



Impact of climatic factors on sexual size dimorphism in ground beetle *Pterostichus melanarius* (Illiger, 1798) (Coleoptera, Carabidae)

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Abstract

Intra-specific body size variation in ground beetles is studied insufficiently, especially in response to climatic factors. Even less studied is the sexual dimorphism (hereinafter referred to as the SSD), its geographic variation patterns and response to climatic factors. We sampled ground beetles *Pterostichus melanarius* in 15 regions of Northern Eurasia along latitude and longitude gradients (in 17 degrees and 121 degrees, respectively), including differing habitats (open and forested) in the spectrum of anthropogenic impact (cities, suburbs, arable lands and natural). 7677 specimens were

measured by six morphometric traits – elytra, pronotum, head length and width, distance between eyes. Our software applied made it possible both to catch the smallest changes in the size of traits in females and males, and to determine their direction. Temperature related factors mostly reduced beetles traits values, but precipitation related factors – enlarged them. Elytra and pronotum parameters were the traits which response differently in males and females to climatic factors, these traits showed more pronounced SSD. Head parameters showed SSD in response to those factors too. That response had the similar direction and was expressed more, either in females or males. The latter processes implemented to a greater extent in relation to the temperature including bioclimatic factors.

Key words: climatic factors; body size variation; sexual size dimorphism; ground beetles; ANOVA.

Introduction

Intergovernmental Panel on Climate Change (IPCC) report in 2013, the climate in southern Europe will become warmer and drier. In northern regions it will become warmer and wetter. With climate change, temperatures in Europe, especially at higher latitudes, are expected to increase more than the average warming worldwide (IPCC, 2007). Increased global average temperatures and varying precipitation patterns promote extreme natural events that affect landscapes and pose a major challenge to the natural environment, agriculture and food security (Shukla *et al.* 2019). Temperature is the major factor affecting plant and animal distribution and abundance patterns due to the physiological limits of individual species (Parmesan & Yohe 2003). Ongoing climate warming allows the cultivation of more crop species but also favours insect pest survival and spread in these regions (Bale & Hayward 2010). In this relation the problem of predatory insects arises. The latter are considered to be the excellent regulators of pests number. Among them ground beetles take pride of place. Carabidae is the large family in Coleoptera. They dwell practically in all terrestrial habitats, imagoes and larvae actively predate on the large spectra of pests. Therefore, it is of great importance to model insects response to climatic factors.

An increase in temperature can affect them directly through physiology, life cycle, or shift in geographic range and indirectly through the presence of resources. The latter factor seemingly is not of great importance because practically of carabid species are predators. In this connection the events on population level become important. Among the most important traits body size occupies a special position. Body size is able to explain many ecological processes and patterns (Peters 1983; Jonsson *et al.* 2005; Brose *et al.* 2006; Bale & Hayward 2010; Riede *et al.* 2011). Consequently, much of current food web theory assumes that body-size-determined consumption is a main driver of community dynamics (Yodzis & Innes 1992; Brose 2010). Besides body size correlates with most performance variables in ectotherms including both survival and reproductive output (Roff 1992; Stearns 1992; Sogard 1997; Hurst 2007). As such, understanding why organisms vary in body size is necessary for developing a full understanding of evolutionary patterns (Arendt & Fairbairn 2012). Therefore, sufficiently large amount of papers are devoted to the problem of body size variation in animals, including insects (Chown & Gaston 2010). In outline temperature and resources are considered to be the main factors affecting their size. In carabids the authors have also identified additional environmental factors. At first, body size in ground beetles varied in latitude gradient and that variation was genus-specific. In *Carabus* species body size declined towards the north and towards the high altitudes and in *Pterostichus* species variation in body size was saw-tooth (Sukhodolskaya & Saveliev 2016; Ananina *et al.* 2020; Sukhodolskaya *et al.* 2021). The authors tended to explain this phenomenon by life-cycle peculiarities. Anthropogenic press affected ground beetles size also (Sukhodolskaya & Saveliev 2014).

Another important trait when analyzing population dynamics is sexual size dimorphism (SSD) – the difference between males and females in the size of traits. It is believed that SSD reflects environmental quality – in severe environment its value decreases. SSD, indeed, varied depending on the environmental conditions. In addition, it is genus-specific. In ground beetles its value was varied in altitude gradient with slight negative trend (Ananina *et al.* 2020; Sukhodolskaya *et al.* 2021). In latitude gradient it did not change significantly (Gordienko *et al.* 2021).

In this article we used the same data set as we have done previously when analyzing *Pterostichus melanarius* (Luzyanin *et al.* 2022a). In the latter publication we showed that body size variation in all traits in general was saw-tooth, both in latitude and in longitude gradients. Regression analysis detected slight trends in general, there was no evidence for the steepness in trait variation in males compared with females.

Thus that analysis revealed that body size variation in geographical gradients was similar in males and females and SSD in that regard was absent.

In this study we analyzed males and females response to climatic factors. We have not found any publication on the topic of body size variation in ground beetles depending on the temperature, snowpack, precipitation etc., based on the large-scaled data and subsequent modeling. Practically all studies include episodic investigations of the single sample in the single plot (Weller & Ganzhorn 2004; Sadler *et al.* 2006; Sukhodolskaya *et al.* 2020b). The only one stuff work now on the carabids body size variation when the beetles are being sampled on the vast territories. Concerning *P. melanarius* those studies showed that dwelling in cities decreased elytra length of the beetles and in suburbs it occurred only in females (Sukhodolskaya 2014). Habitat type affected beetles size also. And that impact was sometimes multidirectional in males and females. In five explored cities *P. melanarius* body size differed sometimes significantly but the authors did not find body size – latitude relationship (Sukhodolskaya *et al.* 2022). It is noteworthy that SSD occurred by all traits and in all cities. Its values varied significantly in six investigated traits and were the lowest in pronotum length and the highest in elytra length.

So the aim of our study was to model climatic factors impact on body size and SSD variation in ground beetle *Pterostichus melanarius*. This issue has not been studied by anyone before and all our hypotheses laid in the stream of our earlier investigations: (i) different traits would response differently to climatic factors; (ii) climatic factors promoting mild vegetation season would impact positively to beetles size but reduce SSD; (iii) males and females response to the certain climatic factor would differ leading to SSD arise.

Materials and Methods

1. Study Organism

Pterostichus melanarius (Illiger, 1798) is a medium-sized beetle. Its range covers Europe and Siberia: from northern Spain and its eastern – to the Amur River (Bousquet 2003). The species successfully dwells in North America (Niemelä & Spence 1994; Niemelä *et al.* 1997). It occurs in meadows, agricultural fields and in all types of forests (Thomas *et al.* 1998; Fournier & Loreau 2001; Sukhodolskyay 2007). *P. melanarius* is a transpalearctic mesophilic zoophagous, generalist species, with a polyvariant life cycle with multiseasonal reproduction and hibernation of larvae and adults of the first and second years of life (Kryzhanovskij *et al.* 1995; Sharova & Denisova 1997; Matalin 2006). Feeding resources of *P. melanarius* are wide (Korolev & Brygadyrenko 2012). Large predators in turn prey on *P. melanarius* (Brygadyrenko & Korolev 2006). As a generalist species, *P. melanarius* is regarded as a good model species for the purposes of studying the morphometric variation in differing environments (Sukhodolskaya 2014). It is abundant in the vast spectra of biotopes, and large database on morphometric variation in this species has been created (Sukhodolskaya *et al.* 2016).

2. Study Design

We used the same database we have done previously when analyzing *P. melanarius* (Luzyanin *et al.* 2022a). It included 7677 specimens, measured by six traits: elytra, pronotum and head length, elytra and pronotum width, distance between eyes. Beetles had been sampled in 15 provinces of Northern Eurasia. Regions of sampling differed in 17 degrees in latitude and 121 degrees in longitude. We sampled beetles in at least three plots in every studied region. Those plots differed in some parameters: anthropogenic impact, vegetation, etc. However, we took into account that our investigation was large in scale. Due to the huge number of sampled and measured beetles, we performed the study by developing a high-throughput approach. This kind of approach has become popular in recent decades. It involves gathering data from scattered publications on the definite item, colligating it, and making conclusions on the given topic, e.g., (Blanckenhorn *et al.* 2006).

3. Statistical Analysis

We used mostly parametric models and tests for sexual dimorphism analysis. The latter assume the normal distribution of parameters. The supposition about the local populations homogeneity is the additional argument in favor to normal distribution.

We supposed outliers occurrence (Gower 1975; Ten Berge 1977; Goodal 1991; Kent 1994). Then we used the robust (resistant to outliers) methods of mean and dispersion estimation. They were realized in rlm

function of MASS package (version 7.3-57). A simple robust model $\text{rlm}(Y \sim 1)$ was used with the default method = "M". The mean and scale were extracted from the fitted model and used to detect outliers. We estimated the probability of normal distribution for each trait with mean and dispersion estimation. The multiple comparisons of all 6 traits took place. That is why we set the value 0.0085 as the significance level threshold for each trait. The latter corresponded to the standard level 0.05 for multiple tests.

After outliers detection with the noted significance level use those values usually are deleted or winsored. There were few outliers in our data, then we have deleted them from the following analysis.

We used the following model to estimate body size variation in males and females in response to different environmental factors:

$$\begin{aligned} \text{Size}_{i,j,k} &= a_{i,0} + a_{i,1} \cdot I_{i,j,k}^{male} + a_{i,2} \cdot X_{i,j,k} + a_{i,3} \cdot I_{i,j,k}^{male} \cdot X_{i,j,k} + \varepsilon_{i,j,k} \\ \varepsilon_{i,j,k} &\sim \text{Norm}(0, \sigma_{i,j}^2) \end{aligned} \quad (1)$$

Here

$\text{Size}_{i,j,k}$ – i -size of the k beetle in j -biotope

$I_{i,j,k}^{male}$ – indicator function, it became 1, if the beetle was male, and 0 if it was female.

$X_{i,j,k}$ – environmental factor. As the latter we used climatic variables from Bioclim data set (<https://worldclim.org/data/bioclim.html>): BIO1 – Annual Mean Temperature, BIO2 – Mean Diurnal Range (Mean of monthly (max temp – min temp)), BIO3 – Isothermality (BIO2/BIO7) ($\times 100$), BIO4 – Temperature Seasonality (standard deviation $\times 100$), BIO5 – Max Temperature of Warmest Month, BIO6 – Min Temperature of Coldest Month, BIO7 – Temperature Annual Range (BIO5–BIO6), BIO8 – Mean Temperature of Wettest Quarter, BIO9 – Mean Temperature of Driest Quarter, BIO10 – Mean Temperature of Warmest Quarter, BIO11 – Mean Temperature of Coldest Quarter, BIO12 – Annual Precipitation, BIO13 – Precipitation of Wettest Month, BIO14 – Precipitation of Driest Month, BIO15 – Precipitation Seasonality (Coefficient of Variation), BIO16 – Precipitation of Wettest Quarter, BIO17 – Precipitation of Driest Quarter, BIO18 – Precipitation of Warmest Quarter, BIO19 – Precipitation of Coldest Quarter.

$\sigma_{i,j}^2$ – error variation, it can differ for different biotopes.

$a_{i,0}, a_1, a_2, a_3$ – the model coefficients;

$a_{i,1}$ – the difference between the average size of females and males in a whole by all data set;

a_2 – the value of shift in female trait size under the certain environmental factor impact; if it was positive, the factor increased females trait size, and vice versa;

a_3 – the difference in regression slopes for males and females and its significance, in other words, the response of males and females for the environmental factor; the significance of a_3 tells that the shifts in trait differs in males and females in value, but tells nothing about the directions of shifts; in order to reveal the direction of shifts we should estimate the sum:

$a_{i,2} + a_{i,3}$ and compare the sign of sum with the sign of $a_{i,2}$

Additional data analysis results (Fig. S1–10, Tables S1–S21) can be downloaded from cloud-based repository Mendeley Data (Luzyanin *et al.* 2022b; <https://doi.org/10.17632/wm9tyhg597.1>).

Results and Discussion

The mode of distribution – skewness and kurtosis matched with normal distribution because their modulo did not exceeded 1 (Table S1a).

At first we tried to compare the real values of traits in *P. melanarius* in different habitats. It was done to show the readers the real values of traits in *P. melanarius*, because some carabidologists dealing with morphometry are interested especially in tangible body size parameters.

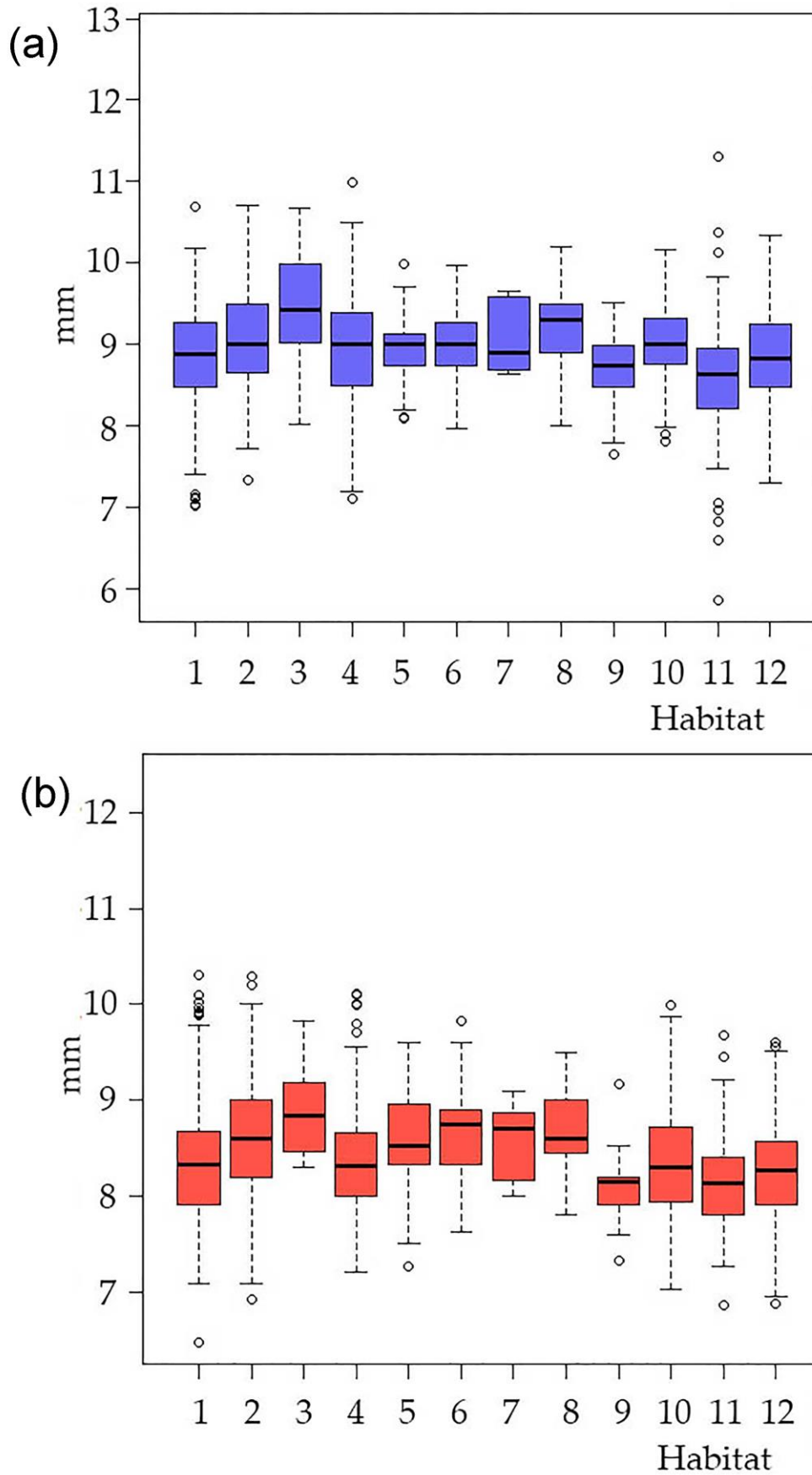


Figure 1. Elytra length variation in *P. melanarius* from different habitats (a – females, b – males). Habitats are designated as follows: 1 – meadow, 2 – birch-forest, 3 – elm, 4 – oak-wood, 6 – pine forest, 7 – willow, 8 – shrubs, 9 – lawn, 10 – fir-forest, 11 – garden, 12 – rape field.

Females did not differ significantly in elytra length, but males in elms and shrubs were significantly larger than in lawns (Fig. 1). Dimensions of elytra width both in females and males were similar in lime-forests, willows, shrubs and fir-woods. And they were significantly larger than in lawns and gardens (Fig. S1,2).

Pronotum length in females were larger in birch-forests and shrubs if compared with lawn populations of *P. melanarius*, but in males another trend occurred that trait was larger in pine, lime-forests and willows compared with elm populations (Fig. S3,4). Pronotum width was just about similar in all habitats, but in females from shrub populations and in males from lime-forests and willows it was significantly larger (Fig. S5,6). Head length in both sexes was significantly larger in lime-forests compared with pine-forests and shrubs (Fig. S7,8) but its width (between eye distance) varied differently: it was larger in females in willow populations compared with elms and lawn, but in male lime-forests populations males had larger head width than meadow ones. In a whole, large beetles inhabited wet biotopes (woody ones) (Fig. S9,10). Thus we concluded that the type of habitat really affected beetles size. This conclusion is consistent with our earlier published works in *P. melanarius* and other carabids (Sukhodolskaya 2014; Sukhodolskaya & Saveliev 2014; Sukhodolskaya & Saveliev 2016).

In any way all phytocenoses (perhaps except agrocenoses) are formed under environmental conditions including climatic parameters. The latter, therefore, must influence beetles body size. We have analyzed this item using linear models. For example, Table 1 shows results of modeling Annual Mean Temperature (Bio1 in terms from Bioclim) impact of beetles traits variation. In regard to elytra length they can be interpreted as follows. In a whole females were larger than males (the coefficient “a1” had a negative sign and p-value of it was significant); the relationship between mean annual temperature and elytra length dimension was negative: the “a2 = -0.032”, had a negative sign and p-value of it was significant, in other word – the higher is annual mean temperature the smaller was elytra length in *P. melanarius* females; coefficient a3 shows males elytra length shifts compared with females shifts (a3 = -0.038): its sign is negative and its value is significantly higher than in females, so males elytra length decreased and to a greater extent than in females; the sum (a2 + a3) shows the similarity of shifts direction in males and females, it has the same sign with a2 coefficient, so the direction of shifts were similar in males and females; the main conclusion on elytra length changes under Bio 1 impact, then, as follows: females and males elytra length responded to annual mean temperature in the same direction. Both decreased elytra length with annual temperature increasing, and males did it more intense than females, so SSD ocured. Similarly, pronotum length varied.

Table 1. ANOVA results on modeling Annual Mean Temperature in traits value in *P. melanarius*.

Trait/ Model	a1	a1.p-val	a2	a2.p-val	a3	a3.p-val	a2+a3
coefficients							
Elytra.Length	-0,56	0	-0,032	0,01	-0,038	0,024	-0,07
Elytra.Width	-0,165	0	-0,02	0,068	0,044	0,003	0,024
Pronotum.Length	-0,174	0	-0,021	0	-0,014	0,03	-0,035
Pronotum.Width	-0,202	0	0,001	0,903	-0,01	0,278	-0,009
Head.Length	-0,116	0	0,255	0	0,058	0	0,313
Eye.Distance	-0,16	0	0,023	0	-0,018	0,001	0,005

Notes. a1– the difference between the average size of females and males in a whole by all data set; a2 – the value of shift in female trait size under the certain environmental factor impact; if it was positive, the factor increased females trait size, and negative – if the trait size decreased; a3 – the difference in regression slopes for males and females and its significance, in other words, the response of males and females for the environmental factor; if a2 was significant, the response of males and females differed, then SSD occurred; sum (a2 + a3) – shows the direction of shifts in trait values in males and females; if this sum and a2 coefficient have the same signs, the direction of shifts in both sexes was the same; if they differ, the direction differed too.

Similar analysis of the other traits variation in response to annual mean temperature allowed us to draw the following conclusion: elytra width in general was smaller in males; annual mean temperature did not affect elytra width (“a2” was not significant); but males significantly differed from females and enlarged elytra width (a3 is positive), so SSD occurred. Pronotum width in general was smaller in males (“a1” had negative sign and it was significant); annual mean temperature did not affect this trait (“a2” was insignificant); difference between males and females in response to this factor was insignificant, so SSD was absent. Head length in general was smaller in males; it increased with increasing annual mean temperature in both sexes, but in males in greater extent, so SSD occurred. Distance between eyes also was smaller in males, it increased with increasing annual mean temperature in both sexes, but in males in a less degree, so SSD occurred again. We summarized those descriptions in the first row of Table 1: five traits out of six investigated showed SSD occurrence in response to Bio1 impact.

ANOVA results showed how the other climatic factors affected beetles size (Tables S2–20). The summary of those models is presented in Table S21: the coefficients “a1” (difference between females and males) were negative in all cases. Thus under the influence of all climatic factors males remained smaller by all traits as it has been shown earlier (Sukhodolskaya *et al.* 2016), and this has been basically the case for Carabidae. Then we carefully analyzed every factor impact, i.e. the values of coefficients in every trait variation, and organized them into two tables. At first about the changes in traits values in a whole when only significant impact with *p*-level < 0.05 was taken into account (Table 2).

Table 2. Engagement of bioclimatic factors into size variation in *P. melanarius*.

Trait	Direction of changes	Factors (number of analyzed cases)	
		Temperature related	Precipitation related
Elytra length	increase	3	2
	decrease	5	0
Elytra width	increase	1	7
	decrease	5	1
Pronotum length	increase	4	1
	decrease	6	4
Pronotumwidth	increase	5	0
	decrease	4	6
Head length	increase	4	7
	decrease	6	1
Distance between eyes	increase	5	7
	decrease	6	1
In total	increase	22	24
	decrease	32	13

Head parameters are the most variable traits in *P. melanarius*, all climatic factors influenced them in one direction or another. Elytra and pronotum parameters were less variable and, sometimes, showed similar variation. For example, they increased with the increasing of Mean Temperature of the Wettest Quarter (Bio8). It is noteworthy than head varied on opposite direction (decreased) as well as in regard to Bio4, Bio7, Bio10. These should be taken into account ahead of area shifts in *P. melanarius* (Avtaeva *et al.* 2021). We paid attention to the climatic factors characters when analyzing Table 2: temperature related factors (Bio1–11) mostly reduce beetles traits values, but precipitation related factors (Bio12–19) – enlarge them. Speaking specifically on the traits two types of factors affected parity on elytra length variation, but elytra width increase is depended on moisture and decrease – on temperature. Head parameters increase practically always is affected by factors, which include precipitation. In general, Bio8 (Mean Temperature of the Wettest Quarter) impact was expected: the higher is its value the more beetles elytra and pronotum increase, i.e. body size enlarge. This is explained by the fact that imagoes size is depended on larva size. The latter develop more successfully in warm and moist soil (Huruk *et al.* 2014). Similar effect has Bio9: the higher is the temperature of the driest quarter the more beetles size decrease. Unstable temperature regime (Bio3) also decreases body size in *P. melanarius*. At the same time, coordination in variation of different traits was not so explainable. For example, the effect of Bio4, Bio7, Bio10 was positive on pronotum size, but negative on head one.

We would like to dwell separately on SSD issue. A quick look at the Table 3 allows us to conclude that the red cells concentrated below the imaginary diagonal, green cells – above it, and yellow cells took place predominantly at upper rows. Filling the picture with biological meaning we can say the following. Elytra and pronotum parameters are the traits which responded differently in males and females to climatic factors, those traits showed more SSD. Head parameters showed SSD in response to those factors too, but those responses had the similar direction and was expressed more, either in females or males. The latter processes implemented to a greater extent in relation to the temperature including bioclimatic factors.

Table 3. Involvement of climatic variables in the manifestation of SSD in *P. melanarius*.

Climatic factor/ Trait	A	B	V	G	D	E
1	Bio1	Bio1	Bio1		Bio1	Bio1
2	Bio2					Bio2
3		Bio3			Bio3	
4	Bio4	Bio4			Bio4	Bio4
5	Bio5		Bio5		Bio5	Bio5
6	Bio6	Bio2	Bio6		Bio6	Bio6
7	Bio7	Bio	Bio7		Bio7	Bio7
8	Bio8		Bio8	Bio8		Bio8
9	Bio9	Bio9	Bio9		Bio9	Bio9
10	Bio10	Bio10		Bio10	Bio10	
11	Bio11	Bio11			Bio11	Bio11
12	Bio12		Bio12			
13	Bio13	Bio13	Bio13			
14			Bio14		Bio14	
15	Bio15	Bio15	Bio15	Bio15		Bio12
16	Bio16	Bio16	Bio16	Bio16		
17						
18	Bio18	Bio18	Bio18	Bio18		
19						

Notes. Columns: A – elytra length, B – elytra width, V – pronotum length, G – pronotum width, D – head length, E – distance between eyes. Left column – climatic variables, numbered according from Bioclim data set Coloration of the cells: red dyed – females and males changed in opposite directions, yellow dyed – females and males changed in the same direction but the males – in the greater degree, green dyed – females and males change in the same direction but the males – in the less degree, without coloration – there was no SSD.

As for SSD representation in a whole practically 50% of analyzed cases showed SSD in response to climatic factors impact. It was most significant in elytra length (79% of cases), elytra width and pronotum length (63%).

Phenotypic traits are the organism's observable characteristics regulated by gene expression, epigenetic modification and environmental and life-history factors (Aubin-Horth & Renn 2009). Our results are the first experience of modeling species life-traits response to climatic factors. We do believe that *P. melanarius* is very plastic species. It can adapt to variety of habitats, beginning from moisturized flood-plain forests and natural mountain beech-fire or beech-fire-spruce forests till arable lands and urban sites. It was all the more interesting to outline the range of climatic factors affecting its size. The novelty of the work lies in the fact that our method allows to record the smallest shifts in body size. The latter is very important because body size mediates the interactions between organisms and their environment and may place stronger selection pressures than other trait on the ecology of organisms in our fast-changing environment.

Our investigation is the first in the item of climatic factors impact on body size and sexual size dimorphism (SSD) variation in Coleoptera. So we do not claim comprehensive conclusions. All known paper on the matter of climate impact included modeling species distribution shifts under the global climate events [see, Namyatova 2020; Zhang *et al.* 2020; Avtaeva *et al.* 2021; Skendžić *et al.* 2021). But body size being the integral trait affects plenty of physiological, developmental and etc. traits which determine species distribution. Surely our investigations should be expanded by attracting the other carabid species. According

to our initial plan the latter should be widespread allowing analysis of beetles from the whole Eurasia. Additionally it will be desirable to get samples from North America. *P. melanarius* was introduced to this continent and successfully expanded (Niemelä & Spence 1994; Niemelä *et al.* 1997). And “residential” populations differ from the ones that dwell at the boundary of expansion. The question is especially interesting in relation of SSD variation. Theoretically SSD can be considered as the “compass of evolution”. In ground beetles the value of SSD differed in different morphological traits (Sukhodolskaya *et al.* 2016). Besides SSD was revealed in relation to shape (Benítez *et al.* 2020).

Thus comparative studies in SSD variation in several species of carabids should shed possible light on traits evolution in this large and progressive family. But such studies should be held by using the unified methodology and similar traits variation must be analyzed. As M. Shelomi said in relation to body size clines: “The type of organ examined for size variation is also important: several studies showed Bergmann clines for some morphological characters and converse-Bergmann clines for others within the same populations” (Shelomi 2012). No less important modern statistics use which allows to catch the smallest changes and differences in body size variation in both sexes. In other words, to reveal SSD.

Body size in different carabid species changed similarly in latitude gradient but sometimes the direction of variation slopes differed in males and females (Sukhodolskaya & Saveliev 2016). The first mention of SSD variation in *P. melanarius* was last ago (Sukhodolskaya & Saveliev 2017). SSD variation in elytra length followed Rensch’s rule at the edge of area, elytra width and pronotum length – at the centre. Head length and width variation followed converse one. More wide investigation showed that in *P. melanarius* regression slopes in body size were nearly zero both in males and females in latitude gradient, but the real SSD values changed from one region to another significantly (Gordienko *et al.* 2021; Luzyanin *et al.* 2022a).

Studies in another species – *Pterostichus oblongopunctatus* – gave similar results (Sukhodolskaya *et al.* 2020a). SSD variation in altitude gradient also was studied: its value varied at different elevations and was genera-specific (Sukhodolskaya *et al.* 2021). What is more, the value of SSD positively correlated with the number of beetles at the corresponding elevation.

Paper in SSD variation are known in the other orders (Bidau *et al.* 2013; Bidau *et al.* 2016; Cooper 2022a,b). In which connection the works in SSD variation in millipedes include environmental factors impact. Unfortunately sampling size in these papers is small and they are done predominantly on inter – specific level.

We do believe, that morphometrics studies should still be performed, particularly in widespread insect orders. Studies of species with overly large geographical ranges will cover many environmental or historical variables affecting body size. Then we conclude that studies of climatic factors impact should focus within species and look at widespread but contiguous populations to account for all sources of variation while minimizing error. Future ecogeographical-morphometrics studies should have species specific and mechanistic hypotheses.

Conclusions

As we suggested different traits responded differently to climatic factors. Especially it was seen in relation to elytra and pronotum length. Temperature – depended climatic factors mostly reduced beetles traits values, but precipitation related factors (Bio12–19) – enlarged them. SSD in response of beetles size variation occurred more than in 50 per cents of analyzed cases. Females and males elytra and pronotum parameters varied in different direction more frequently.

Our findings will enable the conservation authorities to initiate preemptive conservation strategies, such as ground beetles habitation and reproduction in different parts of their area. We also encourage conservation authorities to employ ecological body size and SSD variation models to map potential species distributions and to forecast range shifts due to climate change.

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