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Sexual Dimorphism of Insects and Conditions of Its Manifestation.

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ABSTRACT

The studies of sexual dimorphism (SD) interspecific change by size is generally state that intraspecific value of this parameter is a stable one. This paper presents the results of sexual dimorphism systematic study according to measuring signs of Coleoptera, Carabidae bugs. The samples of six eurytopic individuals among widespread species were taken in a large-scale aspect - in the most part of the area, in the spectrum of a human impact and different vegetation habitats - and integrated into a single database, original for each species. More than 15,000 individuals were studied in total. Among all studied species of ground beetles females are larger than males according to all measurements. Using the second type of the reduced regression models allowed to show that the slope angle of the regression curve for male and female sizes is a positive one, which indicates that the change of female size has one vector with the changes of male size, but the magnitudes of regression coefficients differ among different species. The values of model constants have different signs. These facts are indicate that the studied species of ground beetles are divided into two groups with respect to environmental factor sensitivity: the first group (Carabus granulatus, Carabus hortensis, Pterostichus niger, Pterostichus oblongopunctatus) is more sensitive to changes in the female environment, and will be reduced with the increase of SD damaging effects in the populations of these species. The second group (*Carabus cancellatus, Carabus aeruginosus, Pterostichus melanarius, Calathus halensis*) includes the species with more sensitive males, and in the harsh environmental conditions among the populations of these species SD will be increased. Thus, we developed the method of secured bioindication for external impacts on biota, based on the assessment of SD value orientation changes in the populations of ground beetles.

Keywords: sexual dimorphism by sizes, ground beetles, the regression models of the second type II, Rench rule, bioindication.

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INTRODUCTION

Sexual dimorphism according to body size is considered as one of the most attractive ones in terms of bioindication (PDR, PD - if there is a sexual dimorphism according to a particular sign size), which is widespread in the animal world [1]. Since the 60s of the last century, PDR became the subject of research during the study of the most diverse groups of animals [2]. One of the main objectives of these studies is to clarify the issue of Rench rule following according to a given taxon. The latter states that PDR increases within a taxon with the increasing of sizes if a male is larger than a female, and, conversely, PDR decreases with the increase of size if if it is larger than a female. If larger sizes of males in this taxon are usually confirmed then in the case of larger females in a taxon the information is contradictory one, and one may say that this rule is not confirmed in 50% of cases [3]. This is especially true in relation to invertebrates, in particular insects. The reviews on PDR topic in this group are the compilation of various research results, carried out during very different periods [4,5]. Apparently, the contradictive nature of the conclusions is explained by PDR vector among insects. Moreover, one feature is taken for the analysis (it is often elytra length) and various researchers estimate PDR on different grounds. This may be elytra length, and the length of a thigh, and the width of a head. Thus, various works are presented by a variety of approaches to PDR assessment. There are more systematic studies, when the authors analyze PDR among a certain type of insects and evaluate the factors influencing PDR value. However, such works are carried out on laboratory cultures of insects, which makes the extrapolation of obtained data on natural populations a difficult one according to PDR.

Thus, the proper evaluation of PDR among a certain group of insects demands the material collection in nature, in different environmental conditions and is treated by one group of researchers using the same methodology with the involvement of several features in the analysis. At the same time it is important to take the species - indicators for the analysis of an anthropogenic or other exposure to register environmental changes according to PDR magnitude and direction. In this regard, a good indicator are bugs - ground beetles (Coleoptera, Carabidae) [6]. They make an essential element of the soil cenosis, and as most of this family species are predators, they are a good model object, which weakly depends on a feed substrate. Ground beetles are attracted in a large number of studies as indicators, but these works are performed at a community level [7]. At a species level there are a few works concerning the variations of body size and the identification of PDR patterns of karabids and the changing of a beetle form in a narrow local scale is considered in a greater degree [8, 9]. The main purpose of this study is the identification of sexual dimorphism among ground beetles (Coleoptera, Carabidae).

MATERIALS AND METHODS

Object. The following species of karabids were studied in the study (the number of analyzed individuals is indicated in parentheses): Carabus granulatus L., 1738 (1168); Carabus cancellatus Ill, 1798 (663).; Carabus aeruginosus Herbst, 1784 (1585); Carabus hortensis L., 1758 (1282); Pterostichus melanarius Ill, 1798 (2912).; Pterostichus niger Schall, 1783 (1034).; Pterostichus oblongopunctatus F. 1787 (300); Poecilus cupreus L. 1758 (2404); Carabus arcensis Herbst, 1784 (43); Calasoma investigator Ill, in 1797 (127).; Calathus halensis Schall., 1783 (299), Carabus odoratus barguzinicus, 1996 (1095).

Study area. The material was collected so that the basic requirements of large-scale studies were observed. In each part of beetle areal the beetles were caught in natural cenoses, as well as in the areas with anthropogenic influence (city, suburbs, agrocenoses). The capture was carried out in all biotypes inhabited by test species beetles (coniferous and deciduous forests, grasslands, etc.). The trapping of bugs in the Republic of Tatarstan is performed in a standard way by Barbera traps during vegetation seasons of 1996 - 2010. The part of the raw material according to morphometric measurements of beetles is taken from the works, where the author of this article acts as its co-author [10, 11]. The rest collections, including the collections of ground beetles from other areal parts of studied species were obtained within the framework of scientific cooperation from the colleagues of different regions of Russia: Kirov region, Udmurtia (the northern boundary of many species areal), Nizhny Novgorod and Sverdlovsk regions, the Republic of Mari El - the center, Stavropol territory - the south and Kemerovo region - the areal east of studied species. The exception is presented by C. aeruginosus and C. odoratus. The first one is the Siberian species, but it is widely distributed from the Ural Mountains to Lake Baikal and Yakutia, the material on this species was collected only in Kemerovo region. The second one is the Baikal subspecies of the Siberian species, the endemic of Barguzin ridge, which is widely represented in all departments of a number of an altitude belt row (460-1800 m above sea level). The material on this species was collected in the appropriate forest habitats. Ground beetle species Cal. halensis were collected only in agrocenoses of the Republic of Tatarstan, as this kind is considered to be purely field one and is not met in other cenoses.

STUDY METHODS

Morphometric features were brought in order to identify PDR patterns. This is related to the fact that if an insect continues to feed during an adult stage, its weight will depend on the feed resources. Thus, the body weight index is a very variable and can not serve as a reliable tool during field collections. Morphological features are less variable among adults and generally depend little on the supply conditions. Therefore, they are usually used as body size indicators [12]. Since PDR patterns among different attributes of the same species individuals may vary [13], six morphometric characters of ground beetles were taken in our analysis. The morphometric measurements were performed under a binocular microscope MBS - 9 at the increase of 1x8. After the determination of sex among beetles six dimensional signs were evaluated using an ocular micrometer: elytra length - the distance from the middle to the top of a rim along a seam; elytra width - the distance between the shoulder angles of the left and the right elytra, front back length - the distance along the midline from the bottom to the top, front back width - the width of the base, head length - the distance from the neck to the upper lip, the distance between eyes.

Statistical processing. PDR was assessed according to the procedures [14] adopted in the world practice: PDR = (female/male mean value of an attribute) - 1. In order to assess PDR allometry the regression models of type II were used, using the method of principal axes (RMA - Reduced Major Axis) [15]. The calculations of logarithm for quantile values distribution are performed in respect of the studied traits of males as a linear function for quantile of distribution logarithms of these female sizes. The model is displayed in a text file, $Y = άXβ$. The positive values of the regression coefficient (β) represent the same vector of a feature change among males and females, in other words, with the increase of characteristic value among females, the values of this attribute among males are also increased. The positive values of the model constant (Intercept) suggest that female sizes increase faster than male sizes, that is females are more sensitive to environmental changes, the negative values suggest otherwise [4].

RESULTS

All studied species of ground beetles have positive PDR values (Table. 1), i.e., females are larger than males according to almost all dimensional characteristics. The exception is the width of elytra among C. granulatus and the head length of P. oblongopunctatus. In these cases, PDR values are negative, therefore, females are less than males among this species according to these attributes (Table 1).

PDR value among the studied species of ground beetles varies considerably by different attributes. If on the average PDR of all studied species according to one attribute may differ three times from PDR according to the other, in Calas. investigator this difference is sevenfold, while it is equal to 1 among P. oblongopunctatus. C. arcensis has the most volatile PD on different attributes. from C. The greatest variation on PD values according to individual features is observed among P. oblongopunctatus, P, cupreus, Cal. halensis and S. odoratus. At the same time an interspecies variability of PD is recorded for each of the studied dimensional characteristics: PD value may vary 9 - 14 times among different species. If on the average PD for the studied species of ground beetles ranges from 0.05 - 1.11, then during the analysis of PD variability the following result is obtained according to individual features: the smallest interspecific PD variations are observed along the elytra length, the largest ones are observed along the length of the front back.

Table 2 shows the results of regression reduced models of female and male sizes among the studied species of karabids. All coefficients obtained after regression analysis are positive ones. This suggests that the values of traits among males and females at the change of conditions vary in the same direction. However, it should be noted that the values of these coefficients vary at an interspecific level and on different grounds. At that, if a regression coefficient makes more than 1, if it is more volatile and, therefore, then male species is more sensitive to the changes in the environment. If the regression coefficient is less than 1 then females are more sensitive to the changes in the environment. According to Table. 2 one may conclude that the sensitivity to environmental factors of males and females among ground beetles is different according to different attributes. Thus, C. granulatus according to the attributes of elytra and head, as well as females are more volatile according to the width and of a front back and males are more volatile according to the length of a front back. Thus, during the environmental change the body size varies among the females of this species: at the deterioration of conditions they will reduce their size faster than males, resulting in PD decrease, and at the improvement of existence conditions the female size will grow faster than male one that will increase PD. A similar analysis of data for other species of ground beetles leads to the conclusion that such patterns are characteristic of P. niger and P. oblongopunctatus, as evidenced by the mean value of the regression coefficient according to all six attributes. An another set of studied ground beetle species has quite another trend. Males are more sensitive to environmental changes among the remaining species of Carabus, P., melanarius and Poec. supreus. Therefore, when the conditions of existence are deteriorated, they are reduced in size to a greater degree than females and PD increases. During the improvement of environmental conditions the males of these species increase the sizes to a greater extent compared with females, thereby reducing the PD values. Cal. halensis data are slightly out of the picture: an average value of the regression coefficient for a set of attributes is equal to 1, wherein females are more sensitive to the environmental changes and males are more sensitive according to other three. However, it is worth noting that a definite trend can be traced for this kind: during the deterioration of existence conditions among males the head size is decreased to a greater extent, while the front back is reduced among females.

The regression coefficient values are correlated with the value of model constants (Table 3): at a positive constant the regression coefficient models are usually less than 1, while it is more than 1 at a negative constant. Spearman rank correlation coefficient of the mentioned values makes (-0,90) (t = -14,93; p <0,00000), which suggests that the regression coefficients and the model constants are related by feedback.

Thus, we conclude that the investigated species of ground beetles show different strategies of PDR expression. The analysis of model constant values shows that C. granulatus, C. hortensis, P. niger, P. oblongopunctatus females are more sensitive to the environmental changes and with the improvement of existence conditions PDR should be increased. C. cancellatus, C. aeruginosus, P. melanarius, Cal. halensis males are more sensitive to environmental changes and with the living conditions improvement PDR shall be decreased among these species. Two remaining species - C. odoratus and Poec. cupreus have a positive and a negative regression coefficient according to three attributes. Such an ambiguity is determined, in our view, by the fact that the databases of these species, in contrast to other databases of the species studied by us include mainly individuals of the same type: C. odoratus - an endemic species and it is found only in natural habitats of Barguzin ridge highlands, and Poec. cupreus - an absolute dominant in the communities of agrocenosis and numerous sample concerning this species were caught in farmlands.

Thus, taking into account the analysis, the regression coefficients and the model constants, we conclude that both values have among a certain type of ground beetles are interconnected and determine a great sensitivity to the environmental factors among C. granulatus, P. niger, P. oblongopunctatus females and C. cancellatus, C . aeruginosus and P. melanarius males. An ambiguous relationships between the regression coefficient and the constants of models are explained among the other studied species, in our opinion, by the fact that Poec. supreus and Cal. halensis dominate in agrocenoses and C. odoratus is not a widespread, endemic species.

In order to find out the observance of Rench rule by ground beetles, we arranged the studied species of ground beetles in the order of elytra length decrease and calculated the correlation coefficient between the elytra length and PD value. It appeared to be equal to 0,61 (p <0,03). Consequently, ground beetles according to the main dimensional characteristic (elytra length) follow Rench rule. The correlation analysis of other feature value dependence and PD did not show a definite trend by their size. For all five other studied traits the correlation coefficient between the elytra length and PD values was not a statistically significant according to this attribute. The same result was obtained for the total body length (total length of elytra, front back and head). Thus, with respect to other features there are no reasons to say, that PDR follows Rench rule according to their sizes.

DISCUSSION

The main outcome of our results is that we showed that PDR may be different if a few attributes are taken into an analysis. PDR studies on insects usually involved 1 or 2 features from dimensional attributes, the body length (skaters, dragonflies, caddisflies), thorax length (diopside, Drosophila, sepsides, skatopsides), hind tibia length (skaters, dung flies). Elytra length is usually taken for PDR analysis among ground beetles. Without belittling the importance of this feature for karabids, we emphasize that the variability of the elytra sizes may differ from the other parts of an insect body, so depending on the chosen sign PD values may vary greatly. This is indicated by other researchers [12, 13]. These conclusions have a direct relevance to the issue of the Rench rule confirmation. Most of the works on this topic is devoted to mammals and birds, where the Rench rule is usually observed. However, this rule is not observed among the birds and the species where females are bigger than males, and the authors conclude that the Rench rule does not exist as an independent scaling phenomenon [16]. Among insects the Rench rule is observed only among half of the studied species, and, most likely, it is not a rule for this class. Besides, it is worth noting that the number of studies and their quality (the presence of amendment for phylogeny or the lack of it) is very uneven in different orders. For example, PDR and its dynamics is assessed in several families among Diptera and bedbugs, while in other groups the data for all families are united and only one family in the order is examined (eg. Caddisflies). On the other hand, the data on Rench rule approval among Diptera and bugs are quite similar, and this rule may be observed on a family level among anteaters, but not on a genus level. Thus, the data confirming Rench rule among insects are rather separated. The studies on ground beetles are met quite rarely, at that PD is studied only according to one feature. Initially B. Rench [17] having investigated the total body length among 9 karabid species, comes to the conclusion that they do not follow the Rench rule in general. Apparently, it was determined by the fact that in general the karabid regression coefficient made 0,97. In other words, the females of studied karabid species were larger than males, and in the phylogenetic series with theincrease of body size PDR values should be decreased (reverse Rench rule).

The data obtained by us may be compared with the authors of a few works. They describe PDR only in general form for invertebrates and the values of PDR are comparable there with those that we obtained [18, 19]. In another work on PDR study among insects PDR values are specified, and for the representatives of the ground beetle family (Sarabus nemoralis) PDR is brought equal to 0,059, which is correlated with our data for PDR on elytra length for the representatives of Carabus species ground beetles [20]. In the work carried out by Belarusian scientists in natural cenoses, PD value among the representatives of the type C. granulatus along elytra length and front back length completely coincides with the data obtained by us [21].

Thus, the contradictory data in the literature, in our opinion, is that the variability of different characters among the same species may be subject to different laws. Depending on the selection of sampling period, a population cycle phase, the features of selection activity and many other reasons a researcher may get quite opposite results. Therefore, the study of such a problem as PDR requires not only a large sampling. This sampling should include the species caught in different parts of an area, with different anthropogenic impact and different type of habitats. In other words, this sampling should be a compilation of material obtained in large-scale aspect in order to neutralize the possible impact of purely local conditions on PDR value. The mechanism of PDR implementation is important here. Two issues are considered usually during the study of this phenomenon. First of all, it is an adaptive PDR value. The generally accepted view is that PDR reflects the different roles of males and females during the implementation of reproductive function. The body size is usually correlated with the suitability, with the fertility among females and with the success among males in the fight for a female. So an optimal size of a female and a male body varies in different environmental conditions. As for PDR concerning the attributes that are not directly related to reproduction (locomotor, associated with food obtaining), this PDR is defined by the segregation of niches. Although it is unlikely that the segregation of niches does not depend on a reproductive success as well as such an attribute, that the development time of the female and male larvae: it was shown that sexual dimorphism thereon is positively correlated with an adaptability of caryopsis populations [22].

Theory predicts that if there is no an independent variability within a sex, in other words, if a genetic correlation between males and females is equal to 1, then PDR can not be formed. However, the genetic correlation between sexes is very rarely equal to 1, so own genes are expressed on the same environmental conditions among each sex and PRD is formed. And the main effect of genes that work in both sexes, is in the maximum deceleration of PDR evolution, different sizes of males and females are preserved sometimes for a long time, although they are far from optimal ones.

The second issue which appears is the the correlated evolution of male and female size, even within the terms of an antagonistic selection. This occurs during the early stages of PDR evolution when the selection for size increase (or decrease) may cause less, but the same vector effect among an opposite sex. The body size of one sex increases, but faster than the other one, leading to a temporary covariance of sizes among different genders and the covariance between average sizes and the sexual dimorphism magnitude. This development of events is known as PDR allometry or the Rench rule. However, the genetic correlation between females and males in terms of development rates is observed only during the very early stages of PDR development evolutionary trajectory, so most researchers reject this explanation of its existence. The only work on water striders, where it was verified experimentally, rejected this hypothesis [23]. The role of genetic constraints and genomic conflicts in PRD development remained largely unknown [20]. A definite step for this problem solution is a series of works on the study of an internal locus sexual conflict [22, 24 Bonduriansky, Chenoweth, 2009; Arnqvist, Rowe, 2013]. An internal locus sexual conflict arises when the direction of selection according to a certain allele depends on its expression among females and males, and it is expressed in the fact that males and females have differebt optimum of phenotypic trait, which is implemented in both sexes. In other words, sexual internal locus conflict leads to the fact that the optimal values of any phenotypic trait have different values among females and males. An internal locus sexual conflict is insufficiently studied, although it has a direct relation to such important processes as adaptation and speciation [25]. Despite the fact that males and females are very similar by genome, they often differ in response to a choice. Theoretically sexual antagonistic loci should result in gender load within the populations as sexual selection on the basis of one particular sex is in danger of being eliminated on the same basis among the other sex. It is not clear still whether such an intralocus sexual conflict is a transitional evolutionary state, or if it is a longer obstacle to adaptation. In any case an intralocus sexual conflict could manifest itself as the correlated evolution between the population adaptability and PD symptoms presented among both sexes.

Although the most part of PDR variability has a genetic basis and, therefore, is subject to selection, some part of it is determined by the sex differences in the phenotypic plasticity of body size [12, 26]. But the way of such differences appearance in the phenotypic plasticity between the representatives of different sexes remain unclear, because males and females have the same genom coding the signs of growth and development [27]. Thus, the issue why females and males reach different sizes and show differences in response to the impact of the same environmental factors remains unresolved [12]. The fact that intrasexual differences among adults also affect the environmental conditions for a long time was known for a long time [28]. PDR appears brighter in the worst resource conditions. At that it has values and biotic factors. For example, PDR values are increased, if a habitat is a poor one for biodiversity, and vice versa, PDR is less noticeable at the amplification of an interspecific competition [29]. Insects in general demonstrate a body weight plasticity which depends on gender in response to the quality / quantity of food [12]. For example, R. Bonduriansky [30] in his experiments with the Australian fly demonstrated that males are more sensitive to the quality of food: with a poor diet the sizes of males and females are almost identical, i.e. PDR was not shown. In a rich medium males were statistically bigger than females, which led to PDR. The data about the effect of temperature on the expression of a gender dependent phenotypic plasticity is contradictory, although the development temperature is considered as a major factor of growth, development and maturation period. Thus, it was shown that males are bigger in the cultures of Callosobruchus maculates at higher temperatures compared to the development of females at the same time. On other sites these patterns were not confirmed, and the PDR value depended on the population development stage [12].

These complex dependencies apparently make the norm in natural populations. This leads to the fact that PDR value may vary in a wide spatio - temporal aspect. PDR values may be significant ones even if there are no genetic differences between the populations of the same species, but they are developing at different temperatures, which leads to a well-known PDR geographic variation [31, 32]. Thus, no species has a fixed PDR value. Allopatric populations tend to live in different ecological conditions, and even in the case of sympatric speciation there are such factors as population density, food resources, and so on. Therefore, the comparative studies on PDR dynamics should include a wide spectrum of species, shall be representative in a sampling aspect and shall encompass a sufficiently large number of factors that influence the body size of the objects under study.

Taking into account this PDR variability one should assess very properly the impact of a particular environmental factor on the size of males and females, involving modern statistical methods for analysis. Most studies on the evaluation of insect size variability carried out in such a way that the factor which determines in this case the increase or decrease of sizes in the populations of insects is not clear, as research area is limited to one locality and it is impossible to determine the significance of discussed factor essence even with the comparative data from another on the change of male and female sizes. Therefore, it is impossible to determine the significance of PDR value. In this regard, the works, where the size variability is evaluated by a complex of signs and uses linear models. This approach allows us to isolate the actions of each environmental factor in its spectrum, irrespective of other existing ones. Thus, it was shown that ground beetles Carabus cancellatus L. have PD along the elytra length (it is bigger among females than among males) which appears under the influence of living in the center of an areal in a natural cenosis, and under the influence of habitat in an agrotcenosis only males become bigger, which leads to the fact that PD is not recorded along elytra length. Within the same species of ground beetles males and females respond differently to living conditions in a city and agrocenoses that leads to the appearance of PD not only along elytra length, but also according to five-dimensional features [33]. In another study, performed on the Siberian species of ground beetles C. aeruginosus, the authors record PD in all studied characteristics, but the PD value on these attributes is dependent significantly on environmental conditions: it increases depending on the biotope vegetation and becomes almost equal to zero under the influence of urbanization [34]. The use of the same linear models during the analysis of other species of ground beetles S. granulatus variability showed that PDR expression degree of various features is also highly dependent on environmental conditions: PD in this species of ground beetles is especially pronounced by elytra length, but it is virtually erased under the influence of city conditions, and also the living on meadows and lawns due to the mixed reaction of male and female size on these factors [35]. This phenomenon was described for ground beetles Harpalus rufipes and Bembidion properans, whose PD by body size appears only in stable environment of natural cenoses and disappears under the influence of recreation due to the fact that a body size in these conditions increases among males only [36].

On the other hand, the reaction on environmental factors depend on gender not among all types of ground beetles. So, elytra length of P. melanarius in city conditions decreases among females and males, while P. niger does not have such changes at all [37] and at that a major role is played by PD according to form [38].

Table 1. The value of sexual dimorphism according to different signs among the studied species of ground beetles (А - elytra length, Б - elytra width, В - front back length, Г - front back width, Д - head length, Е - the distance between eyes)

Species/Signs	А	Б	В	Г	Д	Е	Average for species	Stand. dev.
C. granulatus	0,10	-0,03	0,04	0,08	0,05	0,07	0,05	0,05
C. cancellatus	0,07	0,02	0,02	0,03	0,04	0,04	0,04	0,02
C. aeruginosus	0,03	0,02	0,01	0,02	0,05	-0,02	0,02	0,02
C. hortensis	0,09	0,09	0,04	0,07	0,03	0,05	0,06	0,03
P.melanarius	0,04	0,05	0,02	0,03	0,03	0,05	0,03	0,01
P. niger	0,06	0,09	0,04	0,05	0,05	0,07	0,06	0,02
P. oblongopunctatus	0,01	0,00	0,00	0,00	-0,01	0,01	0,00	0,01
P. cupreus	0,02	0,01	0,03	0,02	0,02	0,01	0,02	0,01
C. arcensis	0,06	0,08	0,14	0,20	0,12	0,12	0,12	0,05
Calas.investigator	0,07	0,01	0,04	0,06	0,07	0,03	0,05	0,03
Cal.halensis	0,05	0,03	0,04	0,05	0,04	0,04	0,04	0,01
C. odoratus	0,03	0,04	0,04	0,06	0,03	0,04	0,04	0,01
Difference order	10,00	9,00	14,00	10,00	12,00	12,00		
Average for an attribute	0,05	0,72	1,11	0,82	0,96	0,96		
Stand.dev.	0,03	0,04	0,03	0,05	0,03	0,04		

Table 2. Regression ratios (β) log (males)/ log (females) according to reduced model results (RLM) (designations, as in table 1).

Species/Signs	А	Б	В	Г	Д	Е	Average for species	Stand. dev.
C. granulatus	0,85	0,69	1,05	0,94	0,94	0,70	0,86	0,14
C. cancellatus	1,08	1,06	1,07	1,07	1,01	0,92	1,04	0,06
C. aeruginosus	1,16	1,26	1,2	1,05	1,14	1,05	1,14	0,08
P.melanarius	1,1	1,02	1,04	1,02	1	0,90	1,01	0,07
P. niger	0,91	0,89	0,84	0,98	1,01	0,89	0,92	0,06
P. oblongopunctatus	0,74	0,86	1	1	1,04	1	0,94	0,12
P. cupreus	1,01	1,58	2,5	3,68	1,67	1,36	1,97	0,97
Cal.halensis	0,97	1,17	0,85	0,93	1,01	1,04	1,00	0,11
C. odoratus	1,14	1,11	1,02	1,06	1,04	0,98	1,06	0,06
Average for an attribute	1,00	1,07	1,17	1,30	1,10	0,98		
Stand.dev.	0,14	0,26	0,51	0,89	0,22	0,18		

Table 3. Regression model constants (Intercept) for ground beetle female/male sizes (designations as in table 1)

Species/Signs	А	Б	В	Г	Д	Е
C. granulatus	0,3	0,5	-0,1	0,03	0,02	0,16
C. cancellatus	-0,3	-0,19	-0,16	-0,14	-0,05	0,04
C. aeruginosus	-0,4	-0,3	-0,19	-0,07	-0,12	0,003
C. hortensis	2,67	1,33	1,46	1,74	1,09	0,9
P.melanarius	-0,25	-0,06	-0,07	-0,06	-0,04	-0,03
P. niger	0,16	0,14	0,17	-0,02	-0,04	0,04
P. oblongopuctatus	0,47	0,08	-1,98E-16	1,96E-16	0,02	0,00E+00
P. cupreus	0,05	-0,2	0,11	0,07	-0,03	-0,03
C. halensis	-1,15	-0,98	-1,7	-3,4	-0,6	-0,2
C. odoratus	-0,27	-0,16	0,01	-0,03	0,03	0,06

CONCLUSION

Ground beetles register sexual dimorphism according to all six dimensional signs. Its focus is the same - females are bigger than males. The magnitude of sexual dimorphism on different signs withion the same species of karabids may vary greatly. The differences of values between the species of sexual dimorphism are marked on the same grounds. The analysis of reduced regression model results concerning male and female sizes shows that the variability of the beetle sizes depends on sex and it is species-specific one. The origin and evolutionary fate of PD is likely determined by the genetic architecture responsible for the expression dependent on gender and an interlocus gender conflict degree. Further comparative studies of PD at the inside - and interspecific levels will help to a better understanding of relationships and constraints that control the evolution of PD among animals.

CONFLICT OF INTEREST

The authors acknowledge that the presented data do not contain any conflict of interest.

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