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Variation in Body Size and Body Shape in Ground Beetle *Pterostichus melanarius* Ill. (Coleoptera, Carabidae)

Raisa Sukhodolskaya*

Laboratory of Biomonitoring, State Budgetary Establishment Research Institute for Problems of Ecology and Mineral Wealth Use of Tatarstan Academy of Sciences

Corresponding Author: Raisa Sukhodolskaya

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ABSTRACT

Research into large-scale ecological rules has a long tradition but has received increasing attention over the last two decades. Our knowledge of the determinants and mechanisms which shape spatial patterns in invertebrate traits is still limited. This study analyzes macroecological patterns in traits variation in *P. melanarius* (Coleoptera, Carabidae). Beetles were sampled in 1996 – 2008 in different regions of Russia and the plots differed in anthropogenic disturbance and type of habitats. We measured six morphometric traits of nearly 3000 specimens and used linear models and General Procrustes Analysis to investigate how different environmental factors contributed to the body size and shape variation. Our results showed that all environmental variables (region, anthropogenic disturbance, vegetation, landscape features) contributed significantly into the size and shape variation in *P. melanarius*. The significant Sex^{x}Environmental Factors interactions indicated a divergence of sexual size and shape dimorphism in different regions and under different anthropogenic disturbance. Various traits in *P. melanarius* had different latitude gradients: variation of elytra length both in males and females followed converse Bergmann rule, variation of pronotum size had no any direction, variation of head size followed Bergmann rule. Urban and suburban conditions decreased beetles elytra but increased their head

Keywords: *Ground Beetles; morphometry, environmental factors, sexual size and shape dimorphism.*

INTRODUCTION

Several parameters, from physiological processes to environmental pressures, play a role in determining the body size and related morphological parameters in insects. Among a wide range of factors, ontogenesis, biomechanical constraints, sexual selection, fecundity, size-specific predation, resource quality and availability, overcrowding, competition and temperature have often been reported as the most prominent ones (Berven, Gill, 1983; Juliano, 1985; Wheeler, 1996; Angilletta, 2003). Most of these factors may vary from one habitat to another and geographic variation in body size has thus been studied extensively (Chown, 2003; Boggs, 2005). At a large geographic scale, clinal variation of morphological parameters within species from different taxa has been found (Hallas, 2002; Blanckenhorn, 2004). The nature of such variation has been addressed frequently along altitudinal and/or latitudinal climatic gradients (Blanckenhorn, 2006; Arthur, 2008). The importance of examining variation of morphological traits was recently re-emphasized because these traits (i) are used extensively for taxonomy, (ii) are partially under genetic control, (iii) are the target of selection, and (iv) reflect intraspecific clinal divergence (Sota, 2007). Moreover, variation in morphology can exhibit clear patterns of differentiation that molecular markers can not detect (Nice, Shapiro, 1999).

In this aspect the studies in Ground Beetles are relatively few. Most of them concern the variation of body size in carabid assemblages where authors divide species pool into several classes – small, middle and large. In the same way researchers describe the clinal variation of body size in carabids (Homburg, 2012). The intraspecific variation of body size in carabids is investigated very poorly. Articles on this subject are not supported by sufficient statistical analysis so that sometimes it is hard to understand what factor impacted beetles body size in certain research (Dorofeev, 2009; Budilov, 2012).

The primary purpose of this paper is to examine variation of body size and shape in Ground Beetle *Pterostichus melanarius* Ill. (Coleoptera, Carabidae) and to clarify environmental factors which determine this phenomena.

MATERIALS AND METHODS

Collection sites and insect sampling. Wild specimens of P. melanarius were sampled in 1996 - 2006 in different provinces of Tatarstan Republic (53 sites). Material from other regions of Russia were kindly.

presented to us from our colleagues from Perm, Kemerovo, Stavropol, Udmurtia Universities and Visim Reserve. The localization of these regions is shown in Table 1 and Figure 1.

Table 1. Sampling localities and number of specimen of P. melanarius used in the morphological analysis

	Region	Latitude, ºN	Longitude, ºE	Number of sites	Type of habitats*	Sample size
1	Stavropol region	45°02’	41°55’	6	Meadow, birch	105
2	Tatarstan Republic	55°47’	49°06’	53	Meadow, birch, oak, elm	1993
3	Mari El Republic	56°42’	47 52’	14	Meadow, birch, oak	237
4	Udmurtia Republic	57°17’	52°45’	16	Birch, oak, elm	109
5	Cis_Ural	57° 01’	57°9’	21	Birch, oak, elm	126
6	Sverdlovsk region	58°42’	61°20’	6	Meadow	136

the prevailing type of vegetation is pointed

Figure 1. Sampling localities of *P. melanarius* (numbers). See Table 1 for locality numbers

Study organism. P. melanarius is a very prolific and widespread European beetle that is introduced to the North America. It occurs in open habitats (meadows, agricultural ones) and in all types of forests and gardens as well (Thomas, 1998; Sukhodolskaya, 2007; Fournier, 2011). Generalist, zoophagous, autumn breeder (Sharova, 1981; Kryzhanovskij, 1995).

Morphometric analysis. All measurements were made with a Leitz RS stereoscopic dissecting microscope at a magnification of 10 diameters, using a calibrated ocular grid with a scale interval of 0.1 mm. For each of specimens six variables were measured, including: elytra length and width.

pronotum length and width, head length and distance between eyes (Figure 2)

Figure 2. Illustration of measurements: 1-2 – elytra length, 3-4 – elytra width, 5-6 – pronotum length, 7-8 – pronotum width, 9-10 – head length, 11–12 – distance between the eyes

Statistical analysis. All dimensions (in millimeters) were $\log_{10}$ transformed to ensure normality. All statistical analyses of the morphometric data were performed using R programs (. R Development Core Team …., 2011).Linear models were used to reveal how different environmental factors affected morphometric traits. The models like these give the possibility to identify the influence of each factor in its range (McCulloch, 2008). Thus, in our case we estimated the contribution of area, anthropogenic disturbance, type of habitat and landscape features into the traits variation in *P. melanarius*. In other words, these variables were considered independent. The contribution of other factors was considered to be random and was summarized as the error of the model. All variables were modeled as categorical using treatment contrasts. As the base (reference) level we used: for regional aspect – Tatarstan as the center of the area, for anthropogenic disturbance – natural cenoses (minimal anthropogenic affect), for habitat type – birch forests (the most favourable habitat for *P. melanarius* reproduction), for landscape features – watersheds (the lands without floods and isolation from mainland). The contributions of area (signed as "region" in tables and "@" in figures in the main text), anthropogenic disturbance ("anthropogen" and "%"), habitat type (habitat" and "$") and landscape features (Isolation" and "*") were considered to be additive and independent. The influence of the listed factors was considered to be different in males and females, besides the affect of sex was taken into account too. In other word the model included sex and its interaction with every listed factor. For example, the model which estimated the variation of elytra length was recorded as follows (using the R syntax): **** Elytra.Length~fSex/(fRegion+fAnthropogen+fHabitat+fIsolation), where fSex – the factor.

representing sex, fRegion- factor, representing the area etc. Variance analysis (ANOVA) of models was used for factors significance test. We estimated the contribution of all variables and their interactions for every trait and pointed confidence intervals (using Student criteria) and residual statistics (errors). Received values and their confident intervals were used to present results in figures and tables: interactions were compared with corresponding base levels (the 95% confident level was used for the normal approximation). Besides the confidence intervals for the additive effects of sex and certain variables were displayed.

For the purposes of shape analysis 12 landmarks were recoded on the beetles body (Fig. 2). These landmarks were chosen for their ability to capture the overall shape of the beetles body. The specimens were scaled to unit centroid size and their landmarks configurations were aligned according to the best overall fit, using the Generalized Procrustes Analysis (GPA) in R and shape variables were obtained as the partial warp scores and uniform component. Centroid size was also calculated and retained for each specimen. To describe shifts in shape under different environmental factors we performed a relative warp analysis (a principal component analysis of the weight matrix) and examined the pattern of shape variation under different environmental effects. Thin-plate spline deformation grids for certain factor effect were generated to facilitate description of shape variation in differing environmental conditions. Additionally, shape variation under differing environmental factors was represented by the matrix of Procrustes distances.

RESULTS AND DISCUSSION

Variation in size.As the example of variation of studied morphometric traits in P. melanarius we present at first the Table 2. Similar tables were obtained for the other studied traits. On their basis we formed the figures (Fig. 3). They showed the real means of body size traits in P. melanarius under various environmental factors. Factor “Sverdlovsk” contributed in the way that elytra length and pronotum size decreased both in males and females. These changes were accompanied by increased elytra width and head size. Factor “Udmurtia” significantly decreased elytra length, but factor “Stavropol” acted in the opposite way. Factor “Stavropol” increased pronotum width in both sexes and the head length. Factors “Cis-Ural” and “Mari El” affected in the same way. As we considered Tatarstan to be the center of the area we concluded that in eurytopic P. melanarius elytra length decreased towards the high latitudes but pronotum width and head dimensions increased toward the area periphery.

Factor “Urban” decreased elytra length in both sexes and factor “Suburban” – only in females. In these conditions elytra width increased in both cases. In urban environment males pronotum was significantly smaller but head width was larger. Factor “Suburbs” decreased females pronotum width, but increased head size in both sexes.

Contribution of vegetation into the traits variation in P. melanarius was seen clearly: in open habitats (meadows) traits means were practically the same as in the base “birch” excluding head length of the beetles. In shadowy habitats (elm, oak, lime) traits means in majority cases decreased.

Landscape factors (isolation on islands, floods in lowlands) in most cases increased traits means, especially head size. We counted all statistically significant shifts in traits means under various environmental impacts in order to determine whether traits variation in P. melanarius were in agreement with Bergmann rule (Fig. 4). Variation of certain traits in P. melanarius differed: variation of elytra length both in males and females followed converse Bergmann rule, variation of pronotum size had no any direction, variation of head size followed Bergmann rule.

Variation in shape. An analysis of variance indicated that sex as well as factors “Region”, “Antrop”, “Habitat” had significant effect on centroid size (Table 3). Moreover, the significant Sex^{x}Habitat and Sex^{x}Isolation interactions indicated a divergence of sexual size dimorphism in different habitats and different landscapes. MANOVA results indicated significant effects of sex and all environmental factors on beetles shape. Highly significant “Sex”^{x}Environmental factors interaction suggested that sex dimorphism in P. melanarius differed considerably in various environment. Allometry contributed to variation in beetles shape (significant main effect of centroid size), but there appeared to be differences in the allometric patterns among beetles in differing environmental conditions (Table 4). Patterns of shape variation under different environmental effects in females and males of P. melanarius are presented in Fig 5.

Discussion. When choosing the methods researchers usually are orient to the main factors that might affect traits variation in certain species. Naturally the range of these factors is very wide. Our study is devoted to Ground Beetles. Thus we have selected four main environmental factors that might affect body size and shape variation in carabids. First, variation over the area (or geographic variation). Patterns of latitudinal or altitudinal variation in body size are common in animals (Chown, 2003; Ashton, 2004; Cabanita, Atkinson, 2006; Blanckenhorn, 2007). Comparative studies show that arthropod species feature a range of relationships of body size with latitude within species. Both Bergmann size clines, showing increased body size at higher latitudes, and converse Bergmann clines, showing decreased body size at higher latitudes, are about equally common (Nylin, 1991; Mousseau, 1997; Chown, 1999; Telfer, 1999). Generation time relative to season length is a crucial parameter in determining which rule applies. Species with long development times relative to season length consequently have only one generation per year, such as the water strider Aquarius remigis, are more prone to experience end of season time constraints (and thus exhibit converse Bergmann clines) than multivoltine species with short generation time and many generations per year, such as Drosophila melanogaster (Blankenhorn, 1995; James, 1997). If the different proximate mechanisms causing Bergmann and converse Bergmann clines instead interact multiplicatively, at least theoretically dome-shaped clines could also occur (Johansson, 2003).

In the their excellent review W. U. Blanckenhorn and M. Demont (2004) conclude that Bergmann and converse Bergmann size clines are not mutually exclusive, in principle they can operate in conjunction and may cancel each other to varying degrees if they interact additively. To our great regret carabids were noted in this review only once where ground beetle Carabus nemoralis showed converse body size clines. The converse Bergmann rule in carabids was also confirmed in another research, where Thalassotrechus barbarae decreased body size towards the northern latitudes (Evans, 1997). Recently the interest to large-scale ecological rules has received increasing attention and there has been shown that body size of carabid beetles increased from northern towards southern Europe and then decreased towards North Africa (Homburg, 2012), but this research has been done on assemblages level.

Table 2. Results of Linear modeling the effects of environmental factors on elytra length in P. melanarius

Factor	Contribution of factor into the trait shift					
	Females			Males		
	Confidence interval limits		Mean of the shift	Confidence interval limits		Mean of the shift
	Left 2,5%	Right 97,5%		Left 2,5%	Right 97,5%	
Sverdlovsk	-0.74	-0.55	-0.65	-0.56	-0.32	-0.44
Udmurtia	-0.69	-0.38	-0.54	-0.54	-0.15	-0.35
Mari El	-1.18	-0.68	-0.93	-1.25	-0.65	-0.95
Cis-Ural	-0.31	0.45	0.07	-0.44	0.13	-0.16
Stavropol	-1.03	0.33	-0.35	0.04	1.74	0.89
Urban	-0.77	-0.37	-0.57	-0.79	-0.39	-0.59
Suburban	-0.72	-0.34	-0.53	-0.42	0.12	-0.15
Meadow	0.03	0.36	0.2	-0.37	0.11	-0.13
Elm	-0.42	-0.23	-0.33	-0.35	-0.07	-0.21
Oak	-0.11	0.07	-0.02	-0.25	0.02	-0.12
Lime	-0.1	0.41	0.16	-0.3	0.18	-0.06
Island	-0.4	-0.14	-0.27	-0.16	0.22	0.03
Lowland	-0.11	0.06	-0.02	-0.04	0.24	0.1

Intraspecific latitudinal variation of body size in Ground beetles has been studied only in a few papers. For Carabus granulatus and P. melanarius there has been shown that these species body size decreased towards the North (Philippov, 2008). At the same time in another paper the authors concluded that these species body size were depended mostly on season length (Timofeeva, 2010). Large-scale estimation of body size variation in another carabid species – Carabus cancellatus – showed that different beetles traits had different type of latitudinal variation: variation in elytra and pronotum followed converse Bergmann rule but width traits increased in high latitudes (Sukhodolskaya, 2011).

Our research showed that different traits in P. melanarius had different latitude gradients: variation of elytra length both in males and females followed converse Bergmann rule, variation of pronotum size had no any direction, variation of head size followed Bergmann rule. Beetles shape variation in area reflected to our mind distribution of resources in area. The latter is considered to be more available in the center of area – Tatarstan.

Anthropogenic impact on intraspecific body size variation in Ground Beetles is studied very poorly. There has been shown that body size in Carabus nemoralis, Carabus aeruginosus decreased in the gradient of urbanization (Weller, 2003; Timofeeva, 2008), but how much factor “urbanization” contributed into the size variation was not clearly estimated. In our study various traits responded differently to the urban or suburban conditions. Enlarged head in urban and suburban conditions seemingly referred to the increased searching activity because beetles in urban and in suburban conditions often suffer from the lack of nutrients.

Impact of vegetation on carabids traits size varied. For example, the beetles P. melanarius from elevated oak forest were heavier than from the same biotope in lowland (Gryuntal, 2010). Our results did not confirm this paper. On the contrary, beetles pronotum and head became larger in lowlands. According to some authors habitat features contributed into the body size variation in carabids (Lenski, 1984; Erikstad, 1989; Gordienko, 2001).But carabids are predators and to our mind the variation in intraspecific body size is affected mainly by an abundance of their preys but not of the habitat vegetation.

CONCLUSION

Environmental factors (latitude, anthropogenic disturbance, habitat and landscape features) contribute significantly into the size and shape variation in Ground Beetle P. melanarius. Various traits change in different ways in latitudinal and urban gradients. In open habitats (meadows) traits means were practically the same as in the base “birch” excluding head length of the beetles. In shadowy habitats (elm, oak, lime) traits means in majority cases decreased. These facts must be taken into attention when new subspecies (or even species) are described. It happens very often that taxonomists present new species having data on the only several traits deviations from “standard type” and does not pay attention to the tremendous amount of variation in nature.

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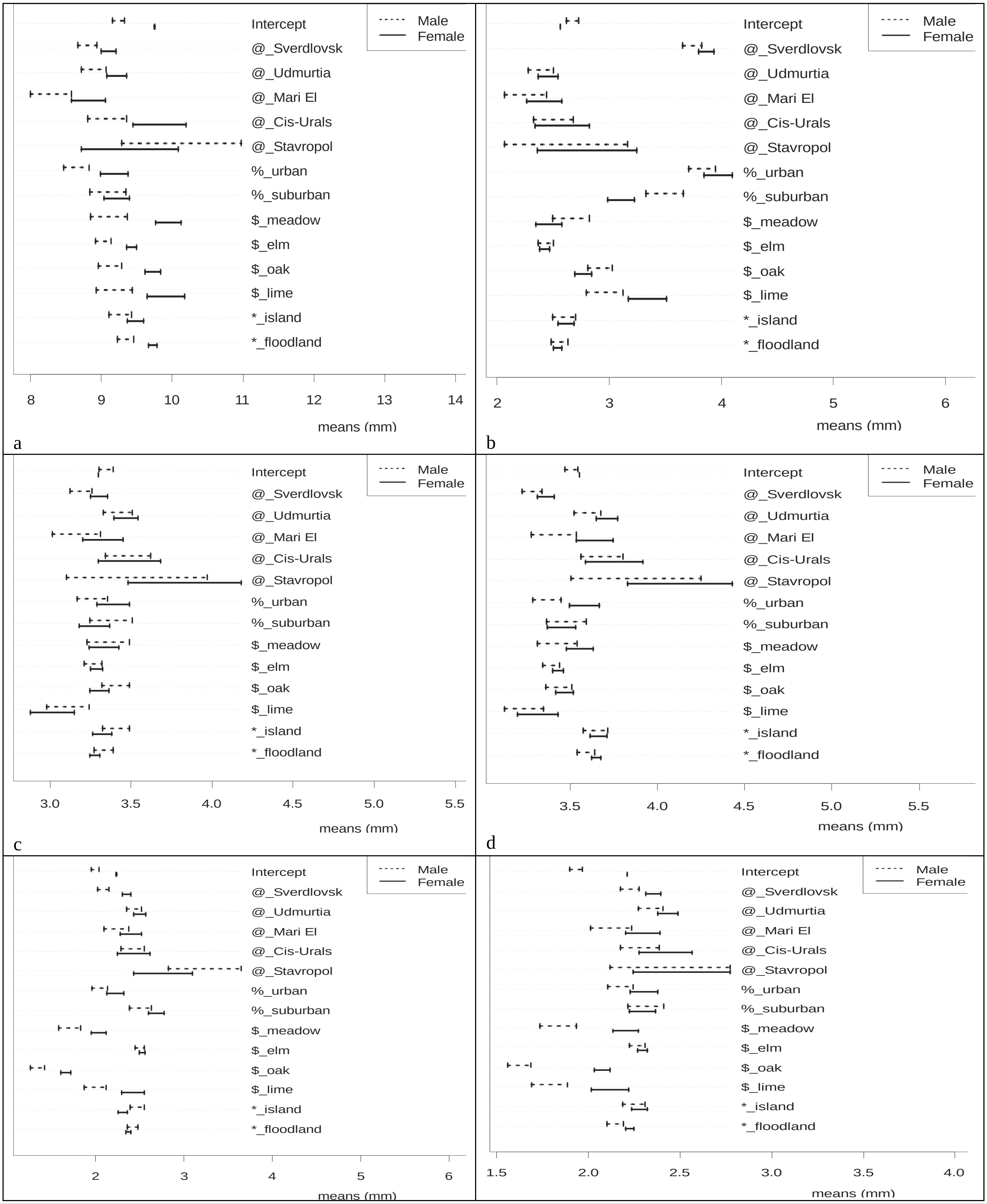
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means (mm)

e	f

Figure 3 Contribution of environmental factors into morphometric traits variation in P. melanarius: a – elytra length, b – elytra width, c – pronotum length, d – pronotum width, e – head length, f – distance between eyes (signed as "@" – the contribution of area, "%"- anthropogenic disturbance, "$" – type of vegetation, "*" – landscape features)

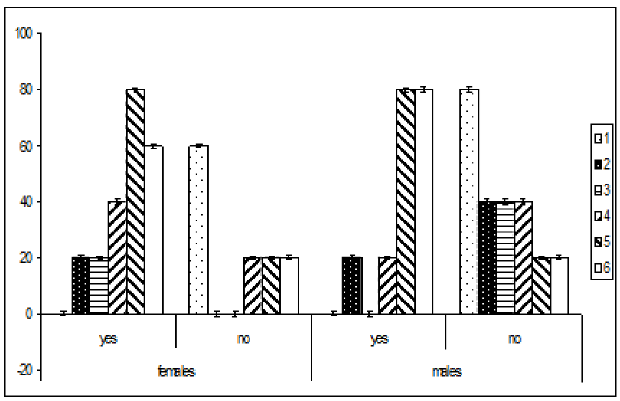


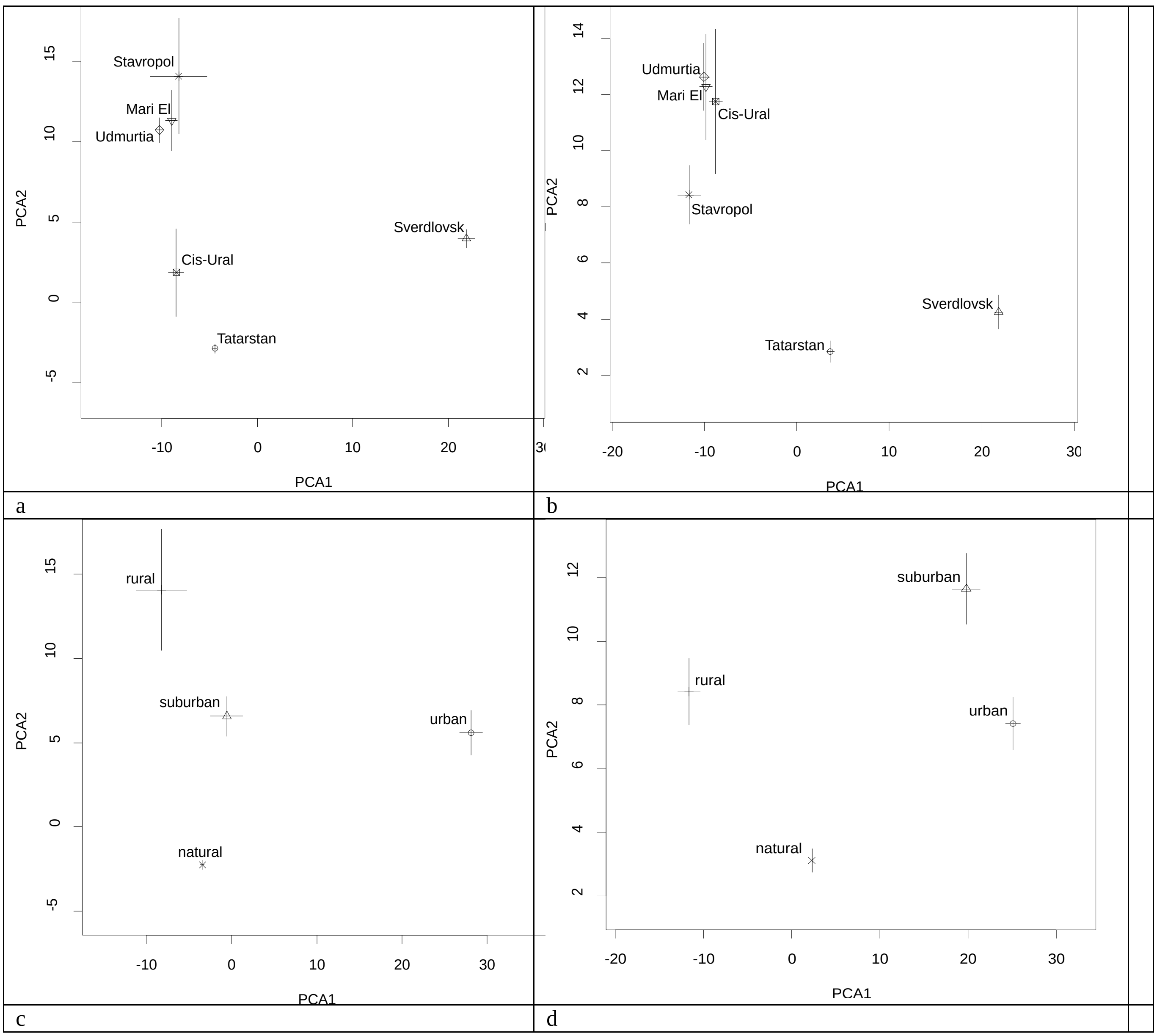
Figure 4. Number of statistically significant shifts in body size traits which follow (signed as "yes") or do not follow Bergman rule (signed as "no") in latitudinal variation of P. melanarius (1 – elytra length, 2 – elytra width, 3 – pronotum length, 4 – pronotum width, 5 – head length, 6 - distance between eyes.

Table 3. The effect of sex, environmental factors and their interaction on centroid size: Results of the analysis of variance (ANOVA)

Effect	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Sex	1	161465	161465	216.1065	< 2.2e-16	***
Region	5	42084	8417	11.2652	8.812e-11	***
Antrop	2	7398	3699	4.9511	0.0071341	**
Habitat	4	14173	3543	4.7423	0.0008166	***
Isolation	2	1290	645	0.8634	0.4218210	
Sex x:Region	5	2476	495	0.6628	0.6517099	
Sex:xAntrop	2	3378	1689	2.2609	0.1044346	
Sex:xHabitat	4	43030	10758	14.3981	1.200e-11	***
Sex:xIsolation	2	4601	2300	3.0788	0.0461627	*
Residuals	2984	2229514	747			

Table 4. The effects of sex, environmental factors and their interaction on beetles shape, tested by multivariate analysis of variance (MANOVA)

Effect	Df	Wilks	approx F	num Df	den Df	Pr(>F)	
Csize	1	0.84120	280.43	2	2971	< 2.2e-16	***
Sex	1	0.82876	306.93	2	2971	< 2.2e-16	***
Region	5	0.39317	353.44	10	5942	< 2.2e-16	***
Antrop	2	0.41494	820.62	4	5942	< 2.2e-16	***
Habitat	4	0.84866	63.51	8	5942	< 2.2e-16	***
Sex:Region	5	0.98693	3.92	10	5942	2.432e-05	***
Sex:Antrop	2	0.94225	44.85	4	5942	< 2.2e-16	***
Sex:Habitat	4	0.97975	7.64	8	5942	3.223e-10	***
Sex:Isolation	4	0.99119	3.29	8	5942	0.0009281	***
Csize:Region	5	0.94736	16.28	10	5942	< 2.2e-16	***
Csize:Antrop	2	0.98011	15.00	4	5942	3.368e-12	***
Csize:Habitat	4	0.99898	0.38	8	5942	0.9326996	
Residuals	2972						



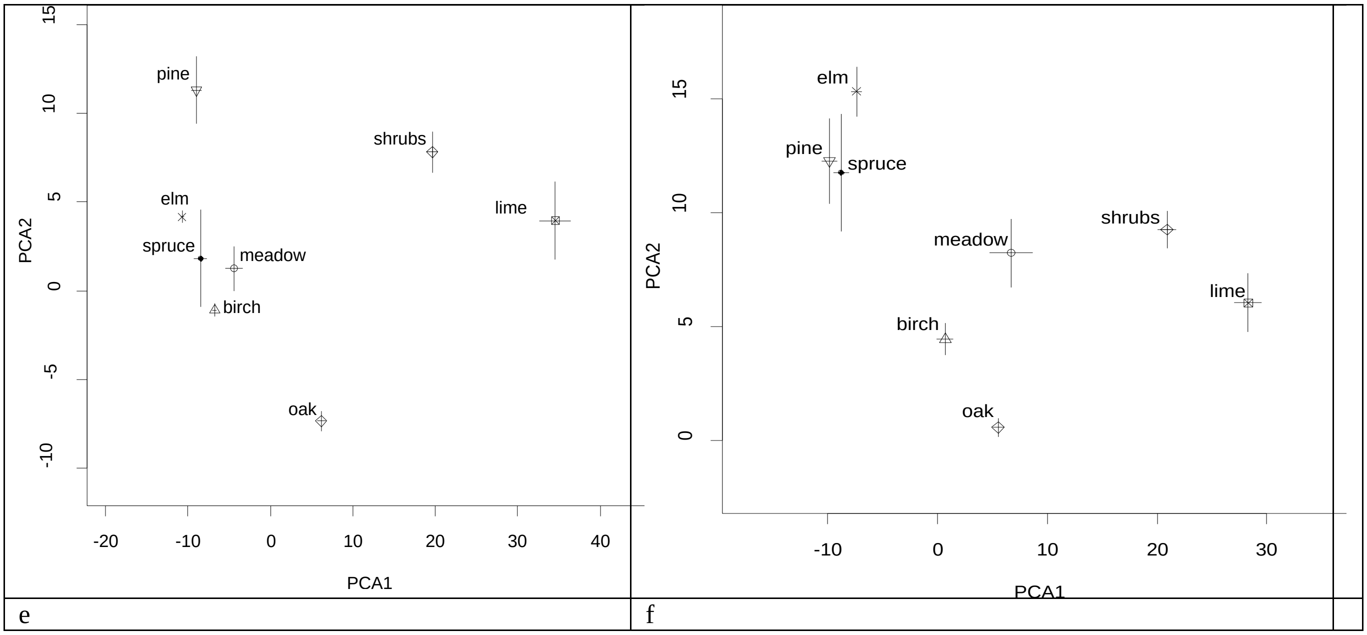


Figure 5. Results of the relative warp analysis (a principal component analysis of the weight matrix) when analyzing effect of environmental factors on body shape shifts in P. melanarius. a – effect of area to females, b – the same to males; c – effect of habitat disturbance to females, d – the same – to males; e – effect of habitat vegetation to females, f – the same – males

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