MORPHOMETRIC VARIABILITY OF GROUND BEETLES *BEMBIDION MINIMUM* (COLEOPTERA, CARABIDAE): WHO SHOULD CHANGE MORE, MALES OR FEMALES?

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Morphological variability can be used as an indicator of the state of invertebrate populations. Microevolutionary processes can show up in the morphological differentiation of populations. This includes differences between morphometric characters in the two sexes. The variability of 12 populations of *Bembidion minimum* (Coleoptera, Carabidae) was assessed by 24 morphometric characteristics and indices in this article. *Bembidion minimum* is a halophile that lives in ecosystems of Protected Areas in Ukraine (Black Sea Biosphere Reserve, Dniprovsko-Orilskyi Nature Reserve, Ornithological Sanctuary «Bulakhovsky Liman», Regional Landscape Park «Dniprovi Porogy», Samara Forest). The coefficients of variation for males, females, and combined populations of males and females were estimated in the article. The studied populations inhabited different soil and plant conditions and were under the influence of anthropogenic factors of varying intensity. The redundancy analysis shows three clusters. In the first cluster, morphometric characteristics and indices in both males and females were linked to environmental variables (herb layer, salt, composition of soil). The second cluster had morphometric characteristics and indices in both males and females with a link to environmental variables (pH, litter, recreational load, cattle grazing). The third cluster formed morphometric characteristics and indices in both males and females that are not affected by any environmental variables. The coefficient of variation for most of the linear morphometric characteristics of *B. minimum* (width of head, length of prothorax, width of prothorax, length of elytra and distance between setae on the elytra) for males was significantly lower than for the combined sample of males and females. The variability of width of elytra and length of body was significantly higher for females than for males. The degree of variability of males, females and their combined sample did not significantly differ for nonlinear morphometric characteristics, as well as for the six morphometric indices (body proportions) studied by us. In general, in the 12 studied populations of *B. minimum*, the coefficient of variation for most of the studied measurements was insignificantly lower in males (CV = 5.59%) than in females (6.10%) or in the combined sample of males and females (6.75%). The lowest variability in populations of *B. minimum* was found for morphometric indices: CV = 3.89% for males, CV = 3.76% for females, and CV = 3.86% for the combined population (males + females). The absence of differences in the mean values of the coefficient of variation between males, females and the combined sample of males and females for each individual population suggests that both males and females make a relatively equal contribution to the polymorphism of *B. minimum* populations. An assessment of the morphological variability of invertebrates, and especially the variation of coefficients of linear parameters and morphometric indices, can be used to indicate the state of ecosystems in Protected Areas in Ukraine and other countries.

Key words: body length, carabids, coefficient of variation, litter invertebrates, population, sexual dimorphism, morphometrics, zoophagous

Introduction

The state of populations of rare invertebrate species in ecosystems can be assessed either by their abundance in ecosystems («rough» estimate) (Gobbi & Fontaneto, 2008; Pakhomov et al., 2019; Pokhylenko et al., 2020) or by changes in the morphological parameters of the body («fine» estimate) (Di Grumo & Lovei, 2016). For a detailed assessment of the state of invertebrate populations, it is possible to use asymmetry indices, the percentage of individuals with deviations in body structure, changes in the average value of linear body parameters and morphological indices, as well as the coefficient of variation (Ernsting & Isaaks, 1997; Barton et al., 2011).

Sexual dimorphism reflects the direction of evolution of a species: if over millions of years of phylogeny, representatives of this species have become larger, now males have become larger than females (for example, humans, gorillas, stag beetles). This phenomenon is described by Geodakjan's theory (Geodakjan, 1982). Sexual size dimorphism is considered to be one of the major evolutionary determinants of mating success in many species. Because larger males are generally more aggressive and more competitive than smaller males, larger males often attain greater reproductive success through intersexual selection. Differences in body size vary greatly among different animal taxa (Fairbairn et al., 2007; Shreeves & Field, 2008). At least in vertebrates, females represent a more conservative part of the population: their ovicells are formed at the initial stages of ontogenesis, and their genome reflects in a greater degree the living conditions during that period. Males constantly renew the composition of spermatozoa, the genome of which corresponds to the environmental conditions at a given time (Zhuk, 2019). This explanation seems plausible at least for vertebrates. For mammals, this point of view seems to be justified in the case of longtime ontogenesis and rather abrupt changes in conditions in time. Geodakjan's theory has probably a number of restrictions regarding insects. If in females of primates and humans, ovicells are laid in the fourth month of intrauterine development of the fetus, then in insects with their variability of life cycles, options are always possible.

The morphological variability of invertebrates is largely dependent on environmental conditions (Gugosyan et al., 2019; Sowa & Skalski, 2019; Kozak et al., 2020). There are groups of species among beetles in which the larvae grows for a short period, and the imago develops for a long time (e.g. Carabidae, Staphylinidae, Silphidae) (Lindroth, 1985; Kryzhanovskij et al., 1995; Hurka, 1996). There are groups in which the larva lives for approximately an equal period with adults (for example, many species of weevils, diving beetles, water scavenger beetles). Finally, the third group consists of species in which the larva grows for a long time, and the imago, on the contrary, has a short life period (for example, many species of Cerambycidae, Lucanidae). It is clear that within each family of beetles, many variants of the ratio of the lifespan of the imago and the larva are possible. However, it seems indisputable that the different habitats of the larva and the imago in beetles should have different effects on the ratio of body sizes in larvae and adults (Jensen, 1990; Vittum & Morzuchi, 1990; Theiss & Heimbach, 1994). The cardinal restructuring of the beetle's body structure at the pupal stage, changes in the dietary spectrum and, often, the habitat in the adult in comparison with the larva, allow us to doubt the linear dependence of sexual dimorphism on a decrease or increase in body size in phylogeny (Shulman et al., 2017; Okuzaki & Sota, 2018).

The second aspect, insufficiently studied in the population ecology of beetles, is how the influence of environmental conditions on the body size of imago ground beetles can manifest itself: in the average size of individuals or in the variability (plasticity) of the population as a whole (Di Grumo & Lovei, 2016; Rusynov & Brygadyrenko, 2017). Probably, the average size of beetles cannot change over tens of generations, but the coefficient of variation (the ratio of the standard deviation to the mean, expressed as a percentage) can change. Reactions of species communities and body size in the population are related to the characteristics of the landscape and changes in the environment (Rueffler et al., 2006; Langraf et al., 2020; Avtaeva et al., 2021). The structure of species populations is also affected by morphometric changes caused by environmental factors (Giglio et al., 2011; Talarico et al., 2011). Morphometric variability in the population indicates that the variation in body size is the result of morphometric adaptation to the environment (Benítez, 2013; Osman et al., 2015; Kawano, 2016). Changes in the body size and an individual species distribution across the space are parameters that indicate the degree of environmental burden (McGeoch, 1998; Lagisz, 2008; Boyko et al., 2019). Environmental quality and resource food availability influence metabolic activity. Depending on body size, we can also predict if an organism is a potential predator or prey (Belaoussoff et al., 2003; Braun et al., 2004; Brygadyrenko, 2015). Rouabah et al. (2015) analysed the influence of vegetation on the diversity of ground beetles in correlation with their body size. They confirmed that corpulent species achieve high population densities in forests, while small species prefer species-rich meadow vegetation. Similar studies have been carried out by other authors (e.g. Tyler, 2010; Benítez et al., 2018). The most pronounced morphological adaptation of ground beetles is associated with a specific diet (Thiele, 1977). The availability of food, the change in the number and nature of food items, as well as the diet itself, is influenced by environmental factors, which subsequently leads to changes in body size. The large size of females also compared to the size of males can be explained by the role of females in the reproduction process (Thornhill & Alcock, 1983).

Riparian ecosystems are of great interest, since they have a variety of habitats and a high species richness of invertebrates (Desender & Verdyck, 2001; Petillon et al., 2007). The species composition of ground beetles (Carabidae) of riparian ecosystems differs from the species composition of other ecosystems (Eyre & Luff, 2004; Putchkov et al., 2020). Representatives of the genus *Bembidion* Latreille, 1802 dominate among ground beetles in riparian ecosystems and are convenient bioindicators of the influence of environmental factors (Andersen, 1985; Abdel-Dayem, 1998; Nitzu, 2003; Knapp & Saska, 2012). The morphological variability of representatives of this genus is poorly studied; therefore it is of interest (Komlyk & Brygadyrenko, 2019a,b, 2020). *Bembidion minimum* (Fabricius, 1792) lives in humid habitats along the shores of seas, rivers, and standing water bodies (Lindroth, 1974). It prefers muddy, moderately humid and slightly shady places, among herbaceous plants. It is a halophile which is usually found in high numbers on salt marshes and clay soils, on the banks of saline water bodies. *Bembidion minimum* has a peak of activity in spring. Larvae develop within 3–4 weeks; adults are active most of the year. *Bembidion minimum* lives in ecosystems of Protected Areas of Ukraine. This species is found in riparian ecosystems of the Black Sea Biosphere Reserve, Dniprovsko-Orilskyi Nature Reserve, Regional Landscape Park «Dniprovi Porogy», in the salt marshes of Ornithological Sanctuary «Bulakhovsky Liman» and in the territory of the Samara Forest (Komlyk & Brygadyrenko, 2019b). *Bembidion minimum* is also found in Protected Areas in other countries, e.g. Strandzha Nature Park (Bulgaria) (Kostova & Guéorguiev, 2016), Serra de Collserola Natural Park, Font Roja Natural Park, S'Albufera de Mallorca Natural Park (Spain) (Serrano, 2013), Sevan National Park (Armenia) (Iablokov-Khnzorian, 1976).

The environmental conditions at the larval stage have the greatest impact on the absolute size and proportions of the body of this species. The morphological variability of the population is determined by the third level of the response of the population system to external influences. The first level is «alive or dead»; the second level is the occurrence of developmental anomalies, deviations in body size; the third level is changes in body proportions (Komlyk & Brygadyrenko, 2019b). Perhaps the quality of the food composition, the amount of food determine the overall size of the body. No studies have been carried out for this species or for the genus *Bembidion* (in the laboratory or under natural conditions). The purpose of this study is to determine how strongly the coefficients of variation of males, females and combined samples of males and females change in populations of *B. minimum* under different habitat conditions.

Material and Methods

The morphological variability of *B. minimum* was investigated. The research was carried out in 12 ecosystems in the Mahdalinovka district, Novomoskovsk district, Pavlograd district and Sinelnikovo district of Dnipropetrovsk Region (Ukraine) (Table 1). Detailed descriptions of the conditions of the study areas are given in articles of some authors (Gritsan et al., 2019; Baranovski et al., 2020, 2021; Gorban et al., 2021). The invertebrate fauna of these territories was also described earlier (Komlyk & Brygadyrenko, 2019b; Puchkov et al., 2020; Kunakh et al., 2021) A brief description of the studied habitats is given in Table 1. The method for determining the mineralisation and pH of soil solution is also described in some articles (Komlyk & Brygadyrenko, 2019a, 2020). Twelve studied populations of *B. minimum* are ranked depending on six ecological characteristics:

– mechanical composition of the soil: three groups are identified: sand (ecosystems 3, 10), sandy loam (1, 2, 7), loam (4, 5, 6, 8, 9, 11, 12) (Appendix 1);

– mineralisation of soil solution: three groups are distinguished: with relatively low mineralisation < 2 g/L (ecosystems 1, 2, 3, 4, 5), average mineralisation 2–4 g/L (6, 7, 8, 9) and high mineralisation of soil solution > 4 g/L (10, 11, 12) (Appendix 2);

Table 1. Brief characteristic of ecosystems (Dnipropetrovsk Region, Ukraine) where specimens of 12 populations of *Bembidion minimum* were collected

Ecosystem	Ecosystem co-ordinates	Mechanical composition of soil	Salt content in soil solution, g/L	pH of soil solution	Density of herb layer (%) and dominating plant species	Average litter thickness, cm	Degree of recreational load, points*	Impact of cattle grazing, points**
1	48.667861° N, 35.338556° E	sandy loam	0.35	8.38	0	0	0	0
2	48.627083° N, 35.353944° E	sandy loam	0.37	8.17	0	0	3	3
3	48.509167° N, 36.078889° E	sand	0.87	8.60	90	0	2	2
4	48.492500° N, 35.363611° E	loam	1.12	8.22	0	4	3	3
5	48.667528° N, 35.338139° E	loam	1.43	7.64	0	0	0	0
6	48.729444° N, 35.008611° E	loam	2.08	8.10	0	4	1	0
7	48.573333° N, 35.870306° E	sandy loam	2.13	7.98	0	0	2	2
8	48.671583° N, 35.310361° E	loam	3.22	7.75	0	2	0	0
9	48.672556° N, 35.355417° E	loam	3.48	7.99	90	2	1	1
10	48.571750° N, 35.865861° E	sand	4.40	7.75	0	0	2	2
11	48.477806° N, 36.022722° E	loam	4.42	7.98	35	0	1	1
12	48.625806° N, 35.339111° E	loam	5.50	8.50	0	0	3	1

Note: * – recreational load: 0 – absent (human traces and household waste are absent), 1 – slight (human traces and household waste are rare), 2 – medium (human traces and household waste occupy 10–30% of land area), 3 – high (human traces and household waste occupy more than 30% of land area); ** – the impact of cattle grazing: 0 – absent (animal trails and their feces are absent), 1 – slight (animal trails and feces are rare), 2 – medium intensity (animal trails and feces occupy 10–30% of land area), 3 – heavy intensity (animal trails and feces occupy more than 30% of land area).

– pH of the soil solution: two groups are distinguished: with the reaction of the soil solution less than 8.0 (ecosystems 5, 7, 8, 9, 10, 11) and more than 8.0 (1, 2, 3, 4, 6, 12) (Appendix 3);

– litter thickness: two groups of ecosystems were identified, one with the absence of a litter layer (ecosystems 1, 2, 3, 5, 7, 10, 11, 12) and one with a litter thickness of 2–4 cm (4, 6, 8, 9) (Appendix 4);

– herb layer: two groups were identified, one with no herb layer (ecosystems 1, 2, 4, 5, 6, 7, 8, 10, 12) and one with a developed herb layer (3, 9, 11) (Appendix 5);

– recreational load: four groups were identified, evaluated in points: 0 points (ecosystems 1, 5, 8), 1 point (6, 9, 11), 2 points (3, 7, 10), 3 points (2, 4, 12) (Appendix 6);

– cattle grazing: four groups are identified: ecosystems without grazing (1, 5, 6, 8), with slight grazing (9, 11, 12), with grazing of medium intensity (3, 7, 10) and with strong grazing (2, 4) (Appendix 7).

Beetles were collected using soil traps and manually using an aspirator in May–July. We collected 410 specimens of *B. minimum* in 12 ecosystems, including 243 females and 163 males (i.e. ecosystem 1: 15 males, 20 females; ecosystem 2: 12 males, 28 females; ecosystem 3: 13 males, 14 females; ecosystem 4: 16 males, 22 females; ecosystem 5: 14 males, 24 females; ecosystem 6: 9 males, 11 females; ecosystem 7: 14 males, 21 females; ecosystem 8: 17 males, 20 females; ecosystem 9: 15 males, 25 females; ecosystem 10: 15 males, 22 females; ecosystem 11: 5 males, 16 females; ecosystem 12: 18 males, 18 females). The morphological characteristics of beetles were assessed according to the methodology previously used by Komlyk & Brygadyrenko (2019a) (Table 2). Measurements were taken for all collected specimens. Photographs of the collected insects were taken using the binocular MBS-10 and a digital camera of 5-megapixel resolution. Morphometric measurements were performed using photographs in the TpsDig 2.17 program (F. James Rohlf, State University of New York at Stony Brook, USA, 2004).

Statistical processing of the results was carried out by calculating the coefficient of variation (CV), expressed as a percentage (the ratio of the standard deviation times 100 to the mean). The samples were compared using ANOVA, corrected for multiple comparison (Bonferroni correction). The post hoc Tukey test was used for a multiple comparison of samples. Calculations were performed using the Statistica 10 software package (StatSoft Inc., USA). Multivariate analysis (redundancy analysis, RDA) was employed to determine the dependencies between objects (morphometric characteristics, index of B. minimum individuals (listed in Table 2) in males, females and environmental variables (salt content in soil solution, pH of soil solution, average litter thickness, density of herb layer, degree of recreational load, impact of cattle grazing, mechanical composition of soil). We tested the statistical significance of those environmental variables with the Monte Carlo permutation test (iterations = 499) in the Canoco 5 program (Ter Braak & Šmilauer, 2012).

Table 2. Brief description of morphometric characteristics and indices used to assess the variability of *Bembidion minimum* populations

Morphometric characteristic or index	Unit of measurement	Description
Lb	mm	length of body
Lc	mm	length of head (from front edge of clypeus to articulation with prothorax)
Lp	mm	length of prothorax
Le	mm	length of elytra
Sc	mm	width of head with eyes
Sp1	mm	width of prothorax between front angles
Sp2	mm	width of prothorax between back angles
Spm	mm	maximum width of prothorax
Se	mm	maximum width of elytra
B	degree ^{o}	the back angles of the prothorax were determined on the left (B1) and right (B2) parts of the body; for the further calculations, their arithmetic mean value was used
P	units of mm^2	density of elytra puncturing was assessed from photographs by counting the quantity of pores on the area 1 mm^2 between the back edge of the scutellar groove and the first groove of the elytra
K	conditional units	the contrast of the light spots at the top of the left (Kl) and right elytra (Kr) was determined in a gradient from 1 (clear) to 4 (poorly discernible), and their arithmetic mean value was calculated for each beetle
L1l	mm	distance from the base of the left elytra to the first setae
L1r	mm	distance from the base of the right elytra to the first setae
L2l	mm	distance between setae on the left elytra
L2r	mm	distance between setae on the right elytra
(Sc+Sp+Se)/3Lb	–	ratio of arithmetic mean value of the width of head, prothorax and elytra to body length
Lp/Sp	–	ratio of prothorax length to its maximum width
Le/Lp	–	ratio of elytra length to prothorax length
Se/Sp	–	ratio of maximum width of elytra to maximum prothorax width
Spm/Sp2	–	ratio of maximum prothorax width to its width at the back edge
Le/Se	–	ratio of elytra length to their width

Note: linear characteristics were measured with an accuracy of ± 1 pixel (0.96 μm); accuracy of photographic measurement of angles was equal to ± 0.1°.

Results

Multivariate analysis of morphometric characteristics and index of *B. minimum* individuals (Table 2) in males, females was determined using redundancy analysis (RDA, SD (length of gradient) = 1.87 on the first ordination axis). We observed relationships between the morphometric characteristics, index of *B. minimum* individuals (males, females) and environmental variables. The values of the explained variability of morphometric characteristics and indices data were 62.1% on the first ordination axis and 51.6% on the second cumulative ordination axis. Using the Monte Carlo permutation test, we identified statistically significant effects of recreational load ($p = 0.0260$, $F_{(1.938)} = 1.952$, $df = 6$), pH ($p = 0.0104$, $F_{(1.854)} = 2.111$, $df = 6$), cattle grazing ($p = 0.0182$, $F_{(1.101)} = 3.089$, $df = 6$), litter ($p = 0.0232$, $F_{(2.213)} = 2.581$, $df = 6$), herb layer ($p = 0.0256$, $F_{(2.121)} = 2.311$, $df = 6$), salt ($p = 0.0280$, $F_{(1.879)} = 2.041$, $df = 6$), composition of soil ($p = 0.0287$, $F_{(1.814)} = 1.924$, $df = 6$) on the morphometric characteristics and index of *B. minimum* individuals in males and females. The selected variables were not mutually correlated with the maximum value of the inflation factor = 4.292. The ordination graph (triplot) had three clusters. In the first cluster, the morphometric characteristics and index in males, females (e.g. Lc_f, Lc_m, Se/Sp_m, Le/Se_f, Le/Lp_f) with a link on environmental variables (herb layer, salt, composition of soil). The second cluster had morphometric characteristics and index in males, females (e.g. K_m, B_m, B_f, L1r_f, L1l_f, Sp2/Spm_m) link with environmental variables (pH, litter, recreational load, cattle grazing). The third cluster was formed by morphometric characteristics and index in males, and females that are not affected by any environmental variables (Fig. 1).

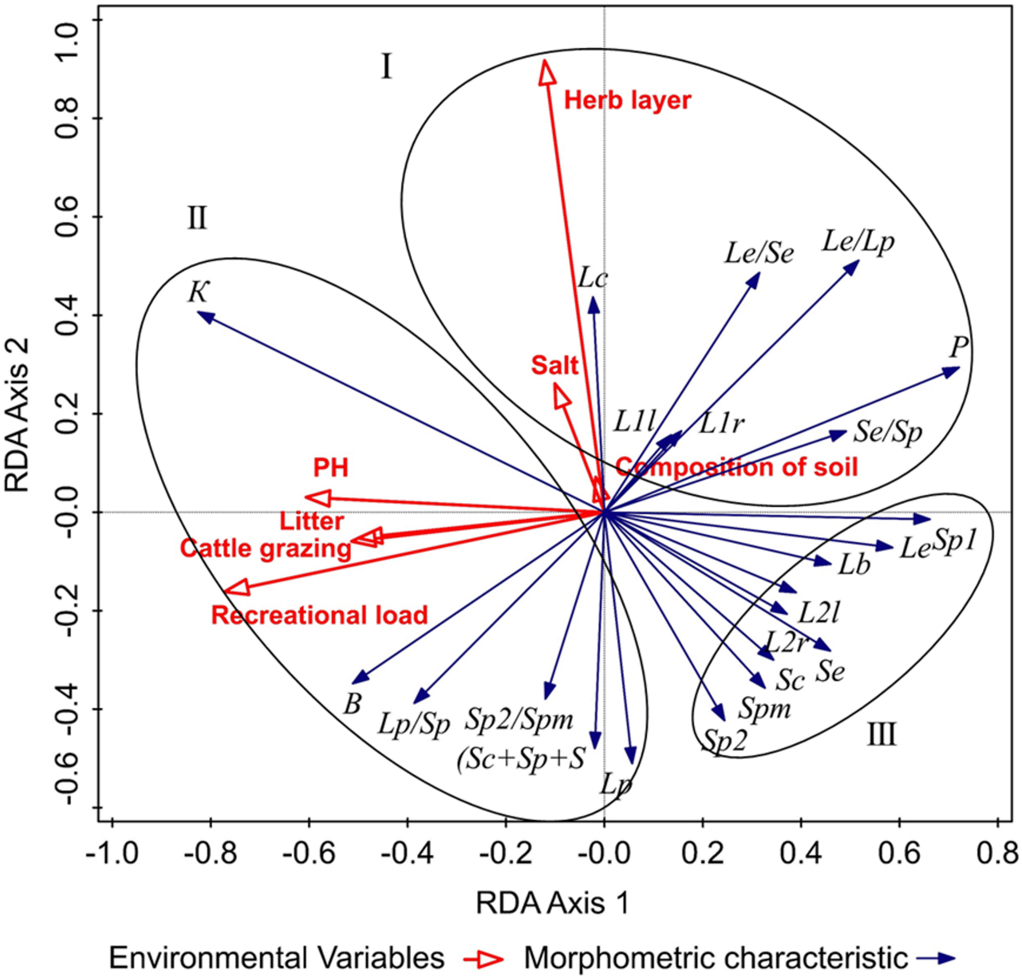

Fig. 1. RDA, redundancy analysis, of morphometric characteristic and indices with respect to environmental variables. Environmental variables (red arrows) are Salt (salt content in soil solution), pH (pH of soil solution), Litter (average litter thickness), Herb layer (density of herb layer (%) and dominating plant species), Recreational load (degree of recreational load), Cattle grazing (impact of cattle grazing), Composition of soil (mechanical composition of soil). The abbreviations of morphometric characteristics are present in Table 2. Females are marked with a green arrow and the ending by «f» in the name of the morphometric trait. Males are marked with a blue arrow and the ending by «m» in the name of the morphometric trait.

The coefficients of variation for most linear morphometric characteristics of *B. minimum* (width of head (Sc), length of prothorax (Lp), width of prothorax (Sp1, Sp2, Spm), length of elytra (Le), distance between setae on the elytra (L2l and L2r, Fig. 2A,B) in males) are significantly lower than in the combined sample of males and females. The variability of elytra width (Se) and body length (Lb, Fig. 2B) is significantly higher in females than in males. The degree of variability in males, females and their combined sample does not significantly differ for nonlinear morphometric characteristics (Fig. 2C) and six morphometric indices (Fig. 2D).

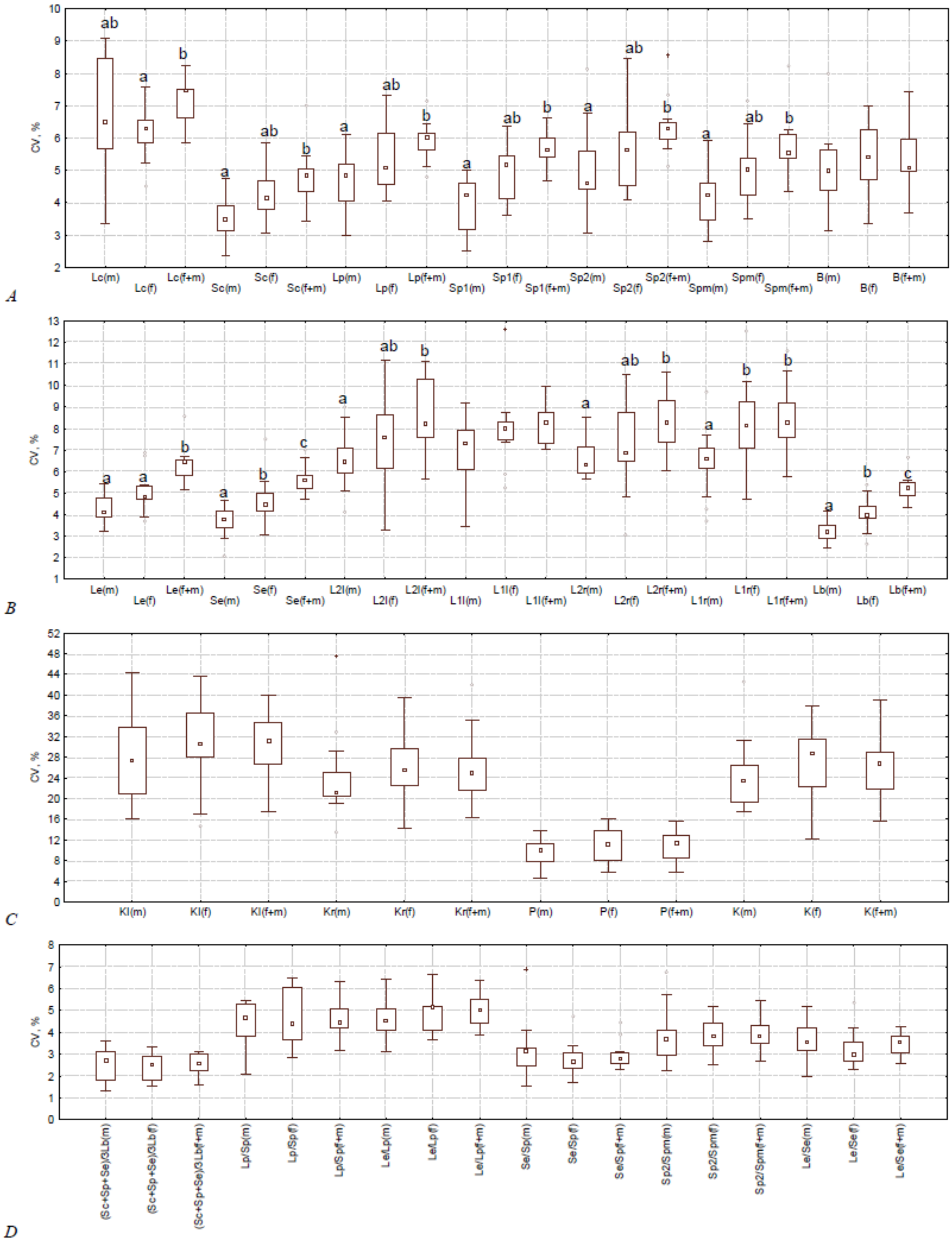

Fig. 2. Variation of morphometric characteristics (A, B, C) and morphometric indices (D) for *Bembidion minimum* males (designation in brackets is «m», n = 163), females (designation in brackets is «f», n = 243), and the combined sample of males and females (designation in brackets is «f+m», n = 406). In each sample, the diagram combines the coefficients of variation of 12 populations of ground beetles. A small square denotes the median of each sample, the lower and upper edges of the rectangle denote the first and third quartiles of the sample, circles and asterisks represent outliers. Different letters above the rectangles denote samples that, within one morphological characteristic or index, significantly ($p < 0.05$) differ from one another according to the results of the Tukey test; if there are no letters above the sample, then none of the three samples for this characteristic differs from any other.

In general, in the 12 studied populations of *B. minimum*, the coefficient of variation in males (CV = 5.59%), females (6.10%) or in the combined sample of males and females (6.75%) for most of the studied measurements are not significant (Table 3). The variability of males, females and the population as a whole does not differ in nonlinear characteristics (distance from the base of the elytra to the first setae, density of elytra puncturing, the back angles of the prothorax) (CV = 25.44%, CV = 24.70% and CV = 25.40%, respectively for males, females and males and females in the combined sample). The lowest variability in *B. minimum* populations was found for morphometric indices (body proportions). The coefficient of variation in the three studied groups did not exceed 4% on average: CV = 3.89% for males, CV = 3.76% for females, CV = 3.86% for the combined population (males + females) (Table 3).

Table 3. Coefficient of variation (CV, %) of morphological characteristics and indices of males, females and the combined sample of males and females in 12 populations of *Bembidion minimum*

Morphometric characteristic or index	Sex	Ecosystem												
		1	2	3	4	5	6	7	8	9	10	11	12	1–12
Sample size (n), specimen	m	15	12	13	16	14	9	14	17	15	15	5	18	163
	f	20	28	14	22	26	11	21	20	25	22	16	18	243
	f+m	35	40	27	38	40	20	35	37	40	37	21	36	406
Linear characteristics														
Lc	m	8.49	4.74	6.36	6.49	9.09	8.95	8.45	8.26	5.66	4.94	3.33	5.64	7.55
	f	6.27	6.53	6.98	4.48	5.22	5.28	6.31	5.90	6.16	7.55	5.83	7.02	6.54
	f+m	7.33	6.60	8.24	5.84	7.48	7.60	7.45	8.20	6.29	7.49	6.19	6.69	7.46
Sc	m	3.10	3.88	3.79	3.44	2.93	3.94	3.08	3.84	3.16	2.35	3.18	4.74	4.06
	f	3.77	3.81	4.13	3.23	3.04	5.45	4.17	4.94	3.95	3.22	4.66	5.85	4.43
	f+m	4.03	5.28	4.29	4.96	3.40	5.43	4.33	4.89	4.66	4.82	4.39	7.00	5.02
Lp	m	3.94	5.17	6.09	4.89	4.94	5.71	3.60	4.29	4.32	2.97	5.54	4.02	4.82
	f	5.08	4.36	5.04	4.43	5.08	7.32	4.56	6.13	6.37	4.02	6.82	5.06	5.76
	f+m	5.18	6.05	5.60	5.99	5.80	7.11	4.79	6.12	6.14	5.11	6.41	5.93	6.08
Sp1	m	3.88	4.22	5.01	3.15	4.13	4.74	4.58	3.02	3.04	2.49	4.51	4.74	4.53
	f	4.08	5.39	5.74	3.59	4.11	5.98	5.14	6.36	4.33	3.66	5.16	5.45	5.07
	f+m	4.65	5.97	6.05	5.07	4.70	6.30	5.82	5.47	5.58	5.64	5.39	6.62	5.77
Sp2	m	4.13	5.57	4.61	4.07	4.39	4.57	6.10	8.10	4.59	3.05	6.74	4.90	5.51
	f	6.18	4.80	7.96	4.48	4.85	6.95	4.50	5.85	5.63	4.06	8.46	4.06	5.88
	f+m	5.82	5.66	6.59	5.95	5.10	6.27	6.00	7.31	6.31	5.94	8.54	6.42	6.46
Spm	m	3.91	5.90	4.95	3.53	3.44	3.39	3.27	4.22	4.60	2.77	5.25	4.57	4.57
	f	4.81	5.03	6.42	3.47	4.08	5.36	4.41	5.29	4.22	3.98	6.19	7.15	5.34
	f+m	5.07	6.10	6.24	5.53	4.34	5.61	4.75	5.37	5.45	5.55	6.18	8.23	5.90
B	m	7.99	5.79	5.75	3.50	3.61	3.11	4.35	5.45	4.36	5.14	4.97	4.60	5.61
	f	6.96	5.81	4.20	3.32	4.69	6.25	4.69	6.42	5.39	5.13	6.64	5.39	6.21
	f+m	7.43	5.79	4.97	3.66	4.31	5.06	4.52	5.94	4.98	5.09	6.60	4.94	5.97
Le	m	4.14	4.76	4.79	4.28	3.54	4.05	3.89	3.20	4.01	3.27	4.44	5.42	4.93
	f	3.71	4.87	4.86	3.90	4.73	4.79	4.82	6.71	4.80	3.88	6.84	5.35	5.33
	f+m	5.44	6.53	5.97	6.67	5.35	5.17	6.01	6.42	5.79	6.43	6.53	8.56	6.54
Se	m	4.54	4.64	4.15	3.45	4.13	3.63	4.15	3.77	3.31	2.09	2.89	3.38	4.46
	f	4.40	4.47	4.81	3.24	4.17	5.01	4.19	5.54	4.05	3.07	7.48	4.68	5.02
	f+m	5.30	5.97	5.27	5.60	4.78	5.21	5.10	5.73	4.68	5.65	6.66	6.98	5.83
L2l	m	6.36	8.97	6.54	6.84	5.11	5.51	5.93	8.52	4.14	6.10	6.46	8.26	7.06
	f	5.78	8.64	3.25	8.58	6.14	6.77	7.56	9.72	4.76	6.23	11.18	10.10	7.80
	f+m	6.96	10.34	6.78	9.12	7.91	7.59	7.78	11.07	5.63	8.17	10.26	11.08	8.79
L1l	m	5.10	6.12	5.17	7.33	9.16	3.42	7.60	8.95	6.40	6.06	7.90	8.87	7.31
	f	8.09	7.86	12.58	7.77	8.30	8.74	7.36	5.23	7.46	5.87	8.19	8.36	7.96
	f+m	7.00	8.68	9.80	9.35	8.74	7.06	7.64	7.53	7.24	7.28	8.39	9.95	8.28
L2r	m	6.75	8.53	5.72	6.94	5.66	6.32	6.00	7.50	5.68	6.02	5.91	7.51	7.14
	f	6.48	8.09	3.05	8.73	5.55	6.87	6.47	8.85	4.79	6.47	9.22	10.51	7.55
	f+m	7.63	9.69	7.38	9.27	6.75	8.09	7.11	10.59	6.01	8.27	8.46	10.42	8.56
L1r	m	6.79	7.58	4.84	7.09	6.12	3.66	7.67	6.29	6.60	4.22	6.23	9.69	6.94
	f	7.70	8.49	12.54	7.56	6.97	10.15	7.10	4.70	8.13	5.88	9.21	9.59	8.18
	f+m	7.58	9.32	10.65	8.71	7.23	8.29	7.94	5.78	7.67	7.53	9.15	11.60	8.47
Lb	m	2.63	3.50	4.13	3.17	3.12	3.23	2.90	2.43	3.04	2.42	3.67	3.17	3.70
	f	3.48	3.88	4.13	3.08	3.97	4.38	3.93	5.39	3.85	2.62	5.12	4.56	4.33
	f+m	4.30	5.52	5.23	5.49	4.85	4.78	4.90	5.56	4.72	5.28	5.00	6.64	5.40
Average for linear characteristics	m	5.13	5.67	5.14	4.87	4.96	4.59	5.11	5.56	4.49	3.85	5.07	5.68	5.59
	f	5.49	5.86	6.12	4.99	5.06	6.38	5.37	6.22	5.28	4.69	7.21	6.65	6.10
	f+m	5.98	6.96	6.65	6.52	5.77	6.40	6.01	6.86	5.80	6.30	7.01	7.93	6.75
Non-linear characteristics														
Kl	m	35.82	26.63	18.54	25.20	44.30	33.92	16.21	34.57	18.52	27.23	21.07	30.97	32.63
	f	40.66	36.67	17.01	14.66	38.53	43.67	32.24	28.60	27.12	36.51	28.04	30.68	30.05
	f+m	38.27	34.84	17.50	19.91	40.05	38.85	26.75	31.10	24.57	33.02	26.68	30.40	31.60
Kr	m	32.90	13.43	19.06	23.83	47.68	20.43	21.02	19.25	21.13	21.14	23.57	25.09	29.31
	f	38.26	27.92	14.27	18.50	39.48	24.02	29.70	24.76	22.47	35.05	21.26	29.26	25.57
	f+m	35.29	24.88	16.43	20.68	41.99	22.17	26.75	22.22	21.76	30.53	21.63	26.86	27.88
P	m	11.34	8.70	11.36	8.05	12.33	4.61	10.02	12.05	7.91	10.89	6.67	6.10	13.87
	f	11.34	8.03	8.10	9.81	15.43	5.79	13.07	13.83	8.60	11.27	16.16	5.88	14.41
	f+m	11.91	8.37	9.84	9.62	15.64	5.90	12.17	12.92	8.56	11.46	14.28	5.92	14.35
K	m	31.39	19.26	18.33	23.65	42.65	26.37	17.54	24.20	18.17	21.23	20.36	26.53	25.96
	f	36.77	29.17	12.25	15.12	37.93	31.62	29.03	24.55	21.82	34.78	22.25	27.75	28.76
	f+m	33.97	27.49	15.65	19.12	39.07	29.03	25.17	24.05	20.40	30.11	21.86	26.76	27.77
Average for non-linear characteristics	m	27.86	17.01	16.82	20.18	36.74	21.33	16.20	22.52	16.43	20.12	17.92	22.17	25.44
	f	31.76	25.45	12.91	14.52	32.84	26.28	26.01	22.94	20.00	29.40	21.93	23.39	24.70
	f+m	29.86	23.90	16.86	17.33	34.19	23.99	22.71	22.57	18.82	26.28	21.11	22.49	25.40
Morphometric indices														
(Sc+Sp+Se)/3Lb	m	2.64	3.48	1.42	3.58	1.81	1.40	3.12	2.60	2.98	1.33	2.85	3.42	2.72
	f	1.84	2.75	2.49	1.56	2.35	1.82	1.69	3.32	3.07	2.17	3.09	2.90	2.57
	f+m	2.27	2.97	2.17	2.59	2.39	1.60	2.45	3.08	3.00	1.86	3.01	3.13	2.68
Lp/Sp	m	5.42	5.45	3.69	5.28	4.88	3.83	4.23	3.65	4.37	2.10	5.02	5.48	4.69
	f	2.85	4.40	6.03	3.29	3.68	5.12	2.83	4.21	6.21	3.70	6.48	6.36	4.77
	f+m	4.25	4.74	5.05	4.21	4.18	4.48	3.42	3.95	5.61	3.17	6.34	6.08	4.74
Le/Lp	m	4.12	6.43	3.53	4.53	5.11	4.83	4.21	4.81	4.43	3.10	3.91	6.34	5.08
	f	3.67	4.78	5.19	4.07	4.23	6.21	3.88	6.25	5.17	3.75	6.65	5.21	5.17
	f+m	4.07	5.25	5.00	4.45	4.49	5.49	4.29	5.59	5.04	3.88	6.35	6.38	5.28
Se/Sp	m	4.09	3.14	2.84	2.47	3.16	1.52	2.49	2.15	3.75	1.76	6.90	3.28	3.19
	f	1.70	2.32	4.76	2.65	2.35	2.81	2.40	3.38	1.98	2.49	3.19	3.08	2.77
	f+m	3.07	2.67	3.90	2.55	2.66	2.30	2.44	2.94	2.81	2.31	4.43	3.14	2.95
Sp2/Spm	m	3.15	5.71	2.23	3.79	2.42	2.93	5.11	6.76	2.84	3.01	4.07	3.71	4.06
	f	2.92	3.54	4.45	3.39	3.06	5.13	4.41	4.17	4.29	2.50	3.69	5.16	3.86
	f+m	3.00	4.27	3.65	3.52	2.82	4.31	4.67	5.43	3.78	2.70	3.85	4.48	3.94
Le/Se	m	3.24	3.84	3.26	5.19	3.17	2.22	4.24	2.04	4.21	1.97	3.68	4.32	3.58
	f	2.64	3.56	2.98	2.68	2.93	3.51	2.30	5.37	4.22	2.95	3.77	2.43	3.41
	f+m	3.04	3.63	3.16	3.93	3.05	2.93	3.30	4.16	4.25	2.60	3.85	3.60	3.55
Average for morphometric indices	m	3.78	4.68	2.83	4.14	3.43	2.79	3.90	3.67	3.76	2.21	4.41	4.43	3.89
	f	2.60	3.56	4.32	2.94	3.10	4.10	2.92	4.45	4.16	2.93	4.48	4.19	3.76
	f+m	3.28	3.92	3.82	3.54	3.27	3.52	3.43	4.19	4.08	2.75	4.64	4.47	3.86

Note: the numbers of the populations correspond to those given in Table 1; the names of the characteristics correspond to those given in Table 2; m – males, f – females, m+f – combined sample of males and females.

The influence of humidity, mechanical composition of soil, litter thickness or other factors on the variability of morphological characteristics or indices were not confirmed in most cases either. For the pH of the soil solution, differences were obtained according to six characteristics or indices, for the litter thickness to two, for the herb layer to 11 (Table 4), for the mechanical composition of soil to two, for the mineralisation of soil solution to one (Table 5), for recreational load to seven, for grazing to four characteristics or indices out of 24 × 3, i.e. of 72 characteristics or indices (Table 6).

Table 4. Coefficient of variation (CV, %) of morphometric parameters of *Bembidion minimum* populations under the influence of pH of soil solution, litter thickness, herb layer

Ecological factor	Morphometric characteristic or index		Sex	Factor values	
pH of soil solution	–	–	–	< 8	> 8
	Sc	width of head with eyes	m	3.09 ± 0.48[a]	3.82 ± 0.55[b]
	Le	length of elytra	m	3.73 ± 0.48[a]	4.57 ± 0.52[b]
	L1r	distance from the base of the right elytra to the first setae	f	7.00 ± 1.59[a]	9.34 ± 1.87[b]
	L1r	–	f+m	7.55 ± 1.09[a]	9.36 ± 1.51[b]
	P	density of elytra puncturing	f	13.06 ± 2.79[a]	8.16 ± 2.18[b]
	P	–	f+m	12.51 ± 2.45[a]	8.59 ± 2.37[b]
Litter thickness, cm	–	–	–	0	2–4
	Lc	length of head	f	6.46 ± 0.73[a]	5.46 ± 0.75[b]
	Le/Se	ratio of elytra length to their width	f	2.95 ± 0.51[a]	3.95 ± 1.14[b]
Herb layer	–	–	–	absent	developed herb layer
	Sp2	width of prothorax between back angles	f	5.08 ± 1.01[a]	7.35 ± 1.51[b]
	Lb	length of body	m	2.95 ± 0.38[a]	3.61 ± 0.55[b]
	Kl	the contrast of the light spots at the top of the left elytra	m	30.54 ± 7.95[a]	19.38 ± 1.47[b]
	Kl	–	f+m	32.58 ± 6.46[a]	22.92 ± 4.81[b]
	Kr	the contrast of the light spots at the top of the right elytra	f	29.66 ± 6.92[a]	19.33 ± 4.43[b]
	K	the average contrast of the light spots at the top of the left and right elytra	f	29.64 ± 6.99[a]	18.77 ± 5.65[b]
	K	–	f+m	28.31 ± 5.78[a]	19.30 ± 3.25[b]
	Lp/Sp	ratio of prothorax length to its maximum width	f	4.05 ± 1.14[a]	6.24 ± 0.23[b]
	Lp/Sp	–	f+m	4.28 ± 0.84[a]	5.67 ± 0.65[b]
	Se/Sp	ratio of maximum width of elytra to maximum prothorax width	m	2.67 ± 0.82[a]	4.50 ± 2.13[b]
	Se/Sp	–	f+m	2.68 ± 0.31[a]	3.71 ± 0.83[b]

Note: two groups were identified by the pH of soil solution: with the reaction of soil solution less than 8 (ecosystems 5, 7, 8, 9, 10, 11) and more than 8 (1, 2, 3, 4, 6, 12); two groups of ecosystems were identified according to the litter thickness: with the absence of litter layer (ecosystems 1, 2, 3, 5, 7, 10, 11, 12) and with litter thickness of 2–4 cm (4, 6, 8, 9); two groups of ecosystems were identified according to the development of herb layer: with absent herb layer (ecosystems 1, 2, 4, 5, 6, 7, 8, 10, 12) and with developed herb layer (3, 9, 11).

Table 5. Coefficient of variation (CV, %) of morphometric parameters of *Bembidion minimum* populations under of influence of mechanical composition of soil, mineralisation of soil solution

Ecological factor	Morphometric characteristic		Sex	Factor values		
Mechanical composition of soil	–	–	–	sand	sandy loam	loam
	Lc	length of head	f	7.27 ± 0.40[a]	6.37 ± 0.14[b]	5.70 ± 0.81[b]
	Lp	length of prothorax	f+m	5.36 ± 0.35[a]	5.34 ± 0.65[ab]	6.21 ± 0.44[b]
Mineralisation of soil solution, g/L	–	–	–	< 2	2–4	> 4
	Se	maximum width of elytra	m	4.18 ± 0.47[a]	3.72 ± 0.35[ab]	2.79 ± 0.65[b]

Note: three groups of soils were identified according to their mechanical composition – sand (ecosystems 3, 10), sandy loam (1, 2, 7), loam (4, 5, 6, 8, 9, 11, 12); three groups were identified according to the intensity of soil solution mineralisation – with relatively low mineralisation < 2 g/L (ecosystems 1, 2, 3, 4, 5), average mineralisation of 2–4 g/L (6, 7, 8, 9) and high mineralisation of soil solution > 4 g/L (10, 11, 12).

Table 6. Coefficient of variation (CV, %) of morphometric parameters of *Bembidion minimum* populations under influence of recreational load, intensity of cattle grazing

Ecological factor	Morphometric characteristic or index		Sex	Factor values			
	–	–	–	0	1	2	3
Recreational load, points	Lc	length of head	f+m	7.67 ± 0.47^{ab}	6.69 ± 0.79^{ab}	7.73 ± 0.45^{a}	6.38 ± 0.47^{b}
	Lp	length of prothorax	f	5.43 ± 0.61^{ab}	6.84 ± 0.48^{a}	4.54 ± 0.51^{b}	4.62 ± 0.39^{b}
	Lp	–	f+m	5.70 ± 0.48^{ab}	6.55 ± 0.50^{a}	5.17 ± 0.41^{b}	5.99 ± 0.06^{a}
	L2r	distance between setae on the right elytra	m	6.64 ± 0.93^{ab}	5.97 ± 0.32^{a}	5.91 ± 0.17^{a}	7.66 ± 0.81^{b}
	Kl	the contrast of the light spots at the top of the left elytra	m	38.23 ± 5.29^{a}	24.50 ± 8.25^{ab}	20.66 ± 5.81^{a}	27.60 ± 3.00^{a}
	P	density of elytra puncturing	m	11.91 ± 0.51^{a}	6.40 ± 1.67^{b}	10.76 ± 0.68^{a}	7.62 ± 1.35^{b}
	Le/Lp	ratio of elytra length to prothorax length	m	4.68 ± 0.51^{ab}	4.39 ± 0.46^{ab}	3.61 ± 0.56^{a}	5.77 ± 1.07^{b}
	–	–	–	absent	slight	medium	strong
Intensity of cattle grazing, points	Lc	length of head	m	8.70 ± 0.39^{a}	4.88 ± 1.34^{b}	6.58 ± 1.77^{ab}	5.62 ± 1.24^{b}
	Lc	–	f+m	7.65 ± 0.38^{a}	6.39 ± 0.26^{b}	7.73 ± 0.45^{a}	6.22 ± 0.54^{b}
	Kl	the contrast of the light spots at the top of the left elytra	m	37.15 ± 4.83^{a}	23.52 ± 6.58^{b}	20.66 ± 5.81^{b}	25.92 ± 1.01^{b}
	Lp/Sp	ratio of prothorax length to its maximum width	f+m	4.22 ± 0.22^{a}	6.01 ± 0.37^{b}	3.88 ± 1.02^{a}	4.48 ± 0.37^{a}

Note: four groups were identified according to the intensity of the recreational load, evaluated in points – from minimum of 0 points (ecosystems 1, 5, 8), 1 point (6, 9, 11), 2 points (3, 7, 10), to maximum 3 points (2, 4, 12); four groups of ecosystems were identified according to the intensity of cattle grazing – without grazing (1, 5, 6, 8), with slight grazing (9, 11, 12), grazing of medium (3, 7, 10) and heavy intensity (2, 4).

Discussion

Changes in the mean values of the morphometric characteristics of population are possibly under the influence of variable environmental factors. However, changes in their coefficient of variation are also more likely (relative to the variability expressed as a percentage in relation to the mean value of the characteristic) (Brygadyrenko & Korolev, 2015; Langraf et al., 2018, 2019). The average value of the characteristic in the gradient of any factor can remain unchanged, and the variation of individuals within a population can increase or decrease (Brygadyrenko & Reshetniak, 2014). According to Geodakjan's theory (Geodakjan, 1982), the variability in males is often higher than in females. The general variance of any morphometric characteristic of populations will be affected by the variance of males, the variance of females and the amount of sexual dimorphism (Sukhodolskaya & Eremeeva, 2013). Sexual dimorphism will make the greatest contribution to the total variance of a characteristic in a population with the same variances of any characteristic of males and females. Sexual dimorphism in male body size is considered as one of the main determinants of mating success (Fincke et al., 1997). Larger males are generally more aggressive and more competitive than smaller males, while larger males often attain greater reproductive success through intrasexual selection (Lagarde et al., 2005).

The results of this study showed that out of 24 × 3 = 72 studied characteristics or indices analysed in the gradient of seven environmental factors (72 × 7 = 504), only 33 of them showed a significant increase in variability (33/504 × 100% = 6.5%). In the gradient of seven environmental factors, in 12 cases, significant differences in the coefficient of variation were noted for males, in ten cases for females, and in 11 cases for the combined sample of males and females. Sexual dimorphism is the connection of sexual selection with natural selection, along with environmental variation, although male competition and the segregation of sexes due to limited resources have produced selective differentiation (Emlen, 2008; Benítez et al., 2011).

The absence of differences in the mean values of the coefficient of variation between males, females and the combined sample of males and females for each individual population suggests that males and females of *B. minimum* make a relatively equal contribution to the population polymorphism. It should also be noted that in the 12 studied populations, sexual dimorphism is relatively weak, i.e. in accordance with Geodakjan's theory, a decrease in size or its increase in the phylogeny of this species could not be observed. Interestingly, the coefficient of variation for most of the linear morphometric characteristics of *B. minimum* is lower in males: width of head (Sc), length of prothorax (Lp), width of prothorax (Sp1, Sp2, Spm), length of elytra (Le), distance between setae on the elytra (L2l and L2r). This also indicates a low rate of microevolutionary processes. The higher variability of width of elytra (Se) and length of body (Lb) in females compared to males indicates the importance of these parameters during reproduction, since the length of elytra is related to the length of abdomen, and hence to the volume of the abdomen, which closely correlates with the number of laid eggs.

Conclusions

The morphological and physiological variability of insect populations is a reflection of the genetic diversity of the population in the gradients of tens of environmental factors. The normal variability of populations should increase under conditions of intense negative impact of the habitat. Such an increase in the coefficient of variation was not found in our study, probably due to the fact that all 12 studied populations were close to the ecological optimum. The lower variability in males compared to females of *B. minimum* was unexpected. The second surprise was the equality of the coefficients of variation within the sex groups and for the combined sample of males and females.

The revealed patterns should be studied in detail for other invertebrate species. Comparison of the obtained patterns for invertebrates, vertebrates and humans should help in understanding the microevolutionary processes that will be observed in the future in isolated populations during space exploration. The method for estimating the coefficient of variation can be used to indicate the state of populations of rare species of invertebrates. In addition, this method can be recommended for assessing the state of ecosystems, the impact of environmental factors on them in Protected Areas of Ukraine and other countries.

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References

Abdel-Dayem M.S. 1998. The Egyptian species of *Bembidion* Latreille, 1802 (Coleoptera, Carabidae). *Bulletin of the Entomological Society of Egypt* 76: 181–198.

Andersen I. 1985. Ecomorphological adaptations of riparian Bembidiini species (Coleoptera: Carabidae). *Entomologia Generalis* 11(1–2): 41–46. DOI: 10.1127/entom.gen/11/1985/41

Avtaeva T.A., Sukhodolskaya R.A., Brygadyrenko V.V. 2021. Modeling the bioclimatic range of *Pterostichus melanarius* (Coleoptera, Carabidae) in conditions of global climate change. *Biosystems Diversity* 29(2): 140–150. DOI: 10.15421/012119

Baranovski B.A., Ivanko I.A., Gasso V.J., Ponomarenko O.L., Dubyna D.V., Roshchyna N.O., Karmyzova L.O., Poleva J.L., Nikolaieva V.V. 2021. Biodiversity of the Regional Landscape Park Samara Plavni within the first large reservoir in Europe. *Biosystems Diversity* 29(2): 160–179. DOI: 10.15421/012121

Baranovski B.A., Karmyzova L.A., Roshchyna N.O., Ivanko I.A., Karas O.G. 2020. Ecological-climatic characteristics of the flora of a floodplain landscape in Southeastern Europe. *Biosystems Diversity* 28(1): 98–112. DOI: 10.15421/012014

Barton P.S., Gibbk H., Manningk A., Lindenmayer D.B., Cunningham S.A. 2011. Morphological traits as predictors of diet and microhabitat use in a diverse beetle assemblage. *Biological Journal of the Linnean Society* 102(2): 301–310. DOI: 10.1111/j.1095-8312.2010.01580.x

Belaoussoff S., Kevan P.G., Murphy S., Swanton C. 2003. Assessing tillage disturbance on assemblages of ground beetles (Coleoptera: Carabidae) by using a range of ecological indices. *Biodiversity and Conservation* 12(5): 851–882. DOI: 10.1023/A:1022811010951

Benítez H.A. 2013. Assessment of patterns of fluctuating asymmetry and sexual dimorphism in carabid body shape. *Neotropical Entomology* 42(2): 164–169. DOI: 10.1007/s13744-012-0107-z

Benítez H., Briones R., Jerez V. 2011. Intra and Inter-population morphological variation of shape and size of the Chilean magnificent beetle, *Ceroglossus chilensis* in the Baker River Basin, Chilean Patagonia. *Journal of Insect Science* 11(1): 94. DOI: 10.1673/031.011.9401

Benítez H.A., Lemic D., Puschel T.A., Gasparic H.V., Kos T., Baric B., Bazok R., Zivkovic I.P. 2018. Fluctuating asymmetry indicates levels of disturbance between agricultural productions: An example in Croatian population of *Pterostichus melas melas* (Coleptera: Carabidae). *Zoologischer Anzeiger* 276: 42–49. DOI: 10.1016/J.JCZ.2018.07.003

Boyko O.O., Gugosyan Y.A., Shendrik L.I., Brygadyrenko V.V. 2019. Intraspecific morphological variation in free-living stages of *Strongyloides papillosus* (Nematoda, Strongyloididae) parasitizing various mammal species. *Vestnik Zoologii* 53(4): 313–324. DOI: 10.2478/vzoo-2019-0030

Braun S.D., Jones T.H., Perner J. 2004. Shifting average body size during regeneration after pollution – a case study using ground beetle assemblages. *Ecological Entomology* 29(5): 543–554. DOI: 10.1111/j.0307-6946.2004.00643.x

Brygadyrenko V.V. 2015. Parameters of ecological niches of *Badister*, *Licinus* and *Panagaeus* (Coleoptera, Carabidae) species measured against eight ecological factors. *Baltic Journal of Coleopterology* 15(2): 137–154.

Brygadyrenko V.V., Korolev O.V. 2015. Morphological polymorphism in an urban population of *Pterostichus melanarius* (Illiger, 1798) (Coleoptera, Carabidae). *Graellsia* 71(1): e025. DOI: 10.3989/graellsia.2015.v71.126

Brygadyrenko V.V., Reshetniak D.Y. 2014. Morphological variability among populations of *Harpalus rufipes* (Coleoptera, Carabidae): What is more important – the mean values or statistical peculiarities of distribution in the population? *Folia Oecologica* 41(2): 109–133.

Desender K., Verdyck P. 2001. Geographic scaling and genetic differentiation in two highly mobile European saltmarsh beetles. *Belgian Journal of Zoology* 131(1): 31–42.

Di Grumo D., Lovei G. 2016. Body size inequality in ground beetle (Coleoptera: Carabidae) assemblages as a potential method to monitor environmental impacts of transgenic crops. *Periodicum Biologorum* 118(3): 223–230. DOI: 10.18054/pb.2016.118.3.3921

Emlen D. 2008. The evolution of animal weapons. *Annual Review of Ecology, Evolution, and Systematics* 39: 387–413. DOI: 10.1146/annurev.ecolsys.39.110707.173502

Ernsting G., Isaaks J. 1997. Effects of temperature and season on egg size, hatchling size and adult size in *Notiophilus biguttatus*. *Ecological Entomology* 22(1): 32–40. DOI: 10.1046/j.1365-2311.1997.00040.x

Eyre M.D., Luff M.L. 2004. Ground beetle species (Coleoptera, Carabidae) associations with land cover variables in northern England and southern Scotland. *Ecography* 27(4): 417–426. DOI: 10.1111/j.0906-7590.2004.03757.x

Fairbairn D., Blankenhorn W., Székely T. 2007. *Sex, size and gender roles: Evolutionary studies of sexual size dimorphism*. Oxford: Oxford University Press. 266 p.

Fincke O., Waage J., Koenig W. 1997. Natural and sexual selection components of odonate mating patterns. In: J.C. Choe, B.J. Crespi (Eds.): *Mating Systems in Insects and Arachnids*. Cambridge: Cambridge University Press. P. 58–74. DOI: 10.1017/CBO9780511721946.004

Geodakjan V.A. 1982. Sexual dimorphism and the evolution of duration of ontogenesis and its stages. In: V.J.A. Novak, J. Mlikovsky (Eds.): *Evolution and Environment*. Praha: ČSAV. P. 229–237.

Giglio A., Giulianini P.G., Zetto T., Talarico F. 2011. Effects of the pesticide dimethoate on a non-target generalist carabid, *Pterostichus melas italicus* (Dejean, 1828) (Coleoptera: Carabidae). *Italian Journal of Zoology* 78(4): 471–477. DOI: 10.1080/11250003.2011.571222

Gobbi M., Fontaneto D. 2008. Biodiversity of ground beetles (Coleoptera: Carabidae) in different habitats of the Italian Po lowland. *Agriculture, Ecosystems and Environment* 127(3–4): 273–276. DOI: 10.1016/j.agee.2008.04.011

Gorban V., Huslystyi A., Espejo J.M.R., Bilova N. 2021. Prediction of SOC in calcic chernozem in the steppe zone of Ukraine using brightness and colour indicators. *Ekológia (Bratislava)* 40(4): 325–336. DOI: 10.2478/eko-2021-0034

Gritsan Y.I., Sytnyk S.A., Lovynska V.M., Tkalich I.I. 2019. Climatogenic reaction of *Robinia pseudoacacia* and *Pinus sylvestris* within Northern Steppe of Ukraine. *Biosystems Diversity* 27(1): 16–20. DOI: 10.15421/011902

Gugosyan Y.A., Boyko O.O., Brygadyrenko V.V. 2019. Morphological variation of four species of *Strongyloides* (Nematoda, Rhabditida) parasitising various mammal species. *Biosystems Diversity* 27(1): 85–98. DOI: 10.15421/011913

Hurka K. 1996. *Carabidae of the Czech and Slovak Republics*. Zlin: Kabourek. 565 p.

Iablokov-Khnzorian S.M. 1976. *Fauna of the Armenian Republic of the USSR. Ground beetles (Carabidae).* Yerevan: Publishing house of the Academy of Sciences of the Armenian SSR. 295 p. [In Russian]

Jensen L.B. 1990. Effect of temperature on the development of the immature stages of *Bembidion lampros* (Coleoptera: Carabidae). *Entomophaga* 35: 277–281. DOI: 10.1007/BF02374803

Kawano K. 2016. Comparative quantification of intralocalityal, interlocalityal, and interspecific variability in stag beetles (Coleoptera: Lucanidae) and the questions of phenotypic plasticity and species selection. *Annals of the Entomological Society of America* 109: 555–566. DOI: 10.1093/aesa/saw011

Knapp M., Saska P. 2012. The effects of habitat, density, gender and duration on overwintering success in *Bembidion lampros* (Coleoptera: Carabidae). *Journal of Applied Entomology* 136(3): 225–233. DOI: 10.1111/j.1439-0418.2011.01643.x

Komlyk V.O., Brygadyrenko V.V. 2019a. Morphological variability of *Bembidion aspericolle* (Coleoptera, Carabidae) populations in conditions of anthropogenic impact. *Biosystems Diversity* 27(1): 21–25. DOI: 10.15421/011903

Komlyk V.O., Brygadyrenko V.V. 2019b. Morphological variability of *Bembidion minimum* (Coleoptera, Carabidae) populations under the influence of natural and anthropogenic factors. *Biosystems Diversity* 27(3): 250–269. DOI: 10.15421/011935

Komlyk V., Brygadyrenko V. 2020. Morphological variability of *Bembidion varium* (Coleoptera, Carabidae) in gradient of soil salinity. *Folia Oecologica* 47(1): 23–33. DOI: 10.2478/foecol-2020-0004

Kostova R., Guéorguiev B. 2016. The ground beetles (Coleoptera: Carabidae) of the Strandzha Mountain and adjacent coastal territories (Bulgaria and Turkey). *Biodiversity Data Journal* 4: e8135. DOI: 10.3897/BDJ.4.e8135

Kozak V.M., Romanenko E.R., Brygadyrenko V.V. 2020. Influence of herbicides, insecticides and fungicides on food consumption and body weight of *Rossiulus kessleri* (Diplopoda, Julidae). *Biosystems Diversity* 28(3): 272–280. DOI: 10.15421/012036

Kryzhanovskij O.L., Belousov I.A., Kabak I.I., Kataev B.M., Makarov K.V., Shilenkov V.G. 1995. *A checklist of the ground-beetles of Russia and Adjacent Lands*. Sofia-Moscow: Pensoft. 271 p.

Kunakh O.M., Lisovets O.I., Yorkina N.V., Zhukova Y.O. 2021. Phytoindication assessment of the effect of reconstruction on the light regime of an urban park. *Biosystems Diversity* 29(3): 276–285. DOI: 10.15421/012135

Lagarde F., Corbin J., Goujon C., Poisbleau M. 2005. Polymorphisme et performances au combat chez les mâles de Lucane cerf-volant (*Lucanus cervus*). *Revue d'Écologie* 60(2): 127–137.

Lagisz M. 2008. Changes in morphology of the ground beetle *Pterostichus oblongopunctatus* F. (Coleoptera; Carabidae) from vicinities of a zinc and lead smelter. *Environmental Toxicology and Chemistry* 27(8): 1744–1747. DOI: 10.1897/07-661.1

Langraf V., David S., Babosová R., Petrovičová K., Schlarmannová J. 2020. Change of ellipsoid biovolume (EV) of ground beetles (Coleoptera, Carabidae) along an urban–suburban–rural gradient of Central Slovakia. *Diversity* 12: 475. DOI: 10.3390/d12120475

Langraf V., Petrovičová K., David S., Kanská M., Nozdrovická J., Schlarmannová J. 2018. Change phenotypic traits in ground beetles (Carabidae) reflects biotope disturbance in Central Europe. *Journal of the Entomological Research Society* 20(2): 119–129.

Langraf V., Petrovičová K., David S., Nozdrovická J., Petrovič F., Schlarmannová J. 2019. The bioindication evaluation of ground beetles (Coleoptera: Carabidae) in three forest biotopes in the southern part of Central Slovakia. *Ekológia (Bratislava)* 38(1): 25–36. DOI: 10.2478/eko-2019-0003

Lindroth C.H. 1974. *Coleoptera, Carabidae. Handbooks for the identification of British insects.* London: Royal Entomological Society of London. 148 p.

Lindroth C.H. 1985. *The Carabidae (Coleoptera) of Fennoscandia and Denmark*. Vol. 1. 226 p.

McGeoch M.A. 1998. The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews* 73(2): 181–201. DOI: 10.1111/j.1469-185X.1997.tb00029.x

Nitzu E. 2003. Contributions to the knowledge of the tribus Bembidiini (Coleoptera: Carabidae) from Romania. *Travaux du Museum National d'Histoire Naturelle Grigore Antipa* 45(1): 179–185.

Okuzaki Y., Sota T. 2018. Predator size divergence depends on community context. *Ecology Letters* 21(7): 1097–1107. DOI: 10.1111/ele.12976

Osman W., El-Samad L.M., Mokhamer E.H., El-Touhamy A., Shonouda M. 2015. Ecological, morphological, and histological studies on *Blaps polycresta* (Coleoptera: Tenebrionidae) as biomonitors of cadmium soil pollution. *Environmental Science and Pollution Research* 22(18): 14104–14115. DOI: 10.1007/s11356-015-4606-4

Pakhomov O.Y., Kunakh O.M., Babchenko A.V., Fedushko M.P., Demchuk N.I., Bezuhla L.S., Tkachenko O.S. 2019. Temperature effect on the temporal dynamic of terrestrial invertebrates in technosols formed after reclamation at a post-mining site in Ukrainian steppe drylands. *Biosystems Diversity* 27(4): 322–328. DOI: 10.15421/011942

Pokhylenko A.P., Didur O.O., Kulbachko Y.L., Bandura L.P., Chernykh S.A. 2020. Influence of saprophages (Isopoda, Diplopoda) on leaf litter decomposition under different levels of humidification and chemical loading. *Biosystems Diversity* 28(4): 384–389. DOI: 10.15421/012049

Putchkov A.V., Brygadyrenko V.V., Nikolenko N.Y. 2020. Ecological-faunistic analysis of ground beetles and tiger beetles (Coleoptera: Carabidae, Cicindelidae) of metropolises of Ukraine. *Biosystems Diversity* 28(2): 163–174. DOI: 10.15421/012022

Puchkov A.V., Brygadyrenko V.V., Faly L.I., Komaromi N.A. 2020. Staphylinids (Coleoptera, Staphylinidae) of Ukrainian metropolises. *Biosystems Diversity* 28(1): 41–47. DOI: 10.15421/012007

Petillon J., Georges A., Canard A., Ysnel F. 2007. Impact of cutting and sheep grazing on ground-active spiders and carabids in intertidal salt marshes (Western France). *Animal Biodiversity and Conservation* 30(2): 201–209.

Rouabah A., Villerd J., Amiaud B., Plantureux S., Lasserre F. 2015. Response of carabid beetles diversity and size distribution to the vegetation structure within differently managed field margins. *Agriculture, Ecosystems and Environment* 200: 21–32. DOI: 10.1016/j.agee.2014.10.011

Rueffler C., Van Dooren T.J.M., Leimar O., Abrams P.A. 2006. Disruptive selection and then what? *Trends in Ecology and Evolution* 21(5): 238–245. DOI: 10.1139/g11-052

Rusynov V.I., Brygadyrenko V.V. 2017. Morphological variability of a population of *Anatolica eremita* (Coleoptera, Tenebrionidae): Constancy of morphometric indices with variation of linear parameters of the body. *Baltic Journal of Coleopterology* 17(2): 205–217.

Serrano J. 2013. *New catalogue of the family Carabidae of the Iberian Peninsula (Coleoptera)*. Murcia: Universidad de Murcia. 192 p.

Shreeves G., Field J. 2008. Parental care and sexual size dimorphism in wasps and bees. *Behavioral Ecology and Sociobiology* 62(5): 843–852. DOI: 10.1007/s00265-007-0510-3

Shulman M.V., Pakhomov O.Y., Brygadyrenko V.V. 2017. Effect of lead and cadmium ions upon the pupariation and morphological changes in *Calliphora vicina* (Diptera, Calliphoridae). *Folia Oecologica* 44(1): 28–37. DOI: 10.1515/foecol-2017-0004

Sowa G., Skalski T. 2019. Effects of chronic metal exposure on the morphology of beetles species representing different ecological niches. *Bulletin of Environmental Contamination and Toxicology* 102(2): 191–197. DOI: 10.1007/s00128-018-02532-7

Sukhodolskaya R.A., Eremeeva N.I. 2013. Body size and shape variation in ground beetle *Carabus aeruginosus* F.-W., 1822 (Coleoptera, Carabidae). *Contemporary Problems of Ecology* 6(6): 609–615. DOI: 10.1134/S1995425513060127

Talarico F., Brandmayr P., Giglio A., Massolo A., Brandmayr T.Z. 2011. Morphometry of eyes, antennae and wings in three species of Siagona (Coleoptera, Carabidae). *ZooKeys* 100: 203–214. DOI: 10.3897/zookeys.100.1528

Ter Braak C.J.F., Šmilauer P. 2012. *Canoco reference manual and user's guide: Software for ordination, version 5.0.* Ithaca, USA: Microcomputer Power. 496 p.

Theiss S., Heimbach U. 1994. Laborzuchtverfahren für laufkäfer der art *Bembidion tetracolum* (Coleoptera: Carabidae). *Entomologia Generalis* 19(1/2): 61–64. DOI: 10.1127/entom.gen/19/1994/061

Thiele H.U. 1977. *Carabid beetles in their environments. A study on habitat selection by adaptation in physiology and behaviour*. Berlin: Springer-Verlag. 369 p. DOI: 10.1007/978-3-642-81154-8

Thornhill R., Alcock J. 1983. *The evolution of insect mating systems*. London: Harvard University Press. 535 p.

Tyler G. 2010. Variability in colour, metallic lustre, and body size of *Carabus arvensis* Herbst, 1784 (Coleoptera: Carabidae) in relation to habitat properties. *Entomologica Fennica* 21(2): 90–96. DOI: 10.33338/ef.84514

Vittum P.J., Morzuchi B.J. 1990. Effect of soil pH on Japanese beetle (Coleoptera: Scarabaeidae) oviposition in potted turfgrass. *Journal of Economic Entomology* 83(5): 2036–2039. DOI: 10.1093/jee/83.5.2036

Zhuk V.V. 2019. *Biology of reproduction and development. Part 1.* Perm: Publishing Center of Perm State National Research University. 232 p. [In Russian]

Appendix 1. Coefficient of variation (CV, %) of morphometric parameters of *Bembidion minimum* populations studied in ecosystems with different mechanical composition of soil

Morphometric characteristic or index	Sex	Sand		Sandy loam		Loam		F, $F_{0.05}$ = 4.256	p
		x	SD	x	SD	x	SD		
n	m	14.00	1.41	13.67	1.53	13.43	4.72	0.017	0.983
n	f	18.00	5.66	23.00	4.36	19.71	5.25	0.666	0.538
n	f+m	32.00	7.07	36.67	2.89	33.14	8.76	0.291	0.754
Lc	m	5.65	1.00	7.23	2.15	6.77	2.11	0.373	0.699
Lc	f	7.27	0.40	6.37	0.14	5.70	0.81	4.439	0.046
Lc	f+m	7.87	0.53	7.13	0.46	6.90	0.87	1.242	0.334
Sc	m	3.07	1.02	3.35	0.46	3.60	0.62	0.577	0.581
Sc	f	3.68	0.64	3.92	0.22	4.45	1.08	0.729	0.509
Sc	f+m	4.56	0.37	4.55	0.65	4.96	1.10	0.270	0.769
Lp	m	4.53	2.21	4.24	0.83	4.82	0.65	0.374	0.698
Lp	f	4.53	0.72	4.67	0.37	5.89	1.05	2.870	0.109
Lp	f+m	5.36	0.35	5.34	0.65	6.21	0.44	4.690	0.040
Sp1	m	3.75	1.78	4.23	0.35	3.90	0.81	0.198	0.824
Sp1	f	4.70	1.47	4.87	0.70	5.00	1.02	0.070	0.933
Sp1	f+m	5.85	0.29	5.48	0.72	5.59	0.67	0.193	0.828
Sp2	m	3.83	1.10	5.27	1.02	5.34	1.50	0.992	0.408
Sp2	f	6.01	2.76	5.16	0.90	5.75	1.53	0.204	0.819
Sp2	f+m	6.27	0.46	5.83	0.17	6.56	1.09	0.685	0.529
Spm	m	3.86	1.54	4.36	1.37	4.14	0.71	0.147	0.865
Spm	f	5.20	1.73	4.75	0.31	5.11	1.29	0.115	0.893
Spm	f+m	5.90	0.49	5.31	0.71	5.82	1.20	0.290	0.755
B	m	5.45	0.43	6.04	1.83	4.23	0.85	3.062	0.097
B	f	4.67	0.66	5.82	1.14	5.44	1.16	0.656	0.542
B	f+m	5.03	0.08	5.91	1.46	5.07	0.97	0.740	0.504
Le	m	4.03	1.07	4.26	0.45	4.13	0.71	0.068	0.935
Le	f	4.37	0.69	4.47	0.66	5.30	1.09	1.188	0.348
Le	f+m	6.20	0.33	5.99	0.55	6.36	1.14	0.149	0.864
Se	m	3.12	1.46	4.44	0.26	3.51	0.39	3.667	0.068
Se	f	3.94	1.23	4.35	0.15	4.88	1.36	0.570	0.585
Se	f+m	5.46	0.27	5.46	0.46	5.66	0.88	0.106	0.900
L2l	m	6.32	0.31	7.09	1.65	6.41	1.62	0.236	0.974
L2l	f	4.74	2.11	7.33	1.44	8.18	2.35	1.988	0.193
L2l	f+m	7.48	0.98	8.36	1.76	8.95	2.03	0.500	0.622
L1l	m	5.62	0.63	6.27	1.26	7.43	2.03	1.021	0.398
L1l	f	9.23	4.74	7.77	0.37	7.72	1.17	0.536	0.603
L1l	f+m	8.54	1.78	7.77	0.85	8.32	1.10	0.332	0.726
L2r	m	5.87	0.21	7.09	1.30	6.50	0.81	1.111	0.370
L2r	f	4.76	2.42	7.01	0.93	7.79	2.09	1.897	0.205
L2r	f+m	7.83	0.63	8.14	1.36	8.51	1.74	0.171	0.846
L1r	m	4.53	0.44	7.35	0.48	6.53	1.77	2.258	0.160
L1r	f	9.21	4.71	7.76	0.70	8.04	1.86	0.284	0.759
L1r	f+m	9.09	2.21	8.28	0.92	8.35	1.81	0.168	0.848

Morphometric characteristic or index	Sex	Sand		Sandy loam		Loam		F, $F_{0.05}$ = 4.256	p
		x	SD	x	SD	x	SD		
Lb	m	3.28	1.21	3.01	0.45	3.12	0.37	0.143	0.869
Lb	f	3.38	1.07	3.76	0.25	4.34	0.79	1.557	0.263
Lb	f+m	5.26	0.04	4.91	0.61	5.29	0.68	0.408	0.677
Kl	m	22.89	6.14	26.22	9.81	29.79	8.91	0.532	0.605
Kl	f	26.76	13.79	36.52	4.21	30.19	9.21	0.806	0.476
Kl	f+m	25.26	10.97	33.29	5.92	30.22	7.33	0.679	0.531
Kr	m	20.10	1.47	22.45	9.81	25.85	9.85	0.357	0.709
Kr	f	24.66	14.69	31.96	5.53	25.68	6.93	0.771	0.491
Kr	f+m	23.48	9.97	28.97	5.55	25.33	7.61	0.374	0.698
P	m	11.13	0.33	10.02	1.32	8.25	2.93	1.287	0.322
P	f	9.69	2.24	10.81	2.56	10.79	4.37	0.070	0.933
P	f+m	10.65	1.15	10.82	2.12	10.41	3.94	0.016	0.984
K	m	19.78	2.05	22.73	7.55	25.99	7.95	0.614	0.562
K	f	23.52	15.93	31.66	4.43	25.86	7.40	0.711	0.517
K	f+m	22.88	10.22	28.88	4.56	25.76	6.83	0.472	0.638
(Sc+Sp+Se)/3Lb	m	1.38	0.06	3.08	0.42	2.66	0.80	3.924	0.060
(Sc+Sp+Se)/3Lb	f	2.33	0.23	2.09	0.57	2.59	0.69	0.678	0.532
(Sc+Sp+Se)/3Lb	f+m	2.02	0.22	2.56	0.36	2.69	0.55	1.472	0.280
Lp/Sp	m	2.90	1.12	5.03	0.70	4.64	0.71	5.238	0.031
Lp/Sp	f	4.87	1.65	3.36	0.90	5.05	1.34	1.835	0.215
Lp/Sp	f+m	4.11	1.33	4.14	0.67	4.98	1.00	1.102	0.373
Le/Lp	m	3.32	0.30	4.92	1.31	4.85	0.76	2.615	0.127
Le/Lp	f	4.47	1.02	4.11	0.59	5.40	1.01	2.265	0.160
Le/Lp	f+m	4.44	0.79	4.54	0.63	5.40	0.79	2.064	0.183
Se/Sp	m	2.30	0.76	3.24	0.80	3.32	1.75	0.370	0.701
Se/Sp	f	3.63	1.61	2.14	0.38	2.78	0.49	2.755	0.117
Se/Sp	f+m	3.11	1.12	2.73	0.32	2.98	0.70	0.205	0.818
Sp2/Spm	m	2.62	0.55	4.66	1.34	3.79	1.44	1.375	0.301
Sp2/Spm	f	3.48	1.38	3.62	0.75	4.13	0.81	0.612	0.563
Sp2/Spm	f+m	3.18	0.67	3.98	0.87	4.03	0.82	0.877	0.449
Le/Se	m	2.62	0.91	3.77	0.50	3.55	1.15	0.861	0.455
Le/Se	f	2.97	0.02	2.83	0.65	3.56	1.02	0.855	0.457
Le/Se	f+m	2.88	0.40	3.32	0.30	3.68	0.52	2.481	0.139

Note: three groups of ecosystems were identified according to the mechanical composition of the soil: sand (ecosystems 3, 10), sandy loam (ecosystems 1, 2, 7), loam (ecosystems 4, 5, 6, 8, 9, 11, 12).

Appendix 2. Coefficient of variation (CV, %) of morphometric parameters of *Bembidion minimum* populations studied in ecosystems with different mineralization of soil solution

Morphometric characteristic or index	Sex	< 2		2–4		> 4		F, $F_{0.05}$ = 4.256	p
		x	SD	x	SD	x	SD		
n	m	14.00	1.58	13.75	3.40	12.67	6.81	0.115	0.893
n	f	22.00	5.48	19.25	5.91	18.67	3.06	0.496	0.625
n	f+m	36.00	5.43	33.00	8.91	31.33	8.96	0.392	0.687
Lc	m	7.03	1.76	7.83	1.48	4.64	1.18	3.824	0.063
Lc	f	5.90	1.02	5.91	0.45	6.80	0.88	1.282	0.324
Lc	f+m	7.10	0.91	7.39	0.80	6.79	0.66	0.449	0.652
Sc	m	3.43	0.42	3.51	0.45	3.42	1.21	0.018	0.983
Sc	f	3.60	0.45	4.63	0.69	4.58	1.32	2.345	0.151
Sc	f+m	4.39	0.75	4.83	0.46	5.40	1.40	1.275	0.325
Lp	m	5.01	0.77	4.48	0.88	4.18	1.29	0.790	0.483
Lp	f	4.80	0.37	6.10	1.15	5.30	1.42	1.989	0.193
Lp	f+m	5.72	0.35	6.04	0.95	5.82	0.66	0.250	0.784
Sp1	m	4.08	0.67	3.85	0.94	3.91	1.24	0.077	0.926
Sp1	f	4.58	0.93	5.45	0.91	4.76	0.96	1.036	0.394
Sp1	f+m	5.29	0.68	5.79	0.37	5.88	0.65	1.271	0.326
Sp2	m	4.55	0.61	5.84	1.67	4.90	1.85	1.026	0.397
Sp2	f	5.65	1.44	5.73	1.00	5.53	2.54	0.014	0.987
Sp2	f+m	5.82	0.54	6.47	0.58	6.97	1.38	1.941	0.199
Spm	m	4.35	1.06	3.87	0.64	4.20	1.28	0.256	0.779
Spm	f	4.76	1.11	4.82	0.59	5.77	1.63	0.875	0.450
Spm	f+m	5.46	0.78	5.30	0.38	6.65	1.40	2.442	0.142
B	m	5.33	1.86	4.32	0.96	4.90	0.28	0.613	0.563
B	f	5.00	1.42	5.69	0.80	5.72	0.81	0.579	0.580
B	f+m	5.23	1.46	5.13	0.59	5.54	0.92	0.126	0.883
Le	m	4.30	0.51	3.79	0.40	4.38	1.08	0.930	0.429
Le	f	4.41	0.56	5.28	0.95	5.36	1.48	1.272	0.326
Le	f+m	5.99	0.61	5.85	0.52	7.17	1.20	3.077	0.096
Se	m	4.18	0.47	3.72	0.35	2.79	0.65	7.882	0.011
Se	f	4.22	0.59	4.70	0.70	5.08	2.23	0.507	0.618
Se	f+m	5.38	0.44	5.18	0.43	6.43	0.69	5.872	0.023
L2l	m	6.76	1.40	6.03	1.83	6.94	1.16	0.391	0.687
L2l	f	6.48	2.24	7.20	2.05	9.17	2.60	1.342	0.309
L2l	f+m	8.22	1.51	8.02	2.26	9.84	1.50	1.036	0.393
L1l	m	6.58	1.70	6.59	2.36	7.61	1.43	0.330	0.727
L1l	f	8.92	2.06	7.20	1.45	7.47	1.39	1.267	0.328
L1l	f+m	8.71	1.06	7.37	0.27	8.54	1.34	2.395	0.147
L2r	m	6.72	1.17	6.38	0.79	6.48	0.89	0.142	0.870
L2r	f	6.38	2.25	6.75	1.67	8.73	2.06	1.346	0.308
L2r	f+m	8.14	1.27	7.95	1.95	9.05	1.19	0.499	0.623
L1r	m	6.48	1.06	6.06	1.70	6.71	2.77	0.127	0.882
L1r	f	8.65	2.24	7.52	2.27	8.23	2.04	0.294	0.752
L1r	f+m	8.70	1.38	7.42	1.12	9.43	2.05	1.686	0.239

Morphometric characteristic or index	Sex	< 2		2–4		> 4		F, $F_{0.05}$ = 4.256	p
		x	SD	x	SD	x	SD		
Lb	m	3.31	0.55	2.90	0.34	3.09	0.63	0.717	0.514
Lb	f	3.71	0.43	4.39	0.71	4.10	1.31	0.829	0.467
Lb	f+m	5.08	0.51	4.99	0.39	5.64	0.88	1.231	0.337
Kl	m	30.10	10.05	25.81	9.79	26.42	5.00	0.291	0.754
Kl	f	29.51	12.59	32.91	7.49	31.74	4.33	0.144	0.868
Kl	f+m	30.11	10.62	30.32	6.30	30.03	3.19	0.001	0.999
Kr	m	27.38	13.41	20.46	0.86	23.27	1.99	0.672	0.534
Kr	f	27.69	11.35	25.24	3.12	28.52	6.92	0.152	0.861
Kr	f+m	27.85	10.56	23.23	2.36	26.34	4.47	0.432	0.662
P	m	10.36	1.87	8.65	3.18	7.89	2.62	1.015	0.400
P	f	10.54	3.06	10.32	3.80	11.10	5.14	0.037	0.964
P	f+m	11.08	2.85	9.89	3.27	10.55	4.25	0.140	0.871
K	m	27.06	10.13	21.57	4.39	22.71	3.34	0.689	0.527
K	f	26.25	11.99	26.76	4.40	28.26	6.28	0.049	0.952
K	f+m	27.06	9.82	24.66	3.55	26.24	4.15	0.127	0.882
(Sc+Sp+Se)/3Lb	m	2.59	0.97	2.53	0.78	2.53	1.08	0.006	0.994
(Sc+Sp+Se)/3Lb	f	2.20	0.49	2.48	0.84	2.72	0.49	0.673	0.534
(Sc+Sp+Se)/3Lb	f+m	2.48	0.32	2.53	0.68	2.67	0.70	0.109	0.898
Lp/Sp	m	4.94	0.74	4.02	0.34	4.20	1.83	1.047	0.390
Lp/Sp	f	4.05	1.24	4.59	1.43	5.51	1.57	1.045	0.391
Lp/Sp	f+m	4.49	0.39	4.37	0.94	5.20	1.76	0.643	0.548
Le/Lp	m	4.74	1.11	4.57	0.30	4.45	1.69	0.072	0.931
Le/Lp	f	4.39	0.60	5.38	1.12	5.20	1.45	1.196	0.346
Le/Lp	f+m	4.65	0.47	5.10	0.59	5.54	1.43	1.119	0.368
Se/Sp	m	3.14	0.60	2.48	0.94	3.98	2.64	0.966	0.417
Se/Sp	f	2.76	1.17	2.64	0.60	2.92	0.38	0.087	0.918
Se/Sp	f+m	2.97	0.56	2.62	0.30	3.29	1.07	0.928	0.430
Sp2/Spm	m	3.46	1.40	4.41	1.89	3.60	0.54	0.515	0.614
Sp2/Spm	f	3.47	0.60	4.50	0.43	3.78	1.33	1.942	0.199
Sp2/Spm	f+m	3.45	0.57	4.55	0.69	3.68	0.90	2.895	0.107
Le/Se	m	3.74	0.85	3.18	1.21	3.32	1.21	0.335	0.724
Le/Se	f	2.96	0.37	3.85	1.29	3.05	0.68	1.385	0.299
Le/Se	f+m	3.36	0.40	3.66	0.65	3.35	0.66	0.397	0.684

Note: three groups of ecosystems were identified according to the mineralisation of the soil solution: with low mineralisation < 2 g/l (ecosystems 1, 2, 3, 4, 5), medium mineralisation 2–4 g/l (ecosystems 6, 7, 8, 9) and high mineralisation of the soil solution > 4 g/l (ecosystems 10, 11, 12).

Appendix 3. Coefficient of variation (CV, %) of morphometric parameters of *Bembidion minimum* populations studied in ecosystems with different soil solution reactions (pH)

Morphometric characteristic or index	Sex	< 8		> 8		$F, F_{0.05} = 4.965$	p
		x	SD	x	SD		
n	m	13.33	4.23	13.83	3.19	0.054	0.822
n	f	21.67	3.61	18.83	6.01	0.978	0.346
n	f+m	35.00	7.13	32.67	7.63	0.300	0.596
Lc	m	6.62	2.31	6.78	1.63	0.018	0.895
Lc	f	6.16	0.78	6.09	1.01	0.017	0.898
Lc	f+m	7.18	0.78	7.05	0.85	0.080	0.783
Sc	m	3.09	0.48	3.82	0.55	5.891	0.036
Sc	f	4.00	0.76	4.37	1.04	0.515	0.489
Sc	f+m	4.42	0.55	5.17	1.05	2.399	0.152
Lp	m	4.28	0.92	4.97	0.87	1.799	0.209
Lp	f	5.50	1.11	5.22	1.08	0.198	0.666
Lp	f+m	5.73	0.64	5.98	0.64	0.449	0.518
Sp1	m	3.63	0.89	4.29	0.69	2.071	0.181
Sp1	f	4.79	0.97	5.04	0.97	0.192	0.670
Sp1	f+m	5.43	0.39	5.78	0.76	0.977	0.346
Sp2	m	5.50	1.83	4.64	0.55	1.197	0.299
Sp2	f	5.56	1.57	5.74	1.54	0.040	0.845
Sp2	f+m	6.53	1.21	6.12	0.36	0.643	0.441
Spm	m	3.93	0.93	4.38	0.96	0.683	0.428
Spm	f	4.70	0.87	5.37	1.29	1.141	0.310
Spm	f+m	5.27	0.65	6.13	1.11	2.665	0.134
B	m	4.65	0.67	5.12	1.79	0.373	0.555
B	f	5.49	0.85	5.32	1.35	0.070	0.797
B	f+m	5.24	0.87	5.31	1.25	0.012	0.915
Le	m	3.73	0.48	4.57	0.52	8.696	0.015
Le	f	5.30	1.20	4.58	0.64	1.675	0.225
Le	f+m	6.09	0.46	6.39	1.21	0.324	0.582
Se	m	3.39	0.80	3.97	0.56	2.085	0.179
Se	f	4.75	1.55	4.44	0.63	0.213	0.655
Se	f+m	5.43	0.74	5.72	0.68	0.494	0.498
L2l	m	6.04	1.47	7.08	1.29	1.687	0.223
L2l	f	7.60	2.42	7.19	2.46	0.085	0.776
L2l	f+m	8.47	1.94	8.65	1.81	0.026	0.875
L1l	m	7.68	1.27	6.00	1.91	3.207	0.104
L1l	f	7.07	1.25	8.90	1.84	4.074	0.071
L1l	f+m	7.80	0.62	8.64	1.32	1.969	0.191
L2r	m	6.13	0.69	6.96	0.98	2.919	0.118
L2r	f	6.89	1.78	7.29	2.53	0.099	0.760
L2r	f+m	7.87	1.62	8.75	1.23	1.126	0.314
L1r	m	6.19	1.12	6.61	2.12	0.184	0.677
L1r	f	7.00	1.59	9.34	1.87	5.429	0.042
L1r	f+m	7.55	1.09	9.36	1.51	5.644	0.039

Morphometric characteristic or index	Sex	< 8		> 8		F, $F_{0.05}$ = 4.965	p
		x	SD	x	SD		
Lb	m	2.93	0.47	3.31	0.49	1.816	0.208
Lb	f	4.15	1.00	3.92	0.56	0.239	0.636
Lb	f+m	5.05	0.31	5.33	0.79	0.624	0.448
Kl	m	26.98	10.77	28.51	6.37	0.09	0.771
Kl	f	31.84	4.77	30.56	12.23	0.057	0.816
Kl	f+m	30.36	5.69	29.96	9.26	0.008	0.930
Kr	m	25.63	10.89	22.46	6.56	0.374	0.554
Kr	f	28.79	7.31	25.37	8.49	0.558	0.472
Kr	f+m	27.48	7.94	24.39	6.44	0.550	0.475
P	m	9.98	2.27	8.36	2.73	1.244	0.291
P	f	13.06	2.79	8.16	2.18	11.517	$6.8*10^{-3}$
P	f+m	12.51	2.45	8.59	2.37	7.917	0.018
K	m	24.03	9.43	24.26	4.92	0.003	0.959
K	f	28.39	6.75	25.45	9.66	0.375	0.554
K	f+m	26.78	6.89	25.34	6.74	0.134	0.722
(Sc+Sp+Se)/3Lb	m	2.45	0.72	2.66	1.02	0.167	0.691
(Sc+Sp+Se)/3Lb	f	2.62	0.64	2.23	0.56	1.253	0.289
(Sc+Sp+Se)/3Lb	f+m	2.63	0.48	2.46	0.56	0.340	0.573
Lp/Sp	m	4.04	1.07	4.86	0.85	2.133	0.175
Lp/Sp	f	4.52	1.49	4.68	1.43	0.035	0.856
Lp/Sp	f+m	4.45	1.26	4.80	0.70	0.367	0.558
Le/Lp	m	4.26	0.71	4.96	1.18	1.548	0.242
Le/Lp	f	4.99	1.24	4.86	0.91	0.045	0.836
Le/Lp	f+m	4.94	0.91	5.11	0.81	0.111	0.745
Se/Sp	m	3.37	1.87	2.89	0.86	0.324	0.582
Se/Sp	f	2.63	0.54	2.89	1.03	0.287	0.604
Se/Sp	f+m	2.93	0.77	2.94	0.57	0.001	0.987
Sp2/Spm	m	4.04	1.65	3.59	1.19	0.291	0.601
Sp2/Spm	f	3.69	0.76	4.10	0.95	0.683	0.428
Sp2/Spm	f+m	3.88	1.05	3.87	0.58	0.001	0.995
Le/Se	m	3.22	1.02	3.68	1.02	0.610	0.453
Le/Se	f	3.59	1.11	2.97	0.47	1.612	0.233
Le/Se	f+m	3.54	0.66	3.38	0.39	0.239	0.635

Note: two groups of ecosystems were identified by pH: with the reaction of the soil solution less than 8.0 (ecosystems 5, 7, 8, 9, 10, 11) and more than 8.0 (ecosystems 1, 2, 3, 4, 6, 12).

Appendix 4. Coefficient of variation (CV, %) of morphometric parameters of *Bembidion minimum* populations studied in ecosystems with different litter thickness

Morphometric characteristic or index	Sex	0 cm		2–4 cm		F, $F_{0.05}$ = 4.965	p
		x	SD	x	SD		
n	m	13.25	3.77	14.25	3.59	0.193	0.670
n	f	20.63	4.75	19.50	6.03	0.126	0.730
n	f+m	33.88	6.60	33.75	9.25	7.4*10–4	0.979
Lc	m	6.38	2.09	7.34	1.53	0.652	0.438
Lc	f	6.46	0.73	5.46	0.75	4.982	0.049
Lc	f+m	7.18	0.65	6.98	1.10	0.163	0.695
Sc	m	3.38	0.73	3.60	0.36	0.295	0.599
Sc	f	4.08	0.88	4.39	0.99	0.306	0.592
Sc	f+m	4.69	1.08	4.99	0.32	0.269	0.616
Lp	m	4.53	1.06	4.80	0.66	0.208	0.658
Lp	f	5.00	0.84	6.06	1.20	3.243	0.102
Lp	f+m	5.61	0.55	6.34	0.52	4.946	0.051
Sp1	m	4.20	0.78	3.49	0.84	2.112	0.177
Sp1	f	4.84	0.77	5.07	1.32	0.142	0.714
Sp1	f+m	5.61	0.67	5.61	0.51	1.1*10^{-15}	0.999
Sp2	m	4.94	1.17	5.33	1.86	0.209	0.657
Sp2	f	5.61	1.74	5.73	1.01	0.015	0.904
Sp2	f+m	6.26	1.03	6.46	0.59	0.128	0.728
Spm	m	4.26	1.08	3.94	0.57	0.301	0.595
Spm	f	5.26	1.18	4.59	0.91	0.987	0.344
Spm	f+m	5.81	1.20	5.49	0.10	0.264	0.619
B	m	5.28	1.31	4.11	1.04	2.388	0.153
B	f	5.44	0.97	5.35	1.42	0.018	0.895
B	f+m	5.46	1.08	4.91	0.94	0.737	0.411
Le	m	4.28	0.71	3.89	0.47	0.991	0.343
Le	f	4.88	0.96	5.05	1.18	0.070	0.797
Le	f+m	6.35	1.00	6.01	0.67	0.367	0.558
Se	m	3.75	0.89	3.54	0.20	0.201	0.663
Se	f	4.66	1.26	4.46	1.02	0.074	0.791
Se	f+m	5.71	0.77	5.31	0.47	0.918	0.361
L2l	m	6.72	1.27	6.25	1.87	0.264	0.619
L2l	f	7.36	2.56	7.46	2.17	4.2*10^{-3}	0.949
L2l	f+m	8.66	1.66	8.35	2.31	0.072	0.794
L1l	m	7.00	1.60	6.53	2.32	0.174	0.685
L1l	f	8.33	1.90	7.30	1.48	0.879	0.371
L1l	f+m	8.44	1.09	7.80	1.05	0.936	0.356
L2r	m	6.51	1.02	6.61	0.79	0.028	0.871
L2r	f	6.98	2.30	7.31	1.91	0.061	0.810
L2r	f+m	8.21	1.28	8.49	1.94	0.089	0.771
L1r	m	6.64	1.72	5.91	1.54	0.513	0.490
L1r	f	8.44	2.06	7.64	2.25	0.379	0.552
L1r	f+m	8.88	1.60	7.61	1.29	1.853	0.203

Morphometric characteristic or index	Sex	0 cm		2–4 cm		$F, F_{0.05} = 4.965$	p
		x	SD	x	SD		
Lb	m	3.19	0.56	2.97	0.37	0.517	0.488
Lb	f	3.96	0.73	4.18	0.97	0.185	0.676
Lb	f+m	5.22	0.68	5.14	0.45	0.042	0.842
Kl	m	27.60	9.36	28.05	7.66	$7.0*10^{-3}$	0.924
Kl	f	32.54	7.56	28.51	11.88	0.526	0.485
Kl	f+m	30.94	7.30	28.61	8.23	0.251	0.627
Kr	m	25.49	10.53	21.16	1.94	0.633	0.445
Kr	f	29.40	8.53	22.44	2.79	2.426	0.150
Kr	f+m	28.05	7.95	21.71	0.72	2.413	0.151
P	m	9.68	2.30	8.16	3.04	0.952	0.352
P	f	11.16	3.66	9.51	3.34	0.572	0.467
P	f+m	11.20	3.13	9.25	2.90	1.080	0.323
K	m	24.66	8.64	23.10	3.49	0.117	0.740
K	f	28.74	8.46	23.28	6.83	1.243	0.291
K	f+m	27.51	7.18	23.15	4.44	1.207	0.298
(Sc+Sp+Se)/3Lb	m	2.51	0.87	2.64	0.92	0.058	0.814
(Sc+Sp+Se)/3Lb	f	2.41	0.50	2.44	0.88	$6.9*10^{-3}$	0.935
(Sc+Sp+Se)/3Lb	f+m	2.53	0.46	2.57	0.68	0.012	0.914
Lp/Sp	m	4.53	1.17	4.28	0.73	0.150	0.707
Lp/Sp	f	4.54	1.54	4.71	1.25	0.035	0.856
Lp/Sp	f+m	4.65	1.14	4.56	0.73	0.021	0.889
Le/Lp	m	4.59	1.25	4.65	0.20	$7.6*10^{-3}$	0.931
Le/Lp	f	4.67	1.01	5.43	1.03	1.468	0.254
Le/Lp	f+m	4.96	0.98	5.14	0.52	0.114	0.743
Se/Sp	m	3.46	1.54	2.47	0.94	1.340	0.274
Se/Sp	f	2.79	0.92	2.71	0.58	0.025	0.877
Se/Sp	f+m	3.08	0.74	2.65	0.28	1.192	0.300
Sp2/Spm	m	3.68	1.24	4.08	1.84	0.208	0.658
Sp2/Spm	f	3.72	0.90	4.25	0.71	1.035	0.333
Sp2/Spm	f+m	3.68	0.77	4.26	0.85	1.422	0.261
Le/Se	m	3.47	0.75	3.42	1.54	$6.0*10^{-3}$	0.940
Le/Se	f	2.95	0.51	3.95	1.14	4.654	0.056
Le/Se	f+m	3.28	0.40	3.82	0.61	3.452	0.093

Note: two groups of ecosystems were identified by litter thickness: with the absence of the litter layer (ecosystems 1, 2, 3, 5, 7, 10, 11, 12) and with a litter thickness of 2–4 cm (ecosystems 4, 6, 8, 9).

Appendix 5. Coefficient of variation (CV, %) of morphometric parameters of *Bembidion minimum* populations studied in ecosystems with different degrees of development of the herb layer

Morphometric characteristic or index	Sex	Absent		Developed herb layer		F, $F_{0.05}$ = 4.965	p
		x	SD	x	SD		
n	m	14.44	2.70	11.00	5.29	2.337	0.157
n	f	20.89	4.83	18.33	5.86	0.575	0.466
n	f+m	35.33	6.04	29.33	9.71	1.685	0.223
Lc	m	7.23	1.77	5.12	1.59	3.331	0.098
Lc	f	6.06	0.96	6.32	0.59	0.192	0.671
Lc	f+m	7.19	0.70	6.91	1.16	0.270	0.615
Sc	m	3.48	0.70	3.38	0.36	0.054	0.820
Sc	f	4.16	1.03	4.25	0.37	0.018	0.897
Sc	f+m	4.90	1.01	4.45	0.19	0.572	0.467
Lp	m	4.39	0.86	5.32	0.91	2.552	0.141
Lp	f	5.12	1.03	6.08	0.93	2.046	0.183
Lp	f+m	5.79	0.69	6.05	0.41	0.376	0.554
Sp1	m	3.88	0.82	4.19	1.02	0.278	0.610
Sp1	f	4.86	1.03	5.08	0.71	0.110	0.747
Sp1	f+m	5.58	0.68	5.67	0.34	0.047	0.832
Sp2	m	4.99	1.46	5.31	1.24	0.119	0.737
Sp2	f	5.08	1.01	7.35	1.51	9.070	0.013
Sp2	f+m	6.05	0.60	7.15	1.21	4.602	0.058
Spm	m	3.89	0.92	4.93	0.33	3.484	0.092
Spm	f	4.84	1.07	5.61	1.21	1.092	0.321
Spm	f+m	5.62	1.11	5.96	0.44	0.255	0.625
B	m	4.84	1.50	5.03	0.70	0.043	0.841
B	f	5.41	1.11	5.41	1.22	$2.1*10^{-5}$	0.997
B	f+m	5.19	1.10	5.52	0.94	0.207	0.659
Le	m	4.06	0.71	4.41	0.39	0.640	0.442
Le	f	4.75	0.92	5.50	1.16	1.331	0.275
Le	f+m	6.29	1.02	6.10	0.39	0.094	0.765
Se	m	3.75	0.77	3.45	0.64	0.374	0.555
Se	f	4.31	0.78	5.45	1.80	2.564	0.140
Se	f+m	5.59	0.63	5.54	1.02	0.013	0.913
L2l	m	6.84	1.40	5.71	1.36	1.479	0.252
L2l	f	7.72	1.61	6.40	4.21	0.707	0.420
L2l	f+m	8.89	1.57	7.56	2.41	1.274	0.285
L1l	m	6.96	1.95	6.49	1.37	0.143	0.713
L1l	f	7.51	1.19	9.41	2.77	3.053	0.111
L1l	f+m	8.14	1.07	8.48	1.28	0.208	0.658
L2r	m	6.80	0.92	5.77	0.12	3.524	0.090
L2r	f	7.56	1.58	5.69	3.18	1.954	0.192
L2r	f+m	8.65	1.41	7.28	1.23	2.218	0.167
L1r	m	6.57	1.82	5.89	0.93	0.366	0.559
L1r	f	7.57	1.71	9.96	2.30	3.794	0.080
L1r	f+m	8.22	1.61	9.16	1.49	0.783	0.397

Morphometric characteristic or index	Sex	Absent		Developed herb layer		F, $F_{0.05}$ = 4.965	p
		x	SD	x	SD		
Lb	m	2.95	0.38	3.61	0.55	5.582	0.040
Lb	f	3.92	0.82	4.37	0.67	0.713	0.418
Lb	f+m	5.26	0.67	4.98	0.26	0.459	0.514
Kl	m	30.54	7.95	19.38	1.47	5.502	0.041
Kl	f	33.58	8.57	24.06	6.12	3.080	0.110
Kl	f+m	32.58	6.46	22.92	4.81	5.518	0.041
Kr	m	24.97	9.98	21.25	2.26	0.386	0.548
Kr	f	29.66	6.92	19.33	4.43	5.684	0.038
Kr	f+m	27.93	6.97	19.94	3.04	3.527	0.090
P	m	9.34	2.69	8.65	2.43	0.156	0.701
P	f	10.49	3.42	10.95	4.52	0.035	0.855
P	f+m	10.43	3.27	10.89	3.00	0.046	0.835
K	m	25.87	7.54	18.95	1.22	2.349	0.156
K	f	29.64	6.99	18.77	5.65	5.838	0.036
K	f+m	28.31	5.78	19.30	3.25	6.330	0.031
(Sc+Sp+Se)/3Lb	m	2.60	0.89	2.42	0.87	0.094	0.765
(Sc+Sp+Se)/3Lb	f	2.27	0.61	2.88	0.34	2.669	0.133
(Sc+Sp+Se)/3Lb	f+m	2.48	0.53	2.73	0.48	0.496	0.497
Lp/Sp	m	4.48	1.14	4.36	0.67	0.029	0.869
Lp/Sp	f	4.05	1.14	6.24	0.23	10.291	0.009
Lp/Sp	f+m	4.28	0.84	5.67	0.65	6.777	0.026
Le/Lp	m	4.83	1.05	3.96	0.45	1.850	0.204
Le/Lp	f	4.67	1.01	5.67	0.85	2.324	0.158
Le/Lp	f+m	4.88	0.84	5.46	0.77	1.141	0.310
Se/Sp	m	2.67	0.82	4.50	2.13	5.187	0.046
Se/Sp	f	2.58	0.49	3.31	1.39	2.104	0.178
Se/Sp	f+m	2.68	0.31	3.71	0.83	11.261	0.007
Sp2/Spm	m	4.07	1.47	3.05	0.94	1.232	0.293
Sp2/Spm	f	3.81	0.96	4.14	0.40	0.327	0.580
Sp2/Spm	f+m	3.91	0.94	3.76	0.10	0.072	0.794
Le/Se	m	3.36	1.13	3.72	0.48	0.268	0.616
Le/Se	f	3.15	0.94	3.66	0.63	0.732	0.412
Le/Se	f+m	3.36	0.51	3.75	0.55	1.305	0.280

Note: two groups of ecosystems were identified according to the intensity of development of the herb layer: with an absent herb layer (ecosystems 1, 2, 4, 5, 6, 7, 8, 10, 12) and with a developed herb layer (ecosystems 3, 9, 11).

Appendix 6. Coefficient of variation (CV, %) of morphometric parameters of *Bembidion minimum* populations studied in ecosystems with different recreational loads

Morphometric characteristic or index	Sex	0		1		2		3		F, $F_{0.05}$ = 4.066	p
		x	SD	x	SD	x	SD	x	SD		
n	m	15.33	1.53	9.67	5.03	14.00	1.00	15.33	3.06	2.278	0.157
n	f	22.00	3.46	17.33	7.09	19.00	4.36	22.67	5.03	0.711	0.572
n	f+m	37.33	2.52	27.00	11.27	33.00	5.29	38.00	2.00	1.863	0.214
Lc	m	8.61	0.43	5.98	2.82	6.58	1.77	5.62	0.88	1.788	0.229
Lc	f	5.80	0.53	5.76	0.44	6.95	0.62	6.01	1.35	1.390	0.315
Lc	f+m	7.67	0.47	6.69	0.79	7.73	0.45	6.38	0.47	4.491	0.040
Sc	m	3.29	0.48	3.43	0.44	3.07	0.72	4.02	0.66	1.421	0.306
Sc	f	3.92	0.96	4.69	0.75	3.84	0.54	4.30	1.38	0.497	0.695
Sc	f+m	4.11	0.75	4.83	0.54	4.48	0.30	5.75	1.10	2.764	0.111
Lp	m	4.39	0.51	5.19	0.76	4.22	1.65	4.69	0.60	0.555	0.659
Lp	f	5.43	0.61	6.84	0.48	4.54	0.51	4.62	0.39	13.609	$1.7*10^{-3}$
Lp	f+m	5.70	0.48	6.55	0.50	5.17	0.41	5.99	0.06	6.185	0.018
Sp1	m	3.68	0.58	4.10	0.92	4.03	1.35	4.04	0.81	0.119	0.946
Sp1	f	4.85	1.31	5.16	0.83	4.85	1.07	4.81	1.06	0.067	0.976
Sp1	f+m	4.94	0.46	5.76	0.48	5.84	0.21	5.89	0.78	2.196	0.166
Sp2	m	5.54	2.22	5.30	1.25	4.59	1.53	4.85	0.75	0.238	0.868
Sp2	f	5.63	0.69	7.01	1.42	5.51	2.14	4.45	0.37	1.853	0.216
Sp2	f+m	6.08	1.13	7.04	1.30	6.18	0.36	6.01	0.38	0.858	0.501
Spm	m	3.86	0.39	4.41	0.94	3.66	1.14	4.67	1.19	0.701	0.577
Spm	f	4.73	0.61	5.26	0.99	4.94	1.30	5.22	1.85	0.116	0.948
Spm	f+m	4.93	0.53	5.75	0.38	5.51	0.75	6.62	1.42	1.969	0.197
B	m	5.68	2.20	4.15	0.95	5.08	0.70	4.63	1.15	0.682	0.588
B	f	6.02	1.19	6.09	0.64	4.67	0.47	4.84	1.33	1.797	0.226
B	f+m	5.89	1.56	5.55	0.91	4.86	0.30	4.80	1.07	0.760	0.547
Le	m	3.63	0.48	4.17	0.24	3.98	0.76	4.82	0.57	2.514	0.132
Le	f	5.05	1.53	5.48	1.18	4.52	0.55	4.71	0.74	0.464	0.715
Le	f+m	5.74	0.59	5.83	0.68	6.14	0.25	7.25	1.13	2.694	0.117
Se	m	4.15	0.39	3.28	0.37	3.46	1.19	3.82	0.71	0.814	0.521
Se	f	4.70	0.73	5.51	1.77	4.02	0.88	4.13	0.78	1.107	0.401
Se	f+m	5.27	0.48	5.52	1.03	5.34	0.28	6.18	0.71	1.118	0.397
L2l	m	6.66	1.73	5.37	1.17	6.19	0.31	8.02	1.08	2.641	0.121
L2l	f	7.21	2.18	7.57	3.28	5.68	2.21	9.11	0.86	1.123	0.396
L2l	f+m	8.65	2.15	7.83	2.32	7.58	0.72	10.18	0.99	1.436	0.303
L1l	m	7.74	2.29	5.91	2.28	6.28	1.23	7.44	1.38	0.680	0.589
L1l	f	7.21	1.72	8.13	0.64	8.60	3.52	8.00	0.32	0.254	0.856
L1l	f+m	7.76	0.89	7.56	0.72	8.24	1.36	9.33	0.64	2.092	0.180
L2r	m	6.64	0.93	5.97	0.32	5.91	0.17	7.66	0.81	4.838	0.033
L2r	f	6.96	1.70	6.96	2.22	5.33	1.97	9.11	1.25	2.172	0.169
L2r	f+m	8.32	2.01	7.52	1.32	7.59	0.61	9.79	0.58	2.061	0.184
L1r	m	6.40	0.35	5.50	1.60	5.58	1.84	8.12	1.38	2.233	0.162
L1r	f	6.46	1.56	9.16	1.01	8.51	3.55	8.55	1.02	0.979	0.450
L1r	f+m	6.86	0.95	8.37	0.74	8.71	1.70	9.88	1.52	2.779	0.110

Morphometric characteristic or index	Sex	0		1		2		3		F, $F_{0.05}$ = 4.066	p
		x	SD	x	SD	x	SD	x	SD		
Lb	m	2.73	0.36	3.31	0.32	3.15	0.88	3.28	0.19	0.837	0.511
Lb	f	4.28	0.99	4.45	0.64	3.56	0.82	3.84	0.74	0.759	0.548
Lb	f+m	4.90	0.63	4.83	0.15	5.14	0.21	5.88	0.66	3.104	0.089
Kl	m	38.23	5.29	24.50	8.25	20.66	5.81	27.60	3.00	4.914	0.032
Kl	f	35.93	6.44	32.94	9.30	28.59	10.25	27.34	11.38	0.520	0.068
Kl	f+m	36.47	4.74	30.03	7.71	25.76	7.81	28.38	7.67	1.239	0.358
Kr	m	33.28	14.22	21.71	1.65	20.41	1.17	20.78	6.40	1.854	0.216
Kr	f	34.17	8.17	22.58	1.38	26.34	10.79	25.23	5.86	1.357	0.324
Kr	f+m	33.17	10.05	21.85	0.28	24.57	7.30	24.14	3.16	1.802	0.225
P	m	11.91	0.51	6.40	1.67	10.76	0.68	7.62	1.35	15.087	$1.2*10^{-3}$
P	f	13.53	2.06	10.18	5.36	10.81	2.52	7.91	1.97	1.488	0.290
P	f+m	13.49	1.93	9.58	4.28	11.16	1.19	7.97	1.88	2.458	0.137
K	m	32.75	9.30	21.63	4.25	19.03	1.94	23.15	3.66	3.531	0.068
K	f	33.08	7.41	25.23	5.54	25.35	11.71	24.01	7.73	0.733	0.561
K	f+m	32.36	7.64	23.76	4.62	23.64	7.35	24.46	4.64	1.377	0.318
(Sc+Sp+Se)/3Lb	m	2.35	0.47	2.41	0.88	1.96	1.01	3.49	0.08	2.588	0.126
(Sc+Sp+Se)/3Lb	f	2.50	0.75	2.66	0.73	2.12	0.40	2.40	0.73	0.349	0.791
(Sc+Sp+Se)/3Lb	f+m	2.58	0.44	2.54	0.81	2.16	0.30	2.90	0.28	1.079	0.411
Lp/Sp	m	4.65	0.91	4.41	0.60	3.34	1.11	5.40	0.11	3.614	0.065
Lp/Sp	f	3.58	0.69	5.94	0.72	4.19	1.65	4.68	1.55	1.957	0.199
Lp/Sp	f+m	4.13	0.16	5.48	0.94	3.88	1.02	5.01	0.96	2.334	0.150
Le/Lp	m	4.68	0.51	4.39	0.46	3.61	0.56	5.77	1.07	4.935	0.032
Le/Lp	f	4.72	1.36	6.01	0.76	4.27	0.80	4.69	0.58	2.011	0.191
Le/Lp	f+m	4.72	0.78	5.63	0.67	4.39	0.57	5.36	0.97	1.676	0.248
Se/Sp	m	3.13	0.97	4.06	2.70	2.36	0.55	2.96	0.43	0.675	0.591
Se/Sp	f	2.48	0.85	2.66	0.62	3.22	1.34	2.68	0.38	0.402	0.756
Se/Sp	f+m	2.89	0.21	3.18	1.11	2.88	0.88	2.79	0.31	0.161	0.920
Sp2/Spm	m	4.11	2.32	3.28	0.69	3.45	1.49	4.40	1.13	0.364	0.781
Sp2/Spm	f	3.38	0.68	4.37	0.72	3.79	1.11	4.03	0.98	0.647	0.606
Sp2/Spm	f+m	3.75	1.46	3.98	0.29	3.67	0.99	4.09	0.50	0.132	0.928
Le/Se	m	2.82	0.67	3.37	1.03	3.16	1.14	4.45	0.68	1.821	0.221
Le/Se	f	3.65	1.50	3.83	0.36	2.74	0.38	2.89	0.59	1.224	0.362
Le/Se	f+m	3.42	0.64	3.68	0.68	3.02	0.37	3.72	0.18	1.189	0.374

Note: four groups of ecosystems were identified according to the intensity of the recreational load, evaluated in points: from a minimum of 0 points (ecosystems 1, 5, 8), 1 point (ecosystems 6, 9, 11), 2 points (ecosystems 3, 7, 10), to a maximum 3 points (ecosystems 2, 4, 12).

Appendix 7. Coefficient of variation (CV, %) of morphometric parameters of *Bembidion minimum* populations studied in ecosystems with different grazing intensity

Morphometric characteristic or index	Sex	Absent		Slight grazing		Medium grazing		Strong grazing		$F, F_{0.05} = 4.066$	p
		x	SD	x	SD	x	SD	x	SD		
n	m	13.75	3.40	12.67	6.81	14.00	1.00	14.00	2.83	0.068	0.975
n	f	19.25	6.18	19.67	4.73	19.00	4.36	25.00	4.24	0.679	0.589
n	f+m	33.00	8.91	32.33	10.02	33.00	5.29	39.00	1.41	0.349	0.791
Lc	m	8.70	0.39	4.88	1.34	6.58	1.77	5.62	1.24	6.398	0.016
Lc	f	5.67	0.51	6.34	0.61	6.95	0.62	5.51	1.45	2.285	0.156
Lc	f+m	7.65	0.38	6.39	0.26	7.73	0.45	6.22	0.54	11.539	$2.8*10^{-3}$
Sc	m	3.45	0.51	3.69	0.91	3.07	0.72	3.66	0.31	0.518	0.682
Sc	f	4.30	1.10	4.82	0.96	3.84	0.54	3.52	0.41	1.079	0.411
Sc	f+m	4.44	0.90	5.35	1.44	4.48	0.30	5.12	0.23	0.765	0.545
Lp	m	4.72	0.78	4.63	0.81	4.22	1.65	5.03	0.20	0.265	0.849
Lp	f	5.90	1.07	6.08	0.91	4.54	0.51	4.40	0.05	3.150	0.086
Lp	f+m	6.05	0.81	6.16	0.24	5.17	0.41	6.02	0.04	2.125	0.175
Sp1	m	3.94	0.71	4.10	0.92	4.03	1.35	3.69	0.76	0.080	0.969
Sp1	f	5.13	1.21	4.98	0.58	4.85	1.07	4.49	1.27	0.172	0.913
Sp1	f+m	5.28	0.78	5.86	0.66	5.84	0.21	5.52	0.64	0.670	0.594
Sp2	m	5.30	1.88	5.41	1.16	4.59	1.53	4.82	1.06	0.193	0.898
Sp2	f	5.96	0.87	6.05	2.23	5.51	2.14	4.64	0.23	0.369	0.778
Sp2	f+m	6.13	0.93	7.09	1.26	6.18	0.36	5.81	0.21	1.116	0.398
Spm	m	3.74	0.40	4.81	0.38	3.66	1.14	4.72	1.68	1.430	0.304
Spm	f	4.89	0.59	5.85	1.49	4.94	1.30	4.25	1.10	0.886	0.488
Spm	f+m	5.10	0.55	6.62	1.44	5.51	0.75	5.82	0.40	1.734	0.237
B	m	5.04	2.21	4.64	0.31	5.08	0.70	4.65	1.62	0.072	0.973
B	f	6.08	0.97	5.81	0.72	4.67	0.47	4.57	1.76	1.912	0.206
B	f+m	5.69	1.34	5.51	0.95	4.86	0.30	4.73	1.51	0.541	0.667
Le	m	3.73	0.44	4.62	0.72	3.98	0.76	4.52	0.34	1.579	0.269
Le	f	4.99	1.25	5.66	1.06	4.52	0.55	4.39	0.69	0.906	0.480
Le	f+m	5.60	0.56	6.96	1.43	6.14	0.25	6.60	0.10	1.801	0.225
Se	m	4.02	0.41	3.19	0.27	3.46	1.19	4.05	0.84	1.005	0.439
Se	f	4.78	0.62	5.40	1.83	4.02	0.88	3.86	0.87	1.099	0.404
Se	f+m	5.26	0.39	6.11	1.25	5.34	0.28	5.79	0.26	1.064	0.417
L2l	m	6.38	1.52	6.29	2.07	6.19	0.31	7.91	1.51	0.652	0.604
L2l	f	7.10	1.79	8.68	3.44	5.68	2.21	8.61	0.04	1.058	0.419
L2l	f+m	8.38	1.83	8.99	2.94	7.58	0.72	9.73	0.86	0.578	0.645
L1l	m	6.66	2.85	7.72	1.24	6.28	1.23	6.73	0.86	0.294	0.829
L1l	f	7.59	1.60	8.00	0.48	8.60	3.52	7.82	0.06	0.148	0.928
L1l	f+m	7.58	0.81	8.53	1.36	8.24	1.36	9.02	0.47	1.058	0.882
L2r	m	6.56	0.77	6.37	1.00	5.91	0.17	7.74	1.12	2.159	0.171
L2r	f	6.94	1.39	8.17	3.00	5.33	1.97	8.41	0.45	1.374	0.319
L2r	f+m	8.27	1.65	8.30	2.21	7.59	0.61	9.48	0.30	0.615	0.625
L1r	m	5.72	1.40	7.51	1.90	5.58	1.84	7.34	0.35	1.246	0.356
L1r	f	7.38	2.25	8.98	0.76	8.51	3.55	8.03	0.66	0.308	0.819
L1r	f+m	7.22	1.06	9.47	1.98	8.71	1.70	9.02	0.43	1.558	0.273

Morphometric characteristic or index	Sex	Absent		Slight grazing		Medium grazing		Strong grazing		F, $F_{0.05}$ = 4.066	p
		x	SD	x	SD	x	SD	x	SD		
Lb	m	2.85	0.38	3.29	0.33	3.15	0.88	3.34	0.23	0.553	0.660
Lb	f	4.31	0.81	4.51	0.64	3.56	0.82	3.48	0.57	1.355	0.324
Lb	f+m	4.87	0.52	5.45	1.04	5.14	0.21	5.51	0.02	0.716	0.570
Kl	m	37.15	4.83	23.52	6.58	20.66	5.81	25.92	1.01	6.695	0.014
Kl	f	37.87	6.53	28.61	1.85	28.59	10.25	25.67	15.56	1.270	0.348
Kl	f+m	37.07	4.05	27.22	2.95	25.76	7.81	27.38	10.56	2.583	0.126
Kr	m	30.07	13.27	23.26	2.00	20.41	1.17	18.63	7.35	1.103	0.403
Kr	f	31.63	8.38	24.33	4.31	26.34	10.79	23.21	6.66	0.696	0.580
Kr	f+m	30.42	9.88	23.42	2.98	24.57	7.30	22.78	2.97	0.782	0.537
P	m	10.08	3.67	6.89	0.93	10.76	0.68	8.38	0.46	1.706	0.243
P	f	11.60	4.22	10.21	5.33	10.81	2.52	8.92	1.26	0.219	0.881
P	f+m	11.59	4.11	9.59	4.27	11.16	1.19	9.00	0.88	0.384	0.768
K	m	31.15	8.24	21.69	4.34	19.03	1.94	21.46	3.10	3.175	0.085
K	f	32.72	6.10	23.94	3.31	25.35	11.71	22.15	9.93	1.128	0.394
K	f+m	31.53	6.46	23.01	3.33	23.64	7.35	23.31	5.92	1.657	0.252
(Sc+Sp+Se)/3Lb	m	2.11	0.61	3.08	0.30	1.96	1.01	3.53	0.07	3.677	0.063
(Sc+Sp+Se)/3Lb	f	2.33	0.70	3.02	0.10	2.12	0.40	2.16	0.84	1.607	0.263
(Sc+Sp+Se)/3Lb	f+m	2.34	0.61	3.05	0.07	2.16	0.30	2.78	0.27	2.916	0.101
Lp/Sp	m	4.45	0.85	4.96	0.56	3.34	1.11	5.37	0.12	3.126	0.088
Lp/Sp	f	3.97	0.95	6.35	0.14	4.19	1.65	3.85	0.78	0.754	0.060
Lp/Sp	f+m	4.22	0.22	6.01	0.37	3.88	1.02	4.48	0.37	8.214	0.008
Le/Lp	m	4.72	0.42	4.89	1.28	3.61	0.56	5.48	1.34	2.044	0.186
Le/Lp	f	5.09	1.34	5.68	0.84	4.27	0.80	4.43	0.50	1.150	0.387
Le/Lp	f+m	4.91	0.75	5.92	0.77	4.39	0.57	4.85	0.57	2.618	0.123
Se/Sp	m	2.73	1.13	4.64	1.97	2.36	0.55	2.81	0.47	2.037	0.187
Se/Sp	f	2.56	0.71	2.75	0.67	3.22	1.34	2.49	0.23	0.413	0.748
Se/Sp	f+m	2.74	0.34	3.46	0.86	2.88	0.88	2.61	0.08	0.942	0.464
Sp2/Spm	m	3.82	1.99	3.54	0.63	3.45	1.49	4.75	1.36	0.335	0.801
Sp2/Spm	f	3.82	1.04	4.38	0.74	3.79	1.11	3.47	0.11	0.443	0.728
Sp2/Spm	f+m	3.89	1.22	4.04	0.39	3.67	0.99	3.90	0.53	0.077	0.971
Le/Se	m	2.67	0.63	4.07	0.34	3.16	1.14	4.52	0.95	3.327	0.077
Le/Se	f	3.61	1.23	3.47	0.93	2.74	0.38	3.12	0.62	0.566	0.653
Le/Se	f+m	3.30	0.58	3.90	0.33	3.02	0.37	3.78	0.21	2.553	0.129

Note: four groups of ecosystems were identified according to the intensity of grazing: without grazing (ecosystems 1, 5, 6, 8), with slight grazing (ecosystems 9, 11, 12), grazing of medium intensity (ecosystems 3, 7, 10) and with strong grazing (ecosystems 2, 4).

МОРФОМЕТРИЧЕСКАЯ ИЗМЕНЧИВОСТЬ ЖУЖЕЛИЦ *BEMBIDION MINIMUM* (COLEOPTERA, CARABIDAE): КТО БОЛЬШЕ ИЗМЕНЯЮТСЯ, САМЦЫ ИЛИ САМКИ?

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Морфологическая изменчивость может служить индикатором состояния популяций беспозвоночных. Микроэволюционные процессы могут проявляться в морфологической дифференциации популяций. Это включает в себя различия между морфометрическими признаками у обоих полов. В данной статье по 24 морфометрическим характеристикам и индексам оценена изменчивость 12 популяций *Bembidion minimum* (Coleoptera, Carabidae). *Bembidion minimum* – галофил, обитающий в экосистемах охраняемых природных территорий Днепропетровской области, Украина (Днепровско-Орельский заповедник, орнитологический заказник «Булаховский лиман», Самарский лес). В статье рассмотрены коэффициенты вариации для самцов, самок и объединенных популяций самцов и самок. Изученные популяции обитали в различных почвенно-растительных условиях, находились под воздействием антропогенных факторов различной интенсивности. Анализ избыточности показал три кластера. В первом кластере морфометрические характеристики и индексы у самцов и самок связаны с такими экологическими переменными, как травянистый ярус, минерализация почвенного раствора, механический состав почвы, во втором кластере – pH почвенного раствора, толщина подстилки, рекреационная нагрузка, выпас скота. Третий кластер сформировали морфометрические характеристики и показатели у самцов и самок, на которые не влияют никакие экологические факторы. Коэффициент вариации для большинства линейных морфометрических характеристик *B. minimum* (ширина головы, длина и ширина переднеспинки, длина надкрыльев, а также расстояние между щетинконосными порами на надкрыльях) у самцов был достоверно ниже, чем для объединенной выборки самцов и самок. Изменчивость ширины надкрыльев и длины тела достоверно выше у самок, чем у самцов. Степень изменчивости самцов, самок и их объединенной выборки достоверно не отличалась для нелинейных морфометрических характеристик, а также для шести изученных нами морфометрических индексов (пропорций тела). В целом в 12 изученных нами популяциях *B. minimum* по большинству изученных измерений коэффициент вариации недостоверно ниже у самцов (CV = 5.59%), чем у самок (CV = 6.10%) или объединенной выборки самцов и самок (CV = 6.75%). Самая низкая изменчивость в популяциях *B. minimum* обнаружена для морфометрических индексов: для самцов CV = 3.89%, для самок CV = 3.76%, для объединенной популяции (самцы + самки) CV = 3.86%. Отсутствие отличий по средним значениям коэффициента вариации между самцами, самками и объединенной выборкой самцов и самок для каждой отдельной популяции позволяет утверждать, что у *B. minimum* в полиморфизм популяций и самцы, и самки вносят относительно равный вклад. Оценку морфологической изменчивости беспозвоночных животных и особенно коэффициентов вариации линейных параметров и морфометрических индексов можно использовать для индикации состояния экосистем на особо охраняемых природных территориях Украины и других стран.

Ключевые слова: длина тела, жужелицы, зоофаги, коэффициент вариации, морфометрия, подстилочные беспозвоночные, половой диморфизм, популяция