

Sexual dimorphism in fire-bellied toads *Bombina* spp. from the central Balkans

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A b s t r a c t The direction and level of sexual size dimorphism (SSD) was examined in fire-bellied toads from the central Balkans. Samples were taken from 12 populations: three *Bombina bombina*, three *B. variegata variegata* and six *B. variegata scabra* populations. Intersexual variation of 20 morphometric characters was analysed. In addition, correspondence analysis of eight qualitative characters was performed. The results showed that, though body length had an inconsistent pattern of intersexual variation across taxa, other traits contributed to statistically significant level of SSD. The analysis on multivariate level revealed a highly significant effect of population in all three taxa, and significant effect of sex on character variation. Discriminant analysis confirmed a higher level of intersexual differences in *B. variegata* compared to *B. bombina*. Correspondence analysis showed that females and males were similar with respect to qualitative traits in all three taxa. At the univariate level, the most prominent features were: significant differences in tibia length in all three taxa, and highly significant differences in head width in *B. bombina* and in humerus length in *B. v. scabra*. These results are discussed with respect to specific reproductive behaviour and possible ecological differences between sexes.

Key words: morphometric characters, sexual size dimorphism, *Bombina* spp., Balkans

Introduction

Sexual dimorphism (SD) is a widespread phenomenon. In numerous species, pronounced differences between the sexes are found in various characteristics of morphology (body size and shape), coloration, ornaments, etc. (e.g. Darwin 1871, Anderson 1994, Halliday & Tejedo 1995). A special case of sexual dimorphism, sexual size dimorphism (SSD), is defined as “any statistically significant difference in the mean length or weight of sexually mature organisms from the same population during a given time interval” (Lovich & Gibbons 1992).

Since Darwin (1871) developed the concept of sexual selection, it has most often been used to explain the observed differences between sexes. Darwin emphasized the distinction between sexual and natural selection, pointing out that they can have opposite directions. Sexual selection can operate through active choice of mates, through differential success in achieving dominance in direct combat or in contests where strength or agility are most important, in competition to attract females or in sperm competition (Halliday 1983, Anderson 1994, Reynolds & Harvey 1994).

Apart from sexual selection, other mechanisms can produce sexual size dimorphism, such as ecological divergence between sexes, i.e. differential resource utilization (Shine

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1989). For instance, as a result of difference in dietary preferences (different types of food or feeding rates) sexes may diverge in head dimensions or total body size. Fecundity selection is also one of the possible explanations. In many animal species, females are larger than males. The general assumption is that selection favors larger females because they can produce more offspring. Positive correlation between fecundity and body size was found in a number of species, but other life-history traits, such as different age at maturation or sex-specific mortality, may have more influence on SSD (Madsen & Shine 1994).

Sexual size dimorphism has been demonstrated in a great variety of species, invertebrates as well as vertebrates (e.g. Clutton-Brock et al. 1977, Price 1984, Cheverud et al. 1985, Fairbairn 1990). In amphibians in general, sexual dimorphism includes a diverse array of characteristics – size and shape differences, dorsal crests, mating calls, etc. (Duellman & Trueb 1986). Many amphibian species exhibit SSD. In a review of published data, Shine (1979) estimated that females are larger than males in approximately 61% of urodeles (of 79 species reviewed) and 90% of 589 anuran species reviewed. The opposite trend was found mainly among species reported to have aggressive behaviour and male combat (19% of urodele and 5% of anuran species). Though these figures were criticized (Halliday & Verrell 1986) on the grounds that heterogeneity of sources and types of data hindered precise estimates, it seems that in amphibians, like in many other poikilothermic vertebrates, the general pattern is that females are larger than males (e.g. Halliday & Verrell 1986, Halliday & Tejedo 1995).

In amphibians and reptiles, the usual explanation for intersexual differences in body size was sexual selection. Thus, Shine (1979) proposed that, in species with male combat, selection is supposed to favor larger males because they are more successful in intrasexual struggles. However, numerous factors and their interactions may influence the total SSD, such as: differences in growth rates (e.g. Cvetković et al. 1997), delayed maturation in one sex (Madsen & Shine 1994) or sex-specific mortality, correlated response to selection (Fairbairn 1997), characteristics of mating system including the operational sex-ratio that may change with time and duration of reproduction period (Halliday & Tejedo 1995).

It has been emphasized (Halliday & Verrell 1986, Madsen & Shine 1994) that the direction of sexual size dimorphism (i.e. which sex is larger) depends on the relative advantage of larger body size – in which sex is larger body size selectively more advantageous. For instance, if large body size gives more advantage to females (through greater fecundity) than to males (through greater reproductive success), females will be the larger sex. In addition, small body size in males may be favored in intrasexual contests where agility is more important than strength; in both sexes, small body size is advantageous in terms of earlier maturation and shorter generation time (Anderson 1994). Thus, the effects of selection in both sexes should be considered (Reynolds & Harvey 1994), as well as correlated size changes in both sexes (e.g. Fairbairn 1997).

European fire-bellied toads (*Bombina* spp.) were subjects of numerous studies (e.g. Arntzen 1978, Gollmann 1984, Szymura 1993, Szymura & Barton 1986, 1991, MacCallum et al. 1998, Szymura et al. 2000), especially those concerning interspecific hybridization and hybrid zones. Diverse aspects of variation at intra- and interspecific level were intensively studied, but sexual dimorphism in *Bombina* populations has attracted little attention so far. Though SSD was examined in anurans in

general, the majority of data concerns species of *Rana*, *Bufo* and *Hyla* (e.g. Howard 1981, Woolbright 1983, Sullivan 1984, Halliday & Verrell 1986, Emerson 1994).

The aim of this study was to examine the direction and magnitude of intersexual differences in two species of European fire-bellied toads, *Bombina bombina* and *B. variegata*. We analysed populations from the central Balkans, the region where both species occur, and where, additionally, two subspecies of *B. variegata* (*B. v. variegata* and *B. v. scabra*) are found.

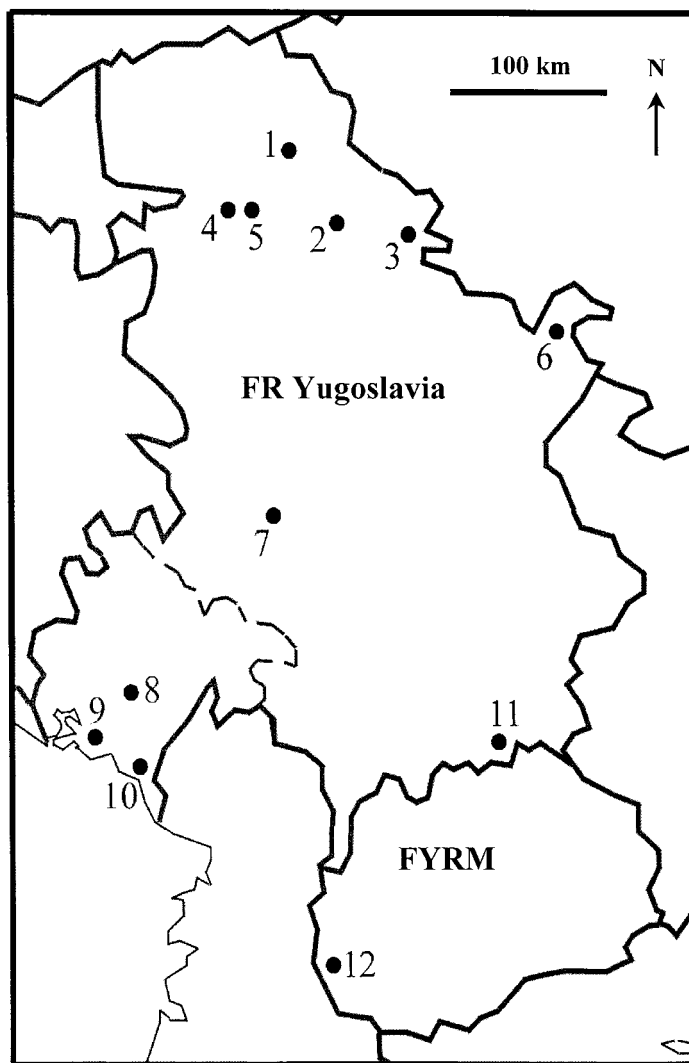


Fig. 1. Map of sampling sites in FR Yugoslavia and Former Yugoslav Republic of Macedonia. *B. bombina*: 1. Melenci, 2. Pančevo, 3. Banatska Palanka; *B. v. variegata*: 4. Andrevlje, 5. Kamenolom, 6. Cvetanovac; *B. v. scabra*: 7. Vasiljev Vrh, 8. Bjeloši, 9. Prekornica, 10. Livari, 11. Prohor Pčinjski, 12. Podgorci.

Material and Methods

Analysis were conducted on 12 *Bombina* spp. populations: three *Bombina bombina*, three *B. v. variegata* and six *B. v. scabra* populations from the central Balkans (Fig. 1). Three *Bombina bombina* samples were collected from ponds near Melenci (n = 65), Pančevo (n = 30) and from Deliblato Sand, locality Banatska Palanka (n = 18). Three samples of *B. v. variegata* were from Fruška Gora Mt. (loc. Andrevlje, n = 28, and Kamenolom n = 21) and from Miroč Mt. (loc. Cvetanovac, n = 28). *B. v. scabra* populations were from: Javor Mt. (Vasiljev vrh, n = 48), Prekornica Mt. (pond Ponikvica, n = 32), Lovćen Mt. (Bjeloši village, n = 31), the Skadar Lake (Livari village, n = 20), Prohor Pčinjski (n = 46) and Starac Mt. (loc. Podgorci, n = 21). All individuals included in analyses were adults.

In order to examine morphological variation, we measured the following 20 morphological characters to the nearest 0.1 mm:

L – body length (from the tip of snout to the edge of cloaca), F – femur length, T – tibia length, N – distance from tibiotarsal ankle to the tip of the longest toe, P – foot length (from the metatarsal ankle to the tip of the longest toe), H – humerus length, M – forearm length (to the tip of the longest finger), DPPA – length of the first finger of fore leg, DSPA – length of the second finger of fore leg, DPPP – length of the first toe of hind leg, CINT – metatarsal tubercle length, LC – head length (from the tip of snout to the edge of jaw), LTC – maximum head width (at the point of jaw articulation), SPP – minimal interorbital distance, SPI – distance between nasal pores, SPCR – snout width (at the front edge of orbits), LO – eye length, LTP – maximum eyelid width, DRO – snout-eye distance, and DNO – distance between nasal pore and eye. For bilateral characters, measurements on the right side of body were taken.

Eight qualitative characters, mostly defined on the basis of previous references (Radovanović 1951, Michałowski & Madej 1969, Lang 1988) were examined as well:

I – pigmentation of dorsal gland structures, II – appearance of dorsal warts, III – colour of ventral side of body, IV – colour of patches on ventral side, V – presence of white spots on ventral side, VI – presence of „neck“ (i.e. slight constriction between head and body), VII – colour of dorsal side of body and VIII – pigmentation of tips of fingers.

The results of gel electrophoresis were used to confirm the subspecies status of different *B. variegata* populations; *B. v. variegata* and *B. v. scabra* showed substantial differences in allelic frequencies on *Idh2* and *Ldh2* loci (unpublished data).

Statistical analyses of morphometric characters included: descriptive statistics, One-way and Two-way analysis of variance (ANOVA) as well as multivariate analysis of variance (MANOVA) and discriminant analysis. Mahalanobis multivariate distances (D^2) between sexes were also calculated. Correspondence analysis was performed to examine differences in qualitative characters between sexes.

Results

Preliminary analyses (Appendix) of 20 morphological traits in female and male *Bombina bombina*, *B. v. variegata* and *B. v. scabra*, revealed a somewhat inconsistent pattern of intersexual size differences. Total length (L), the trait most commonly used as indicator of body size, showed higher mean values in *B. bombina* males than in females, and the opposite trend in both *B. variegata* groups, though none of these differences was statistically

significant. When other traits are considered, males were larger in all cases where significant intersexual differences were found. This raises the question of differences between sexes at the multivariate level. The results of One-way MANOVA showed significant SSD in all three taxa (Rao's R: *Bombina bombina* = 1.69, $p < 0.05$; *B. v. variegata* = 2.75, $p < 0.01$; *B. v. scabra* = 7.86, $p < 0.001$).

Since the sample was heterogeneous in a geographic sense, Two-way ANOVA with sex as fixed and locality as random factor was performed, in order to separate the effects of sex from the effects of locality (i.e. population) on morphological variation. The results are given in Table 1. The effect of sex was significant for three traits in *B. bombina* (T, LTC, SPI), two traits in *B. v. variegata* (L,T) and seven traits in *B. v. scabra* (T, N, P, H, SPCR, DRO, DNO). Factor population showed a strong effect in all three taxa, being highly significant in *B. bombina* and *B. v. scabra*. The effect of interaction was, with almost no exception, insignificant. The most prominent features were: significant differences in T in all three taxa, and highly significant difference in traits LTC in *B. bombina* and H in *B. v. scabra*.

Multivariate analysis (Two-way MANOVA, Table 2) showed highly significant effects of population and insignificant effects of interaction in all three taxa, and the growing significance of the effect of sex on character variation in *B. bombina*, *B. v. variegata* and *B. v. scabra*, respectively.

Discriminant analysis confirmed higher level of intersexual differences in *B. variegata* compared to *Bombina bombina*. Discriminant scores centroids (Fig. 2) show that, while species and subspecies are delimited along the first and the second discriminant axis, sexes are clearly separated along the third discriminant axis. The same general pattern is observed when the population centroids (Fig. 3) are analysed, with the exception that in *Bombina bombina* sexes are not clearly separated along the third discriminant axis.

Mahalanobis multivariate distances between females and males were calculated within each group. The significance of Mahalanobis distance between sexes was lowest in *B. bombina* and highest in *B. v. scabra* (Z values: *B. bombina* = 1.67, $p = 0.05$; *B. v. variegata* = 2.40, $p < 0.01$; *B. v. scabra* = 7.97, $p < 0.001$).

Correspondence analysis, employed to examine differences in qualitative characters, showed that females and males were similar with respect to all analysed qualitative traits in all three taxa. The proximity of sexes in the space of correspondent axes indicates that distributions of character states between females and males are very similar. All dissimilarities in qualitative traits were related to distinction of the taxa (appearance of dorsal warts, colour of ventral side of body and the patches, presence of white spots on the ventral side of body and the presence of slight constriction between head and body). Thus, none of the analysed qualitative characters showed sexual dimorphism.

Discussion

Our results revealed the existence of statistically significant dimorphism in size (SSD) in the *Bombina* species and subspecies analysed. The pattern of intersexual differences was complex. Body length (L), the trait most often used in this kind of study, showed inconsistent differences across taxa. In *B. bombina* males were larger than females, in *B. v. scabra* females were larger, but in both cases the differences were not statistically significant. Only in *B. v. variegata* were females significantly larger than males. However, intersexual differences on

Table 1. Two – way ANOVA for the effects of sex, population and their interaction for 20 morphometric characters in *Bombina* spp. (*p < 0.05, **p < 0.01, ***p < 0.001, ****p < 0.0001). See text for explanation of character codes.

Trait	<i>B. bombina</i>				<i>B. v. variegata</i>				<i>B. v. scabra</i>			
	Sex	Population	Interaction	Sex	Population	Interaction	Sex	Population	Interaction	Sex	Population	Interaction
L	0.01	22.44 ***	1.29	4.81 **	3.57 *	1.16	0.35	26.87 ***	1.45	0.35	26.87 ***	1.45
F	0.51	18.44 ****	0.36	1.48	6.42 ***	0.60	2.01	11.97 ***	2.49 *	2.01	11.97 ***	2.49 *
T	3.91 *	21.98 ***	0.28	7.22 **	1.02	0.94	16.42 ***	24.06 ***	2.57 *	16.42 ***	24.06 ***	2.57 *
N	1.49	49.41 ****	0.35	0.11	3.34 *	1.02	4.40 *	20.53 ***	1.63	4.40 *	20.53 ***	1.63
P	3.22	41.49 ****	0.56	0.97	6.33 **	1.98	6.81 **	15.83 ***	1.08	6.81 **	15.83 ***	1.08
H	0.02	38.77 ****	1.44	1.42	5.43 **	0.28	40.11 ***	10.03 ***	0.83	40.11 ***	10.03 ***	0.83
M	1.63	33.35 ****	0.12	0.79	7.16 **	0.05	1.14	16.23 ***	1.11	1.14	16.23 ***	1.11
DPPA	0.35	9.53 ****	2.24	0.88	0.86	0.56	0.51	6.94 ***	1.30	0.51	6.94 ***	1.30
DSPA	2.09	13.93 ****	0.96	3.89	2.74	0.02	0.48	7.50 ***	2.08	0.48	7.50 ***	2.08
DPPP	1.80	21.10 ****	0.43	0.04	3.75 *	1.94	0.09	11.12 ***	2.14	0.09	11.12 ***	2.14
CINT	3.56	54.60 ****	0.32	0.69	1.85	1.15	0.24	4.84 ***	0.27	0.24	4.84 ***	0.27
LC	0.98	22.98 *	0.68	1.24	8.79 ***	1.40	1.39	10.32 ***	1.95	1.39	10.32 ***	1.95
LTC	13.99 ****	24.13 ****	1.88	0.68	0.25	0.05	0.64	13.37 ****	1.16	0.64	13.37 ****	1.16
SPP	2.89	2.24	0.99	0.37	7.72 ***	1.05	0.04	6.53 ***	1.94	0.04	6.53 ***	1.94
SPI	8.20 **	20.56 ****	0.44	0.32	1.98	1.20	3.50	5.72 ***	1.88	3.50	5.72 ***	1.88
SPCR	3.20	21.09 ****	0.58	0.60	2.98	2.00	4.81 *	4.78 ***	1.54	4.81 *	4.78 ***	1.54
LO	0.04	4.27 ****	0.41	0.47	0.41	0.38	0.11	4.84 ***	1.81	0.11	4.84 ***	1.81
LTP	1.56	6.49 **	1.66	0.65	2.52	2.28	0.16	3.47 *	2.23	0.16	3.47 *	2.23
DRO	2.09	10.70 ****	1.03	0.35	0.16	0.93	7.26 **	6.35 ***	1.04	7.26 **	6.35 ***	1.04
DNO	0.30	2.43	0.43	0.20	0.02	4.43*	4.99 *	3.68 *	0.94	4.99 *	3.68 *	0.94

Table 2. Two-way MANOVA for the effects of sex, population, and their interactions in *Bombina* spp. (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Effect	<i>B. bombina</i>		<i>B. v. variegata</i>		<i>B. v. scabra</i>	
	Wilks' λ	Rao's R	Wilks' λ	Rao's R	Wilks' λ	Rao's R
Population	0.061	13.364***	0.161	3.876***	0.117	4.529***
Sex	0.693	1.947*	0.505	2.552**	0.562	6.514***
Interaction	0.670	0.974	0.459	1.237	0.503	1.241

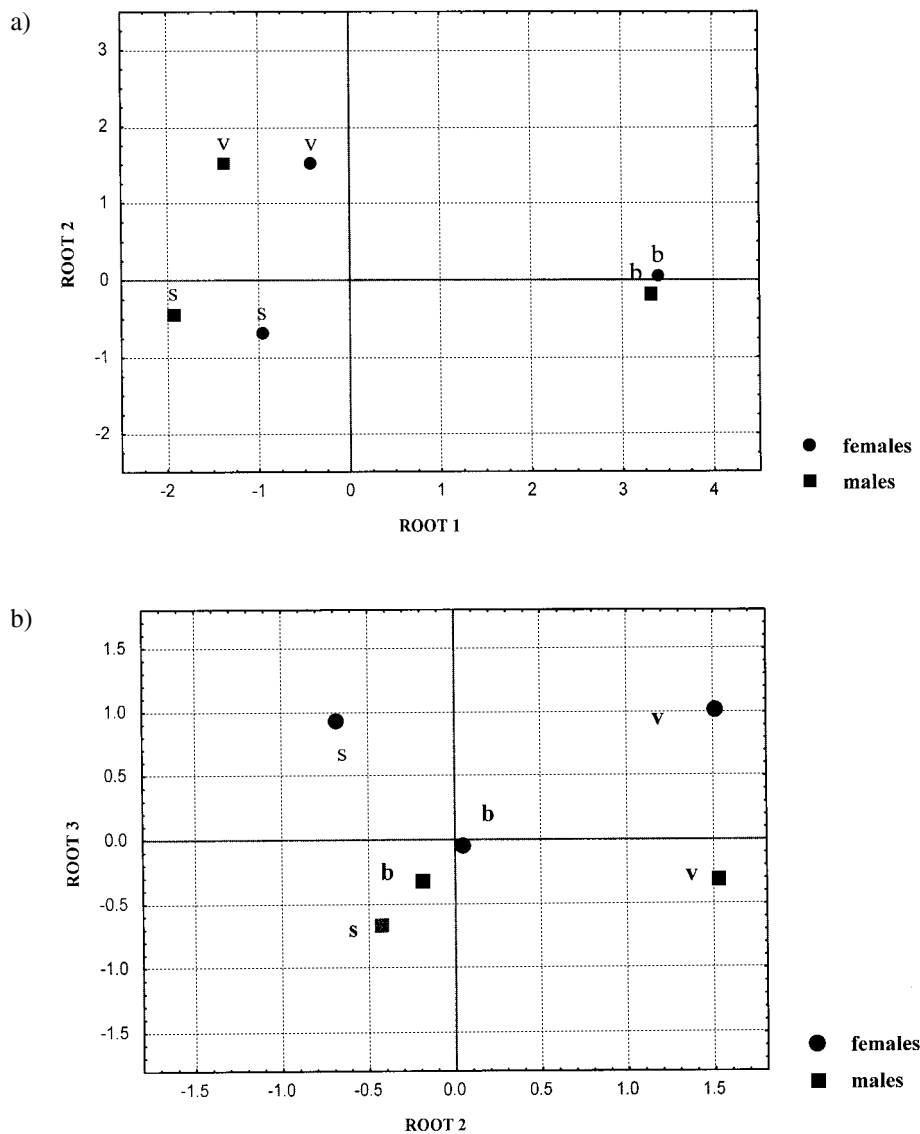


Fig. 2. a) Discrimination of *B. bombina* (b), *B. v. variegata* (v) and *B. v. scabra* (s) along the first and the second discriminant axis; b) discrimination of sexes along the second and the third discriminant axis.

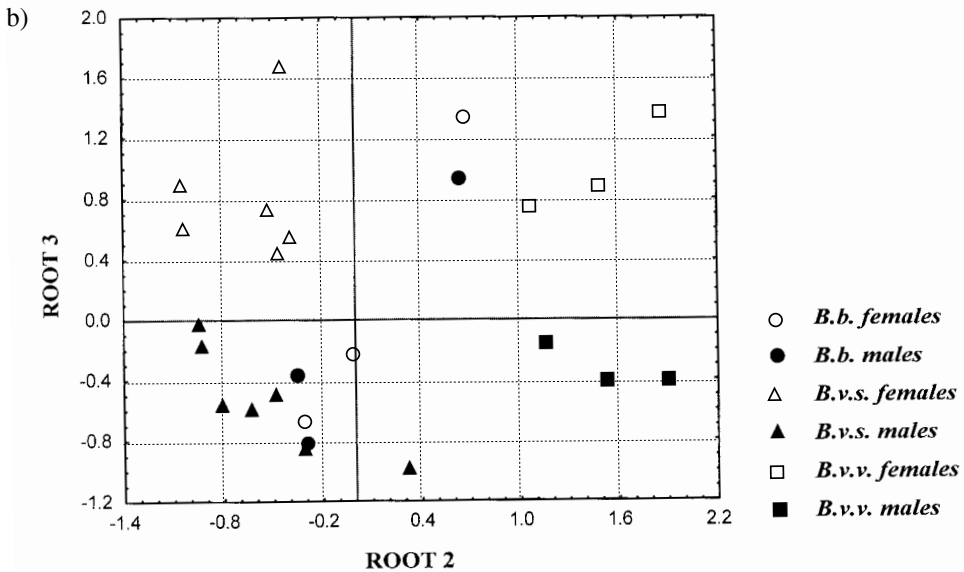
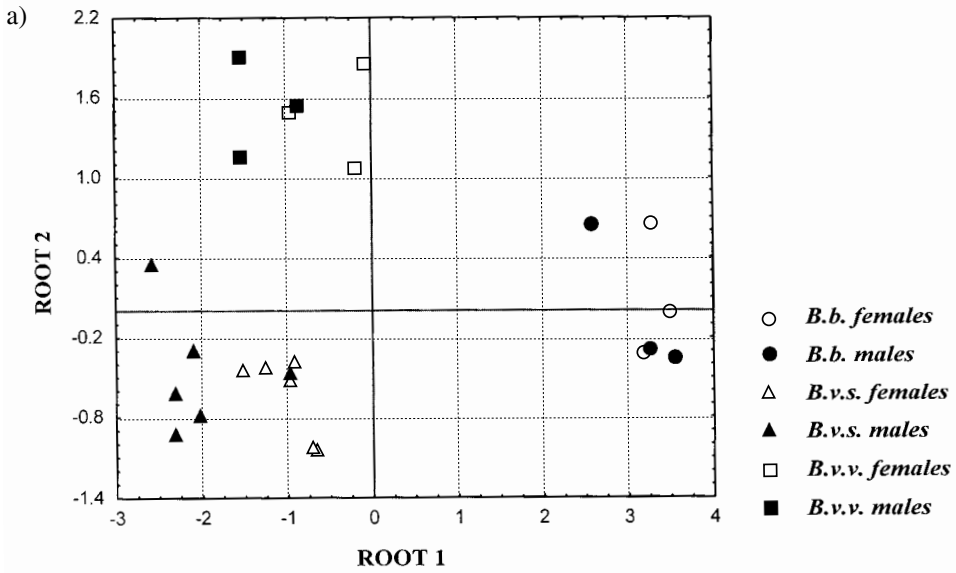


Fig. 3. a) Ordination of population centroids along the first and the second discriminant axis; b) ordination of population centroids along the second and the third discriminant axis.

multivariate level were statistically significant in all three taxa, with growing level of significance of the effect of sex on character variation in *B. bombina*, *B. v. variegata* and *B. v. scabra*, respectively. It is interesting to note that S z y m u r a (1993), in the analysis of

Appendix. Means and standard errors ($\bar{x} \pm S.E.$, in mm) for 20 morphometric characters in *Bombina* spp. (f – females, m – males, n – sample size) and the significance of intersexual differences; (ANOVA; *p < 0.05, **p < 0.01, ***p < 0.001). See text for explanation of character codes.

Trait	<i>B. bombina</i>										<i>B. v. variegata</i>										<i>B. v. scabra</i>					
	n = 52		n = 61		n = 28		n = 49		n = 87		n = 111		n = 52		n = 61		n = 28		n = 49		n = 87		n = 111			
	f	x	SE	m	x	SE	f	x	SE	m	x	SE	f	x	SE	m	x	SE	f	x	SE	m	x	SE	ANOVA	
L	37.6	0.48	0.18	38.4	0.51	1.35	45.8	0.68	44.5	0.45	2.81	44.6	0.67	43.5	0.52	1.66										
F	12.7	0.18	0.19	13.1	0.19	1.98	15.9	0.39	16.6	0.23	2.63	17.7	0.22	17.7	0.21	0.03										
T	12.1	0.14	0.15	12.6	0.15	6.12*	15.9	0.14	16.6	0.17	9.35***	16.2	0.17	16.8	0.17	6.76**										
N	19.7	0.29	0.31	20.5	0.31	3.84	24.8	0.30	25.2	0.24	0.72	24.8	0.28	25.2	0.29	1.18										
P	14.2	0.28	0.28	15.3	0.28	7.28**	15.8	0.29	16.3	0.21	2.02	16.1	0.19	16.6	0.20	2.69										
H	6.4	0.14	0.16	6.7	0.16	2.25	9.1	0.42	9.7	0.17	2.69	9.2	0.15	10.5	0.17	33.58***										
M	12.4	0.18	0.18	12.9	0.18	4.15*	16.0	0.24	15.9	0.17	0.10	16.5	0.19	16.5	0.19	0.00										
DPPA	3.6	0.08	0.07	3.8	0.07	3.52	4.0	0.08	3.9	0.08	0.78	4.2	0.07	4.2	0.06	0.07										
DSFA	5.1	0.09	0.08	5.4	0.08	6.12*	6.2	0.12	5.9	0.08	2.54	6.3	0.09	6.3	0.08	0.08										
DPPP	4.4	0.08	0.09	4.6	0.09	5.33*	5.1	0.09	5.1	0.09	0.14	5.4	0.07	5.4	0.07	0.19										
CINT	1.3	0.05	0.06	1.5	0.06	5.04*	1.7	0.26	1.5	0.03	0.86	1.4	0.03	1.4	0.02	0.16										
LC	6.7	0.12	0.12	7.1	0.12	4.23*	8.0	0.14	7.9	0.12	0.21	8.0	0.14	8.1	0.10	0.61										
LTC	10.7	0.12	0.21	11.9	0.21	19.99***	13.7	0.23	13.5	0.17	0.60	14.3	0.19	14.2	0.16	0.09										
SPP	2.3	0.04	0.04	2.4	0.04	3.47	2.8	0.06	2.8	0.05	1.03	2.6	0.04	2.6	0.03	0.39										
SPI	2.3	0.04	0.04	2.4	0.04	10.28**	2.4	0.04	2.5	0.04	0.23	2.4	0.03	2.4	0.03	1.43										
SPCR	4.3	0.06	0.07	4.5	0.07	3.63	5.6	0.11	5.5	0.08	0.76	5.3	0.05	5.4	0.06	2.91										
LO	3.0	0.04	0.05	3.0	0.05	0.12	3.3	0.05	3.2	0.04	0.28	3.4	0.04	3.4	0.03	0.02										
LTP	2.5	0.03	0.05	2.5	0.05	0.71	3.1	0.05	3.1	0.05	0.08	3.1	0.04	3.1	0.03	0.52										
DRO	4.2	0.05	0.07	4.3	0.07	3.26	4.9	0.12	5.0	0.07	0.64	4.8	0.06	5.0	0.06	6.12*										
DNO	2.4	0.04	0.043	2.5	0.043	1.59	3.22	0.07	3.2	0.05	0.04	3.1	0.04	3.2	0.04	3.65										

patterns of genetic variation, found that *B. variegata* populations were more differentiated than *B. bombina* populations and that, within *B. variegata*, northern groups of populations were more similar than the southern ones.

Body length, which is commonly used as the indicator of body size (many comparative studies of SSD are based on this trait), is not always appropriate for this purpose. In some species, as is clearly the case here, differences in other characters (related to specific reproductive behaviour, feeding, locomotion) could be more important. This is in line with models based on ecological divergence between sexes and differences in food utilization (e.g. Shine 1989). It has been already suggested (e.g. Howard & Kluge 1985, Halliday & Verrell 1986) that body length is not always the most important factor for male mating success in amphibians.

In addition, one of the patterns revealed in our study is the strong effect of populations (i.e. localities) on character variation, indicating the substantial level of geographic differentiation among populations. This raises another issue – to reach the accurate estimate of SSD for a certain species, samples from different populations are needed. When the effect of population was separated from the effect of sex, the most prominent results were: significant intersexual differences in tibia length (T) in all three taxa, and highly significant intersexual difference in head width (LTC) in *B. bombina* and humerus length (H) in *B. v. scabra*. Longer legs in males could be explained with respect to reproductive behaviour; agility is generally considered important in competition to attract females. Longer legs may also be connected with sex-specific territorial behaviour. In this context, it is interesting to mention that, though *B. variegata* males were not considered to be territorial (e.g. Szymura 1993), Seidel (1999) reported that a number of males performed sex-specific territorial behaviour, producing water-waves that demarcated territories with their hind legs.

Humerus was significantly longer in male than in female *B. v. scabra*; contrary to expectations, differences in this trait in the other two taxa were insignificant. Arm length is considered important for male mating success in anurans, and the general assumption is that longer arms allow a more secure grip of females. Howard & Kluge (1985) reported that arm length was more important for reproductive success than body length in male *Rana sylvatica*. Highly significant difference in head width in *B. bombina* is related to the presence of vocal sacs in males and their role in reproduction, but the possibility of a certain degree of trophic divergence may be also worth examining.

Thus, we conclude that the pattern of SSD in analysed taxa was complex, body size was insignificantly different, but all significantly different traits were larger in males, the only exception being L in female *B. variegata variegata*. The general level of SSD was higher in *B. variegata* than in *B. bombina*. In addition, our results emphasize that great caution is needed when analysing SSD on basis of body length only. This problem is pronounced in comparative studies based on previously published data, with heterogeneous indicators of body size, in studies where body length (L) is the only indicator of body size, and studies on geographically differentiated species where samples are not taken from different populations.

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