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Article

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Simple Summary

The topic of sexual dimorphism has fascinated researchers since Darwin, but there remains a lack of consistent research on the mechanisms underlying this phenomenon. Most studies have been conducted at the interspecies level, using various methods and analyzing the variability of a single trait, leading to contradictory results. Sexual dimorphism is considered an indicator of habitat, and in some cases, a kind of "compass" of evolutionary change. Therefore, its study must be accompanied by fundamental research. These include meta-analyses, where authors compile data from the literature and draw certain fundamental conclusions. In particular, the proposition that SSD increases with increasing size in insects. In fact, the authors conclude that confirming this conclusion requires studies at the intraspecies level, using a larger data set. We decided to continue their research.

Abstract

The study was based on a large database of morphometric measurements of the ground beetle *Carabus granulatus*. It was compiled between 2006 and 2025 and includes over 10,000 individuals of this species, captured in 14 major regions of Russia and Western Europe. Beetles were captured with Barber traps across a spectrum of anthropogenic impacts—urban areas, suburbs, agricultural lands, and natural biotopes. They were then transported to the Institute of Ecology of the Academy of Sciences of the Republic of Tatarstan, where they were measured using a unified method for six linear traits. SSD was assessed using two methods. Using the standard Lovich formula, SSD for all traits was significantly higher, on average in all six traits, in beetle populations from suburban areas. Application of the second method, RMAII, showed that the slope of the regression curve is generally

higher in females, indicating greater sensitivity of *Carabus granulatus* females to environmental factors. At the same time, a comparison of the results obtained by the aforementioned methods did not support the thesis that SSD increases with beetle size. The curves for SSD variability in both urban and non-urban populations were sawtooth-shaped. This conclusion may be due to the fact that the variability of both structural traits and SSD for them is not described by a monotonic curve. This necessitates studying the variability of SSD in other ground beetle species (or genera) using the same data set and a unified methodology.

Keywords: Sexual Size Dimorphism; ground beetles; gradient of urbanization; RMAII models; sex-biased sensitivity

1. Introduction

Land-use change is considered the primary source of biodiversity loss worldwide [1], and urbanization represents one of the most intense and long-lasting modifications of natural systems [2]. Urbanization gradients, typically extending from rural areas to highly developed city centers, have long been a major target of ecologists' research. Such gradients include extensive changes in habitat structure, including habitat loss and fragmentation [3] and increased soil impermeability, leading to the subsequent urban heat island effect.

With all this diversity of changes in the urban environment, it is not surprising that the response of the biotic component to urbanization can be diametrically opposed. For example, it has been shown that some butterfly species are completely absent from cities, although they inhabit adjacent areas [4], while the abundance of some midge and spider mite species in urban ecosystems increases [5].

As for ground beetles, a meta-analysis based on publications from 14 European and American cities showed that it is not so much the number of beetles that changes in cities, but rather the structure of communities. Changes occur in size composition (in favor of small species), flight ability (in favor of macropterans and dimorphic species), and trophic preference (in favor of herbivorous species and species with mixed feeding) [6]. At the same time, these authors note that despite the close relationship with these parameters, other sources of variability in urban ground beetle communities must be considered, as no correlation with either city size or its history (date of foundation) has been established, and some ground beetle species demonstrate diametrically opposed spatial exploration strategies in the cities studied.

Anthropogenic transformation in invertebrates leads to increased plasticity of physiological traits, while plasticity of morphological traits decreases. Anthropogenic influence is more detrimental to animal populations compared to fluctuations in the natural environment, since it leads to more rapid restructuring [7]. Thus, changes in the external environment in general, and anthropogenic influence in particular, can lead to maladaptation of populations. To avoid extinction, populations develop responses (increased fitness, population size, etc.). Recently, increasing attention in this regard has been paid to phenotypic plasticity [8,9], which is defined as changes in the phenotype of an organism under the influence of the environment. In some cases, such plasticity is adaptive and allows a population to "jump" from one peak of fitness to another, by passing the "passage" of fitness valleys [8,10].

Morphological features make it possible to expand the scope ecological-functional responses of a guild (in this case, ground beetles) from local to global scales, thus bypassing a purely taxonomic approach based on a regional species pool [11]. A similar concept from local to global is outlined by Pizzolotto et al. [12], but only for chorological traits, where a new index of biogeographic specificity is proposed that emphasizes the value of endemic species for different types of biotopes. The use of species traits in terrestrial habitats provides a new opportunity to assess the degree of disturbance of a biotope if the ecology, morphology, physiology, and life cycles of a taxon are well studied.

Morphology is the main phenotype of an organism, directly related to how it interacts with the environment [13]. Therefore, the study of the morphological characteristics of species, their diversity,

and variability complements knowledge about populations and communities, provides insight into factors influencing organisms' responses to environmental changes.

Our research was inspired by a review publication by Estonian researchers, where sexual dimorphism was assessed based on the degree of variability in the sizes of females and males, which, according to the authors, reflects the sensitivity of the sexes to environmental factors [14]. To quantitatively describe the relationship between the sizes of females and males, we used type II regression (RMA II), which involves constructing a regression curve of the logarithm of male sizes on the logarithm of female sizes. The model constant (Intercept), slope, and statistical significance are also calculated. The results of the regression analysis were interpreted as follows. A positive slope of the regression curve indicated that environmental conditions influenced the sizes of females and males in the same direction, i.e., male size increased with increasing female size. This result allowed us to unambiguously rank the samples according to the degree of favorability of environmental conditions. Furthermore, a zero model constant implied a proportional increase in the sizes of males and females as conditions improved. A positive model constant indicated that females increased in size relatively faster than males, with males being more sensitive to environmental conditions. A negative model constant indicated the opposite trend. These parameters allowed us to draw conclusions about the dependence of sexual dimorphism on environmental conditions. In particular, it is easy to see that sex differences in the sensitivity of body size to environmental conditions should lead to different size ratios of females and males in different environments. Accordingly, with increasing environmental quality, the greater sensitivity of female body size will lead to more pronounced sexual dimorphism in species with larger females. The latter includes the ground beetle species *C. granulatus*, which we studied. If the model constant is negative, the slope of the regression curve will be greater than 1, and, accordingly, males are more sensitive in this case. All conclusions about the dependence of sexual dimorphism on body size and environmental conditions were made at the meta-level. For this purpose, a vote-counting method was used (positive versus negative slopes; positive or negative model constants). The parameters of each intraspecific relationship were treated as separate observations.

In our study, we essentially replicated the methodology discussed above, but applied RMA II models specifically to the analysis of beetle size variability depending on collection location within a range. *Carabus granulatus* L. was chosen as the model species due to its widespread distribution, sufficient eurybionticity, and well-studied ecology. Similar studies have been conducted previously on other ground beetle species. Thus, in relation to the mountain ground beetle *Carabus cummanus*, different sensitivity of females and males to the vegetation conditions of the biotope was shown [15], and in other species of ground beetles - *Carabus odoratus*, *Carabus exaratus*, *Pterostichus montanus* - different patterns of variability of individual organs in females and males at different altitudes in the mountains [16]. In the present study, we aimed to determine the nature of variability in the sizes of beetles of both sexes depending on the habitat. The latter was assessed by the degree of urbanization - cities, suburbs, natural biotopes. At the same time, we predicted: (i) the direction of size variability should be the same for females and males at all captured points; (ii) in urban habitats, males will be more sensitive to environmental conditions, that is, their size will increase at a greater rate compared to females; (iii) accordingly, sexual dimorphism in urban habitats will be expressed to a lesser extent compared to suburbs and natural biotopes.

2. Materials and Methods

2.1. Object of Study

C. granulatus is a large beetle that measures 18-26 mm in length, with a bronze or copper upper surface, often with a green sheen, and sometimes bronze black (Figure 1). The femora is sometimes red. The pronotum is uniformly densely punctate. The antennae are long, reaching halfway along the elytra in males. The elytra are sinuate before the apex with elytral eripleura abruptly near the upper

edge of sinuation and have a sharp sculpture consisting of ridges and chains of tubercles. The pits on the elytra are small and barely noticeable [17,18].

This species is hygrophilous and eurytopic with a transpalaeartic distribution throughout the Eurasian continent from the lowlands to the mountains. It inhabits riparian ecosystems or moist floodplain meadows with dense vegetation. The species has a life cycle; in the northern taiga, it is found only in meadows, while in floodplain forests, its occurrences are rare [19]. In more southern regions, this moisture-preferential species is observed in moist to wet forests, especially floodplain [20,21]. In general, it is a spring breeder without larvae, but with an obligatory adult diapause [21]. It hibernates, often gathering in groups, under the loose bark of trees. Both adults and larvae are predators. The larva moults three times before pupation and, in the laboratory, beetles have been successfully reared from eggs in 53 days.



Figure 1. *Carabus granulatus* in nature. Photos were taken from Internet.

2.1. Study Area and Trapping

This study is part of a larger project on the morphometric variability of the ground beetle *C. granulatus*. As part of this study, a large team of carabidologists has been collecting samples of this beetle for many years, which are then transported to the Institute of Ecology and Subsoil Use of the Academy of Sciences of the Republic of Tatarstan (Kazan, Russia) for morphometric analysis. A detailed description of the beetle collection sites and collection methods is provided in our recent publication, which examined the latitudinal gradient of size variability in this species of beetle [22]. Since then, we have added beetle samples from Italy, Czech Republic, some regions from Russia. Thus, the database with morphometric measurements of six linear traits of beetles has reached 10,172 individuals.

The sampling area included a vast territory in different provinces of Russia, and several sites in six European countries (Figure 2, Table 1).

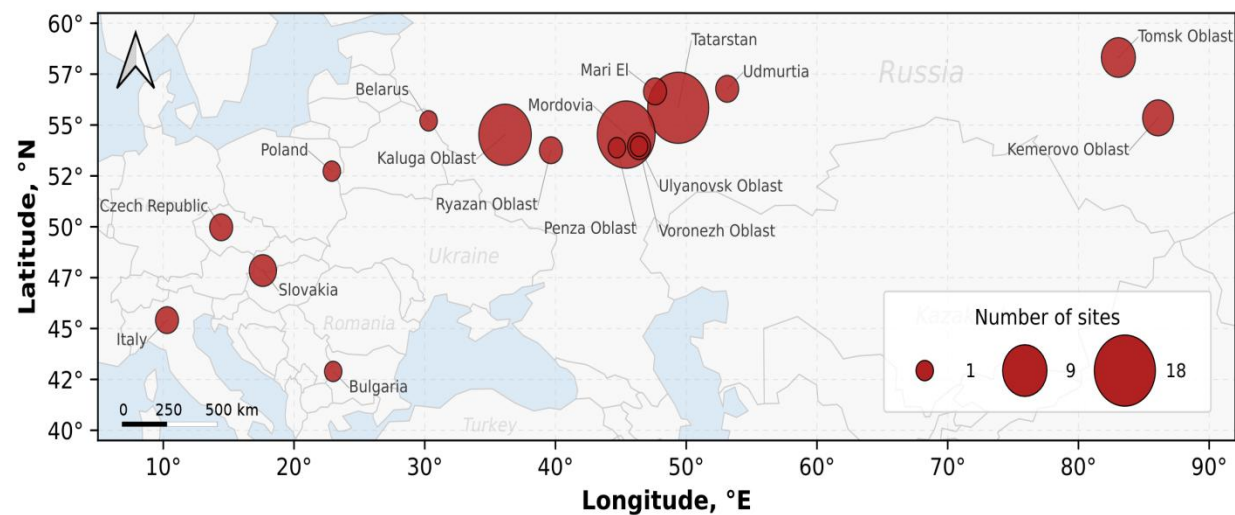


Figure 2. Map of the study area.

Table 1. Regions of sampling plots, geographical coordinates, number of plots, and sample size.

Country/Region in Russia	Number of Plots	Latitude	Longitude	Females	Males	Total
Tatarstan Republic ^a	18	55.846	49.387	1193	1245	2438
Kemerovo Oblast ^a	4	55.352	86.091	96	112	208
Udmurtia Republic ^a	2	56.777	53.134	301	307	608
Mariy El Republic ^a	2	56.649	47.616	84	131	215
Belarus	1	55.205	30.293	39	90	129
Kaluga Oblast ^a	13	54.521	36.143	1530	3733	5263
Bulgaria	1	42.891	22.999	60	34	94
Slovakia	3	47.848	17.616	71	72	143
Poland	1	52.731	22.893	80	80	160
Mordovia Republic ^a	16	54.529	45.407	256	200	456
Penza Oblast ^a	1	53.885	44.700	1	2	3
Ryazan Oblast ^a	2	53.761	39.652	18	25	43
Ulyanovsk Oblast ^a	2	53.960	46.392	118	110	228
Voronezh Oblast ^a	1	53.951	46.392	12	1	13
Italy	2	45.412	10.285	53	52	105
Czech Republic	2	49.974	14.430	16	52	66
Total	71			3928	6246	10172

Legend: the apex “a” corresponds to Russia. The Region number refers to a database of ground beetles constantly updated as beetles are collected from new regions. The species *C. granulatus* analyzed in our study, was not collected in all regions of the database. Therefore, the region numbering is not sequential. Beetles in every region were pitfall trapped using the standard methodic in the period 2006-2025.

2.2. Morphometric Data

All measurements were conducted using a unified methodology adopted by us, described in previously published articles [23–25]. Studied plots differed in some environmental parameters. But taking into account that our investigation was large-scale and remembering the huge number of sampling plots and measured individuals, we argue that our approach was the high-throughput one. The last became very popular the last decades, when the authors compiled data even not their own research and make conclusions on the given topic [26].

Measurements included six traits: elytra length, elytra width, pronotum length, pronotum width, head length and distance between eyes (Figure 3).



Figure 3. Male (left) and female (right) of *C. granulatus*. Males are slightly smaller than females, the main difference when differentiating the sample by sex is the expanded segments of the front legs of males.

2.3. Statistical Analysis

We used the R statistical environment.

An ANOVA was conducted to assess the influence of environmental factors.

Specific SSD values were calculated using the generally accepted Loveich and Gibbson formula: $SSD = \text{females/males} - 1$.

To estimate the allometry of the PDR, type II regression models were used, using the reduced major axis method (RMA). The logarithm of the quantile distribution of the studied male traits was calculated as a linear function of the logarithms of the quantile distribution of these sizes in females. The model is output to a text file, $Y = \alpha X\beta$. Positive values of the regression coefficient (β) indicate the same direction of change in the trait in males and females; in other words, as the trait value increases in females, the values of the same trait in males also increase. Positive values of the model constant (Intercept) indicate that females increase in size faster than males, meaning that females are more sensitive to environmental changes; negative values indicate the opposite [14]. RMA and SMA should be used when there is a high correlation (we have this - on average about 75% and higher with a high level of reliability $p < 0.001$ according to Pearson), and also when the number of points is more than 67 (we had that) [27]. The lmodel2 library was used to calculate the RMA regression coefficients [28]. For example

```
result_ <- lmodel2(el_l_male_log ~ el_l_female_log, data = data,
range.y = "relative",
range.x = "relative",
nperm = 1000)
print(result_)#(factor «range» was taken for estimation of Ranged Major Axis)
Regression results
```

	Method	Intercept	Slope	Angle (degrees)	P-perm (1-tailed)
1	OLS	3.914979	0.7519160	36.94009	0.000999001
2	MA	1.189834	0.9910264	44.74177	0.000999001
3	SMA	1.165074	0.9931990	44.80450	NA
4	RMA	1.397337	0.9728197	44.21066	0.000999001

Confidence intervals

	Method	2.5%-Intercept	97.5%-Intercept	2.5%-Slope	97.5%-Slope
1	OLS	2.0799836	5.749974	0.5911750	0.912657
2	MA	-1.5281748	3.384476	0.7984635	1.229511
3	SMA	-0.8141801	2.849755	0.8453812	1.166863
4	RMA	-1.2463576	3.567658	0.7823908	1.204783

Eigenvalues: 0.7612505 0.1052455

H statistic used for computing C.I. of MA: 0.01142403

To calculate the regression, we used logarithmic mean trait values for males, based on the mean trait value for females from each sampling point. There were 67 sampling points in total, including 43 from natural habitats, 10 from suburbs, and 14 from cities.

The fragment of data frame used:

locality	anthropel_1	male_logel_1	female_log	
<int>	<int>	<dbl>	<dbl>	
1	1	1	2.56	2.42
2	2	1	2.56	2.44
3	3	1	2.56	2.42
4	4	1	2.55	2.42
5	5	1	2.56	2.44
6	6	2	2.54	2.41
7	7	2	2.52	2.41
8	8	3	2.53	2.48
9	9	3	2.52	2.48
10	10	3	2.55	2.42

3. Results

The ANOVA showed that the level of anthropogenic impact on ground beetle habitats influenced the size of their traits. Table 2 presents the results for the effect of anthropogenic pressure on elytra length, showing that the level of anthropogenic impact and sex, as well as their interaction, influence elytra size in the studied ground beetle species.

Table 2. Results of the ANOVA for the effect of anthropogenic pressure and sex on elytra length in *C. granulatus*.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
anthrop	2	23	11.4	14.64	4.50e-07 ***
sex	1	2007	2007.1	2578.79	< 2e-16 ***
anthrop:sex	2	24	11.9	15.29	2.37e-07 ***
Residuals	8160	6351	0.8		

Roughly similar results were obtained for other traits (Appendix A, Tables A1-A11), but there were some differences. For example, no statistically significant combined effects of the "Anthropogenic" and "Gender" factors or the effect of suburban habitat were observed for elytra width. No effects of urban and suburban habitat were observed for pronotal length. Variability in pronotum width depended solely on gender, and the interaction of the "Anthropogenic" and "Gender" factors affected head parameters.

Thus, it was demonstrated that not only the level of anthropogenic impact but also its interaction with gender influenced beetle size. The involvement of gender in regulating the biota's response to anthropogenic impact led to changes in SSD.

We first calculated the average SSD values in plots with different levels of anthropogenic impact (Figure 4). To our surprise, the highest SSD values were consistently recorded for all six studied traits in suburban areas: SSD values for elytra and pronotal length, as well as distance between eyes, were statistically significantly higher in suburban populations compared to those from the city and natural habitats. SSD values for elytra and pronotum width did not differ between beetles from natural habitats and suburban areas, and for head length, they were similar between beetles from suburban and urban areas.

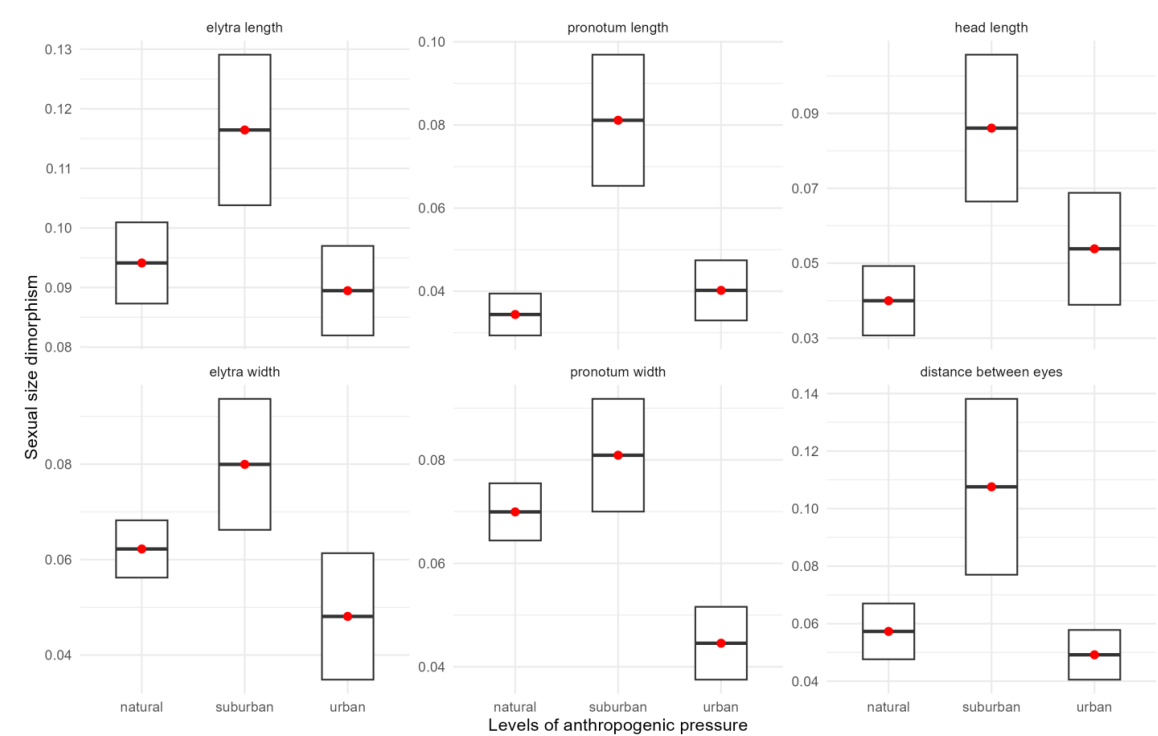


Figure 4. SSD values in different traits in localities with differing anthropogenic press.

To further our understanding of the mechanisms underlying this SSD variability, we analyzed the data using the RMAII method (Table 3).

Table 3. RMAII results in *C. granulatus* populations.

Factor_	Parameter	N	Intercept	Slope	p_val
Urban	Elytra.Length	642	0.23	0.87	0.00
Urban	Elytra.Width	642	-0.19	1.08	0.00
Urban	Pronotum.Length	642	0.01	0.99	0.00
Urban	Pronotum.Width	642	0.03	0.93	0.00
Urban	Head.Length	642	0.04	0.94	0.00
Urban	Eye.Distance	642	0.22	0.71	0.00

Suburban	Elytra.Length	537	0.22	0.88	0.00
Suburban	Elytra.Width	537	-0.04	0.98	0.00
Suburban	Pronotum.Length	537	0.00	0.97	0.00
Suburban	Pronotum.Width	537	-0.10	1.01	0.00
Suburban	Head.Length	537	-0.06	1.00	0.815
Suburban	Eye.Distance	537	-0.02	0.96	0.00
Natural	Elytra.Length	1790	0.40	0.80	0.00
	Elytra.Width	1790	0.04	0.93	0.00
Natural	Pronotum.Length	1790,00	0.03	0.93	0.00
Natural	Pronotum.Width	1790	0.15	0.85	0.00
Natural	Head.Length	1790	0.05	0.90	0.00
Natural	Eye.Distance	1790	-0.09	1.01	0.00

The slope of the regression curve was positive in all cases, meaning that the sizes of females and males vary in the same direction depending on habitat. Generally, a pattern was observed: if the model constant was negative, the slope of the regression curve was greater than 1; if it was positive, it was less than 1. The two curves examined were an exception (12%).

If we consider each trait separately, we see that, under virtually all types of anthropogenic impact (cities, suburbs, and natural habitats), females exhibited greater sensitivity to environmental conditions. Regression curve slopes were greater than 1 in only three cases: elytra width in cities, pronotum width in suburbs, and interocular distance in natural habitats. In other words, urban habitat increased male sensitivity to the "elytra width" trait; suburban habitat increased sensitivity to the "pronotum width" trait; and in natural habitats, males were sensitive to the "interocular distance" trait. It should be noted that, regardless of the factor, body width traits were involved in the phenomenon of increased male sensitivity.

The final aspect of our research concerns the confirmation of the hypothetical figure presented in the article by Teder and Tammaru [14], whose work we relied on for our experiments. The figure presented by the aforementioned authors suggests that SSD should decrease with a negative Intercept and, accordingly, a regression slope greater than 1. This is observed because male size increases faster than female size, and in species with female-biased SSD.

We conducted a generalized RMAII analysis, which results in a logmale/logfemale regression curve for *C. granulatus* beetles as a whole for each studied trait. Specific beetle collection locations are indicated by colored circles in these same figures (Figure 5, Appendix B, Figures B1-B5).

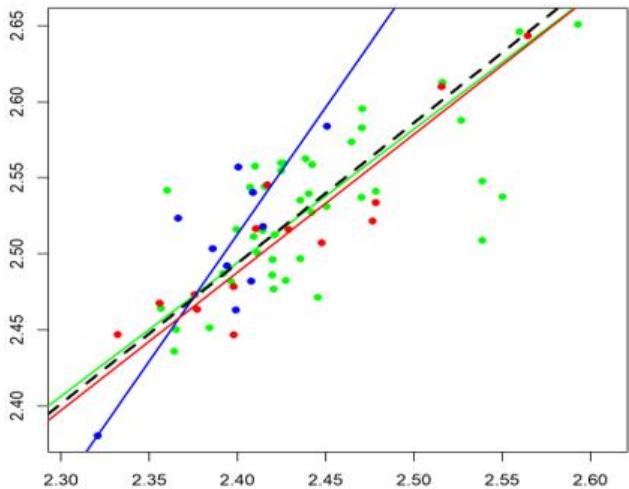


Figure 5. Regression curve log of males/log of females in elytra length variation in *C.granulatus* (dotted line). Painted over circles denote samples, taken in city (red), suburbs (blue) and natural (green) habitats.

Since each point marked in Figure 5 corresponded to a specific beetle sample (identified by a number in our database), we were able to calculate the SSD value for each sample to test whether SSD value indeed increases with beetle size and how this applies to samples from urban, suburban, and natural habitats.

To implement this hypothesis, we calculated the SSD value in each of the studied localities, arranging the data in the figures sequentially in order of increasing trait size. To illustrate this analysis, we present Figure 6, which presents SSD variability for a number of traits in *C. granulatus* populations in urban habitats.

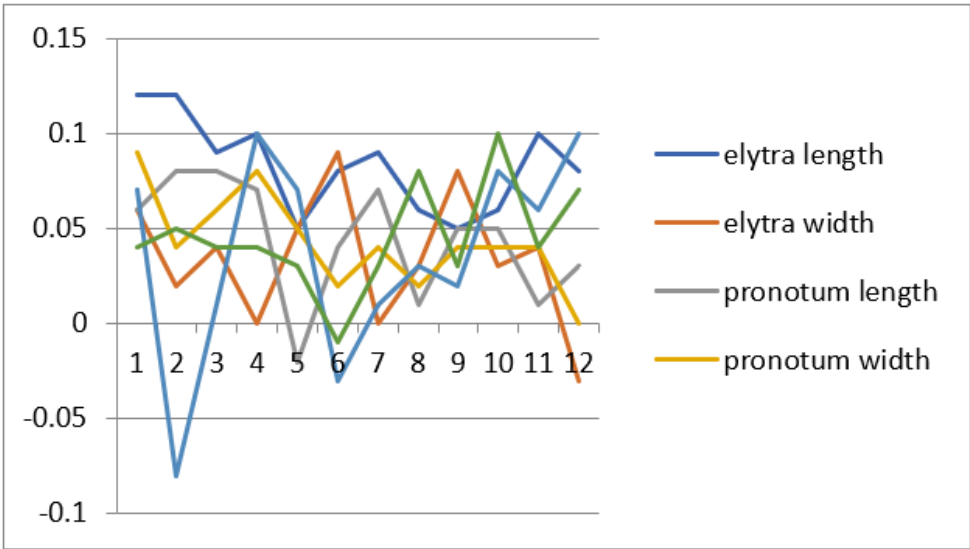


Figure 6. SSD variation in different traits in city habitats in *C. granulatus*.

For each curve, we calculated the R2 value of the trend line. Similar calculations were performed for *C. granulatus* populations inhabiting suburban and natural habitats, figures for which are presented in the Appendix B, Figures B1, B2.

Next, we analyzed the hypothesis that SSD values should decrease with a negative Intercept of the models, and increase with a positive one [14]. In conducting our analysis, we relied on the same hypothetical assumptions [14] that SSD values should decrease with a negative Intercept of the models, and increase with a positive one. Similar regression curves for other traits are shown in Appendix B, Figures B3-B7. We estimated the direction of actual changes in SSD values with increasing trait size based on the slope of the regression curves for trait variability. The results are presented in Table 4, which shows that the assumption of directional variability in SSD with increasing trait value was not confirmed. Only in 8 cases out of 18 did the actual calculated SSD values corresponded to their position on the regression curve.

Table 4. Correspondence between the direction of SSD values variation in real populations and the hypothetical figure of the cited article [14].

Traits/Biotopes	Urban		Suburbs		Natural	
	Expected change in SSD value	Direction and R ² in the linear trend of trait variation	Expected change in SSD value	Direction and R ² in the linear trend of trait variation	Expected change in SSD value	Direction and R ² in the linear trend of trait variation
Elytra length	↑	↓ 0.286	↑	↑ 0.137	↑	↓ 0.001
Elytra width	↓	↓ 0.053	↓	↑ 0.462	↑	↓ 0.040
Pronotum length	↑	↓ 0.212	↑	→ 0.008	↑	↑ 0.112
Pronotum width	↑	↓ 0.499	↓	↓ 0.237	↑	↑ 0.114
Head length	↑	↑ 0.137	→*	→ 0.008	↑	↓ 0.004
Distance between eyes	↑	↑ 0.128	↓	↓ 0.012	↓	↑ 0.212

→- statistically insignificant value.

4. Discussion

The topic of SSD in relation to ground beetles raised in this article is not new. In the past decade, a significant number of studies have appeared presenting data on the different patterns of size variability in female and male carabids. Sexual dimorphism in ground beetles is female-biased, and this has been confirmed across a fairly large number of species [29]. Latitudinal size variability has typically been studied, and the curves for male size variability have always been lower than those for females [23,25]. Statistically significant size differences were observed in the ground beetle *Carabus aeruginosus* between populations at different edges of its range, due in part to sexual differences [30]. In some regions, the sizes of females and males were comparable, but even for small ground beetle species, for example, in the genus *Poecilus*, the phenomenon persists that the curves of male size variation across a latitudinal gradient, although mirroring those of females, are significantly lower [31].

Similar sex-related size differences are also observed when analyzing ground beetle variability across an altitudinal gradient. In both *Carabus* and *Pterostichus* beetles, males are generally smaller than females at all altitudinal levels [32,33]. Moreover, many of the cited studies provide specific data on sexual dimorphism across both latitudinal and altitudinal gradients. The curve of sexual dimorphism variability along the latitudinal gradient is sawtooth-shaped, with SSD values increasing or decreasing abruptly from one region to another. Even more interesting findings were observed along the altitudinal gradient. The curve of SSD variability is concave, with minimal values in the mid-mountain regions, and correlates with the population sizes of the studied ground beetle species at these altitudes [16].

Regarding the species discussed in this article—*C. granulatus*—recently published studies have shown that the sizes of both females and males in this species tended to decrease across a latitudinal gradient, with the male variation curve also located at a lower level [22,24].

The topic of SSD was also addressed in these studies: its variation curve across a latitudinal gradient was sawtooth-shaped with a slight downward trend. Moreover, the highest SSD values were observed for elytral length and pronotum width.

In this article, we are more interested in studies that estimate SSD values based on RMAII results rather than directly calculated using the generally accepted formula [35]. The first such study on ground beetles was published quite a while ago [29]. The analysis of regression curves for 12 species presented there showed that their slopes were generally less than 1, indicating that the SSD in carabids was female-biased. This topic was subsequently raised repeatedly at conferences [e.g., 36, 37], where evidence was presented of variability in the position of the regression curve depending on the beetles' habitat—city, suburb, or natural habitat.

Our article also showed that urbanization influenced RMAII results. Looking at the RMAII results for all six traits (figures in Appendix B), we see that the regression curve plotted separately for biotopes with varying degrees of anthropogenic pressure (urban, suburban, natural) could change its position. However, this variability did not have a specific direction.

Our experimental data in no way detract from the merits of the Estonian authors, who were among the first to conduct a meta-analysis of SSD variability in insects. In recent decades, this approach has become increasingly popular because, as the saying goes, "big things can be seen from afar." In such publications, authors collect a large body of literature, extract factual data from it, compile information on a specific issue, and draw a general conclusion. Such publications are certainly welcome, if only because they address fundamental issues.

Some discrepancies between experimental data and hypothetical concepts of SSD variability are easily explained by logic.

Linear morphometric traits commonly used in field entomology do not correspond to simple theoretical expectations derived from body mass. The observed variability likely reflects complex, nonlinear response norms across multiple traits, rather than the uniform, monotonic response typically associated with biomass.

Given advances in computer technology, it is reasonable to assume that the use of RMAII cannot address the researchers' intended objectives. A more appropriate approach is the use of iteratively reweighted least square (IRLS) methods, which we have begun to explore.

Given that meta-analysis is increasingly becoming a practice for synthesizing data from different researchers and formulating general biological patterns, greater attention should be paid to large-scale studies conducted at the intraspecific level and using a unified methodology.

5. Conclusions

Our data demonstrate a non-monotonic response of SSD to the urbanization gradient. The peak values in suburbs may indicate that moderate anthropogenic environmental transformation (the ecotone effect) creates conditions for the maximum realization of potential differences in growth and development between males and females. In turn, under conditions of severe stress (urban) or a stable environment (nature), these differences are neutralized.

Deviations from the general pattern were observed exclusively for traits related to body width. This suggests that these "volume" characteristics are the most sensitive indicator of male physiological state under anthropogenic stress, possibly due to differences in energy accumulation and expenditure strategies between the sexes.

Despite the lack of a universal trend across all traits, R^2 analysis revealed that the highest proportion of explained variance in SSD change with increasing body size was observed for elytra and pronotum length in urban biotopes, elytra width in suburbs, distance between eyes in natural biotopes. This suggests that different body parts obey different allometric rules in response to urbanization.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

Table A1. Results of the ANOVA for the effect of anthropogenic pressure and sexon elytra length in *C. granulatus*.

	Estimate	Std.Error	t-value	Pr(> t)
(Intercept)	12.23332	0.02167	564.454	<2e-16***
sex2	-1.1369	0.02656	-42.801	<2e-16***
anthrop1	-0.1527	0.04101	-3.723	0.000198***
anthrop2	-0.31692	0.04478	-7.078	1.58e-12***
sex2:anthrop1	0.21852	0.051	4.285	1.85e-05***
sex2:anthrop2	0.24729	0.05556	4.451	8.66e-06***

Residual standard error: 0.8822 on 8160 degrees of freedom.Multiple R-squared: 0.2443,Adjusted R-squared: 0.2439.F-statistic: 527.7 on 5 and 8160 DF, p-value: < 2.2e-16.

Table A2. Results of the ANOVA for the effect of anthropogenic pressure and sexon elytra width in *C. granulatus*.

	Df	SumSq	MeanSq	F value	Pr(>F)
anthrop	2	13	6.25	12.162	5.32E-06***
sex	1	194	194.5	378.222	<2.00E-16***
anthrop:sex	2	2	0.78	1.521	0.219
Residuals	8160	4196	0.51		

Table A3. Results of the ANOVA for the effect of anthropogenic pressure and sexon elytra width in *C. granulatus*.

	Estimate	Std.Error	t-value	Pr(> t)
(Intercept)	5.19321	0.01762	294.79	<2e-16***
sex2	-0.34364	0.02159	-15.916	<2e-16***
anthrop1	-0.09227	0.03334	-2.768	0.00566**
anthrop2	0.06919	0.0364	1.901	0.05733.
sex2:anthrop1	0.0721	0.04145	1.739	0.08201.
sex2:anthrop2	0.01402	0.04516	0.31	0.75624

Residual standard error: 0.7171 on 8160 degrees of freedom. Multiple R-squared: 0.04735, Adjusted R-squared: 0.04677. F-statistic: 81.12 on 5 and 8160 DF, p-value: < 2.2e-16.

Table A4. Results of the ANOVA for the effect of anthropogenic pressure and sexon pronotum length in *C. granulatus*.

	Df	SumSq	MeanSq	F value	Pr(>F)
anthrop	2	20.3	10.145	99.53	2.00E-16***
sex	1	22.6	22.648	222.21	2.00E-16***
anthrop:sex	2	7.1	3.537	34.7	9.84E-16***
Residuals	8160	831.7	0.102		

Table A5. Results of the linear regression for the effect of anthropogenic pressure and sexon pronotumlengthin *C. granulatus*.

	Estimate	Std.Error	t-value	Pr(> t)
(Intercept)	3.377645	0.007843	430.669	<2e-16***
sex2	-0.154943	0.009612	-16.119	<2e-16***
anthrop1	0.021276	0.014841	1.434	0.15174
anthrop2	0.011181	0.016203	0.69	0.49018
sex2:anthrop1	0.153176	0.018454	8.3	<2e-16***
sex2:anthrop2	0.055421	0.020105	2.757	0.00585**

Residual standard error: 0.3193 on 8160 degrees of freedom. Multiple R-squared: 0.05672, Adjusted R-squared: 0.05614. F-statistic: 98.14 on 5 and 8160 DF, p-value: < 2.2e-16.

Table A6. Results of the ANOVA for the effect of anthropogenic pressure and sexon pronotumwidth in *C. granulatus*.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
anthrop	2	0.1	0.06	0.317	0.728
sex	1	162.7	162.7	925.94	<2e-16***
anthrop:sex	2	0.8	0.39	2.201	0.111
Residuals	8160	1433.8	0.18		

Table A7. Results of the linear regression for the effect of anthropogenic pressure and sexon pronotum width in *C. granulatus*.

	Estimate	Std.Error	t-value	Pr(> t)
(Intercept)	4.39367	0.0103	426.663	<2e-16***
sex2	-0.29819	0.01262	-23.627	<2e-16***

anthrop1	-0.02255	0.01949	-1.157	0.247
anthrop2	0.02515	0.02127	1.182	0.237
sex2:anthrop1	0.03106	0.02423	1.282	0.2
sex2:anthrop2	-0.03404	0.0264	-1.289	0.197

Residual standard error: 0.4192 on 8160 degrees of freedom. Multiple R-squared: 0.1024, Adjusted R-squared: 0.1019. F-statistic: 186.2 on 5 and 8160 DF, p-value: < 2.2e-16.

Table A8. Results of the ANOVA for the effect of anthropogenic pressure and sexon head length in *C. granulatus*.

	Df	SumSq	MeanSq	F value	Pr(>F)
anthrop	2	25.5	12.742	82.939	<2e-16***
sex	1	20	20.034	130.402	<2e-16***
anthrop:sex	2	1.3	0.634	4.128	0.0161*
Residuals	8160	1253.6	0.154		

Table A9. Results of the linear regression for the effect of anthropogenic pressure and sexon head length in *C. granulatus*.

	Estimate	Std. Error	t-value	Pr(> t)
(Intercept)	2.445742	0.009629	253.997	<2e-16***
sex2	-0.106944	0.011801	-9.062	<2e-16***
anthrop1	0.037445	0.018221	2.055	0.0399*
anthrop2	-0.087249	0.019893	-4.386	1.17e-05***
sex2:anthrop1	0.043252	0.022657	1.909	0.0563.
sex2:anthrop2	-0.039606	0.024684	-1.605	0.1086

Residual standard error: 0.392 on 8160 degrees of freedom. Multiple R-squared: 0.03598, Adjusted R-squared: 0.03539. F-statistic: 60.91 on 5 and 8160 DF, p-value: < 2.2e-16.

Table A10. Results of the ANOVA for the effect of anthropogenic pressure and sexon distance between eyes in *C. granulatus*.

	Df	SumSq	MeanSq	F value	Pr(>F)
anthrop	2	14	6.984	79.05	<2e-16***
sex	1	19.4	19.419	219.81	<2e-16***
anthrop:sex	2	12.3	6.159	69.72	<2e-16***
Residuals	8160	720.9	0.088		

Table A11. Results of the linear regression for the effect of anthropogenic pressure and sexon distance between eyes in *C. granulatus*.

	Estimate	Std. Error	t-value	Pr(> t)
(Intercept)	2.022138	0.007302	276.944	<2e-16***
sex2	-0.162509	0.008949	-18.16	<2e-16***
anthrop1	-0.041885	0.013817	-3.031	0.00244**
anthrop2	-0.085441	0.015085	-5.664	1.53e-08***
sex2:anthrop1	0.200894	0.017181	11.693	<2e-16***
sex2:anthrop2	0.084315	0.018718	4.505	6.74e-06***

Residual standard error: 0.2972 on 8160 degrees of freedom. Multiple R-squared: 0.05962, Adjusted R-squared: 0.05904. F-statistic: 103.5 on 5 and 8160 DF, p-value: < 2.2e-16.

Appendix B

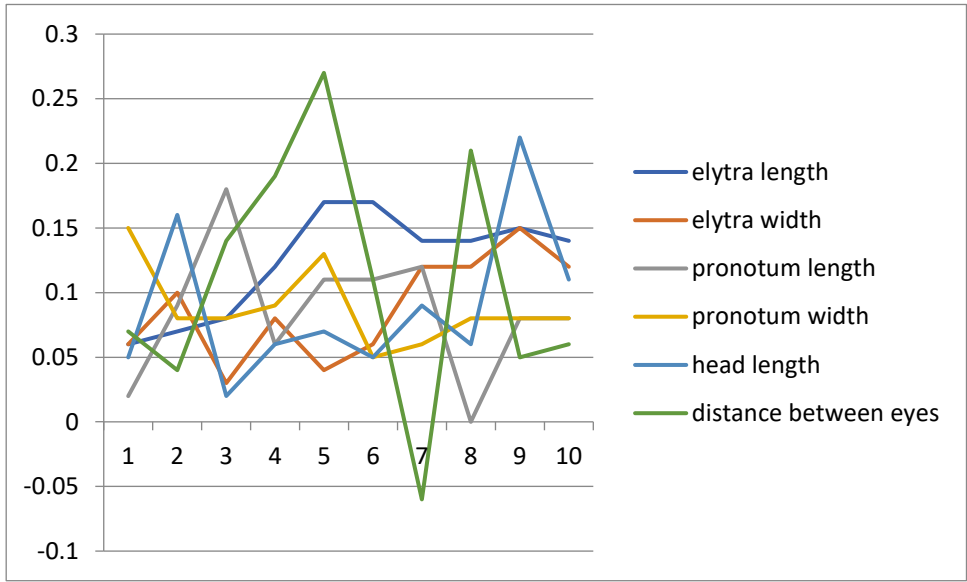


Figure A1. SSD variation in different traits in suburbs habitats in *C. granulatus*.

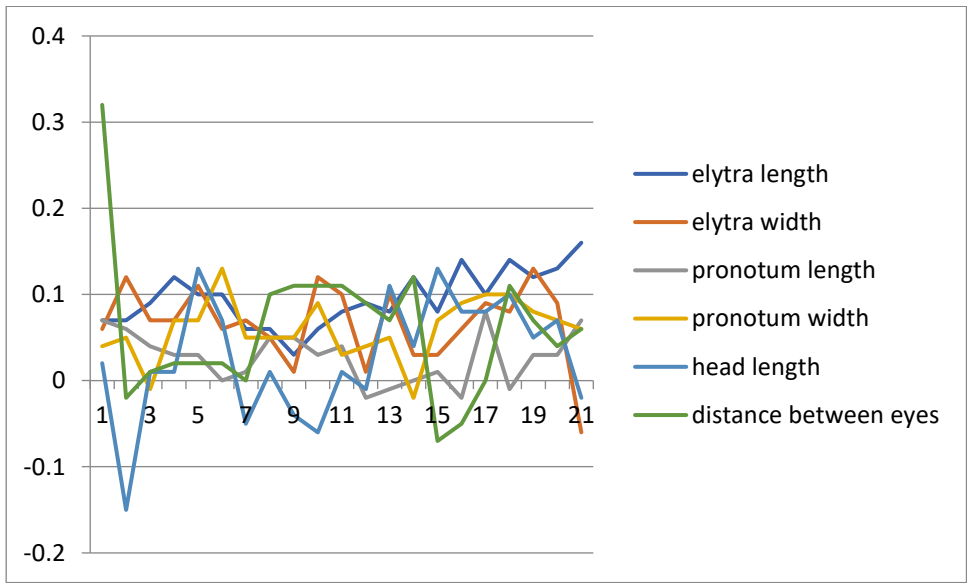


Figure A2. SSD variation in different traits in natural habitats in *C. granulatus*.

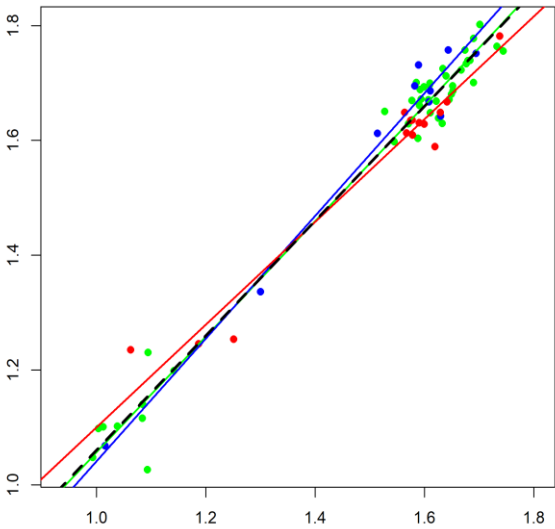


Figure A3. Regression curve log of males/log of females in elytra width variation in *C.granulatus* (dotted line). Painted over circles denote samples, taken in city (red), suburbs (blue) and natural (green) habitats.

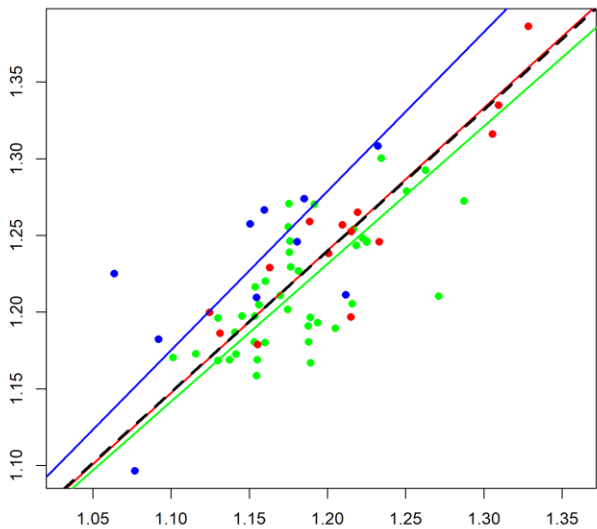


Figure A4. Regression curve log of males/log of females in pronotum length variation in *C.granulatus* (dotted line). Painted over circles denote samples, taken in city (red), suburbs (blue) and natural (green) habitats.

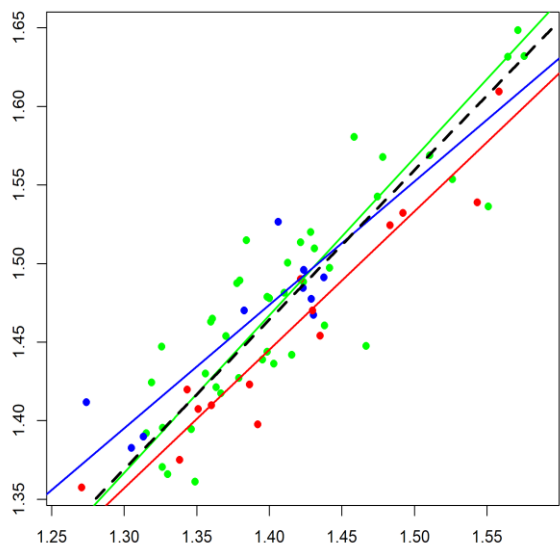


Figure A5. Regression curve log of males/log of females in pronotum width variation in *C.granulatus* (dotted line). Painted over circles denote samples, taken in city (red), suburbs (blue) and natural (green) habitats.

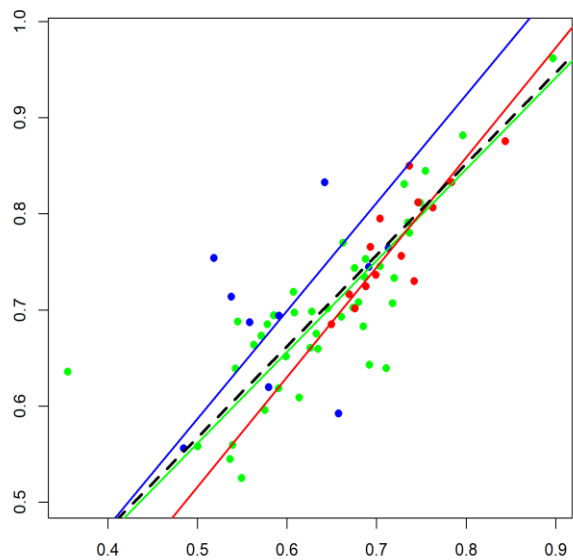


Figure A6. Regression curve log of males/log of females in head length variation in *C.granulatus* (dotted line). Painted over circles denote samples, taken in city (red), suburbs (blue) and natural (green) habitats.

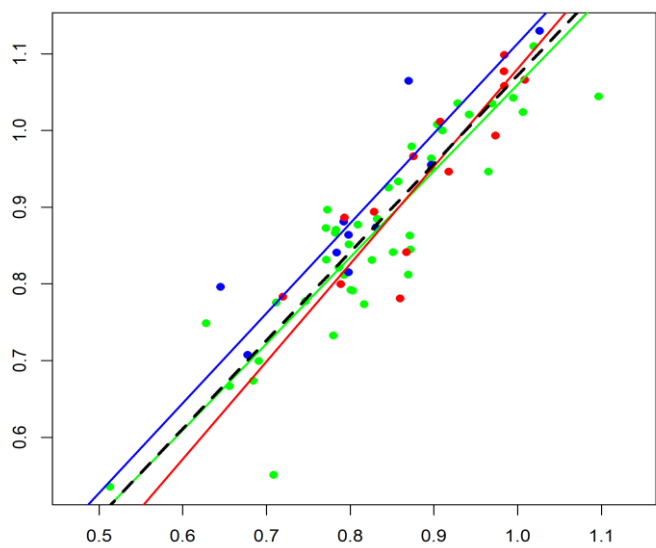


Figure A7. Regression curve log of males/log of females in distance between eyes variation in *C.granulatus* (dotted line). Painted over circles denote samples, taken in city (red), suburbs (blue) and natural (green) habitats.

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