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RESEARCH ARTICLE

Geographic gradients in a functional trait: variation of body size and size diversity in ground beetle *Poecilus cupreus* (Linnaeus, 1758) (Coleoptera, Carabidae)

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Abstract

The aim of this study was to test the character of body size variation and its diversity in the widespread ground beetle *Poecilus cupreus* in geographical gradients. Beetles were sampled in 14 regions of Europe and the Asia, and sampling territories differed by 17° in latitude and 121° in longitude. We measured six linear traits in each captured beetle and formed a data set that included 6745 individuals. In the latitudinal gradient, three of the six traits studied decreased their values (direct trends), and the variability curve of four of the six features studied is hump-shaped with a maximum value in the middle latitudes (polynomial trends). In the longitudinal gradient, three traits decreased their values (direct trends), and the variability of three ones had the form of a concave curve with minimum values in the middle longitudes. The variability coefficients of the features themselves behave differently. Their value increased in the latitudinal gradient and decreased in the longitudinal gradient (direct trends). Polynomial trends show a hump-shaped curve – the greatest variability of feature values is observed in the middle latitudes and middle longitudes. We worked according to a single methodology and our analysis is intraspecific, so we insist that such eco-geographic and morphometric studies be conducted in the same way.

Keywords

Body size variation, geographical gradients, eco-geographical rules, ground beetles, coefficient of variation, morphometry

Introduction

Our report is based on the results of research that has been going on for more than 20 years – the variability of sizes and sexual dimorphism of ground beetles. One of the sections is related to the clarification of general biological ecological-geographical rules, in particular, Bergmann's rule. It states that the sizes of animals of taxonomically close groups increase towards the north. According to the most recent and thorough critical translation of the original German manuscript (Salewski and Watt 2017), the rule states that, all else equal, "within species and among closely related species of homeothermic animals (those that maintain a constant internal body temperature), a larger size is often achieved in colder climates than in warmer ones, which is linked to the temperature budget of these animals".

Bergmann assumed that an animal's surface area determines its rate of heat dissipation and its volume determines its heat production, which means that the surface area-to-volume ratio (SA:V) represents its thermoregulatory ability. Because volume increases faster than surface area because of the square-cube law, the SA:V of an organism decreases as it gets larger, also implying less heat loss per heat generated or less heat production needed to maintain body temperatures. Thus, Bergmann's rule can be summarized as saying that homeothermic animals will have a lower SA:V at higher latitudes and/or altitudes. And if for warm-blooded animals this rule is generally observed and is explained by thermoregulation mechanisms, then for poikilotherms – and this is an incomparably larger part of the terrestrial biota – no intelligible assumptions have yet been made (Blanckenhorn and Demont 2004).

In ectotherms, however, heat is not generated but absorbed from the external environment. Animals with larger surface areas lose and gain heat faster, and larger volumes mean more heat can be stored, but more heat is needed to affect a change in body temperature. Thus, selection for faster heat transfer should lead to larger SA:V ratios, while selection for more stable internal temperatures should lead to smaller SA:V ratios, and either can be preferable for hot or cold climates (Ashton and Feldman 2003).

The highly unpredictable variation in size clines shows data on insects, with different species within the same genus often showing contrasting relationships to latitude (Shelomi 2012). In addition to Bergmann and converse-Bergmann clines, there are nonlinear clines: cases where, for example, organisms are largest at the middle (Vamosi et al. 2007) or the extremes (Johansson 2003) of their latitudinal range, or where an increasing cline stops or resets periodically (stepwise or saw-tooth cline), usually due to changes in voltinism and seasonality (Masaki 1972; Nylin and Svärd 1991; Sukhodolskaya et al. 2021; Luzyanin et al. 2022). Many species showed no clines at all (Nylin and Svärd 1991; Shelomi 2012). Experimental design elements such as measured body parts, inter-/intraspecific variability, geographical range size, and contiguousness (whether the samples come from one continuous range or several, unconnected sites) all had effects on the results (Shelomi 2012). However, some general patterns appeared at the taxonomic level of orders. For example:

Coleoptera are more likely to show converse Bergmann clines, Diptera demonstrates Bergmann rule, and Plecoptera no cline at all (Shelomi 2012). Notably absent from the literature are ecogeographical data on the stick and leaf insects (order Phasmatodea), or Carabidae, though these orders are generally poorly studied, the lack of morphometrical data is particularly surprising due to the evolutionary importance of size on these orders.

The issue became relevant in the late 1990s in connection with the impact of climate change on animal habitats. A large number of studies conducted in different regions of the world and at different sites have yielded an equally large number of contradictory results, when: (i) the size of animals increased towards the north, inverse Bergmann's rule; (ii) more often it decreased, inverse Bergmann's rule; (iii) or it did not change at all.

As a result, in a number of review articles, reviewers of these studies came to the conclusion that the implementation of Bergmann's rule for poikilotherms is idiosyncratic. That is, it cannot be predicted. However, one of the masters made a reservation that, first of all, it is necessary to correctly scale the studies, that is, to conduct them simultaneously both on a large scale (within the continent) and in sufficient detail by location.

Since we had every reason to do this work, we began it, using beetles – ground beetles – as a model. We have chosen carabids for several reasons:

- To clarify Bergmann's rule, we needed material collected on approximately the entire continent, i.e., species distributed from Western Europe to Yakutia and from the southern regions of Russia to the tundra were needed. Ground beetles are a species rich and progressive family, and such species have been found; we currently have 18 of them in our work.

- Ground beetles have been well studied biologically and ecologically, that is, when we assessed the variability of sizes, we could rely on literary data on the influence of certain factors on the beetles of the studied species.

- Ground beetles have a complete metamorphosis, i.e., the hatched imagoes no longer grow during the growing season, and we could take a sample consisting of several generations into the analysis in order to increase the number of beetles measured.

- The measurement process was automated, using a custom-written program in Python, which speeds up the process and minimizes the influence of the human factor. Thus, the database was formed, which currently includes more than 60 thousand records.

As a result of our research, the idiosyncracies of the data according to Bergmann's rule were questioned. In other words, the implementation of Bergmann's rule in ground beetles seems to be quite predictable. For example, the working hypothesis is confirmed that the variability of ground beetles in the latitudinal gradient is genus-specific; in other words, it depends on the genus to which the species belongs. Therefore, for species of the *Carabus* genus, beetle sizes were shown to decrease monotonically towards high latitudes or in the altitudinal gradient, that is, the inverse Bergmann rule is observed (Sukhodolskaya and Saveliev 2016a, b; Ananina et al. 2020). For species of the genus *Pterostichus*, the picture is different (Luzyanin et al. 2022). The size variability curve is saw-toothed, that is, when moving north, the size can increase abruptly, then decrease, then increase again. At the same time, the regression curve has practically no slope; that is, if another researcher takes only a few points for analysis, he would come to the conclusion that the sizes of this species do not change in the latitudinal gradient.

Work on the morphometric variability of *P. cupreus* has been carried out before. Therefore, when there were only four points of the range in the analysis, the regression of the length of the curve of variation in the elytra in this species was practically zero, although males were recorded that males in the Stavropol region (in the south of the range) were significantly larger than in Tatarstan (the center of the range), Kemerovo and Novosibirsk regions (Sukhodolskaya and Saveliev 2015, 2016a, b). In another similar study, *P. cupreus* beetles were larger in Ukraine compared to Chechnya, Tatarstan and the Kostroma region (Sukhodolskaya et al. 2018).

In another work, the influence of anthropogenic factors and cultivated plants on body size and shape in the ground beetles *P. cupreus* (Sukhodolskaya and Saveliev 2016a,b; Sykhodolskaya et al. 2017): in agrocenoses the beetles were larger than in the city, and in natural cenoses only females were larger. Furthermore, the shape of the beetles living in the rye fields was significantly different from that of all other cultures. In general, the morphometric structure of *P. cupreus* populations living in different fields differed statistically significantly (Teofilova and Sukhodolskaya 2021; Teofilova et al. 2022).

This study aims at (1) estimating the variation in body part size variation in geographical gradients and (2) revealing the variability of these traits in those gradients.

Materials and methods

1. Study organism

Poecilus cupreus is a widespread Palearctic species 8.5 to 13.5 mm in length. The humeral tooth of the elytra is indistinct. The head is densely dotted. The elytra are somewhat wider than the base of the pronotum. The upper surface is copper-red, bronze, green, black, and blue; sometimes the femora, rarely the legs, are red (Fig. 1). The coloration is very diverse, sometimes two-colored, and the legs are always black. This is a meadow field species with a high population of agrocenoses. It is of great importance as an entomophage. It also finds favorable conditions for living in urban areas and has a wide range of requirements for the habitat.

Figure 1. Appearance of *Poecilus cupreus* beetles.

2. Sampling regions

The material was obtained under scientific cooperation agreements from researchers from 14 regions of Russia and abroad. Ground beetles were caught using the standard Barber trap method. The sample from each region included beetles caught at a range of sites that differed in the degree of anthropogenic impact and vegetation: cities, suburbs, agrocenoses, and natural biotopes. The number of individuals in each raft was at least 35 individuals (Table 1).

To catch ground beetles, Barber's soil traps have always been used, in accordance with generally accepted methods. Soil traps are cylinders (jars), the upper opening is placed flush with the soil surface, but so that pieces of soil and debris do not fall into the trap. A small amount of soil is poured into the cylinders (jars). In some cases, attractants are used. Traps should be inspected regularly. They are often used to collect ground beetles. Wine or apple cider vinegar, fermented beer, and sugar-yeast starter (mash) are used as bait for ground beetles. The use of soil traps has its own characteristics. The choice of location is a particularly important point. It is necessary to understand where the beetles that are needed for research can live. For ground beetles, these are forests, forest edges, grassy screes, mountain meadows with scattered stones, bush thickets, ravine bottoms, and canals. In places with a low population density of running insects (dry steppe areas, semi-desert and desert, meadows), it is recommended to place cups in trapping grooves 1.5–2 meters long and 20 x 20 cm deep and wide, 1 to 2 pieces per each. After pickling, it is recommended to rinse and dry ground beetles and then lay them on cotton mattresses.

3. Study design

Individuals were photographed 5 to 6 specimens at a time and the parameters were measured in a self-written program in Python 2.7 using the NumPy and openCV libraries. The program is necessary to achieve greater measurement accuracy, automate the process, and reduce subjectivity. They are measured according to six dimensional traits (Fig. 2). A total of 6791 insect specimens were measured, with the last column indicating the number of specimens measured in each region (Table 1). Data are collected in Excel tables for subsequent statistical analysis.

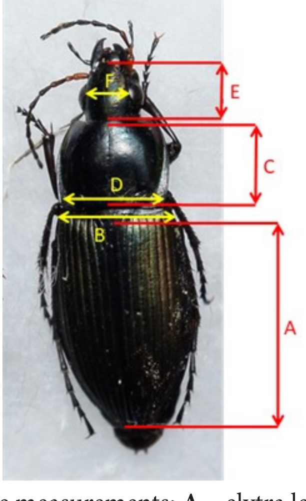

Figure 2. The scheme of beetle measurements: **A** – elytra length; **B** – elytra width; **C** – pronotum length; **D** – pronotum weight; **E** – hat length; **F** – distance between eyes.

Table 1. Description of sampling localities of *P. cupreus*

Region	Latitude	Longitude	Number of sites	Type of habitats	Sample size
Switzerland	47°0.096'N	8°0.078'E	1	rape	148
Germany	51°5.496'N	9°0.078'E	4	rape	569
Bulgaria	42°19.458'N	25°1.392'E	3	rape	698
Romania	44°15.108'N	26°22.218'E	9	rape	1174
Slovakia	48°1.200'N	18°15.000'E	1	meadows, pasture	146
Turkmenistan	40°27.000'N	58°46.2003'E	1	arable	40
Russia:					
Krasnodar Krai	44°22.998'N	38°58.002'E	1	rape	154
Kostroma Region	57°27.636'N	40°33.354'E	1	meadow	100
Stavropol Krai	44°27.600'N	44°2.400'E	1	meadow	71
Chechen Republic	43°10.314'N	45°27.204'E	1	arable	187
Republic of Tatarstan	55°28.386'N	49°4.320'E	9	barley, pea, spring wheat, rye, vetch and oat, alfalfa, carrot, lawn	2643
Sverdlovsk Region	57°24.540'N	59°34.320'E	1	meadow	200
Kemerovo Region	55°15.120'N	86°42.000'E	1	meadow	67
Novosibirsk Region	55°16.200'N	79°19.800'E	2	meadow	548

4. Data Analysis

Statistical processing was carried out in the Excel program. Methods of one-dimensional statistical analysis were used. The mean, standard deviation, error of the mean, and variation coefficient were calculated. The variation coefficient is calculated using the formula standard deviation/mean*100. Graphs were constructed based on the data obtained, and the results were entered into a table.

Results

When analyzing body size variation in *P. cupreus*, we generated a series of graphs to illustrate these patterns. As there were 6 traits in analysis and we analyzed their variation in two gradients (latitude and longitude) and estimated not only linear variation but also its coefficient variation, we received 48 figures. Here we present figures only in the elytra length variation. Results on the other 5 traits variation will be only described in text.

The Elytra length changed insignificantly in the latitudinal gradient, this applied to both straight and polynomial trends, and in the latter there was a tendency for a slight increase in the middle of the studied latitudes (Fig. 3A, B). In the longitudinal gradient, the values also changed slightly, both in straight and polynomial trends (Fig. 4A, B).

The coefficients of variation of the length of the elytra tended to increase slightly in the latitudinal gradient and to decrease in the longitudinal gradient (Figs 5A, B; 6A, B).

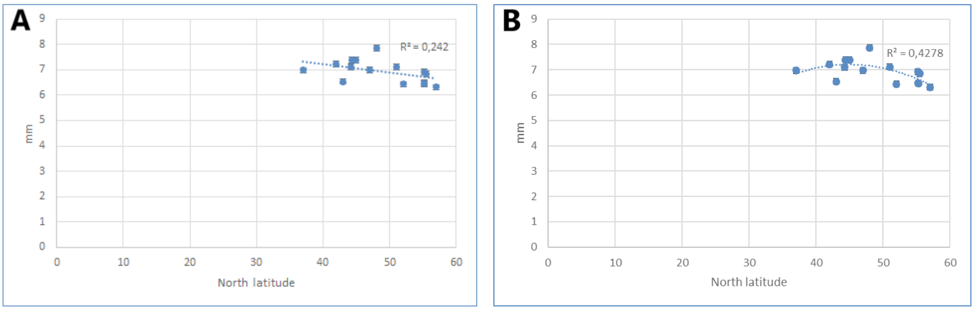

Figure 3. Variation in elytra length in *P. cupreus* in latitude gradient: **A** – straight trend; **B** – polynomial trend.

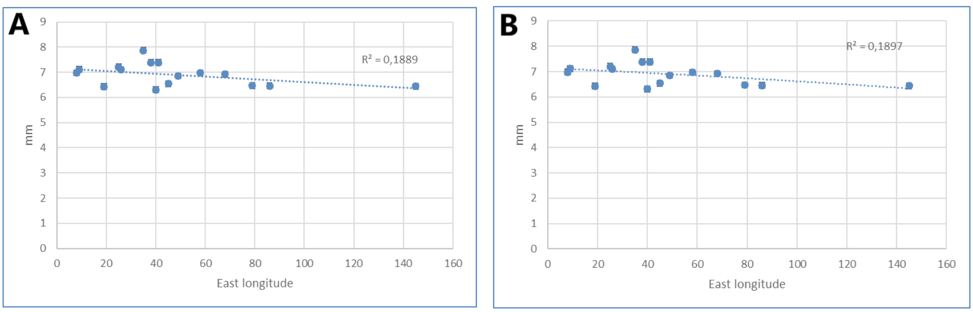

Figure 4. Elytra length variation in *P. cupreus* in longitude gradient: **A** – straight trend; **B** – polynomial trend.

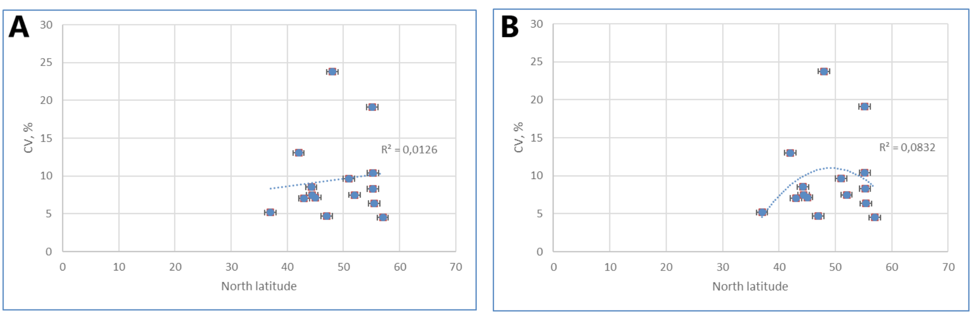

Figure 5. Variation of the coefficient of variance in the length of *P. cupreus* elytra in latitude gradient: **A** – straight trend; **B** – polynomial trend.

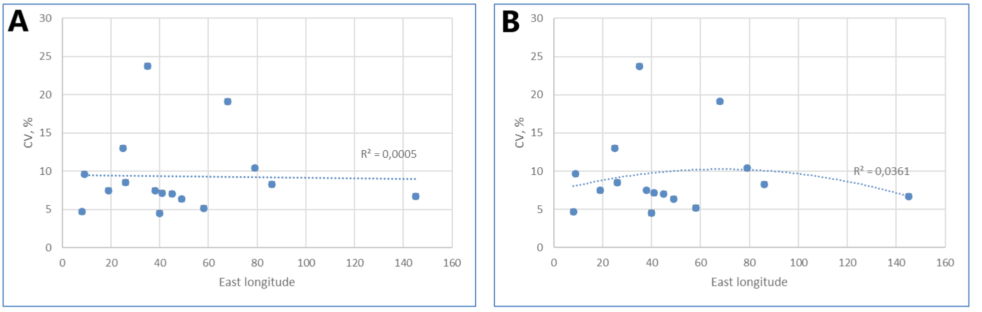

Figure 6. Variation of the coefficient of variance in the length of *P. cupreus* elytra in longitude gradient: **A** – straight trend; **B** – polynomial trend.

The variation of means and coefficients of variance in other traits studied is presented in Table 2. The elytra width in the latitudinal gradient increased when moving toward northern latitudes in straight and polynomial trends. In the longitudinal gradient, the changes were insignificant in straight lines, and in the polynomial trend, a slight increase in size occurred in the central longitudes.

Variation coefficients tended to increase in the latitudinal gradient and decreased in the longitudinal one. The length of the pronotum practically did not change in both the latitudinal and longitudinal gradients, but in the polynomial trends an increase was visible in the central latitudes. In the longitudinal gradient, no changes were observed. The variation coefficients tended to increase in the latitudinal and decrease in the longitudinal, whereas in the polynomial trend an increase was noticeable in the central part of the graph.

The width of the pronotum decreased when moving in the latitudinal gradient and slightly decreased in the longitudinal in straight trends. As for the polynomial trends, in the latitudinal gradient, an increase in size in the central latitudes was noticeable. In the longitudinal gradient, a slight tendency to decrease in the central longitudes was noticeable.

The variation coefficients were practically unchanged, and there was only a noticeable increase in the central latitudes in the polynomial trend. The head length changed insignificantly in the latitudinal gradient; this applied to both straight and polynomial trends, and in the latter there was a tendency for a slight increase in the middle of the studied latitudes. In the longitudinal gradient, the values also changed slightly, both in straight and polynomial trends, and in polynomial trends there was a slight tendency to decrease in the middle of the studied longitudes.

The head length variation coefficients tended to increase slightly in the latitudinal gradient and decrease in the longitudinal gradient. The distance between the eyes changed insignificantly, both in the latitudinal and longitudinal gradients. This was applied to both straight and polynomial trends.

Variation coefficients tended to increase in the latitudinal gradient and slightly decreased in the longitudinal gradient. In the longitudinal gradient with polynomial trend, there was a tendency to increase in the middle of the studied longitudes.

Table 2 shows the squares of the regression coefficients (R^2). The reliability of the slope curves can be seen by providing data on the calculated R values (Table 3). First, it is worth checking the coincidence of the R values in the straight and polynomial trends, which showed that in about half of the cases such values do not coincide. This must be borne in mind when calculating trends of different levels, when conducting regression analysis. Second, we obtained statistically reliable R values only in three cases, so we can conclude that in the variability latitudinal gradient, the curves of the elytra length and the pronotum width had a hump-shaped form with maximum values in the middle latitudes. In the longitudinal gradient, only the length of the elytra changed reliably, monotonously decreasing towards the east. If we take into account all the indicated trends (with values of $R > 0.1$), we can say the following:

- in the latitudinal gradient, three of the six studied traits decreased their values (direct trends), the variability curve of four of the six studied features is hump-shaped with a maximum value in the middle latitudes (polynomial trends);

- in the longitudinal gradient, three traits decreased their values (direct trends) and the variability of three ones had the form of a concave curve with minimum values in the middle longitudes.

Table 2. Statistical analysis of trait size variation across geographical gradients in *P. cupreus*

Traits / Regression coefficients	Linear R^2 lat	Linear R^2 long	Polynom R^2 lat + form info	Polynom R^2 long+ form info	Linear CV lat R^2	Linear CV long R^2	Polynom CV lat R^2+ form info	Polynom CV long + form info R^2
Elytra length	0.15	0.29	0.32 Weak∩*	0.29 —	0.02	0.00	0.10 ∩	0.03 Weak∩
Elytra width	0.05	0.00	0.06 —	0.05 Weak∩	0.06	0.03	0.06 Weak∩	0.05 Weak∩
Pronotum length	0.04	0.03	0.15 Weak∩	0.03 —	0.03	0.00	0.04 Weak∩	0.10 Weak∩
Pronotum width	0.27	0.07	0.56 Weak∩	0.12 WeakU	0.00	0.00	0.09 ∩	0.00 —
Head length	0.02	0.18	0.14 Weak∩	0.20 WeakU	0.11	0.05	0.16 Weak∩	0.06 Weak∩
Distance between eyes	0.01	0.01	0.02 Weak∩	0.01 —	0.13	0.00	0.14 Weak∩	0.14 Weak∩

Note: *Coefficient of variation regression and the form of its variation curve.

The variability coefficients of the features themselves behave differently. Their value increased in the latitudinal gradient and decreased in the longitudinal gradient (direct trends). Polynomial trends show a hump-shaped curve – the greatest variability of feature values is observed in the middle latitudes and middle longitudes.

Here we can note some correlation: the higher the value of the trait at a given latitude, the higher its variation coefficient. The opposite situation was observed with respect to the longitudinal gradient: at lower values of the trait, its variation coefficient was the highest.

Table 3. Geographical variation in *P. cupreus* trait size: regression analysis (R^2) and statistical significance ($p < 0.05$)

Traits / Regression coefficients	Linear R lat	Linear R long	Polynom R lat	Polynom R long	Linear CV lat R	Linear CV long R	Polynom CV lat R	Polynom CV long R
Elytra length	0.38	0.54	0.57	0.54	0.15	0.04	0.31	0.18
Elytra width	0.23	0.06	0.24	0.23	0.24	0.18	0.25	0.22
Pronotum length	0.21	0.18	0.39	0.18	0.18	0.07	0.21	0.32
Pronotum width	0.52	0.27	0.75	0.34	0.07	0.01	0.31	0.05
Head length	0.14	0.42	0.37	0.45	0.32	0.23	0.40	0.25
Distance between eyes	0.08	0.11	0.15	0.11	0.37	0.03	0.38	0.37

Discussion

In this regard, a methodological aspect of conducting experiments emerges, which has been repeatedly mentioned by some researchers working on the problem of geographic gradients (e.g. Shelomi 2012). Therefore, our studies are consistent with the work on the variability of the sizes of soil invertebrates collected for several years in the NEON pitfall trap network to quantify the geography of the average and diversity of body size from Alaska to Puerto Rico (Kaspari et al. 2024). In the mentioned work, the authors calculated the size of the animals at the community level and found that different taxa exhibited directly opposite trends in size variability in the latitudinal gradient. Thus, if in dipterans and mites, the size clearly increased in the latitudinal gradient, then in beetles and Orthoptera, it clearly decreased. Moreover, in the first two taxa, the increase in size was accompanied by a decrease in the coefficient of variation of sizes, and in the last two taxa, the coefficient of variation also decreased, as did the sizes themselves.

The obtained results, of course, can be attributed to the taxon-specificity of size variability and the coefficient of size variation in the latitudinal gradient. But we are inclined to agree with the opinion of M. Shelomi, who wrote that "general explanations for ectotherm size clines, like the cline rules themselves, will not apply to a given species with any predictability and are influenced by experimental bias and design. Trends in one species cannot be expected to apply even to closely related species. Future ecogeographical-morphometric studies should have species specific and mechanistic hypotheses" (Shelomi 2012). At least we worked according to a single methodology, and our analysis was intraspecific.

Nowadays, it is common to write articles based purely on literary material without thinking about when and where the material was collected. Moreover, sometimes the sizes of insects are simply calculated using a formula that only has data on body weight. And this, as is clear, is unacceptable. Sometimes they use museum exhibits, also collected at different times and using different methods. But this does not in any way diminish the scientific significance of such works as, for example, Shelomi's article on the temporal size variability of Scarabeid beetles (Maher and Shelomi 2022) or a compilation of studies on the life-history of arthropods (Logghe et al. 2024). Therefore, we can fully confirm the scientific relevance of our methods for assessing the nature of size variability in geographic gradients of one of the representatives of such an important family among arthropods – ground beetles.

Conclusions

The problem of Bergmann's rule clarification for ectotherms is far from being resolved. This is due not only to the lack of unified methods of sampling and processing the material but also to the fact that latitudinal clines are often followed by variation of accompanying parameters (temperature, resource availability), which often correlate with latitude. The fact of the presence of local body sizes variation, caused by intrapopulation or other reasons, is of no small importance. We believe that the solution to the problem of variability of animal sizes in geographic gradients should consist of successive systematic collections of animals and be solved at the intraspecific level.

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