

ALTITUDINAL VARIATION IN POPULATION DENSITY, BODY SIZE AND MORPHOMETRIC STRUCTURE IN *CARABUS ODORATUS* SHIL, 1996 (COLEOPTERA: CARABIDAE)

Raisa A. Sukhodolskaya, Tatyana L. Ananina

Sukhodolskaya R.A., Ananina T.L. 2015. Altitudinal variation in population density, body size and morphometric structure in *Carabus odoratus* Shil, 1996 (Coleoptera: Carabidae). *Acta Biol. Univ. Daugavp.*, 15 (1): 179 – 190.

We sampled 1300 specimens of Ground Beetle *Carabus odoratus* in 30 -km high-altitude transect at three elevations (500-700 m, 701-1300 m and 1301 -1700 m) in 1988 – 2012. Morphometric analysis included six traits – lengths and widths of elytra, pronotum and head. Beetles mean densities were similar at low and high altitudes and were significantly higher than at middle elevation. Beetles size monotonically decreased from low altitudes to high ones. Canonical Correspondence Analysis showed that morphometric structure of *C. odoratus* populations differed at different altitudes with the first axis reflecting altitude gradient. Principal Component Analysis, conducted separately for the each trait, revealed that all traits variation, except head length, in middle mountains had intermediate values between low and high mountains ones.

Key words: Carabids, altitudinal variation, morphometric structure, body size variation.

Raisa A. Sukhodolskaya. State Budgetary Establishment Research Institute for Problems of Ecology and Mineral Wealth, Daur'skaya str., 28 Kazan Tatarstan 420087 Russian Federation, e-mail: sukhodolskayaraisa@gmail.com
Tatyana L. Ananina. FGBU "Zapovednoe Podlemorie" Komsomolskaya str. 44 – 64, Ulan Ude, 679945, Russian Federation, e-mail: a_ananin@mail.ru

INTRODUCTION

Population differentiation is a crucial step in the speciation process (Turelli et al. 2001). The latter, defined in a broad sense, is not restricted by the evolution of reproductive isolation (as assumed under the biological species concept), but includes the diversification of all aspects of the phenotype (Barton 2001). This means that it is essential to (i) study the relative influence of the evolutionary forces (e.g. gene flow, natural selection, genetic drift) that interact to produce

a given pattern of differentiation and variability before complete reproductive isolation and, (ii) conduct studies with a wide array of markers (Garnier et al. 2005).

In such a context, studies of morphological differentiation are essential. First, most organismal taxonomy, including intra-specific variation, is based on morphological traits. Thus, one is able to appraise and interpret morphological variation at all levels of integration. Secondly, it is likely that

morphological traits are, to a large extent, under polygenic control. Studying differentiation of such characters then provides a good assessment of the amount of divergence between different entities. It has even been reported that morphology could exhibit clear patterns of differentiation, where molecular markers failed to detect population structure (Nice & Shapiro 1999). Thirdly, most morphological traits are the target of selection; their study is central in the evaluation of its strength and its impact in the differentiation process. Finally, the understanding of phylogeographical history of species, or the evaluation of the action of the different evolutionary forces, all need a comparison of the patterns of geographical variation obtained from different markers, for

example genetic, morphological etc.

Body size is one of the most important traits in animals because it directly relates to fitness – to development and reproduction (Tammeru et al. 2002, Berger et al. 2008), somatic and reproductive tissues growth (Blanckenhorn 2006, Etile & Despland 2008), thermoregulation (Kingsolver et al. 2004) and dispersal abilities (Gutierrez & Menendes 1997). Body size variation research clarifies morphoadaptation of organisms to the environment changes and intra- and interpopulations relations, which can not be revealed by other methods and do not yield to the experimental check (Gelashvili et al. 2011). In this aspect the studies in Ground Beetles are relatively few. Most of them concern the

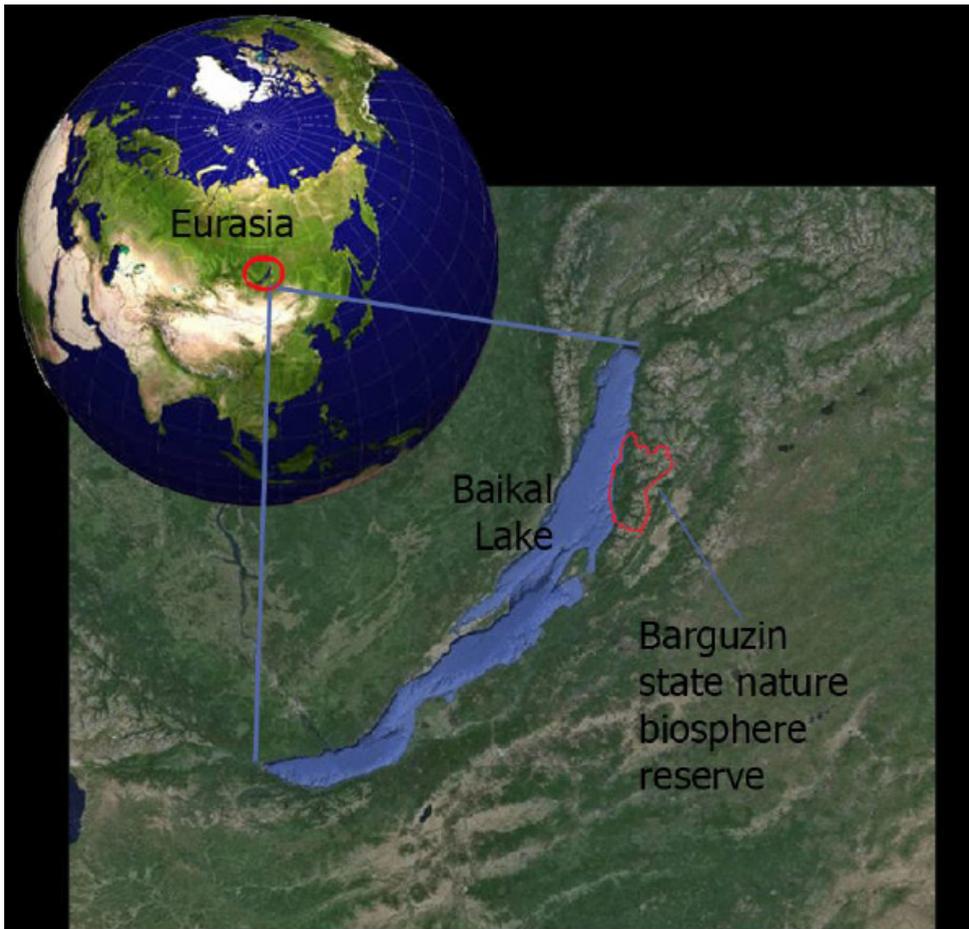


Fig. 1 Region, where study in *C. odoratus* took place.

variation of body size in carabid assemblages, where authors divide species pool into several classes – small, middle and large. In the same way researchers describe the clinal variation of body size in carabids (Maveety et al. 2011, Homburg et al. 2012). The intraspecific variation of body size in carabids is investigated very poorly though Ground Beetles are charged as the sensitive environment indicators (Koivula 2011). Several papers described carabids intraspecific body size variation in latitudinal and anthropogenic gradients (Venn 2007, Sukhodolskaya 2013 Sukhodolskaya & Eremeeva 2013, Sukhodolskaya & Saveliev 2013). The effects of spatial gradients (e.g., altitudinal and latitudinal) on species assemblages remain a central theme of biogeography (Hodkinson 2005, Willig & Bloch 2006). They highlight fundamental mechanisms of species adaptation and also serve a more applied mandate: an example of using latitudinal

or elevational transects to test climate change predictions (Parmesan 2006).

The purposes of this study were to measure the variation in population size of *C. odoratus* across years and elevation; to identify morphological differences in *C. odoratus* across spatial parameters, and to determine, whether morphometric structure of populations varied across elevation.

MATERIAL AND METHODS

Study Sites

We conducted our study in north-east region of Baikal Lake (N 54° 20'; E 109° 30') (National Park “Zapovednoe Podlemorie”, Republic of Buryatia, Russian Federation) (Fig. 1). Beetles were sampled in 30 -km high-altitude transect.

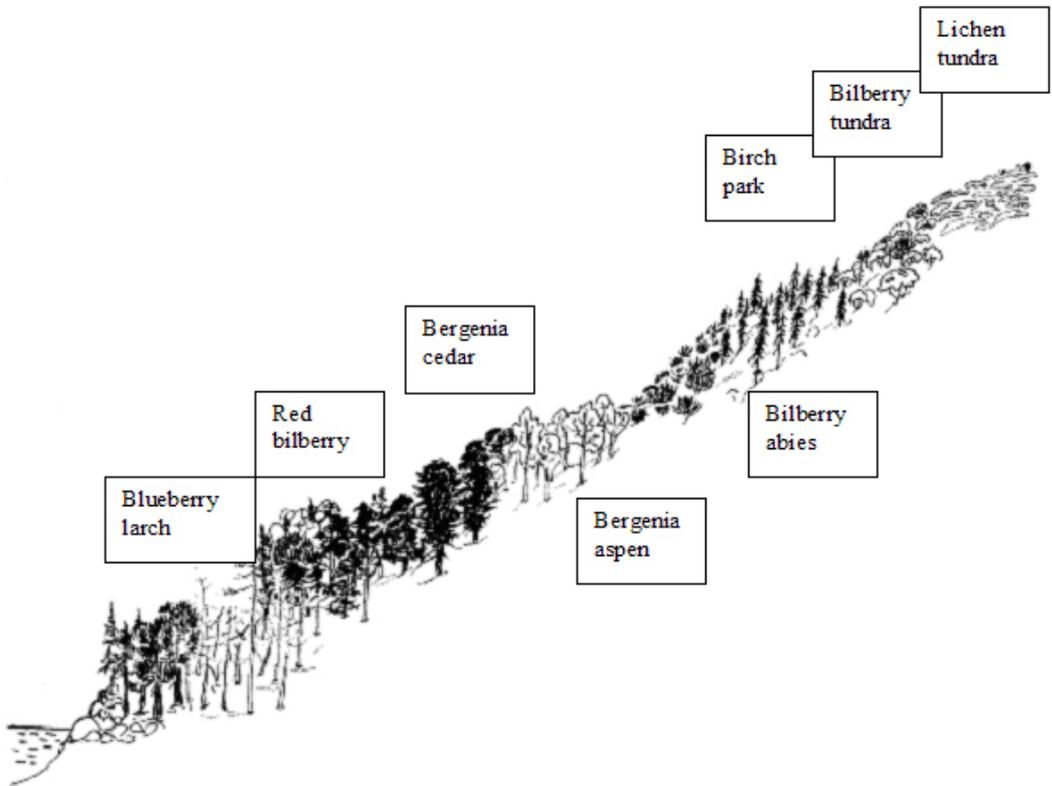


Fig. 2. Sampling localities of *C. odoratus*.

It was situated in Davsha river valley and stretched from the coast of Baikal Lake to the bald Barguzin zone. The transect was divided into three plots designated as low (5-17 km from Baikal Lake shore, 500-700 m altitude), medium (20-25 km, 701-1300 m) and high part of the range (25-30 km, 1301 -1700 m). Bottom part of the mountain forest zone (Low Mountain) included biotopes with Blueberry larch, Red bilberry pine. Middle mountains biotopes included Bergegia cedar, Bergegia aspen and Bilberry abies, High mountains - Birch park, Blueberry tundra, Lichen tundra (Fig. 2).

We had conducted the previous research in this region when the majority of environmental factors had been investigated with thermographs, precipitation cylinderes, the soil thermometers: snow depths had been measured in altitude belts before melting (in March), (Ananin, Ananina, 2011). We had concluded that environment surroundings were less optimal for Ground Beetles at high altitude.

Study Organism

Carabus odoratus Motschulsky, 1844 is distributed from the Yamal Peninsula, and all around Siberia to Magadan area and Kamchatka Peninsula; in southern Siberia from Altai up to the Khabarovsk territories. In the south of Far East Russia the species is absent. The wide area of this species is inhabited by many unequally differing populations. Some of the groups of populations, undoubtedly, must be considered as subspecies. At the same time, the majority of populations constitute a continuous sequence of forms slightly different in size, coloration and ratios, but it is hardly possible to consider these forms as subspecies. At present a considerable number of forms of *C. odoratus* are described. The majority of infraspecific names must be treated as synonyms. The species has a large number of subspecies and local forms. In the Siberia and north of Far East Russia the species is represented by 20 subspecies. In the southern part of the area the species occurs in the mountain tundra and in the scree, at altitudes from 1500 to 2600 m above sea level; in the

northern part of the area it usually inhabits plain tundra and forest tundra (Obydov 2006).

In our study we used *Carabus odoratus barguzinicus* Shil., 1996. It is Baikal subspecies of Siberian species, endemic and generalist in Barguzin ridge (Shilenkov 1996). It is much higher in number than other carabids there and is considered to be the dominant species together with *Pterostichus dilutipes* Motsch.,



Fig. 3. Illustration of measurements: 1-2 – elytra length (hereafter “A”, 3-4 – elytra width (“B”), 5-6 – pronotum length (“C”), 7-8 – pronotum width (D), 9-10 – head length (E), 11-12 – distance between the eyes (signed as “head width” or “F” in the figures).

1844 and *Pterostichus montanus* Motsch., 1844 (Ananina, 2010).

Study design

Our study took place in 1988 – 2010. Ten pitfall traps were set per site in a transect with traps separated from each other by a minimum of 15 m to ensure independence of samples. Each trap was 10 cm diameter, 15 cm in depth and contained approximately 3 cm of silicate-free ethylene glycol as a killing and preserving agent. Traps were open between 8 June and 24 August. Trap contents were collected every 2 weeks and stored in 70% ethanol until processed. Studied specimens were identified using V. Shilenkov (1996).

Morphometric analysis was made with a Leitz RS stereoscopic dissecting microscope at a magnification of 10 diameters, using a calibrated ocular grid with a scale interval of 0.1 mm. For each of specimens six variables were measured, including: elytra length and width, pronotum length and width, head length and distance between eyes (Fig. 3). In total 1300 specimens from 8 local populations were measured. All measurements were log-transformed for analysis.

Statistical analysis was made in Software Statistica 6.0. We applied regression, correspondence and principal component analyses to evaluate trends in population density at different elevation plots, to identify the patterns of morphological variation within the populations at different elevation based on data of the similarity matrix and to reveal the role of different traits in beetles adaptation to different altitudes.

RESULTS

Beetles abundance did not differ significantly in the populations of *C. odoratus* at different altitudes (Fig. 4), but in the half of the cases population density at the middle mountains plots was lower. We summarized data on the beetles density at different altitudes taking the whole period on investigations into account and found, that beetles abundance was significantly lower at middle mountains (Fig. 5).

We used regression analysis to reveal trends in metric traits means in the populations of *C. odoratus*. We calculated means of each studied trait in *C. odoratus* populations in altitude gradient over the 22 – year of investigations (Fig. 6). The coefficients R^2 were not statistically significant, but trends of decreasing in traits values occurred. Then we summarized data concerned low-, middle- and high-mountains into three separate data sets and calculated descriptive statistics for each morphometric trait in different altitude populations over the whole period. All traits, except elytra and head lengths, tended to be larger in the populations of *C. odoratus* at low altitudes. Elytra and head lengths of the beetles were similar at low- and high elevation populations and were longer compared with middle-elevation populations (Fig. 7).

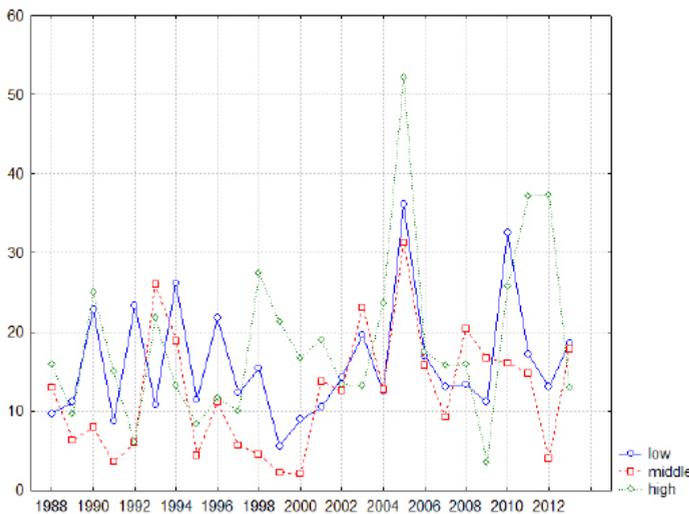


Fig. 4. Populations dynamics of *C. odoratus* in the plots at different altitudes.

Canonical Correspondence Analysis revealed that morphometric structure of *C. odoratus* population differed at different altitudes (Fig. 8). Though Wilk's λ was high and cohesiveness of values was low, significant values of Mahalanobis distances proved structural differences in *C. odoratus* populations in altitude gradient (Table 1).

The first series of PCA included each studied traits variation at different altitudes (Fig. 9). In all cases two main components explained about 70% of variance. For elytra length and width, pronotum and head widths we found similar

type of variation with precise altitude gradient according the PC2. Variation of pronotum and head lengths showed another pattern, with centroid "high" being distanced from others in the case with pronotum length and being the similar with centroid "middle" - in the case of head length.

In the second series of statistical analysis we used data on beetles traits from each altitude separately. It is thought that the first Principal Component reflects variation in size and the second – in the shape of the beetles (Table 2). Together, both Principal Components (PC) explained more than 60% of the variation for the beetles from low-, middle- and high mountains. In low mountains first PC represented negative association with elytra length and width, pronotum and head width. The second PC represented positive association with head length. In middle mountains all traits, except the head length, represented negative association with first axis, data from high mountains demonstrated similar results. In other words allometry in low- and middle mountains was more uttered for head length and was compensated by the second component. But the second component loadings in low- and middle mountains had different directions. We suggested that head shape of the beetles at low- and middle mountains differed. Body shape of

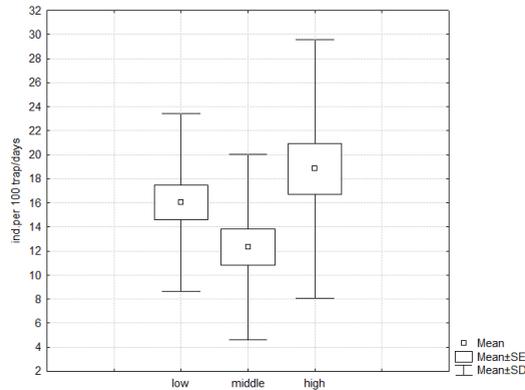


Fig. 5. Descriptive statistics of *C. odoratus* abundance in the plots at different altitudes.

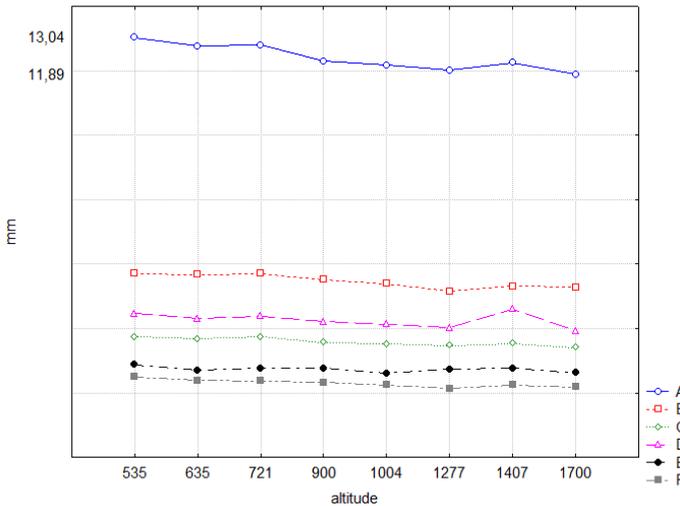


Fig. 6. Means of traits size in *C. odoratus* over a 22-year period in studied plots.

the beetles from high mountains had the most peculiar features: traits association with the first axis was about the same as in low- and middle mountains, but there was no any allometry. This fact suggested that there was no any dependence between size and shape in high altitudes and traits means varied there synchronically. It was noteworthy that pronotum length association with the first axis was high and similar in middle- and high mountains, but at the low altitudes pronotum length variation did not play significant role.

Table 1. Squared Malalanobis Distances from Group Centroids of Traits Variation in *C. odoratus* populations from different altitudes (Wilks' Lambda: ,8196133 approx. F (12,1724) = 15,02405 p < 0,0000)

	Low mountains	Middle mountains	High mountains
Low mountains	0,000000		
Middle mountains	0,409195	0,000000	
High mountains	1,122687	0,264188	0,000000

Table 2. PCA results in *C. odoratus* populations at different altitudes (e.l.-elytra length, e.w.- elytra width, p. l. – pronotum length, p.w. – pronotum width, h.l. – head length, h. w. – head width)

	Low mountains		Middle mountains		High mountains	
	Factor 1	Factor 2	Factor 1	Factor 2	Factor 1	Factor 2
e.l.	-0,779113	-0,170352	-0,839960	0,084893	-0,825769	0,101703
e.w.	-0,701675	0,081866	-0,784728	0,087004	-0,772627	-0,025403
p.l.	-0,640446	-0,410584	-0,726496	0,281532	-0,792336	0,019872
p.w.	-0,743287	0,114584	-0,741721	0,076255	-0,772297	-0,043061
h.l.	-0,460811	0,811168	-0,339142	-0,913945	-0,607153	0,561133
h.w.	-0,709191	-0,170231	-0,713236	-0,127189	-0,565686	-0,685079
Expl. var.(%)	46,3	15,07	50,38	15,85	53,20	13,29

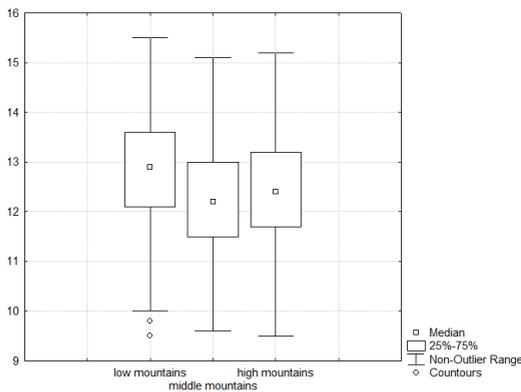


Fig. 7. Descriptive statistics of elytra length means in *C. odoratus* at the plots on different altitudes.

DISCUSSION

Relief features, altitude above the sea level and the distance from Baikal Lake significantly influenced climatic conditions at the certain plots of Barguzin mountain range (Ananin, Ananina 2011). Climatic parameters (the depth of snow cover, air ground interface average temperatures, soil horizons temperature, humidity, soil moisture) varied continually

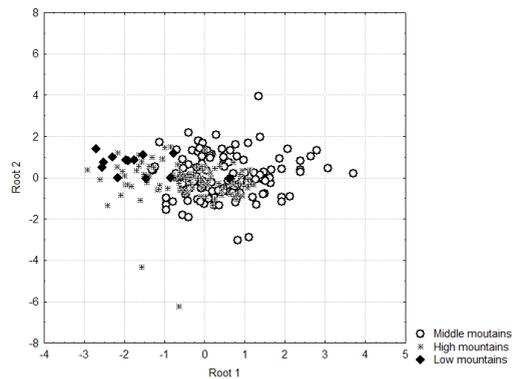


Fig. 8. Results of CCA analysis in *C. odoratus*.

in altitude gradient. Beginning from 700 m (flattening border, middle altitude) steepness of slopes, depth of snow cover, hydrothermal index sharply increased. On the contrary air ground interface temperatures and attached to them soil horizons ones became lower in altitude gradient. Soil temperatures did not necessarily correlate with air temperatures. Besides altitude and landscape features, spring – summer temperature inversions influenced soil temperatures (it is mountain systems character). Thus at low altitudes plots were warmer but less

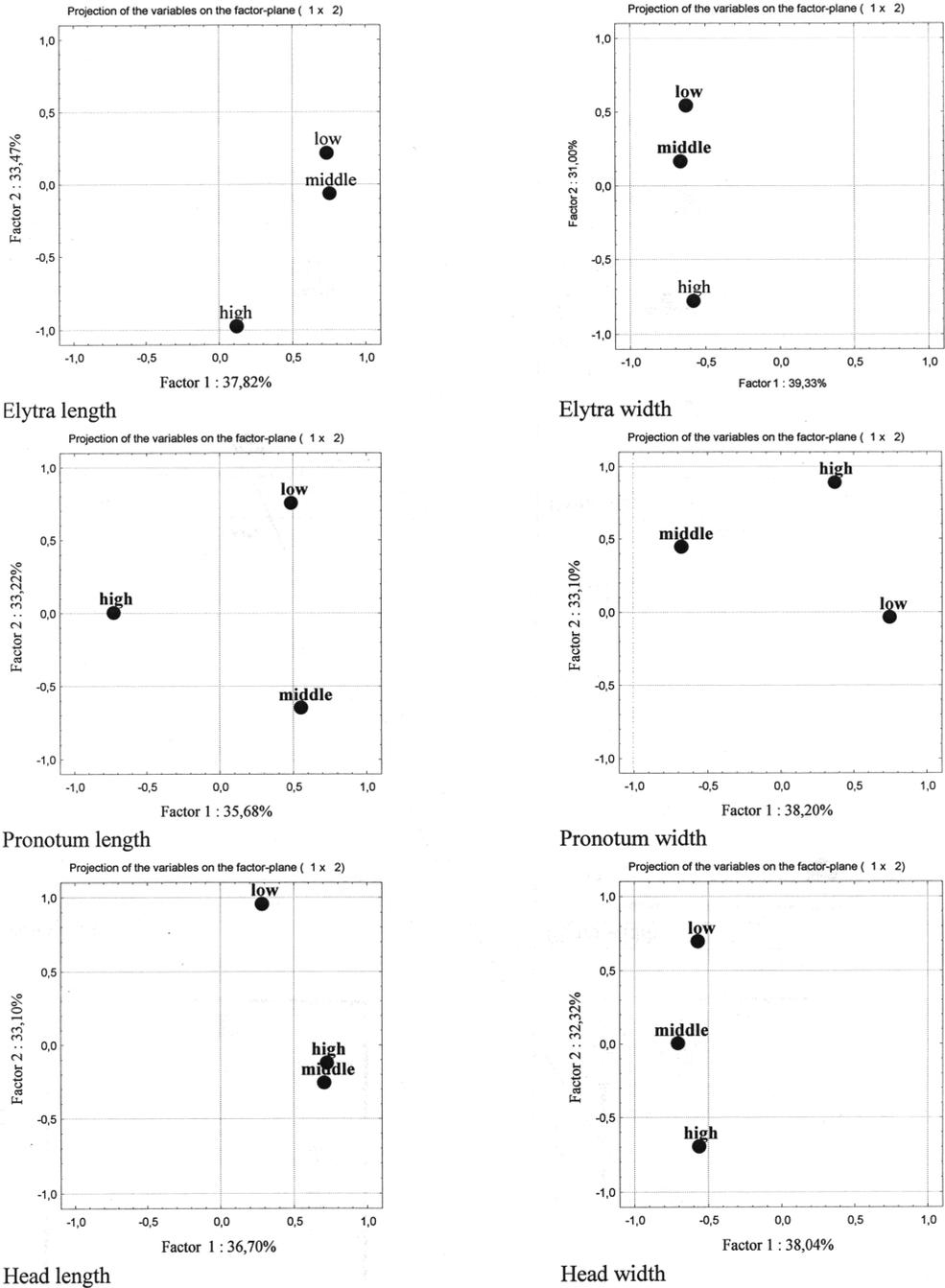


Fig. 9. Results of each trait variation in *C. odoratus* at different altitudes.

moisturized if compared with middle – and high altitude plots.

Two tendencies in morphometric traits variation in Ground Beetle *C. odoratus* at different altitudes were revealed in our study. The first is body size decrease towards the high mountains plots. This is, on the first glance, in opposite to the temperature – size rule in insects (Atkinson 1994). But data on body size variation in altitudinal gradient in insects is contradictory: some of them increased in size in high altitudes (Alonzo 1999, Smith et al. 2000), another altered in opposite direction (Sota 1996, Kubota et al. 2007). Sometimes the only one trait of organism changed, but another remained the same in altitudinal gradient (Tantowijolo & Hoffman 2011).

There were six traits in our study and they showed similar size variation. We suggested several mechanisms of that phenomena. Life-cycles did not coincide in the beetles inhabiting different altitude plots. At low altitude the life-cycle was longer (Ananina 2010), in the whole life-cycles of Ground Beetles in the mountains might be as long as 3 – 4 years. As the consequences the stars have more time to develop and imago became greater. This explanation is in concordance with hypothesis that insects body size decrease in high latitude is determined by shorter reproductive season (Chown & Klock 2003). This explanation is confirmed by intraspecific investigations. Body size of two carabid species was smaller at the high altitudes (Mrazović et al. 2011).

The second explanation is the female-biased sexual size dimorphism in carabids. In low altitude populations of *C. odoratus* sex ratio was female-biased (Ananina 2010). So the increased average body size of the beetles at the low latitude populations might have been determined by females prevailing in the samples.

Mountain habitats are spatially and structurally complex when trees or large shrubs form part of the landscape, producing a mosaic of different habitat types with their own particular vegetation

and/or microclimate (Haslett 1997, Hodkinson 2005). Utilization of these mosaic patches by different plants and animals may reflect more their specific life history strategies and affect special morphometric traits. Patterns in the altitudinal distribution of species richness have frequently been cited as compelling evidence for hypotheses that propose associations with productivity and ambient energy, as well as past and current climates, since these factors vary with altitude (Rahbek 2005). Two patterns in the altitudinal distribution of species richness are frequently observed. The first is a monotonic decrease with altitude. This is expected if resource limitation and thermal constraints govern species diversity and other parameters (Fiedler & Beck 2008). The second is the pattern of hump-shaped variation, the mid-domain effect. For the first time it was described for species richness in latitude gradient (Colwell & Lees 2000). Similar pattern was discovered in interspecific variation of size in the carabid assemblages in the transect from Norway till Southern Africa (Homburg et al. 2012). In the centre of the area beetles body size was larger. Intraspecific study in another carabid *Pterostichus niger* Schal. showed mid-domain effect in body size variation too: beetles were larger in Tatarstan Republic, compared with Kemerovo region (more south) and Sverdlovsk region (more north) (Sukhodolskaya 2012).

Mid-domain effect was detected to wings structure in carabid populations – the share of brachioptery specimens was larger at the middle elevations (Mrazović et al. 2011). We argue that domains can be structural and functional as well. In our study beetles from middle altitude showed intermediate type of variation in PCA. To our mind the PC1 included environmental variation, humidity – temperature regime being the main. Climate factors affected by Baikal Lake play the leading role. Ice melting at this lake, which is situated not far from low mountains, is synchronized with snow cover melt in high mountains. As the result temperature – humidity regimes at these altitudes are similar and environment is relatively severe for carabids. Thus, we revealed similar types of pronotum

and head length variation in low- and high mountains. Those might be associated with heightened locomotor and searching activity in severe environment. In middle mountains carabid diversity is higher (Ananina 2010). Assemblages structure can affect beetles body size too because in sympatric populations imago size is smaller (Sota et al. 2000).

ACKNOWLEDGEMENTS

We thank administration of Barguzinsky Reserve and the staff of the Laboratory of Biomonitoring (Institute of Ecology Tatarstan Academy of Sciences) for the opportunity of field works and our paper illustrations.

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Received: 16.02.2015.

Accepted: 08.06.2015.