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SEXUAL SIZE DIMORPHISM AND LIFE HISTORY TRAITS OF TWO EUROPEAN SPADEFOOT TOADS *(PELOBATES FUSCUS* AND *P. SYRIACUS)* IN ALLOPATRY AND SYMPATRY

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ABSTRACT

We studied the variation in sexual size dimorphism (SSD) and life history traits in two spadefoot toad species (Pelobates fuscus *and* P. syriacus) *across the part of southeastern European geographic distribution (Panonnian Plain and the Balkans), including the area of their sympatry. Species differ considerably in the body size of adult individuals, in the direction and the extent of SSD, while the differences in tadpole and juvenile sizes prior to or after metamorphosis, as well as in longevity and time of attainment of sexual maturity, appeared to be much smaller and without consistent variation pattern. Significant intraspecific variation was found in both species for body size, magnitude of SSD, average longevity and time of sexual maturity attainment. Intraspecific variation in these traits was much more pronounced in* P. syriacus *than in* P. fuscus. *Adult individuals of* P. syriacus *from the zone of strict sympatry were significantly smaller but larger as tadpoles and with the lower level of SSD. Also, these individuals had shorter life span and earlier sexual maturity (at least one year) than conspecific individuals from the geographically remote allopatric part of the species range.*

Key words: spadefoot toads, body size, longevity, sexual maturity, intersex size difference

DIMORFISMO SESSUALE DI TAGLIA E TRATTI EVOLUTIVI DI DUE SPECIE DI ROSPO EUROPEO *(PELOBATES FUSCUS* E *P. SYRIACUS)* IN ALLOPATRIA E SIMPATRIA

SINTESI

Gli autori hanno studiato le variazioni nel dimorfismo sessuale di taglia (SSD) e nei tratti evolutivi di due specie di rospi pelobati (Pelobates fuscus *e* P. syriacus) *dell'Europa sud-orientale (Pianura Pannonica e Balcani), considerando anche l'area della loro simpatria. Le specie si differenziano considerevolmente per le dimensioni degli individui adulti, che ne caratterizzano, inoltre, il dimorfismo sessuale di taglia. Le differenze riscontrate nelle dimensioni di girini ed individui in stadi giovanili, prima e dopo la metamorfosi, nella longevità e nel tempo di raggiungimento della maturità sessuale, appaiono minori e sprovviste di un modello di variazione consitente. Alcune significanti variazioni intraspecifiche sono state invece riscontrate in entrambe le specie per quanto riguarda le dimensioni corporee, l'ampiezza dell'SSD, la longevità media ed il tempo di raggiungimento della maturità sessuale. Le variazioni intraspecifiche di questi tratti sono risultate più marcate in* P. syriacus *che in* P. fuscus. *Gli individui adulti di* P. syriacus *provenienti dalle zone di simpatria stretta, esattamente come i girini, si sono rivelati significativamente più piccoli ma più tozzi, e con un livello minore di SSD. Questi individui hanno inoltre manifestato una durata della vita inferiore e una maturità sessuale anticipata (di almeno un anno) rispetto ai loro conspecifici provenienti dalla geograficamente distante parte allopatrica dell'estensione della specie.*

Parole chiave: rospi pelobati, dimensioni corporee, longevità, maturità sessuale, differenze intersessuali di dimensioni

INTRODUCTION

The spadefoot toad genus *Pelobates* includes three species in Europe (*P. cultripes, P. fuscus* and *P. syriacus*) and one in extreme northwestern Africa (*P. varaldii*). Common spadefoot toad, *P. fuscus*, has an extensive range, which covers most of the plains and hilly regions of central, eastern and southeastern Europe (Nollert, 1998). The eastern spadefoot toad, *P. syriacus*, has a contemporary distribution extending from the southern part of the Panonnian Plain and southeastward into Romania, Bulgaria, Greece, and southwestern Asia (Sofianidou, 1997). These species have a narrow zone of sympatry along the lower course of the Danube, as well as further south in the vicinity of the Bosphorus.

The morphology and natural history of the three spadefoot species is quite similar. These amphibians are obligatory subterranean habitat specialists. Typical terrestrial habitats include sandy areas, heathlands and deciduous woodland on light density soils. They actively forage and are opportunistic feeders with a wide trophic niche (*e.g. P. fuscus*; Cogalniceanu *et al.*, 1998). During the day and dry periods they hide in deep burrows. When above ground, during migrations or when searching for food, they are strictly nocturnal. The spawning biotopes include a variety of mostly stagnant, meso- to eutrophic permanent water bodies. It might be that *P. fuscus* and *P. syriacus* differ in their ecological characters as they occur over different geographical ranges - *P. fuscus* has wider latitudinal and narrower altitudinal range than *P. syriacus*. In this regard, sympatric populations on the margins of their range may be non-representative for both species.

Components of life history (principal sources of fitness) represent selective compromises to a suite of environmental variables accumulated over evolutionary time (Wilbur *et al.*, 1974). The assessment of life history traits among closely related species and/or conspecific populations within different habitats and regions should reveal potential sources of life history variation (*e.g.* Tilley & Bernardo, 1993). Also, differences in life history pattern observed in the field may sometimes be attributable to phenotypic or developmental plasticity expressed in response to variation in environmental variables (Stearns, 1992). However, the study of sympatric populations, especially syntopic ones, can potentially remove the obfuscating effects of environment differences. In other words, because two strictly sympatric species share habitat features to a large degree (including the same ponds for breeding in case of amphibians), interspecific differences in life history patterns are probably not due to phenotypic or developmental plasticity expressed in response to differences in environment, except for possible differences in sensitivity to population and predator densities. Foraging mode, phylogenetic inertia and morphological constraints (body size and shape) may also be factors potentially influencing variation of life history traits as in many ectotermic groups (Dunham & Miles, 1985).

For spadefoot toad species, the extent of sexual size differences and life history traits, assessed on a good sample size of a number of populations, are little known. Here we compare life history traits of two spadefoot toads, *P. fuscus* and *P. syriacus* across the Panonnian Plain and the Balkans, which include the area of sympatry with syntopically breeding sites. We were particularly interested in inter- and intraspecific variation in a number of life history characteristics, such as: tadpoles, juveniles and adult body sizes, age of adult individuals and time of attaining sexual maturity, as well as in direction and the extent of sexual size dimorphisms.

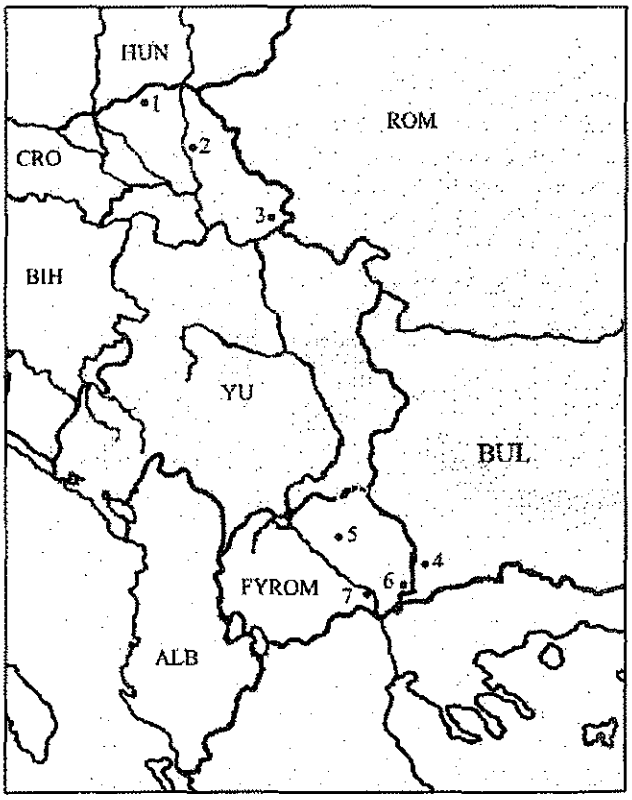

Fig. 1: Distribution of the sampling sites of the spadefoot toads included in the analyses.
Localities: 1 - Cavolj, 2 - Lesino kopovo, 3 - Utrine, 4 - Kresna, 5 - Saramzalino, 6 - Sekirnik, 7 – Prdejci.
Sl. 1: Geografska razporeditev vzorčevalnih mest česnovk, vključenih v analizo.
Lokalitete: 1 - Cavolj, 2 - Lesino kopovo, 3 - Utrine, 4 - Kresna, 5 - Saramzalino, 6 - Sekirnik, 7 – Prdejci.

MATERIAL AND METHODS

Study areas and population samples

As an area where *P. fuscus* lives allopatrically with other spadefoot species, we chose the Subotica-Horgos Sand (Cavolj locality) and the river Tisa inundation area (Lesino kopovo locality, see figure 1). The Deliblato Sand (Utrine locality), situated in the extreme southeastern part of the Panonnial depression, is the area where *P. fuscus* lives in sympatry with *P. syriacus* (Džukić & Pasuljević, 1983). Lesino kopovo lies in an area with quite different geological and edaphic characteristics in comparison to the two Sands. The depression soil of the area is salt-affected and may be regarded as solonetz type according to edaphic classification (Nejgebauer *et al.*, 1959). Allopatric *P. syriacus* populations, from which samples were taken, came from Bulgaria (one breeding unit) and the Former Yugoslav Republic of Macedonia, FYROM (three breeding units, Fig. 1). Locality position data (UTM code, longitude, latitude, altitude) as well as sample sites of tadpoles (at the stage 39; Gosner, 1960), juveniles (just after the metamorphosis) and of sexually matured individuals are presented in table 1. In order to obtain an adequate number of adult individuals of allopatric *P. syriacus*, we pooled individuals collected from these localities neglecting possible population effect on the studied characters' variabilities.

The specimens used in this study are housed in the Georg Džukić's batrachological collection (Institute for Biological Research, Belgrade) and in the collection of the Macedonian Museum of Natural History, Skopje, FYROM.

Morphometrics

Individuals were weighed to the nearest 0.01 g. Nineteen morphometric measurements were taken on each adult specimen's right side using digital caliper (to the nearest 0.01 mm): L - total body length (measured from the snout to cloaca), F – femur length (from the cloaca to the distal end of femur measured on bent hindlimb), T – tibia length, P - pes length (measured from the metatarsal wrist to the apex of the longest, fourth, toe), Lpa - forelimb length (humerus length + length from the proximal articulation of humerus to the apex of the longest, 3rd finger), Lpp - hindlimb length (foot length to the apex of the longest toe, the 4th one), DpPa - length of forelimb first toe (from the proximal end of tubercle to the apex of the 1st finger), DsPa - forelimb second finger length (from the proximal end of tubercle to the apex of the 2nd finger), DpPp - length of hindlimb first toe (from the distal end of inner metatarsal tubercle to the apex of the toe), Cint - inner metatarsal tubercle length, Lc - head length (snout to mouth corner), Ltc - head width (between mouth corners), Spp - minimum interorbital space, Spi - minimum internarial space, Spcr - intercanthal distance, Lo - eye length, Ltp - upper eyelid width, Dro - snout to eye distance, Dno - nostrils to anterior eyelid commisure. Tadpoles and juveniles were measured for the total body length only (from the snout to the tail's tip for tadpoles and from the snout to cloaca for juveniles).

Tab. 1: Locality position data (UTM code, longitude, latitude, altitude) and sample sizes.
Localities: 1 – Cavolj, 2 – Lesino kopovo, 3 – Utrine, 4 – Kresna, 5 – Saramzalino, 6 – Sekirnik, 7 – Prdejci
Tab. 1: Lokaliteta (UTM, zemljepisna dolžina in širina, nadmorska višina) in velikost vzorcev.
Lokalitete: 1 – Cavolj, 2 – Lesino kopovo, 3 – Utrine, 4 – Kresna, 5 – Saramzalino, 6 – Sekirnik, 7 – Prdejci

	1	2	3	4	5	6	7
UTM code	CS91	EQ26	EQ26	FM81	EM72	FL58	FI26
Longitude	46°10'	44°50'	44°50'	41°43'	41°47'	41°26'	41°12'
Latitude	19°40'	21°18'	21°18'	23°9'	21°57'	22°48'	22°31'
Altitude (m)	100	80	95	180	280	210	65
P. fuscus							
Adults - females	8	27	26	-	-	-	-
Adults - males	39	16	5	-	-	-	-
tadpoles	20	-	8	-	-	-	-
juveniles	17	-	14	-	-	-	-
P. syriacus							
Adults - females	-	-	30	4	1	2	4
Adults - males	-	-	21	14	2	1	2
tadpoles	-	-	10	-	-	-	10
juveniles	-	-	15	-	-	-	10

Age and time of sexual maturation

Individual ages were assessed by skeletochronology. A general description of this histological method can be found elsewhere (*e.g.* Castanet *et al.*, 1993). Frozen sections of the demineralized bones were cut at 16 μm and stained in Ehrlich's hematoxylin. Second phalange's diaphyseal portion of the forelimb's third digit was used for counting the lines of arrested growth (LAG), which corresponded to annual resting growth periods. A comparison of the number of LAGs in the phalanges and in the femur of the same individuals (three toads of both species) revealed the same LAG numbers. We managed to assess an individual onset of sexual maturity as a sudden decrease in bone growth and concomitant rapprochement of LACs (see Kleinenberg & Smirina, 1969; Francillon-Vieillot *et al.*, 1990). Possible resorption of the first LAG, due to endosteal cavity growth, was taken into account when age was estimated, and one year added to the estimated age when resorption was obvious.

Statistical analyses

Various parametric and nonparametric tests were used to analyze data. One way ANOVA was used to analyze differences in body weight and morphometric traits between species and between sexes. Mahalanobis distances were calculated to measure overall morphometric differences between genders using the set of all 19 characteristics. A non-parametric Mann-Whitney U test described differences in age and time of attaining sexual maturity, while frequency distributions of age classes in females and males were tested by the Kolmogorov-Smirnov test. We used the Tukey-Kramer test for multiple comparisons among means. Correlations between morphometric traits and between body measures and age were analyzed by the Spearman correlation test (Rs).

All statistical analyses were performed using various STATISTICA program procedures.

RESULTS

Body size measures - intersexual and interlocality comparisons

Descriptive statistics of adult body measures are presented for both species (Tabs. 2a-2e). Intersexual differences between *P. fuscus* toads from Cavolj and Utrine, but not from the Lesino kopovo locality, were significant in respect to almost all analyzed characteristics. Females were significantly larger than males, being apparently twice as massive. Among morphometric traits only toe lengths did not differ significantly between sexes. Males from Cavolj showed significantly larger values only for eye-length (ANOVA, $p < 0.001$) and interorbital distance (ANOVA, $p < 0.05$). In the Utrine population, even these measurements were not significantly larger in males. Mahalanobis distance between sexes in *P. fuscus* from Cavolj was estimated to be $D^2 = 20.23$ ($p < 0.001$), and from the Lesino kopovo locality $D^2 = 12.92$ ($p < 0.01$). This measure was not computed for the Utrine population due to the small sample size of males. Males and females from Lesino kopovo locality were very similar in respect to age at maturity and age range and therefore presented a good sample for analyses. Interestingly, intersexual differences were not significant, except that females were more massive and had longer femurs.

Sexual dimorphism in the common spadefoot toad was seen, not only in overall body-size, but also in specific morphological characters such as limbs. Elongated fore- and hindlimbs in males can be regarded as characters that are favored in male-male competition for females and such sexual dimorphism has been found for some anuran species (Halliday & Tejedo, 1995), but the fight between *Pelobates* males (paired-unpaired) has not been documented yet (Eggert, *pers. comm.)*. Much larger fore- and hindlimbs in males than in females, relative to body length, were confirmed for the common spadefoot toad from Cavolj (Lpa/L, $p < 0.05$; Lpp/L, $p < 0.01$). Also, Cint/L index (inner metatarsal tubercle length/body length) appeared to be significantly larger in males compared to females (ANOVA, $p < 0.001$). However, such sexual dimorphism was not found in the other two population samples, Utrine and Lesino kopovo.

Interpopulation comparisons between *P. fuscus* samples revealed that individuals from Utrine and Cavolj did not differ statistically in respect to most morphometric traits, but in a few cases differences were apparent. Notably, hind limbs and head dimensions were significantly larger in males from Cavolj (ANOVA, $p < 0.05$), while females from the same population were smaller than their counterparts from Utrine in respect to all traits that showed significant differences; *i.e.* hind limbs, inner metatarsal tubercle, eye-length and interorbital distance. However, when samples from Cavolj and Lesino kopovo were compared, significant differences appeared in almost all characters (ANOVA, $p < 0.001$), individuals of both genders from Cavolj being larger. Differences were not significant only for total body length and intercanthal distance in males and for intercanthal distance and minimum interorbital space in females. Utrine *vs.* Lesino kopovo comparison revealed significant differences only in females (in all characters except for minimum interorbital space and eye length), with Lesino kopovo individuals being smallest in comparison to the other two populations.

P. syriacus from Utrine did not show any intersexual differences in morphometric characters. Mahalanobis distance between sexes in *P. syriacus* from this population was estimated to be $D^2 = 9.758$ ($p > 0.05$). Neither females nor males of this species differed significantly in hindlimb lengths and the size of metatarsal tubercle relative to body size (ANOVA, $p > 0.05$). However, forelimbs were much larger in males in comparison to females (ANOVA, $p < 0.001$). Contrary, intersexual differences in allopatric *P. syriacus* individuals from FYROM+Bulgaria were statistically significant in respect to all analyzed traits. Males appeared to be larger than females. The most prominent differences were in weight, body length, fore- and hindlimbs and toe length (ANOVA, $p < 0.001$). Mahalanobis distance between the sexes of *P. syriacus* from this sample was significant ($D^2 = 41.22$, $p < 0.05$). Elongated fore- and hindlimbs in males vs. females appeared to be statistically significant (ANOVA: Lpa/L, $p < 0.05$; Lpp/L, $p < 0.01$), but the size of metatarsal tubercle relative to body size failed to show dimorphism (ANOVA, $p > 0.05$). Males being larger than females is a very interesting result for it is not common in amphibians. Yet, both male and female samples lack young adults (Fig. 3) and the individuals that we compared might have been close to the maximum size they would reach.

Interpopulation comparison within the eastern spadefoot revealed that allopatric females and males (FYROM + Bulgaria) were significantly larger than individuals living in sympatry with the common spadefoot (Utrine) for most morphometric traits in females (except in nostrils to anterior eyelid commisure distance) and all traits in males with the most prominent differences being in total body length and weight (ANOVA, $p < 0.001$). Again, in allopatric population both male and female samples lack young adults and the differences in body sizes could be due to differences in age classes in samples compared, and not to presumable allopatry/sympatry differences.

Tab. 2a: Differences in morphometric characters between sexes in* Pelobates syriacus *from Utrine locality.
X - mean value, SD - standard deviation, SSD - female/male size ratio values. Symbols (* P<0.05; ** P<0.01; *** P<0.001; n.s. - non significant) denote the significance level of SSD, obtained by ANOVA test.
Tab. 2a: Morfometrične razlike med spoloma* Pelobates syriacus *z lokalitete v Utrinah.
X - srednja vrednost, SD - standardni odklon, SSD (VRS) je velikostno razmerje med spoloma. Simboli (* P<0,05; ** P<0,01; *** P<0,001; n.s. – ni signifikantno) ponazarjajo interval zaupanja SSD, dobljen s testom ANOVA.

***Pelobates syriacus* (Utrine)**						
	Males (N=21)		Females (N=30)			
Variable	X ± SD	range	X ± SD	range	SSD	signif.
Weight	28.91 ± 13.49	10.26-60.76	32.01 ± 15.68	11.63-71.92	1.15	n.s.
L	61.13 ± 8.97	47.55-75.62	60.83 ± 8.93	47.84-79.56	1.00	n.s.
F	28.90 ± 4.92	20.47-37.81	29.27 ± 4.75	22.47-40.47	1.01	n.s.
T	23.86 ± 3.60	18.54-32.45	23.77 ± 3.13	17.84-32.54	1.00	n.s.
P	30.63 ± 5.04	22.64-38.44	28.15 ± 4.65	18.51-37.39	0.92	n.s.
Lpa	41.65 ± 8.47	30.90-58.18	38.85 ± 6.41	28.20-53.04	0.93	n.s.
Lpp	93.52 ± 14.95	67.81-121.91	92.96 ± 13.21	73.63-128.22	0.99	n.s.
DpPa	10.24 ± 1.57	7.66-12.81	9.99 ± 1.59	7.22-14.33	0.98	n.s.
DsPa	8.92 ± 1.76	6.12-12.43	8.61 ± 1.66	6.40-13.09	0.97	n.s.
DpPp	5.69 ± 1.25	3.65-8.12	5.41 ± 0.95	3.56-7.80	0.95	n.s.
Cint	5.78 ± 0.97	4.40-7.53	5.73 ± 1.12	4.12-8.24	0.99	n.s.
Lc	16.47 ± 2.92	12.30-20.37	16.44 ± 2.62	11.24-23.62	1.00	n.s.
Ltc	20.01 ± 3.83	14.46-26.55	19.42 ± 2.73	14.53-30.76	0.97	n.s.
Spp	7.26 ± 1.10	4.76-9.81	7.30 ± 1.03	4.78-9.67	1.01	n.s.
Spi	4.38 ± 0.70	3.49-5.89	4.67 ± 0.68	3.46-6.44	1.07	n.s.
Spcr	8.72 ± 1.02	6.64-11.08	8.93 ± 1.21	6.34-11.26	1.02	n.s.
Lo	6.62 ± 0.91	5.01-8.40	6.81 ± 0.87	4.98-8.88	1.03	n.s.
Ltp	5.30 ± 0.54	4.60-6.37	5.04 ± 0.79	2.77-6.79	0.95	n.s.
Dro	9.42 ± 1.28	7.42-11.33	9.62 ± 1.37	6.65-12.79	1.02	n.s.
Dno	5.84 ± 1.01	4.30-7.64	5.94 ± 0.73	4.48-9.30	1.02	n.s.

Tab. 2b: Differences in morphometric characters between sexes in* Pelobates syriacus *from FYROM & Bulgaria localities (for legend see table 2a).

Tab. 2b: Morfometrične razlike med spoloma* Pelobates syriacus *z lokalitet v Makedoniji in Bolgariji (legenda: glej tabelo 2a).

***Pelobates syriacus* (FYROM & Bulgaria)**						
	Males (N=19)		Females (N=11)			
Variable	X ± SD	range	X ± SD	range	SSD	signif.
Weight	53.89 ± 6.44	43.28-66.81	44.80 ± 6.39	35.15-56.35	0.81	***
L	75.81 ± 3.06	68.75-79.73	70.51 ± 4.08	66.14-79.34	0.93	***
F	36.53 ± 1.87	31.48-39.73	33.24 ± 2.31	29.74-36.93	0.91	***
T	29.90 ± 1.35	27.31-33.46	27.71 ± 1.91	24.24-30.25	0.93	**
P	42.01 ± 2.36	37.07-46.09	36.47 ± 2.77	31.48-40.47	0.87	***
Lpa	55.60 ± 2.43	50.46-59.77	48.91 ± 5.39	42.49-62.77	0.88	***
Lpp	120.45 ± 5.55	106.09-130.43	107.64 ± 6.81	97.27-117.83	0.89	***
DpPa	15.09 ± 1.01	13.21-16.53	12.53 ± 1.60	8.34-14.55	0.83	***
DsPa	15.63 ± 0.82	13.51-16.53	13.68 ± 0.87	12.12-14.88	0.88	***
DpPp	16.10 ± 1.14	13.54-17.60	15.40 ± 1.11	13.75-17.17	0.96	n.s.
Cint	7.08 ± 0.44	6.17-7.72	6.74 ± 0.55	5.67-7.71	0.95	n.s.
Lc	25.06 ± 0.99	23.34-27.61	23.25 ± 1.31	21.86-25.91	0.93	***
Ltc	29.72 ± 1.77	25.10-32.03	28.09 ± 1.62	25.90-30.73	0.95	*
Spp	8.18 ± 0.77	6.36-9.74	8.10 ± 1.06	6.36-10.37	0.99	n.s.
Spi	6.47 ± 0.45	5.48-7.19	5.99 ± 0.47	5.31-6.76	0.93	**
Spcr	10.90 ± 0.72	9.58-12.54	10.77 ± 1.06	8.86-12.45	0.99	n.s.
Lo	9.05 ± 0.51	8.03-9.90	8.44 ± 0.57	7.78-9.59	0.93	**
Ltp	6.23 ± 0.28	5.62-6.70	6.02 ± 0.26	5.67-6.50	0.97	n.s.
Dro	11.82 ± 0.60	10.55-12.74	11.10 ± 0.50	10.41-11.78	0.94	**
Dno	6.73 ± 0.52	5.57-7.64	6.34 ± 0.37	5.70-6.73	0.94	*

Tab. 2c: Differences in morphometric characters between sexes in* Pelobates fuscus *from Utrine locality (for legend see table 2a).

Tab. 2c: Morfometrične razlike med spoloma* Pelobates fuscus *z lokalitete v Utrinah (legenda: glej tabelo 2a).

***Pelobates fuscus* (Utrine)**						
	Males (N=5)		Females (N=26)			
Variable	X ± SD	range	X ± SD	range	SSD	signif.
Weight	10.37 ± 1.18	8.73-12.06	17.18 ± 6.45	10.22-32.95	1.66	*
L	44.79 ± 2.77	41.21-48.08	53.71 ± 5.22	46.45-65.16	1.20	***
F	20.46 ± 1.35	18.99-22.30	23.44 ± 2.56	19.34-27.95	1.15	**
T	16.65 ± 0.98	15.24-17.79	20.00 ± 1.90	16.50-24.64	1.20	***
P	20.24 ± 1.44	18.45-22.21	24.65 ± 3.02	19.46-31.92	1.22	****
Lpa	30.39 ± 2.42	27.61-33.89	35.01 ± 3.39	28.54-40.96	1.15	*
Lpp	66.05 ± 3.48	62.01-71.46	75.53 ± 7.47	66.47-92.02	1.14	n.s.
DpPa	7.70 ± 1.01	6.43-9.12	8.75 ± 1.16	6.55-11.99	1.14	n.s.
DsPa	6.70 ± 1.17	5.66-8.17	7.94 ± 1.27	5.11-10.63	1.19	n.s.
DpPp	4.10 ± 0.34	3.80-4.56	4.24 ± 0.59	3.33-5.58	1.03	n.s.
Cint	4.02 ± 0.31	3.69-4.50	4.75 ± 0.57	3.67-6.04	1.18	*
Lc	11.95 ± 0.92	12.75-0.92	14.66 ± 1.37	11.22-18.65	1.23	***
Ltc	14.40 ± 1.79	12.10-17.11	18.66 ± 2.37	14.65-24.26	1.30	***
Spp	5.48 ± 0.48	4.77-6.02	5.84 ± 0.75	4.42-7.60	1.07	n.s.
Spi	3.92 ± 0.37	3.28-4.24	4.57 ± 0.69	3.52-6.31	1.17	n.s.
Spcr	6.16 ± 0.86	5.20-7.42	7.26 ± 0.75	6.14-9.20	1.18	**
Lo	5.30 ± 0.55	4.80-6.07	5.04 ± 0.81	3.99-6.75	0.95	n.s.
Ltp	3.86 ± 0.43	3.27-4.20	4.51 ± 0.44	3.64-5.36	1.17	**
Dro	6.85 ± 0.59	6.02-7.63	8.03 ± 0.94	6.22-10.11	1.17	*
Dno	3.88 ± 0.44	3.24-4.30	4.68 ± 0.65	3.02-5.62	1.21	*

Tab. 2d: Differences in morphometric characters between sexes in** Pelobates fuscus **from Cavolj locality (for legend see table 2a).
Tab. 2d: Morfometrične razlike med spoloma** Pelobates fuscus **z lokalitete v Cavolju (legenda: glej tabelo 2a).

***Pelobates fuscus* (Cavolj)**						
	Males (N=39)		Females (N=28)			
Variable	X ± SD	range	X ± SD	range	SSD	signif.
Weight	12.54 ± 2.69	7.79-18.57	19.14 ± 5.82	8.87-32.49	1.53	***
L	46.00 ± 3.12	40.57-56.65	54.02 ± 4.46	47.07-62.15	1.17	***
F	22.76 ± 2.09	16.44-25.67	23.99 ± 2.15	20.15-30.57	1.05	*
T	18.61 ± 1.25	16.19-20.79	19.95 ± 1.70	16.10-23.29	1.07	***
P	23.66 ± 1.67	20.03-26.18	28.73 ± 4.19	21.89-36.19	1.21	***
Lpa	31.98 ± 3.88	13.60-37.85	34.51 ± 3.45	28.22-41.48	1.08	**
Lpp	74.12 ± 4.67	63.16-83.66	73.40 ± 9.21	59.07-90.18	0.99	n.s.
DpPa	8.13 ± 0.86	6.01-9.56	7.89 ± 0.88	6.52-9.77	0.97	n.s.
DsPa	6.76 ± 0.62	5.50-8.07	7.24 ± 0.98	5.83-9.27	1.07	*
DpPp	4.40 ± 0.55	3.26-5.72	4.62 ± 0.70	3.51-6.13	1.05	n.s.
Cint	4.24 ± 0.35	3.19-5.12	4.36 ± 0.50	3.30-5.68	1.03	n.s.
Lc	12.88 ± 1.05	11.04-15.96	14.07 ± 1.20	11.80-17.20	1.09	***
Ltc	15.72 ± 1.86	12.61-20.30	18.86 ± 1.78	14.66-22.01	1.20	***
Spp	5.81 ± 0.54	4.90-6.79	5.53 ± 0.55	4.50-6.67	0.95	*
Spi	4.43 ± 0.48	3.17-5.95	4.63 ± 0.71	3.29-6.27	1.05	n.s.
Spcr	7.07 ± 0.57	5.99-8.15	7.64 ± 0.60	6.63-8.79	1.08	***
Lo	5.42 ± 0.77	3.81-6.67	4.34 ± 1.04	3.25-7.47	0.80	***
Ltp	3.81 ± 0.52	2.63-5.13	4.28 ± 0.56	3.27-5.96	1.12	***
Dro	7.37 ± 0.76	6.24-9.33	8.19 ± 0.77	6.96-9.99	1.11	***
Dno	4.31 ± 0.55	3.51-6.27	4.7 ± 0.50	3.68-6.18	1.09	**

Comparisons between species from the zone of sympatry (Utrine) revealed statistically significant differences in almost all analyzed traits. Both males and females of *P. syriacus* were significantly larger than their *P. fuscus* counterparts (ANOVA, at least at $p < 0.05$). On average, the largest tadpoles and juveniles were those of *P. fuscus* from the zone of sympatry (Utrine) and the smallest ones were preadult individuals of the same species from the zone of allopatry (Cavolj, Tab. 3).

We only compared tadpoles and juveniles from the same locality, since it is known that tadpole size in anurans is strongly related to tadpole density and the amount of food available in the pond. Interspecific differences (Utrine locality) were not statistically significant neither in tadpoles nor in juveniles (ANOVA, $p>0.05$). *P. fuscus* juveniles reached on average only 35.7% (Cavolj) and 33.8% (Utrine) of the tadpole size prior to metamorphosis, while in *P. syriacus* populations figures were 34.9% (FYROM) and 35.2% (Utrine). It was also interesting to compare juvenile with the adult body size. On average, *P. fuscus* juveniles were from 58.1% (Cavolj) to 61.0% (Utrine) of adult females, and from 68.5% (Cavolj) to 73.2% (Utrine) of adult male body size. In *P. syriacus*, on average, juveniles reached 53.1% of adult female body size in Utrine population and 43.9% of female body size in the FYROM+Bulgaria population.

Age and time at sexual maturation

The life span of adult spadefoot toad species studied ranged from 3 to 16 yr. in *P. fuscus*, and from 2 to 16 yr. in *P. syriacus* species (Tab. 4). Such an old individuals in both species has not been recorded so far. Biegler (1966) noticed an 11 years old *P. fuscus* in captivity, while Eggert & Guyetant (1999) and Wiener (1997) reported 9 years old individuals in the field. On average, the oldest were males of the common spadefoot from Cavolj locality (10.21 ± 2.73 yr.), while the youngest were females of the eastern spadefoot from Utrine (4.59 ± 1.56 yr.). Distributions of age classes are given in figures 2 and 3. Differences between genders within locality, as well as differences between localities within sex appeared to be insignificant except in few cases. Males from Cavolj were significantly older then males from Lesino kopovo (Mann-Whitney U test, $p < 0.05$), and males from Utrine locality ($p < 0.01$). Also, intersexual difference in age was significant in the Utrine population sample (females were older than males, Mann-Whitney U test, $p < 0.05$). However, as we managed to score age for only four Utrine males, these differences should be taken with caution. If we exclude an exceptionally old male of 16 yr. from the Utrine sample of *P. syriacus*, even nine years older than the oldest other males, difference between genders in this population appeared insignificant.

Tab. 2e: Differences in morphometric characters between sexes in** Pelobates fuscus **from Lesino kopovo locality (for legend see table 2a).
Tab. 2e: Morfometrične razlike med spoloma** Pelobates fuscus **z lokalitete Lesino kopovo (legenda: glej tabelo 2a).

***Pelobates fuscus* (Lesino kopovo)**						
	Males (N=16)		Females (N=27)			
Variable	X ± SD	range	X ± SD	Range	SSD	signif.
Weight	8.43 ± 3.10	4.00-14.83	12.81 ± 4.37	4.50-24.01	1.52	**
L	43.93 ± 3.89	36.36-49.51	45.38 ± 9.17	41.40-57.94	1.03	n.s.
F	18.63 ± 3.16	14.41-23.13	20.79 ± 3.18	12.46-26.19	1.12	*
T	17.23 ± 1.76	14.12-20.16	18.20 ± 1.77	13.87-21.85	1.06	n.s.
P	20.59 ± 2.33	16.98-24.92	21.55 ± 2.56	16.25-25.14	1.05	n.s.
Lpa	29.25 ± 3.71	22.67-36.56	29.77 ± 3.65	22.43-38.64	1.01	n.s.
Lpp	63.55 ± 6.79	51.42-72.46	68.20 ± 7.87	49.02-82.09	1.07	n.s.
DpPa	6.93 ± 0.71	5.83-8.62	7.24 ± 0.95	4.54-9.25	1.04	n.s.
DsPa	5.88 ± 0.87	4.47-7.38	6.23 ± 0.97	4.32-9.11	1.06	n.s.
DpPp	3.46 ± 0.50	2.62-4.16	3.46 ± 0.43	2.80-4.31	1.00	n.s.
Cint	4.02 ± 0.61	3.15-5.05	4.35 ± 0.65	2.92-5.67	1.08	n.s.
Lc	11.85 ± 1.52	9.57-15.14	12.63 ± 1.48	9.85-14.94	1.07	n.s.
Ltc	14.68 ± 2.16	11.93-18.32	15.37 ± 3.75	10.18-19.95	1.05	n.s.
Spp	5.27 ± 0.47	4.53-6.12	5.74 ± 0.57	4.48-7.04	1.09	**
Spi	4.00 ± 0.54	3.24-5.10	3.98 ± 0.52	2.66-4.86	1.00	n.s.
Spcr	6.09 ± 0.89	4.74-7.55	6.87 ± 0.67	5.17-8.05	1.13	**
Lo	5.23 ± 0.83	3.82-6.52	5.05 ± 0.90	3.40-6.69	0.97	n.s.
Ltp	3.44 ± 0.33	2.88-4.15	3.69 ± 0.52	2.91-5.15	1.07	n.s.
Dro	7.09 ± 0.69	6.04-8.13	6.67 ± 0.78	3.58-7.62	0.94	n.s.
Dno	4.16 ± 0.39	3.56-4.84	4.36 ± 0.37	3.72-5.02	1.05	n.s.

The average life spans of females and males of the other *P. syriacus* sample (FYROM+Bulgaria) were also very similar in spite of the presence of an exceptionally old female of 15 years. Intraspecific difference in age between allopatric and sympatric individuals was statistically significant for both sexes (Mann-Whitney U test, $p < 0.01$). Individuals from Utrine were much younger than spadefoot toads from the southern part of the species range (FYROM+Bulgaria, Tab. 4). Frequency distributions of age classes in females and males were similar in *P. fuscus*, regardless of population, and in *P. syriacus* (Kolmogorov-Smirnov test, $p > 0.05$).

The common spadefoot toads reached sexual maturity at the age of two to five years, while those of eastern spadefoot species at the age of two to four years (Tab. 5). Intersexual differences in this life history trait were negligible in both species (Mann-Whitney U test, $p < 0.05$). Still, male sample from Cavolj lacks young adults (younger than 6 years) which may not allow to obtain accurate results when compared with female sample from the same locality (our analysis shows that both sexes matured at the same age). Also, our male sample from Utrine was not large enough, so these results should not be taken as definite ones. However, within-species variation existed. Thus, both genders of the Cavolj population matured earlier than individuals from Lesino kopovo (Mann-Whitney U test, $p < 0.05$), while males from Utrine locality matured much earlier than males from Lesino kopovo (Mann-Whitney U test, $p < 0.05$). The eastern spadefoot toads of both genders from FYR Macedonia and Bulgaria attained sexual maturity significantly later than individuals from Utrine population (Mann-Whitney U test, $p < 0.001$).

Comparison between spadefoot toads from the zone of sympatry (Utrine) revealed that *P. fuscus* females had a significantly longer life span and they matured later than *P. syriacus* of the same gender (see Tabs. 4 and 5; Mann-Whitney U test, $p < 0.001$ and $p < 0.05$, respectively). On the contrary, *P. syriacus* males were older and they attained sexual maturity later than *P. fuscus* ones (Mann-Whitney U test, $p < 0.001$ and $p < 0.05$, respectively).

Relation between age and size

None of the morphometric characters in the analyzed samples showed significant correlation with age (Rs test, $p > 0.05$). From our data, we concluded that body length is a poor predictor of age as there is considerable size variability observed within most age-classes. For example, 10 years old males of the common spadefoot toad from Cavolj can be as large as 40 to 56 mm, or females of that age from Lesino kopovo range in size from 42 to 65 mm (Fig. 2). Among the eastern spadefoot toads females in the fourth year of age varied in size from 50 to 77 mm (Fig. 3). One should bear in mind that anuran growth generally follows Von Bertalanffy curve, that is, growth is faster at earlier stages than after reaching sexual maturity. After sexual maturation annual growth rate will strongly decrease and become quite low. But, young adults are smaller than old adults because growth does not stop at sexual maturity, but only decreases rapidly.

Tab. 3: Ranges, mean (X) and standard deviations (SD) for body length (mm) in analyzed tadpole and juvenile spadefoot toad samples.
Tab. 3: Razpon, srednje vrednosti (X) in standardni odkloni (SD) v dolžini telesa (mm) pri analiziranih paglavcih in mladostnih osebkih česnovk.

	Tadpoles			Juveniles		
sample	N	X±SD	range	N	X±SD	range
	Pelobates fuscus					
Utrine	8	96.89±9.06	80.93-113.16	14	32.74±3.08	27.38-36.64
Cavolj	20	84.61±6.99	70.42-96.19	17	30.26±1.46	27.97-34.01
	Pelobates syriacus					
Utrine	10	91.50±8.54	79.93-104.71	15	32.16±3.41	26.30-37.90
FYROM	10	88.74±15.25	60.63-108.18	10	30.94±1.78	28.18-33.44

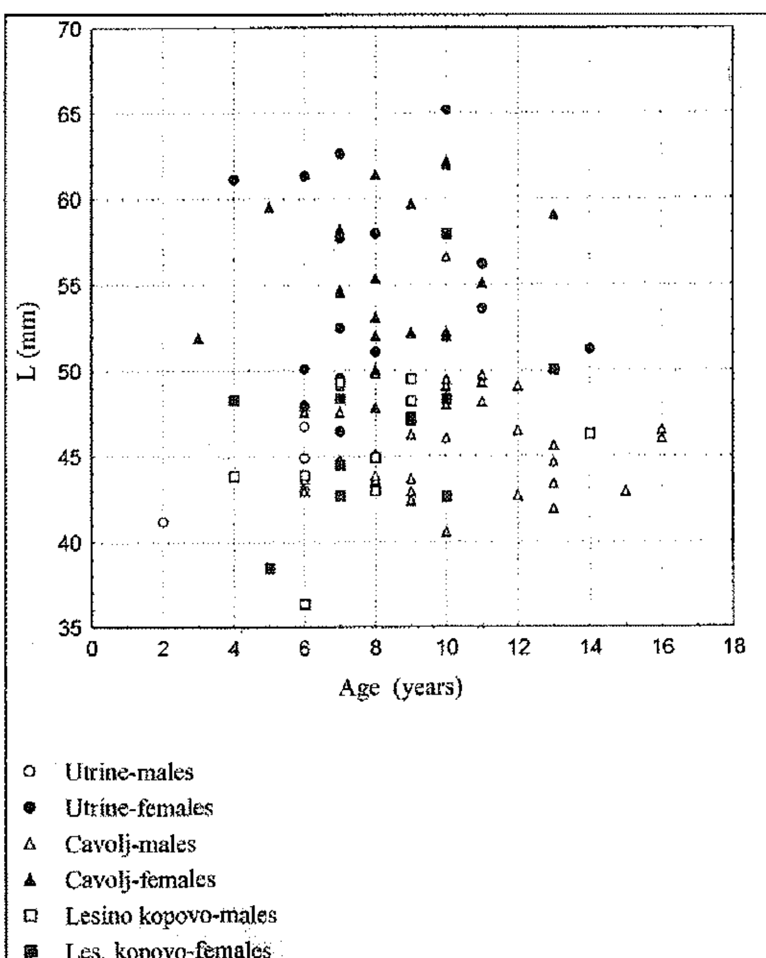

Fig. 2: Distribution of body size (L) and age in the adult** Pelobates fuscus **individuals.
***Sl. 2: Velikostna (L) in starostna razporeditev pri odraslih osebkih** Pelobates fuscus.*

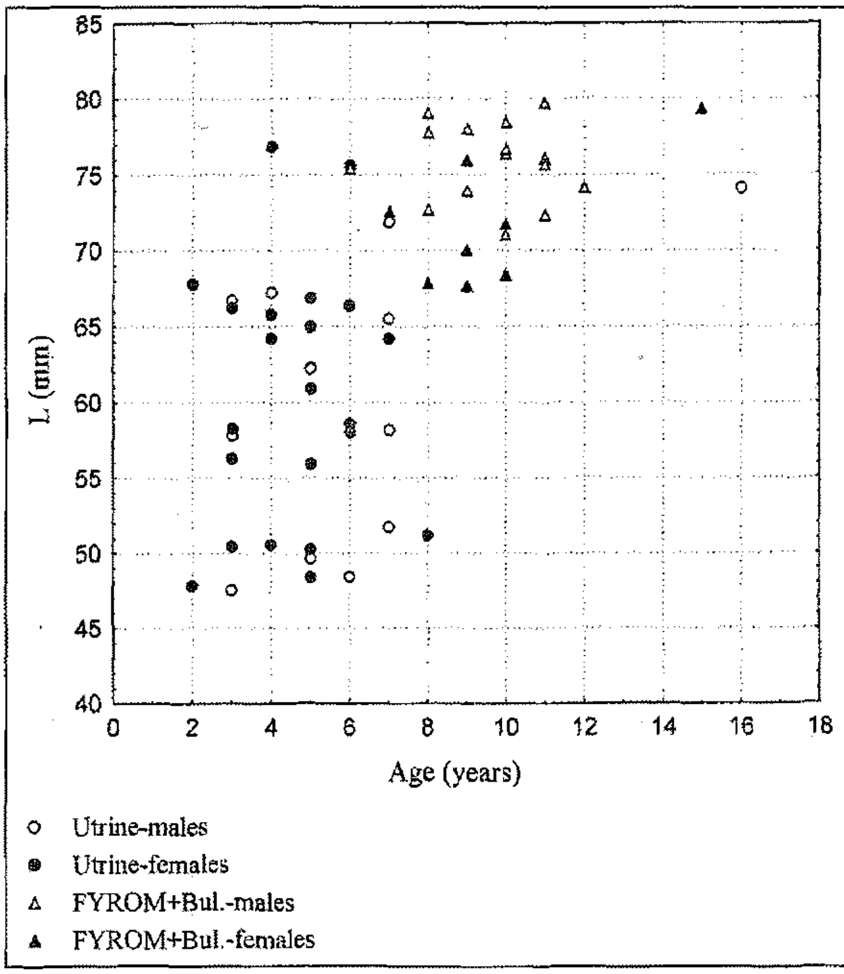

Fig. 3: Distribution of body size (L) and age in the adult *Pelobates syriacus* ***individuals.***
Sl. 3: Velikostna (L) in starostna razporeditev pri odraslih osebkih *Pelobates syriacus.*

Tab. 4: Descriptive statistics for the age in *Pelobates fuscus* ***and*** *Pelobates syriacus samples* ***(for legend see table 2a).***
Tab. 4: Opisna statistika za starost osebkov *Pelobates fuscus* ***in*** *Pelobates syriacus* ***(legenda: glej tabelo 2a).***

	Females			Males			
sample	N	X ± SD	range	N	X ± SD	range	sign.
Pelobates fuscus							
Utrine	15	7.93 ± 2.55	4 -14	4	5.00 ± 2.00	2-6	*
Cavolj	22	8.32 ± 2.10	3 -13	37	10.21 ± 2.73	6-16	n.s.
Lesino kopovo	11	8.00 ± 2.64	4 -13	9	7.89 ± 2.80	4-14	n.s.
Pelobates syriacus							
Utrine	22	4.59 ± 1.56	2 - 8	14	6.00 ± 3.26	3-16	n.s.
FYROM & Bul. Macedonia	8	9.63 ± 2.39	7 -15	16	9.38 ± 1.78	6-12	n.s.

Tab. 5: Descriptive statistics for the time of attaining sexual maturity in* Pelobates fuscus *and* Pelobates syriacus *samples (for legend see table 2a).
Tab. 5: Opisna statistika za starost, ko osebki* Pelobates fuscus *in* Pelobates syriacus *dosežejo spolno zrelost. (legenda: glej tabelo 2a).

	Females			Males			
sample	N	X ± SD	range	N	X ± SD	range	sign.
Pelobates fuscus							
Utrine	11	3.27 ± 0.79	2 - 4	2	2.00 ± 0.00	2 - 2	n.s.
Cavolj	12	2.75 ± 0.62	2 - 4	18	2.78 ± 0.55	2 - 4	n.s.
Lesino kopovo	10	3.60 ± 0.84	2 - 5	6	3.50 ± 0.84	3 - 5	n.s.
Pelobates syriacus							
Utrine	10	2.30 ± 0.49	2 - 3	9	2.67 ± 0.50	2 - 3	n.s.
FYROM & Bulgaria	4	3.50 ± 0.58	3 - 4	10	3.10 ± 0.52	3 - 4	n.s.

Apparently, spadefoot toads are among many tailless amphibians where body size is strongly influenced by juvenile growth rate followed by a reduction in somatic growth after sexual maturation (Halliday & Verrell, 1988; Platz & Lothrop, 1993; Hota, 1994). A sudden decrease in bone growth and concomitant rapprochement of LAGs in *P. fuscus* and *P. syriacus* was obvious in approximately 56% of the individuals studied. In other individuals the absence of such a pattern was probably due to a prolonged period of growth after the onset of sexual maturity. However, if we take into account only individuals which did not show such a LAG pattern (i.e. that did not show sudden decrease in bone growth and grew rather evenly), a statistically significant positive correlation between size and age was found for the *P. syriacus* ($Rs = 0.672$, $p < 0.001$), but not for the *P. fuscus* where correlation was negative, though insignificant ($Rs = -0.191$, $p > 0.05$).

There were significant differences in size among age-classes when tested on pooled data for species. Age-classes were organized in the following way: I (2-7 yr.), II (8-11 yr.) and III (12-16 yr.). In *P. fuscus* intersexual differences in body size in all age-classes were statistically significant (Mann-Whitney U test; I: $p < 0.001$, II: $p < 0.001$; III: $p < 0.01$), females being larger than males. In *P. syriacus* most individuals belonged to age-class II, and intersexual differences in body size were significant ($p < 0.001$), but males had larger body length than females. A posterior analysis among age-classes did not reveal significant differences in size between age-classes (Tukey-Kramer test, $p > 0.05$). Distribution of total body length in respect to age clearly showed, especially when analyzing *P. fuscus* population from Cavolj, that females had greater body length than males from the same age class (Fig. 2). In *P. syriacus* such relation was not present (Fig. 3).

DISCUSSION

Sexual size dimorphism

Among anuran species females appear to be larger than males in 90 % of cases (Shine, 1979). This pattern was found to be true in *P. fuscus*, *P. cultipres* and *P. varaldii* (Halliday & Tejedo, 1995) in many parts of their range. The magnitude of sexual dimorphism (average body size of females *vs.* males) in the common spadefoot toad known so far range from 1.03 (Lesino kopovo, this study) to 1.13 (Poland, Andrzejewski *et al.*, 1977). However, the eastern spadefoot toad males and females show more similar body lengths (1.01, Serbia, this study) or males are significantly larger than females (0.88 in Turkey, Zaloğlu, 1964; 0.93 in FYR Macedonia and Bulgaria, this study). In the case of FYR Macedonia and Bulgaria sample we fail to have young adults in both sexes and the intersexual comparison was done on individuals that probably, in both genders, were close to the maximum size they would reach. Therefore, an interesting result appeared - males were larger than females which is not common in amphibians.

In general, sexual size dimorphism in any species may be a consequence of differences in some life history traits and the action of sexual and/or natural selection, including fecundity selection. Thus, the direction and the degree of SSD may be the result of different selective regimes usually acting separately on females and males. The importance of these regimes varies among species and populations, or even with time in the same population (*e.g.* Howard, 1981; Halliday & Verrell, 1986). Several hypotheses, not mutually exclusive, have been proposed for the evolution of sexual size dimorphism. The most fundamental ones are (1) sexual selection (competition between males and female choice which mostly favors large males), (2) fecundity selection which favors large females, and (3) intersexual niche divergence (for amphibians see reviews in Halliday & Verrell, 1986; Shine, 1989; Halliday & Tejedo, 1995). The evolution of SSD is likely to evolve by interrelationships and correlated trade-offs between life-history adaptations, sexual selection and parameters of fecundity.

In general, as far as proximate determinants of sexual size difference in poikilothermic vertebrates are concerned, of especial importance are difference in age at maturity, longevity, differential growth and mortality rates, in relation to either body-size and age during preadult (larval and juvenile) and adult phases of ontogeny. Among life history characteristics, the timing of maturation is a critical event influencing both morphology and fitness (*i.e.* lifetime reproductive success) of the individuals, as well as the demographic structure of populations and species (Stearns, 1992; Ryan & Semlitsch, 1998). A delay in first reproduction, as large as two years, by females in comparison to males is common in amphibian populations (Halliday & Tejedo, 1995). By delaying maturation, females attain larger body-size at first breeding with a resulting benefit in reproductive performance. The timing of maturation seems to be rather conservative in the genus *Pelobates*, regardless of the region studied, ranging from 2 to 5 years in both genders (Halliday & Tejedo, 1995; this study). Interestingly, in one population of the western spadefoot toad females breed at earlier age than males, which is correlated with a lower level of SSD in comparison with conspecific populations, where females breed later than males, showing higher level of SSD in favor of females (Talavera, 1989). However, in both spadefoot toad species we studied, the time of sexual maturity did not vary significantly between sexes and concomitantly did not affect SSD extent. In comparison to other life history traits with potential effect on the magnitude of SSD studied here, individual age appears not to be sex-specific in any of the spadefoot toad species studied.

Intra- and interspecific differences in life history traits

Size is a dominant ecological factor, particularly among groups with indeterminate growth. Together with age, size is important in determining mortality and fecundity, and in influencing competition within and between species. The importance of body size in the ecology, life history, and reproductive success has been widely acknowledged for years (*e.g.* Fairbairn, 1997). Thus, the pattern of interspecific variation in body size is expected to reflect pattern of adaptive divergence within the species range. That is why one may expect differences in size between individuals of species living in sympatry with other cognate species in comparison to conspecific individuals living in allopatry to decrease and/or escape between-species competition. Contrary to the expectations, spadefoot toads of species living in sympatry appeared not to be consistently larger than conspecific individuals from allopatric parts of the species range. Moreover, sympatric eastern spadefoot toads are significantly smaller than individuals from allopatric populations. However, this finding appears not to be related to sympatry/allopatry at all as deficit of young adult males and females was observed in the allopatric population. Also, males and females reached maturity later and were older in allopatric than in sympatric population, which resulted in larger individuals in the allopatric situation.

As for the interpopulation differences in some life history traits assessed by means of skeletochronology, significant variation was found in both species in the average individual longevity and time of attaining sexual maturity. Of special interest is the fact that *P. syriacus* from the zone of sympatry with *P. fuscus* have shorter life span and breed at least one year earlier in comparison to individuals from allopatric parts of the species range. Thus, our study provides evidence that local environment influences some intraspecific variation in life history traits. However, syntopic spadefoot toad individuals, which share habitat features to a large degree, show number of differences in life-history traits. First, *P. syriacus* adult individuals are significantly larger than *P. fuscus* ones. Most likely this is due to substantial difference in the growth rate of juveniles. Namely, our preliminary results (unpublished) revealed that the juvenile growth rate during the first month was almost twice in *P. syriacus* than in *P. fuscus* living syntopically (Utrine locality). In addition, these two species differ in the magnitude of SSD. They have a different life span and reach sexual maturity at a different age, especially in the females. It might be that our analysis substantiates the possibility that lineage-specific effects can explain some of the pattern of covariation in life history data within the European spadefoot toads.

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VELIKOSTNE RAZLIKE MED SPOLOMA IN ŽIVLJENJSKE ZNAČILNOSTI DVEH EVROPSKIH ČESNOVK *(PELOBATES FUSCUS* IN *P. SYRIACUS)* V ALOPATRIJI IN SIMPATRIJI

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POVZETEK

Avtorji pričujočega znanstvenega dela so preučevali velikostne razlike med spoloma (VRS) in življenjske značilnosti dveh česnovk (Pelobates fuscus *in* P. syriacus) *v delu njunega areala v jugovzhodni Evropi (Panonski nižini in na Balkanu), vključno z območjem njune simpatričnosti. Vrsti se močno razlikujeta po velikosti odraslih osebkov in glede na stopnjo VRS, medtem ko so bile velikostne razlike pri paglavcih in mladostnih osebkih kot tudi v življenjski dobi in času, potrebnem za spolno zrelost, videti precej manjše in brez kakšnega doslednega variacijskega vzorca. Pomembne razlike znotraj vrst so bile odkrite tako pri* P. syriacus *kot* P. fuscus, *in sicer v telesni velikosti, stopnji VRS, povprečni življenjski dobi in času, potrebnem za spolno zrelost. Razlike znotraj vrst v teh značilnostih so bile veliko bolj poudarjene pri vrsti* P. syriacus *kot pri* P. fuscus. *Odrasli osebki vrste* P. syriacus *iz območja striktne simpatrije so bili neprimerno manjši, vendar večji kot paglavci in z manjšo stopnjo VRS. Osebki so imeli tudi krajšo življenjsko dobo in so postajali spolno zreli hitreje (najmanj leto dni) kot istovrstni osebki iz geografsko oddaljenih alopatričnih delov specifičnega areala.*

Ključne besede: rod česnovk, *Pelobates fuscus* in *P. syriacus*, velikost, življenjska doba, spolna zrelost, velikostne razlike med spoloma

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