ceklin individuals. They also attained sexual maturity at smaller size. This study confirms that at least some males matured while possessing a larval morphology. To the best of our knowledge, this is the first report of fully sexually mature crested newts with well developed gills that can therefore be considered paedomorphic.

The most common life-history pathway in newts leads to obligate metamorphosis. This path is followed by newts from Ceklin. However, juveniles are more

aquatic than elsewhere; it appears that the surrounding terrestrial environment, which is arid and unproductive, does not support juvenile growth sufficiently.

Individuals from Lokanj have a plastic life-history including facultative paedomorphosis. The Lokanj larvae have three possible fates during ontogeny: (1) some larvae transform in the same year they were hatched; (2) a considerable number of larvae have a prolonged period of growth, overwintering in the pond and then metamorphosing to immature juveniles; (3) in some larvae a prolonged period of growth is followed by attaining sexual maturity and then metamorphosing into adults. Larvae with an initial growth advantage are more likely to take this life-history pathway. Body size advantage, at a time when larvae are most vulnerable, may account for increased survival through size-specific mechanisms. This increased growth results in earlier sexual maturation of aquatic larvae, in comparison to terrestrial or aquatic juveniles of the same year class.

Moreover, there is evidence that paedomorphs breed earlier within a season, providing their larvae with an early growth advantage over the offspring of metamorphs (Semlitsch, Harris & Wilbur, 1990). Apart from an increase in potential survivorship, other advantages gained through a fully aquatic life cycle, such as elimination of energetic costs of metamorphosis and terrestrial migration, play an important role in the maintenance of paedomorphosis. Males are prime candidates to follow this ontogenetic pathway since they reach sexual maturity earlier than females (e.g. Duellman & Trueb, 1986: 169).

A prerequisite for a polymorphic life-history in newts, is an extended residence in water. It is strongly supported by our data: in both ponds adults as well as subadults are abundant out of the breeding season and numerous juveniles are found in water during autumn. That the juveniles returned to water shortly after the

terrestrial phase, as was found for the crested newt in England (Verrell, 1985), is less likely. Metamorphic individuals would be exposed to stress of heat, desiccation and starvation in dry karst habitat. Moreover, in xeric environment there is a critical surface/volume ratio for metamorphosis above which terrestrial activity is disadvantageous (Bruce, 1976).

In newts, growth in the aquatic environment is greater than in the surrounding terrestrial environment (Verrell & Halliday, 1985). Larger size in amphibians may also be advantageous in terms of fecundity (Kaplan & Salthe, 1979; Verrell & Francillon, 1986). However, though several newt species, such as *Notophthalmus viridescens* (Healy, 1973, 1974) and *Triturus vulgaris* (Bell, 1977), show higher growth rates in aquatic habitat, they have lower mortality rates in terrestrial habitat. It is possible that the above trade-off contributes to the maintenance of both life strategies.

Variation in life-history traits may arise from both genetic and non-genetic sources (e.g. Stearns, 1977; Berven & Gill, 1983; Semlitsch & Gibbons, 1985; and references therein). Non-genetic differences may result from plastic phenotypic responses to local environmental conditions or may be due to non-genetic maternal effects (e.g. Falconer, 1981), as stated for egg quality in some anuran species (Travis, 1980; Berven, 1982).

Though the option for paedomorphosis is under genetic control, it is also highly susceptible to environmental conditions (Harris, 1987; Semlitsch 1987; Semlitsch & Wilbur, 1989; Semlitsch *et al.*, 1990). The agent of selection could be the desiccation history of a pond (Semlitsch *et al.*, 1990). According to local inhabitants, Ceklin pond undergoes more drastic changes of water level, though it never dries completely. Thus, it is possible that the Lokanj population has been subject to long term natural selection for overwintering larvae and for paedomorphosis. In Ceklin pond selection for metamorphosis predominates since falling water level, concomitant deterioration of the water quality and increased larval density, would accelerate metamorphosis.

Significant differences in size-shape trajectories for juveniles and adult males might be the consequence of different ontogenetic pathways followed by Lokanj and Ceklin individuals. The more similar size-shape trajectories for females may be due to absence of paedomorphosis in this sex.

Another consequence of different ontogenetic pathways is a reduced size difference in Lokanj females and males. Rapid larval growth, prolonged time of metamorphosis, earlier sexual maturation of males (more time for growth) and the incidence of paedomorphosis apparently reduced sexual size difference in the Lokanj population. Facultative paedomorphosis has the same effect in the alpine newt (*Triturus alpestris*) and to a lesser degree in the smooth newt (*Triturus vulgaris*) (Kalezic, Crnobrnja, Djorovic & Dzukic, 1992).

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