Arch. Biol. Sci., Belgrade, 65 (2), 685-695, 2013

DOI:10.2298/ABS1302685C

MORPHOLOGICAL DIFFERENTIATION OF THE COMMON TOAD *BUFO BUFO* (LINNAEUS, 1758) IN THE CENTRAL PART OF THE BALKAN PENINSULA

NATALIJA ČAĐENOVIĆ[1], TANJA VUKOV[2], ESTER POPOVIĆ[3] and KATARINA LJUBISAVLJEVIĆ[2]

[1] *The Natural History Museum of Montenegro,* 81000 Podgorica, Montenegro
[2] *Department of Evolutionary Biology, Institute for Biological Research "Siniša Stanković", University of Belgrade,* 11060 Belgrade, Serbia
[3] *Department of Biology and Ecology, Faculty of Science, University of Novi Sad,* 21000 Novi Sad, Serbia

Abstract - This study analyzes the degree of morphological differentiation among populations of the common toad *Bufo bufo* in the central part of the Balkan Peninsula. Variations in a number of morphometric and qualitative characters in 14 population samples were analyzed using univariate and multivariate statistics. We found a high degree of female-biased sexual size dimorphism. Morphological variation among the samples was more expressed in morphometric than in qualitative characters. The significant size differences that exist between northern and southern population groups could be the result of phenotypic plasticity. Our results do not support a clear split between northern and southern populations, contrary to the current taxonomic treatment of these groups as *B. b. bufo* and *B. b. spinosus*, respectively.

Key words: Bufonidae, geographic variation, morphology, Serbia, Montenegro

INTRODUCTION

The common toad, *Bufo bufo* (Linnaeus, 1758) is a widely distributed species inhabiting almost all of Europe, northern Africa and western Asia (Borkin and Veith, 1997). According to literature data, three subspecies are recognized (Lüscher et al., 2001; Geniez and Cheylan, 2005). The nominotypical subspecies (*B. b. bufo*) inhabits the largest part of the species range including the British Isles, northern and central Europe and western Siberia. *B. b. spinosus* occurs in northern Africa, western and central France and the Mediterranean parts of Europe, while *B. b. gredosicola* occupies a limited range in central Spain.

The common toad has been the object of numerous studies (Gittins et al., 1982; Hemelaar, 1983, 1988; Reading, 1988, 1991; Hoglund and Saterberg, 1989; Reading et al., 1991; Scribner et al., 2001; Brede and Beebee, 2006; Kutrup et al., 2006). However, data from the southern part of the range on the Balkan Peninsula were mainly limited to demographic parameters (Cvetković et al., 2003, 2005; Tomašević et al., 2007, 2008).

To date, it was believed that the central part of the Balkan Peninsula (Serbia and Montenegro) was inhabited by two subspecies: *B. b. bufo* in the continental part and B. *b. spinosus* in the Mediterranean part. *B. b. spinosus* is traditionally determined by its greater body size and higher degree of development of the integumentary warts. However, there was an assumption that the subspecies *B. b. spinosus* is poorly defined and that it should be synonymized with the nominal subspecies (Lanza, 1993). Although recent molecular data rejected the monophyly of *B. b. bufo* and B. *b. spinosus* (Garcia-Porta et al., 2012), comparative morphological analyses of populations from the Mediterranean and inland regions of the Central Balkans have not been carried out.

Hence, the basic aim of this study is to establish the degree of morphological differences in population groups of the common toad that inhabit the central part of the Balkan Peninsula. For this purpose, we analyzed numerous quantitative and qualitative traits. Based on characterization of pattern of morphological variation, we tried to determine a possible intraspecific geographical pattern of differentiation in order to shed more light on the geographic variation of this species.

MATERIALS AND METHODS

Samples

Morphological analysis included a total of 353 individuals belonging to 14 populations of *B. bufo*, out of which four samples belonged to a northern population group (Nos. 11-14, see Fig. 1) located in Serbia, while 10 samples belonged to a southern population group (Nos. 1-10) located in Montenegro.

Most of the material was collected in the mating period and preserved in 70% ethanol. Samples from Serbia were from the herpetological collection of the Institute for Biological Research, Belgrade. The specimens from other localities belong to the herpetological collection of Natural History Museum of Montenegro in Podgorica.

Studied characters

Morphometric analysis was performed on 8 traits which determine the size and form of the body and head of tailless amphibians. Measured traits were: L – length of the body from the top of head to the opening of the cloaca; Lpa – length of the front extremity; F – length of femur measured from the opening of cloaca to the knee joint; T – length of tibiofibula from the knee joint to tibiotarsal joint; P – distance from tibiotarsal joint to the tip of the longest finger; n – length of metatarsus from the internal metatarsal ridgelet to the tip of the longest finger; Lc – head length from the top of the head to jaw joint; Ltc – head width measured between the jaw joints. Statistical analysis of morphometric characters included only mature individuals. Reproductively mature males and females were identified on the dissection and gonads survey basis.

We also examined three qualitative traits with three conditions on four body regions (dorsal and ventral side of the head, dorsal side of the body and abdomen). Qualitative traits were: Warts shape – WS (a - round warts, b - oval warts, c - kidney-like warts); Warts convexity – WC (a - very protuberant warts, b - protuberant warts, c - drawn in warts); Prominence of thorn-like wart endings – PE (a - very marked thorn-like ends of warts, b - medium marked thorn-like ends of warts; c - weakly marked thorn-like ends of warts)

Statistical analyses

Descriptive statistics (mean, standard error and minimal and maximal values) were calculated for non-transformed morphometric characters. The differences between population groups (northern and southern) for non-transformed morphometric characters were determined by Tukey HSD test for the samples of unequal size.

As size can confound comparisons of variance patterns (i.e., traits with greater means typically have greater variances (Cheverud 1989)), the morphometric data was size-corrected (transformed) by computing standardized residuals from least-squares regressions (on body length). This adjustment removed isometric size but not size-related (allometric) shape. In order to estimate the extent of differences on different levels, between groups (northern and southern), among populations, and between sexes, variance was partitioned for transformed data by a variance component test with nested design. Since the sample sizes were not equal, Satterthwaite's approximation was used to test for significance. A more detailed analysis of sexual dimorphism was performed by ANOVA using non-transformed and transformed data (corrected for size). In order to reduce the dimensionality for multivariate data sets and graphically present differences between populations, Canonical Discriminant Analysis (CDA) was used on transformed data. The frequencies of qualitative traits were calculated (%), and the significance of differences between relative frequencies of two groups of toads was analyzed by difference between two proportion tests. All statistical analyses were performed using the computer package Statistica® (STATISTICA for Windows. StatSoft, Inc., Tulsa, OK), considering a significance level of alpha = 0.05.

RESULTS

Morphometric characters

Descriptive statistics of non-transformed morphometric characters of sexually mature males and females for the northern and southern population groups are presented in Tables 1 and 2. Values for each population were omitted to make the data more comprehensive. The Tukey HSD test showed significant differences in all studied characters (except Wg in males) between the southern and northern group. It was found that the specimens from the southern group had larger values of all characters, both for males and females (Tables 1 and 2).

The variance partitioning procedure revealed that between group (northern and southern), among population, and between sex variations in transformed morphometric characteristics was significant for most of the traits but minimal, except for the femur where the variation between the sexes was significant and high (Table 3). A great deal of variation existed within populations (see error values in Table 3).

ANOVA on non-transformed data revealed a pronounced sexual dimorphism, where the females had higher average values of the analyzed traits (P<0.05 for all traits) in all samples. However, when the size effect was excluded, most of the sexual differences disappeared (ANOVA on transformed data, full versions of the tables are available from the first author upon request). The characteristics that showed sexual dimorphism after removing the size effect were Vršački breg (Lpa, P, n, F), Bela Crkva (Lpa, Lc, F), Velje Brdo (Lpa, F), Rijeka Crnojevića (Lpa, n, F), Biogradsko jezero (T, F), Kuči (T, P, n, F).

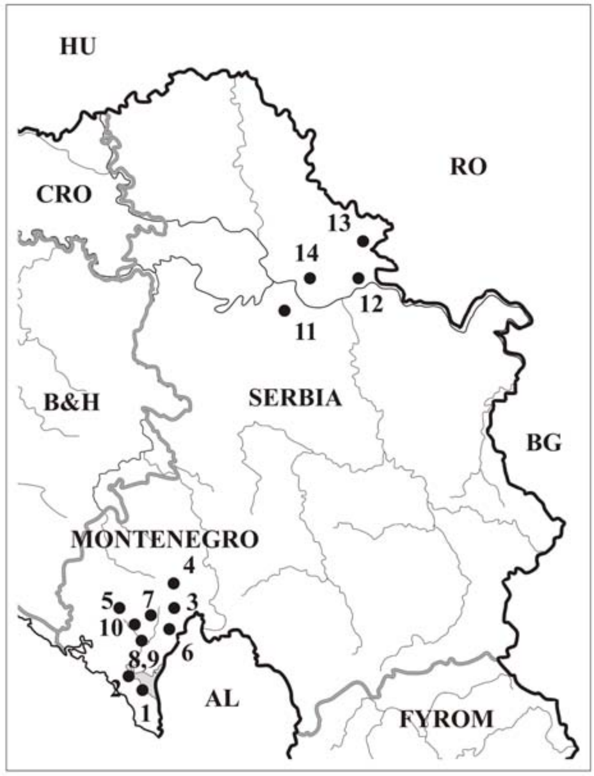

Fig. 1. Map of sampling localities. Southern population group in Montenegro: 1. Skadarsko jezero; 2. Rijeka Crnojevića; 3. Mateševo; 4. Biogradsko jezero; 5. Prekornica; 6. Kuči; 7. Piperi; 8. Velje brdo; 9. Lješanska nahija; 10. Bjelopavlići. Northern population group in Serbia: 11. Trešnja; 12. Bela Crkva; 13. Vršački breg; 14. Deliblatska peščara.

The first three canonical variate axes (CAN1 -3), calculated from CDA on transformed data, accounted for about 85% and 89% of the total variance for males and females, respectively (Table 4). The values of standardized coefficients of canonical variables showed that the discrimination in males and for the first axis was significantly contributed by the differences femur length (F). Moving from the left to the right side along the first canonical axis for males, and in the opposite direction for females, populations with individuals with small femurs were being re-

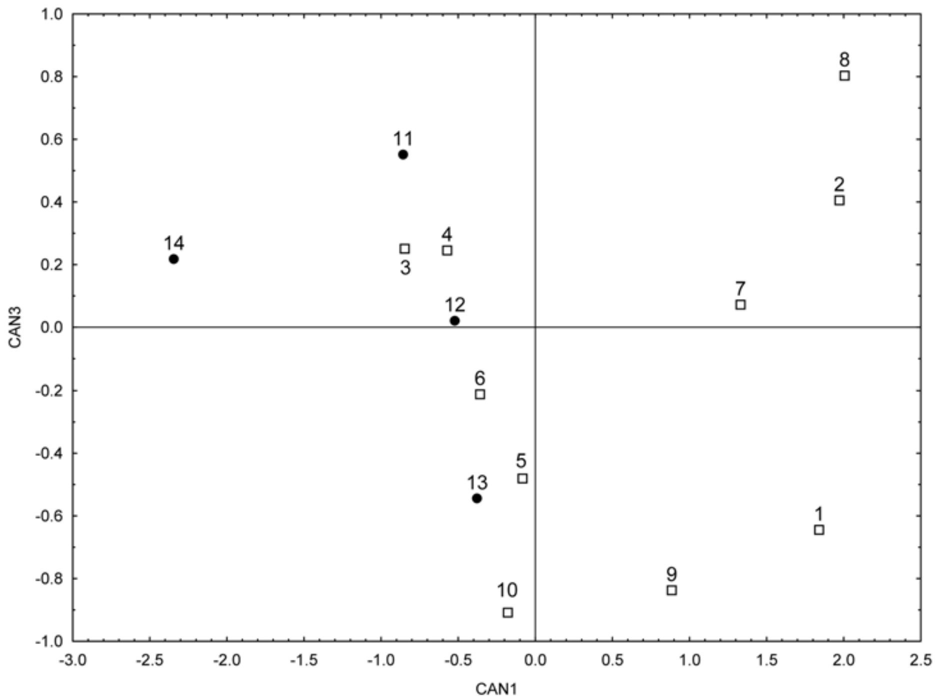

Fig. 2. Scatterplot of the first and second canonical axes (CAN) for morphometric characters in male *Bufo bufo.*

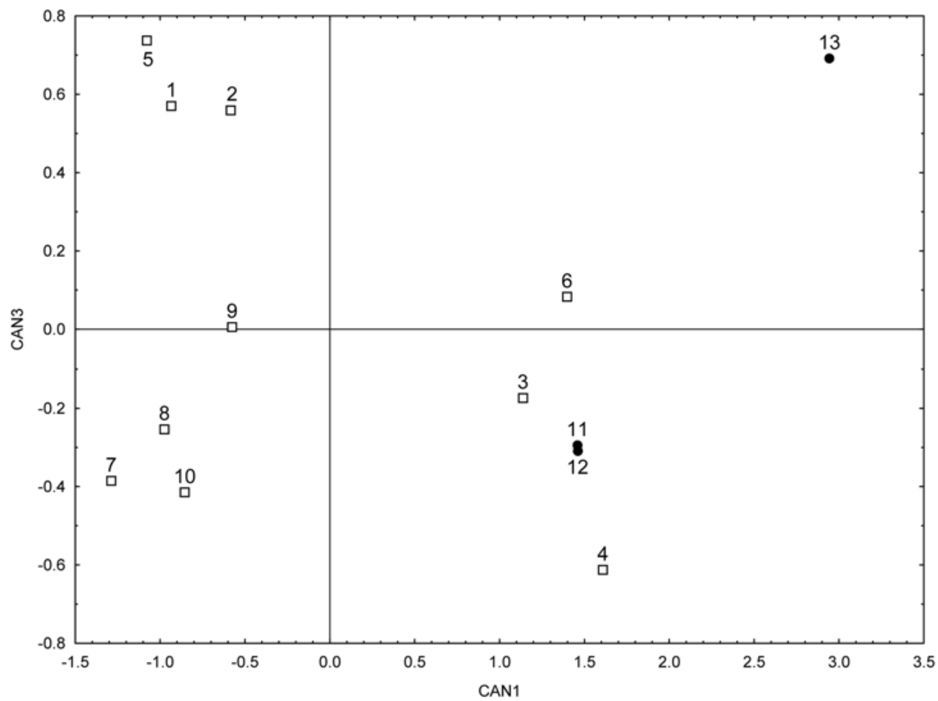

Fig. 3. Scatterplot of the first and second canonical axes (CAN) for morphometric characters in female *Bufo bufo.*

Table 1. Descriptive statistics of morphometric characters examined for male *B. bufo* from Northern and Southern population groups. Sample size (N), Mean value (in mm), Standard error (SE), range and statistical significance of differences between the groups tested by Tukey HSD test for unequal sample sizes (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns – non significant). Abbreviations of characters are given in "Materials and Methods".

	Northern group					Southern group					
Characters	N	Means	SE	Min	Max	N	Means	SE	Min	Max	Tukey test
L	72	71.72	0.58	58.88	78.66	126	77.55	0.57	60.27	97.30	***
Lpa	72	51.40	0.47	41.24	58.79	126	56.95	0.47	41.40	69.24	***
F	72	30.90	0.37	21.70	37.05	126	33.34	0.34	25.32	41.76	***
T	72	22.59	0.24	17.87	26.62	126	24.50	0.19	18.08	29.01	***
P	72	34.43	0.38	24.88	40.80	126	37.71	0.32	25.80	45.50	***
n	72	48.34	0.49	37.17	54.70	126	53.49	0.41	40.43	61.92	***
n-P	72	13.91	0.35	7.21	19.41	126	15.79	0.26	7.26	22.45	***
DpPa	72	7.01	0.09	4.52	8.50	126	7.65	0.11	4.80	10.85	***
DpPp	72	5.78	0.09	3.93	7.97	126	6.64	0.08	4.44	8.95	***
Cint	72	4.02	0.06	2.87	5.85	126	4.71	0.06	3.33	6.64	***
Lc	72	17.20	0.14	13.06	19.92	126	18.55	0.15	14.28	24.37	***
Ltc	72	21.70	0.19	17.04	24.62	126	23.44	0.22	17.78	32.04	***
Spp	72	8.51	0.11	6.85	11.38	126	9.10	0.10	6.72	13.34	***
Spi	72	3.17	0.06	2.28	4.34	126	4.02	0.05	2.82	5.59	***
Spcr	72	7.51	0.07	6.30	8.95	126	8.16	0.08	6.28	10.67	***
Lo	72	6.72	0.08	5.04	8.49	126	7.08	0.10	4.95	9.74	*
Ltp	72	5.70	0.08	4.41	7.33	126	6.18	0.08	4.05	8.55	***
Dro	72	7.40	0.09	3.86	8.44	126	7.96	0.08	3.59	10.50	***
Dno	72	3.22	0.05	2.53	4.55	126	3.52	0.06	2.33	7.64	***
Lh	72	3.32	0.06	1.89	4.58	126	3.64	0.05	2.34	5.64	***
Lg	72	14.02	0.19	10.14	18.05	126	15.43	0.18	11.04	20.66	***
Wg	72	6.09	0.10	4.50	8.30	126	6.27	0.08	4.40	8.89	ns

placed with individuals with larger femurs (northern populations are replaced by southern populations). At the second axis, discrimination was contributed by the length of metatarsus (N) for males, and the head width (Ltc) for females. At the third axis, discrimination was contributed by the head width (Ltc) for males, and the head length (Lc) for females (Table 4, Figs. 2 and 3).

Qualitative characters

By comparing relative frequency of states of qualitative characteristics, it was observed that the same states had the highest frequency in both sexes from the northern populations. The exception was convexity of warts on the dorsal part of the head (most of the males of the northern group had convex warts, while most of the females of the same group had very convex warts). Among the males and females of the southern group there was a much bigger difference in the occurrence of some states. In general, the highest number of specimens of both sexes had round warts on all body regions. Males and females differed by the fact that most of the males were characterized by inserted and poorly expressed warts with thorn-like ends, while the biggest number of females had very convex warts with very developed thorn-like ends. These differences were present on the head region and on the back. Both sexes of the southern group had a similar abdominal part with poorly developed

Table 2. Descriptive statistics of morphometric characters examined for female *B. bufo* from Northern and Southern population groups. Sample size (N), Mean value (in mm), Standard error (SE), range and statistical significance of differences between the groups tested by Tukey HSD test for unequal sample sizes (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns – non significant). Abbreviations of characters are given in the "Materials and Methods".

	Northern group					Southern group					
Characters	N	Means	SE	Min	Max	N	Means	SE	Min	Max	Tukey test
L	18	94.00	1.50	83.78	104.23	137	113.38	0.96	85.86	135.25	***
Lpa	18	63.90	1.62	54.66	75.21	137	78.63	0.66	61.52	97.08	***
F	18	38.27	1.15	30.72	46.14	137	47.19	0.52	31.98	61.61	***
T	18	27.53	0.61	23.33	31.89	137	32.66	0.34	23.14	44.40	***
P	18	39.29	1.08	30.21	47.41	137	48.07	0.44	34.95	58.51	***
n	18	57.22	1.52	42.32	66.77	137	69.32	0.63	47.02	86.35	***
n-P	18	18.12	0.78	12.11	23.77	137	21.25	0.38	7.83	31.22	**
DpPa	18	9.82	0.34	6.28	11.95	137	12.94	0.20	6.63	18.64	***
DpPp	18	6.23	0.26	3.82	7.83	137	9.03	0.12	5.27	12.61	***
Cint	18	5.13	0.24	3.46	7.78	137	7.04	0.09	4.19	9.76	***
Lc	18	22.48	0.56	17.86	25.26	137	27.17	0.23	18.49	32.60	***
Ltc	18	29.74	0.71	25.72	34.66	137	36.85	0.37	26.04	45.41	***
Spp	18	11.07	0.30	9.06	13.59	137	13.60	0.15	9.18	18.54	***
Spi	18	4.06	0.13	3.26	5.00	137	5.71	0.07	2.61	7.81	***
Spcr	18	10.23	0.22	8.17	11.65	137	12.62	0.11	8.56	15.50	***
Lo	18	8.47	0.19	6.89	10.07	137	10.22	0.11	5.97	12.82	***
Ltp	18	7.54	0.22	5.82	10.21	137	8.32	0.09	4.76	10.95	**
Dro	18	9.78	0.19	8.53	11.18	137	11.65	0.11	8.64	14.04	***
Dno	18	4.00	0.12	2.94	4.89	137	4.89	0.07	1.63	6.66	***
Lh	18	4.58	0.18	3.49	6.22	137	5.66	0.08	2.45	7.73	***
Lg	18	19.01	0.57	14.77	22.77	137	23.71	0.28	15.60	31.76	***
Wg	18	7.77	0.28	5.64	10.37	137	9.61	0.15	5.21	13.09	***

warts and thorn-like extensions (Tables 5 and 6).

DISCUSSION

The body size for *B. bufo* observed in this study is generally within the range recorded so far (Radovanović, 1951; Arnold and Burton, 1978; Đurović et al., 1979). We found a high degree of female-biased sexual size dimorphism, which is also known for other populations of the common toad (Gittins et al., 1980; Hemelaar, 1988; Cvetković et al., 2005, 2007). The most used explanation of the sexual dimorphism in the body size is the advantage that bigger females have in producing a greater number of eggs (Gibbons and McCarthy, 1986; Halliday and Verrel, 1986; Cvetković et al., 2007).

The northern and southern populations differed in numerous size characteristics, e.g. the southern specimens tended to be larger than the northern ones. However, interpopulation variability within each group was also significant, and more expressed between the populations of the southern group. The differences between the two groups were less expressed in qualitative traits. Contrary to earlier studies (Lüscher et al., 2001), there was no clear separation of previously defined subspecies according to integumentary characteristics both among males and

Table 3. Components of variance for morphometric characters expressed as a percentage of the total variance (%). Error variation represents variation within populations plus basic error variance. (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns – non significant). Abbreviations of characters are given in the "Materials and Methods".

Character	Between groups		Among populations		Between sexes		Error
	%	P	%	P	%	P	%
Lpa	11.1	*	3.8	*	0.0	ns	84.9
F	7.0	*	4.2	***	80.2	***	8.6
T	1.5	ns	0.3	ns	2.1	*	96.1
P	9.2	*	6.5	***	6.4	***	77.8
n	15.3	**	1.3	ns	6.5	***	76.9
Lc	0.0	ns	4.8	**	0.6	ns	94.6
Ltc	0.0	ns	15.2	***	2.3	*	82.5

Table 4. Standardized coefficients of variation of the first three canonical variates of male and female *B. bufo* calculated on transformed (size corrected) data. The largest coefficients are underlined. Abbreviations of characters are given in the "Materials and Methods".

	males			females		
Characters	CAN 1	CAN 2	CAN 3	CAN 1	CAN 2	CAN 3
Lpa	0.1473	0.4441	0.0573	0.0085	-0.7697	-0.1449
F	<u>1.1108</u>	-0.1380	0.1954	<u>-1.0526</u>	-0.1633	0.1602
T	-0.1830	0.1908	0.3544	0.1579	-0.0513	0.2155
P	-0.1717	0.1803	0.0697	-0.2292	0.3970	-0.7327
n	-0.1668	<u>0.5998</u>	-0.3496	0.1820	-0.3778	0.1132
Lc	0.2211	0.1782	-0.3292	0.0246	-0.4664	-0.7895
Ltc	0.1729	-0.1291	<u>1.0846</u>	-0.5339	<u>1.2752</u>	0.3793
Eigenvalue	1.1923	0.4344	0.2633	1.8411	0.7279	0.2204
Cumulative % of variance	53.84	73.45	85.35	58.57	81.72	88.73

females. Therefore, our results do not clearly suggest a primary morphological divergence between populations of the northern (Serbian) and southern (Montenegrin) groups, seemingly opposing the previous predictions related to the taxonomic subdivision of the species.

Differences in morphometric characteristics were related to body size, but not to body shape, which usually follows intraspecific taxonomic differentiation of the population groups. In addition, our results indicate the existence of a relatively wide zone of clinal variation of the analyzed morphometric characteristics in the northern part of Montenegro. The absence of clear differentiation between the northern and southern population groups of common toad were also recorded in Italy (Andreone and Luiselli, 2000). The common toad shows extensive gene flow between populations (Seppa and Laurila, 1999; Lüscher et al., 2001; see Brede and Beebee, 2004 for opposite results). Martínez-Solano and Gonzales (2008) also suggested that populations of this species maintain relatively high levels of gene flow on a wider spatial scale. The dispersal capabilities of juvenile individuals maintain high levels of gene flow and account for small morphological and genetic differences between the populations in this species, in spite of a high site fidelity of adults (Reading et al., 1991).

The detected size differences between the northern and southern population groups may be caused by environmental factors and reflect pheno-

Table 5. Relative frequencies (in %) of qualitative traits in male *Bufo bufo* and statistical significance of differences between two population groups (*P*) (*, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001; ns – non-significant). Abbreviations of characters are given in the "Materials and Methods".

Body region	Character	State	Relative frequency (%)		P
			Northern group	Southern group	
Head-dorsal side	WS	a	88	97	*
		b	12	3	*
		c	0	0	/
	WC	a	16	16	ns
		b	55	31	***
		c	29	53	**
	PE	a	0	4	ns
		b	11	15	ns
		c	89	81	ns
Body-dorsal side	WS	a	89	98	**
		b	11	2	**
		c	0	0	/
	WC	a	12	1	***
		b	45	31	*
		c	43	68	***
	PE	a	0	4	ns
		b	20	15	ns
		c	80	81	ns
Head-ventral side	WS	a	100	100	ns
		b	0	0	/
		c	0	0	/
	WC	a	4	16	*
		b	29	37	ns
		c	67	47	**
	PE	a	13	30	**
		b	59	30	***
		c	28	40	ns
Abdominal part	WS	a	100	100	ns
		b	0	0	/
		c	0	0	/
	WC	a	1	7	ns
		b	16	10	ns
		c	83	83	ns
	PE	a	5	7	ns
		b	33	7	***
		c	62	85	***

typic plasticity. Factors such as climatic conditions, trophic resources, predatory effect, intra- and interspecific competition could have complex influence on size variation. Cvetković et al. (2009) found that *B. bufo* exhibits a converse Bergmann cline along latitudinal gradient, with a body size increase with mean environmental temperature during the activity period, which is in accordance with our results. In warmer and drier parts of the species range, individuals are bigger compared to those in colder and more humid parts of the range, because larger specimens have greater desiccation tolerance due to the relative decrease in body surface (Duellman and Trueb, 1994). In addition, in the southern parts of the range toads are active a longer period (the hibernation period is shorter), they have greater food

Table 6. Absolute and relative (in %) frequencies of qualitative traits in female *Bufo bufo* and statistical significance of differences between two population groups (*P*) (*, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001; ns – non-significant). Abbreviations of characters are given in the "Materials and Methods".

Body region	Character	State	Relative frequency (%)		*P*
			Northern group	Southern group	
Head-dorsal side	WS	a	92	88	ns
		b	8	9	ns
		c	0	3	ns
	WC	a	48	80	***
		b	40	14	**
		c	12	6	ns
	PE	a	8	45	***
		b	28	30	ns
		c	64	25	***
Body-dorsal side	WS	a	88	96	ns
		b	12	4	ns
		c	0	0	/
	WC	a	28	62	**
		b	56	26	**
		c	16	12	ns
	PE	a	8	60	***
		b	28	24	ns
		c	64	16	***
Head-ventral side	WS	a	100	100	ns
		b	0	0	/
		c	0	0	/
	WC	a	20	68	***
		b	36	22	ns
		c	44	10	***
	PE	a	32	68	***
		b	56	20	***
		c	12	12	ns
Abdominal part	WS	a	100	98	ns
		b	0	2	ns
		c	0	0	/
	WC	a	4	16	ns
		b	12	27	ns
		c	84	57	*
	PE	a	4	15	ns
		b	40	29	ns

availability and therefore a larger body size can be expected. Garcia-Porta et al. (2012) also suggested that the greater body size and greater level of keratinization of the Mediterranean populations of the common toad are adaptations to dry environments and that both could be related to desiccation tolerance.

Therefore, we can conclude that our study does not clearly support the validity of a *B. b. spinosus* subspecies in Montenegro. Although significant morphometric differences existed between the Serbian and Montenegrin population groups, they could also be attributed to adaptations to different environmental conditions in these regions.

Acknowledgments - We wish to thank Georg Džukić and Miloš L. Kalezić for their advice and support. This study was partly funded by the Serbian Ministry of Education, Science and Technological Development Grant No. 173043.

REFERENCES

Andreone, F., and *L. Luiselli* (2000). The Italian batrachofauna and its conservation status: a statistical assessment. *Biol. Conserv.* **96**, 197-208.

Arnold, E. N., and *J. A. Burton* (1978). *A Field Guide to the Reptiles and Amphibians of Britain and Europe.* Harper Collins Publishers, London, UK, 1-272.

Borkin, L. J., and *M. Veith* (1997). *Bufo bufo* Linnaeus, 1758, In: *Atlas of Amphibians and Reptiles in Europe* (Eds. J. P.Gasc, A. Cabela, J. Crnobrnja-Isailović, D. Dolmen, K. Grossenbacher, P. Haffner, J. Lescure, H. Martens, J. P. Martinez Rica, H. Maurin, M. E. Oliveira, T. S. Sofianidou, M. Veith and A. Zuiderwijk), 118-119. Societas Europea Herpetologica, Museum National d'Histoire Naturelle, Paris, France.

Brede, E. G., and *T. J. C. Beebee* (2004). Contrasting population structures in two sympatric anurans: implications for species conservation. *Heredity* **92**, 110-117.

Brede, E. G., and *T. J. C. Beebee* (2006). Large variations in the ratio of effective breeding and census population sizes between two species of pond-breeding anurans. *Biol. J. Linnean Soc.* **89**, 365-372.

Cheverud, J.M. (1989). A comparative analysis of morphological variation patterns in the Papionins. *Evolution* **43**, 1737-1747.

Cvetković, D., Aleksić, I., and J. Crnobrnja-*Isailović* (2003). Reproductive traits in common toad *Bufo bufo* from the vicinity of Belgrade. *Arch. Biol. Sci.* Belgrade **55**, 25P-26P.

Cvetković, D., Tomašević, N., Aleksić, I., and J. Crnobrnja-*Isailović* (2005). Assessment of age and intersexual size differences in *Bufo bufo*. *Arch. Biol. Sci.* Belgrade **57**, 157-162.

Cvetković, D., Tomašević, N., Aleksić, I., and J. Crnobrnja-*Isailović* (2007). Phenotypic selection in common toad (*Bufo bufo*). *Arch. Biol. Sci.* Belgrade **59**, 327-333.

Cvetković, D., Tomašević, N., Ficetola, G. F, J. Crnobrnja-Isailović and *C. Miaud* (2009). Bergmann's rule in amphibians: combining demographic and ecological parameters to explain body size variation among populations in the common toad *Bufo bufo. J. Zool. Syst. Evol. Res.* **47**, 171-180.

Duellman, W. E., and *L. Trueb* (1994). *Biology of Amphibians*. The John Hopkin University Press, Baltimore, Maryland, USA, 1-670.

Đurović, E., Vuković, T. and *Z. Pocrnjić* (1979). *Vodozemci Bosne i Hercegovine*. Zemaljski muzej BiH, Sarajevo, 1-94.

Garcia-Porta, J., Litvinchuk, S. N., Crochet, P. A., Romano, A., Geniez, P. H., Lo-Valvo, M., Lymberakis, P., and *S. Carranza* (2012). Molecular phylogenetics and historical biogeography of the west-palearctic common toads (*Bufo bufo* species complex). *Mol. Phyl. Evol.* **63**,113-130.

Geniez, P., and *M. Cheylan* (2005). *Reptiles et Batraciens de France*. CD-rom, Educagri, Dijon, France.

Gibbons, M. M., and T. K. McCarthy (1986). The reproductive output of frogs Rana temporaria (L.) with particular reference to body size and age. J. Zool. **209**, 579-593.

Gittins, S. P., Parker, A. G. and *F. M. Slater* (1980). Population characteristics of the common toad (*Bufo bufo*) visiting a breeding site in Mid-Wales. *J. Anim. Ecol.* **49**, 161-173.

Gittins, S. P., Steeds, J. E., and *R. Williams* (1982). Population age structure of the common toad (*Bufo bufo*) at a lake in Mid-Wales determined from annual growth rings in the phalanges. *Brit. J. Herpet.* **6**, 249-252.

Halliday, T. R., and *P. A. Verrell* (1986). Sexual selection and body size in amphibians. *Herp. J.* **1**, 86-92.

Hemelaar, A. S. M. (1983). Age of *Bufo bufo* in amplexus over the spawning period. *Oikos* **40**, 1-5.

Hemelaar, A. S. M. (1988). Age, growth, and other population characteristics of *Bufo bufo* from different latitudes and altitudes. *J. Herpetol.* **22**, 369-388.

Höglund, J., and *L. Säterberg* (1989). Sexual selection in common toads correlates with age and body size. *J. Evol. Biol.* **2**, 367-372.

Kutrup, B., Yilmaz, N., Canakci, S., Belduz, A. O. and *S. Doglio* (2006). Intraspecific variation of *Bufo bufo*, based on 16S Ribosomal RNA sequences. *Amphibia-Reptilia* **27**, 268-273.

Lanza, B. (1993). Amphibia, Reptilia. In: *Checklist delle specie della Fauna italiana* (Eds. A. Minelli, S. Ruffo and S. La Posta), 2-74. Calderini, Bologna, Italia.

Lüscher, B., Grossenbacher, K., and *A. Scholl* (2001). Genetic differentiation of the common toad (*Bufo bufo*) in the Swiss Alps. *Amphibia-Reptilia* **22**,141-154.

Martínez-Solano, I. and *E. G. Gonzalez* (2008). Patterns of gene flow and source-sink dynamics in high altitude populations of the common toad *Bufo bufo* (Anura, Bufonidae). *Biol. J. Linnean Soc.* **8**, 824-839.

Radovanović, M. (1951). *Vodozemci i gmizavci naše zemlje*. Naučna knjiga, Beograd, 1-249.

Reading, C. J. (1988). Growth and age at sexual maturity in common toads (*Bufo bufo*) from two sites in Southern England. *Amphibia-Reptilia* **9**, 277-288.

Reading, C. J. (1991). The relationship between body length, age, and sexual maturity in the common toad *Bufo bufo*. *Holarct. Ecol.* **14,** 245-249.

Reading, C. J., Loman, J., and *T. Madsen* (1991). Breeding pond fidelity in the common toad, *Bufo bufo*. *J. Zool*. **225**, 201-211.

Scribner, K. T., Arntzen, J. W., Cruddace, N., Oldham, R. S., and *T. Burke* (2001). Environmental correlates of toad abundance and population genetic diversity. *Biol. Conserv.* **98**, 201-210.

Seppa, P., and *A. Laurila* (1999). Genetic structure of island populations of the anurans *Rana temporaria* and *Bufo bufo*. *Heredity* **82**, 309-317.

Tomašević, N., Cvetković, D., Aleksić, I., and *J. Crnobrnja-Isailović* (2007). Effect of climatic conditions on post-hibernation body condition and reproductive traits of *Bufo bufo* females. *Arch. Biol. Sci.* Belgrade **59,** 51P-52P.

Tomašević, N., Cvetković, D., Miaud, C., Aleksić, I., and *J. Crnobrnja-Isailović* (2008). Interannual variation in life history traits between neighbouring populations of the widespread amphibian *Bufo bufo*. *Rev. Ecol.-Terre Vie* **63**, 73-83.