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Body size patterns of *Pholidoptera frivaldskyi* (Orthoptera) in very isolated populations

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Abstract

We studied geographical body-size variation and sexual size dimorphism in three isolated populations of the bush-cricket *Pholidoptera frivaldskyi* in Central Europe (Slovakia). We measured six body traits in females and seven in males, from 93 individuals (46 males and 47 females): lengths of body, right hind femur, right hind tibia, pronotum, right cercus or ovipositor, length of wing (only in males) and body weight. Not all linear traits in both sexes were correlated with body weight. Generally, females were significantly bigger than males in all parameters. Although discriminant function analysis indicated some significant differences in male traits, there were no strong morphological difference among local populations. Morphological variability among the three populations was not higher than that within populations. This relative somatic uniformity should be verified on the level of genetic variability of the studied populations, since cryptic species diversity can be expected.

Key words

Orthoptera, Tettigoniidae, bush-cricket, morphology, sexual size dimorphism, endangered species, isolated population, body mass, femur length

Introduction

Many species show nested distributional patterns due to habitat changes, including fragmentation and loss of biocorridors (Schouten *et al.* 2007). Such isolation can lead to significant genetic differentiation among populations. This is seen in alpine Orthoptera, where isolation of populations in separate mountain regions and on different slopes has led to reciprocally monophyletic, deeply differentiated, lineages (Trewick *et al.* 2000).

Because genetic differentiation often produces morphological differentiation (*e.g.*, Brower 1994, for moths), morphological differentiation can be used as an indicator of possible underlying genetic differentiation. In the Orthoptera, body size changes latitudinally and altitudinally (Bidau & Marti 2007a,b; Kaňuch & Krištín in press), and these morphological differences often derive from underlying genetic differences. Furthermore, loss and fragmentation of habitat can lower migration rates and genetic connectivity among remaining populations of native species, increasing genetic differences between populations, but reducing genetic variability within populations and increasing extinction risk (Vandergast *et al.* 2007). This is especially true for flightless or nondispersing organisms, where isolation and limited mobility can contribute to local or even global extinction (Streiff *et al.* 2006).

If we are to preserve genetically distinct populations, we must first identify them. Comparing morphologies among isolated populations is the first step toward this goal. Such studies can also shed light on evolutionary patterns among populations.

In this paper, we compare the morphologies of three isolated populations of the endangered bush-cricket, *Pholidoptera frivaldskyi* (Herman, 1871) (Orthoptera: Tettigoniidae). Our immediate goals were to 1) determine if isolated populations differed in morphological traits, and, if so, by how much; 2) analyse multivariate differentiation by traits among populations, and 3) to examine the extent of sexual size dimorphism. Our ultimate goal is to understand and aid the conservation of this endangered species.

Material and methods

Study species.— *Pholidoptera frivaldskyi* (= *Thamnotrizon friwaldszkyi* in Obenberger 1926) is an endangered species inhabiting traditionally managed fragments of mountain hay meadows (Fig. 1). It has existed as fragmented and very isolated populations for at least 100 y in mountainous areas (elevations 550-1800 m) of central and southeastern Europe (Carpathian Mts and montane areas in Bulgaria, Serbia, Bosnia and Macedonia), implying high risk of local extinction (Harz 1969, Krištín 2000). However, there has been no published record of this species outside Slovakia for at least 40 y (Nagy 2005). Presently, this species is known to occur in central Europe in only three isolated areas, each consisting of small scattered plots (up to 3 to 12 ha). Movement out of these isolated sites is very limited, because this species is flightless: males are brachypterous and the females nearly apterous (Fig. 1).

Study sites.— Every May and October from 1994 to 2008, we inspected 508 sites in 211 mapping squares (one square having the area of 132 km^2) using the Slovak Fauna Databank (49% of the total number of squares in Slovakia). All three current populations within central Europe (Slovakia) were studied. They occur in mountainous habitats, with similar habitat features, but with different population density and size: 1) Veľká biela voda (VBV, Slovenský raj National park, 610 m a.s.l., 48°56´12N, 20°20´14E), average annual temperature (AAT) = 4.2°C (Šťastný *et al.* 2002), average population size 28 singing males (M) / 0.1 ha (July 13, 2008), occupied plot size *ca* 5 ha (574-620 m); habitat: mountain forest meadow in valley along road and forest edge, within mixed spruce and pine forests, N and NE aspect, slope 0-5°. 2) Hrochotská Bukovina (HRB, Poľana Mts, 880 m a.s.l., 48°39´52N, 19°25´48E), AAT = 4°C, average population size 12 M / 0.1 ha (July 20, 2008), the smallest occupied plot size *ca* 3 ha (800-930 m); habitat: traditionally managed and pastured mountain mesophilous hay meadow surrounded by beech-spruce forest, SW

Fig. 1. Males of *P. frivaldskyi* from VBV a) and HRB b) study sites and females from PUP c) and VBV d) study sites in Slovakia. Photo by V. Hrúz from VBV, by A. Krištín from HRB and PUP. See Plate I.

aspect, slope 10-25°. 3) Pusté pole (PUP, Slanské vrchy Mts, 670 m a.s.l., 48°56´19N 21°26´05E), AAT = 4.8°C, average population size 16 M / 0.1 ha (July 13, 2008), the biggest occupied plot size *ca* 12 ha (655-680 m); habitat: mountain mesophilous hay meadow surrounded by beech forests, W and SW aspect, slope 0-10°. Study sites were separated by 73 km (HRB - VBV), 80 km (VBV - PUP) and 148 km (HRB - PUP). During a long-term survey of species distribution in 1994-2008, no other populations of this species were found in Central Europe (Nagy 2005, and unpub. results).

Data collection and analysis.— Individual *P. frivaldskyi* were collected and measured during the time of peak adult activity between July 13 and 20, 2008 (VBV = 21 males and 21 females, HRB = 20 and 21, PUP = 5 and 5). For each individual, we measured body weight and lengths of: pronotum along midline, right hind femur and hind tibia, right cercus in males or ovipositor in females, right forewing or elytron (only in males). All males used for analysis were heard singing, *i.e.*, spermatophore development (weight) was in the equal precopulation phase (Loher & Dambach 1989). The measurement of live individuals was performed by the same person, using digital calipers (accuracy ± 0.03 mm). Weight was determined by pocket digital scale (accuracy ± 0.1 g). Immediately after measurement, individuals were released at their site of capture.

Although morphological traits should have normal distributions in natural populations, this was not so because of small sample size in one population (PUP); so we tested differences in all body measurements between the three studied sites using a nonparametric Kruskal-Wallis ANOVA. To learn how one can discriminate among the three isolated populations, based on selected measures of morphological traits, we performed Discriminant Function Analysis. Results were visualized in scatterplots of the discriminant functions of Canonical Analysis. Differences in relevant body measurements between two sexes of whole material were tested using nonparametric Mann-Whitney *U*-tests (STATISTICA 7, StatSoft, Inc.).

Table 1. Descriptive statistics of *P. frivaldskyi* male and female measurements of three isolated populations in Slovakia (SD, standard deviation; Var, variance; Min–Max, minimum and maximum values).

Measurement	Mean±SD	Var	Min–Max	Mean±SD	Var	Min–Max	Mean±SD	Var	Min–Max	Mean±SD	Var	Min–Max
Males	VBV (n = 21)			HRB (n = 20)			PUP (n = 5)			All males (n = 46)		
Femur (mm)	21.5±1.0	1.0	20.1-23.2	22.6±1.2	1.5	19.9-25.1	22.3±1.1	1.3	21.0-23.4	22.1±1.2	1.5	19.9-25.1
Tibia (mm)	19.2±1.0	0.9	17.4-21.8	19.9±0.9	0.9	18.7-21.4	19.7±1.3	1.6	17.4-20.5	19.6±1.0	1.0	17.4-21.8
Pronotum (mm)	7.1±0.4	0.1	6.4-7.7	7.6±0.4	0.1	6.9-8.5	7.2±0.6	0.4	6.6-7.9	7.3±0.4	0.2	6.4-8.5
Wing (mm)	7.9±0.5	0.2	7.4-8.8	8.7±0.6	0.3	7.6-9.6	7.8±0.7	0.5	7.3-8.9	8.3±0.7	0.5	7.3-9.6
Cercus (mm)	2.8±0.3	0.1	2.4-3.3	2.8±0.3	0.1	2.3-3.1	2.4±0.4	0.2	1.8-2.9	2.7±0.3	0.1	1.8-3.3
Body (mm)	22.4±1.3	1.6	19.7-24.1	23.3±1.8	3.1	19.9-26.1	22.1±0.7	0.5	21.5-23.3	22.8±1.5	2.4	19.7-26.1
Weight (g)	0.8±0.1	0.0	0.6-1.0	1.0±0.1	0.0	0.8-1.2	0.7±0.1	0.0	0.6-0.8	0.9±0.1	0.0	0.6-1.2
Females	VBV (n = 21)			HRB (n = 21)			PUP (n = 5)			All females (n = 47)		
Femur (mm)	23.2±1.0	0.9	21.4-24.9	22.4±1.2	1.4	20.4-24.6	24.3±0.9	0.8	23.3-25.3	23.0±1.2	1.4	20.4-25.3
Tibia (mm)	20.5±1.4	2.0	17.0-23.7	20.4±1.6	2.4	16.5-23.4	22.1±1.2	1.5	20.9-23.8	20.6±1.5	2.4	16.5-23.8
Pronotum (mm)	7.6±0.5	0.2	6.8-8.4	7.4±0.4	0.2	6.7-8.1	7.8±0.3	0.1	7.4-8.2	7.5±0.4	0.2	6.7-8.4
Ovipositor (mm)	18.7±2.0	2.6	17.2-24.8	18.4±1.0	1.1	16.1-20.1	18.6±0.3	0.4	18.4-19	18.6±1.5	2.2	16.1-24.8
Body (mm)	24.1±1.6	0.0	21.4-27.4	23.3±1.0	0.1	21.8-25.6	25.8±0.7	0.0	25.0-26.5	23.9±1.5	0.0	21.4-27.4
Weight (g)	1.0±0.2	0.0	0.7-1.5	1.0±0.3	0.0	0.7-1.8	1.0±0.1	0.0	0.9-1.1	1.0±0.2	0.0	0.7-1.8

Table 2. Differences of body measurements between three isolated populations of *P. frivaldskyi* (results of Kruskal-Wallis ANOVA; df = 46, 2 in males and 47, 2 in females).

Measurement	*H*	*p*
Males		
Femur	9.3	0.009
Tibia	5.5	0.063
Pronotum	9.9	0.007
Wing	17.9	0.001
Cercus	4.6	0.098
Body	4.9	0.084
Weight	18.2	0.001
Females		
Femur	10.5	0.005
Tibia	5.8	0.054
Pronotum	2.4	0.307
Ovipositor	1.3	0.531
Body	12.3	0.002
Weight	0.5	0.796

Table 3. Correlations of linear morphological traits with body weight in males and females of *P. frivaldskyi*.

Measurement	*r*	*p*
Males		
Femur	0.46	0.002
Tibia	0.38	0.011
Pronotum	0.41	0.006
Wing	0.53	0.001
Cercus	0.02	0.896
Body	0.37	0.013
Females		
Femur	0.27	0.069
Tibia	0.30	0.042
Pronotum	0.32	0.029
Ovipositor	0.12	0.421
Body	0.09	0.567

Results and discussion

Morphological variability in isolated populations.— Table 1 summarizes morphology data from three isolated populations of *P. frivaldskyi*. For males, populations differed significantly in femur, pronotum, wing length, and mass, and for females, populations differed in femur, and body length (Table 2). Paradoxically, the largest (based on femur, pronotum, and wing length) and heaviest males and the smallest females (based on femur and body length), were found at the same site (HRB), in the northwesternmost of our three sites. There were no significant morphological differences between our other two populations (both from east Slovakia) (Fig. 2). In males all linear traits but one (cercus) were correlated with body weight. In females weight did not generally correlate well with linear traits, which is expected because female mass fluctuates during the gonotrophic cycle (Table 3). In general, for all morphological traits, within-population trait variation was greater than among-population variation, suggesting that the individual populations were not dramatically different from one another. An examination of raw data (Table 1) shows that standard deviations and variance for individual populations were in some cases larger than those for all populations combined.

Table 4. Standardized coefficients for canonical variables.

Variable	Root 1	Root 2
Males		
Femur	0.165	-0.475
Pronotum	-0.266	-0.391
Wing	-0.590	0.111
Cercus	-0.168	0.831
Weight	-0.637	0.213
Eigenvalues	1.170	0.350
Cumulative proportion	0.770	1.000
Females		
Femur	-0.837	1.208
Tibia	0.380	-1.531
Body	-0.602	-0.338
Eigenvalues	0.517	0.091
Cumulative proportion	0.850	1.000

Overall, our study showed higher morphological variability than that of Harz (1969). Unfortunately, Harz did not give the sizes and origins of his samples; however, we believe that they probably derived from Romania, and represent the *terra typica*. We also noted that most males and females from VBV, but not HRB or PUP, had conspicuously large blackish markings on the lateral pronotum, but exact quantitative data on the presence and size of these are needed (Fig. 1).

Our three study sites differed in Orthoptera species richness. HRB, the 3-ha site with the largest male *P. frivaldskyi*, contains 37 species of Orthoptera (less in PUP: 28 species / 12 ha and in VBV: 17 species / 5 ha). On the other hand, HRB has the lowest *P. frivaldskyi* population size (total population-size estimate is max. 360 males / 3 ha) against highest in PVP (1920 males / 12 ha). At this point we do not know if the morphological differences among populations have genetic or environmental causes. Orthoptera are well known to alter body size and color via phenotypic plasticity in response to many habitat factors (climate, food supply, disease, inter- and intra-specific competition, *etc*. (Bidau & Marti 2008, Chapuis *et al*. 2008, Wason & Pennings 2008, Whitman & Ananthakrishnan 2009).

Discrimination of isolated populations.— In males, both discriminant functions were statistically significant ($\chi^2 = 44.1$, df = 10, p = 0.0001). The first discriminant function (root 1) was weighted most heavily by body weight and wing length. The second function (root 2) seemed to be marked mostly by the variables, length of cercus and length of femur, less by pronotum length. The first function explained nearly 77% of the variance (Table 4). According to total *a priori* classification probability, we could successfully predict the type of population in 85% of all cases, based on five male measurements (lengths of tibia and body did not enter into the model).

To summarize the findings, it appears that the clearest discrimination is possible for male individuals from the HRB population. The first discriminant function is marked by negative coefficients for body weight and length of wings, while the second function is marked by a positive coefficient for the length of cercus and nega-

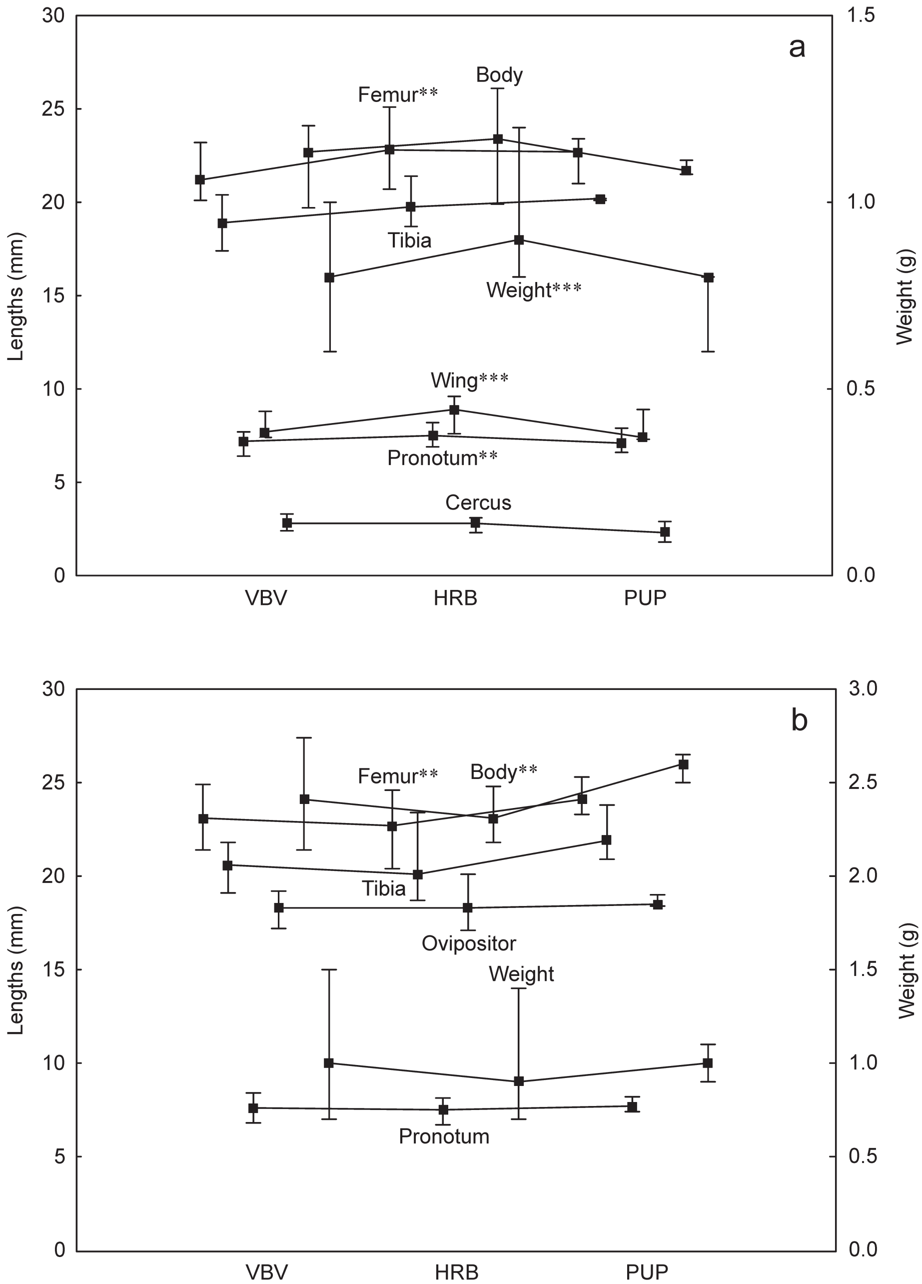


Fig. 2. Comparison of selected morphological traits (medians ± nonoutlier ranges) in males (a) and females (b) among three isolated populations of *P. frivaldskyi* (**, p < 0.01; ***, p < 0.001).

tive coefficients for the length of femur and pronotum (Table 4). Thus, a heavier male with longer traits (wings, femur, pronotum), but not cercus, is likely to be from HRB (Fig. 3a). In females only the first discriminant function (root 1) was significant ($\chi^2 = 21.7$, df = 6, p = 0.001). It was weighted mostly by the lengths of femur and body, accompanied by length of tibia. The function explained around 85% of the variance (Table 4), but we could not reliably predict the type of population (prediction ratio only 60%), based on the three variables entering the model (lengths of body, femur and tibia, Fig. 3b). Hence, in our study, males showed higher morphological divergence than females. Our study mirrors that of Heller *et al.* (2004), who also found that male morphology (wings and cerci patterns) and stridulating frequency enabled discrimination among species of *Isophya* bush-crickets.

In all populations, females were significantly bigger than males for all measurements (Mann-Whitney *U*-test: femur, Z = -3.2, p = 0.001; tibia, Z = -3.8, p = 0.0001; pronotum, Z = -2.2, p = 0.028; body, Z = -3.2, p = 0.001; weight, Z = -3.0, p = 0.002). However, these differences were small, in comparison to some ensiferan species which exhibit much greater sexual size dimorphism (see articles, this volume). Overall, our results corroborate general knowledge about sexual dimorphism patterns in Orthoptera, where size dimorphism tends to be lower in the Ensifera than in the Caelifera (Harz 1969, Ingrisch & Köhler 1998, Cepeda *et al.* 2003).

In conclusion, we find moderate, but significant, variability among some traits, but little or no variability among most traits, when comparing three isolated populations of *P. frivaldskyi* in Slovakia. Multivariate discrimination based on morphological differences suggests the possibility of genetic differences among the populations, which must now be verified, since cryptic species

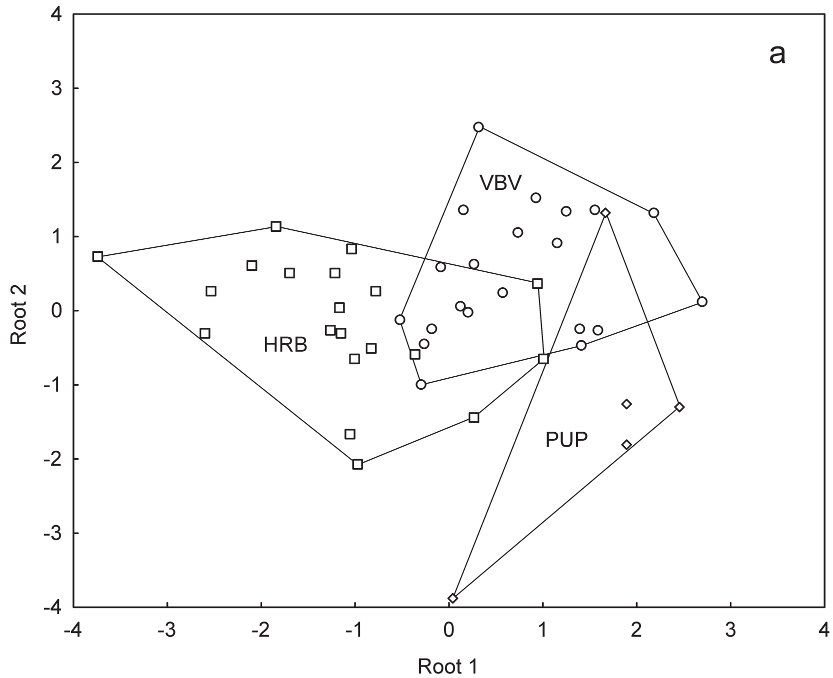
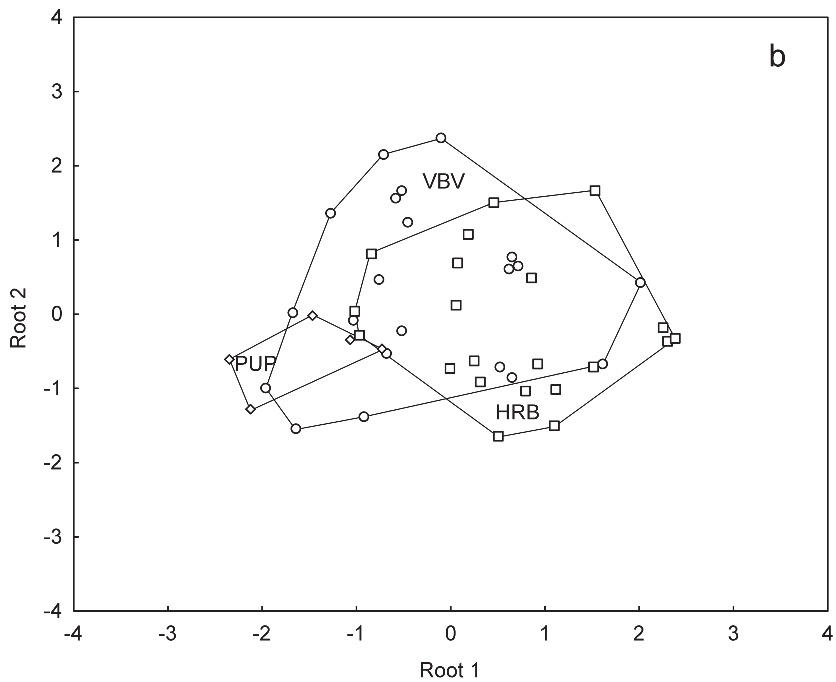


Fig. 3. Discrimination among males (a) and females (b) in three isolated populations of *P. frivaldskyi* in scatterplots of canonical analysis (variables entering models are shown in Table 4).



diversity can be expected. If these exist, they could be an important factor in the conservation of this endangered species.

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