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BODY SIZE DECREASES IN ALTITUDE GRADIENT BUT SEXUAL SIZE DIMORPHISM DOES NOT IN GROUND BEETLE *CARABUS ODORATUS* SHIL.

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Author's contribution
RAS and TLA designed the study and wrote the paper. TLA collected the data and performed the morphometric analysis. AAS and TAG performed statisticalanalysis and illustrations.

Key words:
Body size variation, ground beetles, altitude gradient, sexual size dimorphism.

ABSTRACT

Attributing biological explanation to observed ecogeographical patterns requires intra-specific studies. Body size variation in latitude/altitude gradient and sexual size dimorphism variation reflect adaptation of the organisms to the varying environment and future climate impact. Investigations took place at Barguzinsky Ridge (North-East part of Baikal Lake, N 54° 20'; E 109° 30', Russia). Beetles of the Ground Beetle *Carabus odoratus* Shil. were sampled in 30 -km transect, divided into four plots – the coast, low-, middle- and high mountains (455-460, 500-720, 721-1300, 1301-1700 m above sea-level, respectively). In total 968 individuals were measured by six traits – the length and the width of elytra, pronotum and head. Our results showed that altitude and sex but not their interaction affected body size in *C. odoratus.* The values of all morphometric characters decreased towards the highlands in females and males. Sexual size dimorphism (SSD) varied in different traits: the highest values of SSD were recorded for the elytra length and the pronotum width (at all altitudes), and the head length (at the coastal and high mountains populations). For the other traits values of SSD at different altitudes did not differ significantly. The mean values of SSD for all the traits were similar at the coastal, low- and high mountains populations but in the middle mountains populations SSD was significantly lower.

1. INTRODUCTION

Body size is a vital trait which affects behavior, physiology and fitness in insects [1]. Large in size specimen can overcome difficulties more easily (food limitation, overwintering etc.) [2, 3, 4, 5]. Frequently larger sized insects cope better with stressful environments. Larger males mate more successfully [6, 7]. Larger females are more fertile [8, 9].

But benefits of large body size are not absolute always: they are limited under certain suboptimal conditions [10], large size requires more food, the longer development leads to increased risk of predation [11]. Thus, intra-species variation in body size is observed in environmental gradients. The most well-known ecogeographical Begrmann rule is devoted to interspecific variation in body size in latitudinal gradients: larger animals have the lower surface-to-volume ratio and then lose less heat in

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*Corresponding Author: t.l.ananina@mail.ru cold environment. However, at the intraspecific level in ectotherms, the validity of this rule is not entirely unambiguous: species can follow the rule, convert, or have some other image [12]. Several explanations for Bergmann rule exist: temperature variation during larval stages [3], food resources [10], season length and voltinism [13, 14].

Body size variation in insects in relation to Bergmann rule accordance is studied successfully in mountain ecosystems. The latter have unique biodiversity as a result of geologic history and specific environmental factors. Furthermore, adaptation of species to changing environment parameters varies along the altitudinal gradients. All this highlights the need for ecological investigations to assess the state of the mountain ecosystems. Insects body size variation in altitude gradient in various species differs: body size can decrease [15, 16, 17], increase [18] or be stable [19].

The females frequently are larger than males (SSD) in insects [20, 2, 21, 22]. Different net selection pressures on sexes affects SSD [23] and different response to abiotic factors in sexes leads to different body size clines in males and females [24, 25]. Generally, it is believed that males produce steeper geographical clines than females [26].

In our study we turned to Ground Beetles – the excellent bioindicators and model species [27]. Their body size variation relatively widely discussed, showing different types of this trait clines in latitude and altitude gradients as well [28, 29, 30, 31]. We put emphasis on sexual size dimorphism (SSD) in studied species of Ground Beetles *Carabus odoratus* and its variation in altitude gradient. So, we tested the following hypotheses: (i) female – biased SSD in *C. odoratus* is similar to the majority of other carabid species; (ii) the trends of body size variation in altitude gradient are similar in females and males; (iii) the value of SSD varies in altitude gradient.

2. MATERIALS AND METHODS

Sites and design: The study was performed in the Barguzinsky State Natural Biosphere Reserve (Republic of Buryatia, Russian Federation). The research area is located on the North-Eastern coast of Baikal Lake in the central part of the Barguzinsky Ridge. We sampled Ground Beetles at 30 km long transect in Davsha river valley. It crosses all high-rise belts from the shore of Lake Baikal to the watershed Davsha-Tarkulik rivers (second-order spur of the Barguzinsky Ridge).The study area is characterized by a relatively gentle rise from the shore of Lake Baikal (455m above sea level) to the low – mountain part of the ridge (at 535 m), steeper – to the upper border of the forest (1407 m), and a sharp rise to the highest point of the watershed – the pass (1700 m). A landscape features were designated as: the coast – 458-500 m above sea level, the low (the lower part of the mountain forest zone – 501-720 m), middle (upper part of the mountain forest zone – 721-1004 m), high (bald belt of vegetation – 1005-1700 m). Coast included biotopes with Bilberry cedar and Grass birch, the bottom part of the mountain forest zone (Low Mountain) – Blueberry larch and Red bilberry pine, middle mountains – Bergenia aspen and Bilberry abies, High mountains – Sparse birch woodland and Lichen tundra (Fig. 1).The climate of the studied region is sharply continental, with sea features. It is characterized by frosty long winters and cool short summers. Humid Baikal type of altitudinal zones, associated with temperature inversions, is formed on the western slopes of the Barguzinsky Ridge. The so-called "false-bald" vegetation belt, consisting of larch forests (*Larix czekanowskii*Szaf.), sparse thickets of cedar dwarf (*Pinus pumila* Reg.), golden rhododendron shrub (*Rododendron aureum* L.) developed from the coastline to 100 m above the lake level. These species grow both on the coast and in the high mountains but are absent in the low- and middle mountain vegetation belts. This fact testifies to the similarity of environmental conditions on the Baikal coast and the high mountains (Tyulina, 1954). Close analogs are noted on the Okhotsk sea coast [32] (Tyulina, 1967). *Carabus odoratus barguzinicus* Shil, 1996 was chosen as a model species for our research. This is the largest ground beetle that dwells here, convenient in measurement. *C. odoratus* is abundant (17.6 % of the total population) in the entire gradient of the Barguzin range. It is endemic there. According to the classification of life forms, *C. odoratus* belongs to walking epigebionts and zoophages with extra-intestinal digestion. The body is convex, the integument is strongly sclerotized. The head is narrower than the pronotum, and there are large compound eyes on the sides. Beetles hunt on the surface of the soil, eating sedentary prey. *C. odoratus* has a two or three-year life cycle with a summer development period and a winter diapause at the imago and larval stages in the study area. Two or three peaks of population growth during seasonal activity are recorded at different altitude levels. The first early peak associated with the emergence from hibernation and the beginning of sexual activity (in the third decade of June) is observed in the low mountains, later (in the first and second decades of July) – in the high mountains [33]. Quantitative counts of beetles were carried out on stationary sites of the altitude transect in 1988-2014 by means of pitfall traps [34] (Barber, 1931). We used glass jars with of 70 mm diameter and a volume of 0.5 liters, and used 4% formalin as a fixative. Pitfall traps were placed in a straight line at 5 m interval. The captured insects were selected every decade from the third decade of May to the second decade of September. The following measurements were made: elytra length and width, pronotum length and width, head length and distance between eyes (Fig. 2).

A –length of the elytra, B –length of the pronotum V– length of the head, G– width of the elytra, D – width of the pronotum, E – the distance between eyes.

We selected undamaged specimens for habitat analysis, but without fixing the selection time (year, month, decade). A total of 883 specimens of ground beetles were selected from 8 biotopes for the period 1988-2014.The sex of beetles was determined by the shape of the segments on the front legs - the segments in males are wide, and in females are narrow.

***Data analysis**:* In the analyses, body size was used as a proxy for describing environmental quality (temperature drops, humidity and as a consequence food availability, food quality): a larger final size was considered to indicate more favorable conditions during the juvenile development (a common practice in insect ecology) [35]. To study variation of sexual size dimorphism (SSD) we calculated the size dimorphism index (SDI) [36] by dividing the trait size of the females by the trait size of males and subtracting one, resulting in negative SDI when male's trait is larger, and positive values of SDI when female's trait is larger. In R environment we used ANOVA to detect effect $\alpha_{\text{coast\_high}}$ of altitude (coast_high), effect of Sex a_{Sex}, and effect of their interaction $\alpha_{Sex,\ coast_high}$the beetles traits variation. The models were as follows:

$$\text{Trait} = a_0+a_{Sex}+a_{coast\_high}+a_{Sex,\ coast\_high}+\varepsilon$$

If the interaction was significant, both variables were considered significant also. If the interaction was not significant, we excluded interaction and conducted the type-II ANOVA to detect the significance of the variables:

$$\text{Trait} = a_0+a_{Sex}+a_{coast\_high}+\varepsilon$$

3. RESULTS

Beetles body size monotonically decreased from the coast to the high mountains (Fig. 3 – 8) in females and males as well. The highest values of SSD were recorded for elytra length (at all altitudes) and for the pronotum width and the head length (at the coastal and high mountains populations). For the other traits values of SSD at different altitudes did not differ significantly (Fig. 9).

We calculated the mean value of SSD for all the traits at the certain altitudes: SSD were similar at the coastal and low mountains populations, then significantly decreased at the middle mountains and then increased again in the high mountains population (Fig. 10).

Sex ratio in all populations were female-biased with significant prevalence of females (Table 1).

Table 1. Sex ratio (females/males) in *C. odoratus* populations at different altitudes populations

	coast	low	middle	high
SR	2,50	1,53	1,51	1,56
χ^2	2,57	13,98	9,36	15,02

ANOVA showed that sampling elevation and sex are significant but their interaction - not in effect on beetles body size. Tables 2, 3 demonstrate elytra length variation.

Table 2. Results of elevation and sex interaction effect on elytra length variation in *C. odoratus* ($A = a_0+a_{Sex}+a_{coast\_high}+a_{Sex,\ coast\_high}+\varepsilon$)

	Df	F value	p-value
$a_{Sex,coast\_high}$	3	0.6391	0.5932

Hereafter: a_0 is constant, a_{sex} – sex effect, a_{coast_high}– altitude effect, and $a_{Sex,coast\_high}$– interaction between the sex and altitude effect, and ε - random error. Since the interaction was not significant, we performed the next model.

Table 3. Results of altitude and sex effects on elytra length variation in *C. odoratus* ($A = a_0+a_{Sex}+a_{coast\_high} +\varepsilon$)

	Df	F value	p-value
a_{Sex}	1	170.098	< 2.2e-16
A_{coast_high}	3	54.439	< 2.2e-16

4. DISCUSSION

In invertebrates, changes in body size with altitude often do not follow Bergmann rule. Rather, it has been shown to decrease with altitude in beetles and butterfly [37, 38], and a number of other studies also indicated converse-Bergmann rule or lack of pattern [39, 40]. Body size often correlates with development time, resulting in a converse-Bergmann cline, i.e., decreasing body size with shorter growing season at higher altitude, and this is conforming to our observations on *C. odoratus*[29]. The size of every 6 treated traits monotonically decreased towards the high altitudes. Smaller body size at high altitude in this study were hypothesized to be linked to high metabolic costs due to low temperature at high altitude which cannot be compensated for by increased feeding rate. At the family level, a negative relationship between altitude and insect (Carabid beetles) body length was found; this was predicted because of a decrease in the diversity of resources, habitat area and primary productivity, and the increase in the unfavorable environment observed at high altitudes [37, 41]. On community level mean individual biomass also decreased in ground beetle communities [42].We analyzed the variation in average body size with height in the studied ground beetle populations. The analysis showed a decrease in average body size with increasing height. However, at low altitudes there are both "large" and "small" individuals, and at high altitudes - mostly "small". This fact indicates a stronger selection pressure in the high mountain areas. Individuals living at high altitudes are probably unable to grow to large size. The adaptability of "small" beetles to difficult mountain conditions is much lower than the adaptability of "large" ones.

However, SSD did not change similarly. We did not investigate males and females sensitivity in the present paper, but in our earlier studies there had been shown that sensitivity in both sexes might be different in relation to different traits at the altitudes studied. Ground beetle *Pterostichus montanus* Motsch. is another dominant ground beetle species inhabiting all biotopes of the Barguzinsky Ridge (19.7% of the total population). It belongs to the group of litter-soil stratobionts, has a one-year life cycle [33]. On the contrary, according to the RMAII, the sensitivity of males was very high in the midlands [42]. Males *Pt. montanus* in the midlands reached larger sizes than females, and the SSD values were lower. A favorable habitat can be determined, in particular, by lower intraspecific competition, since the population density of *C. odoratus* is lower in middle mountains than in low and high mountains [43, 44]. In addition, there were significant differences in the interpopulation morphometric structure. The latter, apparently, reflects the height difference. Two relatively different environments often exist on the mountains: the 'upper mountain' environment, treeless and the subject to more extreme cold temperatures or different rainfall patterns (and often above the tree line), and the 'lower mountain' environment, which is covered with forest. There is a transitional zone between them - "middle mountain". In the Barguzinsky Ridge, the mid-mountain belt is steeper and colder than the low-mountain belt [45]. Another explanation for mid elevation diversity maxima is the 'mid-domain effect' (MDE). It argues that if all species ranges are scattered randomly between the limits of the top and bottom of a mountain, there will be a 'bulge' of maximum numbers of overlapping species in the mid elevations. A recent advance of MDE theory has been to include a midpoint attractor – a unimodal gradient of environmental favorability, using a Bayesian simulation model to estimate the location and strength of the attractor from empirical species distribution data along the elevations, within geometric constraints [46]. It has been suggested that gradients of environmental favorability, together with the geometric constraints imposed by the base of a mountain and its summit, will more parsimoniously explain elevational species richness patterns.

Information on sex-specific within-population variation along an altitudinal gradient could provide insight into mechanisms generating altitudinal clines in sexual size dimorphism, for example, by revealing that phenotype canalization in females is increased under harsh high-altitude conditions, that is, within population variability in female body size decrease. In general, patterns observed at scales within a population can provide useful additional information to patterns observed at scales between populations. Nevertheless, the sex bias in all the studied populations of *C. odoratus* indicates that the ecological conditions for this species are quite favorable at all altitudes.

5. CONCLUSION

Overall, considering that body size is a master trait driving fundamental characteristics of organisms, its study along altitudinal gradients under different bioclimates may allow better understanding of the factors driving elevational patterns in the populations' structure of Carabidae and ecogeographical rules as well. The proposition that Carabidae generally follow Bergmann rule or any common pattern is clearly challenged by available studies. The results suggest that to improve understanding of the drivers of the observed patterns further investigations on changes in ground beetles communities along altitudinal gradients should consider different species and bioclimatic contexts and use similar sampling designs.

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7. CONFLICT OF INTEREST

All authors have declared that there is no conflict of interests regarding the publication of this article.

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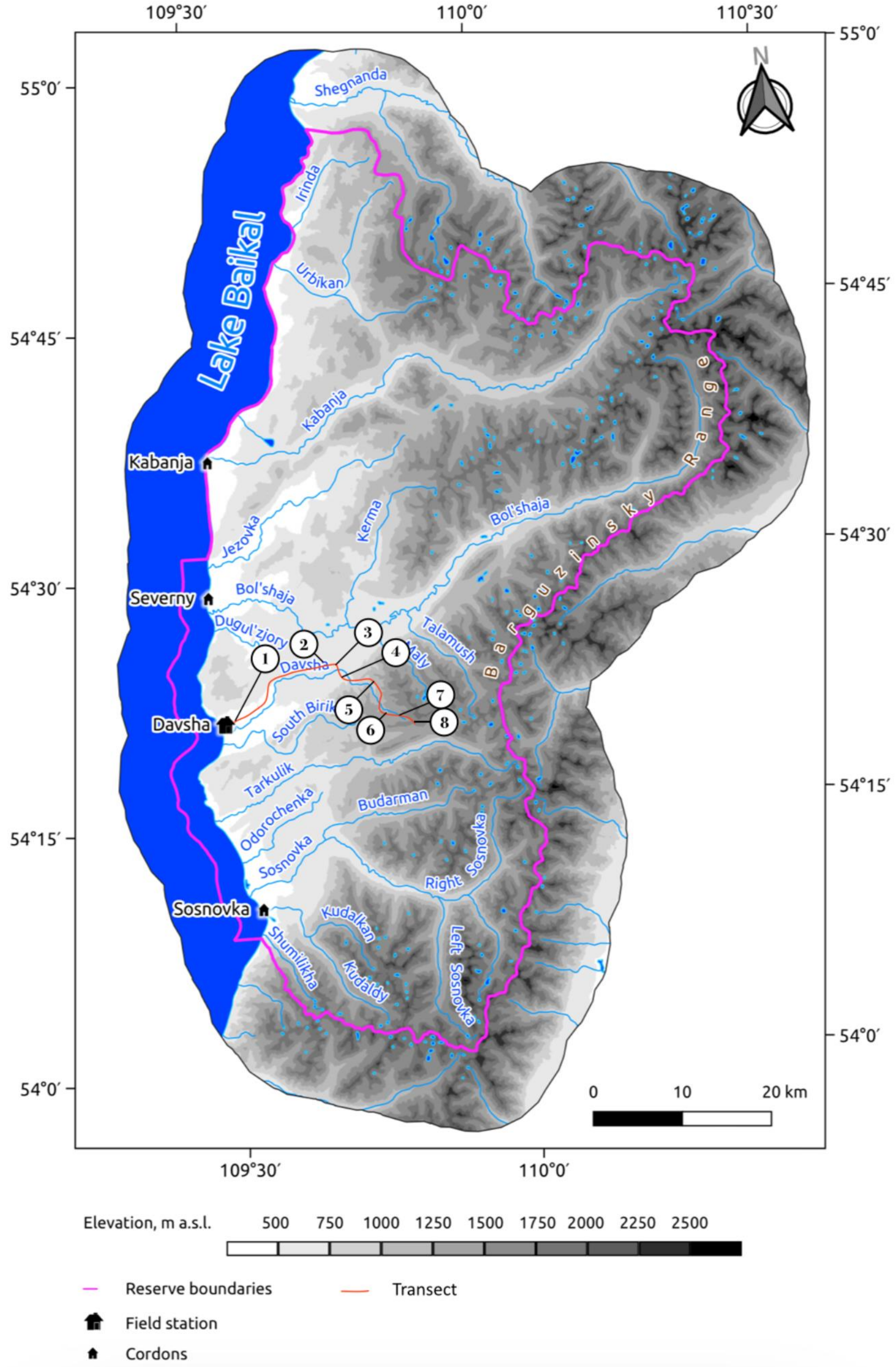

Fig.1. Location of entomological sites on the high-altitude transect of the Barguzinsky ridge: 1 – Bilberry cedar, 2 – Grass birch, 3 – Blueberry larch, 4 – Red bilberry pine, 5 – Bergenia aspen, 6 – Bilberry abies, 7 – Sparse birch woodland, 8 – Lichen tundra.

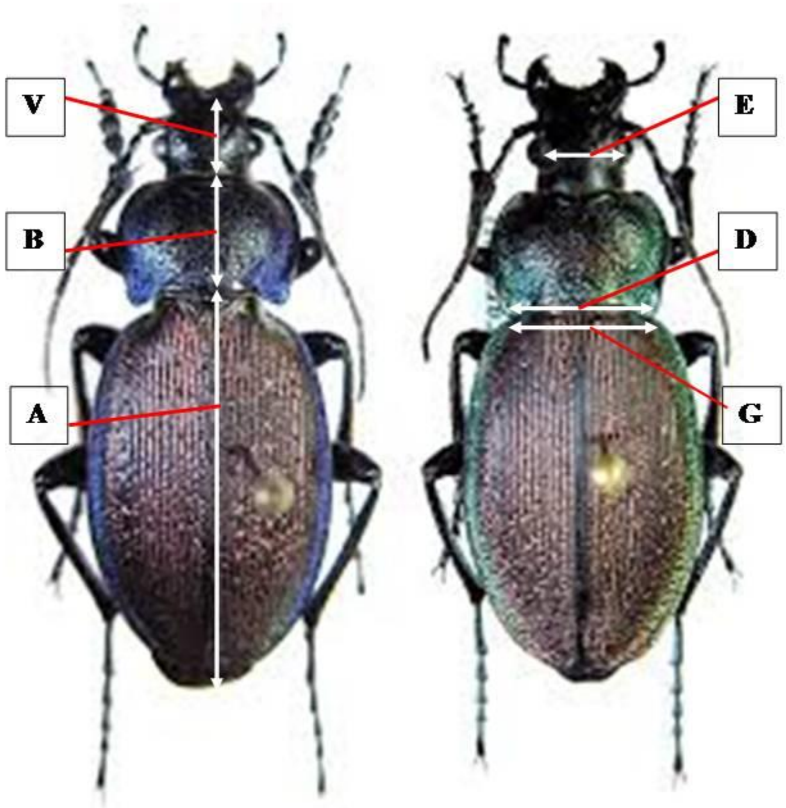

Fig. 2. Measured morphometric features *C. odoratus:*
A –length of the elytra, B –length of the pronotum V– length of the head, G– width of the elytra, D – width of the pronotum, E – the distance between eyes.

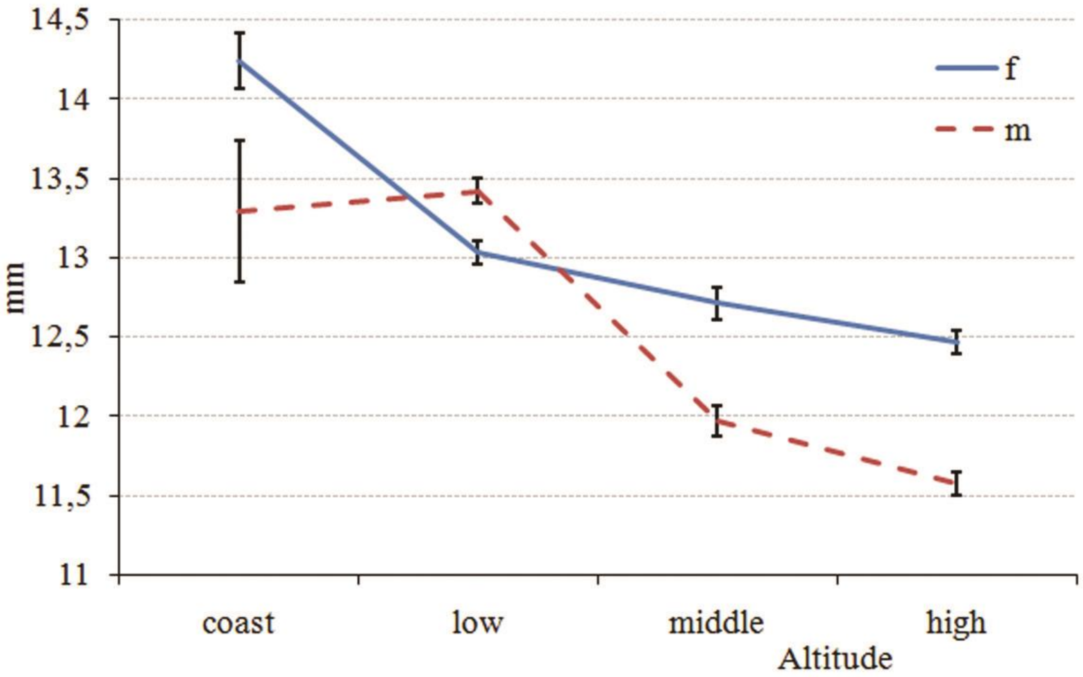

Fig. 3. Elytra length variation in *C. odoratus*

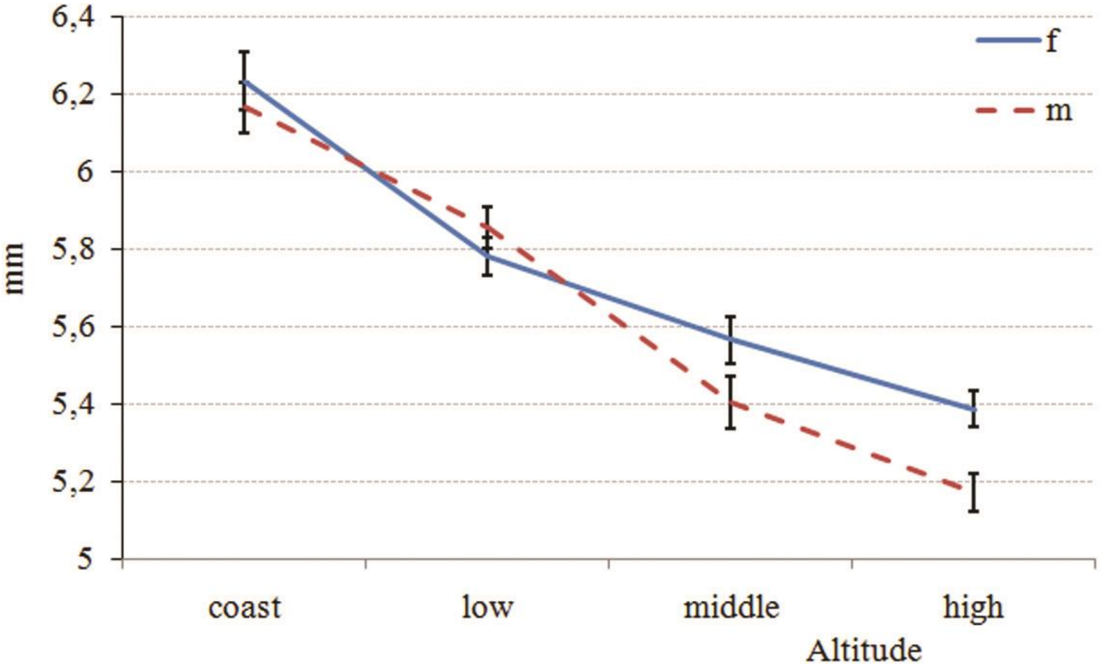

Fig. 4. Elytra width variation in *C. odoratus*

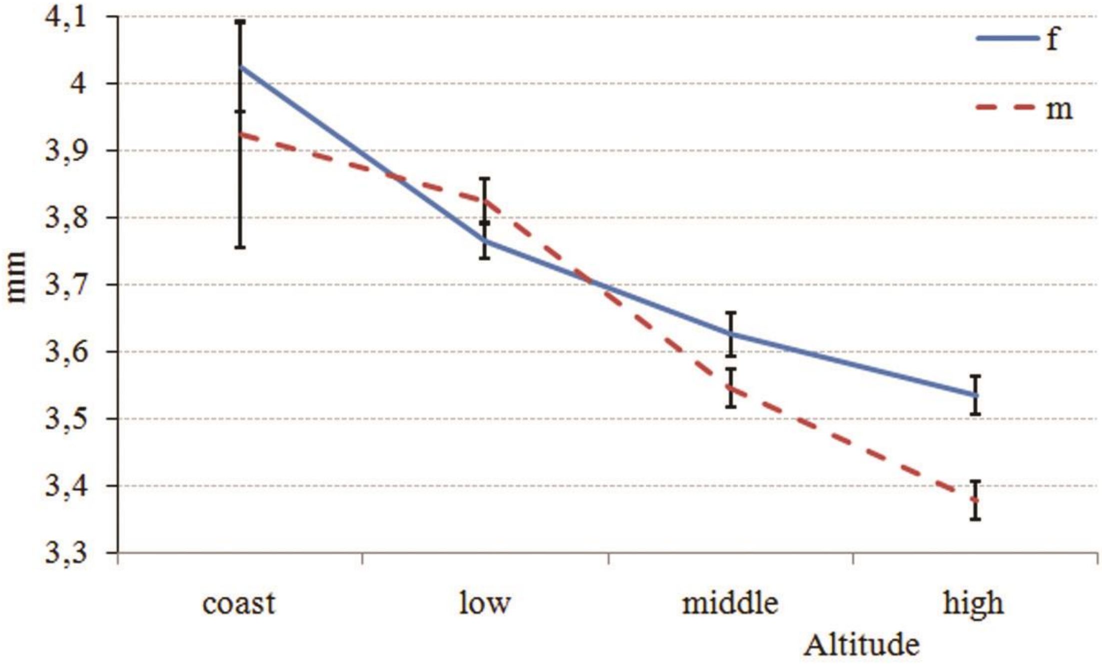

Fig. 5. Pronotum lengh variation in *C. odoratus*

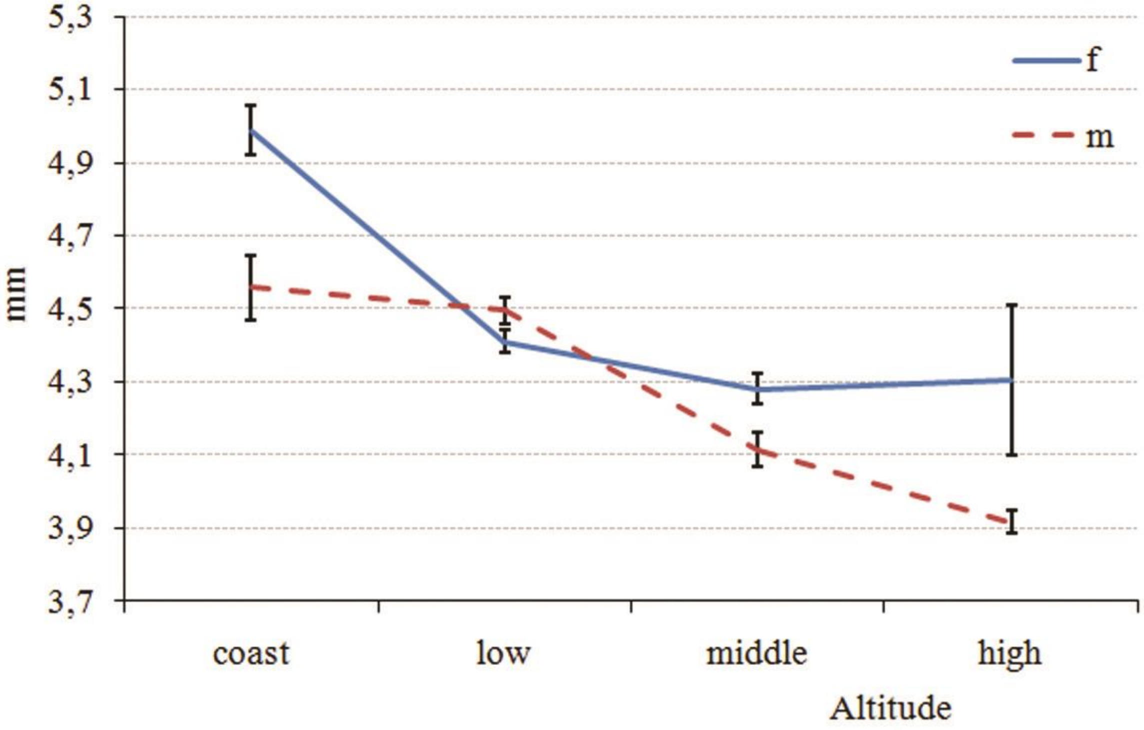

Fig. 6. Pronotum width variation in *C. odoratus*

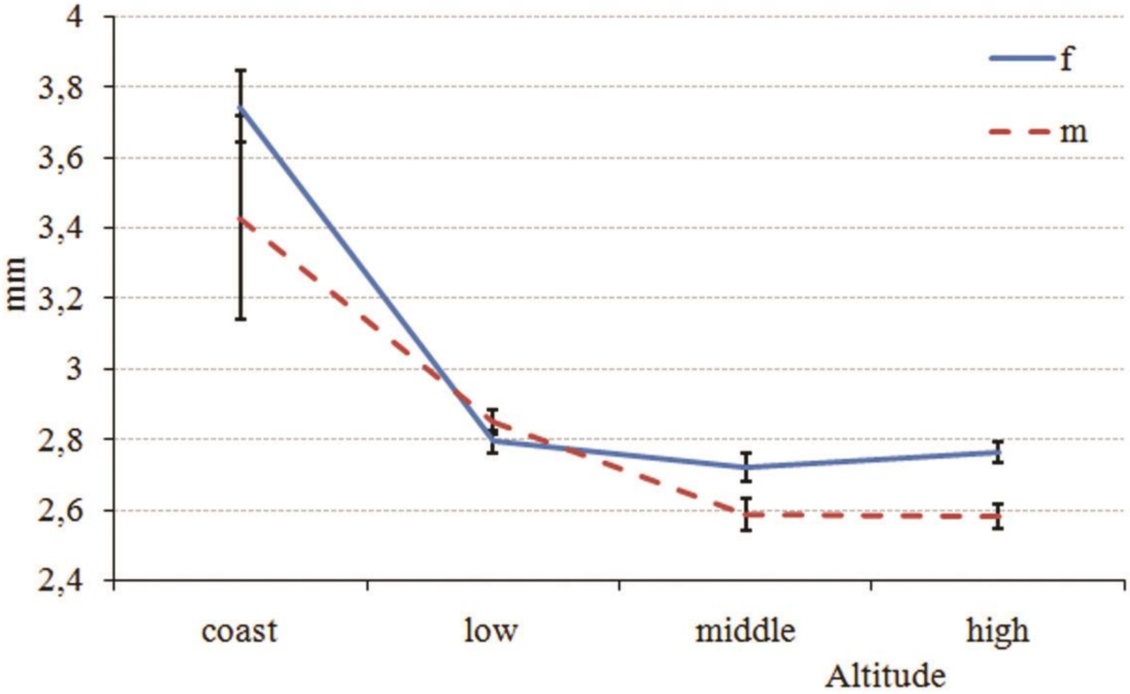

Fig. 7. Head length variation in *C. odoratus*

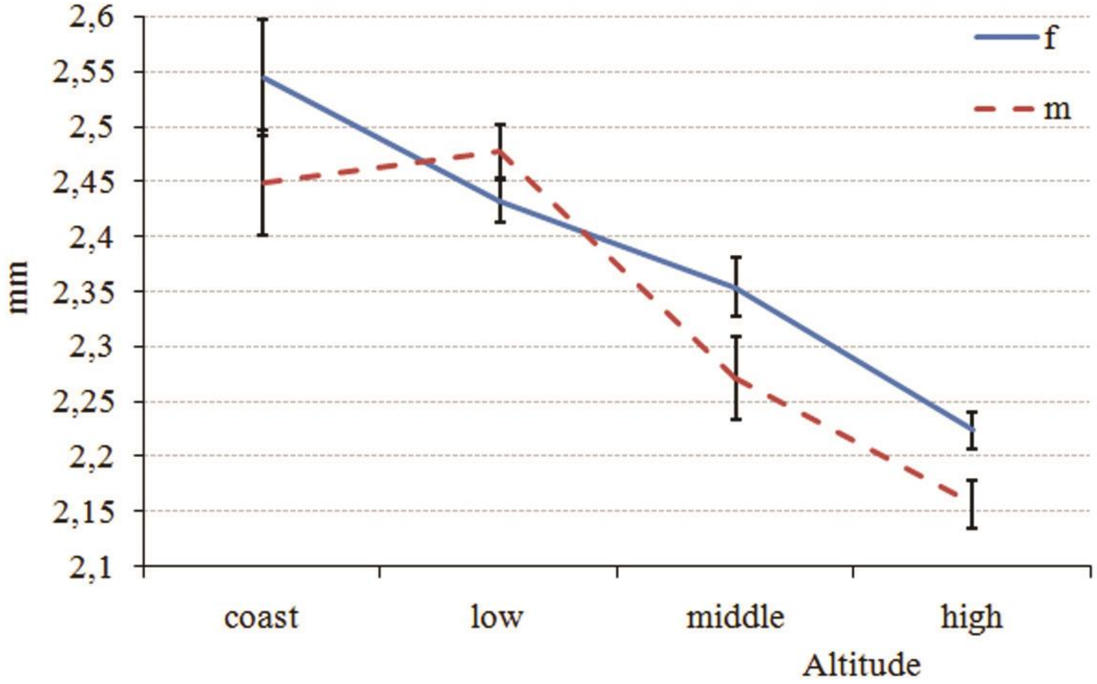

Fig. 8. Distance between eyes variation in *C. odoratus*

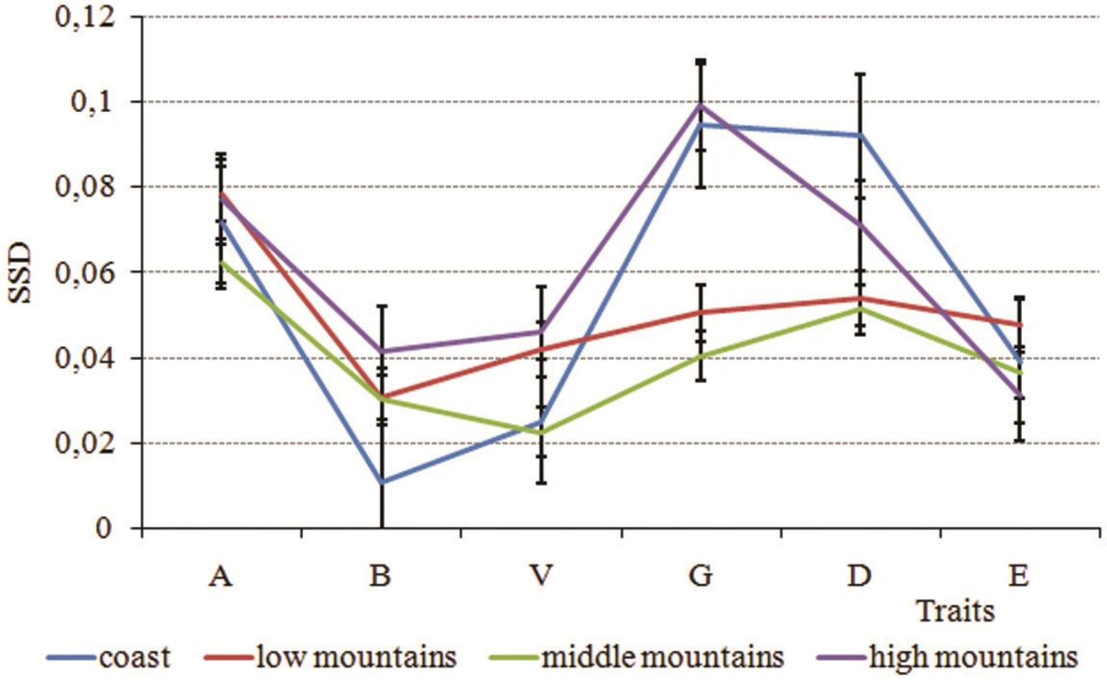

Fig. 9. Sexual Size Dimorphism values in different traits at different altitude in *C. odoratus*

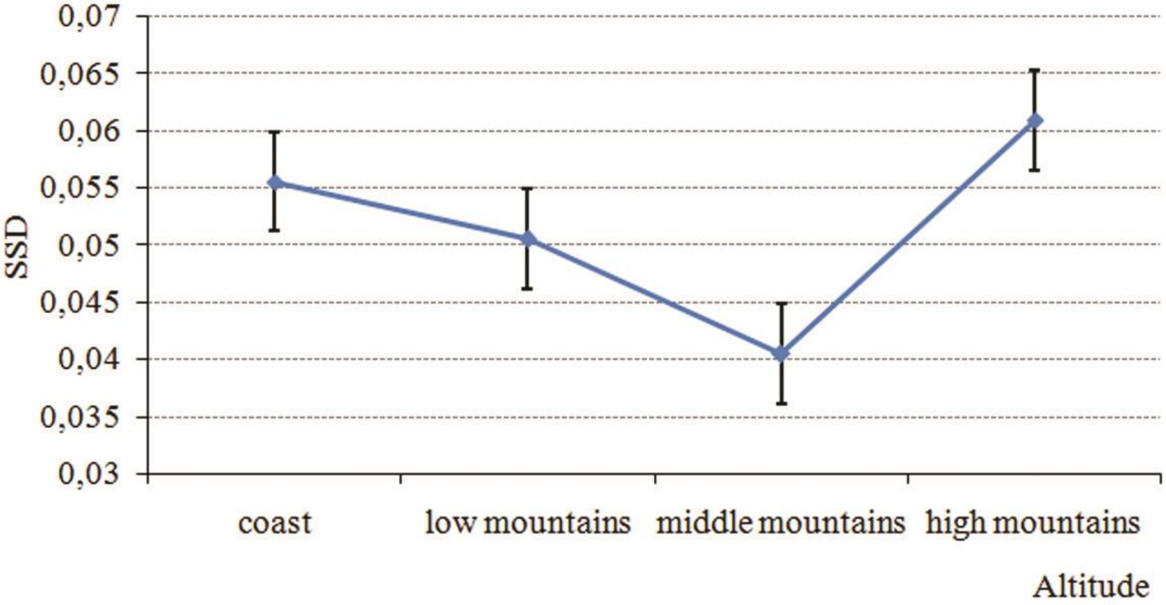

Fig. 10. Mean values of Sexual Size Dimorphism over 6 traits in *C. odoratus*