УДК 595.762.12: 574.24

[1]T.L. Ananina , [2]A.A. Saveliev, [3]R.R. Shagidullin,
[3]T.A. Gordienko, [3]R.A. Sukhodolskaya

[1]Zapovednoe Podlemorie, [2]Kazan (Volga Region) Federal University
[3] Research Institute for Problems of Ecology and Mineral Wealth Use of Tatarstan Academy of Sciences,
sukhodolskayaraisa@gmail.com

CLIMATIC FACTORS CAN DIFFERENTLY AFFECT BODY SIZE IN CLOSELY RELATED SPECIES (THE CASE STUDY IN GROUND BEETLES)

The study of body size variation in the altitudinal gradient showed the presence of shifts in the morphometric characteristics of ground beetle populations under the influence of bioclimatic factors. Ground beetles were collected on the Barguzinsky Ridge (Russia, Buryatia) in eight characteristic biotopes in four high-altitude sections: on the coast of Lake Baikal, low, middle and high mountains (458-1667 m above sea level). At each site in 2004–2017, we carried out a quantitative account of ground beetles and recorded the main climatic parameters using thermochrons, sedimentary cylinders, soil thermometers, and a snow gauge. We took two common species – *Carabus odoratus* and *Pterostichus montanus* (2200 specimens) for morphometric analysis. The six features of the body organs – the length and width of the elytra, the length and width of the pronotum, and the length of the head and distance between the eyes were measured. Using linear modeling, we investigated how climatic variables affected body size in the studied species. Comparing the reaction of the two species to hydroclimatic parameters, we noted that the reaction was directly opposite to temperature indicators, and the similar to factors that depend on humidity. The higher was the soil temperature at a 5 cm depth, the greater was the length of the elytra, pronotum, and head in *C. odoratus*, but the same characters were smaller in *P. montanus*. High population density led to body size decrease in *C. odoratus*, but *P. montanus* responded in lesser degree. By genus, *C. odoratu*s turned out to be more sensitive to changes in bioclimatic factors.

Keywords: ground beetles; body size variation; climatic factors; number, mountains.

DOI: https://doi.org/10.24852/2411-7374.2023.3.04.11

Introduction

The causes of morphological variation of organisms along climatic gradients are the main historical and present challenges of ecology (Hodkinson, 2005). Different patterns or theories discuss body size as the most studied trait in a wide variety of organisms and along different geographic thermic gradients. The most known is the “Bergmann rule” which states that larger size is often achieved in colder climates than in warmer ones, which is linked to the temperature budget of these animals. Bergmann (Bergmann, 1848) proposed that larger animals are better enabled to conserve heat in colder climates. Bergmann’s patterns in ectotherms has yielded highly heterogeneous results. Some studies conform Bergmann’s rule, but others show other patterns, including positive relationships between body size and temperature (converse Bergmann’s rule), or no relationship at all (Shelomi, 2012; Vinarski, 2014).

The comparison of morphological features of organisms has been a central element of biology for centuries (Adams et al., 2004). There are numerous investigations dealing with morphological traits of carabids and their life strategies among different habitats (Braun et al., 2004; Gutiérrez, Menéndez, 1997; Magura et al., 2006; Niemelä et al., 2002; Ribera et al., 2001; Szyszko et al., 2000; Weller, Ganzhorn, 2004). But there are no investigations, concerning climatic factors impact on their body size variation. Few studies dealt with insects in a whole and suggested that climate warming would lead to body size decrease, especially in terrestrial taxa (Colinet et al., 2015; Verberk et al., 2021). Temporal decrease in size was already revealed in Scarabeidae species (Maher, Shelomi, 2022). As for carabids Szyszko et al. (2000) suggested the «mean individual biomass» (MIB) as an indicator of the state of succession in the environment.

Without diminishing the importance of this approach, it should nevertheless be emphasized that all microevolutionary processes take place on the population level. So intra-specific measuring should be processed to analyze drivers of body size variation in organisms. As for ground beetles the majority of studies, as mentioned above, were done exactly on assemblages level. But studies on population level is notable. Their body size varied in geographical and anthropogenic impact gradients (Sukhodolskaya, Eremeeva, 2013; Sukhodolskaya, 2014; Sukhodolskaya, Ananina, 2015). Modeling procedures also confirmed habitats vegetation cover effect on beetles size variation (Sukhodolskaya, Saveliev, 2016, 2017). Significant part of them concerns altitude variation in size (Ananina et al., 2020; Sukhodolskaya et al., 2021a): beetles size varied in elevation gradient declining in some species towards high mountains. Undoubtedly, severity of environmental conditions at high altitudes leads to such the consequences. Despite the absolute logic of those statements, none of those authors studied the specific climatic factors that might influence beetles body size. It has been done in relation to other species. Modeling climatic factors impact on ground beetle *Pterostichus melanarius* Ill. along its area and using BIOCLIM date base showed that temperature related factors mostly reduced beetles traits values, but precipitation related factors – enlarged them (Luzyanin et al., 2022). Mentioned paper dealt with generalist species distributed all over Eurasia. In mountain ecosystem, such the investigations did not take place. However, elevation changes in species traits, as the response to environmental factors effect in altitude gradient, reflect possible changes in population structure as the response to global climate changes. Besides, the problem of Sexual Size Dimorphism (SSD) exists. Females and males sometimes showed different patterns in body size variation in geographical gradients (Ananina et al., 2020; Sukhodolskaya et al., 2021b).

Wishing to fill this gap, we aimed our study to model bioclimatic factors impact on body size variation in two mountain ground beetle species – *Carabus odoratus* Shil. and *Pterostichus montanus* Motch. Beetles imagoes size mainly is affected by temperature and humidity of soil where their larvae grow. Then we hypothesized that: (a) beetles body size would correlate with annual temperatures; (b) beetles body size would correlate with soil mean humidity; (c) beetle body size would negatively correlate with population density; (d) response of species studied would vary due to the differences in their life-histories.

Materials and methods

Studied species

Two species of ground beetles were chosen as models (fig. 1).

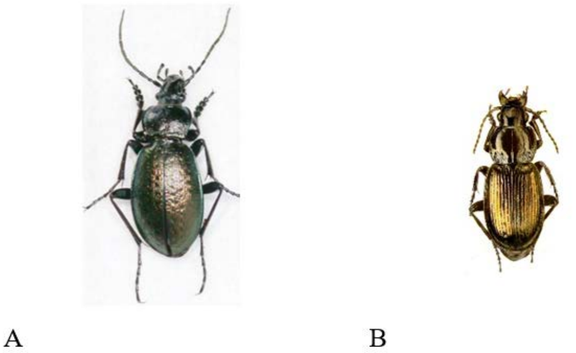


Fig. 1. Images of the studied species:
A – C. odoratus barguzinicus Shil, 1996;
photo by T.L. Ananina
B – P. (Petrophilus) montanus Motschulsky, 1844
(Carabidae of the world, 2017)

C. odoratus barguzinicus is the Baikal subspecies of *C. odoratus*. It is distributed from the Yamal Peninsula and all-around Siberia to the Magadan area and the Kamchatka Peninsula. The species has a large number of subspecies and local forms. In Siberia and north of the Russian Far East, the species is represented by 20 subspecies (Obydov, 2006). *C.odoratus bargusinicus* is endemic, and generalist in Barguzin Ridge (18.4% of the total population) (Shilenkov, 1996), an eurytopic species with mountain-forest features, early summer species by type of reproduction, recycling. Previous studies of carabid beetles at high altitudes have demonstrated the prolonged adult life cycles (more than one or two years) because the annual length of the growing season is too short (Sharova, Dushenkov, 1979; Sharova, Khobrakova, 2005). The species lives in all altitude zones from the Lake Baikal shore to the high mountains.

P. montanus is another boreal Eastern Palaearctic species distributed from the Ural to the Far East and northern Mongolia (Sharova, Dushenkov, 1979), generalist ground beetle species (19.7% of the total population). In adjacent territories the species lives exclusively in the mountains. In the conditions of the Barguzin Ridge, the species descends to the coast of Baikal. Therefore, the *P. montanus* is eurytopic mountain-forest species and belongs to the ecological group "lowered alpines" (Sharova, Khobrakova, 2005). It has one-year life cycle, early summer-spring type of reproduction, monocyclic (Ananina, 2020).

Study sites

The studied territories are located in the Southern Siberian Mountain. The key plot of entomological research is located at Barguzin State Natural Biosphere Reserve, S = 375 thousand hectares (N 54°20'; E 109°30'; Republic of Buryatia, Russia) on the western macroslope of the same name Ridge. It is on the northeastern coast of Lake Baikal.

The study area is a part of the Baikal-Dzhugdzhur mountain-taiga region of North Asia. The climate is sharply continental, with marine features. Average long-term annual air temperatures are –2.7°C. The coldest months of the year are January (–22.7°C) and February (–21.4°C). The warmest months of the year are July (12.9°C) and August (13.5°C). The average annual level of atmospheric precipitation is 421 mm (in the warm period of the year – 251 mm, in the cold period of the year – 170 mm).

The area has frosty long winters and cool short summers. The continentality decreases during the transitional seasons of the year: in spring, Baikal cools the air, and in autumn, it gives heat off. Here, the development of a special wet Baikal type of zonation associated with the inversion phenomenon is noted. Thus, on the shores of Lake Baikal, a pseudo subalpine belt formed (larch forests and clumps of dwarf cedar). The lattter does not rise above 100 m above the lake level (Tyulina, 1967). Eight entomological sites were located in experimental biotopes along a 30-km high-altitude transect in the Davsha river valley, from the coast of Lake Baikal to the subalpine belt. The altitude sections: coast, 458–500 m above sea level; low mountains (the lower part of the mountain forest belt, 501–720 m); middle mountains (the upper part of the mountain–forest belt, 721–1004 m), and high mountains (subalpine vegetation belt, 1005–1667 m). In the coastal transect part we investigated beetles in Blueberry cedar and Herbaceous birch forest; in the low mountains – Blueberry larch and Bergenia cedar; in the middle mountains – Bergenia aspen and Blueberry fir; in the high mountains – Blueberry tundra and Lichen tundra biotopes (tab. 1).

At each plot we recorded climatic parameters. Their list and mean annual values are presented in table 2.

Ground beetle sampling

We used pitfall traps for beetles sampling – glass jars with of 70 mm in diameter and 0.5 liters in volume, with 4% formalin as a fixative. Pitfall traps were placed in a straight line at 5 m interval. We selected captured insects every decade (every 10 days) from the third decade of May to the second decade of September in 2004 – 2017. In each biotope, during the study period, we worked out 1708 trap-days on the coast, 1400 trap-days in the low-mountain belt, and 1260 trap-days in the middle and high mountains. In total, 45673 ground beetles were caught.

We selected undamaged specimens for analysis, but without fixing the selection time (year, month, and decade). In total 2200 specimen of *C. odoratus* and *P. montanus* were selected and measured individually for six traits: elytra length (distance between posterior end of scutellum and terminus of right elytron, in the case of absence of intact right elytron, left one is acceptable) and width (distance between anterior-distal corners of elytra), pronotum length (measured along of central furrow) and width (distance between posterior corners of the pronotum), head length (distance between labrum and juncture of occiput and postgena) and distance between eyes in each beetle.

Statistical analysis

Table 1. Characteristics and location of studied biotopes on the altitudinal transect in the Barguzin Ridge

№	Biotope name	Main forest-forming species	Land cover	Hight, abs. m	Coordinates
1	Blueberry cedar	*Pinus sibirica* Du Tour	*Vaccinium myrtillus* L.	460	54.36 N 109.49 E
2	Herbaceous birch	*Betula baikalensis* Suk.	*Pyrola incarnata* (DC.), *Arctostaphylos uva-ursi* (L.)	485	54.358 N 109.50 E
3	Blueberry larch	*Larix sibirica* Ledeb.	*Vaccinium uliginosum* L.	518	54.21 N 109.30 E
4	Bergenia cedar	*Pinus sibirica* Du Tour	*Vaccinium myrtillus* L,	635	54.46 N 109.85 E
5	Bergenia aspen	*Populus tremula* L.	*Bergenia crassifolia* L.	712	54.23 N 109.43 E
6	Blueberry fir	*Abies sibirica* Led.	*Vaccinium myrtillus* L.	1278	54.39 N 109.69 E
7	Blueberry tundra	*Pinus pumila* Pall.	*Vaccinium myrtillus* L.	1637	54.34 N 109.83 E
8	Lichen tundra	*Rhododendron aureum* G.	*Cladonia rangiferina* L.	1701	54.34 N 109.83 E

Table 2. Climatic parameters and abundance of species studied

Factors/Biotopes	Blueberry cedar	Herbaceous birch	Blueberry larch	Bergenia cedar	Bergenia aspen	Blueberry fir	Blueberry tundra	Lihen tundra
Soil temp., depth 5 cm, ºC	12.1	14.5	12.3	11	11.2	9.5	10.4	7.9
Soil temp., depth 10 cm, ºC	11.9	13.7	11.3	10.5	10.7	7.8	10	7.5
Min soil temp., ºC	4.1	5.3	3.3	4.5	8.2	-	4.3	3.9
Precipitation, mm	153	153	200	178	178	252	-	453
Beginning t >0°C, months-decades	V-3	V-3	V-1	V-2	V-2	VI-1	VI-3	VI-3
Snow cover thickness, cm	42	42	43	58	76	138	167	167
Snow cover duration, days	171	171	180	180	230	230	245	245
Frost-free period, days	123	123	140	140	135	135	113	113
Min temperature in July, ºC	8.8	8.8	10	10.5	10.5	9.5	8.7	8
Min temperature in January, ºC	-31.4	-12.5	-12.9	-11.5	-5.8	-1.7	-1.7	-1.6
P. montanus abundance, ind. 100 trap/day	8	10.5	11.9	27.8	19.3	22.6	5.3	5.6
C. odoratus abundance, ind. 100 trap/day	1.3	2.1	14.8	15.9	16.7	17.3	18.5	19.3

We used linear models to evaluate environmental factors impact on beetles' body size variation. Independent variables: soil humidity, soil temperature at 5 and 10 cm depth, minimal temperatures at the soil surface, precipitation level, the date of positive temperatures of soil, population number, snow depth, frost-free period, snowpack, minimal soil temperatures in July and January.

We processed data in R using linear models (R Development Core Team, 2021). The latter permited us to conclude what environmental factor affected beetles size and led to the different responses in males and females.

$$Size_{i,j,k} = a_{i,0} + a_{i,1} \cdot I^{male}_{i,j,k} + a_{i,2} \cdot X_{i,j,k} + a_{i,3} \cdot I^{male}_{i,j,k} \cdot X_{i,j,k} + \varepsilon_{i,j,k}$$

$$\varepsilon_{i,j,k} \sim Norm(0, \sigma^2_{i,j})$$

a_{i1}–the difference between the average size of females and males in a whole by all data set;

a_{i2}–the value of shift in female trait size under the certain environmental factor impact; if it was positive, the factor increased female's trait size, if it was negative – the factor decreased females size;

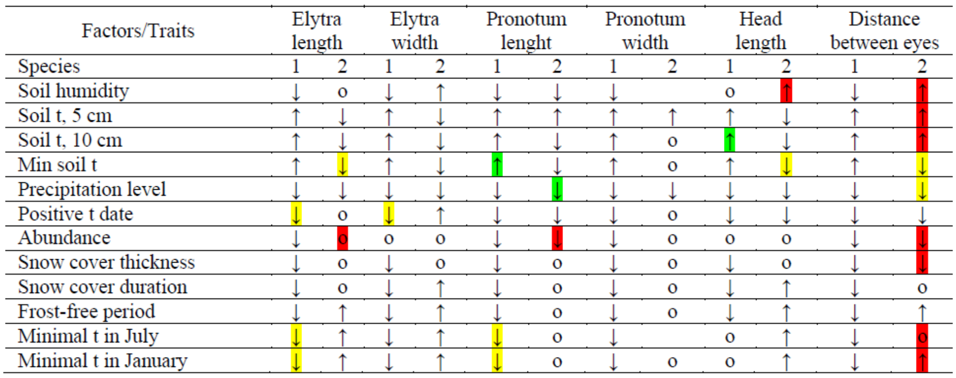
a_{i3} – the difference in response to the certain climatic factor in males compared with of females and its significance; in other words, a_{i3} told that the shifts in traits differed in males and females in value (or SSD was recorded).

Results

Results of bioclimatic factors impact on beetles' body size variation are presented in Table 3.

Comparing two species response to the climatic factors, we noted that response was exactly the opposite. We have studied 72 cases (12 factors multiplied by 6 traits) and in 52 cases (72%) the response discussed was the opposite. If we differentiate climatic factors according to their nature, the result was as follows. Temperature-depended factors in 81% of cases influenced *C. odoratus* and *P. montanus* in different directions. For instance, the higher was soil temperature at the 5 cm depth the longer were

Table 3. Directions of shifts in traits value under climatic factors impact in studies species



Factors/Traits	Elytra length		Elytra width		Pronotum lenght		Pronotum width		Head length		Distance between eyes	
Species	1	2	1	2	1	2	1	2	1	2	1	2
Soil humidity	↓	o	↓	↑	↓	↓	↓		o	🟥↑	↓	🟥↑
Soil t, 5 cm	↑	↓	↑	↓	↑	↑	↑	↑	↑	↓	↑	🟥↑
Soil t, 10 cm	↑	↓	↑	↓	↑	↓	↑	o	🟩↑	↓	↑	🟥↑
Min soil t	↑	🟨↓	↑	↓	🟩↑	↓	↑	o	↑	🟨↓	↑	🟨↓
Precipitation level	↓	↓	↓	↓	↓	🟩↓	↓	↓	↓	↓	↓	🟨↓
Positive t date	🟨↓	o	🟨↓	↑	↓	↓	↓	o	↓	↓	↓	↓
Abundance	↓	🟥o	o	o	↓	🟥↓	↓	o	o	o	↓	🟥↓
Snow cover thickness	↓	o	↓	o	↓	o	↓	o	↓	o	↓	🟥↓
Snow cover duration	↓	o	↓	↑	↓	o	↓	o	↓	↑	↓	o
Frost-free period	↓	↑	↓	↑	↓	o	↓	o	↓	↑	↓	↑
Minimal t in July	🟨↓	↑	↓	↑	🟨↓	o	↓		o	↑	↓	🟥o
Minimal t in January	🟨↓	↑	↓	↑	🟨↓	o	↓	o	o	↑	↓	🟥↑

Notes: 1 – *C. odoratus*, 2 – *P. montanus*, ↑ – positive correlation, ↓ – negative correlation, o – no correlation; arrows colour: yellow – males changed in the same direction with females, but to a lesser degree than females; green – males changed in the same direction with females, but to a greater degree than females; red – males changed in an opposite direction compared with females

elytra length in *C. odoratus*, but the shorter were in *P. montanus* etc.

Similarly snow-depended factors acted, and the only in one case (impact of snow cover thickness on the trait «distance between eyes») the response of both species was similar. Humidity-depended factors influenced both species in the same way and in the only 33% of cases the response of species trait was the opposite.

We could not conclude that different traits reaction on climatic factors was specific: elytra parameters as well as pronotum and head ones responded just about similarly in both species.

Population density affected beetles size more often in *C. odoratus*, decreasing traits size. Therefore, that species was more sensitive for environmental factors variation.

Sexual Size Dimorphism appeared more frequently in *P. montanus*. Among 72 cases studied SSD in *C. odoratus* was observed only in eight cases and in all of them direction of traits shifts were similar in both sexes. In *P. montanus* we observed 10 cases with multidirectional changes in males and females among 15 registered. So *P. montanus* seemed to be more labile under the climatic factors impact. What factors lead to SSD appearance? In relation to temperature-dependent factors, we had 36 cases for analysis. Among them 15 ones (42%) with SSD result. The latter appeared quantitatively similarly in *C. odoratus* and P. *montanus*. Humidity-dependent factors only in 33% of cases studied lead to SSD and snow-dependent factors lead to SSD only in one case (5%). Therefore, we concluded that temperature was the main factor that increased traits variation and consequently led to SSD appearance.

Discussion

Body size at *C. odoratus* and *P. montanus* varied differently in altitude gradient. *C. odortus* traits decreased monotonically (Ananina et al., 2020). *P. montanus* had saw-tooth curve of body size variation with regression coefficient about zero. In other words, *P. montanus* size did not change in elevational gradient (Sukhodolskaya et al., 2021a).

Preliminary results in bioclimatiac factors impact on beetles' body size were published in some conference papers (Sukhodolskaya et al., 2022a, b).

Humidity-depended factors (humidity, precipitation) level affected *C. odoratus* negatively: the higher was those factors value the smaller was beetles size. Temperature-dependent factors, on the contrary, positively influenced beetles size: the higher was soil temperature at depth of 5 and 10 cm the larger were the beetles (Sukhodolskaya et al., 2022a). For *P. montanus* the results were somewhat different. Beetles size decreased with decreasing temperature at the 10 cm depth and minimal temperature of the soil, but it decreased with the precipitation increasing and late dates of positive temperatures at the surface (Sukhodolskaya et al., 2022b). Positive effect on beetles' size had snow cover depth, frost-free period duration, and minimal temperatures of the soil surface in July and under snow in January.

Our study with comparative analysis in two species body size variation showed that studied species response to bioclimatic factors was directly opposite in the majority of cases. SSD in response to climatic factors emerged in them differently also.

Thus, those two species demonstrated two different life strategies: different ways of body size variation in altitude gradient and different response to climatic factors as well. SSD was more pronounced in *P. montanus*. It is believed that SSD is more pronounced in severe environment (Geodakyan, 1991). Extreme weather events such as heat waves are predicting to increase in the course of global climate change. Widespread species are exposing to a variety of environmental conditions throughout their distribution range, often resulting in local adaptation (Günter et al., 2020). The latter authors working with butterfly *Pieris napi* showed 'pace-of-life' syndrome when northern populations had a slower life style and invested more strongly into maintenance, while those from warmer regions showed the opposite pattern. In our case, populations from different elevations could also vary in their capacity to deal with challenging conditions such as thermal stress. *C. odoratus* и *P. montanus* habitate similar biotopes at Barguzin Ridge. They are generalists, and have colonized all altitude belts. Both are mountain – forest species (Sharova, Dushenkov, 1979). Nevertheless, they differ significantly in life-style histories, namely specific ways of adaptation (Chernov, 2008) to Barguzin Ridge environment (Matalin, 2007). *C. odoratus* has 2 or 3-year cycle with delayed development during several seasons. Both imagoes and larvae hibernate. *P. montanus* has strict life cycle: it finishes development in a single season and only imagoes hibernate.

The above features determine the cyclicity of reproduction: *C. odoratus* is the polycyclic and *P. montanus* is the monocyclic. Species differ in reproduction phenology also. *C. odoratus* comes to the surface at the second or third decades of June, it is middle-summer species. *P. montanus* imagoes comes to the soil surface in the third decade of May, it is early-summer species. *C. odoratus* is «walking epigeont», it dwells on the soil surface. *P. monatus* lives in litter. They differ in body sizes also, *C. odoratus* being larger than *P. montanus*. All above-mentioned characters allow us to suggest that the ways of adaptation to environment are different in two studied species. We consider *C. odoratus* to have inert type of adaptation. It adaptively acclimatizes to the short vegetation season. The latter allows it to habitat open biotopes in high mountains. *P. montanus* conceivably has active adaptation, striving to complete life cycle in a single season. Its refuge is a thick layer of litter, which is more common in low mountains. Therefore, adaptation to climatic factors appeared to be genera-specific. Natural environmental factors (e.g., climate and elevation) often jointly affect species. It is important to identify the real effects of individual factors for understanding the environmental process. Our field experiment was controlled as we took instrument readings systematically at our plots and then modeled factors impact on beetles size. Elevational gradients are closely associated with abiotic factors at small spatial scales and is an instrument to reveal species' adjustments to climatic and other environmental factors. Genera-specific response to them shown in our work seems to be not altitude-dependent. Perhaps other factors, not included into the study design, were responsible to such results. Similar propositions the other author made when working with dark bush-crickets (Jarčuška et al., 2023). Environmentally-induced plasticity can be explained by resource-based habitat concept or the plants richness at the habitats (Schuldt et al., 2019; Hansen et al., 2023).

Funding: The study was carried out within the framework of State Assignment on the topic 730000P.16.1.OH17AA33OOO «Investigations in East Europe Diversity in Conditions of Nature-Climate and Anthropogen Impact in Historical and Modern Contexts»

Acknowledgments: We are grateful to the administration of «Zapovednoe Podlemorie» for our expeditions processing.

References

1. Adams D.C., Rohlf F.J., Slice D.E. Geometric morphometrics: ten years of progress following the 'revolution'// Italian journal of zoology. 2004. 71(1). P. 5–16. https://doi.org/10.1080/11250000409356545.

2. Ananina T.L. Results of Long-Term Monitoring of the Genus Carabus (Coleoptera: Carabidae) in the Barguzinsky Range (Northern Baikal Region) // Contemporary Problems of Ecology. 2020. 13(4). P. 391–400 (in Russian). https://doi.org/10.1134/S1995425520040046.

3. Ananina T., Sukhodolskaya R., Saveliev A. Altitudinal variation of sexual size dimorphism in ground beetle *Carabus odoratus* Shill. //GSC Biological and Pharmaceutical Sciences. 2020. 12(2). P. 27–36. https://doi.org/10.30574/gscbps.2020.12.2.0216.

4. Bergmann C. Über die Verhältnisse der Wärmeökonomie der Thierezuihrer Grösse. 1848. 125 p.

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

6. Carabidae of the World. http://www. carabidae.org (accessed 12.08.2023).

7. Chernov Y.I. Ecology and biogeography: selected studies. Moscow: KMK, 2008. 580 p. (in Russian)

8. Colinet H., Sinclair B.J., Vernon P., Renault D. Insects in fluctuating thermal environment // Annual review of entomology. 2015. 60. P. 123–140.

9. Geodakyan V.A. Evolutionary theory of sex // Priroda. 1991. №8. P. 9–60. (in Russian)

10. Günter F., Beaulieu M., Franke K., Toshkova N., Fischer K. Clinal variation in investment into reproduction versus maintenance suggests a 'pace-of-life'syndrome in a widespread butterfly. Oecologia. 2020. 193(4). P. 1011–1020. https://doi.org/10.1007/s00442-020-04719-4.

11. Gutiérrez D., Menéndez R. Patterns in the distribution, abundance and body size of carabid beetles (Coleoptera: Carabidea) in relation to dispersal ability // Journal of biogeography. 1997. 24(6). P. 903–914.

12. Hansen R.R., Damgaard R.F., Kjær C., Rasksen M.B., Thomsen P.F., Strandberg M.T. Quantification of arthropod species resources using distance-based measures – Ground beetles as focal group // Ecological indicators. 2023. 147. P. 110026. https://doi.org/10.1016/j.ecolind.2023.110026.

13. Hodkinson I.D. Terrestrial insects along elevation gradients: species and community responses to altitude // Biological reviews. 2005. 80(3). P. 489–513. https://doi.org/10.1017/S1464793105006767.

14. Jarčuška B., Krištín A., Kaňuch P. Body size traits in the flightless bush-cricket are plastic rather than locally adapted along an elevational gradient // Evolutionary ecology. 2023. 37(3). P. 1–22. https://doi.org/10.1007/s10682-023-10231-x.

15. Luzyanin S.L., Gordienko T.A., Saveliev A.A., Ukhova N.L., Vorobeva I.G., Solodovnikov I.A., Anciferov A.L., Nogovitsyna S.N., Aleksanov V.V., Teofilova, T.M., Sukhodolskaya R.A. Impact of climatic factors on sexual size dimorphism in ground beetle *Pterostichus melanarius* (Illiger, 1798) (Coleoptera, Carabidae) // Ecologica Montenegrina. 2022. 58. P. 1–13. https://doi.org/10.37828/em.2022.58.1.

16. Magura T., Tóthmérész B., Lövei G.L. Body size inequality of carabids along an urbanisation gradient // Basic and applied ecology. 2006. 7(5). P. 472–482. https://doi.org/10.1016/j.baae.2005.08.005.

17. Maher I.M., Shelomi M. Increasing body sizes in *Anomala expansa expansa* (Coleoptera: Scarabaeidae) // Populations in response to rising temperatures over time. 2022. 51(4). P. 798–805. doi: 10.1093/ee/nvac032. PMID: 35641116.

18. Matalin A.V. Typology of life cycles of ground beetles (Coleoptera, Carabidae) in Western Palaearctic // Entomological review. 2007. 87(8). P. 947–972. (in Russian) https://doi.org/10.1134/S0013873807080027.

19. Niemelä J., Kotze D.J., Venn S., Penev L., Stoyanov I., Spence J., Hartley D., De Oca E.M. Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison // Landscape ecology. 2002. 17(5). P. 387–401.

20. Obydov D. A new subspecies of *Carabus (Morphocarabus) odoratus* Motchulsky, 1844 (Coleoptera, Carabidae) from Eastern Siberia // Munis entomology & zoology. 2006. 1(1). P. 149–154.

21. R Development Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2021. http://www.R-project.org (accessed: 20.05.2023).

22. Ribera I., Dolédec S., Downie I.S., Foster G.N. Effect of land disturbance and stress on species traits of ground beetle assemblages // Ecology. 2001. 82(4). P. 1112–1129. https://doi.org/10.1890/0012-9658.

23. Schuldt A., Ebeling A., Kunz M., Staab M., Guimarães-Steinicke M., Bachmann D., Durka W., Fichtner A., Fornoff W., Härdtle W., Hertzog L.R., Klein M., Roscher C., Schaller J. von Oheimb G. Multiple plant diversity components drive consumer communities across ecosystems // Natural Communities. 2019. 10(1). P. 1460.

24. Sharova I.K., Dushenkov V.M. Types of Development and Types of Seasonal Activity in Ground Beetles (Coleoptera, Carabidae) // Fauna I ekologiya bespozvonochnykh. M:MGPI, 1979. P. 15–25. (in Russian).

25. Sharova I.K., Khobrakova L.T. Features of the life cycles of *Pterostichus montanus* (Motschulsky, 1844) and *Carabus loschnikovi* (Fischer-Waldheim, 1822) (Coleoptera, Carabidae) in conditions of the mountain taiga belt in the Eastern Sayan // Biology bulletin. 2005. 32(1). P. 27–37. (in Russian)

26. Shelomi M. Where are we now? Bergmann's rule sensu lato in insects // The American naturalist. 2012. 180(4). P. 511–519. https://doi.org/10.1086/667595.

27. Shilenkov V.G. Ground Beetles of Carabus L. genus of Southern Siberia. Irkutsk: Irkutsk State University Publ.,1996. 80 p. (in Russian)

28. Sukhodolskaya R.A. Variation in body size and body shape in ground beetle *Pterostichus melanarius* Ill. (Coleoptera, Carabidae) // Journal of agri-food and applied sciences. 2014. 2(7). P. 196–205.

29. Sukhodolskaya R.A., Ananina T.L. Altitudinal variation in population density, body size and morphometric structure in *Carabus odoratus* Shil, 1996 (Coleoptera: Carabidae) // Acta biologica Universitasis Daugavpiliensis. 2015. 15(1). P. 179–190.

30. Sukhodolskaya R.A., Eremeeva N.I. Body size and shape variation in Ground Beetle Carabus aeruginosus F.-W., 1822 (Coleoptera, Carabidae) // Contemporary problems of ecology. 2013. 6(6). P. 609–615.

31. Sukhodolskaya R.A., Saveliev A.A. Crop impact on body size variation in carabid beetle Poecilus cupreus Linnaeus (Coleoptera, Carabidae) // Ukrainska entomofaunistyka. 2016. 3(7). P. 85–91. https://doi.org/10.2991/isees-18.2018.3.

32. Sukhodolskaya R.A., Saveliev A.A. Biotope vegetation role in body size variation in ground beetles (Coleoptera, Carabidae) // Biological systems: sustainability, principles and functioning mechanisms / Materials of the V All-Russia conference. Nizsniy Tagil, 2017. P. 311–315. (in Russian)

33. Sukhodolskaya R.A., Ananina T.L., Saveliev A.A. Variation in Body Size and Sexual Size Dimorphism of Ground Beetle *Pterostichus montanus* Motsch.(Coleoptera, Carabidae) in Altitude Gradient // Contemporary problems of ecology. 2021a. 14(1). P. 62–70. https://doi.org/10.1134/S199542552101008X.

34. Sukhodolskaya R., Ananina T., Avtaeva T., Saveliev A. Sexual size dimorphism in ground beetles and its variation in altitude gradient // Advances in medicine and biology. 2021b. 191 p.

35. Sukhodolskaya R.A. Ananina T.L., Saveliev A.A. Impact of environmental factors on the variability of body size and sexual size dimorphism of *Carabus odoratus* Shill. (Carabidae, Coleoptera) // Actual problems of ecology / Proceedings of the conference. Grodno, 2022a. P. 160–161.

36. Sukhodolskaya R.A., Ananina T.L., Savelyev A.A. Influence of environmental factors on the variability of the size of ground beetles in high mountains // Biological diversity of the Caucasus and the South of Russia / Proceedings of the XXIV international scientific conference. Magas, Makhachkala, 2022б. P. 457–459. (in Russian)

37. Szyszko J., Vermeulen H.J.W., Klimaszewski K., Abs M., Schwerk A. Mean individual biomass (MIB) of ground beetles (Carabidae) as an indicator of the state of the environment // Natural history and applied ecology of carabid beetles. Sofia, Moscow: Pensoft, 2000. P. 289–294.

38. Tyulina L.N. The vegetation zones in the western and eastern coasts of Northern Baikal. Geobotanicheskie issledovaniya na Baikale (Geobotanical studies in the Baikal Region). Moscow, 1967. P. 3–44. (in Russian)

39. Verberk W., Atkinson D., Hoefnagel K.H., Hirst A.G., Horne C.R., Siepel H. Shrinking body sizes in response to warming: explanations for the temperature – size rule with special emphasis on the role of oxygen // Biologocal reviews. 2021. 96. P. 247–268. https://doi/10.1111/brv.12653.

40. Vinarski M.V. On the applicability of Bergmann's rule to ectotherms: the state of the art // Biology bulletin reviews. 2014. 4(3). P. 232–242. https://doi.org/10.1134/S2079086414030098.

41. Weller B., Ganzhorn J.U. Carabid beetle community composition, body size, and fluctuating asymmetry along an urban–rural gradient // Basic and applied ecology. 2004. 5(2). P. 193–201. https://doi.org/10.1078/1439-1791-00220.

Ананина Т.Л., Савельев А.А., Шагидуллин Р.Р., Гордиенко Т.А., Суходольская Р.А. **Климатические факторы могут по-разному влиять на размер тела у близкородственных видов (на примере жуков-жужелиц).**

Изучение изменчивости размеров тела в высотном градиенте показало наличие сдвигов в морфометрических характеристиках популяций жуков жужелиц под влиянием биоклиматических факторов в горах. Жужелицы были собраны на Баргузинском хребте (Россия, Бурятия) в восьми характерных биотопах на четырех высотных участках: на побережье озера Байкал, в низких, средних и высоких горах (458–1667 м над уровнем моря). На каждом участке в 2004–2017 гг. проводили количественный учет жуков и регистрировали основные климатические параметры с помощью термохронов, осадочных цилиндров, почвенных термометров и снегомера. Для морфометрического анализа были взяты два вида *Carabus odoratus* и *Pterostichus montanus* (2200 экземпляров). Измеряли шесть признаков – длину и ширину надкрылий, длину и ширину переднеспинки, длину и расстояние между глазами головы. С помощью линейного моделирования исследовали, как климатические переменные влияют на размеры тела изучаемых видов. Сравнивая реакцию двух видов на гидроклиматические параметры, отметили, что на температурные показатели реакция была прямо противоположной, а на факторы, зависящие от влажности, – сходной. Например, чем выше температура почвы на глубине 5 см, тем больше длина надкрылий, переднеспинки и головы у *C. odoratus*, но те же признаки были меньше у *P. montanus* и др. Увеличение численности популяции у *C. odoratus* привело к уменьшению большего числа признаков, чем у *P. montanus*. По родовому признаку *C. odoratus* оказался более чувствительным к изменению биоклиматических факторов.

Ключевые слова: жуки-жужелицы; изменчивость размеров тела; климатические факторы; численность; горы.

Раскрытие информации о конфликте интересов: Автор заявляет об отсутствии конфликта интересов / Disclosure of conflict of interest information: The author claims no conflict of interest

Информация о статье / Information about the article
Поступила в редакцию / Entered the editorial office: 31.07.2023
Одобрено рецензентами / Approved by reviewers: 17.08.2023
Принята к публикации / Accepted for publication: 28.08.2023

Сведения об авторах

Ананина Татьяна Львовна, кандидат биологических наук, ведущий научный сотрудник, ФБГУ «Заповедное Подлеморье», 671623, Россия, г. Усть-Баргузин, ул. Ленина, 71, E-mail: t_l_ananina@mail.ru.

Савельев Анатолий Александрович, доктор биологических наук, профессор, Казанский (Приволжский) федеральный университет, 420097, Россия, г. Казань, ул. Товарищеская, 5, E-mail: anatoly.saveliev.aka.saa@gmail.com.

Шагидуллин Рифгат Роальдович, доктор химических наук, член-корреспондент АН РТ, директор, Институт проблем экологии и недропользования АН РТ, 420087, Россия, г. Казань, ул. Даурская, 28, E-mail: Shagidullin_@mail.ru.

Гордиенко Татьяна Александровна, научный сотрудник, Институт проблем экологии и недропользования АН РТ, 420087, Россия, г. Казань, ул. Даурская, 28, E-mail: eiseniata@gmail.com.

Суходольская Раиса Анатольевна, кандидат биологических наук, старший научный сотрудник, Институт проблем экологии и недропользования АН РТ, 420087, Россия, г. Казань, ул. Даурская, 28, E-mail: ra5suh@rambler.ru.

Information about the authors

Tatyana L. Ananina, Ph.D. in Biology, Leading Researcher, FBSE «Zapovednoe Podlemorie», 71, Lenin st., Ust-Barguzin, 671623, Russia, E-mail: t_l_ananina@mail.ru

Anatoliy A. Saveliev, D.Sci. in Biology, Professor, Kazan Federal University, 5, Tovarisheskaya st., Kazan, 420097, Russia, E-mail: anatoly.saveliev.aka.saa@gmail.com.

Rifgat R. Shagidullin, D.Sci. in Chemistry, Corresponding Member of Tatarstan Academy of Sciences, Director, Research Institute for Problems of Ecology and Mineral Wealth Use of Tatarstan Academy of Sciences, 28, Daurskaya st., Kazan, 420087, Russia, E-mail: Shagidullin@mail.ru.

Tatyana A. Gordienko, Researcher, Research Institute for Problems of Ecology and Mineral Wealth Use of Tatarstan Academy of Sciences, 28, Daurskaya st., Kazan, 420087, Russia, E-mail: eiseniata@gmail.com.

Raisa A. Sukhodolskaya, Ph.D. in Biology, Senior Researcher, Research Institute for Problems of Ecology and Mineral Wealth Use of Tatarstan Academy of Sciences, 28, Daurskaya st., Kazan, 420087, Russia, E-mail: ra5suh@rambler.ru.