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Body Size Variation of Ground Beetles (Coleoptera: Carabidae) in Latitudinal Gradient

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Abstract

Background and purpose: *Despite plenty of data, papers on latitudinal intraspecific body size variation in insects are scarce and in Ground Beetles are absent at all. The aim of this research was to: (i) model the effect of the latitude into the body size variations in widespread carabid species; (ii) describe elytra length variation and body shape variation in latitude gradient in studied species of Ground Beetles.*

Material and methods: *Six carabid species from different provinces of Russia (situated on different latitudes) were analyzed for six morphometric traits. We used linear models to quantify contribution of provinces latitude to traits variation. We applied relative warp analysis (a principal component analysis of the weight matrix) when analyzing effect of latitude on body shape deviation in studied carabid species.*

Results: *Different traits of certain species varied in differing ways under the influence of the same environmental factor. In three* Carabus *species and* Pterostichus niger *elytra length decreased towards the high latitudes,* Pterostichus melanarius *demonstrated saw-tooth elytra length variation in latitude gradient and* Poecilus cupreus *– the counter-gradient one.*

Conclusion**:** *Closely related species of carabids could act very differently, each individual species following or countering Bergmann's rule in its own way. Explanation that takes into account the natural history, climatic correlations and sexual size dimorphism is needed to assess the observed contrasting geographic patterns and differences between species, morphometric traits and sexes, since size clines (e.g. Bergmann's clines) may obey to multiple selection pressures.*

INTRODUCTION

Body size and body parts proportions tend to follow some ecogeographical patterns, such as Bergmann's or Allen's rules. Those empirical postulates were originally formulated for endotherms, but subsequent work showed that ectotherms, either vertebrate or invertebrate, may show geographic body size patterns that sometimes do agree with the rules' predictions *(1, 2, 3)*. The literature on ecogeographical rules, both in endotherms and ectotherms, is abundant and the subject has received considerable attention in recent years *(4, 5, 6)*. In the case of ectotherms either invertebrate or vertebrate, several hypotheses concerning body size variation have also been proposed, reflecting the evidence that some groups follow Bergmann's and Allen's rules, some show converse or compound patterns, and some do not show any pattern at all. Converse Bergmann's clines are much more frequent in ectotherms than

Table 1. *Sampling localities and sample size*

	Region	Latitude, °N	Longitude, °E	Number of sites	Type of habitats	Sample size
1	Stavropol region	45°02’	41°55’	6	Meadow, birch	76
2	Kemerovo region	54°56’	87°14’	20	Meadows, birch, lawn	1954
3	Novosibirsk region	55°27’	79°33’	14	Meadows, farmlands	360
4	Tatarstan Republic	55°47’	49°06’	53	Meadow, birch, oak, elm	11312
5	Maiy El Republic	56°42’	47 52’	14	Meadow, birch, oak	67
6	Udmurtia Republic	57°17’	52°45’	16	Birch, oak, elm	396
7	Cis_Ural	57° 01’	57°9’	21	Birch, oak, elm	58
8	Sverdlovsk region	58°42’	61°20’	6	Meadow	458

in endotherms, especially in insects *(2, 3, 7)*. Body size in insects probably obeys to different ecophysiological factors and evolutionary pressures than those in endotherms. Several authors have proposed, that size clines result from climatic selection on the duration of egg and nymphal development which indirectly affects body size and can produce different geographic patterns according to the nature of the life cycle *(8, 9, 10)*.

When revealing the mechanisms of clinal variation arising, several factors must be taken into account. A systemic review of the known literature on inter- and intraspecific variation in insect size along latitudinal or altitudinal clines was done to see how often such clines appeared and if they reflected class-wide, species-specific, or experimentally biased tendencies *(11)*. Nearly even numbers of studies showed Bergmann clines and converse Bergmann’s clines, where insects get smaller as latitude/altitude increases. In fact, the majority of studies suggested no clines at all. Small ranges may have obscured certain clines, while giant ranges may have introduced artifacts. Researchers examining interspecific patterns found clines less frequently than those examining intraspecific patterns due to variation among species within the clades, which renders interspecific studies unhelpful. Bergmann’s rule does not apply to hexapods with nearly the same consistency as it does to endothermic vertebrates. The validity of Bergmann’s rule for any group and range of insects is highly idiosyncratic and partially depends on the study design *(11)*. M. Shelomi concluded that studies of „Bergmann’s Rule“ should focus within species and look at widespread but contiguous populations to account for all sources of variation while minimizing error.

Thus in our study we tried to design investigations in the way to obtain data that will allow us to reveal intraspecific body size variation in carabid populations sampled in different areas of large provinces of Russia (cities and their suburbs, natural cenosis with different vegetation). We studied elytra length variation in latitudinal gradient in six carabid species, taking into account all published and newly analyzed results.

Figure 1. *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).*

MATERIAL AND METHODS

Collection sites and insect sampling. The material from 8 large provinces have been analysed (Table 1). Wild specimens of carabids were sampled in different provinces of Tatarstan Republic (53 sites) from 1996 till 2012. For the sake of this research, specimens from other 7 provinces of Russia were kindly presented to us from our colleagues from Perm, Kemerovo, Stavropol, Udmurtia, Mariy El Universities, Institute of Systematic and Zoology UD RAN and Visim Reserve and we measured those beetles ourselves (Table 1). Sample size of studied species varied from one site in each province to another, but was not less than 100 specimens per species. In Tatarstan we tried to sample beetles in their usual habitats, that were mainly similar between studied regions for all studied species as well as our collegues from other provinces. Beetles in every province were pitfall trapped in natural biotopes, cities, suburbs and arable lands. Details on sample sizes are given in table S1 as supporting material.

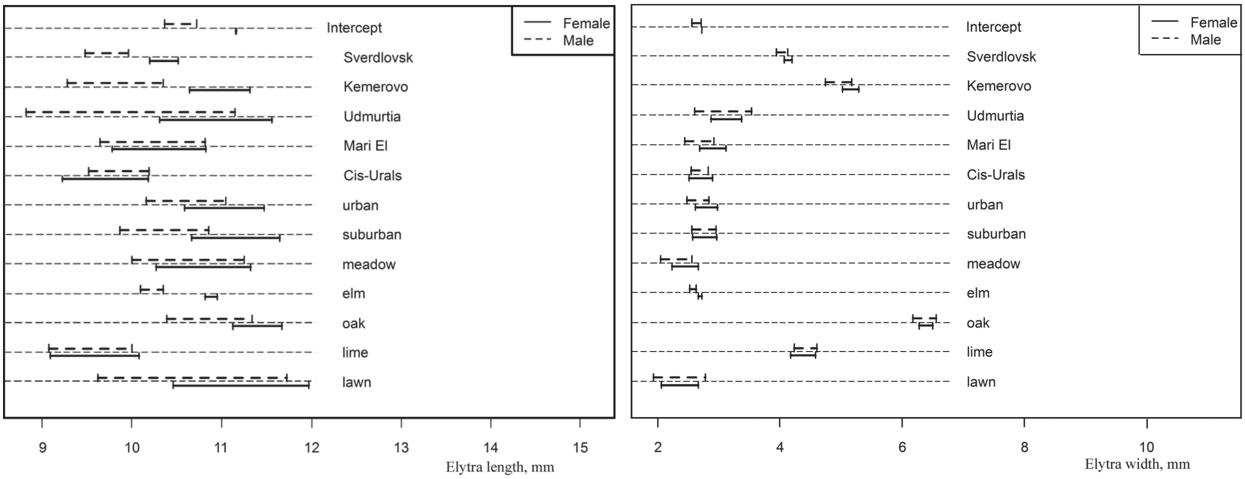


Figure 2. *Effect of environmental factors into elytra variation in P. niger: a – elytra length, b – elytra width.*

Study organisms. We analyzed six carabid species: *Carabus (Carabus) granulatus* Linnaeus 1758, *Carabus (Tachypus) cancellatus* Illiger 1798, *Carabus (Oreocarabus) hortensis* Linnaeus 1758, *Pterostichus melanarius* Illiger 1798, *Pterostichus niger* Schaller 1783, *Poecilus cupreus* Linnaeus 1758. All of them are widespread in Paleartic, generalists, zoophagous and mesophilous.

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 specimen six variables were measured, including: elytra length and width, pronotum length and width, head length and distance between eyes (Fig. 1). Mentioned points were used as landmarks in Procrustes analysis.

Statistical analysis. All statistical analyses of the morphometric data were performed using R system (12). In this paper we present profound analysis of the one species – P. niger. At first we formed data set, coding each specimen for the province and region, where it was sampled and for other environmental factors. The list of variables and codes used in each column are presented as supporting material in Tables S2 and S3. Then we used linear models to reveal, which factor (province, anthropogenic or habitat type) affected significantly to traits variation. 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), where fSex – the factor, representing sex, fRegion-factor, representing the area, etc. Variance analysis (ANOVA) of models was used for effects significance test. We estimated the effects for all variables and their interactions for every trait and confidence intervals (using Student criteria) and residual statistics (errors). Results were presented as estimated effects and their confidence intervals were used to present modeling results in figures and tables; interaction effects were compared with that of the base of comparison (the 95% confidence level and a normal approximation was used). Besides the confidence intervals for the main effects of sex, some other variables were also displayed. Modeling results in *P. niger* are shown as supporting information in table S4. Table S5 shows the impact of studied factors to elytra length variation.

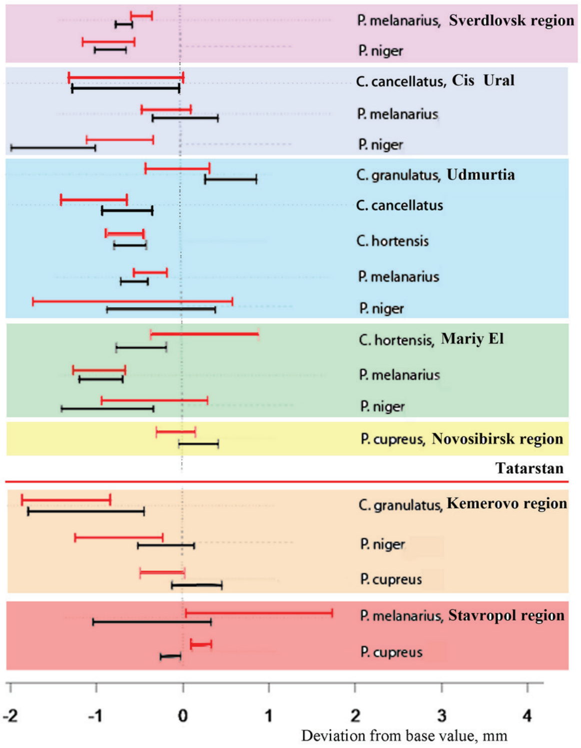
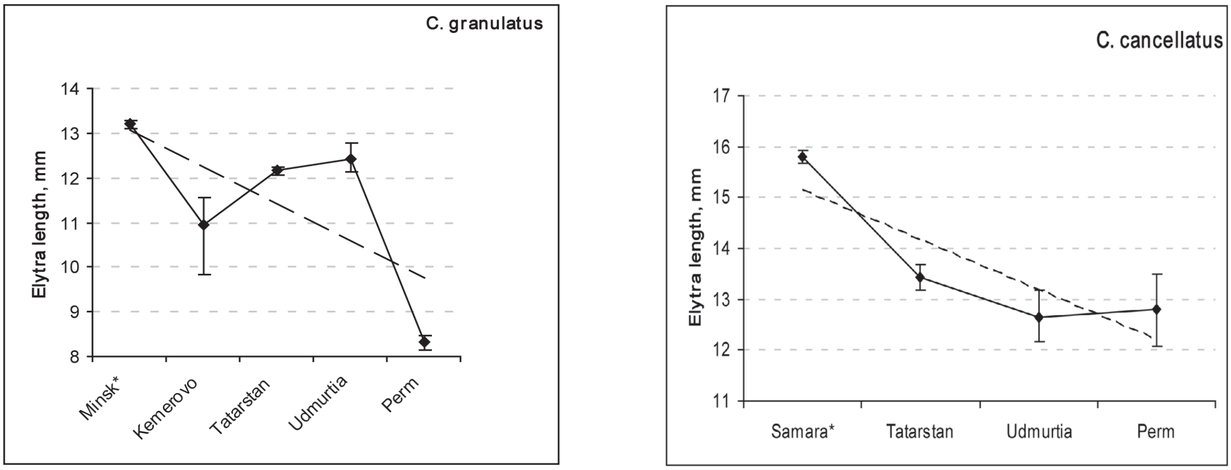


Figure 3. *Effect of latitude into the elytra length variation in different species of carabids; the vertical dotted line denotes the normalized basic means of elytra length in concrete species in the centre of its area; each region has its own color, colors change in rainbow turn – from the bottom (low latitudes, red color) to the top (high latitudes, violet color): – females, – males.*

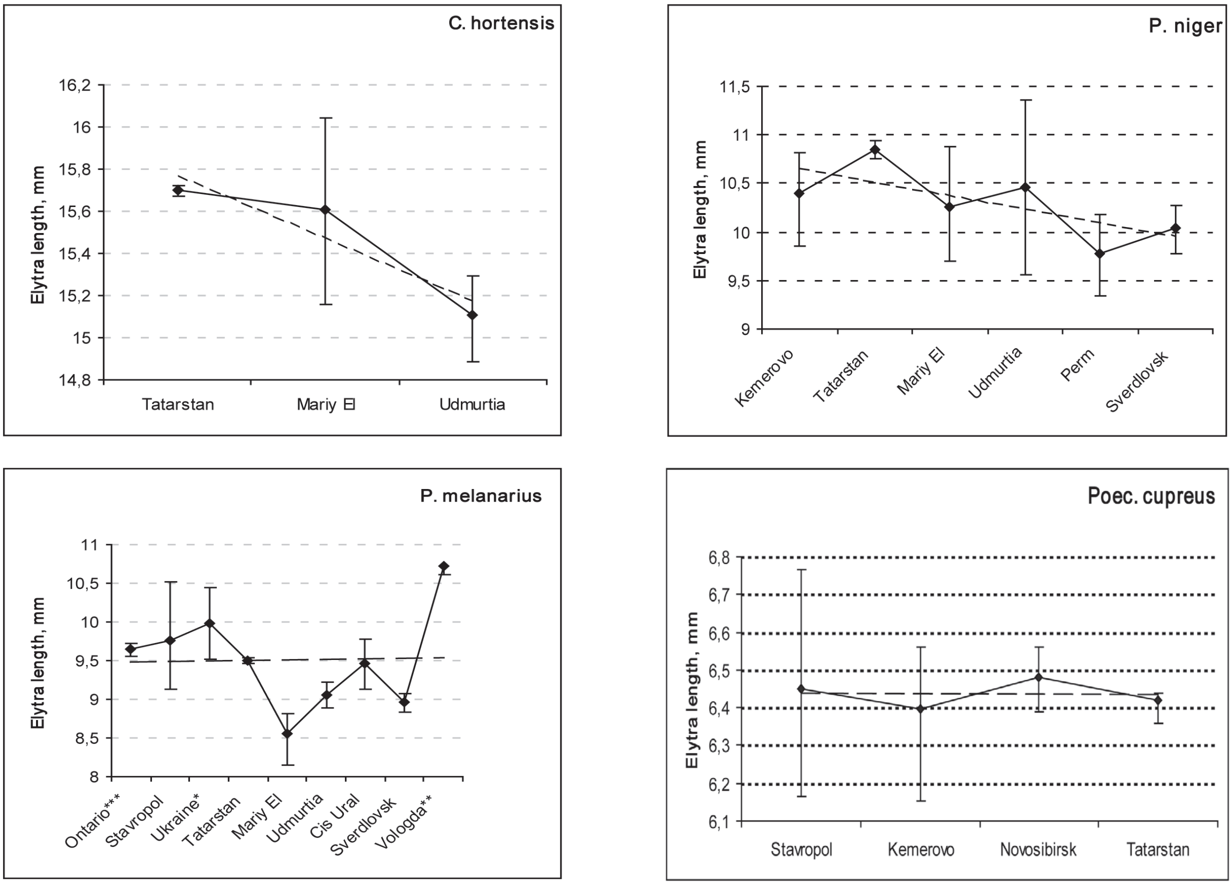
The other five species had been treated in the same way and results had been published earlier *(13, 14, 15, 16, 17)*. In this paper we discuss results only how latitude contributed to the elytra length variation

For the purposes of shape analysis 12 landmarks were recorded on the beetles body (Fig. 1). These landmarks were chosen for their ability to capture the overall shape of the beetles' body. The specimens were scaled to unit



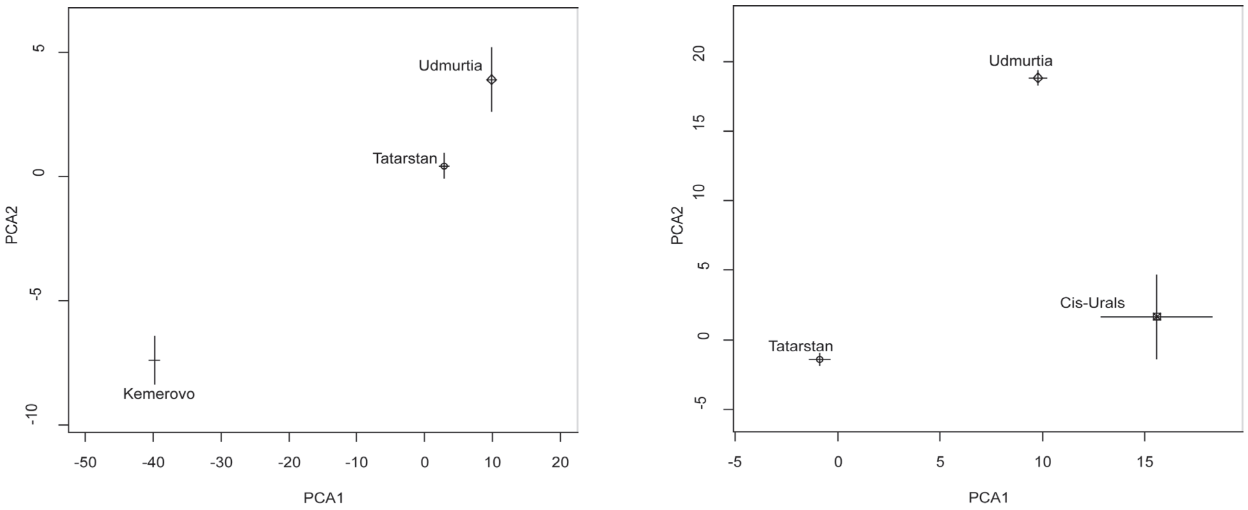
* – data was taken from M.L.Minetz, V. V. Grichik *(18)*

* – data was taken from I. N. Isaeva *(19)*

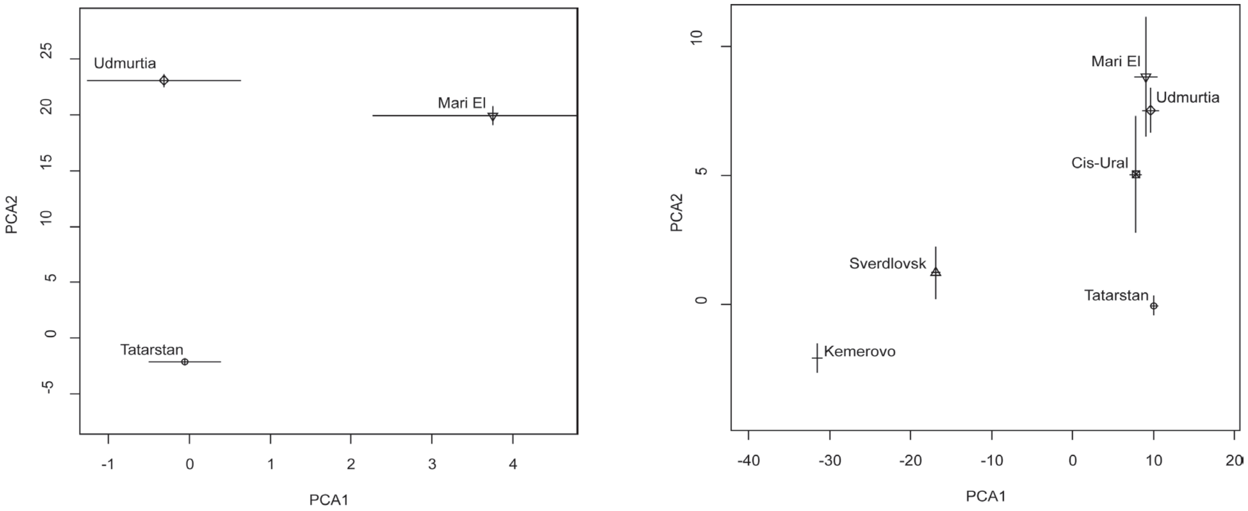


* – data was taken from V. V. Brygadyrenko, O. V., Korolev *(20)*, ** – the same – from Y. N. Belova *(21)*, *** – the same – from S. L. Kallio *(22)*

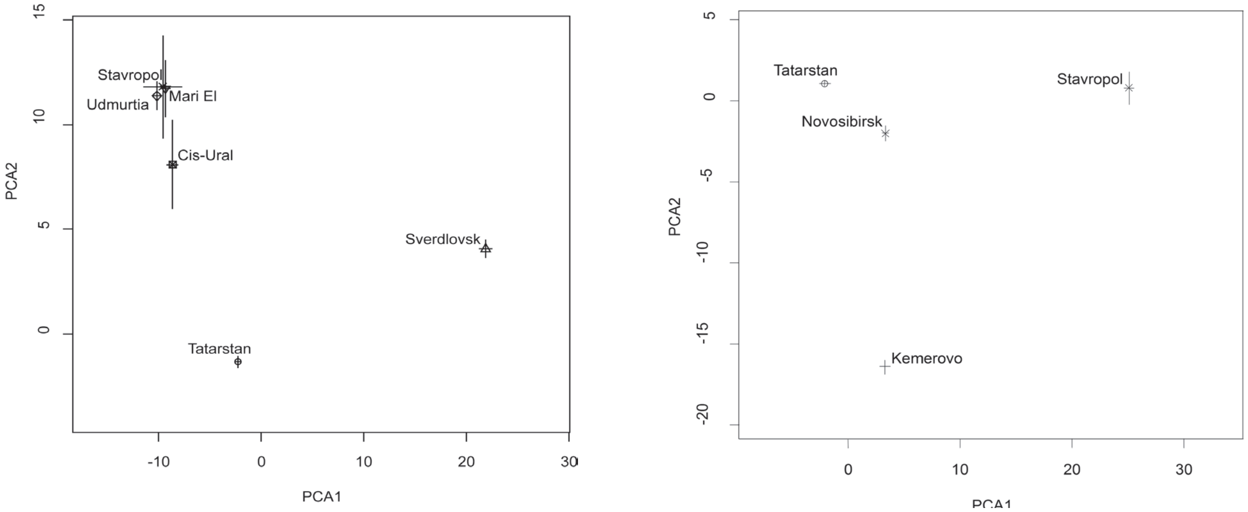
Figure 4. *Elytra length variation in latitudinal gradient (from left to right in the images = from low latitudes towards high latitudes; --- – linear trends).*



C. granulatus *C. cancellatus*



C. hortensis *P. niger*



P. melanarius *Poec. cupreis*

Figure 5. *Results of the relative warp analysis (a principal component analysis of the weight matrix) when analyzing effect of latitude on body shape shifts in studied species of carabids.*

centroid size and their landmarks configurations were aligned according to the best overall fit, using the Generalized Procrustes Analysis (GPA) 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 size changes 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

In order to illustrate the way of our analysis we demonstrate the results of linear models when estimating the role of main environmental factors in body size variation in one of the studied species – *P. niger* (Fig. 2). The other species were treated in the same way.

Factor of latitude position affected different traits in different ways: elytra length decreased in the regions northwards of Tatarstan (see Table 1) (Intercept in our model). On the contrary, elytra width was broader in those regions. The other traits did not vary significantly. As for other environmental factors (anthropogenic state, vegetation), they did take part in the *P. niger* traits variation in size, e. g. in shadowed biotopes (elm, lime) elytra length decreased but elytra width increased.

Then we compiled data concerning the only elytra length variation in latitudinal gradient, taking results in *P. niger*, mentioned above, and the results in five carabid species, that had been published (See „Materials and methods") (Fig. 3): deviations in elytra length in latitude gradient were not similar in all six species. For example, southwards from Tatarstan (it is the centre of the areas), in Kemerovo region, elytra length in *C. granulatus* decreased, in *P. niger* alters only males and in *Poec. cupreus* no deviations were observed. Another example: northwards from Tatarstan, in Udmurtia, elytra length in *C granulatus* became longer only in females, in *C. cancellatus, C. hortensis* and *P. melanarius* elytra length decreasd in both sexes, but in *P. niger* that trait did not change at all.

Because of the cognitive value of the elytra length (the majority of carabidologists equate this trait to the body size) we tracked elytra length value variation in latitudinal gradient in studied carabid species. Results demonstrated three types of that variation: in *C. granulatus*, as well as in *C. cancellatus*, *C. hortensis* elytra length decreased towards the high latitudes. The same tendency in a lesser degree demonstrated *P. niger*. *P. melanarius* showed „saw-tooth" variation of elytra length in latitudinal gradient, when trait value periodically increased and decreased towards the high latitudes. In *Poec. cupreus* means of elytra length did not show significant deviations in latitude gradient (Fig. 4).

Such differences echoed shape variation as well. Results of relative warp analysis (a principal component analysis of the weight matrix) showed that in studied species centroids of southern regions stood lower relatively to the 2-nd axis, than the centroids of more northern regions, the second axis reflected then systematic body shape variation in latitude gradient. On the contrary, in *P. melanarius* distribution of coding regions cenroids in the factor plane was irregular (Fig. 5).

DISCUSSION

The earlier studies showed that relatively large insects with long development times tended to express converse Bergmann clines, whereas relatively small insects with short development times trended to express Bergmann's clines *(2)*. When the available time for growth decreases, the insect will be selected to mature earlier at the cost of a reduced adult size that could also reduce fecundity. This scenario results in a detectable pattern in development time and size along an environmental gradient; with a monotonic increase with season length *(23)*. In univoltine insects, which can only overwinter at a particular developmental stage, their developmental time is restricted by habitat temperature. The decrease in body size in cooler habitats can be explained by selection for a shorter developmental time, which results in smaller body size. Therefore, the converse of Bergmann's rule is considered to be a result of climatic adaptation in univoltine arthropods *(8, 10)*. This is the so-called „converse Bergmann's rule" *(24,)* that has been well documented *(25, 26, 27, 28)*. In our study we registered body size decrease in *Carabus* species and *P. niger*. They confirmed the previous studies in *C. granulatus*, when body size in that species decreased from Middle Taiga towards Forest Tundra *(29)*. It is noteworthy that in *Carabus* species nor bivoltine, nor biennial cycles are implemented *(30)*. These facts explained continuous decrease of body size in our studied species of *Carabus* genus in latitude gradient. In other words elytra length variation in those species followed converse Bergmann rule.

The second opinion on the body size clines is that variation in number of generations per season (i.e. voltinism) affects time constraints. The traditional view about how latitudinal or altitudinal gradient in season length affects the evolution of development time and body size in potentially multivoltine insects was developed by S. Masaki *(8, 9)* and formalized by D. Roff *(10, 23)* and Y. Iwasa *(31)*. They assumed that development time and body size are positively correlated among genotypes, and insects, use all available time for growth to maximize adult body size and thus fecundity. Consequently, both development time and body size are expected to increase along a gradient of increasing season length (i.e. with decreasing latitude or altitude) as long as voltinism does not change, giving rise to a converse Bergmann cline. However, sharp decreases in both traits are expected at the season lengths that facilitate the emergence of a new generation within the season, because time available per generation decreases at these transitions. Thus, the traditional saw-tooth cline arises across phenologies because of genetic adaptation to local conditions. The examples of saw-tooth variation were presented in recent years *(32, 33).*

To our view that mechanism worked in our study in relation to *P. melanarius*. According to A. V. Matalin *(34, 35)* this species has polyvariant life cycle. At middle latitudes (primarily, in forest steppe and mixed coniferous and broad-leaved forests) with the long growing season (not less than 5.5–6 months) and with a significant coenotic diversity (including meso- and microclimatic diversity) the period of activity is prolonged, often covering hot summer months. As a result, a partial or complete development of the second generation is observed in this species throughout the season. Since there are two generations, body size of the beetles is not large. Further to the north the duration of the reproductive season decreases and life-cycle in *P. melanarius* becomes univoltine, hence allowing more time for this single generation. There is enough time to the larva development and the body size of imago becomes larger. Similar processes were observed in other insects *(32, 33, 36, 37, 38).* Further to the north because of the temperature constraints, breeding period becomes shorter and body size of the beetles again decreases. Onwards further to north *P. melanarius* has biennial life cycle *(39)* and its body size, correspondingly, increased again by reasons of prolonged time of development.

In addition the third pattern of body size variation in latitude gradient can occur. It is counter-gradient variation, known as the hypothesis of latitude compensation *(40).* The mechanism can be described as follows: in high latitudes specimen compensate short breeding period by higher (it is genetically coded) rate of growth, compared with conspecificians in low latitudes. In simplest case the rate of growth is the body size per the unit of development time, the utterly exact compensation of breeding season constraints at the certain latitude (the environmental component) will occur in that situation, when growth rate (genetic component) evolves in the way to keep phenotypic body size equal at all latitudes. If increasing growth rate perfectly compensates for the decrease in generation time, body size remains constant over the whole gradient of season length. Possibly that pattern of latitudinal elytra size variation we observed in *Poec. cupreus*. Additionally, the lack of the pronounced fluctuations in elytra length in *Poec. cupreus* might be determined by the lack of samples in northern regions: the highest latitude where that species was sampled in our study was 55°47'N.

As for latitude shape variation in studied species, we failed to find papers concerning this subject. Very scarce data in beetles shape variation dealt one – two species in very local scale *(41, 42).* Discussion on this subject is probable after the confound investigations of carabids intra – specific shape variation, including common garden experiments as well.

CONCLUSION

Previous studies in body size clines in arthropods resumed that taken as a whole these studies suggest no general latitudinal relationship with respect to body size among all insect groups, although positive, negative or null relationships may occur in specific taxa in any particular biogeographical region. That occurred, to our mind, because of the irrespective designs of investigations, which must take into account that even very close species and their certain traits may act differently in latitude gradient. We showed three types of latitude body size variation in carabids. Our data confirmed that this parameter can follow converse Bergmann rule, demonstrate saw-tooth or counter gradient variation. Explanation that takes into account the natural history, climatic correlations and sexual size dimorphism is needed to assess the observed contrasting geographic patterns and differences between species, morphometric traits and sexes, since size clines (e.g. Bergmann's clines) may obey to multiple selection pressures that are not only dependent on temperature constraints but also on other climatic and biotic factors that could influence body size.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

S1	Sample size of carabid species, sampled in different provences
S2	Data set for *P. niger*
S3	Denotations for columns in S2
S4	Results of modeling of different factors effect on traits variation in *P. niger*
S5	Effects of environmental factors on elytra length variation in *P. niger*, results of linear modeling

S1 Sample size of carabid species, sampled in different provences

Sample size of carabid species, sampled in different regions

Region/Species							
	C. granulatus	*C. cancellatus*	*C. hortensis*	*P. melanarius*	*P. niger*	*Poec. cupreus*	total
Stavropol region				5		71	76
Kemerovo region	104				83	84	271
Tatarstan Republic	993	1664	1170	2394	690	1865	8776
Mariy El Republic			24	38	9		71
Udmurtia Republic	71	114	97	110	14		494
Cis_Ural		14		12	18		44
Sverdlovsk region				138	120		258
Novosibirsk region						360	360
total	1168	1792	1291	2697	934	2380	10350

S2 Data set for *P. niger*

7	1	3	5	4	4	2	9.7	2.1	3.5	3.6	3	2.1	-999	-999	-999	-999	-999	-999
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7	5	-999	-999	1	4	3	11	2.9	4	4.4	3	2.3	10	10	1	-999	-999	-999
7	5	-999	-999	1	4	3	11	3	4	4.3	3	2.3	10	10	1	-999	-999	-999
7	5	-999	-999	1	4	3	11	3	4	4.5	3	2.5	10	10	1	-999	-999	-999
7	5	-999	-999	1	4	3	10.5	2.7	3.8	4.3	2.8	2.4	10	10	1	-999	-999	-999
7	5	-999	-999	1	4	3	10.7	2.8	4	4.4	3	2.5	10	10	1	-999	-999	-999
7	5	-999	-999	1	4	3	10.8	2.7	4	4.3	3	2.4	10	10	1	-999	-999	-999
7	5	-999	-999	1	4	3	10.1	2.8	3.8	4.5	3	2.2	10	10	2	-999	-999	-999
7	5	-999	-999	1	4	3	10	2.6	3.8	4	2.5	2.2	10	10	-999	-999	-999	-999

S3 Denotations for columns in S2 (Data set for *P. niger*)

1. A – species
2. B – region
    1. Tatarstan
    2. Sverdlovsk region
    3. Kemerovo region
    4. Novosibirsk region
    5. Udmurtia
    6. Mariy El
    7. Cis_Ural
    8. Stavropol
3. C – district
4. D – settlement
5. E – biotope type
    1. meadow
    2. birch
    3. swamps
    4. elm
    5. oak
    6. pine
    7. lime
    8. carr
    9. shrubs
    10. barley
    11. maize
    12. vetch&oat
    13. pea
    14. wheat
    15. carrot
    16. spring wheat
    17. alfalfa
    18. rye
    19. lawn
    20. spruce
6. F – degree of anthropogenic impact
    1. urban
    2. suburban
    3. rural
    4. natural
7. G – isolation
    1. island
    2. floodland
    3. table-land
    4. urbancenosis
8. H – elytra length
9. I – elytra width
10. J – pronotum length
11. K – pronotum width
12. L – head length
13. M – distance between eyes
16. P – sex
    1. female
    2. male

-0,999 – no data

S4 Results of modeling of different factors effect on traits variation in *P. niger*

Call:						
lm(formula = Elytra.Length~ fSex/(fRegion +fAntrop +fHabitat),						
data = cur.data, weights = Wts, contrasts= list(fRegion = ct.Region,						
fAntrop= ct.Antrop, fHabitat= ct.Habitat))						
Residuals:						
Min	1Q Median	3Q	Max			
-2.59375 -0.337	45 0.09114	0.31719	2.51620			
Coefficients: (4 not defined because of singularities)						
	Estimate	Std. Error	t value	Pr(>|t|)		
(Intercept)	11.159580	0.042215	264.353	< 2e-16	***	
fSex2	-0.620452	0.099986	-6.205	6.79e-10	***	
fSex1:fRegion2	-0.804024	0.091794	-8.759	< 2e-16	***	
fSex2:fRegion2	-0.822461	0.152199	-5.404	7.42e-08	***	
fSex1:fRegion3	-0.181747	0.165567	-1.098	0.272473		
fSex2:fRegion3	-0.726118	0.258056	-2.814	0.004951	**	
fSex1:fRegion5	-0.227226	0.317668	-0.715	0.474523		
fSex2:fRegion5	-0.558479	0.587493	-0.951	0.341931		
fSex1:fRegion6	-0.859580	0.271180	-3.170	0.001552	**	
fSex2:fRegion6	-0.314127	0.312907	-1.004	0.315564		
fSex1:fRegion7	-1.459580	0.248151	-5.882	4.85e-09	***	
fSex2:fRegion7	-0.689127	0.195227	-3.530	0.000426	***	
fSex1:fAntrop1	-0.131618	0.223884	-0.588	0.556686		
fSex2:fAntrop1	0.058000	0.207494	0.280	0.779874		
fSex1:fAntrop2	-0.003409	0.247297	-0.014	0.989003		
fSex2:fAntrop2	-0.177778	0.236242	-0.753	0.451838		
fSex1:fHabitat1	-0.365332	0.272107	-1.343	0.179573		
fSex2:fHabitat1	0.086991	0.332695	0.261	0.793758		
fSex1:fHabitat4	-0.276175	0.053915	-5.122	3.35e-07	***	
fSex2:fHabitat4	-0.318162	0.111294	-2.859	0.004303	**	
fSex1:fHabitat5	0.238194	0.133626	1.783	0.074834	.	
fSex2:fHabitat5	0.323333	0.225449	1.434	0.151701		
fSex1:fHabitat6	NA	NA	NA	NA		
fSex2:fHabitat6	NA	NA	NA	NA		
fSex1:fHabitat7	-1.576647	0.257562	-6.121	1.14e-09	***	
fSex2:fHabitat7	-1.004367	0.253019	-3.970	7.49e-05	***	
fSex1:fHabitat1	9 0.053785	0.388683	0.138	0.889957		
fSex2:fHabitat1	9 0.128991	0.545208	0.237	0.813002		
fSex1:fHabitat2	0 NA	NA	NA	NA		
fSex2:fHabitat2	0 NA	NA	NA	NA		

Signif. codes:	0 ‘***’ 0.	001 ‘**’ 0.	01 ‘*’ 0	.05 ‘.’ 0	.1 ‘	’ 1
Residual standard error: 0.599 on 1753 degrees of freedom						
Multiple R-squared: 0.2791, AdjustedR-squared: 0.2688						
F-statistic: 27.15 on 25 and 1753 DF,p-value: < 2.2e-16						
Analysis of Variance Table						
Response: Elytra.Length						

	Df Sum Sq	Mean Sq F v	alue	Pr(>F)		
fSex	1 114.94	114.939 320	.358 < 2	.2e-16 **	*	
fSex:fRegion	10 42.90	4.290 11	.957 < 2	.2e-16 **	*	
fSex:fAntrop	4 46.51	11.627 32	.407 < 2	.2e-16 **	*	
fSex:fHabitat	10 39.17	3.917 10	.919 < 2	.2e-16 **	*	
Residuals 1	753 628.94	0.359				

Signif. codes:	0 ‘***’ 0.	001 ‘**’ 0.	01 ‘*’ 0	.05 ‘.’ 0	.1 ‘	’ 1

Call:						
lm(formula = Elytra.Width~ fSex/(fRegion + fAntrop +fHabitat),						
data = cur.data, weights = Wts, contrasts= list(fRegion = ct.Region,						
fAntrop= ct.Antrop, fHabitat= ct.Habitat))						
Residuals:						
Min	1Q Median	3Q	Max			
-1.44115 -0.116	42 0.00000	0.09885	1.19688			
Coefficients: (4 not defined because of singularities)						
	Estimate	Std. Error	t value	Pr(>|t|)		
(Intercept)	2.71634	0.01702	159.638	< 2e-16	***	
fSex2	-0.08481	0.04030	-2.104	0.03548	*	
fSex1:fRegion2	1.41329	0.03700	38.197	< 2e-16	***	
fSex2:fRegion2	1.40180	0.06135	22.850	< 2e-16	***	
fSex1:fRegion3	2.44160	0.06674	36.586	< 2e-16	***	
fSex2:fRegion3	2.33067	0.10402	22.407	< 2e-16	***	
fSex1:fRegion5	0.40168	0.12804	3.137	0.00174	**	
fSex2:fRegion5	0.43595	0.23680	1.841	0.06580	.	
fSex1:fRegion6	0.18366	0.10931	1.680	0.09309	.	
fSex2:fRegion6	0.04347	0.12612	0.345	0.73039		
fSex1:fRegion7	-0.01634	0.10002	-0.163	0.87023		
fSex2:fRegion7	0.05180	0.07869	0.658	0.51042		
fSex1:fAntrop1	0.07868	0.09024	0.872	0.38342		
fSex2:fAntrop1	0.02000	0.08364	0.239	0.81103		
fSex1:fAntrop2	0.05341	0.09968	0.536	0.59216		
fSex2:fAntrop2	0.12556	0.09522	1.319	0.18750		
fSex1:fHabitat1	-0.27045	0.10968	-2.466	0.01377	*	
fSex2:fHabitat1	-0.33220	0.13410	-2.477	0.01334	*	
fSex1:fHabitat4	-0.02817	0.02173	-1.296	0.19503		
fSex2:fHabitat4	-0.05856	0.04486	-1.305	0.19190		
fSex1:fHabitat5	3.67350	0.05386	68.203	< 2e-16	***	
fSex2:fHabitat5	3.73667	0.09087	41.120	< 2e-16	***	
fSex1:fHabitat6	NA	NA	NA	NA		
fSex2:fHabitat6	NA	NA	NA	NA		
fSex1:fHabitat7	1.65897	0.10382	15.980	< 2e-16	***	
fSex2:fHabitat7	1.78962	0.10199	17.548	< 2e-16	***	
fSex1:fHabitat1	9 -0.35662	0.15667	-2.276	0.02295	*	
fSex2:fHabitat1	9 -0.28220	0.21976	-1.284	0.19927		
fSex1:fHabitat2	0 NA	NA	NA	NA		
fSex2:fHabitat2	0 NA	NA	NA	NA		

Signif. codes:	0 ‘***’ 0.	001 ‘**’ 0.	01 ‘*’ 0	.05 ‘.’ 0	.1 ‘	’ 1
Residual standard error: 0.2414 on 1753 degrees of freedom						
Multiple R-squared: 0.9425, AdjustedR-squared: 0.9417						
F-statistic: 1150 on 25 and 1753 DF,p-value: < 2.2e-16						
Analysis of Variance Table						
Response: Elytra.Width						

	Df Sum Sq	Mean Sq F	value	Pr(>F)		
fSex	1 15.98	15.982 2	74.18 <	2.2e-16 *	**	
fSex:fRegion	10 1133.12	113.312 19	43.91 <	2.2e-16 *	**	
fSex:fAntrop	4 92.11	23.029 3	95.06 <	2.2e-16 *	**	
fSex:fHabitat	10 434.31	43.431 7	45.08 <	2.2e-16 *	**	
Residuals 1	753 102.18	0.058				

Signif. codes:	0 ‘***’ 0.	001 ‘**’ 0.	01 ‘*’ 0	.05 ‘.’ 0	.1 ‘	’ 1

Call:						
lm(formula = Pronotum.Length ~ fSex/(fRegion+ fAntrop+ fHabitat),						
data = cur.data, weights = Wts, contrasts= list(fRegion = ct.Region,						
fAntrop= ct.Antrop, fHabitat= ct.Habitat))						
Residuals:						
Min 1Q	Median	3Q M	ax			
-1.2116 -0.1114	-0.0042 0	.0951 4.29	52			
Coefficients: (4 not defined becauseof singularities)						
	Estimate	Std. Error	t value	Pr(>|t|)		
(Intercept)	3.803593	0.018334	207.456	< 2e-16	***	
fSex2	-0.040763	0.043425	-0.939	0.34802		
fSex1:fRegion2	-0.070260	0.039868	-1.762	0.07819	.	
fSex2:fRegion2	-0.129496	0.066102	-1.959	0.05027	.	
fSex1:fRegion3	0.097967	0.071908	1.362	0.17325		
fSex2:fRegion3	-0.066527	0.112077	-0.594	0.55287		
fSex1:fRegion5	0.134774	0.137968	0.977	0.32878		
fSex2:fRegion5	0.033473	0.255156	0.131	0.89564		
fSex1:fRegion6	0.156407	0.117777	1.328	0.18435		
fSex2:fRegion6	0.062170	0.135900	0.457	0.64739		
fSex1:fRegion7	-0.220260	0.107775	-2.044	0.04113	*	
fSex2:fRegion7	-0.071163	0.084790	-0.839	0.40142		
fSex1:fAntrop1	-0.101471	0.097236	-1.044	0.29684		
fSex2:fAntrop1	-0.058000	0.090118	-0.644	0.51992		
fSex1:fAntrop2	-0.134091	0.107405	-1.248	0.21203		
fSex2:fAntrop2	-0.138889	0.102603	-1.354	0.17602		
fSex1:fHabitat1	-0.026560	0.118180	-0.225	0.82220		
fSex2:fHabitat1	0.003698	0.144494	0.026	0.97959		
fSex1:fHabitat4	-0.098791	0.023416	-4.219	2.58e-05	***	
fSex2:fHabitat4	-0.142256	0.048337	-2.943	0.00329	**	
fSex1:fHabitat5	-0.020833	0.058036	-0.359	0.71966		
fSex2:fHabitat5	-0.093333	0.097916	-0.953	0.34062		
fSex1:fHabitat6	NA	NA	NA	NA		
fSex2:fHabitat6	NA	NA	NA	NA		
fSex1:fHabitat7	-0.490544	0.111863	-4.385	1.23e-05	***	
fSex2:fHabitat7	-0.301840	0.109890	-2.747	0.00608	**	
fSex1:fHabitat1	9 0.199910	0.168810	1.184	0.23648		
fSex2:fHabitat1	9 -0.038302	0.236792	-0.162	0.87152		
fSex1:fHabitat2	0 NA	NA	NA	NA		
fSex2:fHabitat2	0 NA	NA	NA	NA		

Signif. codes:	0 ‘***’ 0.	001 ‘**’ 0.	01 ‘*’ 0	.05 ‘.’ 0	.1 ‘	’ 1
Residual standard error: 0.2601 on 1753 degrees of freedom						
Multiple R-squared: 0.1093, AdjustedR-squared: 0.09662						
F-statistic: 8.607 on 25 and 1753 DF,p-value: < 2.2e-16						
Analysis of Variance Table						
Response: Pronotum.Length						

	Df Sum Sq	Mean Sq F	value	Pr(>F)		
fSex	1 2.169	2.16890 32	.0481 1.	754e-08 *	**	
fSex:fRegion	10 1.534	0.15338 2	.2663	0.01245 *		
fSex:fAntrop	4 6.098	1.52440 22	.5248 <	2.2e-16 *	**	
fSex:fHabitat	10 4.761	0.47612 7	.0353 6.	512e-11 *	**	
Residuals 1	753 118.637	0.06768				

Signif. codes:	0 ‘***’ 0.	001 ‘**’ 0.	01 ‘*’ 0	.05 ‘.’ 0	.1 ‘	’ 1

Call:						
lm(formula = Pronotum.Width ~ fSex/(fRegion +fAntrop+ fHabitat),						
data = cur.data, weights = Wts, contrasts= list(fRegion = ct.Region,						
fAntrop= ct.Antrop, fHabitat= ct.Habitat))						
Residuals:						
Min	1Q Median	3Q	Max			
-0.85324 -0.129	88 0.00564	0.12969	1.19451			
Coefficients: (4 not defined becauseof singularities)						
	Estimate	Std. Error	t value	Pr(>|t|)		
(Intercept)	4.144138	0.017232	240.493	< 2e-16	***	
fSex2	-0.133123	0.040814	-3.262	0.001129	**	
fSex1:fRegion2	-0.281175	0.037470	-7.504	9.79e-14	***	
fSex2:fRegion2	-0.277682	0.062127	-4.470	8.34e-06	***	
fSex1:fRegion3	-0.138391	0.067583	-2.048	0.040738	*	
fSex2:fRegion3	-0.266688	0.105337	-2.532	0.011436	*	
fSex1:fRegion5	0.490086	0.129670	3.779	0.000162	***	
fSex2:fRegion5	0.421508	0.239811	1.758	0.078979	.	
fSex1:fRegion6	0.115862	0.110694	1.047	0.295390		
fSex2:fRegion6	0.238985	0.127727	1.871	0.061503	.	
fSex1:fRegion7	-0.394138	0.101294	-3.891	0.000104	***	
fSex2:fRegion7	-0.144349	0.079691	-1.811	0.070256	.	
fSex1:fAntrop1	0.070588	0.091388	0.772	0.439981		
fSex2:fAntrop1	-0.072000	0.084698	-0.850	0.395397		
fSex1:fAntrop2	0.061364	0.100945	0.608	0.543340		
fSex2:fAntrop2	-0.066667	0.096433	-0.691	0.489451		
fSex1:fHabitat1	-0.330748	0.111072	-2.978	0.002943	**	
fSex2:fHabitat1	-0.094327	0.135804	-0.695	0.487410		
fSex1:fHabitat4	-0.138836	0.022008	-6.308	3.56e-10	***	
fSex2:fHabitat4	-0.129501	0.045430	-2.851	0.004415	**	
fSex1:fHabitat5	0.099537	0.054546	1.825	0.068195	.	
fSex2:fHabitat5	0.006667	0.092027	0.072	0.942258		
fSex1:fHabitat6	NA	NA	NA	NA		
fSex2:fHabitat6	NA	NA	NA	NA		
fSex1:fHabitat7	-0.846268	0.105135	-8.049	1.52e-15	***	
fSex2:fHabitat7	-0.585777	0.103281	-5.672	1.65e-08	***	
fSex1:fHabitat1	9 -0.236336	0.158658	-1.490	0.136512		
fSex2:fHabitat1	9 -0.122327	0.222551	-0.550	0.582624		
fSex1:fHabitat2	0 NA	NA	NA	NA		
fSex2:fHabitat2	0 NA	NA	NA	NA		

Signif. codes:	0 ‘***’ 0.	001 ‘**’ 0.	01 ‘*’ 0	.05 ‘.’ 0	.1 ‘	’ 1
Residual standard error: 0.2445 on 1753 degrees of freedom						
Multiple R-squared: 0.3075, AdjustedR-squared: 0.2976						
F-statistic: 31.14 on 25 and 1753 DF,p-value: < 2.2e-16						
Analysis of Variance Table						
Response: Pronotum.Width						

	Df Sum Sq	Mean Sq F	value	Pr(>F)		
fSex	1 9.850	9.8496 16	4.762 <	2.2e-16 *	**	
fSex:fRegion	10 13.897	1.3897 2	3.247 <	2.2e-16 *	**	
fSex:fAntrop	4 13.674	3.4185 5	7.183 <	2.2e-16 *	**	
fSex:fHabitat	10 9.117	0.9117 1	5.250 <	2.2e-16 *	**	
Residuals 1	753 104.796	0.0598				

Signif. codes:	0 ‘***’ 0.	001 ‘**’ 0.	01 ‘*’ 0	.05 ‘.’ 0	.1 ‘	’ 1

Call:						
lm(formula = Head.Length ~fSex/(fRegion + fAntrop + fHabitat),						
data = cur.data, weights = Wts, contrasts= list(fRegion = ct.Region,						
fAntrop= ct.Antrop, fHabitat= ct.Habitat))						
Residuals:						
Min	1Q Median	3Q	Max			
-1.03269 -0.129	06 0.02845	0.13896	1.85556			
Coefficients: (	4 not defin	ed because	of singu	larities)		
	Estimate	Std. Error	t value	Pr(>|t|)		
(Intercept)	2.869763	0.018684	153.597	< 2e-16	***	
fSex2	-0.158036	0.044253	-3.571	0.000365	***	
fSex1:fRegion2	-0.225318	0.040627	-5.546	3.37e-08	***	
fSex2:fRegion2	-0.078393	0.067361	-1.164	0.244672		
fSex1:fRegion3	-0.888531	0.073278	-12.126	< 2e-16	***	
fSex2:fRegion3	-0.920849	0.114212	-8.063	1.37e-15	***	
fSex1:fRegion5	-0.249986	0.140596	-1.778	0.075570	.	
fSex2:fRegion5	-0.152653	0.260017	-0.587	0.557220		
fSex1:fRegion6	-0.269763	0.120021	-2.248	0.024723	*	
fSex2:fRegion6	0.013273	0.138489	0.096	0.923656		
fSex1:fRegion7	-0.569763	0.109829	-5.188	2.38e-07	***	
fSex2:fRegion7	-0.270060	0.086405	-3.126	0.001804	**	
fSex1:fAntrop1	0.208824	0.099088	2.107	0.035220	*	
fSex2:fAntrop1	0.138000	0.091834	1.503	0.133095		
fSex1:fAntrop2	0.034091	0.109451	0.311	0.755478		
fSex2:fAntrop2	-0.008889	0.104558	-0.085	0.932260		
fSex1:fHabitat1	0.143768	0.120431	1.194	0.232725		
fSex2:fHabitat1	0.279122	0.147247	1.896	0.058176	.	
fSex1:fHabitat4	-0.070412	0.023862	-2.951	0.003212	**	
fSex2:fHabitat4	-0.123355	0.049257	-2.504	0.012360	*	
fSex1:fHabitat5	-0.431944	0.059141	-7.304	4.23e-13	***	
fSex2:fHabitat5	-0.673333	0.099781	-6.748	2.03e-11	***	
fSex1:fHabitat6	NA	NA	NA	NA		
fSex2:fHabitat6	NA	NA	NA	NA		
fSex1:fHabitat7	-0.412459	0.113994	-3.618	0.000305	***	
fSex2:fHabitat7	-0.315253	0.111983	-2.815	0.004929	**	
fSex1:fHabitat1	9 0.169945	0.172026	0.988	0.323338		
fSex2:fHabitat1	9 0.421122	0.241303	1.745	0.081124	.	
fSex1:fHabitat2	0 NA	NA	NA	NA		
fSex2:fHabitat2	0 NA	NA	NA	NA		

Signif. codes:	0 ‘***’ 0.	001 ‘**’ 0.	01 ‘*’ 0	.05 ‘.’ 0	.1 ‘	’ 1
Residual standard error: 0.2651 on 1753 degrees of freedom						
Multiple R-squared: 0.3635, AdjustedR-squared: 0.3544						
F-statistic: 40.04 on 25 and 1753 DF,p-value: < 2.2e-16						
Analysis of Variance Table						
Response: Head.Length						

	Df Sum Sq	Mean Sq F	value P	r(>F)		
fSex	1 12.391	12.3906 17	6.3040 <	2e-16 ***		
fSex:fRegion	10 45.358	4.5358 6	4.5391 <	2e-16 ***		
fSex:fAntrop	4 0.476	0.1190	1.6926 0	.1490		
fSex:fHabitat	10 12.124	1.2124 1	7.2506 <	2e-16 ***		
Residuals 1	753 123.200	0.0703				

Signif. codes:	0 ‘***’ 0.	001 ‘**’ 0.	01 ‘*’ 0	.05 ‘.’ 0	.1 ‘	’ 1

Call:						
lm(formula = Eye.Distance~ fSex/(fRegion + fAntrop +fHabitat),						
data = cur.data, weights = Wts, contrasts= list(fRegion = ct.Region,						
fAntrop= ct.Antrop, fHabitat= ct.Habitat))						
Residuals:						
Min	1Q Median	3Q	Max			
-0.60100 -0.083	35 -0.00340	0.06650	1.59900			
Coefficients: (4 not defined becauseof singularities)						
	Estimate	Std. Error	t value	Pr(>|t|)		
(Intercept)	2.229185	0.010865	205.176	< 2e-16	***	
fSex2	-0.040080	0.025733	-1.558	0.119529		
fSex1:fRegion2	0.033778	0.023625	1.430	0.152970		
fSex2:fRegion2	-0.089105	0.039171	-2.275	0.023040	*	
fSex1:fRegion3	-0.027803	0.042612	-0.652	0.514181		
fSex2:fRegion3	-0.096967	0.066416	-1.460	0.144466		
fSex1:fRegion5	0.082963	0.081758	1.015	0.310372		
fSex2:fRegion5	0.093033	0.151202	0.615	0.538447		
fSex1:fRegion6	0.090815	0.069793	1.301	0.193363		
fSex2:fRegion6	0.210895	0.080532	2.619	0.008901	**	
fSex1:fRegion7	0.070815	0.063866	1.109	0.267672		
fSex2:fRegion7	0.102561	0.050245	2.041	0.041380	*	
fSex1:fAntrop1	0.041176	0.057621	0.715	0.474944		
fSex2:fAntrop1	0.132000	0.053403	2.472	0.013538	*	
fSex1:fAntrop2	-0.029545	0.063647	-0.464	0.642555		
fSex2:fAntrop2	0.073333	0.060801	1.206	0.227937		
fSex1:fHabitat1	0.023618	0.070032	0.337	0.735975		
fSex2:fHabitat1	-0.082138	0.085625	-0.959	0.337555		
fSex1:fHabitat4	-0.001841	0.013876	-0.133	0.894482		
fSex2:fHabitat4	0.019933	0.028644	0.696	0.486582		
fSex1:fHabitat5	0.130787	0.034391	3.803	0.000148	***	
fSex2:fHabitat5	0.060000	0.058024	1.034	0.301250		
fSex1:fHabitat6	NA	NA	NA	NA		
fSex2:fHabitat6	NA	NA	NA	NA		
fSex1:fHabitat7	0.177345	0.066288	2.675	0.007535	**	
fSex2:fHabitat7	-0.020109	0.065119	-0.309	0.757510		
fSex1:fHabitat1	9 0.077441	0.100035	0.774	0.438952		
fSex2:fHabitat1	9 -0.124138	0.140320	-0.885	0.376452		
fSex1:fHabitat2	0 NA	NA	NA	NA		
fSex2:fHabitat2	0 NA	NA	NA	NA		

Signif. codes:	0 ‘***’ 0.	001 ‘**’ 0.	01 ‘*’ 0	.05 ‘.’ 0	.1 ‘	’ 1
Residual standard error: 0.1542 on 1753 degrees of freedom						
Multiple R-squared: 0.1003, AdjustedR-squared: 0.08745						
F-statistic: 7.816 on 25 and 1753 DF,p-value: < 2.2e-16						
Analysis of Variance Table						
Response: Eye.Distance						

	Df Sum Sq	Mean Sq F v	alue	Pr(>F)		
fSex	1 0.954	0.95429 40.	1547 2.9	76e-10 **	*	
fSex:fRegion	10 1.643	0.16433 6.	9148 1.0	90e-10 **	*	
fSex:fAntrop	4 1.364	0.34100 14.	3485 1.5	70e-11 **	*	
fSex:fHabitat	10 0.682	0.06819 2.	8692 0.	001487 **		
Residuals 1	753 41.661	0.02377				

Signif. codes:	0 ‘***’ 0.	001 ‘**’ 0.	01 ‘*’ 0	.05 ‘.’ 0	.1 ‘	’ 1

S5 Effects of environmental factors on elytra length variation in *P. niger*, results of linear modeling

Factor	Contribution of factor into the trait deviation						Contribution of factor into the trait mean					
	Females			Males			Females			Males		
	Confidence interval limits		Mean of the deviation	Confidence interval limits		Mean of the deviation	Confidence interval limits		Trait mean	Confidence interval limits		Trait mean
	Left 2,5%	Right 97,5%		Left 2,5%	Right 97,5%		Left 2,5%	Right 97,5%		Left 2,5%	Right 97,5%	
Sverdlovsk region	-0.98	-0.62	-0.8	-1.12	-0.52	-0.82	10.2	10.52	10.36	9.48	9.96	9.72
Kemerovo region	-0.51	0.14	-0.18	-1.23	-0.22	-0.73	10.64	11.31	10.98	9.28	10.35	9.81
Udmurtia	-0.85	0.4	-0.23	-1.71	0.59	-0.56	10.3	11.56	10.93	8.82	11.15	9.98
Mariy El	-1.39	-0.33	-0.86	-0.93	0.3	-0.31	9.77	10.83	10.3	9.64	10.81	10.22
Cis-Ural	-1.95	-0.97	-1.46	-1.07	-0.31	-0.69	9.22	10.18	9.7	9.51	10.19	9.85
Urban	-0.57	0.31	-0.13	-0.35	0.46	0.06	10.58	11.47	11.03	10.15	11.04	10.6
Suburban	-0.49	0.48	0	-0.64	0.29	-0.18	10.66	11.65	11.16	9.87	10.86	10.36
Meadow	-0.9	0.17	-0.37	-0.57	0.74	0.09	10.27	11.32	10.79	10	11.25	10.63
Elm	-0.38	-0.17	-0.28	-0.54	-0.1	-0.32	10.82	10.95	10.88	10.09	10.35	10.22
Jak	-0.02	0.5	0.24	-0.12	0.77	0.32	11.12	11.67	11.4	10.39	11.34	10.86
Lime	-2.08	-1.07	-1.58	-1.5	-0.51	-1	9.08	10.08	9.58	9.07	10	9.53
Lawn	-0.71	0.82	0.05	-0.94	1.2	0.13	10.46	11.97	11.21	9.61	11.72	10.67