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GEOGRAPHICAL VARIABILITY IN THE CRYPTIC COLORATION OF THE COMMON GREEN GRASSHOPPER (*OMOCESTUS VIRIDULUS* (LINNAEUS, 1758), ORTHOPTERA: ACRIDIDAE)

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Abstract. Based on the study of photographs posted on three Internet sites, as well as field collections, the representation of four colour forms of the grasshopper *Omocestus viridulus* in different parts of its distribution area from Western Europe to Altai and Tien Shan was analyzed. A conclusion was made about a regular decrease in the representation of the green form (viridis) from west to east up to its complete disappearance. It is shown that within the studied part of the distribution area, *O. viridulus* populations can be grouped into three clusters: British-Scandinavian (the largest proportion of representatives of the viridis form), East Eurasian (a very weak representation of the viridis form up to its complete absence), and Western European (intermediate position). In addition, the rarity of males of the hyalosuperficies form (green top and gray or brown sides), females of the rubiginosa form (gray or brown sides and top) and females of the purpurata form (purplish-red flanks and a green top) is shown throughout the entire studied part of the distribution area of *O. viridulus*. A close connection between the representation of the viridis form among both sexes and the rubiginosa form among *O. viridulus* females with the degree of climate continentality was proved. Increasing climate continentality (in particular, the greater the annual temperature range) is correlated with a decrease in the proportion of the viridis form and increase in the proportion of females of the rubiginosa form.

INTRODUCTION

Over the past decades, the range of data sources available to biologists significantly expanded thanks to the Internet. The significance of this circumstance is well known to molecular biologists, but it should not be underestimated also in relation to general biodiversity. The Internet has opened certain possibilities, including for studying the geographical variability of animals, plants and other organisms. This also applies to quantitative patterns of intraspecific geographic variation in the colour of animals, which are of interest for research in the field of population biology, ecology and evolutionary theory. As examples of well-known similar patterns, we can mention the industrial melanism of the peppered moth *Biston betularia* (Linnaeus, 1758), the ecologically determined colour polymorphism of the two-spotted ladybird *Adalia bipunctata* (Linnaeus, 1758) and the clinal colour variability of the tawny owl *Strix aluco* Linnaeus, 1758 (Timofeeff-Ressovsky 1940; Steward 1977; Sergievsky and Zakharov 1981; Yablokov 1987; Galeotti and Cesaris 1996; Zakharov and Rubanovich 2018a, b, 2023).

Important objects for studying colour variability, including the geographic one, are orthopteran insects, including acridid grasshoppers. It is generally accepted that one of the most important functions of coloration in this group of insects is cryptic, protecting against predators (Morse 1907; Rowell 1972). In particular, it is generally accepted that geophilous grasshoppers are characterized by earthy coloration, while the inhabitants of vegetation are characterized by coloration similar to the colours of living or dried plants (Bey-Bienko and Mistshenko 1951; Rowell 1972). Based on this point of view, further in this paper the coloration of the upper and lateral sides of the body of grasshoppers, similar to the colour of the soil or vegetation, is regarded as cryptic.

This work, in addition to solving particular problems related to the issue of the variability of the cryptic coloration of a phytophilous acridid species, the common green grasshopper *Omocestus viridulus* (Linnaeus, 1758), is intended to illustrate some of the possibilities of the Internet as a source of biological data, as well as to show the value of scientific volunteering ("Citizen Science"), an effort by amateur naturalists to make the data they collect available to the public.

The main goal of this paper is to continue a series of works (Ozerskiy 2018; Ozerski 2022) aimed at studying the patterns of variability in the cryptic coloration of acridoids, including in connection with their life forms and with the concept of life form in general. The grasshopper chosen as the model species, *O. viridulus*, is convenient in that its range of colour forms can be relatively easily reduced to just four basic colour variants. Among these colour forms the viridis form (Rubtzov 1935) is characterized by a predominance of green elements in colour and can be easily recognized directly in nature (Figure 1). We can assume a specific adaptive value of this coloration variant – providing camouflage against a uniform green background (which, however, needs to be experimentally verified). In addition, *O. viridulus* has a wide trans-Palaearctic distribution area (Sergeev 1986), which increases the value of this species as a model for studying the patterns of geographic variability. Due to its wide distribution area, *O. viridulus* inhabits several different natural zones and, accordingly, its local populations live under different climatic conditions. Theoretically, it is possible to assume the influence of climate on the quantitative relationships between colour forms in local populations of *O. viridulus* – for example, due to differences in thermoregulation among representatives of different colour forms or, indirectly, through the state of the vegetation (in particular, the colour of the above-ground parts of plants and projective cover), which should have different effects on the effectiveness of different variants of cryptic coloration.

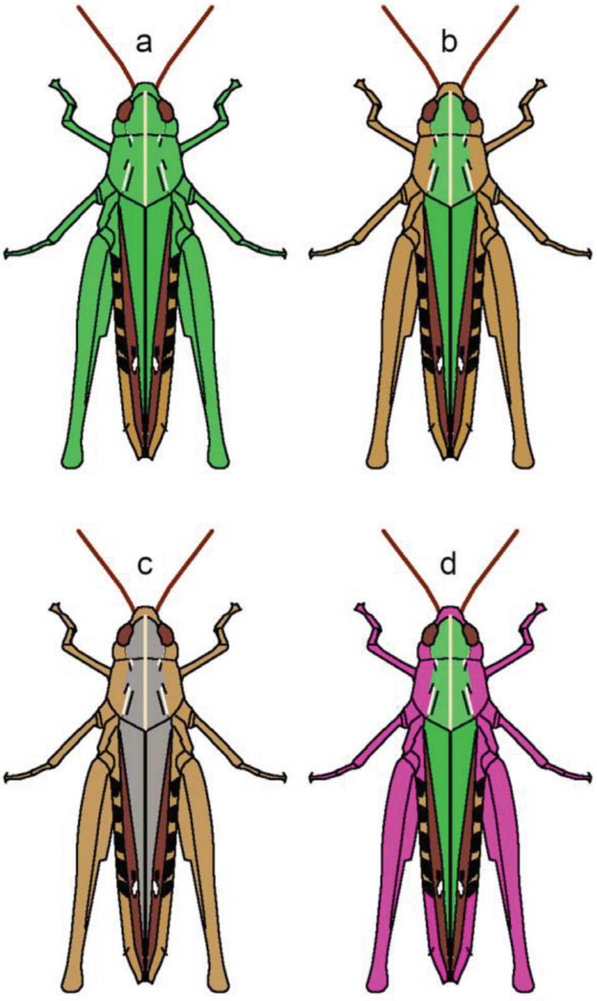

Figure 1. Colour forms of *O. viridulus* (simplified schemes): a – *viridis*; b – *hyalosuperficies*; c – *rubiginosa*; d – *purpurata*.

Previous attempts to quantitatively study the representation of different colour forms in natural populations of this species were predominantly regional in nature: populations of the Scandinavian Peninsula (Petersen and Treherne 1949), Great Britain (Richards and Waloff 1954), and north-western regions of Russia (Ozerskiy 2018; Ozerski 2022) were investigated. This work is an attempt to analyze the regularities in the representation of this form over a much larger area stretching from Western Europe to Western Siberia and Northern Tien Shan, mainly based on data that are publicly available on Internet resources.

MATERIALS AND METHODS

The Internet sites A Community for Naturalists – iNaturalist (https://www.inaturalist.org), Global Biodiversity Information Facility (GBIF) (https://www.gbif.org) and Observation.org (https://observation.org) were used as a data source, aggregating photographic and other data on the location of various species of animals and plants around the globe. At present, these sites provide the possibility of interactive construction of point ranges of taxa based on information about finds stored in its database. Using the tools provided by these sites, electronic maps of recorded *O. viridulus* finds in Eurasia and adjacent islands were built. Using the tools provided by the site, elliptical and rectangular areas were identified on this map, visually distinguished by a particularly large number of *O. viridulus* finds. A total of 22 such areas were identified, within which 2000 findings of *O. viridulus* specimens were identified, accompanied by photographic images (Figure 2; Table 1). Another area (No. 21 with a single point – Medeu in the vicinity of Almaty, Kazakhstan) was surveyed directly in the field using the method of route accounting, as in previous works (Ozerskiy 2018; Ozerski 2022).

In further analysis, the images of adults and larvae of the last instar were used. Based on visual inspection, each of these individuals, despite a certain variability in the shades of non-green colour elements, was assigned to one of the four colour forms in accordance with the classification adopted by I.A. Rubtzov (1935). The following colour forms were distinguished (Figure 1): viridis (green colour predominates, including the head, disk and lateral lobes of the pronotum, pleurites of the meso- and metathorax and femora of the hind legs); hyalosuperficies

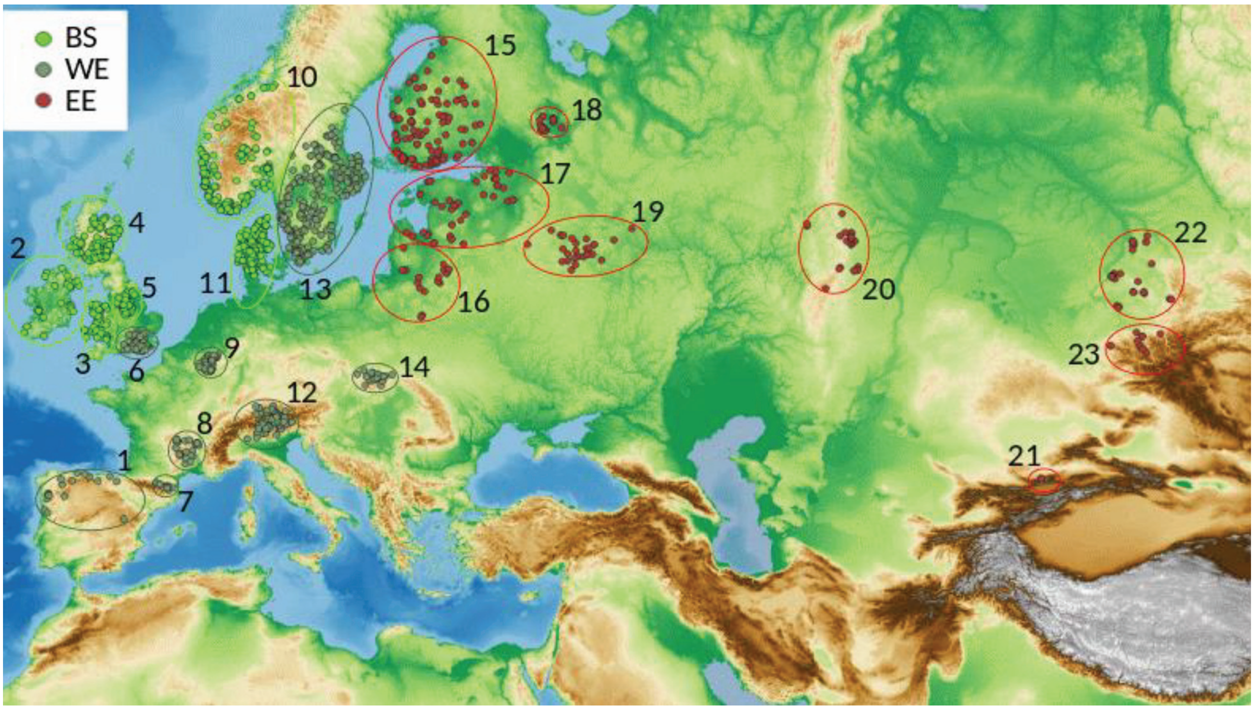

Figure 2. Map of areas – data sources for analysis. Coloured circles indicate *O. viridulus* finds used in the study. The colour of the circles indicates that the respective regions belong to one of the three selected clusters: British-Scandinavian (BS, light green); Western European (WE, dark green); East Eurasian (EE, red).

(grayish, brownish or buffy tones predominate, however, vertex, occiput, top of pronotum and posterior (upper when folded) part of elytra are coloured green); rubiginosa (grayish, brownish, buffy, sometimes olive tones predominate, but green elements are practically absent); purpurata (green colour elements are located, as in representatives of the hyalosuperficies form, and the lateral parts of the head and chest are coloured purple).

Further, for each of the 23 areas identified on the map, the representation of the viridis form was determined separately (calculated as a percentage of the total number of *O. viridulus* individuals identified within the given area). Since it is known that in this species the colour form does not change after imaginal molting (Richards and Waloff 1954) and the proportion of the viridis form is approximately the same (statistically indistinguishable) among males and females (Ozerskiy 2018), the developmental phase and sex of individuals were not considered.

In addition, the representation of all colour forms was determined separately for males and females (calculated as a percentage of the total number of individuals of the corresponding sex). The division by gender was made, since the representation of the forms rubiginosa and hyalosuperficies among males and among females of *O. viridulus* differs significantly (Petersen and Treherne 1949; Richards and Waloff 1954; Ozerskiy 2018; Ozerski 2022).

To visually display geographic differences, the data were plotted on an electronic map using the QGIS 3.28 “Firenze” software. The raster basis of the map was created using GIS data available on the Internet resource https://ows.terrestris.de provided by terrestris (terrestris – WebGIS mit Freier und OpenSource-Software).

Statistical analysis was carried out, except where otherwise noted, using the Past 4.11 software (Hammer et al. 2001). Holm–Bonferroni corrections were calculated using the statistical software R Statistics 4.0.4. Fisher’s exact test was used to compare proportions. The cluster analysis used the UPGMA method and the Euclidean distance. For post hoc assessment of the influence of the factor, the Kruskal-Wallis test was used. To compare the actual ratios with the expected ones, the chi-square fit test implemented in the LibreOffice 7.5.5 spreadsheet (CHITEST function) was used.

When constructing 95% confidence intervals for the proportions, the EBCIC 0.0.4 software (EBCIC: Exact Binomial Confidence Interval Calculator) was used, which implements the exact Clopper-Pearson algorithm.

Spearman’s rank correlation coefficient was used to estimate the relationship between the geographical location of the areas and the proportion of individuals of the viridis form. The calculations used the median values of the geographic latitude and longitude of the finds, calculated for local sampling sets of individuals corresponding to the 23 areas mentioned above.

To estimate the relationship between natural zones in the places where *O. viridulus* was found and the proportions of individuals of the viridis form, natural zones were numbered in the direction from north to south (boreal –

Table 1. Material studied by regions and natural zones.

№	Brief characteristics of areas	Natural zones*	Latitude (median, range in parentheses)	Longitude (median, range in parentheses)	Individuals studied (males/females)**
1	Portugal and north-western Spain	Temperate and submeridional	42.080255 (40.480126 – 43.499492)	−8.173732 (−8.541717 – −1.704907)	24 (6/18)
2	Ireland (including Northern Ireland)	Temperate	53.172205 (51.678209 – 55.257627)	−6.570033 (−10.281903 – −5.580324)	37 (24/13)
3	Wales and adjacent territories of England	Temperate	52.416055 (51.497613 – 53.393102)	−4.0555065 (−5.071323 – −3.126035)	70 (27/43)
4	Scotland	Boreal and temperate	56.014828 (55.617055 – 57.774109)	−3.808658 (−6.364497 – −2.063781)	231 (82/149)
5	Central England	Temperate	53.289696 (52.818636 – 54.120158)	−1.601134 (−2.274347 – −0.804288)	95 (30/65)
6	Southeast England	Temperate	51.078618 (50.82542 – 51.864243)	−0.1116225 (−1.724123–0.452692)	96 (39/57)
7	South-western France, Andorra and adjacent territories of Spain	Submeridional (mountain area)	42.624012 (42.394988–42.851392)	1.9570035 (1.074258–2.466207)	20 (6/14)
8	Southeast France	Temperate	45.3878115 (44.080907–45.637163)	3.640613 (2.753667–4.737599)	34 (12/22)
9	Belgium, Luxembourg and adjacent territories of Germany	Temperate	50.107099 (49.679693–50.637649)	5.752558 (4.749175–6.38196)	123 (52/71)
10	Western Norway	Boreal and temperate	59.466638 (57.731857–63.490476)	7.4557565 (4.874528–11.239945)	208 (70/138)
11	Denmark	Temperate	56.4524895 (54.891708–57.738876)	9.8441005 (8.085575–10.912178)	216 (69/147)
12	Northern Italy and adjacent territories of Austria and Switzerland	Temperate and submeridional (mountain area)	46.725833 (45.662772–47.67741)	11.127588 (8.897391–12.720506)	105 (33/72)
13	Sweden	Boreal and temperate	58.18032 (55.49508–62.488422)	14.333975 (11.72239–19.01912)	328 (95/233)
14	Southeast Poland and northern Slovakia	Temperate (mountain area)	49.397289 (48.875292–49.749641)	20.0581255 (18.333982–21.327373)	36 (17/19)
15	Finland	Boreal and temperate	61.686608 (60.078655–65.143558)	23.471862 (21.376944–28.914115)	145 (67/78)
16	Lithuania	Temperate	54.89941 (52.709389–56.261398)	24.0075665 (22.213855–26.20637)	22 (7/15)
17	Estonia, Latvia and northwest Russia	Boreal and temperate	58.522777 (56.456069–59.895944)	26.7795725 (22.593998–31.728526)	54 (23/31)
18	Republic of Karelia, Russia	Boreal	61.8197305 (61.609137–62.224707)	34.4778165 (33.986275–35.896391)	26 (16/10)
19	Central Russia	Temperate	56.141794 (55.165233–57.212925)	37.284474 (32.968286–41.922157)	31 (16/15)
20	Middle and Southern Ural, Russia	Temperate	56.601588 (54.225483–57.921491)	60.7809805 (56.961345–61.344762)	28 (13/15)
21*	Southeast Kazakhstan	Submeridional (mountain area)	43.1519321748411	77.0631257748435	52 (27/25)
22	Southern Siberia, Russia	Temperate	54.8305935 (53.202819–56.854862)	84.971621 (83.091532–88.242242)	52 (29/23)
23	Altai (Russian part)	Temperate and submeridional (mountain area)	51.142666 (50.147311–51.870944)	85.589947 (83.025063–87.917206)	19 (7/12)

1, moderate – 2, submeridional – 3), and the numbers of natural zones obtained in this way were subsequently used when calculating the Spearman rank correlation coefficient. Each of the 23 areas was assigned a specific natural zone (or specific zones). Areas located within the same natural zone were assigned a rank equal to the number of this zone. The regions located on the borders of two natural zones were assigned intermediate ranks.

When studying the relationship between the proportions of different colour forms and the climatic conditions of the respective geographical areas, data on average monthly temperatures and precipitation for the period from 1991 to 2021 were used, as provided by the Climate Data for Cities Worldwide website (https://en.climate-data.org). Due to a strong influence of altitude, solar exposure and other relief-related factors on temperature conditions in mountainous areas, high-mountain areas were excluded from consideration (7, 12, 14, 21 and 23). Due to the lack of data on the local climate directly in the places of photo registration of individuals, for each of the 18 areas considered below, climatic conditions were extrapolated for 5 geographical points in accordance with Table 2 and Figure 3 (median values were used). In the correlation analysis (also using the Spearman's rank correlation coefficient), both directly the average monthly values of temperatures and precipitation and the indicators of climate continentality based on them – the Zenker (C_Z), Khromov (C_K) and Schwer (C_S) indices were used:

$$C_Z = \frac{6}{5}\frac{A}{\varphi} - 20\,,$$

$$C_K = \frac{A - 5.4\sin\varphi}{A}\cdot 100\%\,,$$

$$C_S = \frac{\sum X_{III-VIII}}{\sum X_{IX-II}}\,,$$

where A is the annual temperature amplitude (°C), φ is the latitude of the area (degrees in the form of a decimal fraction), $\Sigma X_{III-VIII}$ is the amount of precipitation in the spring-summer period (mm), and ΣX_{IX-II} is the total precipitation in the autumn-winter period (mm) (Zenker 1888; Schwer 1976; Khromov and Petrosyants 2006; Kuznetsova and Sokolov 2019).

In addition to continentality indicators, the de Martonne (A_{dM}) (average annual and average monthly) and Gorczyński (A_G) aridity indices were also calculated using the following formulas (Stenz 1946; Dajoz 1975):

$$A_{dM} = \frac{P}{T+10}\,,$$

$$A_g = \frac{A\Delta R\,\mathrm{cosec}\,\varphi}{3R}\cdot\left(1+\frac{ka}{100}\right),$$

where P and T are, respectively, the amount of precipitation (mm) and the average temperature (°C) for a given time period (year or month), A is the annual temperature range (°C), ΔR is the amplitude of average monthly precipitation (mm), R is the annual amount of precipitation, φ is the latitude of the area (degrees as a decimal fraction), and k_a is a correction factor depending on the duration of observations, the value of which in the case of 21 years (1999–2019) is 23 (Gorczyński 1943).

RESULTS AND DISCUSSION

General characteristics of the variability of cryptic coloration of O. viridulus

Within the studied geographic areas, the diversity of colour forms of *O. viridulus* can be reduced to 4 basic ones: viridis, hyalosuperficies, rubiginosa, and purpurata (Figure 4). In most of the areas studied, the most common colour form in *O. viridulus* males was rubiginosa; and in females, hyalosuperficies. The exceptions were areas 2 (Ireland), 3 (Wales), 4 (Scotland), 5 (central England), 10 (Norway) and 11 (Denmark), where the representatives of the viridis form accounted for about half of the individuals (comparison with the expected 1:1 ratio using the chi-square test: $p > 0.05$) or even predominated. At

Figure 3. Map of climate data sources (shown by points). The ovals represent the 18 geographic areas used in the study of the relationship between the proportions of representatives of different colour forms of *O. viridulus* and climatic conditions.

Table 2. Geographical points used to assess climatic conditions in the studied areas.

Area	Locality	Geographic coordinates	
		Latitude	Longitude
1	León	42.605556	−5.57
	Braga	41.551111	−8.428333
	Lugo	43.016667	−7.55
	Pamplona	42.816667	−1.65
	Teruel	40.343611	−1.107222
2	Lisburn	54.512	−6.031
	Greystones	53.144	−6.072
	Clonakilty	51.621944	−8.886389
	Waterville	51.827583	−10.172181
	Athenry	53.3	−8.746
3	Llanidloes	52.449	−3.5402
	Llanrug	53.147	−4.193
	Ponterwyd	52.411667	−3.84
	Carmarthen	51.856	−4.316
	Cardiff	51.481667	−3.179167
4	Tomintoul	57.251	−3.378
	Westhill	57.154	−2.284
	Falkirk	56.0011	−3.7835
	Largs	55.795	−4.87
	Benderloch	56.492222	−5.403611
5	Leeds	53.7975	−1.543611
	Derby	52.921667	−1.476667
	Bolton	53.578	−2.429
	Buxton	53.259	−1.911
	Bakewell	53.214	−1.676
6	Oxford	51.75	−1.25
	Polegate	50.8216	0.2442
	Bishop’s Stortford	51.872	0.1725
	Winchester	51.0632	−1.308
	St Albans	51.755	−0.336
8	Lyon	45.76	4.84
	Lablachire	44.4644	4.215
	Montbrison	45.6083	4.0658
	Issoire	45.545	3.2497
	Rodez	44.3506	2.575
9	Saint-Hubert	50.025	5.372222
	Bastogne	50.004167	5.72
	Leudelange	49.5667	6.0667
	Marche-en-Famenne	50.216667	5.333333
	Houffalize	50.133333	5.783333
10	Sauda	59.6875	6.437222
	Lyngdal	58.169167	7.055833
	Trondheim	63.429722	10.393333
	Ringebu	61.535556	10.308056
	Drammen	59.737778	10.205

Area	Locality	Geographic coordinates	
		Latitude	Longitude
11	Herning	56.133333	8.983333
	Skagen	57.716667	10.583333
	Aalborg	57.05	9.916667
	Aabenraa	55.044444	9.418056
	Oksbøl	55.625833	8.279167
13	Karlskoga	59.333333	14.516667
	Hudiksvall	61.733333	17.116667
	Oskarshamn	57.265	16.45
	Landskrona	55.870556	12.831111
	Mölndal	57.65	12.016667
15	Äänekoski	62.6	25.725
	Kannus	63.9	23.916667
	Paimio	60.45	22.7
	Sulkava	61.783333	28.366667
	Nilsiä	63.205	28.083333
16	Alytus	54.401389	24.049167
	Białystok	53.135278	23.145556
	Varėna	54.211111	24.572222
	Švenčionys	55.133333	26.155556
	Telšiai	55.983333	22.25
17	Ostrov	57.35	28.35
	Ogre	56.818611	24.605556
	Ludza	56.55	27.716667
	Vyritsa	59.411111	30.347222
	Veliky Novgorod	58.55	31.266667
18	Kondopoga	62.2	34.283333
	Petrozavodsk	61.783333	34.333333
	Pudozh	61.8	36.516667
	Medvezhyegorsk	62.9	34.466667
	Povenets	62.85	34.816667
19	Zvenigorod	55.733333	36.85
	Noginsk	55.85	38.433333
	Dmitrov	56.35	37.533333
	Elektrostal	55.783333	38.466667
	Podolsk	55.431111	37.545556
20	Snezhinsk	56.083333	60.733333
	Miass	55	60.1
	Sysert	56.5	60.816667
	Kamensk-Uralsky	56.4	61.933333
	Kungur	57.433333	56.933333
22	Iskitim	54.64	83.306111
	Leninsk-Kuznetsky	54.6575	86.161667
	Toguchin	55.233333	84.416667
	Suzun	53.7825	82.3189
	Kislovka	56.4127568741916	84.8657948663249

The numbering of the regions is as in Figure 2. Natural zones for Europe up to and including the Urals (1–20) are given according to Bohn et al. (2004); and for territories east of the Urals (21–23), according to Grigor and Zemtsov (1961), with changes in terminology.
*Area 21 is represented by field material; other areas, by material from Internet sources.

the same time, the proportion of males of the rubiginosa form is closely related to the proportion of females of the hyalosuperficies form ($\rho = 0.89$; $p < 0.001$). Fisher's exact test revealed statistically significant differences between these two proportions ($p < 0.01$) only for area 15 (Finland); however, accounting for the multiplicity of comparisons using the Holm–Bonferroni correction led to a loss of statistical significance of the differences ($p > 0.05$) also in this case. Thus, taking into account the data obtained for relatively closely related (belonging to the same tribe) species (Sansome and La Cour 1935; Gill 1981; Schielzeth and Dieker 2020; Winter et al. 2021) and indicating the hereditary nature of colour forms, it can be assumed that in *O. viridulus*, the belonging of males to the rubiginosa form and the belonging of females to the hyalosuperficies form are determined by the same allele.

In addition to both sexes of the viridis form, males of the rubiginosa form and females of the hyalosuperficies form, three more colour variants were found among the examined specimens of *O. viridulus*: males of the hyalosuperficies form, females of the rubiginosa form, and females of the purpurata form. The proportion of such individuals was very small and never exceeded 10% of the total number of representatives of the corresponding sex in the corresponding geographical area. Further, these three colour forms are designated as rare.

It is noteworthy that among the examined individuals not a single male of the purpurata form was identified. To explain this phenomenon, one can pay attention to the fact that the colour pattern characterized by a combination of green top and non-green sides is generally uncharacteristic of males of this species. Even the widespread hyalosuperficies form in females, characterized by a similar pattern, is very rare in males. Given that, as noted above, the tribe Gomphocerini is characterized by a genetic determination of body coloration, I would suggest that in male *O. viridulus* the formation of this coloration pattern is determined by a rare allele, phenotypically manifested only in the male sex. At the same time, the presence of purple elements in the colour of females is also observed relatively rarely, which leads to the assumption that in this case we are also talking about a rare allele. Thus, the formation of the phenotype of male f. *purpurata* would only be possible if two rare alleles were combined in the genotype of one individual, which is unlikely regardless of whether we are talking about one or different genes. It should be noted, however, that testing this hypothesis would require special genetic research.

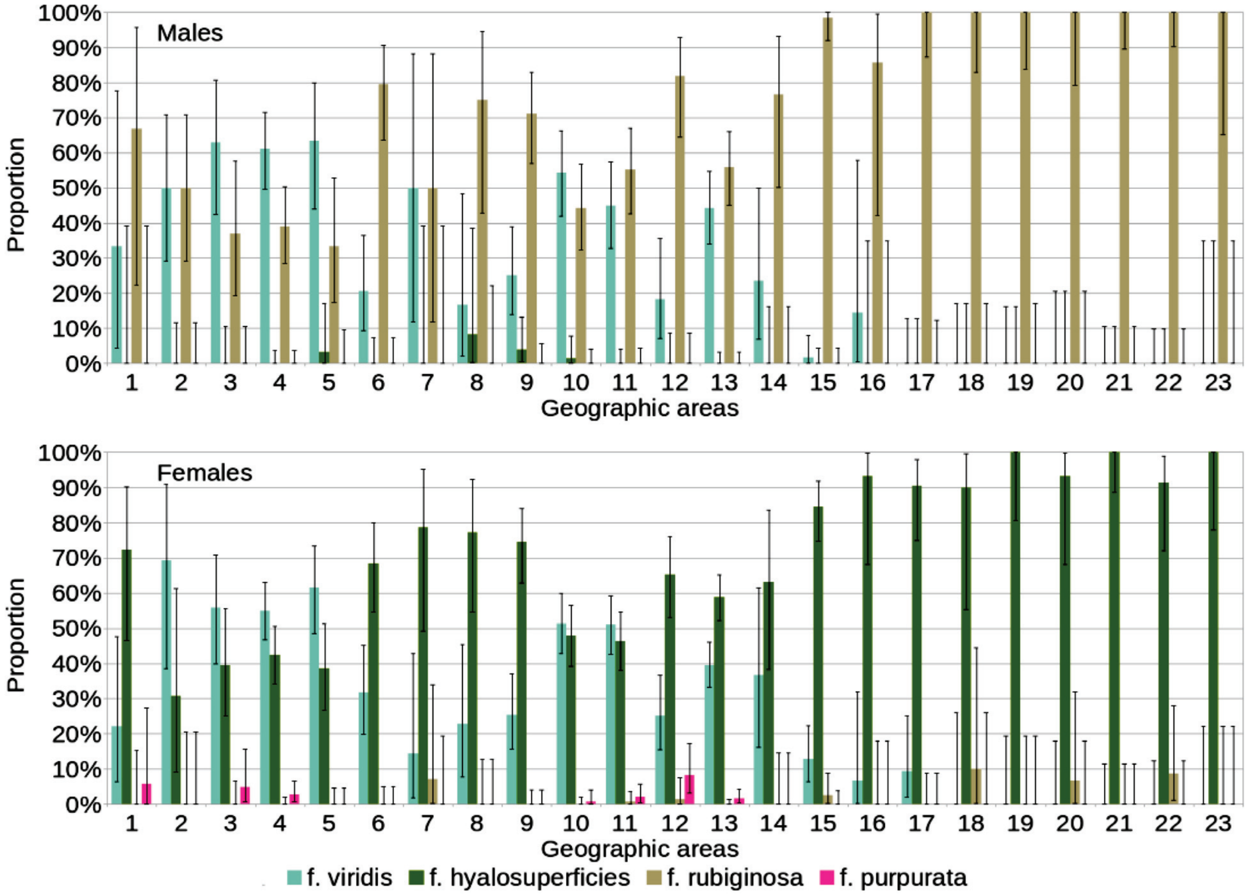

Figure 4. Representation (percentage of the total number of individuals of the same sex) of basic colour forms in the studied geographical areas. Designations of areas are as in Table 1 and in Figure 2. 95% confidence intervals are given.

Representation of the viridis form in different parts of the distribution area of O. viridulus

The representation of individuals of the viridis form varies greatly in different parts of the distribution area of *O. viridulus* (Figure 5). The highest percentage of such individuals was found in area 5, located in the western part of the species distribution area (in central England), and amounted to 62.1% (95% confidence limits – from 51.6% to 71.9%). In the six easternmost regions (18–23), the specimens of the viridis form were not detected at all (with the upper 95% confidence limit in such cases not exceeding 14.6%).

Correlation analysis using the Spearman coefficient showed that the proportion of representatives of the viridis form does not show a statistically significant relationship with either the median (by regions) geographic latitude of their locations (taking into account mountainous regions: $\rho = -0.08$; $p > 0.05$; without taking into account mountainous areas: $\rho = -0.24$; $p > 0.05$), or with the location of finds in certain natural zones (taking into account mountainous areas: $\rho = -0.14$; $p > 0.05$; excluding mountain areas: $\rho = 0.07$; $p > 0.05$). At the same time, the proportion of representatives of the viridis form shows a strong and statistically significant negative relationship with the median (by region) geographic longitude (both with and without mountain regions: $\rho = -0.83$; $p < 0.001$). Thus, in *O. viridulus*, there is a tendency for the proportion of individuals of the viridis form to decrease from west to east.

As can be seen from Figure 5, the occurrence is complex and non-linear. Therefore, a more illustrative use of cluster analysis was done. As can be seen from the dendrogram (Figure 6), according to the representation in densely populated populations of *O. viridulus* of the viridis form, three clusters are clearly distinguished: 1) British-Scandinavian (BS), characterized by a high proportion of such individuals (from 49.1% to 62.1%); 2) Western European (WE), characterized by their moderate representation (from 20.6% to 40.9%); and East Eurasian (EE), where the viridis form is represented by an extremely low percentage or is absent (from 0.0% to 9.1%).

Noteworthy is the fact that the manifestation of this pattern is not prevented by the fact that the south-western (corresponding to area 1 in the terminology of this work) populations of *O. viridulus* belong to a subspecies, *O. viridulus kaestneri* (Harz, 1972), characterized by specific coloration features (the presence of signal elements on the abdomen that are not characteristic of the nominative subspecies). Despite this feature, area 1 in terms of the representation of *O. viridulus* f. viridis fits well into the Western European cluster, to which it also gravitates from a geographical point of view.

The post hoc test of the influence of the cluster membership of regions on the proportion of *O. viridulus* f. viridis showed a statistically significant effect of this factor (Kruskal-Wallis test value adjusted for related values: $H_c = 19.75$; $p < 0.001$).

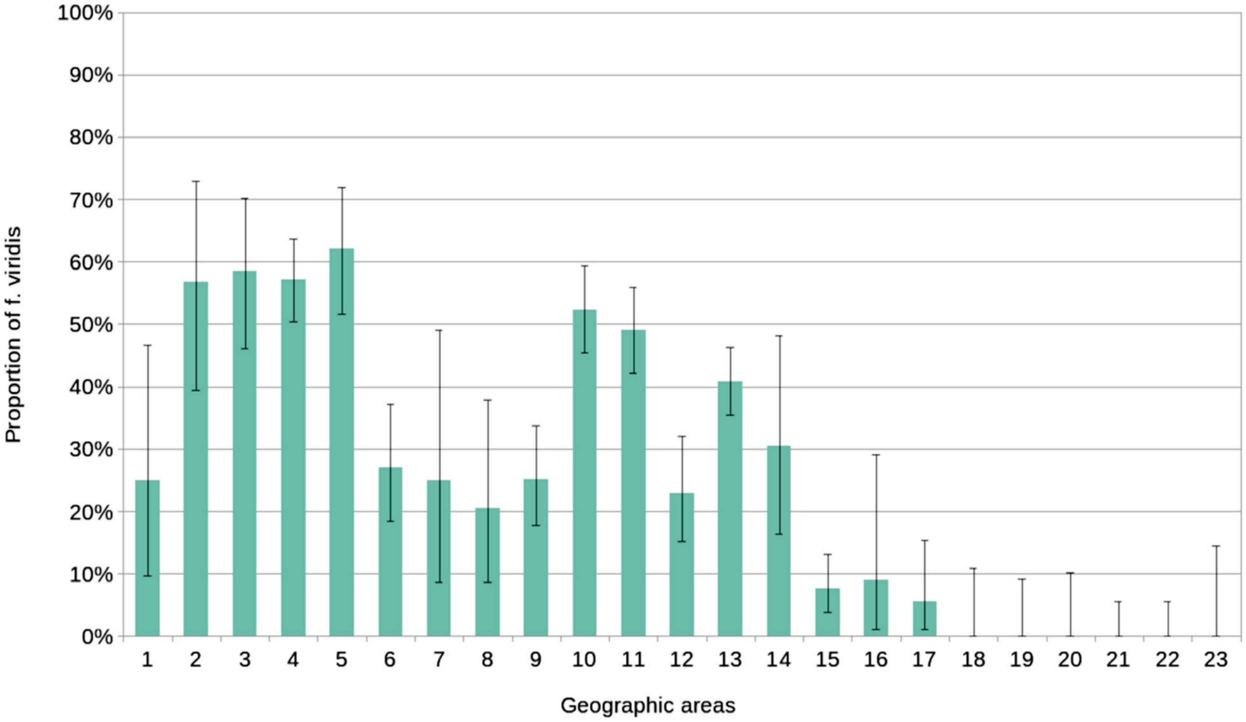

Figure 5. Percentage of representatives of the viridis form among *O. viridulus* individuals in the studied geographic areas. The numbering of areas increases in the direction from west to east. Designation of areas are as in Figure 2. 95% confidence intervals are given.

Of particular interest is the comparison of the obtained results with the available published data (Figure 6; Table 3). At the same time, it should be emphasized that in previous publications of both the author of this work and other researchers, the quantitative analysis of colour variability in grasshoppers was always based on field counts or material collection, and not on Internet content. At the same time, the geographical points of collections and counts that formed the basis of these publications correspond, to one degree or another, to the areas identified in this work or are adjacent to them. So, in the work of Petersen and Treherne (1949), *O. viridulus* populations were studied within areas 10 (western Norway) and 13 (Sweden), in the work of Richards and Waloff (1954) within region 6, and in the works of the author of this study (Ozerskiy 2018; Ozerski 2022) within region 17 (Pskov, Leningrad and Novgorod provinces) and its immediate environs.

An analysis of data previously published for Scandinavia (Petersen and Treherne 1949), Great Britain (Richards and Waloff 1954) and north-western Russia (Ozerskiy 2018; Ozerski 2022) showed their significant similarity with the materials given on iNaturalist and GBIF for respective territories (Fisher's exact test was used for comparison). In the case of points located in Sweden within area 13 (Petersen and Treherne 1949), statistically significant differences were revealed in the total proportion of the viridis form from materials given on the iNaturalist and GBIF sites for both areas located in the west of the Scandinavian Peninsula: $p < 0.01$ for area 10 and $p < 0.001$ for area 13. This data was included in the British-Scandinavian cluster, like area 10 (Figure 6: B). In all other cases (southern Great Britain, Norway, north-western Russia), the literature data did not show statistically significant differences from the iNaturalist and GBIF data for the territorially corresponding regions (6, 10 and 17, respectively) and were included in common clusters with them (Figure 6: C, A, D).

In general, noteworthy is a high correspondence between the proportions of *O. viridulus* f. viridis determined using traditional accounting methods and the proportions calculated for the respective geographic areas from the indicated websites. It was observed in two cases out of four (data for the southeast of England and northwest Russia), and in one more case (data for Norway), despite a statistically significant difference from the Internet data for the corresponding area, the conformity of the proportion of the viridis form to the expected British-Scandinavian cluster was confirmed. The only exception were the localities in Sweden given in the work of Petersen and Treherne (1949), which, in terms of the representation of the viridis form, corresponded not to the area within which they fell geographically but to the neighbouring one. This discrepancy can have various explanations, ranging from the mosaic distribution of the viridis form, which was not taken into account due to insufficient Internet data, to a possible real change in the quantitative relationships between colour forms over time (it should be noted that more than 70 years have passed since the publication of the above-mentioned work by Petersen and Treherne). In any case, however, this deviation does not affect the general trend.

It can be considered a proven trend towards a decrease in the proportion of individuals of the viridis form, up to their complete disappearance, in the direction from west to east (in the absence of a similar trend in the latitudinal direction). It is noteworthy that this pattern is consistent with the data published for the north-western region of Russia and indicating that the territory of the Novgorod province is the boundary between the western populations of *O. viridulus*, in which representatives of the viridis form are regularly found, albeit in small numbers, and the eastern populations of the same species, in which the viridis form is practically absent (Ozerski 2022).

Ecological reasons for geographical differences in representation f. viridis in different parts of the distribution area of O. viridulus

Controversial opinions have been expressed regarding the ecological significance of the variability of cryptic coloration in *O. viridulus*. Petersen and Treherne (1949), based on the results of surveys at two points located in the southeast of Sweden (Sävja and Malsta), concluded

Table 3. Representation of the viridis form in *O. viridulus* populations according to the published data.

Area	Region	Source	Decimal coordinates***		N (males/females)	Percentage of f. viridis		
			Latitude	Longitude		Males	Females	Both sexes
A	Norway	Petersen and Treherne 1949	61.77	9.53	71 (21/50)	61.9 (38.4–81.9)	66.0 (51.2–78.8)	64.8 (52.5–75.8)
B	Sweden	Petersen and Treherne 1949	59.82 (59.77–63.19)	17.70 (14.65–18.92)	1162 (462/700)	62.1 (57.5–66.6)	66.0 (62.4–69.5)	64.5 (61.6–67.2)
C	SE England	Richards and Waloff 1954	51.41	–0.64	2515 (1019/1496)	30.0 (27.2–32.9)	30.3 (28.0–32.7)	30.2 (28.4–32.0)
D	NW Russia	Ozerskiy 2018; Ozerski 2022	57.88 (56.25–59.73)	30.95 (28.08–36.21)	2276 (1086/1190)	4.4 (3.3–5.8)	6.0 (4.7–7.5)	5.2 (4.4–6.2)

***The coordinates are determined from Google maps. The ranges of latitudes and longitudes are given in parentheses.

that in humid habitats the proportion of *O. viridulus* f. viridis is higher than in dry ones, and suggested two possible mechanisms for this phenomenon: selective elimination by predators of individuals with colours that do not match the background and differences in the behaviour of *O. viridulus* individuals belonging to different colour forms. At the same time, however, these authors failed to identify statistically significant differences in the behaviour of representatives of different colour forms (including in relation to the thermal preference, the choice of ambient air humidity and the choice of the ambient background). In addition, my analysis of the data presented in their work was able to confirm the statistical significance of these differences only for the first of these localities (Fisher's exact test: $p < 0.01$).

A few years after the publication of the work of Petersen and Treherne, Richards and Waloff (1954), studying the colour variability of *O. viridulus* in the vicinity of London and comparing data from different years (which differed in hydrothermal conditions and, as a result, in the predominant colour of grass cover), came to the conclusion that the proportion of representatives of the viridis form does not depend on the moisture content of habitats. Finally, in my recent work (Ozerski 2022), on the example of *O. viridulus* populations in northwestern Russia (within the southern taiga and mixed forests), the absence of the pronounced dependence of the proportion of individuals of the viridis form on the natural zones in which their habitats are located was demonstrated. These results are also consistent with the absence of a statistically significant correlation between the natural zones in the places where *O. viridulus* was found and the proportion of the representatives of the viridis form demonstrated above in this work.

Worthy of special attention is the work of Köhler and Schielzeth (2020), in which for two grasshopper species from the same tribe Gomphocerini, *Gomphocerus sibiricus* (Linnaeus, 1767) and *Pseudochorthippus parallelus* (Zetterstedt, 1821), the effect of colour on body temperature was demonstrated by direct measurements in nature: brown individuals warmed up in the sun by about 1.5 °C more than green ones, and the differences were statistically significant. It is important to note that in this work an assumption was made about the relationship between the revealed regularity and the phenomenon of colour polymorphism in acridid grasshoppers.

Developing this assumption, one would expect a higher proportion of dark-coloured individuals (representatives of the forms rubiginosa and hyalosuperficies) in *O. viridulus* populations inhabiting regions with a colder climate compared to populations of warm regions. Indeed, being poikilothermic organisms, acridoids must react to greater body warming by accelerating their development, which, in turn, would provide them with a selective advantage under the conditions of a temporary limitation of the warm season. Indeed, Berner and co-authors (Berner et al. 2004; Berner and Blanckenhorn 2006) experimentally showed that, when kept under the same conditions, the rate of embryonic and larval development in *O. viridulus* directly depends on the altitude at which their initial populations live: the higher the altitude (and, accordingly, the colder the local climate and the shorter the warm season), the faster the grasshoppers reach sexual maturity. However, it should

Table 4. Correlation between the proportion of representatives of the viridis form and some average monthly climatic indicators in the areas inhabited by populations of *O. viridulus*.

Indicator	Values of the Spearman correlation coefficient (ρ) by months											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Average monthly temperature	0.81^{***}	0.80^{***}	0.68^{*}	0.48	−0.26	-0.70^{**}	-0.80^{***}	-0.59^{*}	0.28	0.60^{*}	0.72^{**}	0.79^{**}
Average monthly precipitation	0.90^{***}	0.87^{***}	0.80^{***}	0.67^{*}	0.59^{*}	0.57^{*}	0.22	0.57^{*}	0.60^{*}	0.74^{**}	0.70^{**}	0.84^{***}
Average monthly de Martonne index	−0.06	−0.06	−0.23	0.61	−0.56	-0.70^{*}	−0.55	−0.56	−0.37	0.40	0.70^{*}	0.71^{*}

Spearman correlation coefficients are given. Asterisks indicate statistically significant correlation coefficients. $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$. For each of the indicators separately, a correction for the multiplicity of comparisons was taken into account (the Holm–Bonferroni method was used).

Table 5. Relationship between the proportion of representatives of the viridis form and some average annual climatic indicators in the areas inhabited by populations of *O. viridulus*.

	Temperature amplitude	Precipitation amplitude	Amount of precipitation		Continentality indices			Aridity indices	
			III–VIII	IX–II	Zenker	Khromov	Schwer	De Martonne	Gorczynski
ρ	-0.905^{***}	−0.422	0.636^{**}	0.803^{***}	-0.943^{***}	-0.939^{***}	-0.673^{**}	0.338	-0.918^{***}

Spearman correlation coefficients are given. Asterisks indicate statistically significant correlation coefficients. $^{**}p < 0.01$; $^{***}p < 0.001$.

be noted that in these works of Berner and co-authors the colour variability of *O. viridulus* specimens was not studied and was not taken into account.

The above facts and assumptions regarding the ecological significance of the colour variability of *O. viridulus* prompted me to compare in more detail the representation of the viridis form with climatic conditions in different parts of the range of this species. At the same time, the existence of strong statistically significant correlations between the representation of the viridis form and a number of climatic indicators was confirmed (Tables 4 and 5).

If we talk about average monthly temperatures, then especially strong relationships can be traced between the representation (percentage of the total number) of *O. viridulus* f. viridis and the average temperatures of the coldest and hottest months in the respective geographical areas (in the first case they are positive, and in the second they are negative). Thus, the absolute values of the Spearman correlation coefficients, corresponding to the average temperatures of December, January, February and July, significantly exceeded 0.75. A somewhat similar picture was also revealed in relation to the average monthly precipitation; however, it applies primarily to the cold half of the year (winter and early spring): a strong positive relationship between the average monthly precipitation and the representation of *O. viridulus* f. viridis in the respective geographic areas, with Spearman correlation coefficient values greater than 0.75, was detected for December, January, February and March. However, especially strong relationships were found between, on one side, the representation of *O. viridulus* f. viridis and, on the other, the annual temperature amplitudes and the Zenker and Khromov climate indices based on them, where the absolute values of the Spearman rank correlation coefficient exceeded 0.9. A similar result was obtained for the Gorczynski aridity index, which is also associated with annual temperature amplitudes. Weaker, but statistically significant relationships were also found between the representation of *O. viridulus* f. viridis and average annual climatic indicators associated with precipitation: the total precipitation in the autumn-winter and spring-summer periods, as well as the Schwer continentality index based on them. It should be noted that the use of the Holm–Bonferroni correction for the amplitudes of temperatures and precipitation, as well as the total precipitation in the autumn-winter and spring-summer periods does not change the described picture in relation to the four indicators listed.

When interpreting these results, it should be borne in mind that the regimes of temperatures and precipitation in the studied areas are closely interrelated. In particular, when comparing data for these 18 regions, a strong positive relationship was found between annual temperature amplitudes and average monthly precipitation ($\rho = 0.78$; $p < 0.001$) and a strong negative relationship between annual temperature amplitudes and annual precipitation amounts ($\rho = -0.77$; $p < 0.001$). Therefore, without involving additional data (for example, physiological) it is impossible to make convincing assumptions regarding not only the mechanisms but even environmental factors that directly determine the revealed relationship between the representation of the viridis form and the climatic conditions of *O. viridulus* habitat. In any case, however, it can be argued that a picture observed in nature is strictly opposite to that which would follow from the above assumptions about the role of the thermoregulatory function of colour. Thus, the relationship between the prevalence of the viridis form and climatic conditions should, apparently, be explained by other reasons.

At least two reasons can be mentioned as possible for the revealed regularity. The first is the differences in the surrounding background due to differences in the hydrothermal conditions of the warm season (which, in turn, determine the state of the vegetation cover, including the colour of the aboveground vegetative parts of plants and the projective cover). It should be noted, however, that this assumption is not entirely consistent with the previously shown (Richards and Waloff 1954) lack of a pronounced relationship between the abundance of *O. viridulus* f. viridis and the moisture content of habitats (it is obvious that the surrounding background of a local habitat, which strongly depends on the growing conditions of plants, should be much more important for such a species with little migratory tendency as *O. viridulus* than the background of the “average” vegetation cover of a large region).

The second possible reason for this relationship may be the different physiological response of *O. viridulus* individuals with different genotypes to hydrothermal conditions (i.e., we can talk about the pleiotropic effect of one of the genes that determine the individual’s belonging to one of the colour forms). For example, one can assume different ability of carriers of different alleles of the corresponding gene to endure severe frosts at the stage of overwintering eggs or their different survival or fecundity during hot summers. Indeed, as can be seen from the results of the correlation analysis, the smallest percentage of representatives of the viridis form is observed in *O. viridulus* precisely in regions characterized by the lowest average temperatures in the winter months and the highest average summer temperatures. As the closest analogy, we can mention the long-described situation with the variability in the colour of the elytra in the two-spotted ladybug *Adalia bipunctata* (Linnaeus, 1758), for which differences in the physiological responses of different colour forms to low and high temperatures (in particular, in different survival rates of individuals with normal and melanistic coloration during wintering) and, as a result, differences between populations living in different climatic conditions in the representation of these forms (Timofeeff-Ressovsky 1940; Sergievsky and Zakharov 1981; Brakefield 1985; Zakharov and Rubanovich 2018a, b, 2023). However, it should be noted that a number of unresolved issues also remain regarding the colour polymorphism of *A. bipunctata*, for example, about the mechanisms that determine a strong negative relationship between the proportion of melanistic individuals in the Crimean populations of this species and summer air temperatures (Zakharov and Rubanovich 2018b). It remains to be hoped that subsequent studies will provide answers to questions about the mechanisms that link colour polymorphism with climatic conditions in both *A. bipunctata* and *O. viridulus*.

Representation of rare colour forms in different parts of the distribution area of O. viridulus

The representation of rare colour forms of *O. viridulus* – males of the hyalosuperficies form, females of the rubiginosa and purpurata forms (the latter form was found only in females) – in the areas under consideration was very low and in no case exceeded 10.0% of the total number of analyzed individuals of corresponding sex (Table 6). In most cases, the relationship between the representation of rare forms (expressed as a percentage of the total number of individuals of the same sex) and geographic latitude and longitude (calculated as median values), as well as the natural zone of the respective areas could not be identified ($p > 0.05$). In three cases, the Spearman correlation coefficients turned out to be statistically significant: this is a positive relationship between the representation of females of the rubiginosa form and geographic latitude and longitude (in both cases, excluding mountain areas 7, 12, 14, 21, 23; respectively, $p < 0.05$ and $p < 0.01$) and a negative relationship between the representation of females of the purpurata form and geographic longitude (both with and without taking into account the same mountainous areas; in both cases, $p < 0.05$). However, it should be noted that in all the above cases, the values of the Spearman correlation coefficient had values corresponding to a weak or very weak correlation. When using the Holm–Bonferroni corrections for each of the rare colour forms, only the relationship between the proportion of females of the rubiginosa form and geographic longitude (excluding mountainous areas) remains statistically significant ($p < 0.05$).

While assessing the correlations between the representation of rare colour forms of *O. viridulus* and average

Table 6. Expression of relationship between the representation of rare colour forms of *O. viridulus*, median geographic coordinates (latitude and longitude) and natural zones of the respective areas.

Colour form	Latitude	Longitude	Natural zone
hyalosuperficies (males)	−0.11 (−0.32)	−0.28 (−0.23)	−0.10 (0.10)
rubiginosa (females)	0.24 (0.49*)	0.33 (0.62**)	−0.03 (−0.22)
purpurata (females)	−0.05 (−0.11)	−0.45* (−0.51*)	−0.00 (0.05)

The values of the Spearman correlation coefficient are given, calculated with and (in parentheses) without taking into account mountainous areas (7, 12, 14, 21, 23). Asterisks indicate statistically significant relationships: $^*p < 0.05$; $^{**}p < 0.01$ (not adjusted for multiple comparisons).

Table 7. Correlation between the proportions of representatives of rare colour forms and some average monthly climatic indicators in the areas inhabited by populations of *O. viridulus*.

Indicator	Values of the Spearman correlation coefficient (ρ) by months											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
hyalosuperficies (males)												
Average monthly temperature	0.14	0.14	0.23	0.30	0.06	−0.08	−0.17	−0.11	0.07	0.23	0.14	0.14
Average monthly precipitation	0.40	0.41	0.43	0.44	0.57	0.56	0.25	0.33	0.51	0.38	0.41	0.48
Average monthly de Martonne index	0.06	0.14	0.07	0.47	−0.50	−0.33	−0.23	−0.24	−0.41	0.08	0.04	0.18
rubiginosa (females)												
Average monthly temperature	−0.65*	−0.66*	−0.69*	−0.69*	−0.45	0.11	0.21	−0.01	−0.48	−0.63*	−0.62*	−0.65*
Average monthly precipitation	−0.66*	−0.69*	−0.59	−0.71*	−0.70*	−0.55	−0.05	−0.17	−0.38	−0.46	−0.44	−0.49
Average monthly de Martonne index	−0.08	−0.12	0.52	−0.32	0.19	0.23	0.09	0.06	−0.02	−0.53	−0.52	−0.63
purpurata (females)												
Average monthly temperature	0.40	0.39	0.36	0.19	−0.17	−0.32	−0.31	−0.19	0.20	0.36	0.33	0.39
Average monthly precipitation	0.48	0.50	0.44	0.45	0.30	0.13	−0.01	0.21	0.21	0.46	0.42	0.43
Average monthly de Martonne index	−0.12	−0.14	−0.16	0.39	−0.31	−0.26	−0.14	−0.19	−0.06	0.28	0.45	0.38

Asterisks indicate statistically significant correlation coefficients. $^*p < 0.05$. For each of the indicators separately, a correction for the multiplicity of comparisons was taken into account (the Holm–Bonferroni method was used).

monthly climatic indicators (temperatures, precipitation, and de Martonne aridity indices; Table 7), statistically significant relationships were identified for females of the rubiginosa form.

First of all, statistically significant negative correlations of moderate strength between the representation of females of the rubiginosa form and the average monthly temperatures of the cold half of the year (from October to April inclusive) were revealed. The statistical significance of these relationships is also preserved in the case of the Holm–Bonferroni correction; however, in all cases, the critical level of significance increases from 0.01 to 0.05.

In addition, statistically significant negative correlations (strong and moderate) between the representation of females of the rubiginosa form and the average monthly precipitation for a number of months were revealed. Without taking into account multiple comparisons, they are traced from December to June (for December and June $p < 0.05$, for other months $p < 0.01$). If the Holm–Bonferroni correction is applied, the statistical significance of these relationships is confirmed only for January, February, April and May (in all cases, $p < 0.05$).

To complete the picture, it should be mentioned that without taking into account multiple comparisons, weak positive relationships are also revealed between the representation of females of the purpurata form and average monthly precipitation in January and February ($p < 0.05$). However, in the case of the Holm–Bonferroni correction, these relationships become statistically insignificant.

While assessing the correlations between the representation of rare colour forms of *O. viridulus* and average annual climatic indicators (Table 8), statistically significant relationships were found for females of the rubiginosa form (with temperature and precipitation amplitudes, with the amount of precipitation in the autumn-winter period, as well as with temperature amplitude-based indices of continentality (Zenker and Khromov) and aridity (Gorczynski). In addition, a statistically significant positive relationship was found between the representation of males of the hyalosuperficies form and the amount of precipitation in the spring-summer period. However, almost all of the identified relationships are relatively weak (the absolute values of the Spearman correlation coefficients are less than 0.65), and when using the Holm–Bonferroni correction for the amplitudes of temperatures and precipitation, as well as the total precipitation in the autumn-winter and spring-summer periods, the only statistically significant ($p < 0.05$) relationship remains between the proportion of females of the rubiginosa form and the annual temperature amplitude.

It should be noted that exactly the annual temperature amplitude underlies the above-mentioned continentality and aridity indices, for which the relationship with the representation of females of the rubiginosa form is also statistically confirmed. In contrast to the situation with the viridis form, in all these cases the relationship is positive, that is, there is a tendency to an increase in the proportion of females of the rubiginosa form as the annual temperature amplitude (and, accordingly, the climate continentality) increases.

Thus, among the rare colour forms, the most pronounced relationship between the representation in populations and the climatic conditions of the habitats is demonstrated by females of the rubiginosa form, which clearly gravitate to areas with relatively low temperatures in the cold half of the year and low rainfall. It should be recognized that, as in the case of the viridis form, the mechanisms responsible for these patterns remain unclear.

Sex ratio in O. viridulus and some general considerations about the representativeness of the analyzed material

The representativeness of the data provided by photographers and other volunteers on Internet resources at the disposal of researchers can naturally be questioned.

Table 8. Correlation between the proportion of representatives of rare colour forms and some average annual climatic indicators in the areas inhabited by populations of *O. viridulus*.

Colour form	Temperature amplitude	Precipitation amplitude	Amount of precipitation		Continentality indices			Aridity indices	
			III–VIII	IX–II	Zenker	Khromov	Schwer	De Martonne	Gorczynski
hyalosuperficies (males)	−0.18	−0.20	0.53^{*}	0.42	−0.17	−0.20	−0.40	0.38	−0.32
rubiginosa (females)	0.58^{*}	0.55^{*}	−0.46	0.49^{*}	0.54^{*}	0.54^{*}	0.38	0.04	0.63^{**}
purpurata (females)	−0.43	−0.19	0.27	0.46	−0.43	−0.41	−0.42	0.05	−0.33

The values of the Spearman correlation coefficient calculated without taking into account mountainous regions are given (7, 12, 14, 21, 23). Asterisks indicate statistically significant correlation coefficients. $^{*}p < 0.05$; $^{**}p < 0.01$ (not adjusted for multiple comparisons).

As a rule, volunteers do not set themselves the task of purposefully observing the real quantitative ratios between the representation of different species, forms, sexes, etc. in the places of photography. Moreover, even with proper precautions the proportion of identified individuals from their actual number in representatives of different species, forms and sexes can still be different − both for objective reasons (different visibility of individuals of different colours on the same ambient background, different mobility of females and males, their different propensity to jump and fly in danger, etc.) and subjective (different degrees of attractiveness of different individuals for photography, which depends on their size, colour, and rarity).

To test this hypothesis, a sample sex ratio was analyzed in *O. viridulus*, based on the analysis of the same data for 22 areas that were obtained from Internet sources and used to analyze the representation of colour forms. It turned out that the sex ratio of *O. viridulus* differs markedly in different geographical areas: the proportion of males varies from 25.0% (area 1 – Portugal and northern Spain) to 64.9% (area 2 – Ireland) (Figure 7). At the same time, as can be seen from the same figure, in more than half of the cases – except for seven regions (1, 4, 5, 10, 11, 12 and 13) – a 1:1 ratio falls into the 95% confidence interval, consistent with the data cited in the literature for this species by chromosomal sex determination with heterogametic males (X0) and homogametic females (XX) (Rees et al. 1978). The same conclusion is confirmed by the chi-square goodness-of-fit test: statistically significant deviations of the sex ratio from the expected 1:1 were detected only for 7 areas (for 6 in the case of the Holm–Bonferroni correction) out of 23 (Table 9).

Thus, it can be assumed that, in relation to *O. viridulus*, the objective and subjective factors discussed above did not have a significant impact on the representativeness of the sample data in about two-thirds of the cases. This gives grounds to believe that the above assessment of the ratios between the representation of different colour forms in different parts of the range of this species also deserves some confidence. It should be noted that the same is indirectly evidenced by the above-mentioned significant degree of agreement between the results of the analysis of Internet materials in relation to the representation of the viridis form with the results of traditional countings. However, the example of sex ratio seems to me more revealing, as it relies on sexual dimorphism,

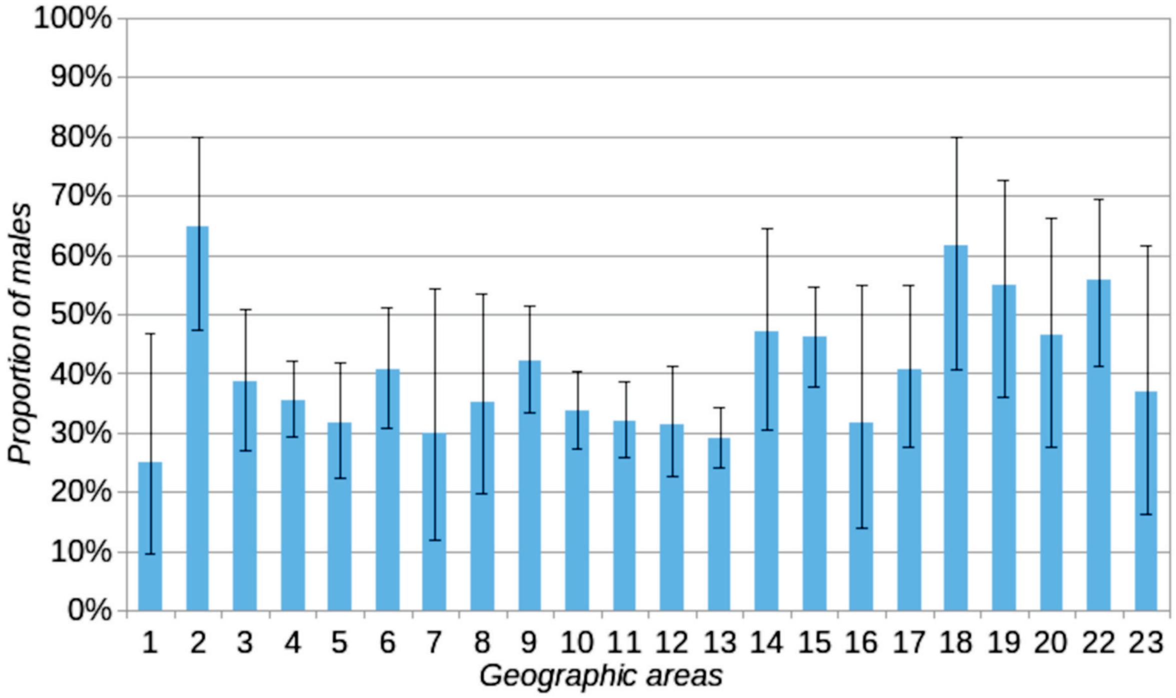

Figure 7. Percentage of males among *O. viridulus* individuals in the geographic areas studied. Designation of areas is as in Figure 2. 95% confidence intervals are given.

Table 9. The degree of conformity of the sex ratio of *O. viridulus* from different geographic areas to the expected 1:1 ratio without adjustment for multiple comparisons and with the Holm–Bonferroni correction.

Area	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	22	23
Without correction		*		***	***					***	***	***	***									
Holm–Bonferroni corrected				***	**					***	***	**	***									

The results of the comparison made using the chi-square goodness-of-fit test are given, without taking into account mountainous areas (7, 12, 14, 21, 23). Asterisks indicate statistically significant correlation coefficients. $^{*}p < 0.05$; $^{***}p < 0.001$.

which affects, among other things, the size and behaviour of individuals. Males in *O. viridulus* are noticeably smaller than females and at the same time have a much greater ability and propensity to fly, thus proving to be less convenient subjects for photography. Despite this, as can be seen above, in most cases, there were no significant differences in the sex ratio revealed during the analysis of photographs from the expected one.

Thus, it can be assumed that Internet resources such as iNaturalist and GBIF and Observation.org, at least in some cases, provide an acceptable degree of representativeness of the data they provide and are quite suitable for use in scientific research.

CONCLUSIONS

1. In the entire studied part of the range, from the western tip of Europe and the British Isles to Altai and the southeast of Western Siberia, the same basic colour forms are represented among *O. viridulus* individuals: rubiginosa, hyalosuperficies, viridis, and purpurata (only in females).

2. Quantitative relationships between colour forms differ in different parts of the distribution area of *O. viridulus*. In general, there is a tendency for the proportion of individuals of the viridis form to decrease up to their complete disappearance from west to east.

3. The relationship between the representation of the viridis form and the geographical latitude and natural areas of *O. viridulus* in the studied part of its distribution area is not statistically significant.

4. According to the representation of the viridis form, the studied geographical areas are grouped into three distinct clusters: British-Scandinavian, Western European, and Eastern Eurasian. The highest proportion of *O. viridulus* f. viridis is in the areas belonging to the British-Scandinavian cluster, while in the areas of the East Eurasian cluster it is very low up to complete absence.

5. A strong correlation was found between the representation of the viridis form and a number of climatic indicators, trending towards decrease in the representation of the viridis form as the continentality and aridity of the climate increase.

6. Males of the hyalosuperficies form and females of the rubiginosa and purpurata forms are rare or absent in the studied part of the species distribution area. Males of the purpurata form were not noted at all. There are weakly pronounced tendencies towards an increase in the proportion of females of the rubiginosa form in directions from south to north and from west to east and to a decrease in the proportion of females of the purpurata form in the direction from west to east.

7. A correlation was found between the representation of rubiginosa females and a number of climatic indicators, trending towards increase in the representation of females of the rubiginosa form as the continentality and aridity of the climate increase.

8. A weak positive correlation was found between the representation of males of the hyalosuperficies form and the amount of precipitation in the spring-summer period. Unfortunately, the available amount of data does not allow me to offer a convincing explanation for the discovered phenomenon.

9. Despite a number of objective and subjective prerequisites for the different photo-registration efficiency of males and females of *O. viridulus*, the selective sex ratio of this species in most of the studied areas does not differ significantly from the expected ratio of 1:1. Indirectly, this indicates a relatively unbiased representativeness of the data provided by volunteer photographers and allows us to regard Internet resources like iNaturalist and GBIF and Observation.org as useful sources of primary data, at least in some cases quite suitable for use in scientific research.

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REFERENCES

A Community for Naturalists – iNaturalist. https://www.inaturalist.org (accessed on 11 May 2023).

Berner, D., & Blanckenhorn, W.U. 2006. Grasshopper ontogeny in relation to time constraints: adaptive divergence and stasis. *Journal of Animal Ecology* 75(1), 130–139. https://doi.org/10.1111/j.1365-2656.2005.01028.x

Berner, D., Körner, Ch., & Blanckenhorn, W.U. 2004. Grasshopper populations across 2000 m of altitude: is there life history adaptation? *Ecography* 27(6), 733–740. https://doi.org/10.1111/j.0906-7590.2005.04012.x

Bey-Bienko, G.Ya., & Mistshenko, L.L. 1951. *Locusts and grasshoppers of the USSR and adjacent Countries*. Vol. 1. Moscow/Leningrad: The USSR Academy of Sciences, 380 pp. [In Russian].

Bohn, U., Gollub G., Hettwer, Ch., Neuhäuslová, Z., Raus, Th., Schlüter, H., & Weber, H. 2004. Karte der natürlichen Vegetation Europas. *Bundesamt für Naturschutz*, Bonn, 512 pp. [In German].

Brakefield, P.M. 1985. Differential winter mortality and seasonal selection in the polymorphic ladybird *Adalia bipunctata* (L) in the Netherlands. *Bio-*

logical Journal of fhe Linnean Society 24, 189–206. https://doi.org/10.1111/j.1095-8312.1985.tb00169.x

Climate Data for Cities Worldwide. https://en.climate-data.org (accessed on 15 September 2023).

Dajoz, R. 1975. *Fundamentals of ecology*. Moscow: Progress, 416 pp. [In Russian].

EBCIC: Exact Binomial Confidence Interval Calculator. https://kazkobara.github.io/ebcic/ (accessed on 15 September 2023).

Galeotti, P., & Cesaris, C. 1996. Rufous and Grey Colour Morphs in the Italian Tawny Owl: Geographical and Environmental Influences. *Journal of Avian Biology* 27(1), 15–20.

Gill, P. 1981. The genetics of color patterns in the grasshopper *Chorthippus brunneus*. *Biological Journal of the Linnaean Society* 16(3), 243–259. https://doi.org/10.1111/j.1095-8312.1981.tb01850.x

Global Biodiversity Information Facility. https://www.gbif.org (accessed on 15 September 2023).

Gorczyński, W. 1943. Aridity factor and precipitation ratio and their relation to world climates. *Bulletin of the Polish Institute of Arts and Sciences in America* 1(3), 602–645.

Grigor, G.G., & Zemtsov, A.A. 1961. Natural zoning of Western Siberia. Voprosy Geografii Sbornik. *Prirodnoe i selskokhozyaystvennoe rayonirovanie SSSR* 55, 82–90. Moscow: Geografgiz. [In Russian].

Hammer, Ø., Harper, D.A.T., & Ryan, P.D. 2001. Past: paleontological statistics software. Package for education and data analysis. *Palaeontologia Electronica* 4(1), Art. 4., 9 pp. http://palaeo-electronica.org/2001_1/past/past.pdf (accessed on 12 September 2023).

Khromov, S.P., & Petrosyants, M.A. 2006. *Meteorology and Climatology: a textbook*. 7th Ed. Moscow: Moscow University, Nauka, 582 pp. [In Russian].

Köhler, G., & Schielzeth, H. 2020. Green-brown polymorphism in alpine grasshoppers affects body temperature. *Ecology and Evolution* 10, 441–450. https://doi.org/10.1002/ece3.5908

Morse, A.P. 1907. Further researches on North American Acrididae. *Carnegie Inst. Washington publication* No 68, 54 pp. Washington: Wilkens-Sheiry.

Observation.org. https://observation.org (accessed on 15 September 2023).

Ozerski, P.V. 2022. On colour variability of the common green grasshopper *Omocestus viridulus* (Orthoptera: Acrididae) in northwestern Russia. *Proceedings of the Zoological Institute RAS* 326 (2), 115–124. https://doi.org/10.31610/trudyzin/2022.326.2.115

Ozerskiy, P.V. 2018. To the color variation in the common green grasshopper (*Omocestus viridulus*, Orthoptera: Acrididae). *Printsipy ekologii* 1, 73–84. [In Russian]. https://doi.org/10.15393/j1.art.2018.7262

Petersen, B., & Treherne, J.E. 1949. On the distribution of colour forms in Scandinavian *Omocestus viridulus* L. *Oikos* 1(2), 175–183. https://doi.org/10.2307/3564711

Rees, H., Shaw, D.D., & Wilkinson, P. 1978. Nuclear DNA variation among acridid grasshoppers. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 202, 517–525. https://doi.org/10.1098/rspb.1978.0083

Richards, O.W., & Waloff, N. 1954. Studies of the biology and population dynamics of British grasshoppers. *Anti-Locust Bulletin* 17, 1–182.

Rowell, C.H.F. 1972. The variable coloration of the acridoid grasshoppers. *Advances in Insect Physiology* 8, 145–198.

Rubtzov, I.A. 1935. Phase variation in non-swarming grasshoppers. *Bulletin of Entomological Research* 26(4), 499–520.

Sansome, F.W., & Cour, L.La 1935. The genetics of grasshoppers: *Chorthippus parallelus*. *Journal of Genetics* 30(3), 415–422.

Schielzeth, H., & Dieker, P. 2020. The green-brown polymorphism of the club-legged grasshopper *Gomphocerus sibiricus* is heritable and appears genetically simple. *BMC Evolutionary Biology* 20(1), 63. https://bmcecolevol.biomedcentral.com/articles/10.1186/s12862-020-01630-7 (accessed on 14 September 2023). https://doi.org/10.1186/s12862-020-01630-7

Schwer, Ts.A. 1976. *Precipitation on the territory of USSR*. Leningrad: Gidrometeoizdat, 304 pp. [In Russian].

Sergeev, M.G. 1986. *Patterns of distribution of orthopteran insects of Northern Asia*. Novosibirsk: Nauka, 238 pp. [In Russian].

Sergievskiy, S.O., & Zakharov, I.A. 1981. Ecological genetics of *Adalia bipunctata* populations: the “rigid” and “flexible” polymorphism concept. *Issledovaniya po genetike* 9, 112–129. [In Russian].

Stenz, E. 1946. *The climate of Afghanistan: its aridity, dryness and divisions*. New York: Polish Institute of Arts and Science in America, 16 pp.

Steward, R.C. 1977. Industrial and non-industrial melanism in the pappered moth, *Biston betularia* (L.). *Ecological Entomology* 2(3), 231–243.

Terrestris – WebGIS mit Freier und OpenSource-Software. https://www.terrestris.de (accessed on 15 September 2023). [In German].

Timofeeff-Ressovsky, N.V. 1940. To the analysis of the polymorphism of *Adalia bipunctata* L. *Biologisches Zentralblatt* 60(3–4), 130–137. [In German].

Winter, G., Varma, M., & Schielzeth, H. 2021. Simple inheritance of color and pattern polymorphism in the steppe grasshopper *Chorthippus dorsatus*. *Heredity* 127, 66–78. https://doi.org/10.1038/s41437-021-00433-w

Yablokov, A.V. 1987. *Population Biology*. Moscow: Vysshaya Shkola, 303 pp. [In Russian].

Zakharov, I.A., & Rubanovich, A.V. 2018a. Ecological genetics of the beetles of the genus Adalia of the population of Norway and Kola Peninsula. *Eko-*

logicheskaya genetika 16(1), 49–52. [In Russian]. https://doi.org/10.17816/ecogen16149-52

Zakharov, I.A., & Rubanovich, A.V. 2018b. Ecological genetics of the beetles of the genus Adalia: the composition of Crimean populations of *A. bipunctata* depends on climate factors. *Ekologicheskaya genetika* 16(1), 45–48. [In Russian]. https://doi.org/10.17816/ecogen16145-48

Zakharov, I.A., & Rubanovich, A.V. 2023. Ecological genetics of the beetles of the genus Adalia: the rebuilding of the composition of populations of *A. bipunctata* as an effect of global warming. *Ekologicheskaya genetika* 21(1), 33–39. [In Russian]. https://doi.org/10.17816/ecogen317164

Zenker, W. 1888. *Die Vertheilung der Wärme auf der Erdoberfläche*. Berlin: Julius Springer, 98 pp. [in German].