Morphological variability among populations of *Harpalus rufipes* (Coleoptera, Carabidae): What is more important – the mean values or statistical peculiarities of distribution in the population?

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Abstract

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The paper analyzes the variability of 19 characteristics (14 linear measurements, 4 angular characteristics and density of elytra downiness), as well as 8 morphometric indices for 391 imagoes of *Harpalus rufipes* (De Geer, 1774) collected in 9 forest, field and steppe ecosystems under various degrees of anthropogenic pressure in four administrative districts of Dnipropetrovsk region, Ukraine. The presence of significant ($P < 0.001$) negative asymmetry in females and absence thereof ($P > 0.05$) in males is typical for body length, head length, elytra length, distance between eyes, head width, prothorax width between the front angle and the back angle, elytra width between humeral angles, and maximum elytra width. For all these characteristics, the excess in males is not significant ($P > 0.05$), while in females in most cases it is significantly positive ($P < 0.05$), which is evidence that there is a large number of females with a greater length of the body and greater width of the head, prothorax and elytra. The absence of significant asymmetry ($P > 0.05$) in males and females proves the absence of directional selection in the populations of *H. rufipes* on the density of elytra downiness and value of the prothorax back angle. A significant negative asymmetry was recorded both in males and females for the maximum width of prothorax ($P < 0.001$) and body height ($P < 0.05$), i.e. unidirectional increase in these characteristics takes place in specimens of both sexes. As distinct from the linear measurements, for all 8 considered proportions of the body in specimens of both sexes the excess is significantly positive ($P < 0.001$), suggesting higher constancy of bodily proportions in *H. rufipes* than of absolute size. For most of the linear characteristics, a significant ($P < 0.001$) sexual dimorphism is recorded. No marked differences between the 9 populations studied within the groups of specimens of the same sex are recorded. In the areas where the annual burning of crop residues and litter is observed, differences between males and females in length are two times higher than the differences between males and females for the ecosystems with no such burning. In the driest areas, maximum elytra width – prothorax width ratio is observed in females. The vertex angle of elytra significantly differs in the populations of the various administrative districts. The average density of elytra downiness in males is 13.3% lower than in females. The results of PCA (principal component analysis) have shown that most of the linear characteristics were connected with the sex of the beetle, while variations in the angular characteristics and degree of elytra downiness bore no relationship to the sex of the *H. rufipes* specimens. The results of our research suggest that the mean values of morphometric characteristics in environmental studies may have less diagnostic value than the type of their distribution in the population.

Key words

Carabidae, Coleoptera, *Harpalus rufipes,* morphometrics, population variability, sexual dimorphism

Introduction

Earlier studies of populations of beetles, primarily ground beetles, were focused on identification of the differences between related species (Pizzo et al., 2006, Talarico et al., 2011), presence of sexual dimorphism (Benítez et al., 2010, 2013a, 2013b), fluctuating asymmetry (Benítez, 2013; Bravi and Benítez, 2013; Daloso, 2014) or changes in the average size of the body under the influence of certain environmental factors or geographic location (Alibert et al., 2001; Bonacci et al., 2006; Okuzaki et al., 2010; Giglio et al., 2011; Sukhodolskaya, 2013). The range of fluctuations and patterns of distribution of morphometric characteristics have been examined in a few studies only (Blake et al., 1994; Sota et al., 2000; Okada et al., 2006; Slin'ko et al., 2008; Benítez et al., 2011; Sukhodolskaya and Eremeeva, 2013). Usage of the methods of multivariate statistics (for example, the geometrical morphometric approach), on the one hand, makes the assessment of changes within populations more clear. However, on the other hand, it does not allow the analysis of characteristics taken separately and comparison of one's own results with the data of other authors. In connection with this, taking one of the most dominant species of ground beetle as our example, we would like to show in this study the importance of not only the analysis of mean values of any characteristic and their joint variability, but to emphasize the importance of analyzing the patterns of distribution of characteristics in a population.

Normal distribution of a particular characteristic may indicate the absence of directional selection on the given parameter (Schluter, 2000). Presence of significant asymmetry is one of the indicators of directional selection on a particular parameter in a specific population (Rueffler et al., 2006). Significant values of excess indicate the intensification of stabilizing selection on the defined attribute. A particularly strong change in the statistical parameters of variation should take place in (1) so called twin species (phylogenetically close species occupying a similar geographic range), as well as in (2) species populating various habitat types (forest, meadow, steppe ecosystems), (3) taxa for which sharp changes in numbers are observed as a result of adaptation to the impact of anthropogenic factors (in various types of agrocenoses, urbanized ecosystems, areas close to industrial enterprises etc.) (Svanbäck et al., 2009).

In this context a convenient object of population studies is *Harpalus rufipes* (De Geer, 1774) (Coleoptera, Carabidae). This is an abundant species corresponding to all three characteristics given above:

- In most habitats it is found together with 3–7 species of the genus *Harpalus*, more often dominating among them in its numbers and having the maximum size among the entire group of ground beetles with mixed (vegetable and animal) diet (Niemelä, 1993; Zhang et al., 1997; Lang et al., 1999; Snyder and Wise, 1999; Thomas et al., 2001; Purvis and Fadl, 2002; Irmler, 2003; Monzo et al., 2011).
- In the steppe zone it is a habitat generalist which populates ecosystems of all moisture gradations (from swampy river banks to the driest positions of ridges which divide ravines) and degrees of soil salination (from salt flats and carbonate soils to humic chernozem soils and areas with insignificant acidification of individual soil horizons), various types of phytocenoses (from dry steppe areas with poorly developed herbaceous vegetation to indigenous floodplain and sandy terrace forests with closed canopy of leaves and shrubs), and inhabiting litter horizons at all degrees of development (from its total absence on arable land to a heavy layer of pine needles or leaf litter in broadleaf forests) (Parmenter and Macmahon, 1988; Frampton et al., 1995; Hawthorne et al., 1998; Magura et al., 2001; Brygadyrenko, 2003; Reshetniak and Brygadyrenko, 2013).
- Particularly high populations are reached in natural communities disturbed by man (on fields of nonperennial and perennial agricultural crops, near major traffic arteries, in industrial zones and human settlements) (Davies, 1953; Dunn, 1981; Kutasi et al., 2004).

H. rufipes is capable of undertaking significant flightless and flight migrations, while forming considerable clusters of individuals in the areas with optimal hydro-thermal conditions, and concentrations of food (vegetable and animal) items. Seeds of plants represent a favorite component of the diet of this ground beetle species, which actually causes considerable damage to agricultural crops (Hartke et al., 1998; Gaines and Gratton, 2010; Meiss et al., 2010; Saska et al., 2010; Bohan et al., 2011; Baraibar et al., 2012). Invertebrates are supplements to the diet of *H. rufipes*, and the list of species it consumes in the steppe zone of Ukraine amounts to several dozen (Reshetniak and Brygadyrenko, 2013). Populations of *H. rufipes* are convenient for assessment of morphological variability in various types of ecosystems and under the influence of different anthropogenic factors, but this subject has remained unexplored so far.

Before beginning our research we raised the following hypotheses: (1) the distribution of morphometric parameters in the studied ecosystems would be normal, (2) as anthropogenic transformation of an ecosystem increases significant changes in mean values should occur, with growing asymmetry and excess of morphometric characteristics and indices, and (3) in the conditions of anthropogenically transformed ecosystems differences between *H. rufipes* males and females will become greater.

Material and methods

We studied 9 populations of *H. rufipes*, located in Novomoskovsk (ecosystems 1–6), Pavlograd (7), Dnipropetrovsk (8) and Petrikovka (9) districts of Dnipropetrovsk region, Ukraine (Table 1). The ecosystems from which the ground beetle imagoes were collected have differing degrees of humidity (xerophilous – 5 and 6, mesoxerophilous – 1 and 8, xeromesophilous – 3 and 4, mesophilous – 2 and 7, mesohygrophilous – 9), types of plant community (agrocenoses – 1, 2 and 8, natural forest – 3 and 9, planted forest – 4 and 7 and steppe ecosystems – 5 and 6), types and degrees of anthropogenic transformation (none – 3 and 9, low – 5 and 7, medium – 4 and 6, high – 1, 2 and 8).

Specimens of *H. rufipes* were collected by soil traps; beetles were killed by freezing at –15 ºC during 24 hours in a cooling chamber and laid onto cotton mats, having been previously stretched out (to maintain proportions, orientation of the head and prothorax was tracked). Photographs of the dried insects were taken through binocular stereoscopic microscope MBS-10 with the use of digital camera with the resolution of 5 megapixels in two (top and side) projections. Each beetle was assigned a serial number including the ecosystem number and sex of the specimen (female, male). Measurements were made by digital photographs in the software package TpsDig 2.17 (2013, Rohlf F.J., Ecology & Evolution, SONY at Stony Brook). 14 linear, 8 angular characteristics and pore density on the elytra were measured.

The following linear characteristics were measured: length of head (Lc), prothorax (Lp), elytra (Le), clypeus (Lcl), distance between eyes (Sa1), length of

Table 1. Brief characteristics of the ecosystems (Dnipropetrovsk region, Ukraine) where *H. rufipes* was collected

Ecosystem	District	Coordinates	Type of moisture	Type of ecosystem	Degree of anthropogenic impact
1	Novomoskovsk	48.790374 N, 35.455946 E	Mesoxerophilous	Lucerne field	High: cutting of vegetation, application of fertilizers
2	Novomoskovsk	48.774368 N, 35.419725 E	Mesophilous	Clover field	High: cutting of vegetation, application of fertilizers
3	Novomoskovsk	48.789978 N, 35.449251 E	Xeromesophilous	Ravine soil cover without grass, elm-ash forest	None
4	Novomoskovsk	48.760904 N, 35.462040 E	Xeromesophilous	Acacia forest belt with catchweed and cow parsley on the upland soil	Medium: burning of leaf litter, contamination with domestic waste
5	Novomoskovsk	48.760452 N, 35.452169 E	Xerophilous	Area of zonal steppe vegetation	Low
6	Novomoskovsk	48.779289 N, 35.468220 E	Xerophilous	Area of zonal steppe vegetation	Medium: excessive grazing of cattle, burning of crop residues
7	Pavlograd	48.602401 N, 35.623144 E	Mesophilous	Soil cover without grass, elm-ash-oak plantation with traces of excessive salination of soil	Low: cattle grazing, soil salination
8	Dnipropetrovsk	48.383352 N, 35.068592 E	Mesoxerophilous	Corn field	High: soil replowing, cultivation of row crops, application of fertilizers
9	Petrikovka	48.495128 N, 34.797109 E	Mesohygrophilous	Bottomland maple-ash forest with nettle	None

eyes (La), width of head with eyes (Sa2), prothorax width between the front angles (Sp1) and back angles (Sp3), maximum width of prothorax (Sp2), width of elytra near humeral angles (Se1), maximum width of elytra (Se2), body height at the level of metathorax (Hb). Total body length (Lb) was determined by combining the length of the head, prothorax and elytra (from the forward edge of upper lip to the top of elytra). Linear characteristics were evaluated by photographs with an accuracy of 1 pixel equal to 0.0024 mm for linear measurements up to 2 mm and 0.0048 mm – for linear measurements over 2 mm.

In order to eliminate the influence of the position of each beetle when the photographs were taken, angular values were measured for the right and left parts of the body, for the further calculations their arithmetical mean value was used. The left (A1) and right angle of prothorax (A2), left (B1) and right back angle of prothorax (B2), left (C1) and right humeral angle of elytra (C2), left (D1) and right vertex angle of elytra (D2) were measured. Measurement of angles was made using photographs with an accuracy of 0.1º.

Elytra pore density (P) was assessed from photographs, by counting the quantity of hairs on an area of 0.15 mm^2 between the backward edge of the scutellar groove and the first groove of the elytra. For each beetle hairs were counted on the right and left elytra; for further processing the arithmetical mean values of the above were taken.

Indices (body proportions) were calculated taking into account methods we have used earlier (Sharova, 1981; Faly and Brygadyrenko, 2007; Brygadyrenko and Fedorchenko, 2008; Korolev and Brygadyrenko, 2014). 8 indices were calculated, namely: ratio of body length to its height (Lb/Hb), ratio of arithmetical mean value of the width of head, prothorax and elytra to body length ((Sc + Sp +Se)/3Lb), ratio of prothorax length to its maximum width (Lp/Sp2), ratio of elytra length to prothorax length (Le/Lp), ratio of maximum elytra width to maximum prothorax width (Se2/Sp2), ratio of maximum prothorax width to its width at the backward edge (Sp2/Sp3), ratio of maximum elytra width to the distance between their front angles (Se2/Se1), and elytra length to width ratio (Le/Se).

The results were processed by standard methods of variation statistics (with the calculation of: x – mean value, SD – standard deviation, Min–Max – minimum and maximum values, D – variation range of characteristics, As – asymmetry, Ex – excess) using Statistica software (version 8, StatSoft, USA). Significance of variations between samples was assessed using one-way anova, for multiple comparisons of samples we used the Tukey test (StatGraphics Plus v5.1 package). Data in the text, in tables and on diagrams (Fig. 7 and 8) are represented as the mean value ± standard deviation.

Results

General variability of distribution of characteristics in males and females

Presence of significant (P < 0.001) negative asymmetry in females and its absence (P > 0.05) in males is typical for body length (Lb, As_{male} = –0.13, As_{female} = –0.88, Fig. 1), head length (Lc, As_{male} = –0.16, As_{female} = –0.79, Fig. 1), elytra length (Le, As_{male} = –0.27, As_{female} = –1.30, Fig. 1), distance between eyes (Sa1, As_{male} = 0.23, As_{female} = –0.62), head width (Sa2, As_{male} = –0.25, As_{female} = –1.02, Fig. 2), prothorax width between the front angles (Sp1, As_{male} = 0.15, As_{female} = –0.67, Fig. 2) and back angles (Sp3, As_{male} = –0.06, As_{female} = –0.80, Fig. 2), width of elytra between the front angles (Se1, As_{male} = –0.17, As_{female} = –0.89, Fig. 3), maximum width of elytra (Se2, As_{male} = 0.05, As_{female} = – 0.74, Fig. 3). For all these characteristics the excess in males is not significant (P > 0.05), while in females in most cases (except Sp1 and Sa1) it is significantly positive (P < 0.05 and P < 0.001). It indicates the presence of selection in females: specimens with greater body length, width of head, prothorax and elytra are more widespread in the population.

Significant (P < 0.001) asymmetry in males and insignificant asymmetry (P > 0.05) in females was recorded for prothorax length (Lp, As_{male} = –0.57, As_{female} = –0.23, Fig. 1). It indicates the higher rate of increase in prothorax length in males compared with females.

The symmetry of distribution of characteristics (absence of significant asymmetry) for males and females is evidence of absence of directional selection in the studied populations of *H. rufipes*. Absence of asymmetry (P > 0.05) was revealed for pore density of the elytra (P, As_{male} = 0.16, As_{female} = 0.01, Fig. 3) and value of the prothorax back angle (B, As_{male} = –0.05, As_{female} = 0.14, Fig. 4). These attributes can be considered among of the most stable for *H. rufipes*.

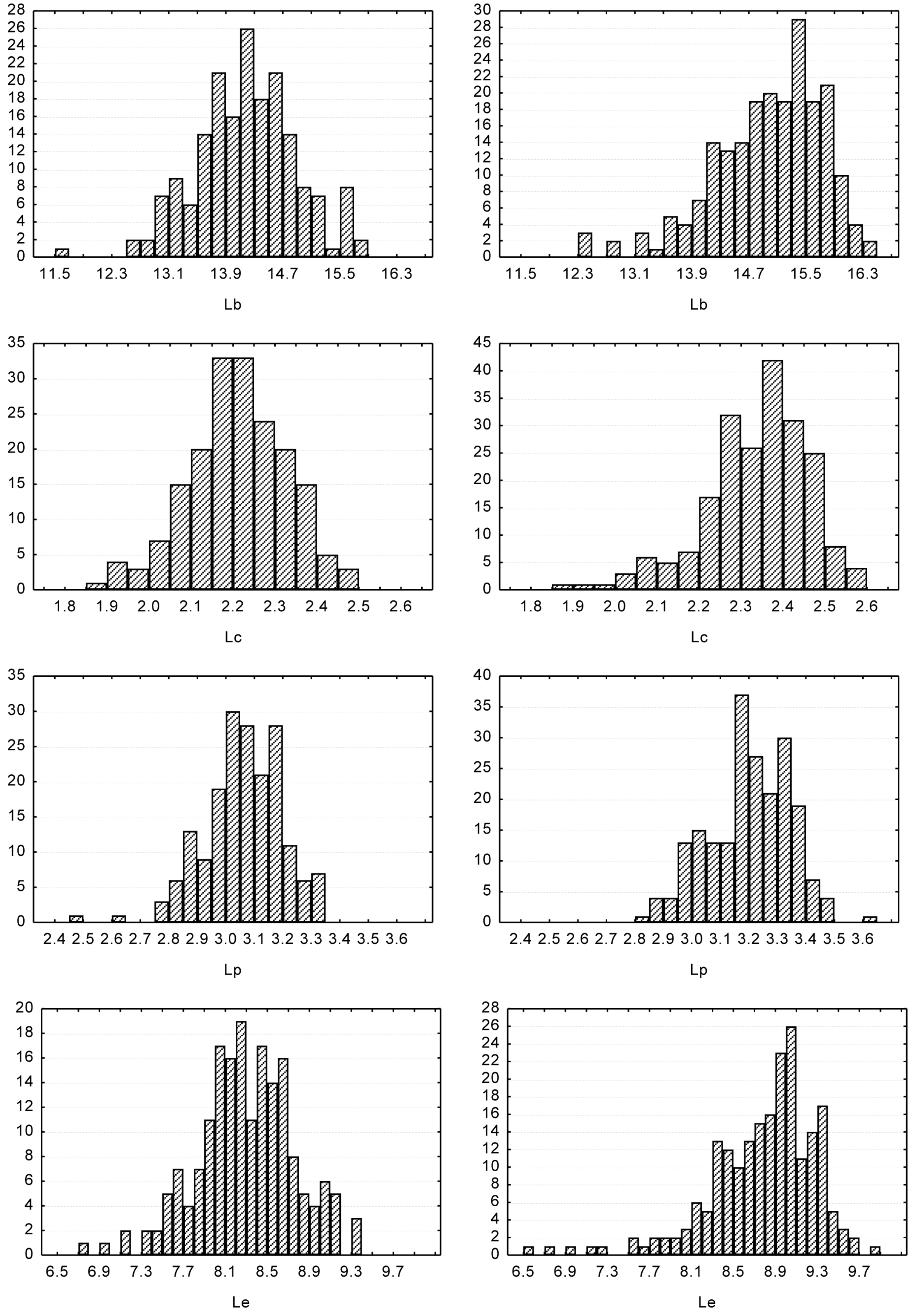

Fig. 1. Variability of length of the body (Lb), head (Lc), prothorax (Lp) and elytra (Le) in *H. rufipes*: on the left – males (n = 183), on the right – females (n = 209); on X-axis – value of characteristics in millimeters, on Y-axis – number of specimens.

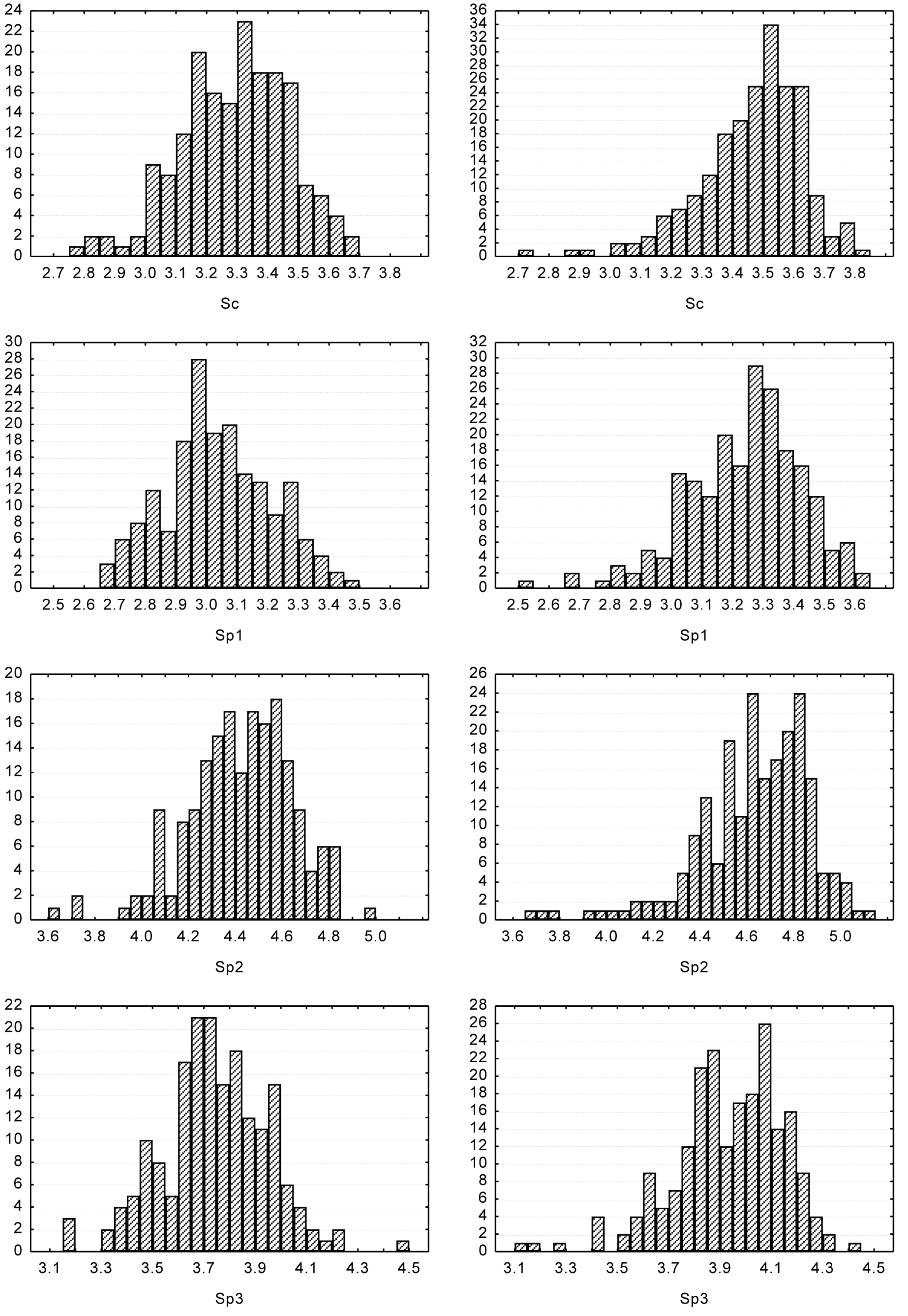

Fig. 2. Variability of head width (Sc), maximum prothorax width (Sp2), prothorax width at the forward edge (Sp1) and backward edge (Sp3) in *H. rufipes*: on the left – males (n = 183), on the right – females (n = 209); on X-axis – values of characteristics in millimeters, on Y-axis – number of specimens.

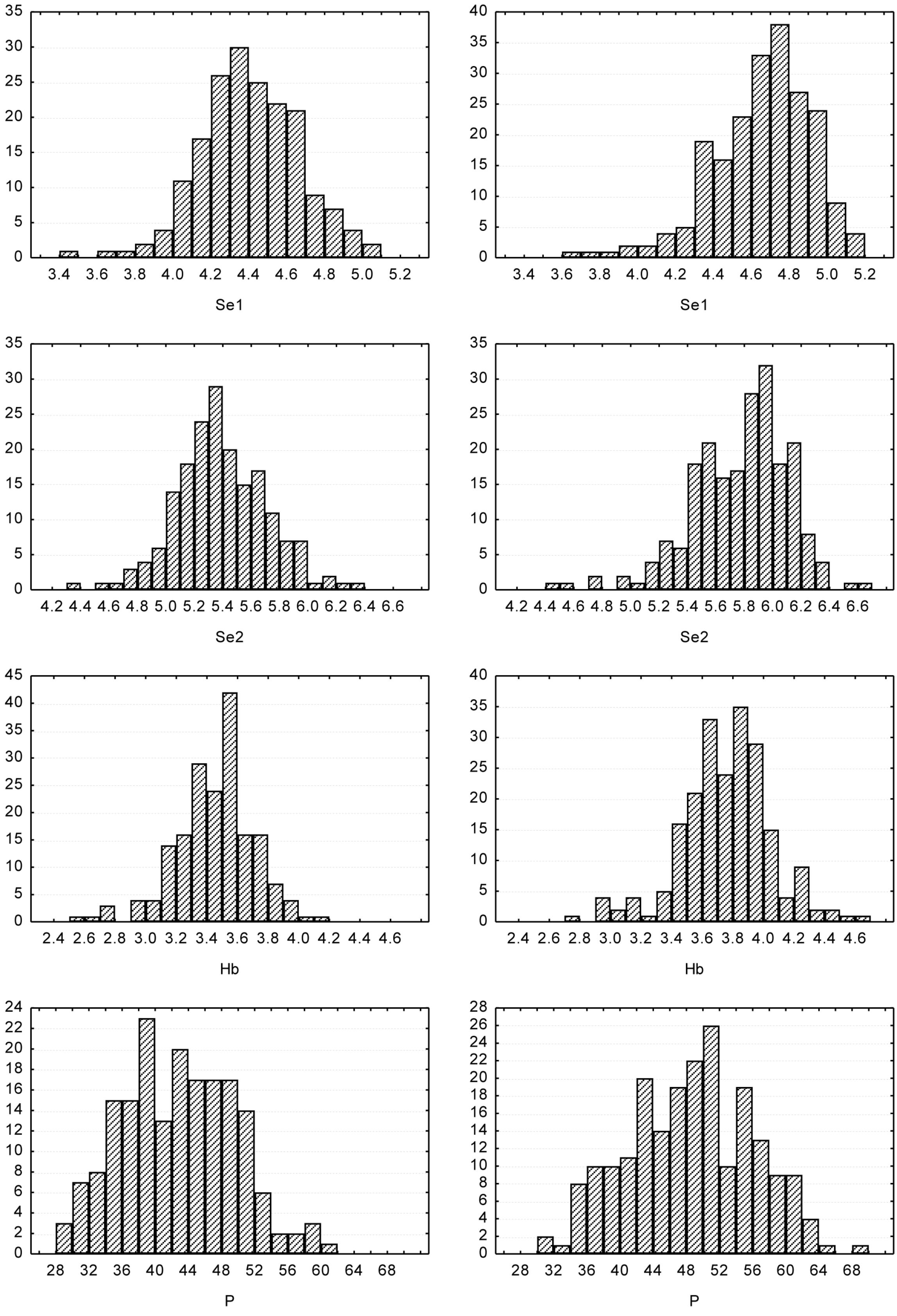

Fig. 3. Variability of distance between humeral angles (Se1, mm), maximum elytra width (Se2, mm), body height (Hb, mm) and quantity of pores on elytron area (P, pc./0.15 mm^2) in *H. rufipes*: on the left – males (n = 183), on the right – females (n = 209); on X-axis – for Se1, Se2 and Hb values of characteristics in millimeters, for P – quantity of pores on elytra (pc./0.15 mm^2), on Y-axis – number of specimens.

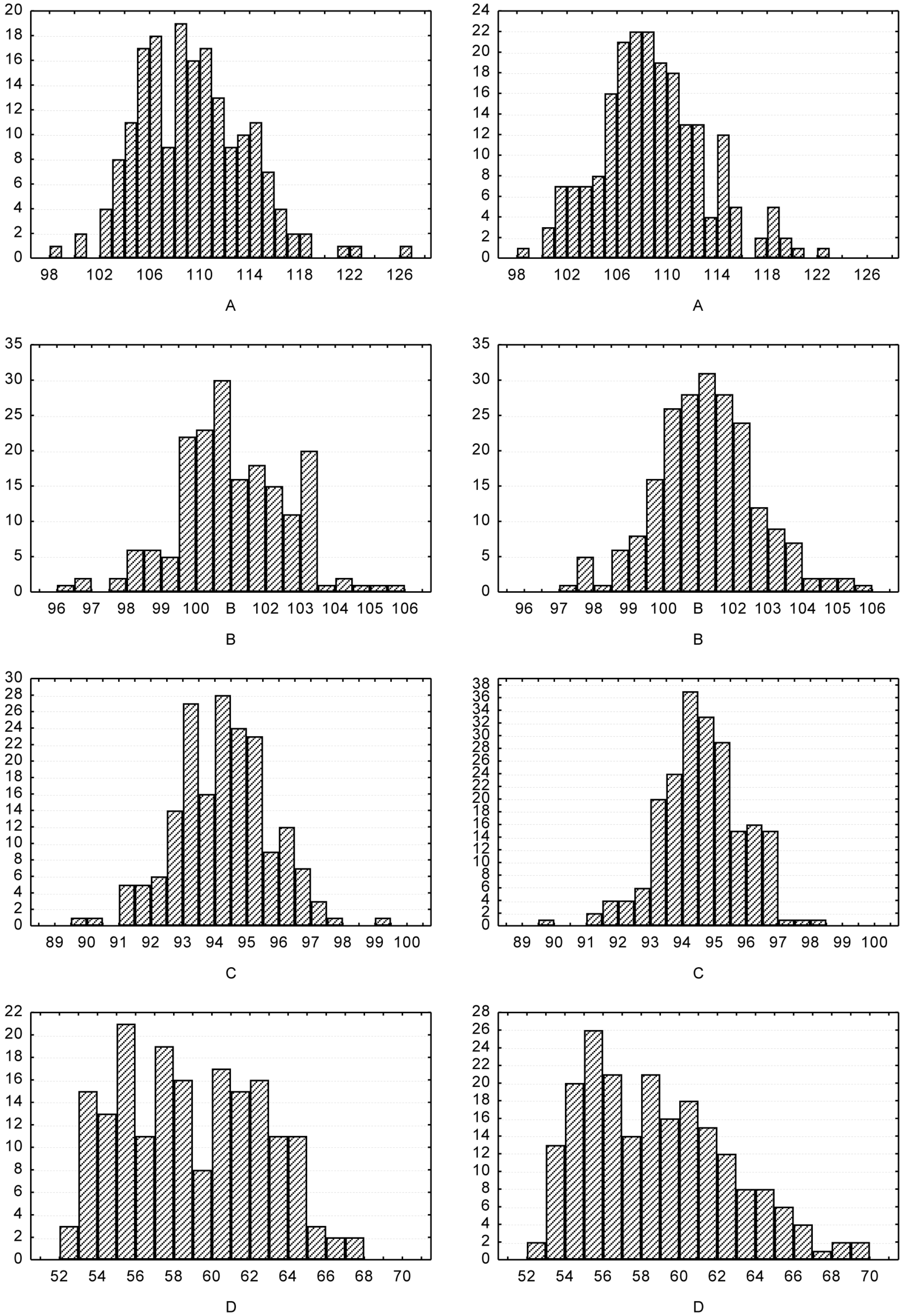

Fig. 4. Variability of front (A) and back (B) angles of prothorax, humeral angles (C) and vertex angles of elytra (D) of H. rufipes: on the left – males (n = 183), on the right – females (n = 209); on X-axis – value of angle in degrees, on Y-axis – number of specimens.

Significant negative asymmetry was also recorded in males and females for the maximum prothorax width (Sp2, As_{male} = –0.56, P < 0.001; As_{female} = –1.11, P < 0.001, Fig. 2) and body height (Hb, As_{male} = –0.49, P < 0.01; As_{female} = –0.28, P < 0.05, Fig. 3), i.e. unidirectional variation (increase) of the given characteristics occurs in males and females.

General variability of distribution of body proportions in males and females

In contrast to linear measurements, the index (ratio of two linear measurements) is a non-dimensional number which describes the change in body proportions. Both absolute value of the index and variability of its values in the studied populations are important. For all 8 body proportions considered (Fig. 5 and 6) the excess values are significantly positive (more often $P < 10^{-10}–10^{-14}$, and always P < 0.001) in both males and in females. It suggests considerably higher constancy of bodily proportions in *H. rufipes* than of absolute size.

Absence of asymmetry in males and females was revealed for the ratio of maximum elytra width to their width between humeral angles (Se2/Se1, As_{male} = –0.06, P > 0.05; As_{female} = –0.13, P > 0.05, Fig. 6), i.e. side faces of elytra do not become more parallel or more rounded.

Positive asymmetry (P < 0.001) is recorded for the ratio of body length to its height (Lb/Hb, As_{male} = 1.61, As_{female} = 0.85, Fig. 5) both in males and in females, i.e. specimens with more convex body prevail in the populations.

With regard to the ratio of body width to its length ((Sc+Sp+Se)/3Lb), no asymmetry in males is found (As_{male} = 0.01, P > 0.05), while it is significantly positive in females (As_{female} = 1.92, P < 0.001, Fig. 5), which indicates the relative decrease in female body width.

For the ratio of prothorax length to its width asymmetry is significantly positive both in males and in females (Lp/Sp2, As_{male} = 2.87, P < 0.001; As_{female} = 2.80, P < 0.001, Fig. 5), i.e. a significant shortening of the prothorax is observed.

Concerning the ratio of elytra length to prothorax length, a significant negative asymmetry (Le/Lp, As_{male} = –1.47, P < 0.001; As_{female} = –2.30, P < 0.001, Fig. 5) is recorded, which proves the presence of selection towards the increase in the relative elytra length.

Maximum width of elytra and prothorax in males and in females varies in different ways. For males, positive asymmetry of their ratio is revealed, while it is negative in females (Se2/Sp2, As_{male} = 0.96, P < 0.001; As_{female} = –0.38, P < 0.05, Fig. 6), i.e. with regard to maximum prothorax width the males' elytra become gradually narrower, while in females, on the contrary, wider.

As to the ratio of maximum width of prothorax to the width between its back angles, no asymmetry is present, whereas it is negative in females (Sp2/Sp3, As_{male} = 0.14, P > 0.05; As_{female} = –0.59, P < 0.001, Fig. 6), i.e. prothorax in females gradually assumes a more distinct heart shape, and in males its shape remains unchanged.

The ratio of the length of elytra to their width features a negative asymmetry both in males and in females (Le/Se, As_{male} = –0.75, P < 0.001; As_{female} = –0.31, P < 0.001, Fig. 6), i.e. elytra become longer in relation to their width.

Values of measured characteristics on the different sampling plots

Significant sexual dimorphism is recorded for *H. rufipes* body length in all the populations studied (Table 2). Average body length of females is 5.6% greater than in males; in population 6 (steppe area) – by 1.27 mm, in population 4 (acacia forest belt) – by 1.18 mm. Annual burning of crop residues (in spring and during the period of summer drought) takes place on both plots (Moroz et al., 2011). Minimal differences in average body length are recorded for populations 9 (maple-ash forest) and 5 (steppe area) – 0.50 and 0.56 mm, respectively. These sampling plots are characterized by minimal anthropogenic impact; the litter horizon is maintained here intact throughout the season.

Distribution of males for all 9 studied populations by body length does not differ from the norm (Table 2). Distribution of females by body length in four (sampling plot 2 – clover field, 6 – steppe area, 8 – corn field and 9 – maple-ash forest) of nine populations deviates from the normal distribution. In all four cases a significant negative asymmetry is manifested, i.e. the population has a larger number of specimens with considerable excess over the average body size.

Differences between body length of males on the examined sampling plots (Fig. 7) are significant as well (Table 2). The size of the males is minimal in sampling plots 3 (elm-ash forest), 6 (steppe area) and 4 (acacia forest belt), and maximal in sampling plots 5 (steppe area), 1 (lucerne field) and 8 (corn field). Minimal body length of females (Fig. 7, Table 2) is observed in sampling plots 3 (elm-ash forest) and 9 (maple-ash forest); differences in body length between females of the other sampling plots are not significant.

As a whole, for the combined 9 samples of males and females (Fig. 1) differences in distribution by body length are typical: it is normal in males, while in females a significant positive excess and negative asymmetry of this characteristic are expressed.

A significant ($P = 1.9 \cdot 10^{-21}$, F = 101.90, $F_{0.05(1, 390)}$ = 3.87) sexual dimorphism (by 5.6%) between males (2.213 ± 0.119 mm) and females (2.337 ± 0.125 mm) is recorded for the head length (Lc). No significant variations between the populations within the group of specimens of the same sex are recorded.

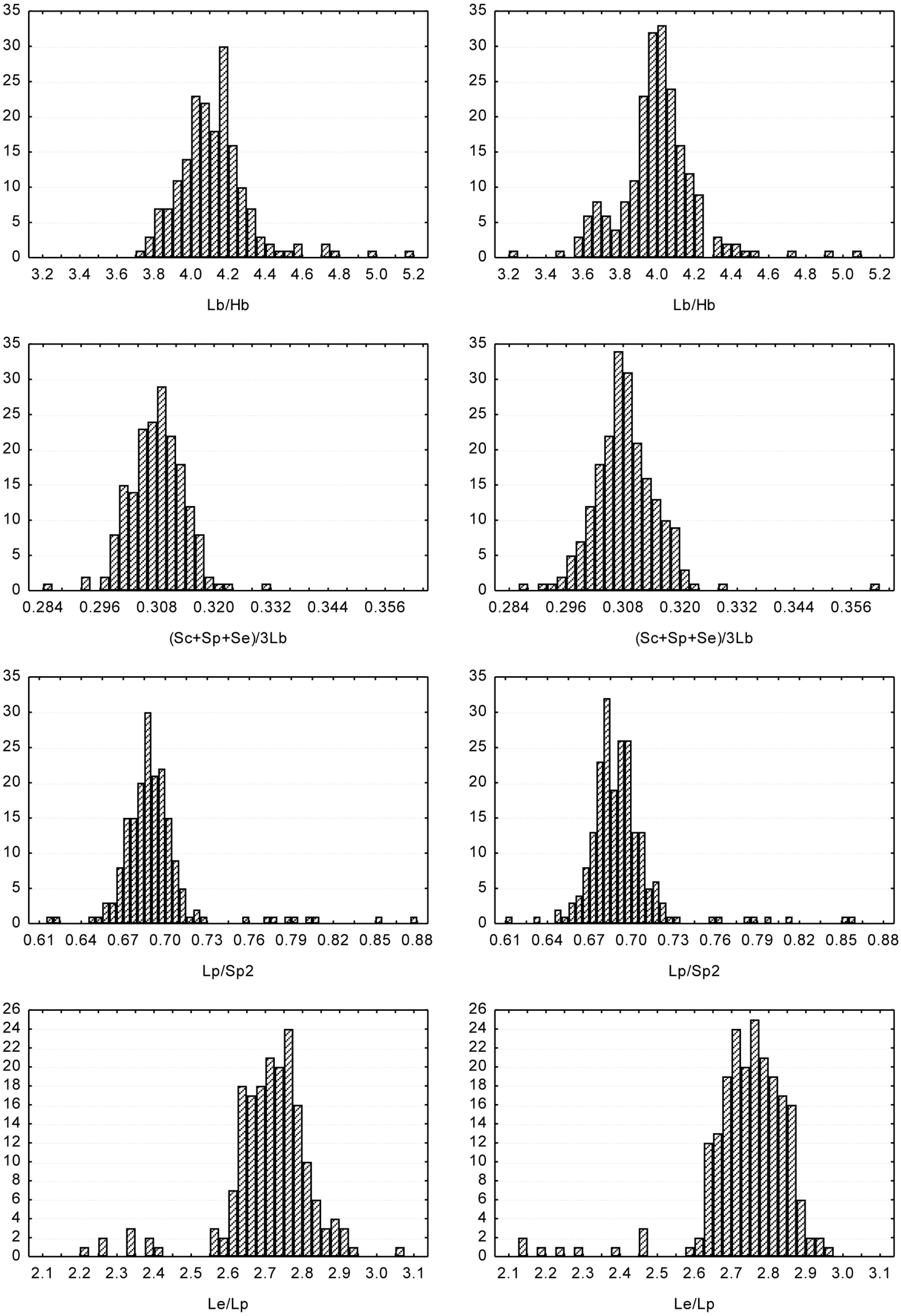

Fig. 5. Variability of morphometric indices of *H. rufipes*: Lb/Hb – ratio of body length to body height, (Sc + Sp + Se)/3Lb – ratio of arithmetical mean value of width of the head, prothorax and elytra to body length, Lp/Sp2 – ratio of prothorax length to maximum prothorax width, Le/Lp – ratio of elytra length to prothorax length; on the left – males (n = 183), on the right – females (n = 209); on X-axis – index value, on Y-axis – number of specimens.

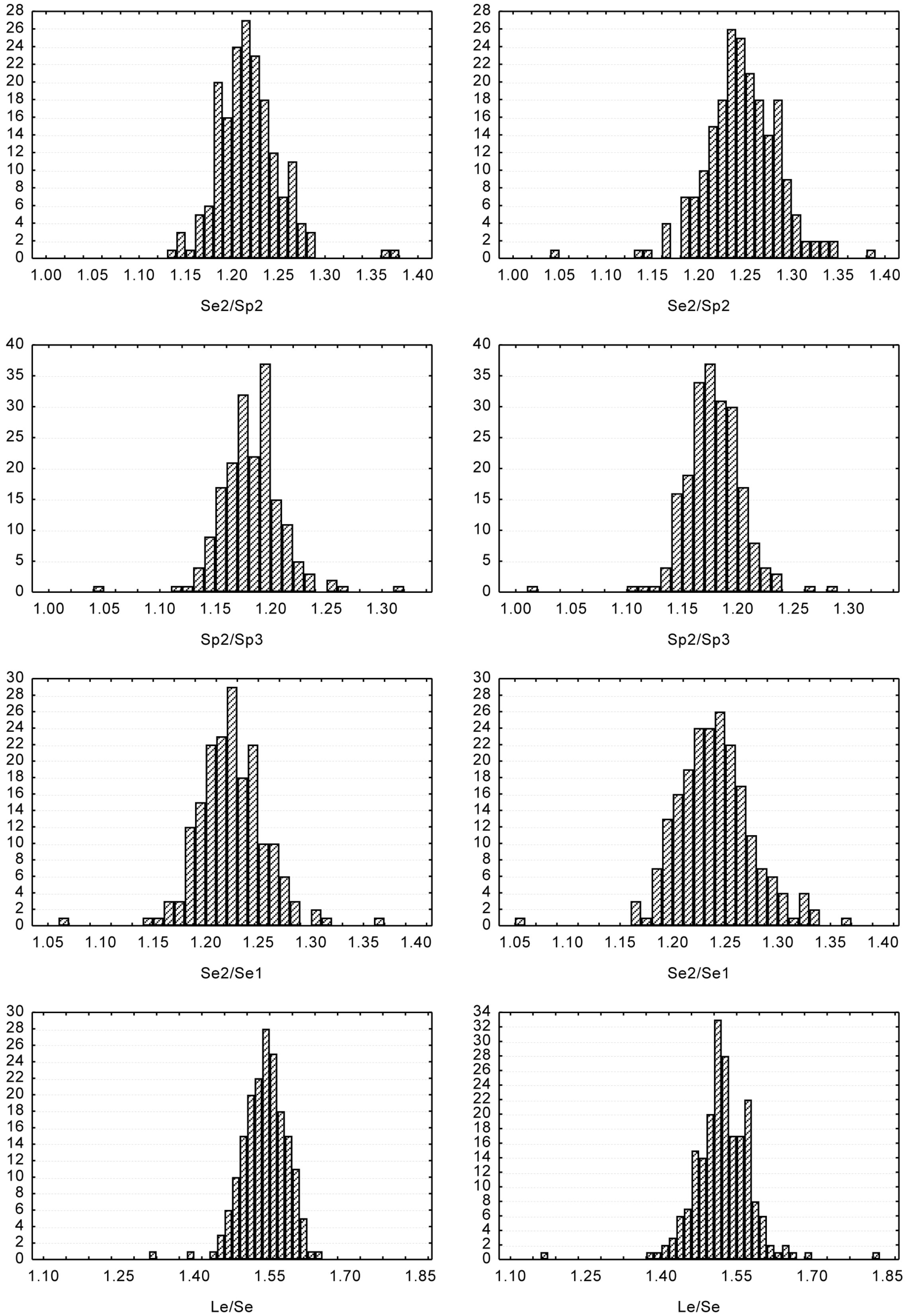

Fig. 6. Variability of morphometric indices of *H. rufipes*: Se2/Sp2 – ratio of maximum elytra width to maximum prothorax width, Sp2/Sp3 – ratio of maximum prothorax width to its width at the backward edge, Se2/Se1 – ratio of maximum elytra width to the distance between their front angles, Le/Se – ratio of elytra length to their width; on the left – males (n = 183), on the right – females (n = 209); on X-axis – index value, on Y-axis – number of specimens.

Table 2. Variability of body length (Lb) in the studied populations of *H. rufipes* (*n* = 392)

Ecosystem	Sex	n	x ± SD [mm]	Min–Max [mm]	D [mm]	Ex ± SD	As ± SD	F	$F_{0.05}$ (df1, df2)	P
1	m	18	14.54 ± 0.63	13.48–15.59	2.12	–0.84 ± 1.02	0.30 ± 0.53	8.42	4.09 (1, 39)	0.006
	f	23	15.11 ± 0.61	13.52–16.01	2.49	0.86 ± 0.93	–0.87 ± 0.48			
2	m	29	14.13 ± 0.67	12.88–15.62	2.73	–0.28 ± 0.84	0.21 ± 0.43	18.97	4.04 (1, 48)	$7.1*10^{-5}$
	f	21	15.10 ± 0.91	12.38–16.12	3.74	2.64 ± 0.96*	–1.46 ± 0.50**			
3	m	17	13.85 ± 0.88	11.64–15.19	3.55	1.21 ± 1.04	–0.76 ± 0.55	6.02	4.16 (1, 31)	0.020
	f	16	14.54 ± 0.73	13.13–15.90	2.77	–0.49 ± 1.07	0.05 ± 0.56			
4	m	29	13.97 ± 0.54	12.53–14.88	2.35	0.67 ± 0.84	–0.73 ± 0.43	38.42	4.03 (1, 51)	$1.0*10^{-7}$
	f	24	15.15 ± 0.84	12.89–16.38	3.49	1.70 ± 0.91	–1.12 ± 0.47			
5	m	19	14.60 ± 0.58	13.60–15.81	2.21	0.11 ± 1.00	0.07 ± 0.52	8.66	4.07 (1, 43)	0.005
	f	26	15.17 ± 0.67	13.53–16.31	2.78	0.07 ± 0.88	–0.54 ± 0.45			
6	m	7	13.94 ± 0.42	13.36–14.54	1.19	–1.11 ± 1.41	0.25 ± 0.77	39.42	4.54 (1, 15)	$1.5*10^{-5}$
	f	10	15.21 ± 0.40	14.24–15.65	1.40	3.72 ± 1.26*	–1.67 ± 0.68*			
7	m	16	14.09 ± 0.75	12.66–15.76	3.10	0.70 ± 1.07	0.35 ± 0.56	10.85	4.13 (1, 34)	0.002
	f	20	14.99 ± 0.85	13.20–16.26	3.05	–0.15 ± 0.98	–0.66 ± 0.51			
8	m	16	14.49 ± 0.70	13.48–15.66	2.18	–0.76 ± 1.07	0.52 ± 0.56	12.88	4.11 (1, 37)	0.001
	f	23	15.25 ± 0.62	13.70–16.21	2.52	0.80 ± 0.93	–1.00 ± 0.48*			
9	m	32	14.15 ± 0.72	12.86–15.56	2.70	–0.85 ± 0.81	–0.22 ± 0.41	7.98	3.97 (1, 76)	0.006
	f	46	14.65 ± 0.80	12.43–15.88	3.45	1.22 ± 0.69	–0.91 ± 0.35*			
Total	m	183	14.19 ± 0.70	11.64–15.08	4.17	0.37 ± 0.36	–0.14 ± 0.18	110.78	3.86 (1, 390)	$5.7*10^{-23}$
	f	209	14.98 ± 0.77	12.37–16.38	4.00	0.87 ± 0.33**	0.88 ± 0.17***			
Differences between males								3.07	1.99 (8, 174)	0.003
Differences between females								2.80	1.98 (8, 200)	0.006

Numbers of ecosystems and their brief characteristic see in Table 1; sex m – male, f – female; Min–Max – minimum and maximum value of the characteristic; D – variation range equal to Max–Min; As – asymmetry; Ex – excess; *, ** and *** – significance of asymmetry and excess $P < 0.05$, 0.01 and 0.001, respectively.

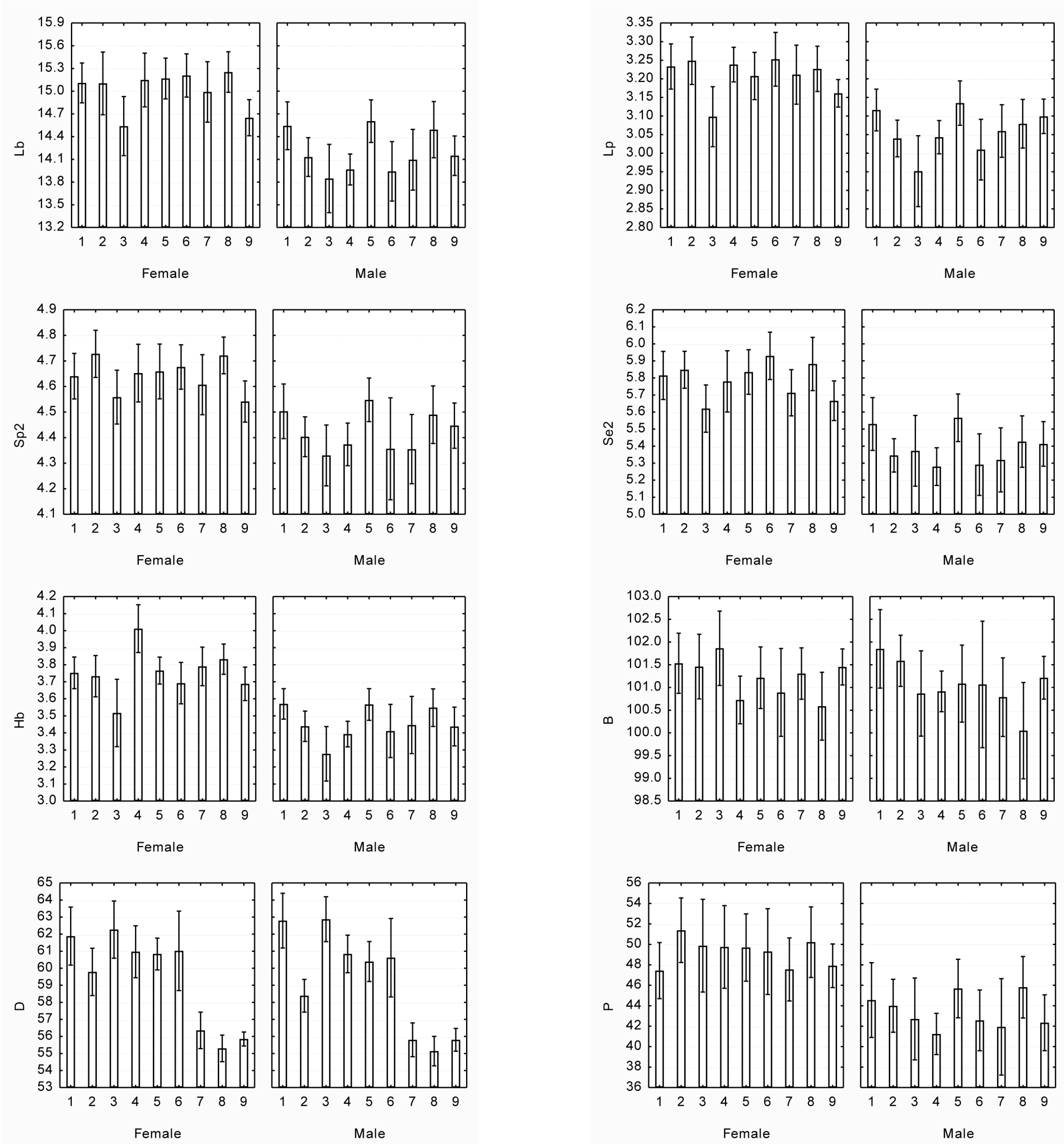

Fig. 7. Mean value and standard deviation of the main morphometric characteristics in *H. rufipes*: Lb – body length (mm), Lp – prothorax length (mm), Se2 – maximum elytra width (mm), Hb – body height (mm), B – prothorax back angle (degrees), D – vertex angle of elytra (degrees) and P – quantity of pores on the elytron area (pc./0.15 mm^2); on the right – males (n = 183), on the left – females (n = 209); on X-axis from 1 to 9 population numbers are indicated (see Table 1), on Y-axis the index value is indicated.

With regard to length (Lp, Fig. 7), sexual dimorphism is also significant ($P = 9.5 \cdot 10^{-21}$, $F = 97.94$, $F_{0.05(1,\ 390)} = 3.87$). Length of prothorax in females is 4.5% greater than in males (3.204 ± 0.143 and 3.064 ± 0.137 mm, accordingly). The shortest prothorax in females and males is recorded for sampling plot 3 (elm-ash forest). Fluctuations of the prothorax length in males are larger than those in females.

Length of elytra in males (8.30 ± 0.47 mm) is also significantly ($P = 9.6 \cdot 10^{-20}$, $F = 92.25$, $F_{0.05(1,\ 390)} = 3.87$) less (by 5.8%) than the length of elytra in females (8.78 ± 0.52 mm). Minimum distance between the inner margin of eyes in males (2.383 ± 0.135 mm) and females (2.527 ± 0.133 mm) significantly ($P = 2.2•10^{–23}$, F = 113.20, $F_{0.05(1, 390)}$ = 3.87) differs by 6.0% as well.

Maximum width of prothorax (Sp, Fig. 7) in females (4.63 ± 0.24 mm) is greater by 4.7% ($P = 7.5•10^{–17}$, F = 76.24, $F_{0.05(1, 390)}$ = 3.87) than in males (4.43 ± 0.23 mm). Minimum length and width of prothorax is typical for males and females of population 3 (elm-ash forest); variations within sex groups between the populations are not significant.

Distance between the humeral angles (Se1) in females (4.66 ± 0.26 mm) is significantly (by 5.7%, $P = 1.3•10^{–19}$, F = 91.46, $F_{0.05(1, 390)}$ = 3.87) greater than in males (4.41 ± 0.26 mm). No significant inter-population differences are recorded.

Maximum width of elytra (Se2, Fig. 7) differs significantly (by 7.0%, $P = 2.1•10^{–25}$, F = 125.24, $F_{0.05(1, 390)}$ = 3.87) between males (5.39 ± 0.32 mm) and females (5.77 ± 0.35 mm). The most pronounced sexual dimorphism on this character is for the populations 6, 4, 2 and 7 (in males of these populations the narrowest elytra are recorded). No significant inter-population differences in the elytra width of females are recorded.

Body height (Hb, Fig. 7) also significantly differs (by 8.9%, $P = 2.0•10^{–24}$, F = 119.23, $F_{0.05(1, 390)}$ = 3.87) between males (3.45 ± 0.26 mm) and females (3.76 ± 0.30 mm). Maximum body height is observed in females of population 4 (acacia forest belt), while minimum body height is recorded in females of population 3 (elm-ash forest).

There are no significant differences recorded on the value of the front (A) and back angle of prothorax (B, Fig. 7) between males and females (mean values differ for A – by 0.5º, for B – by 0.1º). Besides, there are no significant population differences. Most identification guides also state as a diagnostic species characteristic of *H. rufipes*, apart from body size, that the back angles of the prothorax should be right angles (Lindroth, 1985; Hůrka, 1996; Freude et al., 2004). In the populations studied the value of prothorax back angle (on average, 101.1º) is actually unchanged (fluctuations do not exceed 1–2º).

The vertex angle of elytra (D, Fig. 7) in the populations 7, 8 and 9 (Pavlograd, Dnipropetrovsk and Petrikovka districts) significantly differs from that of populations 1–6 (Novomoskovsk district). These differences require additional analysis taking into account the likely variability of the vertex angle of elytra in other populations. Because of considerable inter-population differences in the elytra vertex angle, sexual dimorphism on the given character is not significant (P = 0.76, F = 0.09, $F_{0.05(1, 390)}$ = 3.87).

Density of hairs on the elytra (P, Fig. 7) in males is 13.3% lower than in females: 289 ± 46 pc./mm^2 in males and 327 ± 50 pc./mm^2 in females ($P = 3.4•10^{–14}$, F = 62.00, $F_{0.05(1, 390)}$ = 3.87). No significant inter-population differences in males (P = 0.31, F = 1.19, $F_{0.05(8, 174)}$ = 1.99) and in females (P = 0.65, F = 0.74, $F_{0.05(8, 200)}$ = 1.98) are recorded.

Values of morphometric indices on the different sampling plots

The ratio of body length to its height (Lb/Hb, Fig. 8) reflects the degree of “convexity” of beetles. More flattened specimens can more easily squeeze into the narrow slots of dry soil, which is solid in its mechanical composition. The mean values of the index show significant sexual dimorphism ($P = 4.2•10^{–9}$, F = 34.72, $F_{0.05(1, 390)}$ = 3.87): they are minimal for females (3.999 ± 0.215), and maximal for males (4.123 ± 0.200). In population 4 (acacia forest belt) the values of this index in females are significantly lower than in other populations. For males and females of other populations no significant values are found.

The ratio of the arithmetic mean of width of head, prothorax and elytra to body length ((Sc + Sp + Se)/3Lb, Fig. 8) reflects the relative “broadness” of the beetles. Sex differences between males (0.308 ± 0.006) and females (0.309 ± 0.007) on this index are not significant (P = 0.339, F = 0.91, $F_{0.05(1, 390)}$ = 3.87). This index is minimal for males and females of populations 1 and 7, females of population 4 and males of population 8 (Fig. 8). The maximum value of the index is recorded in females of populations 2 and 3 and males of the population 3.

The ratio of length and maximum width of prothorax (Lp/Sp2) is one of the most stable characteristics of this species. No significant variations between males and females of population 1 (lucerne field), 2 (clover field), 6 (disturbed steppe area), 7 (oak plantation with the traces of cattle grazing) and 8 (corn field) on the given characteristic are found (Table 3). Therefore, on the most anthropogenically transformed plots no sexual dimorphism in the ratio of length and maximum width of prothorax is manifested.

In males (Fig. 8, Table 3) the mean values of the index Lp/Sp2 do not differ significantly (P = 0.829, F = 0.05, $F_{0.05(1, 390)}$ = 3.87) from females (0.693 ± 0.030 and 0.692 ± 0.028 respectively). Distribution of the ratio of length to width of prothorax in females and males of populations 2 and 6, as well as males of populations 5 and 8 is normal (asymmetry and excess are not significant, Table 3). Significant negative asymmetry (specimens with high values of the index prevail in the population) is recorded in males and females of population 3 and females of population 8. In males and females of populations 1, 4, 7, 9, as well as in females of population 5, significant positive excess on the ratio of length and width of prothorax (a larger number of specimens with lower values of the index) is recorded.

The ratio of elytra length to prothorax length (Le/Lp, Fig. 8) significantly differs (P = 0.009, F = 6.85, $F_{0.05(1, 390)}$ = 3.87) between males and females (2.709

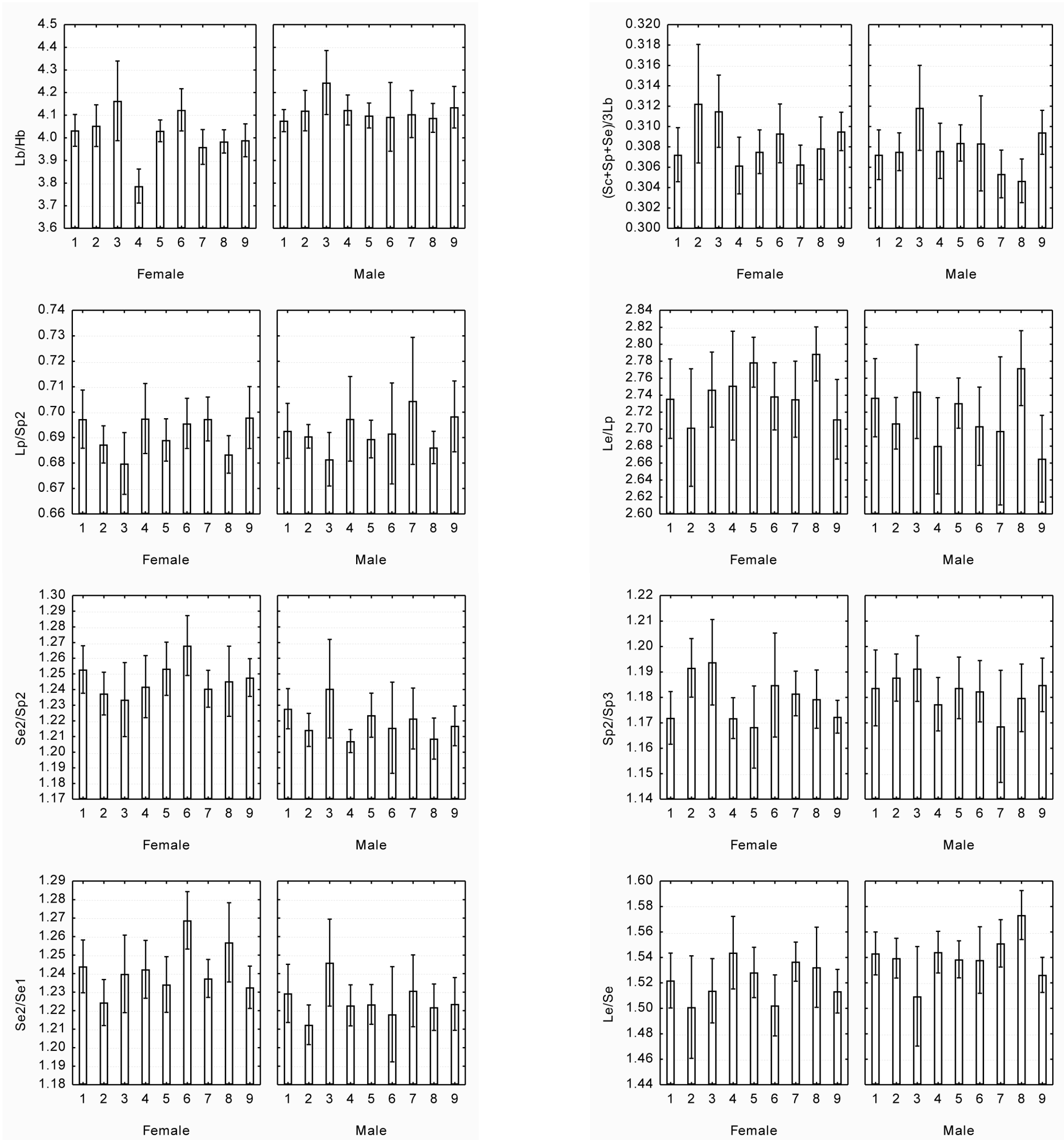

Fig. 8. Mean value and standard deviation of morphometric indices of *H. rufipes*: Lb/Hb – ratio of body length to body height, (Sc + Sp + Se)/3Lb – ratio of arithmetic mean value of width of the head, prothorax and elytra to body length, Lp/Sp2 – ratio of length and maximum width of prothorax, Le/Lp – ratio of elytra length to prothorax length, Se2/Sp2 – ratio of maximum elytra width to maximum prothorax width, Sp2/Sp3 – ratio of maximum width of prothorax to width between its back angles, Se2/Se1 – ratio of maximum elytra width to the distance between their humeral angles, Le/Se – ratio of elytra length to their width; on the right – males (n = 183), on the left – females (n = 209); on X-axis from 1 to 9 population numbers are indicated (see Table 1), on Y-axis the index value is indicated.

± 0.118 and 2.741 ± 0.122 accordingly). This index shows no significant differences between populations. Maximum values of this index for males and females are recorded in population 8 (corn field).

For the ratio of maximum elytra width to maximum prothorax width (Se2/Sp2, Table 4, Fig. 8) between males (1.218 ± 0.034) and females (1.246 ± 0.040) significant sexual dimorphism ($P = 1.3 \cdot 10^{-12}$, $F = 53.84$, $F_{0.05(1, 390)} = 3.87$) is recorded. On the driest areas (1 – lucerne field, 5 and 6 – steppe areas) the maximum ratio of elytra width to prothorax width is recorded in females.

Table 3. Variability of the ratio of prothorax length to its maximum width (Lp/Sp2) in the studied populations of *H. rufipes* (n = 392)

Ecosystem	Sex	n	x ± SD	Min–Max	D	Ex ± SD	As ± SD	F	$F_{0.05}$ (df1, df2)	P
1	m	18	0.693 ± 0.022	0.657–0.756	0.099	3.45 ± 1.02**	1.19 ± 0.53*	0.356	4.09 (1, 39)	0.554
	f	23	0.697 ± 0.026	0.657–0.782	0.124	3.71 ± 0.93***	1.27 ± 0.48*			
2	m	29	0.691 ± 0.012	0.667–0.715	0.048	–0.24 ± 0.84	–0.02 ± 0.43	0.639	4.04 (1, 48)	0.428
	f	21	0.687 ± 0.016	0.647–0.720	0.073	1.21 ± 0.96	–0.24 ± 0.50			
3	m	17	0.682 ± 0.020	0.621–0.705	0.084	4.10 ± 1.04**	–1.78 ± 0.55**	0.049	4.16 (1, 31)	0.827
	f	16	0.680 ± 0.023	0.615–0.710	0.095	3.51 ± 1.07**	–1.56 ± 0.56*			
4	m	29	0.697 ± 0.044	0.615–0.876	0.260	10.41 ± 0.84***	2.68 ± 0.43***	0.001	4.03 (1, 51)	0.990
	f	24	0.697 ± 0.033	0.667–0.799	0.133	5.10 ± 0.91***	2.21 ± 0.47***			
5	m	19	0.689 ± 0.015	0.659–0.722	0.063	0.37 ± 1.00	–0.09 ± 0.52	0.005	4.07 (1, 43)	0.946
	f	26	0.689 ± 0.021	0.648–0.760	0.112	5.03 ± 0.88***	1.49 ± 0.45**			
6	m	7	0.692 ± 0.021	0.663–0.726	0.063	–0.42 ± 1.41	0.40 ± 0.77	0.215	4.54 (1, 15)	0.649
	f	10	0.696 ± 0.014	0.678–0.719	0.040	–1.11 ± 1.26	0.40 ± 0.68			
7	m	16	0.704 ± 0.047	0.673–0.850	0.177	6.56 ± 1.07***	2.59 ± 0.56***	0.389	4.13 (1, 34)	0.537
	f	20	0.697 ± 0.018	0.677–0.760	0.083	6.71 ± 0.98***	2.13 ± 0.51***			
8	m	16	0.686 ± 0.012	0.667–0.760	0.039	–0.99 ± 1.07	–0.05 ± 0.56	0.304	4.11 (1, 37)	0.585
	f	23	0.683 ± 0.017	0.633–0.708	0.075	2.08 ± 0.93*	–1.17 ± 0.48*			
9	m	32	0.698 ± 0.039	0.645–0.808	0.163	2.78 ± 0.81**	1.76 ± 0.41***	0.002	3.97 (1, 76)	0.960
	f	46	0.698 ± 0.041	0.655–0.859	0.204	9.42 ± 0.69***	3.05 ± 0.35***			
Total	m	183	0.693 ± 0.030	0.615–0.876	0.260	12.99 ± 0.36***	2.87 ± 0.18***	0.047	3.87 (1, 390)	0.829
	f	209	0.692 ± 0.028	0.615–0.859	0.244	13.29 ± 0.33***	2.80 ± 0.17***			
Differences between males								0.948	1.99 (8, 174)	0.479
Differences between females								1.360	1.98 (8, 200)	0.216

Numbers of ecosystems and their brief characteristic see in Table 1; sex m – male, f – female; Min–Max – minimum and maximum value of the characteristic; D – variation range equal to Max – Min; As – asymmetry; Ex – excess; *, ** and *** – significance of asymmetry and excess $P < 0.05$, 0.01 and 0.001, respectively.

Table 4. Variability of the ratio of maximum elytra width to maximum prothorax width (Se2/Sp2) in the studied populations of *H. rufipes* ($n = 392$)

Ecosystem	Sex	n	x ± SD	Min–Max	D	Ex ± SD	As ± SD	F	$F_{0.05}$ (df1, df2)	P
1	m	18	1.228 ± 0.026	1.188–1.280	0.092	–0.50 ± 1.02	0.38 ± 0.53	6.427	4.09 (1, 39)	0.015
	f	23	1.253 ± 0.035	1.189–1.335	0.146	0.24 ± 0.93	0.05 ± 0.48			
2	m	29	1.214 ± 0.028	1.149–1.266	0.117	–0.03 ± 0.84	–0.14 ± 0.43	7.998	4.04 (1, 48)	0.007
	f	21	1.237 ± 0.030	1.195–1.291	0.096	–0.96 ± 0.96	0.59 ± 0.50			
3	m	17	1.240 ± 0.061	1.143–1.377	0.233	1.15 ± 1.04	0.97 ± 0.55	0.137	4.16 (1, 31)	0.714
	f	16	1.234 ± 0.044	1.140–1.309	0.169	–0.13 ± 1.07	–0.32 ± 0.56			
4	m	29	1.207 ± 0.019	1.167–1.256	0.089	0.40 ± 0.84	0.38 ± 0.43	13.23	4.03 (1, 51)	$6.4*10^{-4}$
	f	24	1.242 ± 0.047	1.147–1.326	0.178	–0.45 ± 0.91	–0.13 ± 0.47			
5	m	19	1.224 ± 0.029	1.166–1.271	0.104	–0.29 ± 1.00	0.09 ± 0.52	6.985	4.07 (1, 43)	0.011
	f	26	1.253 ± 0.042	1.210–1.388	0.179	3.56 ± 0.88	1.78 ± 0.45			
6	m	7	1.216 ± 0.031	1.181–1.269	0.088	–0.41 ± 1.41	0.70 ± 0.77	13.77	4.54 (1, 15)	0.002
	f	10	1.268 ± 0.027	1.235–1.325	0.090	1.19 ± 1.26	1.18 ± 0.68			
7	m	16	1.221 ± 0.036	1.150–1.286	0.136	–0.29 ± 1.07	0.01 ± 0.56	3.424	4.13 (1, 34)	0.073
	f	20	1.241 ± 0.025	1.193–1.281	0.088	–0.79 ± 0.98	–0.29 ± 0.51			
8	m	16	1.209 ± 0.025	1.166–1.246	0.080	–0.94 ± 1.07	–0.44 ± 0.56	6.890	4.11 (1, 37)	0.013
	f	23	1.245 ± 0.052	1.161–1.349	0.188	–0.47 ± 0.93	–0.01 ± 0.48			
9	m	32	1.217 ± 0.035	1.131–1.284	0.153	–0.06 ± 0.81	–0.23 ± 0.41	12.10	3.97 (1, 76)	$8.4*10^{-4}$
	f	46	1.248 ± 0.041	1.048–1.311	0.263	12.21 ± 0.69	–2.59 ± 0.35			
Total	m	183	1.218 ± 0.034	1.131–1.377	0.246	3.62 ± 0.36	0.96 ± 0.18	53.84	3.87 (1, 390)	$1.3*10^{-12}$
	f	209	1.246 ± 0.040	1.048–1.388	0.340	3.02 ± 0.33	–0.38 ± 0.17			
Differences between males								1.859	1.99 (8, 174)	0.069
Differences between females								0.970	1.98 (8, 200)	0.461

Numbers of ecosystems and their brief characteristic see in Table 1; sex m – male, f – female; Min–Max – minimum and maximum value of the characteristic; D – variation range equal to Max–Min; As – asymmetry; Ex – excess; *, ** and *** – significance of asymmetry and excess $P < 0.05$, 0.01 and 0.001, respectively.

The ratio of maximum width of prothorax to width between its back angles (Sp2/Sp3, Fig. 8) features no significant difference (P = 0.075, F = 3.17, $F_{0.05(1, 390)}$ = 3.87) between males (1.183 ± 0.028) and females (1.178 ± 0.027). Inter-population differences are also not significant.

The ratio of maximum elytra width to distance between their humeral angles (Se2/Se1, Fig. 8) has a pronounced sexual dimorphism (P = $2.7 \cdot 10^{-5}$, F = 18.02, $F_{0.05(1, 390)}$ = 3.87) between males (1.225 ± 0.033) and females (1.240 ± 0.037). It shows significant difference between individual populations of females only. The index Se2/Se1 is maximal for females of populations 6 (steppe area) and 8 (corn field).

The ratio of elytra length to width (Le/Se, Fig. 8) shows significant sexual dimorphism (P = $1.6 \cdot 10^{-3}$, F = 10.05, $F_{0.05(1, 390)}$ = 3.87) between males (1.539 ± 0.044) and females (1.522 ± 0.060). Inter-population differences for females of various populations are not significant on the given index. For males maximum values of the index are recorded in population 8 (corn field), and minimum values in populations 3 (elm-ash forest) and 9 (maple-ash forest).

General variability parameters

Analysis of joint variability of 19 characteristics (14 linear measurements, 4 angular characteristics and density of elytra downiness – see Material and methods) for 391 specimens of beetles showed a complex pattern of interdependencies among the studied characteristics. In view of results of the PCA (Fig. 9) more than 60% of the effect on the sample variability is created by Factor 1, which determines the joint variability of all linear characteristics except for length of eyes (La). Angular characteristics (A, B, C and D) are also not affected by factor 1 (Fig. 10a). Since in the previous parts of this paper we thoroughly established that for most of the characteristics the significant differences were based on sex, we consider that factor 1 can be identified as the sex of the ground beetles. This is confirmed by the distribution of specimens in the factor space of factors 1 and 2 (Fig. 11).

Factor 2 determining 7.3% of the dispersion was interpreted by us as the geographic location of the ecosystem. Most specimens collected outside Novomoskovsk district (sampling plots 7, 8 and 9) have maximum values on the given factor (Fig. 11). Factors 2, 3, 4 and 5 are determined by the values of predominantly angular characteristics (Fig. 10a, b): value of humeral angles of elytra (C), vertex angle of elytra (D), front (A) and back angles or prothorax (B). Factor 6 determining only 3.6% of total sample dispersion (Fig. 10c), correlates to the density of elytra downiness. Factor 7 (3.2% of total dispersion, Fig. 10d) correlates to eye length (La), while factor 8 (2.6% of total dispersion, Fig. 10d) – to clypeus length (Lcl).

Therefore, PCA results showed that the most of linear characteristics were connected with the sex of the beetle, while angular characteristics and the degree of elytra downiness varied regardless of the sex of the *H. rufipes* specimens.

Discussion

Identification guides state that the body length of *H. rufipes* varies from 11 to 16 mm (Lindroth, 1985; Hůrka, 1996; Freude et al., 2004). On the basis of the results of our study, the size of this species of beetle fluctuates within the limits of 11.6 to 16.4 mm. Our data are shifted towards the literature data, which fact may prove not only a simple rounding up to the nearest whole number (in mm), but a slight increase in beetle body length as well.

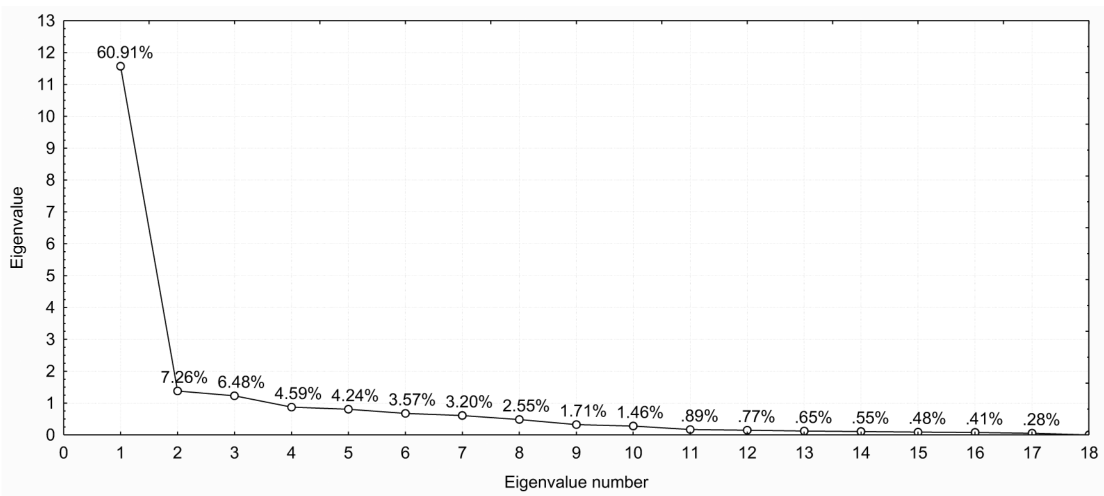

Fig. 9. Eigenvalues of correlation matrix of PCA of studied *H. rufipes* populations.

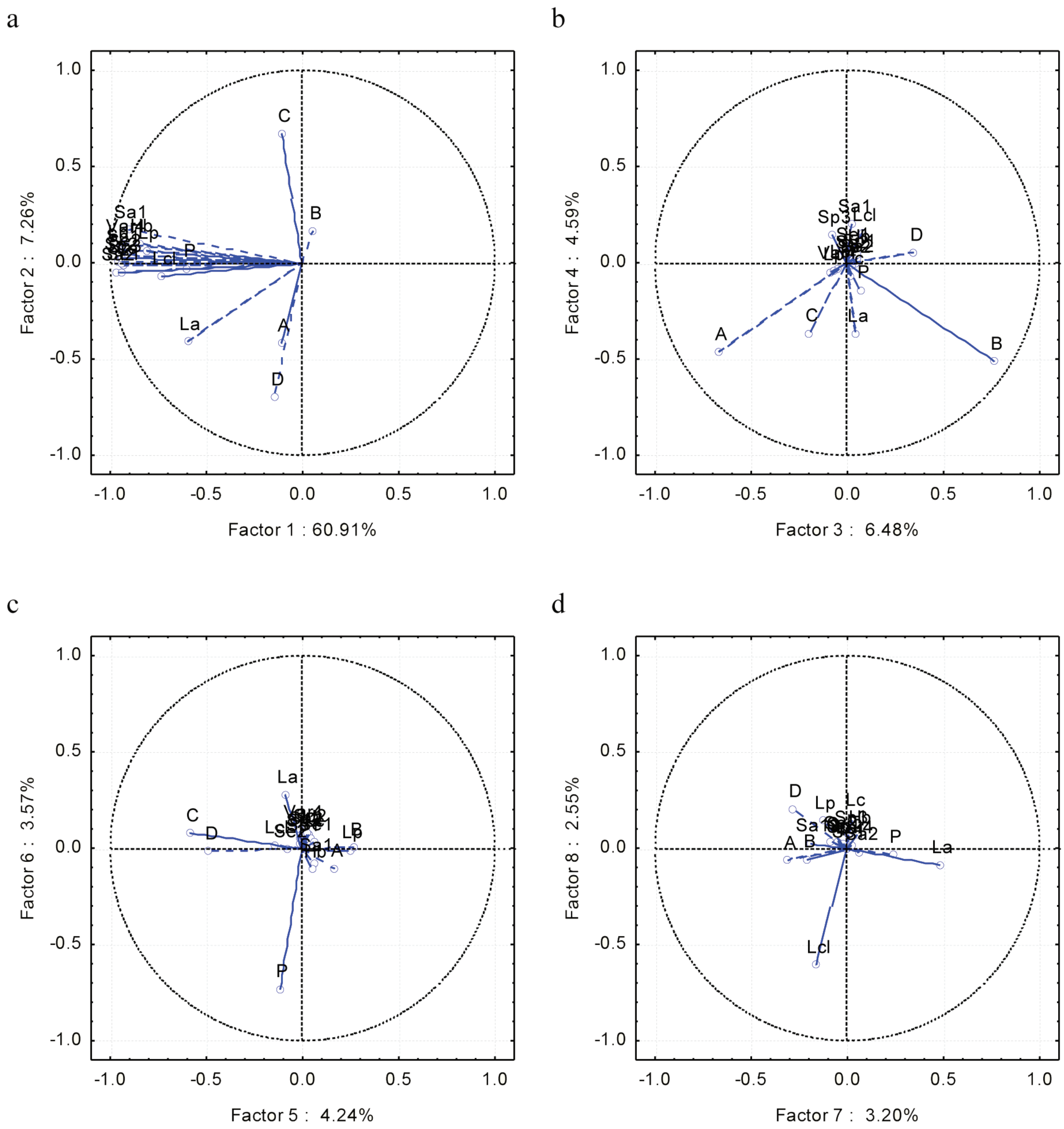

Fig. 10. Results of PCA analysis of studied *H. rufipes* populations in the factor space (a–d) of 8 most significant factors.

As a result of assessment of the body length of *H. rufipes* it was found that for the forest ecosystems (forests with closed canopy and heavy layer of litter) a minimum size of both males and females is typical. At the same time in agrocenoses the body length reaches its maximum in males. In our opinion, this fact can be explained by two reasons. Firstly, in the examined agrocenoses *H. rufipes* is the largest of the dominant species of ground beetles (on the fields there are numerous species of the geni *Poecilus*, *Calathus*, *Amara*, *Bembidion*, *Microlestes*, and other species of the genus *Harpalus*). In contrast to the other types of ecosystem studied, larger ground beetles of the geni *Pterostichus*, *Carabus* and *Calosoma*, capable of feeding on specimens of *H. rufipes* on the fields examined, were virtually absent. Therefore, in the agrocenoses of the area under study *H. rufipes* is one of the top links of the trophic chain among invertebrate animals (Brygadyrenko, 2003; Korolev and Brygadyrenko, 2012, 2014). Secondly, in spite of the fact that the studied species is a ubiquitous habitat generalist, living in a wide variety of moisture conditions from ultra-hygrophilous meadow ecosystems

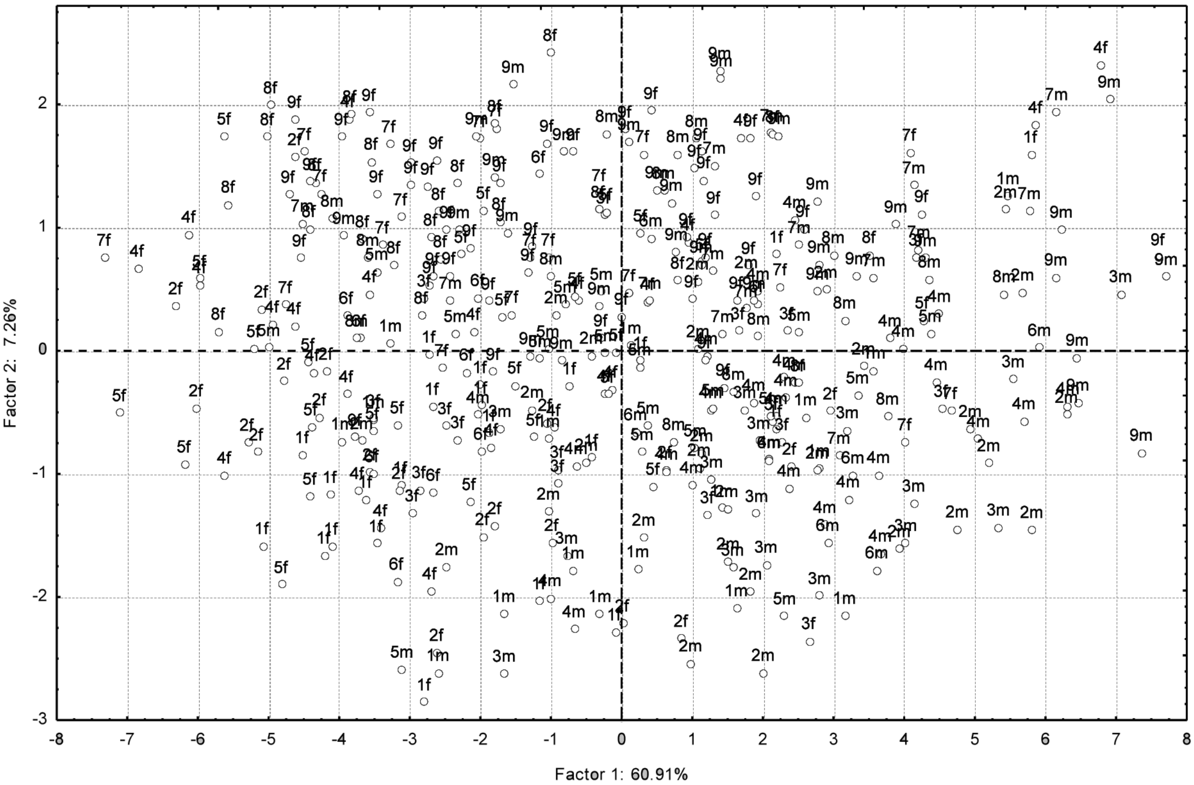

Fig. 11. Distribution of specimens of *H. rufipes* in the factor space of factor 1 (sex: positive values – males, negative values – females) and 2 (ecosystem: positive values – predominantly, ecosystems 7, 8, 9, located in Pavlograd, Dnipropetrovsk, and Petrikovka districts, negative values – all the other ecosystems, located in Novomoskovsk district).

and reed beds on banks of water bodies to xerophilous sand ecosystems on secondary river terraces (Kryzhanovsky et al., 1995; Hůrka, 1996; Brygadyrenko, 2003), *H. rufipes* finds its optimal living environment in the mesoxerophilous and xeromesophilous conditions of agrocenoses (Luff, 1980; Wallin, 1988; Shearin et al., 2007, 2008; Reshetniak and Brygadyrenko, 2013). Here the species reaches its highest numbers, since these habitats offer *H. rufipes* the most varied trophic resources of both vegetable and animal origin (Briggs, 1965; Birthisel, 2013; Birthisel et al., 2014; Brygadyrenko and Reshetniak, 2014).

The presence of sexual dimorphism (males tend to be smaller than females) revealed for most of the linear characteristics of the species may have various ecological interpretations (Slatkin, 1984). In accordance with the evolutionary theory of sex (Geodakyan, 1983) we may suggest the reduction of the absolute size of the body in the process of phylogenesis. However, the significant ($P < 0.001$) negative asymmetry in females and its absence ($P > 0.05$) in males found in our study is evidence, on the contrary, of increase in female size and maintenance of constant body size in males. *H. rufipes* is one of the largest representatives of the genus *Harpalus*. It is probable that the ancestral form of this species had a considerably smaller body than that observed in modern populations of *H. rufipes*. In its size, it should be closer to the modern species *H. griseus* (Panzer, 1797). In our opinion, it would be rewarding to assess the manifestation of sexual dimorphism in populations living in environments under varying degrees of anthropogenic pressure or in proximity to varying numbers of competitor species (Niemelä, 1993; Blake et al., 1994; Roy et al., 2013).

The degree of manifestation of sexual dimorphism can be evidence not only of presence of sexual selection in the population but also of extreme microclimatic conditions affecting the beetles (high temperature and low humidity in summer period) which limit the survival of certain groups of specimens in the population (Lande, 1980; Andersson, 1994; Daly et al., 1998; Bolnick and Doebeli, 2003; Fairbairn, 2007; Cooper et al., 2011; Bobyliov et al., 2014). Fluctuations of numbers and survival rate of *H. rufipes* in the ecosystems where litter horizon is absent (agrocenoses, steppe areas with over-grazing by cattle, areas with regular burning of crop residues) may lead to disappearance of smaller ground beetle species from the macrofauna, as well as elimination of smaller specimens from the populations of *H. rufipes* (Den Boer, 1985; Holland, 2002; Denno et al., 2005; Davis and Raghu, 2010). On the other hand, in the given ecosystems the trophic pressure of predators may grow considerably; in the agrocenoses such predators on *H. rufipes* are first of all rodents and birds, and in areas with sufficient moisture also reptiles and amphibians (Parmenter and Macmahon, 1988; Churchfield et al., 1991; Denno et al., 2005; Guerrero et al., 2010). The diet of the species under study varies both in different periods of the season and in different habitats, their ability to reach a wide variety of food sources being promoted by their characteristic flight migrations and well developed wing musculature (Thiele, 1977; Hamon et al., 1990; Lovei, 1996; Kromp, 1999; Midtgaard, 1999; Collins et al., 2002; Honek et al., 2003; Irmler, 2003; Matalin, 2003; Harrison and Gallant, 2012). Possibly, the morphology of imagoes of *H. rufipes* is also affected by the type of life cycle: Matalin (2007) has found that for part of the population reproduction was typical during the first year of life, and for another part – during the later period of ontogenesis. Specimens with a one-year and two-year lifecycle may coexist in the studied ecosystems (Matalin, 2007).

For many species of plant-eating invertebrates dependence of mandible shape on the diet (Patterson, 1984; Bernays, 1991) has been traced. For *H. rufipes* such dependence has not been traced so far, whereas for other dominant species of ground beetles, *Pterostichus melanarius* (Illiger, 1798), we have found differences in mandible shape (unpublished data).

In our opinion, the most valuable diagnostic character of the state of a population studied in the course of environmental research is not the mean value of any characteristic, but the type of its distribution. Absence of the normal distribution (significant excess or asymmetry of the sample) can be evidence of directional selection in the populations of *H. rufipes* (Schluter, 2000; Rueffler et al., 2006). Over time, this selection may lead to the fixation of certain characteristic values at the genetic level.

Our findings will form the basis for environmental monitoring of the population status of this species in anthropogenically disturbed ecosystems. Possibly, comparison with the reference values of the characteristics given in this paper will provide an opportunity for further identification of indicator characteristics and wider use of this dominant species in bio-indicator studies (Rainio and Niemelä, 2003).

Conclusions

The result of this study is the finding of significant ($P < 0.001$) negative asymmetry in females and its absence ($P > 0.05$) in males for body length, head length, elytra length, distance between eyes, head width, prothorax width between the front and back angles, elytra width between humeral angles, and maximum width of elytra. For all these characteristics the excess in males is not significant ($P > 0.05$), while in females in most cases it is significantly positive ($P < 0.05$), which is evidence of the large number of females with greater body length, and greater width of head, prothorax and elytra. Thus, in the populations of *H. rufipes* females gradually increase their size, while males retain a constant size.

Absence of the significant asymmetry ($P > 0.05$) for males and females suggests the absence of directional selection in the populations of *H. rufipes* on the density of elytra downiness and value of the prothorax back angle. Significant negative asymmetry is recorded in males and females on maximum prothorax width ($P < 0.001$) and body height ($P < 0.05$), i.e. unidirectional increase in these characteristics occurs in specimens of both sexes.

Analysis of body proportions shows that for all 8 considered morphometric indices the values of excess are significantly positive ($P < 0.001$) in males and in females. This suggests a much higher constancy of body proportions than of full size.

For most of linear characteristics the significant ($P < 0.001$) sexual dimorphism is recorded.

In the areas where annual burning of crop residues and litter is observed, differences between males and females in length are two times higher than differences between males and females for the ecosystems with no such burning.

In the most anthropogenically disturbed areas, as distinct from natural areas, sexual dimorphism in the ratio of length and maximum width of prothorax is not manifested.

In the driest areas, maximum ratio of elytra width to prothorax width is recorded in females.

Vertex angle of elytra significantly differs in the populations of various administrative districts.

Average density of elytra downiness in males is 13.3% lower than in females.

The results of PCA have shown that most of the linear characteristics are connected with the sex of the beetle while the angular characteristics and degree of elytra downiness change regardless of the sex of *H. rufipes* specimens.

The hypotheses formulated in the introduction to this paper were not confirmed as a whole: (1) distribution of a considerable part of the morphometric parameters was not normal in the ecosystems under study, (2) significant changes in mean values typically did not occur with the increase of anthropogenic transformation of ecosystems; in some cases asymmetry and excess of morphometric characteristics and indices grew, and (3) in the conditions of anthropogenically transformed ecosystems differences between males and females of *H. rufipes* did indeed show an increase for most characteristics.

The results of this paper have shown that in bio-indication studies during assessment of the anthropogenic load or variability of populations in natural ecosystems of various types the mean values of morphometric characteristics and indices could have the less diagnostic value, than the type of their distribution in the population.

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