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Sexual Size Dimorphism in Ground Beetle *Carabus cumanus* Fischer von Waldheim, 1823 (Coleoptera, Carabidae) and its Variation in Different Traits

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We analyzed six morphometric traits variation (elytra, pronotum, head length and width) in two samples of Ground Beetle *Carabus cumanus*. The latter were taken in two biotopes – steppe mountain slope and flood plain forest (Chechen Republic, Russia). In total more than 100 specimen were measured. Both females and males in forest stand had longer elytra, pronotum and head. Traits widths were similar in both samples. Sexual Size Dimorphism (SSD) in *Carabus cumanus* was female-biased and varied in different traits and in different biotopes. It was most pronounced in the head length. RMA resulted in positive slopes in all traits, showing similar direction in traits variation in females and males. ā-coefficient was significant in four out of six traits treated, showing females more sensitive to environmental conditions than males. Scaling of SSD with body size indicated that *C. cumanus* follows converse Rensch's rule.

Key words: body size variation, sexual size dimorphism, Carabidae, RMA II, biotopic factors, steppe slopes.

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INTRODUCTION

Phenotypic plasticity is the ability of an organism to express different phenotypes depending on the environmental conditions faced (Agrawal 2001). Such plasticity is therefore the consequence of the interaction between environmental variability and the developmental program (genotypic × environmental interaction) (Scheiner 1993) and is thus, one solution to the problem of adaptation to heterogeneous environments (Via et al. 1995). Plasticity arises because environmental variability induces developmental changes, which alter the expression and connection between traits (Relyea 2004). As a developmental response, plastic traits allow species to cope with environmental variability (temporal or spatial), enabling a fitness optimization (such as acclimatization) to these conditions (Ghalambor et al. 2007). Although phenotypic plasticity has an effect on fitness, this effect could be adaptive, maladaptive or neutral (Scheiner 1993; Pigliucci 2005; Ghalambor et al. 2007). Because any environmentally induced plasticity places phenotypes into different selective regimes, the fitness consequence, in both the short and long run, will determine whether the response is adaptive.

Morphological traits have been one of the characters most widely used to study phenotypic plasticity. Insect body size and shape strongly respond to changes in temperature, with responses ranging from population differences to thermal clines in body size (Griffiths et al. 2005; van Heerwaarden & Sgrņ 2011). The latter are well-known and relate to geographical variation in body size, the most common pattern being for increasing body size with latitude, which is called Bergmann’s rule. This pattern is observed in many endotherms and in some ectotherms such as insects (Blanckenhorn et al. 2006; Stillwell 2010; Stillwell et al. 2007). Because the body surface–volume ratio generally decreases with increasing body size, body size plays an important role in thermoregulation of endotherms, in starvation resistance and desiccation resistance in ectotherms. In contrast, clinal body size variation in arthropods often follows the converse of Bergmann’s rule (Masaki 1967; Mousseau 1997). In univoltine insects, which can only overwinter at a particular developmental stage, their developmental time is restricted by habitat temperature. The decrease in body size in cooler habitats can be explained by selection for a shorter developmental time, which results in smaller body size. Therefore, the converse of Bergmann’s rule is considered a result of climatic adaptation in univoltine arthropods (Masaki 1967; Roff 1980). Such adaptations can predict communities alterations, when climate changes. Data on body size variation in altitudinal gradients in insects is contradictory: some of them increased in size in high altitude (Alonzo 1999; Smith et al. 2000) but another – decreased (Sota et al. 2000; Kubota et al. 2007; Sukhodolskaya & Ananina 2015). Sometimes only one trait of the organism changed, but another remained the same in the altitudinal gradient (Tantowijoyo & Hoffman 2010) or body size variation was humped (Sukhodolskaya & Ananina 2017).

As size and shape impact performance and fitness (van Heerwaarden & Sgrņ 2011), these traits are of interest for the study of phenotypic plasticity. Environmental variables are spatially structured, and this structuring could also lead to hierarchically structured morphological variation that could be either continuous (such as a cline) or discontinuous. Therefore, the recognition of such morphological discontinuities can lead to an understanding of the shaping of not only species boundaries but also intraspecific patterns of variation and covariation (Mateus et al. 2013).

Differences in body size between sexes (sexual size dimorphism, SSD) are pervasive in the animal kingdom and thus, a fundamental component of body size variation (Darwin 1871; Andersson 1994; Fairbairn 2013). SSD is a controversial aspect of evolutionary biology for several reasons. On one side, although sexual selection has traditionally been assumed as the key process behind SSD, it is now well known that natural selection can also produce size differences between males and females and that both processes are not completely independent from one another (Isaac 2005; Carranza 2009). This problem includes the study of the adaptive significance of SSD, the genetic constraints to its evolution, and its proximate and ultimate causes (Fairbairn, 2007). Secondly, a problem which has not received a satisfactory explanation is that of the allometric scaling of SSD with body size. Rensch (1950, 1960) proposed that in phylogenetically related species, SSD increases with general body size when males are larger than females and decreases when females are larger. This pattern was termed Rensch´s rule (Abouheif & Fairbairn 1997), but despite numerous studies in very diverse taxa (Fairbairn 2007) there is little evidence to support this rule and no convincing mechanism for its operation has been proposed (Reiss 1989; Webb & Freckleton 2007; Bidau & Marti 2008a; Martinez et al. 2014). Further problems regarding the scaling of SSD with body size remain. In the first place, there is the question of the taxonomic level at which it is studied, and if Rensch’s rule operates (if it does) in any taxonomic entity. Most studies of the scaling of SSD with body size were either phylogenetically-based or not have been performed across species at different levels (Fairbairn et al. 2007), and only a few intraspecifically as for example, in insects, some grasshoppers and beetles (Blanckenhorn et al. 2007b; Bidau & Marti 2008b; Stillwell & Fox 2009). In this regard recently some publications appeared in Ground Beetles (Sukhodolskaya et al. 2016, 2018). There has been shown, that SSD in carabids is female-biased and its values varied in the latitude gradient. In those papers the widespread generalist species were discussed. The aim of this investigation was to analyze variation of SSD in the endemic species *Carabus cumanus* L.

Carabus (Eucarabus) cumanus Fischer, 1823 (Coleoptera, Carabidae) is caucasian endemic with expanding area. It is abundant in the Northern Caucasus. In Russia it is recorded in Stavropole and Krasnodar Regions, Kabardin – Balkar, Dagestan, Chechnya and Ingushetiya Republics. Recently it appeared in Penza city (brought with seedlings) and in Alma-Ata city (Kabak 2013; Polumordvinov & Glebov 2017). In Chechnya *C. cumanus* inhabits flood land forests in steppe zone, mountain mixed forests and mountain stepwise slopes. It has the annual life cycle with spring – summer reproduction, multivariate development with hibernating immature, generative and postgenerative stages the next season (Avtaeva et al. 2017).

The main aim of our study was to estimate differences between females and males body size (SSD) in contrasting environment. In connection with this the following hypotheses were investigated: (i) SSD in *C. cumanus* is female-biased just like other Carabidae species; (ii) abiotic factors in studied sites affect SSD variation (iii) SSD would be more pronounced in forest biotope as more favourable for carabids. Additionally we intended to verify if

C. cumanus follows (or unfollows) Bergmann2s and Rensch2s rules.

MATERIAL AND METHODS

In our study we used collections of *C. cumanus,* gathered by the second author in Chechen Republic in 2009, 2010 and 2015. Detailed description of this researches was published previously (Avtaeva et al. 2017). We advisedly chose material from two sites, located in contrasting environment. Material from two seasonal field stations was analyzed:

(1) Vicinity of Kalinovskaya station, $43^{0}34^{2}$ N $45^{0}31^{2}$ E 69, 600 m a.s.l. The plot was located in flood plain forest in steppe zone with prepotency of oak, willow, elm, wild apple and pear trees. Further in the text - “forest”.

Fig. 1. Studied morphometric characteristics in *C. cumanus (*A – elytra length, B – elytra width, V – pronotum length, G – pronotum width, D – head length, E – distance between eyes)

(2) Kenhi village, $42^{0}38^{2}$ N $45^{0}38^{2}$ E 1558 m a.s.l. The plot was located on the mountain stepwise slope, alpine meadows. Further in the text - “steppe”.

The two field stations were considerably different in their temperature regime, precipitation, total solar radiation. The beetles had been collected in pitfall traps made of 250-ml plastic beakers with the upper diameter 75 mm, filled with 4% formalin solution to 1/3 of their volume. Twenty traps had been placed in each plot at a distance of 10 m; the material was removed from them every 10 days. Selected beetles were stored in 70% solution of ethanol, after which they were air dried. Annual average activity density had been 10,5 individuals / 10 trap × fortnight in the forest biotope and 1,4 – in the steppe biotope.

We chose randomly from the each year collections 26 females and 24 males in steppe biotope and 27 females and 39 males in the forest biotope. The dried beetles were photographed with a digital camera Nicon D5100 with resolution 16 Megapixels. The measuring was done using “Manual Carabid morphometric measurement for the method by Sukhodolskaya” (Mukhametnabiev 2018).. Initial code of the later is available under the free – permissive license MIT (Mukhametnabiev 2018). The selected 116 specimen were measured for 6 linear characteristics (Fig. 1). We researched the elytra length (A, as distance between posterior end of scutellum and terminus of right elytron), elytra width (B, as distance between anterior-distal corners of elytra), pronotum length (V, measured along of central furrow), pronotum width (G, at the backward edge between back angles), head length (D, as distance between labrum and juncture of occiput and postgena), head width (E, between the inner edge of the eyes).

For the evaluation of variation of characteristics depending upon the studied traits, we carried out

Box Analysis (Fig. 2) for males and females. 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 favourable conditions during the juvenile development (a common practice in insect ecology) (Awmack & Leather 2002).

To study variation of sexual size dimorphism (SSD) we calculated the size dimorphism index (SDI, Lovich & Gibbons 1992) by dividing the trait size of the females by the trait size of males and subtracting one, resulting in negative SDI when males trait is larger and positive values of SDI when females trait is larger.

To examine the dependence of SSD on environmental conditions male trait size was plotted against female one separately for each trait. The scaling of SSD with body size was analyzed using a Model II regression method: Reduced Major Axis (RMA) regression; ordinary least-squares (OLS) regression is inadequate for this type of analysis. We run the regressions using the software R, smart package (R Development Core Team 2011). The use of RMA regression of log10 (male size) on log10 (female size) is also justified because RMA is symmetric which means that a single regression line defines the bivariate relationship independently of which variable is X and which is Y, and this is the case for SSD comparisons: Rensch's rule is supported when the slope āRMA is significantly > 1.0, while slopes < 1.0 signal its reversion. Slopes not significantly different from 1.0 indicate sexual isometry. Furthermore, a zero intercept implied proportional increase of male and female sizes with conditions improving. A positive intercept indicated that female size increased relatively faster than male size, the former being then more sensitive to environmental conditions. A negative intercept indicated the opposite tendency.

These parameters allowed us to draw conclusions about the dependence of SSD on environmental conditions. In particular, it is easy to see that sex-related differences in sensitivity of body size to environmental conditions should lead to different female/male size ratios in different environments (Teder & Tammaru 2005).

RESULTS

Females from forest biotope had longer elytra, pronotum and head than from steppe slope, but the traits characterizing the width of the beetle were similar in steppe and forest females (Fig.

Table 1. Results of RMA regression in *C. cumanus* traits (* - p<0.05 *** - p<0.001)

Biotope	Trait	Intercept	Slope
Steppe	Elytra length	-0.05	0.91
	Elytra width	0.11	0.14
	Pronotum length	0.09	0.88***
	Pronotum width	-0.04	0.97
	Head length	0.03	0.85***
	Distance between eyes	0.03	0.83***
Forest	Elytra length	1.23	0.47***
	Elytra width	-0.007	0.94
	Pronotum length	0.16	0.82*
	Pronotum width	0.04	0.91
	Head length	0.02	0.93
	Distance between eyes	-0.29	1.2

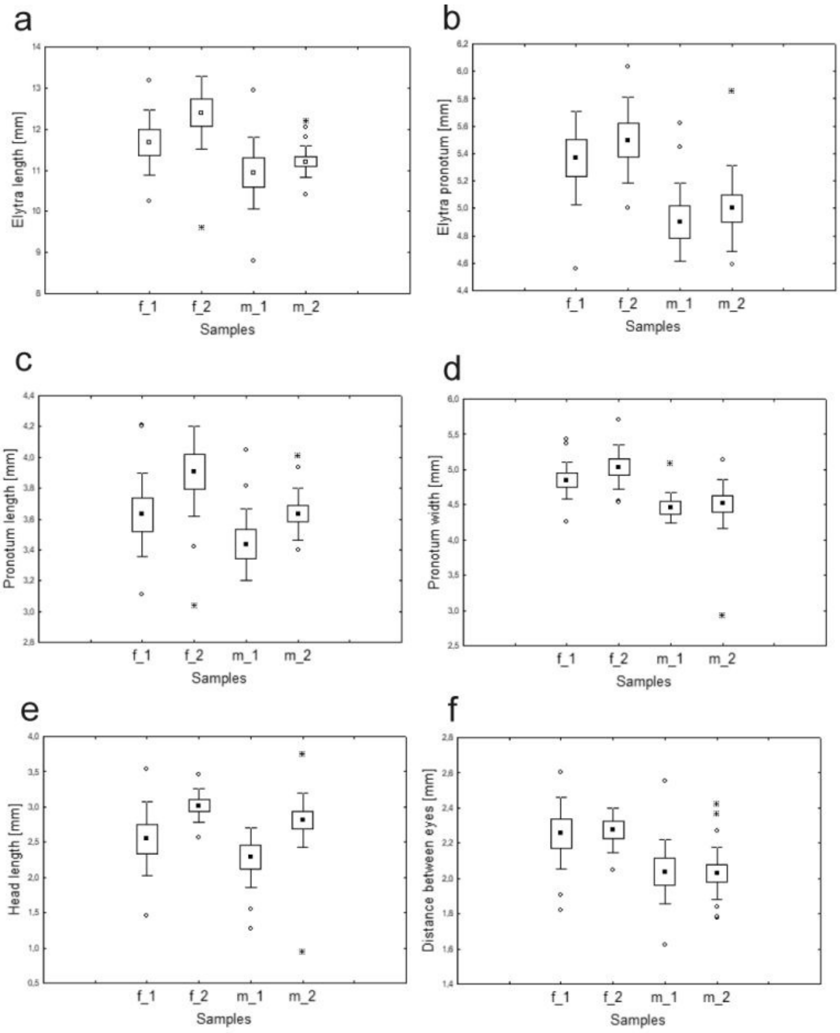

Fig. 2. Descriptive statistics of morphometric traits in *C. cumanus*: a - elytra length, b - elytra width, c - pronotum length, d - pronotum width, e - head length, f - distance between eyes (Mean, ▫ Mean±2*SE, I Mean±SD, - Outliers, * Extremes, f - females, m - males, 1 - steppe slope, 2 - flood plain forest)

2). The same tendencies (excluding head length) were observed in males. Both in forest and steppe samples females were larger than males in the majority of studied traits. The exception was the length of the head in both samples.

When conducting RMA, all slopes were positive (Table 1, Fig. 3). That fact indicated that environmental conditions affected female and male size in the same direction, i.e. male size increased with female size increasing. Such a result allowed to unambiguously rank traits in the samples according to favourability of environmental conditions. Zero intercept implied proportional increase of male and female trait sizes with conditions improving. In our case we concluded that elytra size and pronotum width in steppe, elytra width in beetles from steppe biotopes, elytra and pronotum widths, head size from forest ones varied isometrically in females and males, the latter

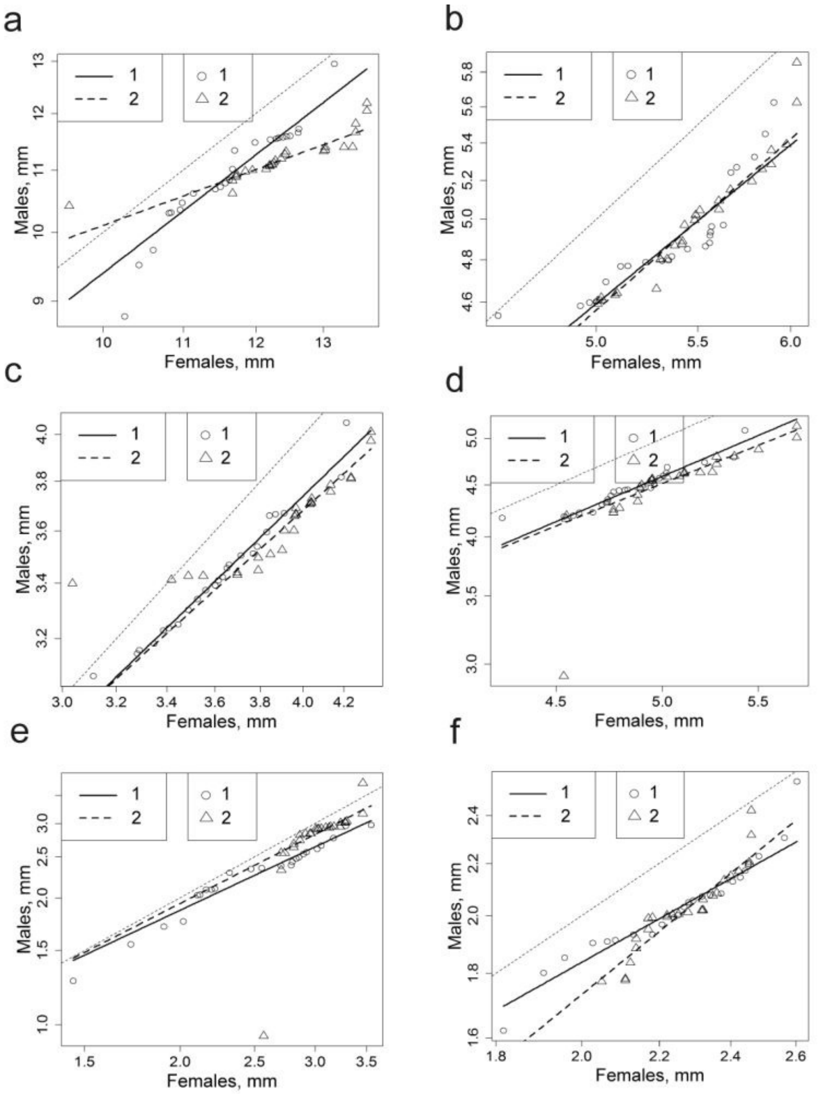

Fig. 3. Results of RMA regression in *C. cumanus* traits: a - elytra length, b - elytra width, c - pronotum length, d - pronotum width, e - head length, f - distance between eyes (1 - steppe biotope, 2 - forest biotope. Circles and triangles denote individuals measured in forest and steppe biotopes respectively. Black dotted line denotes isometry)

having similar sensitivity to environmental conditions. However, regression curves in pronotum length in beetles from both biotopes, elytra length – from the forest, and head parameters – from steppe ones, had significant positive intercepts. A positive intercept indicated that female size increased relatively faster than male size, the former being then more sensitive to environmental conditions. Hereby, by those traits females of *C. cumanus* were more sensitive to the environment in the corresponding biotope. Significant slopes in males/females size traits occurred in elytra, pronotum, head lengths and distance between eyes (Table 1). In those traits the values of SSD were significant. Those results supplemented

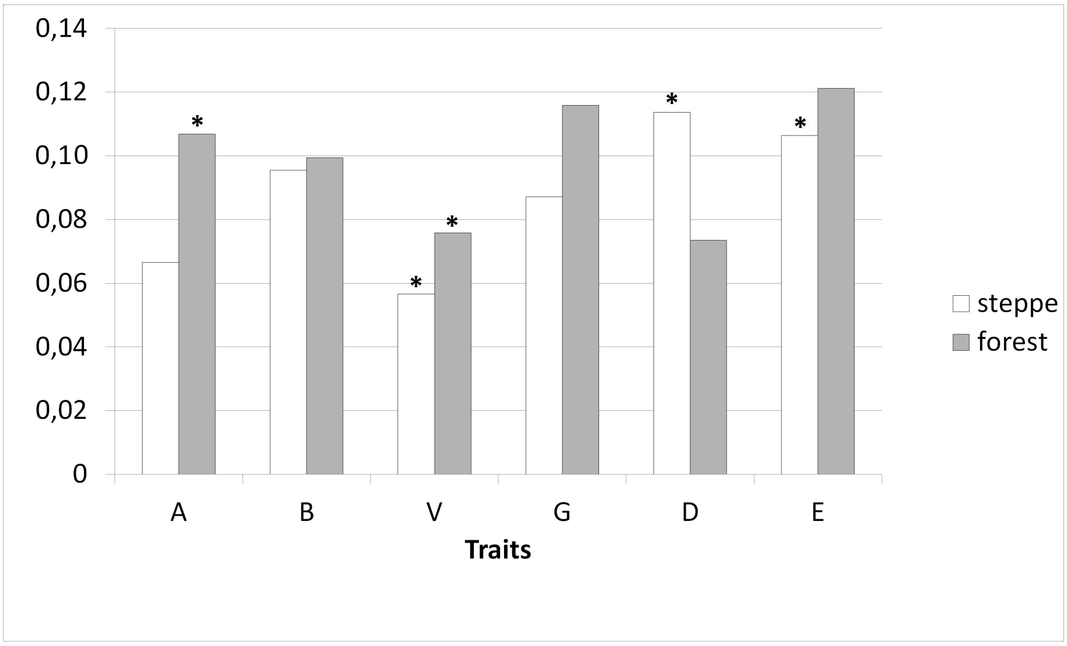

Fig. 4. Values of SSD in different traits in *C. cumanus*. Significant values of SSD (due to Fig. 3, where deviation from isometric curve were significant) are marked by asterisks (A - elytra length, B - elytra width, V - pronotum length, G - pronotum width, D - head length, E - distance between eyes)

Fig. 4: in steppe biotope significant values of SSD occurred in three traits out of the six researched, in the forest biotope in two. However, there was a trend, that in forest biotope SSD was more pronounced.

DISCUSSION

As we assumed, SSD in *C. cumanus* is female-biased. This is common in carabids and in many other insect taxa as well (Teder & Tammaru 2005; Cheng & Kuntner 2014; Sukhodolskaya et al. 2016). In those species in which females are larger than males, it is assumed that natural selection on female body size (via increased fecundity) overrides sexual selection (through competition advantages during mate acquisition) on male body size. However, many other ecological pressures (e.g. habitat, substrate use, length of life cycle) can determine body size evolution in one or both sexes and contribute to shape observed patterns of SSD (Blanckenhorn et al. 2007a; Fairbairn et al. 2007; Fairbairn 2013). Because body size in insects is affected by multiple factors and due to the different plasticity of this trait in males and females, SSD in turn can vary (Blanckenhorn et al. 2007b). It has been shown that in orthopteroid species SSD varied in latitude and longtitude gradients (Bidau et al. 2016). In our earlier publications SSD also varied in the area in the ground beetle *Carabus granulatus*, being the most pronounced at the margins of distribution (Sukhodolskaya & Saveliev 2017a), but in another species, *Pterostichus melanarius*, the highest values of SSD were registered in the centre of its area (Sukhodolskaya & Saveliev 2017b). These results are in agreement with studies of Venn (2007), where has been shown that SSD in Ground Beetles occurred in favourable conditions. Modeling SSD variation in a latitude gradient also showed the trend to decrease toward high latitudes in six carabid species studied (Sukhodolskaya et al. 2018). In our case SSD differences between samples might be related to two factors: altitude and vegetation cover. In *P. melanarius*, for example, the character of vegetation affected females and males differently (Sukhodolskaya 2014). In that study the authors used models, which estimated biotope contribution to regression curves. The latter made it possible to conclude, that in different biotopes SSD in different traits would differ. This fact can explain rather contradictory results on SSD variation in insects, when only a single trait was analysed. In our study we researched six traits in the beetles from two biotopes and SSD and regression coefficients differed among them. With environmental quality increasing, higher sensitivity of female body size would lead to more pronounced SSD in species with female-biased SSD (Teder & Tammaru 2005). In our study environmental conditions for carabids are more favourable in the forest biotope (sufficient humidity, stability of temperature conditions etc.). Moreover, as it was shown in the forest biotope SSD would be more pronounced. According to Fig. 4. we confirm our hypothesis for the variation of elytra and pronotum length and distance between eyes. Indeed, in the forest biotope SSD in those traits were higher than in the steppe biotope. However, for the head length variation our assumption was not justified. In all cases females trait size increased faster than males one, so with increasing body size SSD increased. It meant that *C. cumanus* followed converse Rensch rule.

As for body size variation beetles from the forest biotope were larger in length traits. In this respect our results correspond with other studies, showing that in severe environment carabids become more stocky also (Grinko 2002). Taking into account that studied sites significantly differed in altitude, and beetles from the higher biotope were smaller, we conclude that *C. cumanus* follows converse Bergmann2s rule.

Our results extend our knowledge regarding allometry patterns across insect orders, supporting the inconsistency and the sensibility of the Rensch's rule to the life history and taxonomic group. The results presented here add evidence to the literature regarding the failure of taxa with female-biased SSD in obeying the rule.

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REFERENCES

Abouheif E., Fairbairn D.J. 1997. A comparative analysis of sexual size dimorphism: assessing Rensch's rule. American Naturalist. 149: 540-562.

Agrawal A.A. 2001. Phenotypic plasticity in the interactions and evolution of species. Science. 294: 321-326.

Alonzo C. 1999. Variation in herbivory by *Yponomeuta mahalebella* on its only host plant *Prunus mahaleb* along the elevational gradient. Ecological Entomology. 24: 371-379.

Avtaeva T. A., Kushalieva Sh. A., Fominikh D. D. 2017. Life-cycles of carabids in genus Carabus Linnaeus, 1758 in Chechen Republic. Eurasian Entomological Journal. 16 (4): 375-378.

Awmack C. S., Leather S.R. 2002. Host plant quality and fecundity in herbivorous insects. Annual Review of Entomology. 47: 817 -844.

Bidau C.J., Martķ D.A. 2008a. Rensch's rule in Dichropluspratensis: a reply to Wolak. Annals of the Entomological Society of America. 101: 802-803.

Bidau, C.J., Martķ D.A. 2008b. Contrasting patterns of sexual size dimorphism in the grasshoppers Dichroplus vittatus and D. pratensis (Acrididae, Melanoplinae). Journal of Orthoptera Research. 17: 201-211.

Bidau C. J., Taffarel A., Castillo E. 2016. Breaking the rule: multiple patterns of scaling of sexual size dimorphism in orthopteroid insects. Revista de la Sociedad Entomológica Argentina. 75 (1-2): 11-36.

Blanckenhorn W.U., Stillwell R.C., Young K.A., Fox C.W., Ashton K.G. 2006. When Rensch meets Bergmann: Does sexual size dimorphism change systematically with latitude? Evolution. 60: 2004-2011.

Blanckenhorn W.U., Dixon A.F.G., Fairbairn D.J., Foellmer M.W., Gibert P., Van Der Linde K., Meier R., Nylin S., Pitnick S., Schoff C., Signorelli M., Teder T., Wiklund C. 2007a. Proximate causes of Rensch's rule, does sexual size dimorphism in arthropods result from sex differences in development time? American Naturalist. 169: 245–257.

Blanckenhorn W.U., Meier R., Teder T. 2007b**.** Rensch's rule in insects, patterns among and within species. In: Fairbairn D. J., Blackenhorn W. U., Szekely T. (eds.): Sex, size and gender roles evolutionary studies of sexual size dimorphism. Oxford University Press. Oxford. pp. 60-70.

Carranza J. 2009. Defining sexual selection as sex-dependent selection. Animal Behavior. 77: 749-751.

Cheng R.C., Kuntner M. 2014. Phylogeny suggests nondirectional and isometric evolution of sexual size dimorphism in argione spiders. Evolution. 68: 2861–2872.

Darwin C. 1871. The Descent of man and selection in relation to sex. John Murray. London: 1-822.

Fairbairn D. J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size inmales and females. Annual Review of Ecology and Systematics. 28: 659-687.

Fairbairn D. J. 2007. Introduction: the enigma of sexual size dimorphism. In: Fairbairn D.J., Blanckenhorn W. U., Szekely T. (eds.): Sex, size and gender roles: Evolutionary studies of sexual size dimorphism. Oxford University Press. Oxford. pp. 1-12.

Fairbairn D. J. 2013. Odd Couples: Extraordinary differences between the sexes in the animal kingdom. Princeton University Press. Princeton.

Ghalambor C.K., Mckay J.K., Carroll S.P., Reznick D.N. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptationin new environments. Functional Ecology. 21: 394–407.

Griffiths J.A., Schiffer M., Hoffmann A.A. 2005. Clinal variation and laboratory adaptation in the rainforest species Drosophila birchii for stress resistance, wing size, wing shape and development time. Journal of Experimental Biology 18: 213-222.

Grinko R. A. 2002. Ecological structure of carabids populations (Coleoptera, Carabidae) in zonal and intrazonal ecosystems with different levels of isolation. Ph. Thesis, Nizshniy Novgorod: 1- 25. (In Russian].

Hoffmann A.A., Shirriffs J. 2002. Geographic variation for wing shape in Drosophila serrata. Evolution. 5: 1068-1073.

Isaac J. L. 2005. Potential causes and life-history consequences of sexual size dimorphism in mammals. Mammal Review. 35:101-115.

Kabak I. I. 2013. Materials to the alien carabid species list (Coleoptera, Carabidae) in Kazakhstan and contiguous territories. Selevinia. 21: 107-111. (In Russian; abstract in English).

Kubota U., Loyola R.D., Almeida A.M., Carvalho D.A., Lewinsohn M. 2007. Body size and host range co-determine the altitudinal distribution of Neotropical teephritid flies. Global Ecology and Biogeography. 16: 632-639.

Lovich J.E., Gibbons J.W. 1992. A review of techniques for quantifying sexual size dimorphism. Growth development and Aging. 56: 269-281.

Martķnez P.A., Amado T.F., Bidau C.J. 2014. A phylogenetic approach to the study of sexual size dimorphism in Felidae and an assessment of Rensch's rule. Ecosistemas. 23: 27-36.

Masaki S. 1967. Geographic variation and climatic adaptation in a field cricket (Orthoptera: Gryllidae). Evolution. 21: 725-741.

Mateus R.P., Moura M.O., Manfrin M.H., Monteiro F.M., Sene S.G. 2013. Contrasting patterns of within-species morphological variation in two cactophilic Drosophila species (Diptera: Drosophilidae). Neotropical Entomology. 42: 384-392.

Mukhametnabiev T.. Manual Carabid morphometric measurement for method by Sukhodolskaya [Electronic resource] // URL:https://github.com/CRTmatrix/-Manual-Carabidmorphometric- measurement-for-method-by-Sukhodolskaya- (date of the application 16.12.2018).

Mousseau T.A. 1997. Ectotherms follow the converse to Bergmann's rule. Evolution. 51: 630-632.

Pigliucci M. 2005. Evolution of phenotypic plasticity: where are we going now? Trends of Ecology and Evolution. 20: 481-486.

Polumordvinov O. A., Glebov I. V. 2017. The record of invasive species population of Caucasian Ground Beetle Carabus cumanus Fischer, 1823 (Coleoptera, Carabidae) in Penza city. In: Entomological and Parasitological Researches in Volga Region. Iss. 14. Saratov. pp. 48 – 52. (In Russian; abstract in English).

R Development Core Team 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org/ (accessed 10 Nov. 2016).

Reiss M.J. 1989.The allometry of growth and reproduction. Cambridge University Press. Cambridge.

Relyea R.A. 2004. Integrating phenotypic plasticity when death is on the line: insights from predator–prey systems. In: Pigliucci M., Preston K. (eds.): The Evolutionary Biology of Complex Phenotypes. University Press. Oxford. pp. 176-194.

Rensch B. 1950. Die Abhängigkeit der relativen Sexualdifferenz von der Körpergröße. Bonner Zoologische Beitrage. 1: 58-69.

Rensch B. 1960. Evolution above the species level. Columbia University Press. New York. pp. 210-280.

Roff D. 1980. Optimizing development time in a seasonal environment: the 'ups and downs' of clinal variation. Oecologia. 45(2): 202-208.
Scheiner S.M. 1993. Genetics and evolution of phenotypic plasticity. Annu. Rev. Ecol. Syst. 24: 35-68.

Smith R.J., Hines A., Richmond S., Merrick M., Drew A., Fargo R. 2000. Altitudinal variation in body size and population density of *Nicrophorus investigator* (Coleoptera: Silphidae). Environmental Entomology. 29: 290-298.

Sota T.Y., Takami Y., Kubota K., Ujiie M., Ishikawa R. 2000. Interspecific body size differentiation in species assemblages of the Carabid subgenus Ohomopterus in Japan. Population Ecology. 3: 279-291.

Stillwell R.C. 2010. Are latitudinal clines in body size adaptive? Oikos. 119: 1387-1390.

Stillwell R.C., Morse G.E., Fox C.W. 2007. Geographic variation in body size and sexual size dimorphism of a seed feeding beetle. American Naturalist. 170: 358-69.

Stillwell R.C., Fox C.W. 2009. Geographic variation in body size, sexual size dimorphism and fitness components of a seed beetle: local adaptation versus phenotypic plasticity. Oikos. 118: 703-712.

Sukhodolskaya R. 2014. Variation in Body Size and Body Shape in Ground Beetle Pterostichus melanarius Ill. (Coleoptera, Carabidae). Journal of Agri-Food and Applied Sciences. 2(7): 196-205.

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.

Sukhodolskaya R., Ananina T. 2017. Elevation changes of morphometric traits structure in *Pterostichus montanus* Motsch. (Coleoptera, Carabidae). Asian Journal of Biology. 2(2): 1-9.

Sukhodolskaya R. A., Saveliev A. A. 2017a. Geographical variation of sexual size dimorphism in Ground Beetle Carabus granulatus L. (Coleoptera, Carabidae). Russian Journal of Applied Ecology. 4: 3-10. (In Russian; abstract in English).

Sukhodolskaya R. A., Saveliev A. A. 2017b. Geographical variation of sexual size dimorphism in ground beetle Pterostichus melanarius (Coleoptera, Carabidae). In: Proceedings of 18 European Carabidologists Meeting. Rennes. p. 61.

Sukhodolskaya R.A., Saveliev A.A., Muhammetnabiev T.R. 2016. Sexual Dimorphism of Insects and Conditions of Its Manifestation. Research Journal of Pharmaceutical, Biological and Chemical Sciences. 7(2): 1992-2001.

Sukhodolskaya R.A., Saveliev A.A., Gordienko T.A., Vavilov D.N. 2018. Sexual size dimorphism in Ground Beetles and its modeling in latitude gradient. GSC Biological and Pharmaceutical Sciences. 3(1): 11-18.

Tantowijoyo W., Hoffman A.A. 2010. Variation in morphological characters in two invasive leafminers, Liriomyza huidobrensis and L. sativae, across a tropical elevation gradient. Journal of Insects Science. 11: 69.

Teder T., Tammaru T. 2005. Sexual size dimorphism within species increases with body size in insects. Oikos. 108: 321-334.

Van Heerwaarden B., Sgrņ C.M. 2011. The effect of developmental temperature on the genetic architecture underlying size and thermal clines in Drosophila melanogaster and D. simulans from the east coast of Australia. Evolution. 65: 1048-1067.

Venn S. 2007. Morphological responses to disturbance in wing-polymorphic carabid species (Coleoptera: Carabidae) of managed urban grasslands. Baltic Journal of Coleopterology. 7 (1): 51-59.

Via S., Gomulkiewicz R., de Jong G., Scheiner S.M., Schlichting C.D., Tienderen P.H. 1995. Adaptive phenotypic plasticity: consensus and controversy. Trends Ecol. Evol. 10: 212-217.

Webb T.J., Freckleton R.P. 2007. Only half right: species with female-biased sexual size dimorphism consistently break Rensch’s rule. PLoSONE. 2(9):897.

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