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A morphometric study of two Carpathian newt populations (*Triturus montandoni*): North-West and South-East Tatra mountains

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Abstract. Morphometric data from the Tatra mountains populations of the Carpathian newt Triturus montandoni were analysed for the presence of sexual and environmentally influenced size and shape variation. The data sets were examined with multivariate methods. Sexual dimorphism in size and body weight was clearly demonstrated in the species. The separation in shape was also highly related to sex. Females had relatively shorter tail and wider head than males. No evidence of size or shape variation was found between two different years. The newts tended to differ in shape between localities. Specimens from SE Tatra locations were relatively shorter with wider head than animals from the NW Tatra mountains. This pattern of variation in shape was independent of sexual size or shape dimorphism in newts. There was found high correlation between body weight in females and their shape variation in tail length and head width. Heavier females had relatively wider head and shorter tail than lighter females. There was not found difference in this pattern of shape in males. But heavier males were relatively longer and had narrower head than their lighter counterparts. The results are discussed in terms of evolution of intersexual dimorphism and adaptation to different environmental conditions.

Introduction

Sexual dimorphism is widespread among vertebrates, and there are several different hypotheses concerning its evolution (e.g. Shine 1979, Fairbairn 1997). The ecological model relates to the idea that sexes differ because they have adapted to different resource utilisation. This model predicts that sexes should differ in, for example, trophic structures (i.e. mouth or head morphology). Under the second hypothesis (the fecundity model), sexual dimorphism is believed to evolve when one sex benefits more from a large body size or different body shape than the other sex, in terms of reproductive outcome. The hypothesis predicts that

intersexual differences in morphological characters should be related to fecundity. The third alternative (the sexual selection model) treats sex differences in external morphology as having evolved by, for example, the active selection of morphological characteristics on one sex by the other. This suggests that individuals with better developed traits have an advantage in competition for mates relative to other individuals of the same sex (Andersson 1994, Malmgren and Thollesson 1999). Dimorphic traits are influenced by developmental processes prior to maturity, and in adults they are mainly under hormonal and seasonal influence (Andersson 1994). Moreover, ecological factors (e.g. food availability, local climate) also contribute to the extent of expression in different sexual features (Shine 1989). Recently, there has been debate over whether ectotherms show the same pattern of body-size variation as endotherms, with some authors suggesting that ectotherms follow Bergmann's rule (Lindsey 1966, Van Voorhies 1996, Atkinson and Sibly 1997), while others have contended that ectotherms follow the inverse of Bergmann's rule (Mousseau 1997). It was claimed that Bergmann's Rule holds for amphibians in general, more clearly for tailed amphibians than for anurans (reviewed by Ashton 2002).

European newts of the genus Triturus show a high degree of sexual dimorphism (Kalezić et al. 1992, Andersson 1994, Krizmanić et al. 1997). Most species show permanent sexual differences in morphology (Kminiak 1971, Sotiropoulos et al. 2001). In most of the species, females are generally larger in body size than males (e.g. Rafinski and Pecio 1989, Kalezić et al. 1992, Miaud et al. 2000), and males and females also differ in shape (Lác 1968, Malmgren and Tholleson 1999). Moreover, newts in general show a trend in accordance with Bergmann's rule with respect to latitude and elevation. The relationship between body size in newts and temperature is also consistent with a trend towards concordance with Bergmann's rule (Ashton et al. 2000).

The Carpathian newt is endemic species of Carpathian mountains. Its typical environment is a coniferous forest at higher altitudes. Females are larger than males (Kminiak 1971). In Slovakian Carpathians, it was found from 350 to 1,850 m a.s.l. (Kminiak 1971). Using the species as a model, in this study, we asked the following principal question: Does exist variation in morphology of newts which is independent on sexual dimorphism? We compared size and shape of newts from two different locations in the Tatra mountains.

Morphometry of Triturus montandoni

Material and Methods

The study is based on an analysis of 82 newts collected at two locations within Slovakia, in the West Tatra (Roháče) and East Tatra (Belianske) mountains. The newt individuals were caught with a net over a period of day sessions in the springs 2002 and 2003. The samples, from two locations were used to characterize the multivariate morphology of the Tatranian Carpathian Newt (T. montandoni). Only mature adults were measured, this was confirmed by inspection of the cloacal area. The use of adult specimens counteracts any problems of allometric growth, with a rapid slowing down in growth being linked to sexual maturity (Francillon-Vieillot et al. 1990). All samples were live specimens, to avoid problems involved in measuring preserved specimens (Lee 1982, Verrell 1985). The samples when measured were placed on a moistened towel (Lantz and Callan 1954). Their morphometric characters were then taken with a vernier calliper to within 0.1 mm, with specimens returned to the field within one hour. All newts were also weighed to the nearest 0.1 g. The morphometric characters measured can be seen in Table 1. Explanations of morphological character

Sex	n	•	g)	Body length (mm) mean ± SD	(mm)
Males Females				81 ± 4.8 88.5 ± 6.1	38.4 ± 3.5 40.9 ± 4.0

Table 1. Descriptive statistics on body related variables for the Carpathian newt, *Triturus montandoni*.

Variable	PC1 (Size)	PC2 (Shape)	PC3 (Shape)		
Body lenght	0.535	0.240	0.809		
Tail lenght	0.675	-0.697	-0.239		
Head width	0.506	0.675	-0.535		
Variability (%)	81.02	15.08	3.9		

Table 2. PCA results for covariance matrix of data sets of morphologic characters of Carpathian newts.

measurements: Total length - distance from snout tip to tail tip, tail length - posterior margin of cloacal lips to tip of tail, head width - largest width of head, in line with the corner of the mouth.

All statistical tests were conducted using a PC running Stagraphics 5 statistical software. Shape and size pattern characters were tested for a significant difference in the within/between group variation using an ANOVA (type III, Strauss 1987) while equivalent tests were carried out on the body size and shape measurements by ANCOVA with environmental characters as the independent variables. Each variable was analysed for normality. In multivariate analyses the variables were analysed using principal components analysis (PCA, Malgmrenn and Tholesson 1999). Principal components of mensural data were computed from the covariance matrix of logarithmically transformed data. The logarithmic transformation preserves allometries, standardizes variances, and produce a scale-invariant covariance matrix (Jolicoeur 1963, Strauss 1985). Principal component analysis is a multivariate technique that may be used for summarizing data sets combining large number of variables The first pricipal component of a set of linear measurements provides an appropriate structural size measure (Rising and Somers 1989). The importance of the second and third principal components in this study can be judged from the amount of variance associated with these components. These variations are independent of general size vector (PC1) and they are most easily attributed to shape of newts. A measure of the size or shape equivalence or difference between two selected groups of newts was identified with ANOVA of the component scores (Somers 1986).

Results

The structures of the principal components and their variance are presented in Table 2. Analysis of covariance matrix shows that the three original variables are aproximatelly equally weighted on first size component. Size and shape (on PC2) characters showed a significant difference among the sexes when working at the 95% significance level. This indicated sexual dimorphism in size

Variable n		Body weight mean (SE)	Mean PC1 Score (SE)	Mean PC2 Score (SE)	Mean PC3 Score (SE)		
Year							
2002	42	3.31 (0.09)	-0.13 (0.20)	-0.01 (0.09)	0.06 (0.06)		
2003	40	3.18 (0.1)	0.39 (0.23)	0.09 (0.11)	0.01 (0.07)		
Sexes							
Males	48	2.49 (0.08)	-0.75 (0.19)	-0.28 (0.09)	-0.04 (0.06)		
Females	34	3.99 (0.1)	1.02 (0.24)	0.37 (0.11)	0.10 (0.07)		
Two-way AN	OVA						
Years		F = 0.98; $p = 0.34$	F = 2.85; p = 0.09	F = 0.55; $p = 0.47$	F = 0.26; p = 0.61		
Sexes		F = 135.9; p = 0.00	F = 32.9; p = 0.00	F = 21.12; p = 0.00	F = 2.56; p = 0.11		
Factor inter	ractions	F = 0.14; p = 0.71	F = 0.37; p = 0.55	F = 0.47; p = 0.50	F = 3.43; p = 0.07		

Table 3. Comparison of body weight, size and shape of newt sexes and newts from different years. Size are represented by means of PC1- principal component scores. Shapes are represented by means of PC2 principal component scores.

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Variable	n	Body mean	weight (SE)	Mean PC1 Score (SE)			Mean PC2 Score (SE)			Mean PC3 Score (SE)	
Sexes											
Males	48	2.42	(0.08)		-0.65	(0.20)		-0.25	(0.09)	-0.1	0 (0.06)
Females	34	3.91	(0.14)		1.26	(0.35)		0.43	(0.16)	0.0	5 (0.09)
Locality											
NW-Tatra m.	61	3.34	(0.07)		0.06	6 (0.17)		0.02	(80.0)	0.0	7 (0.05)
SE-Tatra m.	21	2.99	(0.15)		0.55	(0.37)		0.15	(0.17)	-0.1	3 (0.10)
Two-way ANO	VA										
Sexes		F = 8	3.3; p =	0.00	F =	21.9; p =	0.00	F =	21.9; p = 0.0) F =	1.80; p = 0.18
Locality		F = 4	.6; p =	0.04	F =	1.46; p =	0.23	F =	0.49; p = 0.4	9 F =	3.32; p = 0.07
Factor intera	ctions	F = 0	.04; p =	0.90	F =	0.52; p =	0.48	F =	0.007; p = 0.9	3 F =	0.91; p = 0.35

Table 4. Comparison of body weight, size and shape of newt sexes and newts from nothern and southern slopes of the Tatra mountains. Size are represented by means of PC1- principal component scores. Shapes are represented by means of PC2 principal component scores.

as well as in shape. Females were larger and had relatively shorter tail and wider head than males. The animals did not differ in size or shape between two seasons (Table 3).

There were found significant differences in shape at the 95% significance level between localities (Table 4). Specimens from SE Tatra locations were relatively shorter with wider head than animals from the NW Tatra mountains. This pattern of variation in shape was independent of sexual size or shape dimorphism in newts. In the NW Tatra (colder conditions), both sexes were significantly heavier than animals from SE Tatra mountains (Table 4, Fig. 1). There was not any interaction between factor locality and factor sex. Females showed a positive relationship between body weight and body shape defined on PC2 (Table 5). Heavier females had relatively wider head and shorter tail than lighter females (Fig. 2). Such differences were not found in males. But males do show a significantly positive overall association between body weight and body shape defined on PC3. Heavier males were relatively longer and had narrower head than their lighter counterparts (Fig. 3).

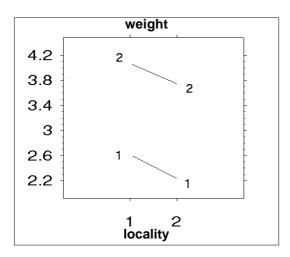


Fig. 1. The relationship between body weight of the newt sexes and localities of their occurence. Both sexes were heavier in the NW than SE Tatra mountains. At both locations, the females were heavier than males.

Discussion

There were high degrees of sexual dimorphism for body-related characters in both populations. The dimorphisms were related to size as well as to shape. Females had relatively shorter tail and wider head than males. Malmgren and Thollesson (1999), whose results agree with ours, described that separation of specimens of T. cristatus and T. vulgaris was highly related to sex. There were some differences between the two species, for example in which sex had the longer tail, the pattern is very similar to intersexual shape differences in the Carpathian newts. Sexual dimorphism in *T. cristatus* and *vulgaris* was also attributed to females showing large values for dimensions related to fecundity, such as standard length and distance of extremities, contrasted with large values for cloaca and limb-related measurements in males. The authors interpreted these results as primarily concordant with the fecundity model. Previous studies on amphibians have shown that females are generally larger than males in body size (e.g. Shine 1979) possibly because fecundity increases with increasing female body size. Generally, female body size correlates with clutch volume in ectothermic vertebrates, presumably owing to constraints on reproductive investment imposed by the size of the female body cavity (Olsson and Shine 1997). Furthermore, female body size and an increased reproductive investment have been shown to correlate positively with mating rate and number of sires (Garner et al. 2002, Garner and Schmidt 2003).

ANOVA	n	PC1	PC2	PC3
Males	48	F = 20.9 p = 0.00 r = 0.56	F = 1.31 p = 0.25 r = 0.16	F = 7.28 p = 0.00 p = 0.00
Females	34	F = 16.8 p = 0.00 r = 0.6	F = 11.6 p = 0.001 r = 0.52	F = 0.39 p = 0.54 r = -0.11

Table 5. Intraspecific relationship between adult body weight and size and shape of newts (ANOVA of linear regression models, F = F-test, p = significance level, r = correlation coefficient).

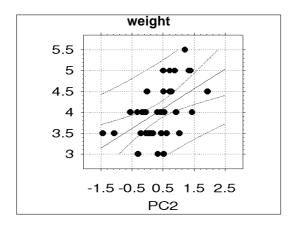


Fig. 2. Positive association between body weight and shape (PC2, see Table 5) in females. Heavier females had relatively wider head and shorter tail than lighter females.

The northern valleys of the West Tatra mountains are generally known as habitats of cooler climate, higher humidity and precipitation than south eastern parts of the Tatras. Direct effects of temperature on body weight and shape may help explain geographic patterns of body-weight variation. Both sexes of newts were heavier and relatively longer with narrower head in the West than in the East Tatra mountains. But in our case, the animals did not differ in size. In fact, a lower development temperature causes a larger body size for ectotherms in general (Ray 1960, Atkinson 1994). The effect of development temperature on body size has been studied in the laboratory for eight species of amphibians (review - Ashton et al. 2000). In all cases, lower development temperatures resulted in larger body sizes. Thus, direct effects of temperature on body size during development may at least partially explain why our newts had a larger body weight in cooler areas. For amphibians, body size might also be more strongly tied to an environmental factor other than temperature. Amphibians are strongly constrained by available moisture because of the need to keep the skin moist to allow respiration and, consequently, they limit desiccation via several means (Duellman and Trueb 1994. Stebbins and Cohen 1995). It is possible that body sizes of newts may be related to the precipitation and humidity. Our results suggest that niche partitioning in terms of feeding is not a likely determinant of sexual dimorphism in the Carpathian newts. Instead, fecundity and, possibly, selection seem more plausible processes underlying the observed dimorphism in the species. But Carpathian newts appear to show a general relationship between body weight and temperature. This body weight and shape variation does not relate to sexual dimorphism. The exact nature of body-size patterns may vary among geographic areas and this may influence the generality of body-size and shape patterns. Some species of newts (e.g. Triturus alpestris) show strong patterns of such variation (Ashton et al. 2000). It is not clear whether Bergmann's rule, larger size within species in cooler areas, holds for any group of ectotherms. Salamanders and newts show body-size patterns consistent with the overall trend, with 13 of 18 species having a larger body size at higher

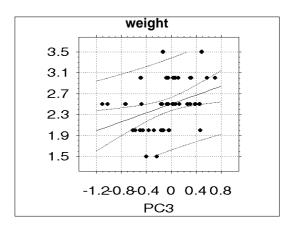


Fig. 3. Positive association between body weight and shape (PC3, see Table 5) in males. Heavier males were relatively longer and had narrower head than lighter males.

latitudes or elevations (Ashton *et al.* 2000). Clearly, more extensive studies of geographic variation in body size among amphibian species relative to environmental factors are needed before strong conclusions can be drawn regarding general patterns.

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