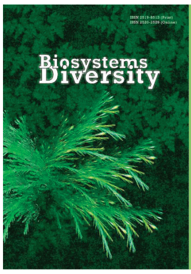

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Morphological variability of *Bembidion minimum* (Coleoptera, Carabidae) populations under the influence of natural and anthropogenic factors

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Morphological variability is the result of interaction between genetic diversity of the population and environmental selection. Despite the large number of studies of morphological variability of ground beetles, there is very little research dedicated to influence of environmental factors on it. This article discusses the influence of natural and anthropogenic factors on the variability of *Bembidion minimum* (Fabricius, 1792). *B. minimum* is a West Palearctic species which is distributed in North Africa, Europe, Western Asia. It is a macropterous species that lives in humid biotopes along the shores of seas, rivers and standing water bodies. 410 specimens were collected from 12 ecosystems differing by plant cover, degree of litter development, mechanical composition of the soil, mineralization and acidity of soil solution, type and intensity of anthropogenic impact. 13 linear characteristics, one angular characteristic, density of elytra puncturing and contrast of spots on the beetles' elytra were measured. Additionally 6 morphometric indices were calculated. More than a third of the variability of imagoes in the studied populations was found to be determined by the general body size. Sexual dimorphism was observed on all linear parameters and most morphometric indices. Females do not differ from males in the back angles of the prothorax. Natural and anthropogenic factors to a greater or lesser degree were shown to affect the morphological variability of *B. minimum*: soil acidity and mineralization have the greatest impact. The soil acidity causes significant variability of most linear parameters; mineralization – body length, head length, prothorax length and width, elytra width. Plant cover and mechanical composition of the soil have a slight impact on imago morphology. The type and structure of vegetation significantly affect head width, prothorax length and width, and the mechanical composition of the soil – body length and head length. Degree of litter development does not cause significant changes in the linear dimensions of beetles. With thickening of the litter the posterior spots on the elytra become brighter, they have sharper contours, and density of elytra puncturing also changes. The mean value of the back angles is affected by the herb layer of meadow vegetation, soil mineralization and acidity. The variability of morphometric indexes under the influence of natural factors was found to be lower than variability of linear characteristics. The recreational load and cattle grazing cause similar changes in linear measurements and morphometric indexes of *B. minimum*. With escalation of these factors, the body length, length and width of elytra of both females and males decrease. Assessing the natural morphological variability of populations in ecosystems whose environmental factors are within extreme and sub-extreme values for a given population is a promising direction of research in modern ecology.

Keywords: population variability; sexual dimorphism; morphometrics; riparian beetles.

Introduction

Insects react in various ways to changes in environmental conditions: changes in numbers, range, morphology etc. Invertebrate populations "accumulate" the influence of environmental factors over a certain time period, therefore they can serve as rather convenient bioindicators of environmental conditions (Moskalev et al., 2015). The results of the influence of a particular factor are determined by the duration and intensity of exposure, on the one hand, and the effectiveness of compensatory mechanisms at the molecular, genetic, cellular, organismic, population, and ecosystem levels, on the other hand (Brygadyrenko & Slynko, 2015). Body size is one of the main characteristics of living organisms, which is associated with the life history of the individual (with the conditions in which its ontogenesis occurred), with its physiological patterns (individual features of gene expression) and environmental interactions within the ecosystem: trophic connections with food objects, predators and parasites (Brygadyrenko & Reshetniak, 2016). The study of the relationship between the body size of insects and the type of habitat is important for understanding the basic regularities of their biotopic distribution and geographical extension (Dangalle et al., 2013). The individuals that make up the population are not identical: they vary in size, duration of ontogenesis, the intensity of anabolism and catabolism. Morphological variability is a property of populations, the total result of the adaptation of individuals to the sum of all effects of environmental factors (Sukhodolskaya & Saveliev, 2014). The study of morphological variability under the influence of environmental factors contributes to the understanding of many ecological processes, makes it possible to assess the potential sustainability of a population, its ability to remain constant under changing conditions, and to identify the boundaries of potential and realized ecological niche (Sota et al., 2000; Barton et al., 2011; Brygadyrenko & Korolev, 2015).

Ground beetles (Coleotera, Carabidae) are sensitive to the effects of abiotic and biotic factors, they quickly respond to environmental changes (Brygadyrenko, 2016a), and therefore they are often used as bioindicators (Grumo & Lovei, 2016). Thiele (1977) suggested that the most pronounced morphological adaptations of carabids are associated with specialized dietary regimes. Erwin (1979), on the other hand, presented observations indicating that there are probably links between the morphology and ecology of carabids. Despite the large amount of data on the morphological variability of abundant species of ground beetles (Brygadyrenko & Reshetniak, 2014), there is very little material on the influence of individual environmental factors on them. The intraspecific morphological variability of carabids is not well studied (Sukhodolskaya & Saveliev, 2017). Usually, research on the influence of environmental factors on the morphometric variability of ground beetles is limited to measuring only the elytra length and is carried out by methods that do not allow one to single out a specific determining (limiting) environmental factor (Sukhodolskaya & Saveliev, 2014). In particular, this applies to the study of ground beetles of riparian ecosystems. The shores of water bodies include a large number of microbiotopes that differ in microclimate and edaphic conditions. The littoral zones of water bodies and estuaries are characterized by the predominance of many species of ground beetles which are absent in other areas (Putchkov, 2012). Species of the genus *Bembidion* occupy most of these biotopes. We previously studied the morphological variability of three species of the genus *Bembidion*: *B. varium* (Olivier, 1795), *B. articulatum* (Panzer, 1796) and *B. aspericolle* (Germar, 1829) (Slinko et al., 2008; Brygadyrenko & Slynko, 2015; Komlyk & Brygadyrenko, 2019). This article is devoted to the study of the morphological variability of *B. minimum* (Fabricius, 1792), which is widely distributed in riparian biotopes.

One of the first references to *B. minimum* (Fabricius, 1792) was made by Band (1892), who described the size, morphological features, and the habitat of this species. *B. minimum* is a West Palearctic species which is distributed in North Africa, Europe, West Asia (Hurka, 1996). In Europe, the species lives in Bosnia, Herzegovina, Bulgaria, Romania (Hieke & Wrase, 1988; Nitzu, 2003) and Lithuania (Tamutis et al., 2011). *B. minimum* is abundant in coastal areas in most of Great Britain: England, Scotland (West Lowlands), Ireland (Lindroth, 1974), its occurrence decreases in the north of the country (Luff, 1998). The only record of the species in Northern Ireland from Johnson & Halbert (1902) indicates that the species was widespread in Ireland in the last century. Lindroth (1985) indicates that *B. minimum* is spread along the coasts of sea and fjords in all districts of Denmark; there are no or few records from the north-west and north-east coasts of Jutland or from the north and west coasts of Zealand. In the south of Sweden *B. minimum* is found exclusively on the sea coasts, generally distributed along the west coast; in Norway, it is a rare species, in Finland it is found along the coast (Lindroth, 1985). In Egypt, the species is very rare in settlements located along the coast of the Mediterranean Sea and the Sinai Peninsula, as these habitats are disturbed by urbanization and tourist settlements (Abdel-Dayem, 1998). In Russia, *B. minimum* is distributed in the northern, central and southern parts of the Russian Plain, in Siberia, Transbaikalia and the Altai-Sayan mountain country (Kryzhanovskij et al., 1995), there are a few records from the Southern Karelian Isthmus (Lindroth, 1985), it is quite common in the Republic of Adygea in coastal areas (Zamotajlov & Nikitsky, 2010). In Ukraine, *B. minimum* is distributed in the Transcarpathian Lowland, in the Carpathians, Right-Bank and Left-Bank Polesie, the zone of broad-leaved forests, the Right-Bank and Left-Bank Forest-Steppes, and the northern subzone of Right-Bank and Left-Bank Steppes (Putchkov, 2011, 2012).

B. minimum lives in humid biotopes along the shores of seas, rivers, and standing water bodies (Lindroth, 1985). It prefers muddy, moderately humid and slightly shady places, among herbaceous plants (for example, plant associations of *Juncus*, *Equisetum* and others) and under bushes. It is a halophile which is usually found in high numbers (sometimes up to 20 ind./m^2) on salt marshes and marine clay soils, on the banks of saline and brackish water bodies (Desender & Maelfait, 1999), less often on the banks of fresh water bodies (Zherebcov, 2000; Zamotajlov & Nikitsky, 2010). *B. minimum* is one of the indicators of soil salinity (Schultz, 2000). *B. minimum* is widely distributed in polders (Meijer, 1974). The beetles often run about in sunny weather on exposed spots (Lindroth, 1985). *B. minimum* is a spring-summer species, breeding occurs in spring (Lindroth, 1985). It is macropterous, having functional flight muscles. *B. minimum* is characterized by high flight activity of both sexes during the entire existence of imago. In this species, both sexes and all ages of beetles participate in migratory activity (Matalin, 2003). It flies towards light, especially to polarized light (Szentkiralyi et al., 2005). *B. minimum* beetles swim well (Turin, 2000).

As a result of studies of the molecular variability of *B. minimum* from the shores of the Baltic Sea, it was deduced that the species has two haplotypes: one haplotype is limited to coastal habitats and the other occurs within the interior. This distribution is contrary to the wide distribution area and high mobility of this species (Kamer et al., 2008). The genetic structure and diversity of *B. minimum* has been studied on a regional and Western European scale for more than 1600 individuals from all remaining salt marshes in Belgium and from a number of European etalon areas. The average value of gene diversity is not related to the habitat or population size of *B. minimum*. From 2% to 6% of the total genetic diversity is explained by differentiation of populations. Genetic differentiation of *B. minimum* is significant at different geographic scales with higher values at a larger scale. Kamer et al. (2008) indicate that habitat fragmentation has not yet led to genetic changes, probably due to the large size of the *B. minimum* population, even in very small salt marshes. The observed genetic differentiation suggests that metapopulations on a relatively large geographical scale still function in this highly mobile species. Reconstruction of even small salt marshes can have a positive effect on the conservation for the long-term survival of these specialized ground beetles (Desender & Verdyck, 2001). The karyotype of *B. minimum* was studied (Rozek & Rudek, 1992).

B. minimum is associated with specific habitats (Eyre & Luff, 2004). The zonal distribution of the species positively correlates with tides in excess of 20–40 cm (Irmler et al., 2002). According to the results of many studies, it is known that this species successfully increases its number in stressed habitats, for example, under the conditions of invasion of some plant species. Despite the negative impact of the invasion of *Elymus athericus* (Link) Kerguelen on the abundance of various halophilous ground beetle species, *B. minimum* increases its abundance in areas covered by this species of cereal. These areas are characterized by a lower percentage of halophilous species of ground beetles and their greater diversity. This species of ground beetle can be used in bioindication (Georges et al., 2011). *B. minimum* increases its abundance in the conditions of mowing and grazing sheep. Grazing and mowing make the areas open and therefore more preferable for some halophilous species, including *B. minimum* (Petillon et al., 2007).

Thus, *B. minimum* is a convenient object for a complex study of the influence of environmental factors on morphological variability. The purpose of this article is to examine the morphological variability of *B. minimum* under the influence of natural and anthropogenic factors (recreational load, cattle grazing) and determine the factors that most affect the variability of this species of ground beetle.

Materials and methods

The research was carried in 12 ecosystems in the Mahdalinovka, Novomoskovsk, Pavlograd and Sinelnikovo districts of Dnipropetrovsk region (Ukraine). The ecosystems differed (Fig. 1, Table 1) in composition of herb layer, thickness of the litter, mechanical composition of the soil, acidity and mineralization of the soil solution, degree of recreational load and the intensity of cattle grazing.

Methodology for determination the total mineralization and acidity of the soil is described earlier in our article (Brygadyrenko & Slynko, 2015). For determination of the composition of the herb layer, a square of 4 m^2 was selected and photographed on each sample plot, and a herbarium was collected. The density of the herb layer was determined from photographs by expert assessment. Thickness of litter was measured in each studied ecosystem using a ruler in 10 locations. Recreational load was determined by direct observation, and also by the number of human traces and amount of household waste detected (Muhar et al., 2002). The effect of cattle grazing was determined visually by the presence of animal trails and feces (Kikoti & Mligo, 2015).

Specimens of *B. minimum* were collected using soil traps and manually using an aspirator. The beetles were frozen during 24 hours in a refrigerating chamber and then laid onto cotton mats, preliminarily straightened (to maintain proportions, we monitored the orientation of the head and prothorax). Each beetle was assigned a serial number including the ecosystem number and sex of the specimen (female, male). Photographs of the collected insects were taken using binocular MBS-10 and a digital camera of 5 megapixel resolution (Fig. 2). 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). 13 linear characteristics, 1 angular characteristic, density of pores on the elytra, contrast of the light spots of the left and right elytra were measured (Brygadyrenko & Fedorchenko, 2008; Brygadyrenko & Korolev, 2015; Komlyk & Brygadyrenko, 2019). Six morphometric indices were calculated (Brygadyrenko & Reshetniak, 2014; Brygadyrenko & Slynko, 2015; Komlyk & Brygadyrenko, 2019).

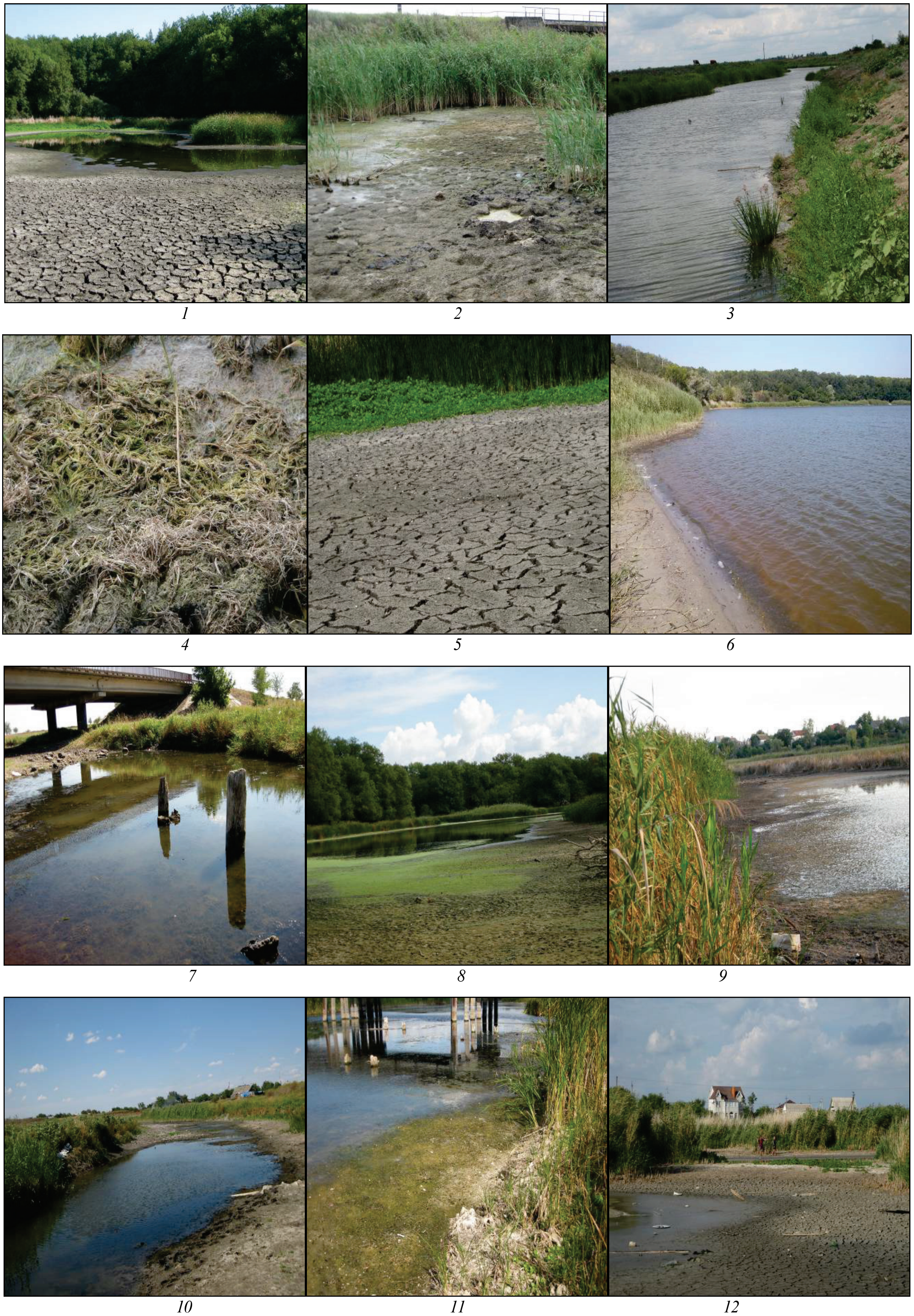

Fig. 1. Vegetation of the sample plots

Table 1
Brief characteristic of ecosystems (Dnipropetrovsk region, Ukraine) where *B. minimum* was collected

Eco-system	Administrative district	Ecosystem coordinates	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**	Number of studied individuals (females and males)***
1	Novo-moskovsk	48°40'04.3"N 35°20'18.8"E	sandy loam	0.35	8.38	0	0	0	0	39 (20f, 19m)
2	Novo-moskovsk	48°37'37.5"N 35°21'14.2"E	sandy loam	0.37	8.17	0	0	3	3	40 (28f, 12m)
3	Pavlograd	48°30'33.0"N 36°04'44.0"E	sand	0.87	8.60	90%: *Xanthium albinum* (Widd.) Scholz (50%), *Chenopodium album* L. (30%), *Bolboschoenus maritimus* (L.) Palla (10%)	0	2	2	27 (14f, 13m)
4	Sinelnikovo	48°29'33.0"N 35°21'49.0"E	loam	1.12	8.22	0	4	3	3	38 (22f, 16m)
5	Novo-moskovsk	48°40'03.1"N 35°20'17.3"E	loam	1.43	7.64	0	0	0	0	40 (16f, 14m)
6	Mahda-linovka	48°43'46.0"N 35°00'31.0"E	loam	2.08	8.10	0	4	1	0	20 (11f, 9m)
7	Pavlograd	48°34'24.0"N 35°52'13.1"E	sandy loam	2.13	7.98	0	0	2	2	35 (21f, 14m)
8	Novo-moskovsk	48°40'17.7"N 35°18'37.3"E	loam	3.22	7.75	0	2	0	0	37 (20f, 17m)
9	Novo-moskovsk	48°40'21.2"N 35°21'19.5"E	loam	3.48	7.99	90%: *Typha angustifolia* L. (90%)	2	1	1	40 (25f, 15m)
10	Pavlograd	48°34'18.3"N 35°51'57.1"E	sand	4.40	7.75	0	0	2	2	37 (22f, 15m)
11	Pavlograd	48°28'40.1"N 36°01'21.8"E	loam	4.42	7.98	35%: *Chenopodium album* L. (30%), *Poa sp.* (5%)	0	1	1	21 (16f, 5m)
12	Novo-moskovsk	48°37'32.9"N 35°20'20.8"E	loam	5.50	8.50	0	0	3	1	36 (18f, 18m)

Notes: * – recreational load: 0 – absent (there are no human traces and household waste), 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 effect of cattle grazing: 0 – absent (there are no animal trails and their feces), 1 – slight (animal trails and their feces are rare), 2 – medium (animal trails and their feces occupy 10–30% of land area), 3 – strong (animal trails and their feces occupy more than 30% of land area); *** – f – females, m – males.

Fig. 2. Male of *B. minimum*

The results were processed by standard methods of variation statistics using Statistica software (version 8, StatSoft, USA). The effect of sex and environmental factors on morphological characteristics and indices was evaluated using MANOVA. Factor analysis was used to determine the similarity of morphological parameters and indices.

Results

The herb layer (Table 3) significantly affects 7 of 16 characteristics (P – density of elytra puncturing, Lp, Sc, Sp2, Spm, B, K) and 3 of 6 morphometric indexes ((Sc+Sp+Se)/3Lb, Le/Lp and Spm/Sp2). The herb layer significantly affects the display of sexual dimorphism of almost all morphometric characteristics (except for B, P, K) and indexes (except for (Sc+Sp+Se)/3Lb, Se/Sp, Spm/Sp2). The interaction between the herb layer and the sex significantly affects Lp, Se and Se/Sp.

Litter thickness affects Sp1, P, K and Le/Lp (Table 4). Litter thickness affects the manifestation of sexual dimorphism for most of the morphological parameters (except for B and K) and indices (except for Lp/Sp, Se/Sp, Spm/Sp2). The interaction of the litter thickness and the sex does not significantly affect any of the studied parameters.

Mechanical composition of soil (Table 5) significantly affects Lc and Se/Sp, Lb. Sex does not affect any characteristics except B, Lp/Sp, Spm/Sp2. The interaction of the mechanical composition of soil and sex does not significantly affect any of the studied characteristics (Table 5).

Soil mineralization (Table 6) significantly affects Lb, Lc, Lp, Sp1, Sp2, Se, B and P. Sex in the gradient of soil mineralization does not affect B, Se/Sp and Spm/Sp2. The interaction of soil mineralization and sex significantly affects Le and Spm.

Soil acidity (Table 7) significantly affects Lb, Lc, Le, Sc, Sp1, Sp2, Spm, Se, B, P, K, L2l, (Sc+Sp+Se)/3Lb. Sex differences in the soil acidity gradient do not appear for B, Lp/Sp, Se/Sp and Spm/Sp2. The interaction of soil acidity and sex significantly affects Lp/Sp and Le/Lp (Table 7). Recreational load (Table 8) significantly affects Lb, Lc, Le, Sc, Sp1, Sp2, Spm, Se, B, P, K, L2l, L2r, Lp/Sp, Le/Lp. Sex does not affect only B, Lp/Sp, Se/Sp and Spm/Sp2. The interaction of recreational load and sex (Table 8) significantly affects Lb, Le, Sc, Se, L1l, L1r and Se/Sp. Cattle grazing (Table 9) significantly causes changes in all characteristics except L1l, L1r, Se / Sp, Spm/Sp2, and Le/Se. The impact of sex does not significantly affect B, Lp/Sp, Se/Sp, Spm/Sp2. The interaction of cattle grazing and sex is not significant for any studied characteristics except Lp/Sp, Le/Lp.

In outermost variants of the herb layer (Fig. 3) – at high values (70%) and the absence of herb layer (0%) – the variability of most studied morphometric characteristics of *B. minimum* is far lower than with average values of herb layer (35%). The maximum similarity between the studied features of females and males was registered for B (Fig. 3*g*), P (Fig. 3*n*), K (Fig. 3*o*) and all studied morphometric indices (Fig. 3*q*–*v*): (Sc+Sp+Se)/3Lb, Lp/Sp, Le/Lp, Se/Sp, Spm/Sp2, Le/Se.

Depending on the litter thickness (Fig. 4), with its increase from 0 to 2 and 4 cm, there is a tendency to a decrease in Le (from 1.62 to 1.60 mm in females and from 1.49 to 1.47 mm in males – Fig. 4*i*), P (from 239 to 212 in males and from 226 to 207 in females – Fig. 4*n*) and Le/Se (from 1.493 to 1.487 in males and from 1.518 to 1.500 in females – Fig. 4*v*).

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

Morphological characteristic or indexes	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 °	the back angles of 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 per 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	conventional 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°.

Table 3
MANOVA results of effect of herb layer on morphometric variability of *B. minimum* populations

Morphological characteristic or index	Factor		Sex		Factor * sex	
	F	P	F	P	F	P
Lb	0.59	0.5522	55.40	<0.0001	2.01	0.1354
Lc	1.58	0.2072	23.39	<0.0001	0.53	0.5895
Lp	5.06	0.0068	11.75	0.0007	3.72	0.0250
Le	0.30	0.7375	43.79	<0.0001	1.69	0.1857
Sc	3.63	0.0285	27.22	<0.0001	1.42	0.2426
Sp1	1.89	0.1526	42.72	<0.0001	0.39	0.6761
Sp2	7.83	0.0005	32.98	<0.0001	0.07	0.9315
Spm	4.39	0.0129	34.00	<0.0001	0.33	0.7174
Se	2.81	0.0612	27.64	<0.0001	3.20	0.0419
B	3.52	0.0305	1.67	0.1976	1.71	0.1816
P	10.37	<0.0001	2.98	0.0851	0.06	0.9437
K	5.64	0.0039	0.05	0.8273	0.97	0.3810
L1l	0.63	0.5357	13.67	0.0002	0.91	0.4037
L1r	0.27	0.7656	18.82	<0.0001	1.15	0.3176
L2l	0.63	0.5335	23.95	<0.0001	1.60	0.2022
L2r	0.98	0.3768	21.82	<0.0001	2.00	0.1367
(Sc+Sp+Se)/3Lb	4.29	0.0145	3.81	0.0519	0.12	0.9324
Lp/Sp	0.06	0.9446	5.70	0.0174	2.53	0.0809
Le/Lp	3.50	0.0312	11.13	0.0009	0.57	0.5635
Se/Sp	1.81	0.1714	3.02	0.0862	4.69	0.0099
Spm/Sp2	3.12	0.0450	0.70	0.4035	0.94	0.3919
Le/Se	2.40	0.0924	7.73	0.0057	0.31	0.7345

Note: names of characteristics are given in section Materials and Methods.

Depending on the mechanical composition of the soil, *B. minimum* head length Lc increases (from 0.393 on sandy to 0.407 mm on loamy soils in females and from 0.363 on sandy to 0.382 mm on loamy soils in males – Fig. 5*a*) and Sp2/Spm index (from 0.647 on sandy to 0.655 on loamy soils in females and from 0.650 on sandy to 0.657 on loamy soils in males – Fig. 5*u*).

Table 4
MANOVA results of effect of litter thickness on morphometric variability of *B. minimum* populations

Morphological characteristic or index	Factor		Sex		Factor * sex	
	F	P	F	P	F	P
Lb	1.18	0.3069	197.64	<0.0001	0.33	0.7468
Lc	2.61	0.0748	46.20	<0.0001	0.25	0.7811
Lp	2.68	0.0699	78.13	<0.0001	0.52	0.5941
Le	1.81	0.1654	153.39	<0.0001	0.47	0.6255
Sc	0.19	0.7794	108.87	<0.0001	0.82	0.4626
Sp1	3.03	0.0487	113.62	<0.0001	0.29	0.7263
Sp2	0.08	0.9189	76.95	<0.0001	0.20	0.8200
Spm	0.50	0.6065	106.67	<0.0001	0.85	0.4301
Se	0.48	0.6062	126.79	<0.0001	0.61	0.5480
B	2.35	0.0967	0.68	0.4087	1.33	0.2657
P	15.74	<0.0001	6.47	0.0113	0.24	0.7852
K	3.96	0.0197	3.03	0.0824	0.36	0.7006
L1l	0.91	0.4037	44.29	<0.0001	0.93	0.3941
L1r	1.34	0.2627	45.56	<0.0001	1.97	0.1404
L2l	0.27	0.7613	96.28	<0.0001	0.05	0.9484
L2r	0.73	0.4836	99.21	<0.0001	0.44	0.6431
(Sc+Sp+Se)/3Lb	0.72	0.5202	6.54	0.0112	0.47	0.6014
Lp/Sp	2.43	0.0925	1.09	0.3051	0.14	0.9269
Le/Lp	3.69	0.0257	11.23	0.0008	0.71	0.4898
Se/Sp	0.12	0.9118	0.47	0.4910	0.62	0.5420
Spm/Sp2	1.03	0.3524	0.21	0.6305	0.60	0.5435
Le/Se	1.13	0.3397	8.38	0.0039	0.31	0.7394

Table 5
MANOVA results of effect of mechanical composition of soil on morphometric variability of *B. minimum* populations

Morphological characteristic or index	Factor		Sex		Factor * sex	
	F	P	F	P	F	P
Lb	3.24	0.0428	236.51	<0.0001	0.92	0.4087
Lc	9.37	0.0001	53.38	<0.0001	2.14	0.1185
Lp	0.71	0.4843	80.19	<0.0001	0.04	0.9948
Le	1.19	0.3037	189.22	<0.0001	0.47	0.5953
Sc	1.40	0.2542	117.23	<0.0001	0.58	0.5750
Sp1	0.11	0.9098	134.13	<0.0001	1.52	0.2159
Sp2	2.82	0.0607	83.18	<0.0001	0.68	0.5075
Spm	1.02	0.3829	113.46	<0.0001	1.50	0.2249
Se	2.04	0.1354	154.71	<0.0001	1.21	0.2959
B	2.29	0.1026	0.04	0.8412	0.29	0.7485
P	0.47	0.6266	11.23	0.0009	0.99	0.3714
K	1.69	0.1859	8.53	0.0037	1.32	0.2684
L1l	0.09	0.9106	46.30	<0.0001	0.30	0.7382
L1r	0.12	0.8905	67.11	<0.0001	0.43	0.6481
L2l	2.10	0.1243	112.25	<0.0001	0.56	0.5724
L2r	2.42	0.0906	115.30	<0.0001	1.21	0.2992
(Sc+Sp+Se)/3Lb	0.80	0.4665	10.57	0.0012	0.09	0.8680
Lp/Sp	0.05	0.9878	1.20	0.2720	1.51	0.2291
Le/Lp	1.42	0.2584	20.93	<0.0001	0.59	0.5734
Se/Sp	3.54	0.0319	4.52	0.0353	1.24	0.2954
Spm/Sp2	1.90	0.1499	0.21	0.6648	0.10	0.8865
Le/Se	0.13	0.8663	11.52	0.0008	0.19	0.7944

Soil mineralization is one of the most significant environmental parameters for invertebrates living on salt marshes: mineralization of the soil solution is less than 3 g/L. With an increase in mineralization of the soil solution, there is a tendency toward an increase in head width in females and a decrease in this parameter in males (Fig. 6*b*). The prothorax width between its front angles in males decreases with increasing mineralization (Fig. 6*d*). The prothorax width between back angles and its maximum width tends to increase in females on highly mineralized soils (Fig. 6*e*, *f*). Similar changes were registered for length and width of the elytra in females (Fig. 6*h*, *i*). There is also a tendency (in both males and females) to decrease in density of elytra puncturing (from 217–245 to 208–209 pores on the area 1 mm^2 – Fig. 6*n*) in areas with high mineralization of the soil. A tendency to increase in the body length of females was revealed, in contrast to males, in areas with saline soil (Fig. 6*p*). The ratio of prothotax length to maximum width (Lp/Sp, Fig. 6*r*) and also the ratio of the elytra length to prothorax length (Le/Lp, Fig. 6*s*) tend to increase in males of *B. minimum*.

Table 6
MANOVA results of effect of soil mineralization
on morphometric variability of *B. minimum* populations

Morphological characteristic or index	Factor		Sex		Factor * sex	
	F	P	F	P	F	P
Lb	3.51	0.0042	313.43	<0.0001	2.04	0.0741
Lc	7.40	<0.0001	67.42	<0.0001	0.61	0.6892
Lp	2.92	0.0138	103.30	<0.0001	0.89	0.5041
Le	1.53	0.1774	251.79	<0.0001	2.54	0.0318
Sc	1.93	0.0861	159.02	<0.0001	1.69	0.1393
Sp1	3.58	0.0031	162.62	<0.0001	0.78	0.5198
Sp2	2.56	0.0271	118.90	<0.0001	1.52	0.2008
Spm	1.72	0.1386	162.11	<0.0001	2.18	0.0500
Se	2.39	0.0359	201.52	<0.0001	2.23	0.0557
B	4.51	0.0005	0.13	0.8157	1.34	0.2795
P	5.32	0.0001	8.04	0.0048	1.08	0.3733
K	1.88	0.0971	4.83	0.0285	0.53	0.7551
L1l	0.89	0.4881	63.18	<0.0001	1.16	0.3275
L1r	0.96	0.4449	88.23	<0.0001	2.17	0.0568
L2l	1.43	0.2138	139.94	<0.0001	0.59	0.7068
L2r	1.62	0.1522	125.95	<0.0001	0.36	0.8774
(Sc+Sp+Se)/3Lb	1.04	0.4222	11.01	0.0010	0.38	0.8640
Lp/Sp	1.23	0.2869	3.92	0.0481	1.57	0.1649
Le/Lp	1.50	0.1924	29.04	<0.0001	1.40	0.2194
Se/Sp	1.52	0.1880	1.63	0.2105	0.29	0.9018
Spm/Sp2	1.48	0.2018	0.13	0.7221	0.72	0.6184
Le/Se	0.82	0.5422	16.60	<0.0001	0.11	0.9879

Table 7
MANOVA results of effect of soil acidity
on morphometric variability of *B. minimum* populations

Morphological characteristic or index	Factor		Sex		Factor * sex	
	F	P	F	P	F	P
Lb	4.02	0.0032	307.86	<0.0001	1.29	0.2723
Lc	3.98	0.0036	64.66	<0.0001	1.45	0.2172
Lp	1.83	0.1354	106.74	<0.0001	1.49	0.1931
Le	3.94	0.0037	248.71	<0.0001	1.36	0.2437
Sc	6.31	<0.0001	165.60	<0.0001	0.89	0.4659
Sp1	13.04	<0.0001	179.58	<0.0001	0.19	0.9500
Sp2	2.70	0.0328	103.54	<0.0001	0.21	0.9105
Spm	4.27	0.0022	156.63	<0.0001	0.89	0.4528
Se	6.11	<0.0001	203.34	<0.0001	1.83	0.1379
B	4.58	0.0013	0.12	0.7599	0.31	0.8803
P	20.32	<0.0001	10.10	0.0016	1.49	0.2034
K	7.36	<0.0001	7.61	0.0061	0.98	0.4305
L1l	1.67	0.1569	61.79	<0.0001	0.59	0.6684
L1r	0.77	0.5482	79.35	<0.0001	0.78	0.5363
L2l	2.54	0.0397	146.29	<0.0001	2.16	0.0728
L2r	2.10	0.0803	139.69	<0.0001	2.37	0.0518
(Sc+Sp+Se)/3Lb	2.67	0.0326	11.73	0.0007	0.40	0.8160
Lp/Sp	1.04	0.4223	2.10	0.1493	2.51	0.0399
Le/Lp	1.79	0.1332	25.11	<0.0001	2.50	0.0424
Se/Sp	1.13	0.3364	2.27	0.1315	1.62	0.1839
Spm/Sp2	0.81	0.5090	1.08	0.2912	1.70	0.1589
Le/Se	0.78	0.5578	15.83	<0.0001	0.59	0.6305

Decrease in the number of pores on the elytra in males and females was observed at the level of tendency in areas with more alkaline soils (Fig. 7*n*). The ratio of prothorax length to its maximum width increases in males, and it decreases in females in areas with higher pH of the soil solution (Lp/Sp, Fig. 7*r*). Opposite changes were noted for the ratio of elytra length to prothorax length (Le/Lp, Fig. 7*s*): in areas with higher pH values this index decreases in males and increases in females. The maximum values of Se/Sp index (Fig. 7*s*) were observed in females in areas with neutral soil solution; the minimum Sp2/Spm (Fig. 7*u*) was recorded in females of *B. minimum* in areas with more alkaline soil solution.

Table 8
MANOVA results of effect of recreational load
on morphometric variability of *B. minimum* populations

Morphological characteristic or index	Factor		Sex		Factor * sex	
	F	P	F	P	F	P
Lb	12.81	<0.0001	312.16	<0.0001	3.21	0.0238
Lc	11.23	<0.0001	66.94	<0.0001	0.36	0.7830
Lp	1.49	0.2042	99.21	<0.0001	2.19	0.0832
Le	15.84	<0.0001	257.05	<0.0001	3.52	0.0165
Sc	12.10	<0.0001	160.32	<0.0001	4.23	0.0061
Sp1	16.59	<0.0001	188.67	<0.0001	2.18	0.0844
Sp2	6.52	0.0003	111.24	<0.0001	0.91	0.4309
Spm	6.87	0.0001	152.86	<0.0001	2.30	0.0725
Se	13.42	<0.0001	198.85	<0.0001	3.76	0.0099
B	10.96	<0.0001	0.43	0.5491	1.84	0.1534
P	35.70	<0.0001	9.09	0.0027	2.33	0.0736
K	13.29	<0.0001	8.59	0.0036	0.63	0.5972
L1l	0.86	0.4623	57.27	<0.0001	2.98	0.0313
L1r	1.00	0.3937	75.37	<0.0001	3.34	0.0194
L2l	2.95	0.0324	139.10	<0.0001	1.30	0.2692
L2r	3.78	0.0107	132.67	<0.0001	1.23	0.2970
(Sc+Sp+Se)/3Lb	2.39	0.0699	12.36	0.0005	0.91	0.4573
Lp/Sp	3.50	0.0156	2.81	0.0959	2.53	0.0594
Le/Lp	10.01	<0.0001	26.95	<0.0001	1.01	0.4154
Se/Sp	2.38	0.0662	1.40	0.2433	3.62	0.0128
Spm/Sp2	1.40	0.2404	0.24	0.6727	0.50	0.7063
Le/Se	1.32	0.2797	16.94	<0.0001	0.11	0.9732

Table 9
MANOVA results of effect of cattle grazing
on morphometric variability of *B. minimum* populations

Morphological characteristic or index	Factor		Sex		Factor * sex	
	F	P	F	P	F	P
Lb	18.02	<0.0001	343.17	<0.0001	1.32	0.2855
Lc	13.47	<0.0001	63.90	<0.0001	0.25	0.8603
Lp	2.60	0.0490	109.06	<0.0001	1.81	0.1428
Le	20.95	<0.0001	288.06	<0.0001	1.39	0.2499
Sc	13.72	<0.0001	178.13	<0.0001	2.50	0.0589
Sp1	10.79	<0.0001	184.35	<0.0001	2.02	0.1128
Sp2	8.03	<0.0001	118.74	<0.0001	0.93	0.4171
Spm	9.74	<0.0001	165.46	<0.0001	1.50	0.2244
Se	17.84	<0.0001	221.87	<0.0001	1.32	0.2783
B	6.47	0.0003	0.01	0.9987	1.71	0.1685
P	21.41	<0.0001	8.14	0.0046	1.82	0.1437
K	9.26	<0.0001	9.23	0.0025	1.01	0.3907
L1l	2.44	0.0636	69.16	<0.0001	2.29	0.0776
L1r	1.36	0.2556	86.42	<0.0001	1.68	0.1716
L2l	3.55	0.0145	143.21	<0.0001	0.53	0.6596
L2r	5.12	0.0017	137.98	<0.0001	1.28	0.2822
(Sc+Sp+Se)/3Lb	2.82	0.0410	12.14	0.0006	0.49	0.6982
Lp/Sp	2.70	0.0456	2.49	0.1171	4.03	0.0080
Le/Lp	8.13	<0.0001	29.83	<0.0001	2.78	0.0399
Se/Sp	2.12	0.0976	2.70	0.1020	2.29	0.0800
Spm/Sp2	1.53	0.2101	0.31	0.5854	0.20	0.9235
Le/Se	0.80	0.4987	18.14	<0.0001	0.59	0.6382

In males the head width (Sc, Fig. 8*b*), the prothorax width between front (Sp1, Fig. 8*d*) and back angles (Sp2, Fig. 8*e*) and also its maximum width (Spm, Fig. 8*f*) decrease in areas with pronounced recreational load. There was a tendency to increase back angles of the prothorax (B, Fig. 8*g*) in both males and females in areas with a recreational load. Recreation in littoral areas – habitats of *B. minimum* – causes a decrease in the elytra length (Le, Fig. 8*h*) in both males and females. Recreational load causes more pronounced decrease in the elytra width (Se, Fig. 8*i*) in males than in females. The distances to the first setae on the left and right elytra (L1l, L1r, Fig. 8*k*, *m*) in areas with a recreational load significantly decrease in males, but they inversely tend to increase in females. The number of pores per unit area of the elytra (P, Fig. 8*n*) decreases in both females and males with increasing degree of recreation.

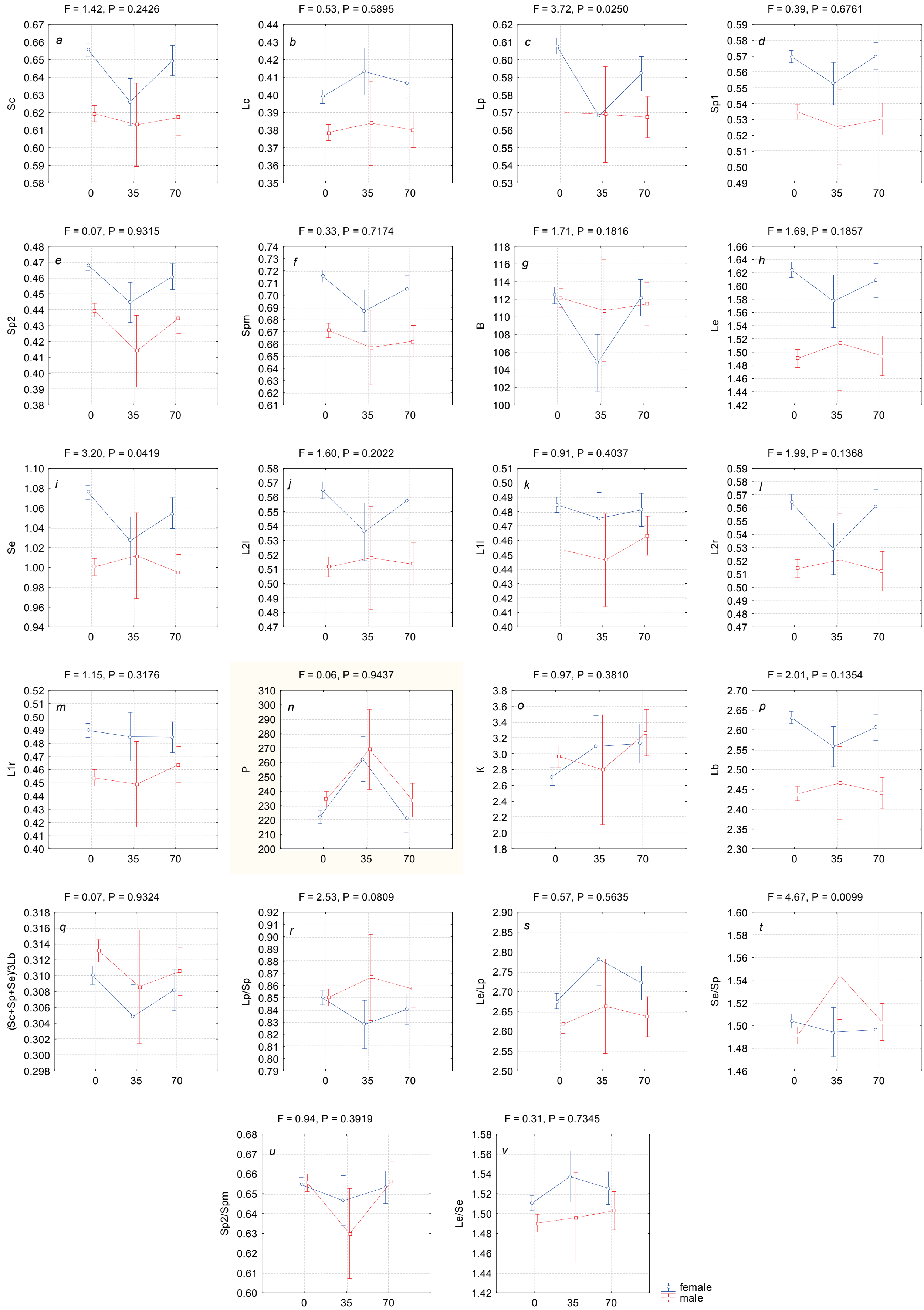

Fig. 3. Variability of morphometric characteristics of *B. minimum* body in studied populations depending on herb layer: on X axis: 0 – there is no herb layer, 35 – average herb layer is 35%, 70 – average herb layer is 70%; other notations see Table 2

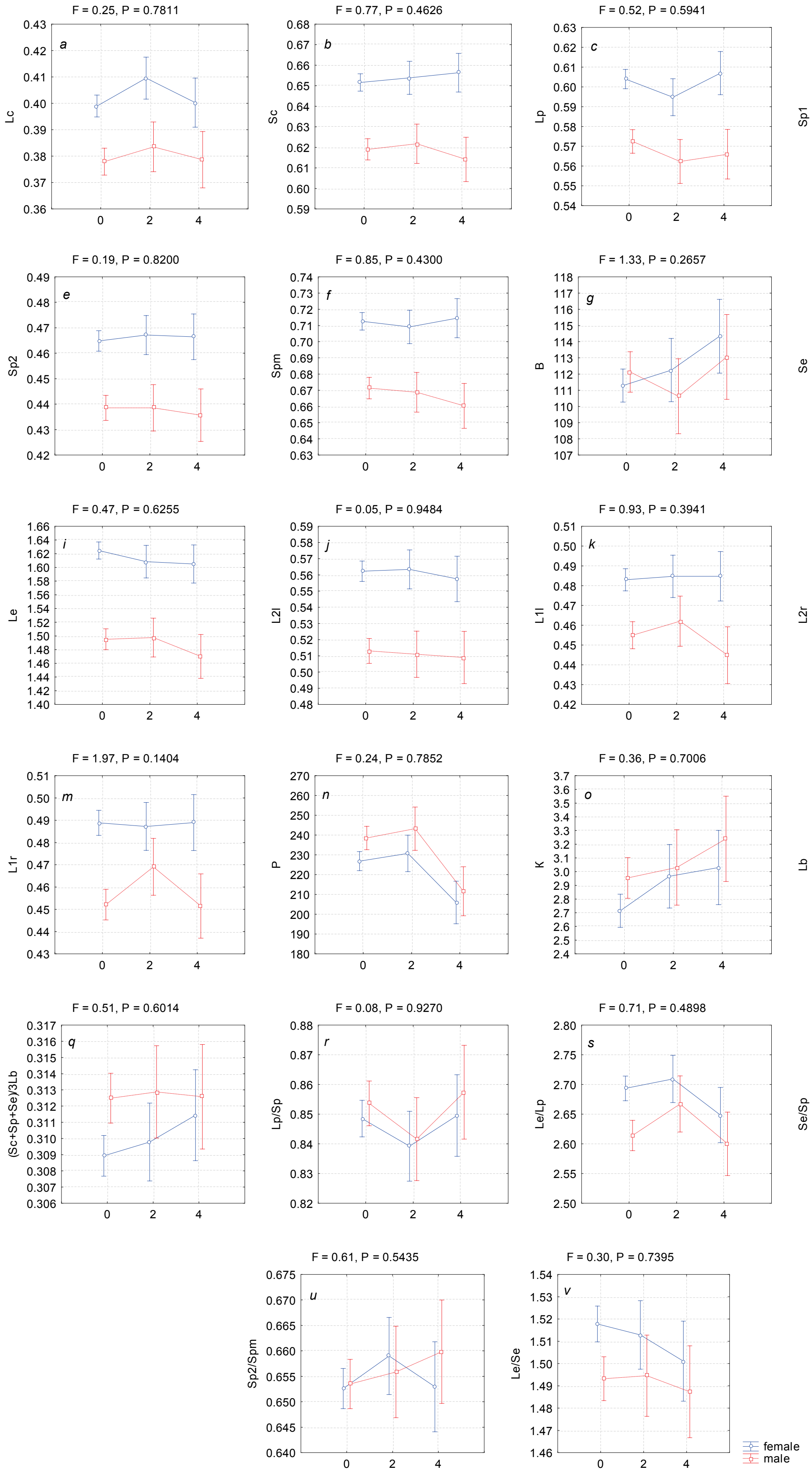

Fig. 4. Variability of morphometric characteristics of *B. minimum* body in studied populations depending on litter thickness: on X axis: 0 – there is no litter, 2 – litter thickness is 2 cm, 4 – litter thickness is 4 cm; other notations see Table 2

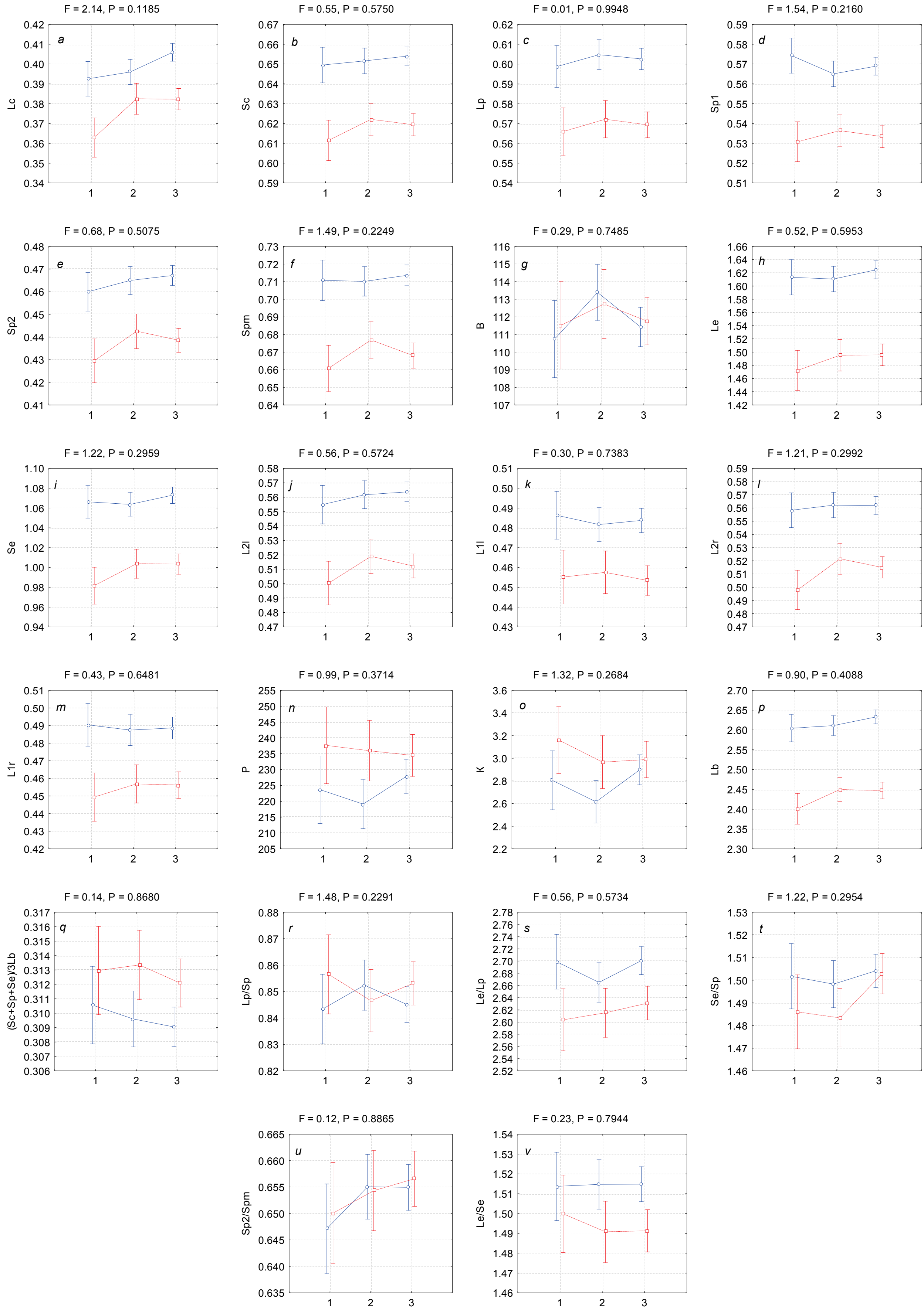

Fig. 5. Variability of morphometric characteristics of *B. minimum* body in studied populations depending on mechanical composition of soil: 1 – sand, 2 – sandy loam, 3 – loam; notations see Table 2

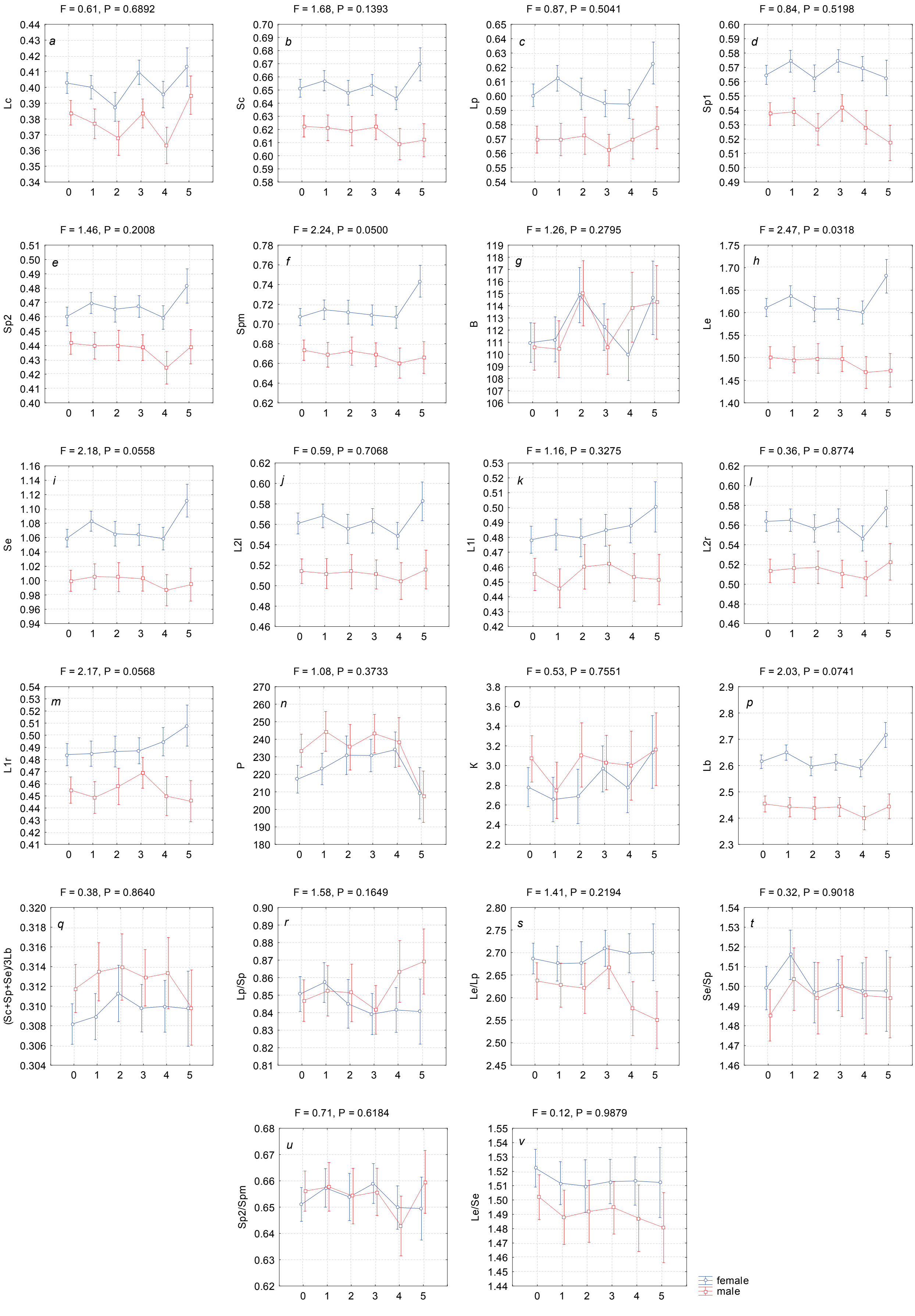

Fig. 6. Variability of morphometric characteristics of *B. minimum* body in studied populations depending on soil mineralization: on X axis: 0 – 0.0–1.0 g/L, 1 – 1.0–2.0 g/L, 2 – 2.0–3.0 g/L, 3 – 3.0–4.0 g/L, 4 – 4.0–5.0 g/L, 5 – >5.0 g/L; other notations see Table 2

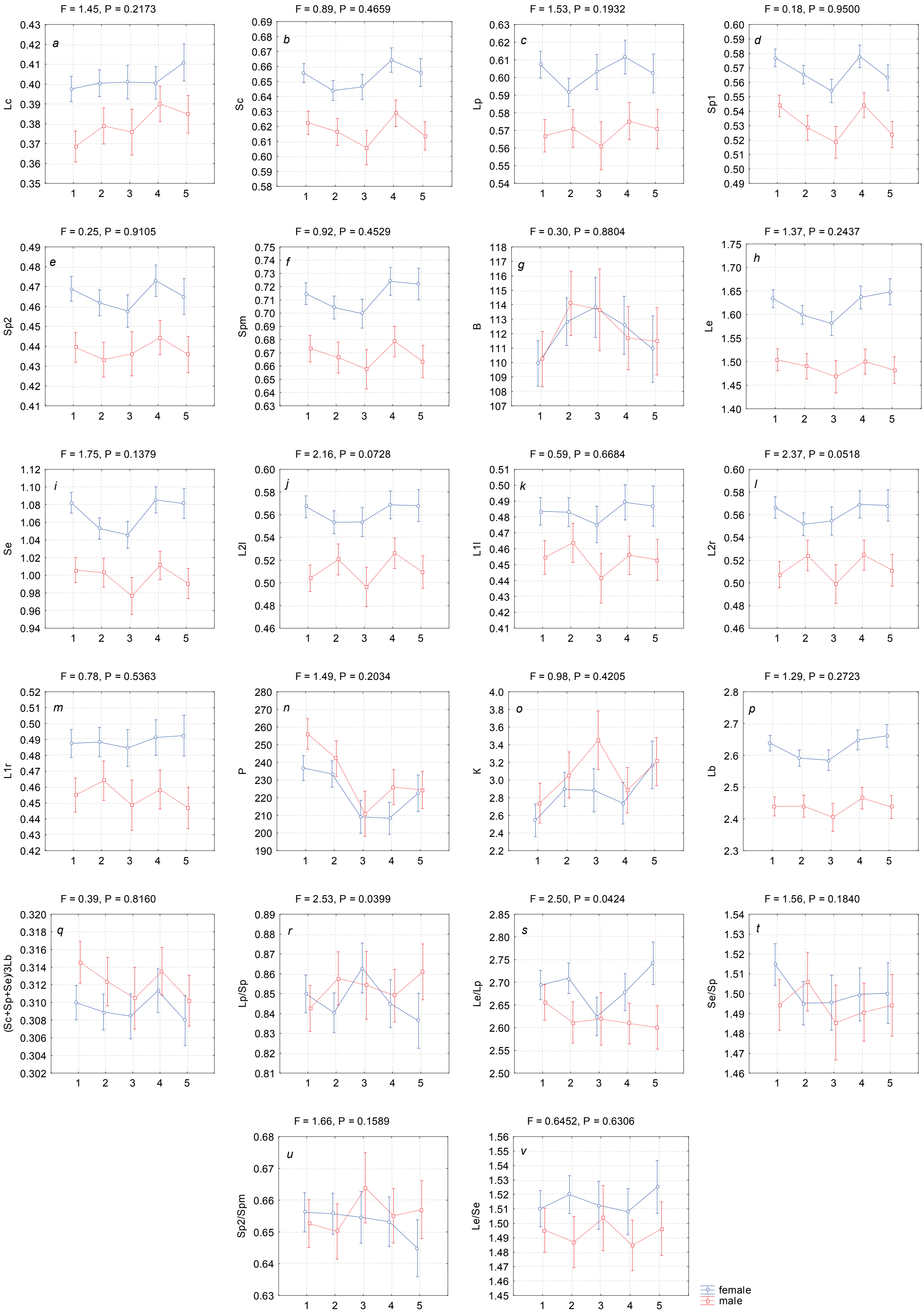

Fig. 7. Variability of morphometric characteristics of *B. minimum* body in studied populations depending on soil acidity: on X axis: 1 – pH < 7.8, 2 – pH = 7.8–8.0, 3 – pH = 8.0–8.2, 4 – pH = 8.2–8.4, 5 – pH = 8.4–8.6; notations see Table 2

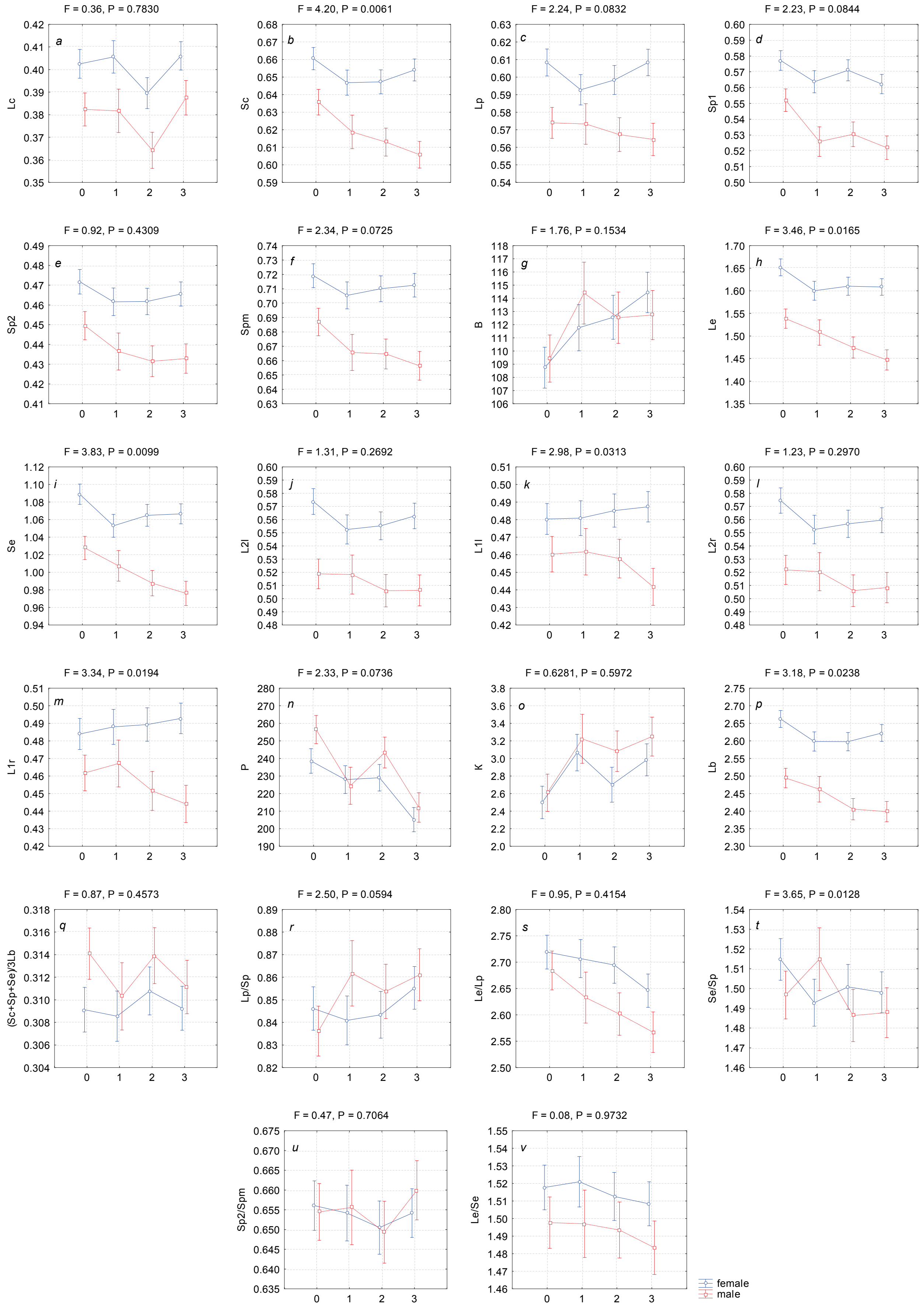

Fig. 8. Variability of morphometric characteristics of *B. minimum* body in studied populations depending on recreational load: on X axis – recreational load: 0 – absent (there are no human traces and household waste), 1 – slight (human traces and household waste are rare), 2 – medium (human traces and household waste occupy 10–30% of land area), 3 – strong (human traces and household waste occupy more than 30% of land area); other notations see Table 2

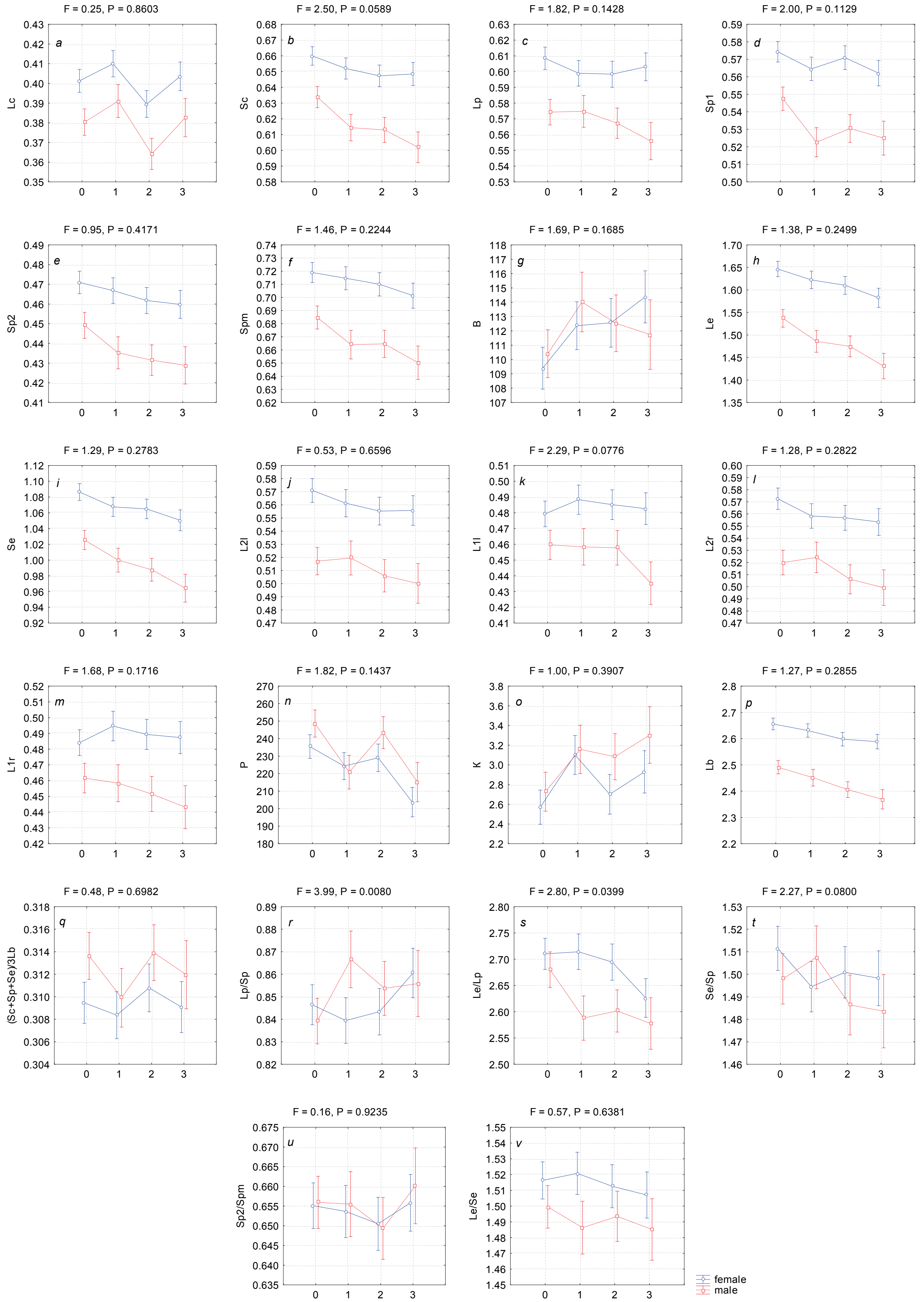

Fig. 9. Variability of morphometric characteristics of *B. minimum* body in studied populations depending on cattle grazing: on X axes –effect of cattle grazing: 0 – absent (there are no animal trails or feces), 1 – slight (animal trails and feces are rare), 2 – medium (animal trails and feces occupy 10–30% of land area), 3 – strong (animal trails and feces occupy more than 30% of land area); other notations see Table 2

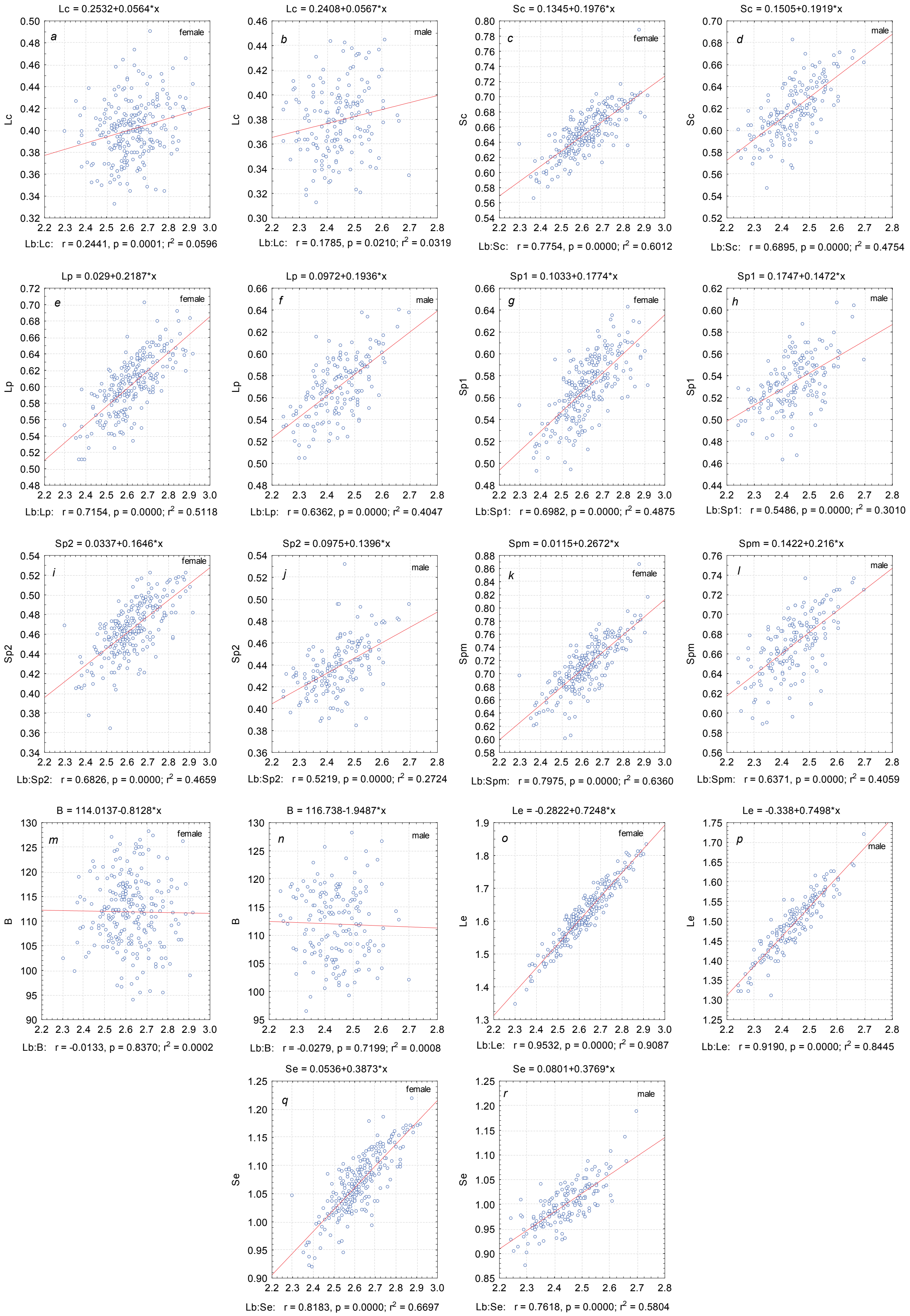

Fig. 10. Scatter diagram of linear characteristics of males and females of *B. minimum* depending on their body length: names of characteristics see Table 2

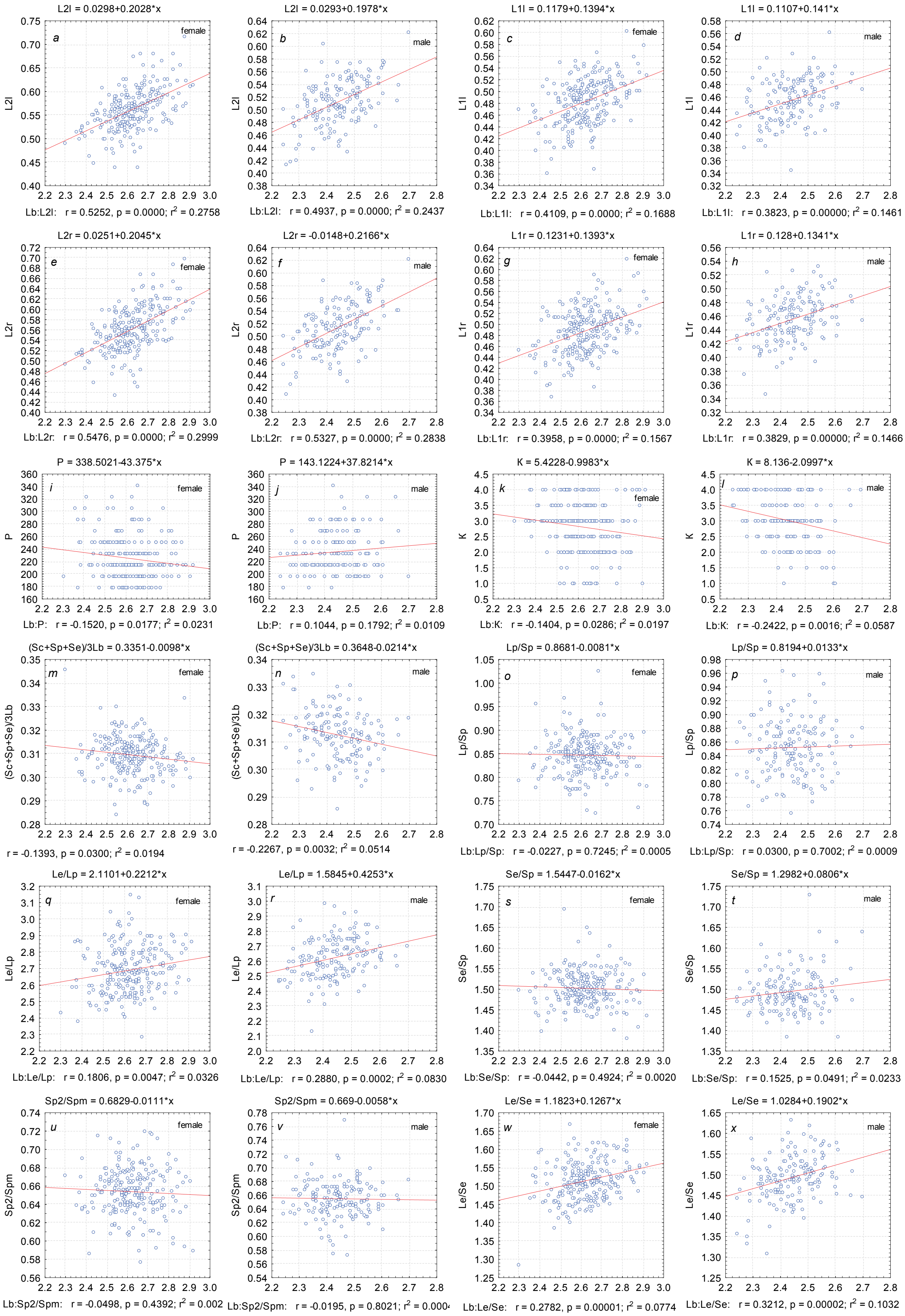

Fig. 11. Scatter diagram of linear characteristics and indices of males and females of *B. minimum* depending on their body length: names of characteristics see Table 2

The body length of *B. minimum* males (Lb, Fig. 8*p*) significantly decreases in conditions of more pronounced anthropogenic load; the ratio of maximum width of elytra to maximum prothorax width also decreases in females (Se/Sp, Fig. 8*t*). Significant decrease in the ratio of elytra length to prothorax length was observed in males of *B. minimum* in areas with intense anthropogenic impact (Le/Lp, Fig. 8*s*).

The head width (Sc, Fig. 9*b*), the length and width of the prothorax (Lp, Sp1, Sp2, Spm, Fig. 9*c–f*), the length and width of the elytra (Le, Se, Fig. 9*h*, *i*) decrease in males in areas with a high degree of cattle grazing; similar but not significant changes also occur in females of this species of beetle. The value of the back angles of the prothorax (B, Fig. 9*g*) increases in areas with high cattle grazing in females, unlike in males. More pronounced changes under the influence of cattle grazing occur in disposition of setae in males than in females (L1l, L1r, L2l, L2r, Fig. 9*j–m*). There are significant changes in three morphometric indices: increase in the ratio of prothorax length to its maximum width in females (Lp/Sp, Fig. 9*r*), decrease in the ratio of elytra length to prothorax length in males and females (Le/Lp, Fig. 9*s*), decrease in the ratio of maximum elytra width to maximum prothorax width in males (Se/Sp, Fig. 9*t*) under the influence of cattle grazing.

After combination of all the measured individuals of *B. minimum* into one sample and their distribution depending on body length (Fig. 10, 11) it was found that the head length (Lc, $r^2 < 0.60$, Fig. 10*a*, *b*), the value of the back angles of the prothorax (B, $r^2 < 0.001$, Fig. 10*m*, *n*), the distance to the first and second setae (L1l, L1r, L2l, L2r, $r^2 = 0.14–0.30$, Fig. 11*a–h*), density of elytra puncturing (P, $r^2 = 0.01–0.02$, Fig. 11*i*, *j*) and the contrast of the light spots of elytra (K, $r^2 = 0.02–0.06$, Fig. 11*k*, *l*) are not related to body size in both females and males. None of the six studied morphometric indices also showed a relationship with the body sizes of males and females of *B. minimum* ($r^2 = < 0.10$, Fig. 11*m–x*).

The head width (Sc, $r^2 = 0.45–0.60$, Fig. 10*c*, *d*), prothorax length (Lp, $r^2 = 0.40–0.51$, Fig. 10*e*, *f*), prothorax width (Sp1, Sp2, Spm, $r^2 = 0.27–0.64$, Fig. 10*g–l*), elytra width (Se, $r^2 = 0.58–0.66$, Fig. 10*q*, *r*) showed average degree of connection with body size.

A strong relationship between the body sizes of males and females was found for the elytra length (Le, $r^2 = 0.84–0.91$, Fig. 10*o*, *p*).

For characteristics with an average and strong degree of relationship with body size, the angle of inclination of the regression line relative to the abscissa is higher for females than for males (Fig. 10, 11).

Factor analysis of the entire array of morphometric data (Fig. 12) showed that more than a third of the variability is determined by the total body size (Lb). Larger length and width of prothorax and elytra (Le, Se, Sc, Spm, Sp1, Sp2, Lp), longer distances to the first and second setae on the right and left elytra (L2r, L2l, L1r, L1l) are associated with larger body sizes. K, Lp/Sp, P correlate with smaller body sizes.

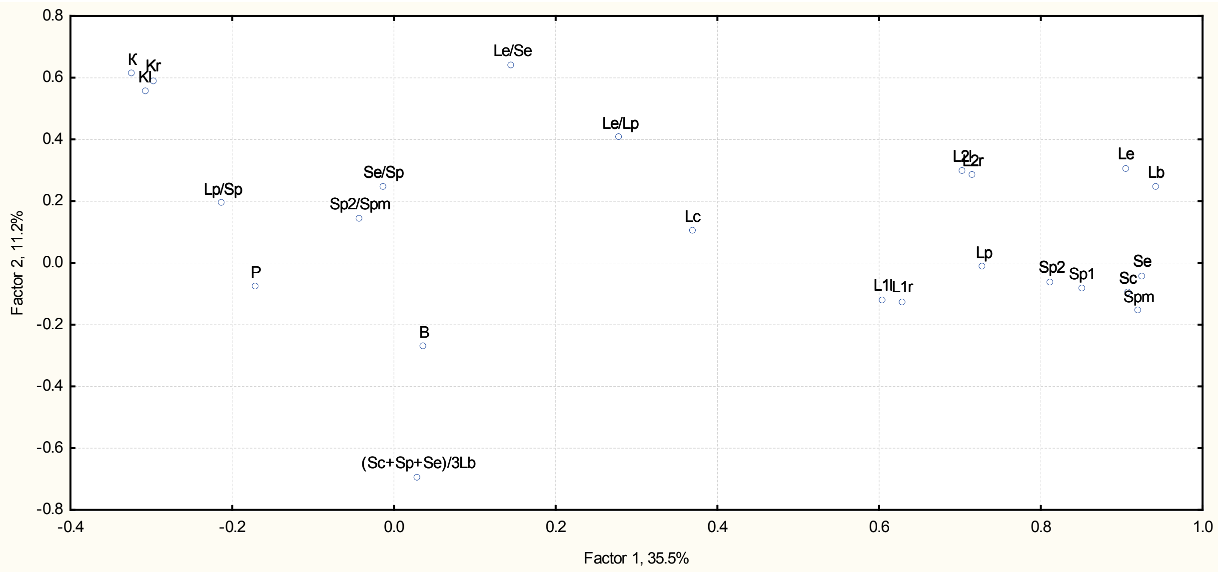

Fig. 12. Factor analysis of similarity of morphometric characteristics and indices of *B. minimum* body: factor 1 – total body length (35.5% of variance: positive values of factor correspond to characteristics that correlate with longer body length, negative – with shorter body length), factor 2 – body width (11.2% of variance: positive values of factor correspond to characteristics that correlate with more "narrow" individuals, negative – with more "wide-bodied")

The second most important factor of variability (Fig. 12) is the relative body width of individuals (11.2% of the variance). Narrower individuals with a larger relative elytra length (Le/Se) correlate K and the ratio of elytra length to the prothorax length Le/Lp. Larger values of back angles of prothorax (B) are associated with larger relative body width (Sc+Sp+Se)/3Lb.

Discussion

Selye (1976, 1982) introduced the concept of stress and identified three stages of organism response to stress factors. The duration and nature of the course of each stage depends on many factors. The presence of stress reactions in insects, as a result of which adaptation to constantly changing environmental conditions occurs, has been proven. The morphological variability of invertebrate animals is the result of the combined effects of genes and the environment and a manifestation of adaptation (Lupi et al., 2015). The choice of habitat in insects depends on the impact of a complex of biotic and abiotic factors. The distribution of invertebrate animals in litter is determined by the influence of many factors: especially the phytocenosis composition, density of the herb layer, humidity, litter thickness and mechanical structure of the soil (Faly & Brygadyrenko, 2018). The influence of many biotic factors on ground beetles was described by Thiele back in 1977. It is difficult to assess the significance and influence of each individual factor. Brygadyrenko (2015a, b; 2016a) assessed the relationship between the forest species *Badister*, *Calathus*, *Dolichus*, *Licinus*, *Panaeus* (Coleoptera, Carabidae) and some environmental factors: he determined the preferences of ground beetles depending on the type of forest ecosystem, tree crown density, composition and density of the herb layer, litter thickness, humidity conditions, mechanical composition and mineralization of the soil, and the presence of ants in ecosystems. Environmental factors can affect important morphometric features of ground beetles. The variability of these features affects the ability of beetles to adapt to new environmental conditions.

There is still no consensus on at what stage of ontogenesis the influence of natural and anthropogenic environmental factors is the most significant and which of them determine and cause morphological variability of carabids. Probably, the direct and indirect influence of factors act most intensively at the larval stage, and are already determined at the adult stage. Change in the quantity and nature of food objects, and the diet itself takes place under the influence of environmental factors, which subsequently affects the rate of reproduction (van Dijk, 1996). The reproduction rate affects the number of eggs laid and their size. Females producing the largest number of eggs lay small eggs. Egg size in turn affects larval survival. It has been experimentally proved that large larvae from the first large eggs live longer than those from small ones (Wallin et al., 1992). The larval stage is probably the most significant in the case of the influence of environmental factors on the morphological variability of imagoes (Ernsting et al., 1992; Arndt & Putchkov, 1997). There is a large amount of research devoted to the influence of temperature and humidity, the size of food objects (van Dijk, 1996; Ernsting & Isaaks, 1997; Okuzaki & Sota, 2018) at the larval stage. The effect of temperature on body length has been proven on representatives of the genus *Hegeter* (Tenebrionidae, Coleoptera); body width is associated with the ability of a species to dig, it is affected by rainfall, vegetation, and the amount of organic matters in the soil (De Los Santos et al., 2000). Intraspecific variability is very often explained by the biogeography of the species (influence of altitude, climate) (Koutroumpa et al., 2013; Sukhodolskaya & Saveliev, 2016; Sukhodolskaya & Ananina, 2017). Very little research has been devoted to other, equally important, environmental factors that can cause morphological variability of beetles.

Andersen (1985) points to the close relationship between body shape and ecological characteristics of species of the tribe Bembidiini. He confirms that dorso-ventrally complanate species with parallel elytra are adapted to live under and between stones on the banks of water bodies, and species with oval shape of the back of the body hide among vegetation, in litter and cracks in the soil; species that occupy an intermediate position between these two forms are eurybionts, and their shape does not depend on the nature of the cover. There is practically no information on the features of the ontogenesis, the description of the egg, larva, pupae for representatives of the genus Bembidion, and there is also limited information on environmental factors that can affect morphological variability at different stages of development. Several attempts have been made to study this question, monitoring the reproduction, oviposition, and development of eggs, larvae, pupae of beetles of *Bembidion* in laboratory and natural conditions, but have not brought positive results in most cases (Mitchell, 1963; Jensen, 1990; Theis & Heimbach, 1994; Knapp & Saska, 2012).

Literature data on the morphometric characteristics of *B. minimum* are limited to information on the total body length. The data on the body length of this species, presented in different sources, are rather uniform and vary within 2.3–3.2 mm (Table 10). The body length of individuals varies from 2.24 to 2.92 mm and in our research averages 2.55 mm. Various authors indicate that *B. minimum* is a macropterous species (Lindroth, 1985; Hurka, 1996). All specimens collected by us also belong to the macropterous form (Matalin, 2003; Szentkiralyi et al., 2005).

Table 10
Sizes of *B. minimum* from various sources

Country	Size, mm	Source
Great Britain	2.3–3.2	Lindroth, 1974
Armenia	2.3–2.8	Iablokov-Khnzorian, 1976
Russia	2.3–3.0	Khotko, 1978
Fennoscandia, Denmark	2.3–3.2	Lindroth, 1985
Czech Republic, Slovakia	2.3–3.1 (2.8)	Hurka, 1996
Tatarstan	2.3–3.0	Zherebcov, 2000
Ukraine	2.24–2.92 (2.55)	This article

Significant morphometric parameters for beetles are the length and relative width of the body. We found that 35.5% of *B. minimum* variability is determined by the size of the body, and the second most important factor is the relative body width of the individual. As a result of the analysis of the obtained data, it was found that head length, value of back angles of prothorax, distance to the first and second setae, contrast of light spots and density of puncturing on the elytra vary greatly within the population and are independent of body length in females and males. All morphometric indices are also independent of the population. Diversity in elytra length is minimal. Differences in body size of ground beetles between populations are largely dependent on environmental conditions (Sukhodolskaya & Saveliev, 2017). It is interesting that a significant effect of ecosystem factors on the linear characteristics of *B. minimum* was found in this research unlike with the previously studied *B. articulatum* (Brygadyrenko & Slynko, 2015). The acidity and mineralization of soil are the most significant among the natural factors considered by us. They cause variability of almost all linear measurements of *B. minimum* individuals. Litter thickness and mechanical composition of the soil have a slight impact. The influence of anthropogenic factors (recreational load, cattle grazing) is pronounced on almost all linear parameters of imagoes.

Larger ground beetles with more massive elytra are found in areas with a more developed herb layer than in open areas (Jelaska et al., 2010; Tyler, 2010; Sukhodolskaya & Eremeeva, 2013); for riparian species of the Cicindelidae family the reverse applies (Dangalle et al., 2013). *Carabus ganulatus* Linnaeus, 1758 has a more complanate body in open areas (Sukhodolskaya & Saveliev, 2017). The type and composition of vegetation also significantly correlates with body size of ground beetles (Palmer, 1994). The effect of the herb layer on the body length of imagoes is not significant for the populations of *B. minimum* studied by us. The prothorax length, head width and prothorax width (Sp2, Spm) significantly change, although no general pattern was found for either males and females. Litter thickness is an important environmental factor that affects structure, abundance and status of the ground beetle complex (Kaizuka & Iwasa, 2015). Increase in litter thickness is accompanied by increase in the total number of macrofauna due to the presence of saprophages in the forests of the steppe zone, the number of species increases mainly due to zoophages (Brygadyrenko, 2016b). Unexpected for us is the fact that litter thickness does not affect the linear dimensions of the body of *B. minimum* but causes changes in parameters such as density of puncturing and contrast of light spots on the elytra. The back spots on the elytra become brighter and acquire clear contours with thickening of the litter in females and males.

The mechanical composition of soil can affect the community of terrestrial beetles, its taxonomic structure, abundance, and morphological variability. This factor significantly affects only the total length of the body and of head of *B. minimum*.

Salinization of soil is one of the most important factors that affect the distribution of characteristics of riparian beetles. Many of them prefer saline areas, since salinization usually negatively affects the herb layer in such manner that saline areas are usually open and well lit. Salinization also inhibits the growth and contagiousness of pathogenic fungi, which is positive for beetles (Dangella et al., 2013). The level of soil mineralization affects the laying of eggs by beetles (Spomer et al., 2015), and the duration of the developmental stages and phenotypic plasticity of insects (Clark et al., 2004). Soil mineralization significantly affects body length, head length, length and width of prothorax (Sp1, Sp2) and elytra width of *B. minimum*. The results obtained in this article indicate that females of *B. minimum* are more sensitive to increased salinization of soil. The size of females of *B. minimum* increases, the length of head, prothorax, the width of prothorax between back angles and of elytra increase. However the prothorax width of females between front angles is minimal compared to females of other populations when soil mineralization is above 5 g/L.

A rather interesting question is the effect of soil acidity on ground beetles. Field and laboratory research has confirmed the presence of specific pH preferences in various species of ground beetles (Paje & Mossakowski, 1984). The effect of soil acidity on the diversity of ground beetles has been proven (Sadej et al., 2012). The abundance of soil macrofauna, including ground beetles, decreases with increasing soil acidity (Kuperman, 1996). Decrease in pH causes decrease in the number of species of ground beetles that are resistant to humidity conditions (mesophile species), which are replaced by hygrophile taxa (Nietupski et al., 2010). Research on *Popillia japonica* Newman, 1838 (Coleoptera, Scarabaeidae) educed no differences in egg laying at pH 5.0–7.9 (Vittum & Mozuchi, 1990). We have not found information regarding changes in the size of insects under the influence of soil pH in analysis of the literature data. The research presented in this article revealed the significant effect of soil acidity on most linear measurements of *B. minimum* body for both females and males. The total body length at the extreme (studied by us) pH values is almost the same in males and does not significantly differ in females. At pH 8.0–8.2 females and males of *B. minimum* have minimum body length, maximum prothorax width, elytra length and width.

Ground beetles have ornamental and quite diverse morphological sculptures on the surface of their elytra. The origin and significance of these sculptures is unknown. Existing theories explain the appearance of such structures as a result of sexual selection or adaptation to the environment, but they almost never result from neutral evolution (Kleisner et al., 2012). However, the absence of the influence of environmental factors on the morphological variability of the sculptures has been proved for ground beetles of the *Carabus* genus, their sculpture is the result of neutral evolution (Kleisner et al., 2012). Schwerk & Jaskula (2018) educed the influence of environmental humidity during the larval stage on the number of pores on the elytra of *Pterostichus oblongopunctatus* (Fabricius, 1787) (Coleoptera, Carabidae). *B. minimum* lives in humid biotopes, therefore we considered other environmental factors that affect the variability of the number of setae per 1 mm^2 of elytra surface. The most interesting fact, which requires further research, is that the number of setae significantly changes under the influence of all the factors studied by us, except for the mechanical composition of soil. This parameter does not depend on the body size of *B. minimum* and is greater in males than in females.

No less interesting and significant body parameters are the contrast of the light spots on the elytra and the back angles of prothorax. From the natural factors, the density of herb layer, the litter thickness and the soil acidity significantly affect the contrast of light spots on the elytra. With an increase in litter thickness the back elytra spots of *B. minimum* become pronounced with clear boundaries. We suppose that brighter colour makes it possible to be camouflaged in variably coloured litter. The density of herb layer, mineralization and acidity of the soil significantly affect the value of the back angles of the prothorax.

Morphometric indices turned out to be less informative than linear parameters for assessing the habitat of *B. minimum*. Whatever the changes in linear dimensions, the proportions of the body basically remain unchanged. We obtained similar results for *B. articulatum* (Brygadyrenko & Slynko, 2015). Mineralization and acidity of the soil does not cause significant changes in any of six considered morphometric indexes of *B. minimum* imagoes. The density of the herb layer, in contrast, is associated with significant variability in half the morphometric indexes. The ratio of prothorax length to its maximum width is a constant for *B. minimum* and does not vary under the influence of the considered natural and anthropogenic factors.

Human activity leads to change in landscapes, affects biodiversity and structure of natural ecosystems. The area of disturbed territories is increasing every year (Sukhodolskaya, 2013). This causes change in soil and vegetation layer, and structure of animal populations. Habitat quality affects the size and weight of ground beetles (den Nijs et al., 1996). The impact of anthropogenic factors on the ground beetle complex can be successfully determined using morphometric methods (Benitez et al., 2018). It is recommended to use body size and other morphological features of beetles to assess impact of human activity on the environment.

The size of the body of some species of ground beetles decreases in urban habitats (Weller & Ganzhorn, 2004; Sukhodolskaya, 2013). Researchers have also identified the effects of heavy metal pollution: zinc, lead, cadmium on the morphometric features of ground beetles (Lagisz, 2008; Osman et al., 2015; Sowa & Skalski, 2019). Females from polluted zones are smaller than females from the control populations. No definite pattern of morphometric parameters was revealed for males of different species: in some the changes concerned only the prothorax, in others – only the elytra, in the third – both of them (Sowa & Skalski, 2019). Different morphometric parameters of individual species vary differently in the gradient of the same anthropogenic factor (Sukhodolskaya & Saveliev, 2014). Head width, elytra length and four morphometric indices significantly change in *B. aspericolle* under the influence of anthropogenic factors (Komlyk & Brygadyrenko, 2019). Changes in the linear dimensions of *B. minimum* body with an increase in recreational load and cattle grazing are similar to those found in our researches. Significant influence of the recreational load on all linear parameters of the body of individuals was observed for the total sample of *B. minimum* except for prothorax length and distance from the base of the elytra to the first setae, and two of the six indices. *B. minimum* is characterized by decrease in body length, length and width of the elytra, width of prothorax between back angles, maximum width of prothorax, ratio of elytra length to prothorax length for both females and males with increase in recreational load. Smaller body size may indicate a low adaptability of this species to recreational load.

The body size of different species of ground beetles decreases in the gradient of intensification of agricultural activity including cattle grazing (Burel et al., 2004). Cattle grazing and trampling is one of the priority factors in the destruction of shore ecosystems in the steppe zone of Ukraine. Almost all linear characteristics of *B. minimum* and three of the six indices of body proportions significantly change under the influence of cattle grazing. Body length, head width, length and width of prothorax, length and width of elytra decrease both in females and males in areas with high degree of cattle grazing.

Expected for us was the dependence of length and width of elytra, length and width of prothorax on body length of *B. minimum*. Deviation from the average values of these characteristics is greater in males than in females. The head length is not related to the total body size in females and males. The fact that the distances from the base of the elytra to the first setae, and the distance between setae of both females and males are independent of their body length is interesting and requires further research on other species of ground beetles. The first and second elytra setae are used to measure the distance between dorsal surface of the imago body and walls of the soil crack in which the beetle is located. The beetle remains in an excited state until all four setae on the elytra are bent to the elytra signaling to the central nervous system that the insect is safe. Probably these setae can also perceive sound vibrations of air. We expected that the distance from the base of elytra to setae would increase with body length of beetle, i.e. that isometric variability would be observed. This was not observed.

The most discernible sexual dimorphism is in evidence for beetles especially for ground beetles (Alibert et al., 2001; Kawano, 2006; Bravi & Benitez, 2013). Intraspecific sexual dimorphism is a stable value. Females are larger than males in most ground beetle species (Sota et al., 2000; Sukhodolskaya & Saveliev, 2017). Ground beetles can be divided into two groups: in some – females are more sensitive to environmental changes, in others – males. In our researches, *B. minimum* females are larger than males, as with *B. articulatum* and *B. aspericolle* (Brygadyrenko & Slynko, 2015; Komlyk & Brygadyrenko, 2019). Sexual dimorphism of *B. minimum* is in evidence in all linear parameters and most morphometric indices. Sexual dimorphism does not appear in value of back angles of the prothorax or in the ratio of maximum width of prothorax to its width between back angles. We can say that there are no differences between females and males in the form of the prothorax.

Conclusions

Despite the availability of research on morphological variability of ground beetles, the features of influence of environmental factors on each stage of ontogenesis are still not disclosed. It is not clear at what stages of development the influence of environmental factors is most significant and which factors mainly determine and cause morphological variability of ground beetles. The dependence shown in this article of variability of linear parameters and morphometric indices of *B. minimum* on natural and anthropogenic factors suggests the need for further research on this issue at the population level. The study of morphological variability will help to identify causes and mechanisms of ground beetle adaptation to existence in natural and anthropogenically transformed ecosystems.

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