Proceedings of the Zoological Institute RAS
Vol. 326, No. 2, 2022, pp. 115–124
10.31610/trudyzin/2022.326.2.115

УДК 595.727, 575.2, 57.018.6

On colour variability of the common green grasshopper *Omocestus viridulus* (Orthoptera: Acrididae) in northwestern Russia

P.V. Ozerski

N.I. Vavilov All-Russian Institute of Plant Genetic Resources, 42–44, Bol'shaya Morskaya Street, 190000, Saint Petersburg, Russia: e-mail: ozerski@list.ru

Submitted December 22, 2021; revised April 15, 2022; accepted May 12, 2022.

ABSTRACT

The diversity of colour forms in the common green grasshopper *Omocestus viridulus* (Linnaeus, 1758) in 19 localities of the Leningrad, Novgorod and Pskov provinces and adjacent districts of the Vologda and Tver provinces is studied. It has been established that the common green grasshopper is represented by three colour forms: rubiginosa (top and sides of brownish or greyish tones), hyalosuperficies (green top, greyish or brownish sides) and viridis (green top and sides). The most characteristic form for males is rubiginosa, for females is hyalosuperficies, while females of the form rubiginosa and (especially) males of the hyalosuperficies form are extremely rare. The proportion of specimens of the form viridis does not depend on sex, does not depend on the natural zone in which the locality is situated, and nowhere exceeds a quarter of the total number of recorded specimens. To the east of the conventional line passing through the town of Chudovo and the settlement of Kresttsy, Novgorod Province, individuals of the form viridis are practically not found, there is only a single record of such a male. At the same time, the representation of the form viridis on different sides of the above-mentioned line is statistically significantly different. The data obtained are consistent with the results of our previous study carried out at 10 localities in the Novgorod and Pskov provinces. In addition, in terms of the representation of the form viridis, our data for northwestern Russia differ statistically significantly from the literature data published in the 1940s for the Scandinavian and British populations of the same species.

Key words: colour forms, grasshoppers, Northwestern Russia, Orthoptera

К вопросу об изменчивости окраски зеленой травянки *Omocestus viridulus* (Orthoptera: Acrididae) на северо-западе России

П.В. Озерский

Всероссийский институт генетических ресурсов растений им. Н.И. Вавилова, Большая Морская ул., 42–44, 190000 Санкт-Петербург, Россия; e-mail: ozerski@list.ru

Представлена 22 декабря 2021; после доработки 15 апреля 2022; принята 12 мая 2022.

РЕЗЮМЕ

Изучено разнообразие цветовых форм у кобылки – зеленой травянки *Omocestus viridulus* (Linnaeus, 1758) в 19 точках Ленинградской, Новгородской и Псковской областей и сопредельных с ними районов Вологодской и Тверской областей. Установлено, что на исследованной территории зеленая травянка представлена тремя цветовыми формами: rubiginosa (верх и бока буроватых или сероватых тонов), hyalosuperficies (зеленый верх, сероватые или буроватые бока) и viridis (зеленые верх и бока). Наиболее характерной формой для самцов является rubiginosa, для самок – hyalosuperficies; при этом самки формы rubiginosa и (особенно) самцы формы hyalosuperficies отмечаются крайне редко. Доля особей формы viridis не зависит от пола и природной зоны, в которой располагается точка учета, и в пределах исследованной территории нигде не превышает четверти от общего количества учтенных особей. Восточнее условной линии, проходящей через город Чудово и поселок Крестцы Новгородской области, особи формы viridis практически не встречаются; имеется лишь единичная находка такого самца. При этом представленность формы viridis по разные стороны от указанной линии статистически значимо различается. Полученные данные согласуются с результатами нашего предыдущего исследования, проведенного в 10 точках Новгородской и Псковской областей. Кроме того, по представленности формы viridis наши данные по северо-западу России статистически значимо отличаются от литературных данных, опубликованных в 40-х и 50-х годах XX века для скандинавских и британских популяций этого же вида.

Ключевые слова: цветовые формы, саранчовые, северо-запад России, прямокрылые

INTRODUCTION

Orthoptera is an order of insects, many of which are characterized by a pronounced protective colouration. Depending on the typical habitat and layer confinement, it can be different and correspond, for example, to the colour of the soil or of the living or dead vegetation. Since many systems of Orthoptera life forms were developed primarily to reflect the relationship of these insects with certain ecofaunas and types of habitats, it is quite natural that the features of protective colouration were also mentioned in the characteristics of life forms as one of important features. At the same time, it was repeatedly noted that representatives of different life forms are characterized by different body colour (see, for example, Bey-Bienko and Mishchenko 1951; Pravdin 1978). However, the above does not negate the prevalence of the phenomenon of intraspecific variability of protective colouration in Orthoptera. Such variability is widespread among bush-crickets (Tettigonioidea) and grasshoppers (Acridoidea), and in the latter it often exhibits similar patterns in different species in accordance with the law of homologous series of N.I. Vavilov (Vorontsovskiy 1928; Rubtzov 1935; Ramme 1950). At the same time, the frequency of occurrence of certain colour forms differs in different species of Orthopteran insects, including closely related ones, often even within the same genus (Ozerski 2012, 2014a).

It can be assumed that this variability demonstrates in different species and in different life forms certain patterns that deserve more detailed study. Such patterns should be of particular interest because they can be considered as possible characters of life forms manifested not at the individual, but at the population level. The latter is important for clarifying the concept of the life form, interpreted in different ways by different authors (see, for example, reviews: Ozerski 2014b; Vasil’ev 2021).

As part of solving the problem of identifying the patterns of variability of protective colouration associated with life forms, we have carried out a long-term study of the grasshoppers and bush-crickets of the fauna of Russia. The current work continues the study of colour variability of a phytophilous species widespread in temperate forest zones, the common green grasshopper *Omocestus viridulus* (Linnaeus, 1758). The choice of the common green grasshopper as a model species is due to the fact that it is easily identified in the field (as a rule, even without requiring catching), and also has a distinct variability of the protective colouration, which makes it possible to distinguish three clearly different colour forms (in the terminology of Rubtzov (1935), f. viridis, f. hyalosuperficies and f. rubiginosa), reflecting the relationship with either living or dead vegetation.

At the present time, the colour variability of common green grasshopper has been studied in some detail. In particular, a number of colour forms characteristic of this species is described (Rubtzov 1935; Petersen and Treherne 1949; Ramme 1950; Richards and Waloff 1954; Blackith and Roberts 1958; Ragge 1965) and patterns of changes in body colour during the individual life of individuals are characterized (Richards and Waloff 1954). In general, it can be assumed that the belonging of *O. viridulus* individuals to one or another colour form is determined mainly, if not exclusively, by genetic mechanisms. First of all, this is demonstrated by the results of intraspecific crossing experiments with grasshoppers of the same tribe Gomphocerini s.l.: *Pseudochorthippus parallelus* (Zetterstedt, 1821) (Sansome and La Cour 1935), *Chorthippus brunneus* (Thunberg, 1815) (Gill 1981), *Ch. dorsatus* (Zetterstedt, 1821) (Winter et al. 2021), *Gomphocerus sibiricus* (Linnaeus, 1767) (Schielzeth and Dieker 2020). In addition, the genetical nature of the body colour polymorphism in *O. viridulus* is indirectly confirmed by population genetic data (Richards and Waloff 1954), according to which, in this species, like in two other representatives of Gomphocerini s. l. of British fauna [*Pseudochorthippus parallelus* and *Stenobothrus lineatus* (Panzer, 1796)], from year to year in populations, a similar quantitative ratio between individuals of different colour forms is more or less stably maintained, approximately consistent with the Hardy–Weinberg law.

In addition to the mentioned work of Richards and Waloff (1954), some information on the representation of various colour forms in the British populations of this species is given in the works of Clark (1943) and Blackith and Roberts (1958). Unfortunately, it does not contain quantitative data, and there are only very rough qualitative estimates. At the same time, the representation of one of the colour forms, viridis, in this species was quantitatively characterized in at least two more works: in an article by Petersen and Treherne (1949), devoted to Scandinavian populations, and in the article by the author of this work (Ozerski 2018) that provided data on micropopulations from 10 localities located on the territory of the Pskov and Novgorod regions. The distribution of colour forms in the Scandinavian and Russian populations turned out to be very different: the proportion of representatives of the viridis form in the second case was significantly lower, and these differences turned out to be statistically significant (Ozerski 2018).

This work supplements these data with materials collected by the author over the past four years in 19 other localities in the European part of Russia.

MATERIALS AND METHODS

The records were done in the summer and autumn of 2018, 2019, 2020 and 2021 in the Leningrad, Novgorod and Pskov Provinces, as well as in the adjacent territories of the Vologda and Tver Provinces, in 19 localities corresponding, according to Aleksandrova and Yurkovskaya (1989), to two natural areas, the taiga (southern subarea) and mixed forests (Table 1, Fig. 1), on mesophytic and hygrophytic meadows.

Counting of grasshoppers was carried out mainly without capture (some individuals were caught in cases of clearly unusual colouration), on non-intersecting transects of arbitrary length and shape, with a distance between parallel sections of at least 1.5 m. Only adults and larvae of the last instar were taken into account (the latter, taking into account the data of Richards and Waloff (1954), indicating that their colouration corresponds to the imaginal one). The sex and colour form of the individuals were recorded. Each of the recorded individuals was assigned to one of the following forms [according to the classification of Rubtzov (1935)].

1. Form rubiginosa. Brown, grey or olive grey colouration; dorsum, elytra, and lateral lobes of pronotum without green admixture. The general tone of the colour of the sides of the body (within the above limits) and the distinctness of the pattern on them are quite variable.

2. Form hyalosuperficies. The sides of the thorax (including the lateral lobes of the pronotum), like the head, are usually greyish or brownish (sometimes yellow or brick-red, but never green), while the dorsum is green (including the vertex, occiput, pronotal disc, and the posterior (located dorsally in a folded state) part of the elytra). The distinctness of the pattern on the sides of the body is quite variable.

3. Form viridis. Dorsum (including dorsal elytra located at rest), head and flanks of thorax (including lateral lobes of pronotum) are green.

Statistical data processing was carried out using PAST 2.17c and PAST 4.10 software (Hammer et al. 2001). To check the normality of the distribution, the Shapiro-Wilk test was used. The distributions were compared using the Mann – Whitney test, the Fisher's exact test, and the paired Wilcoxon test. The non-parametric Mann – Whitney and Wilcoxon tests were selected due to the statistically significant ($p < 0.05$) differences of the corresponding sample distributions from the normal distribution. The standard significance level $p = 0.05$ was adopted.

Separately, for males and females, the proportions of individuals belonging to the viridis, hyalosuperficies, and rubiginosa forms were calculated. Since there were no statistically significant differences between the representation of the viridis form in males and females (the paired Wilcoxon test value: $W = 137$; $p = 0.09$), the total (for both sexes) proportion of viridis form individuals was also determined. 95% confidence limits were calculated using the Clopper – Pearson algorithm in the EBCIC 0.0.1 software (https://github.com/KazKobara/ebcic).

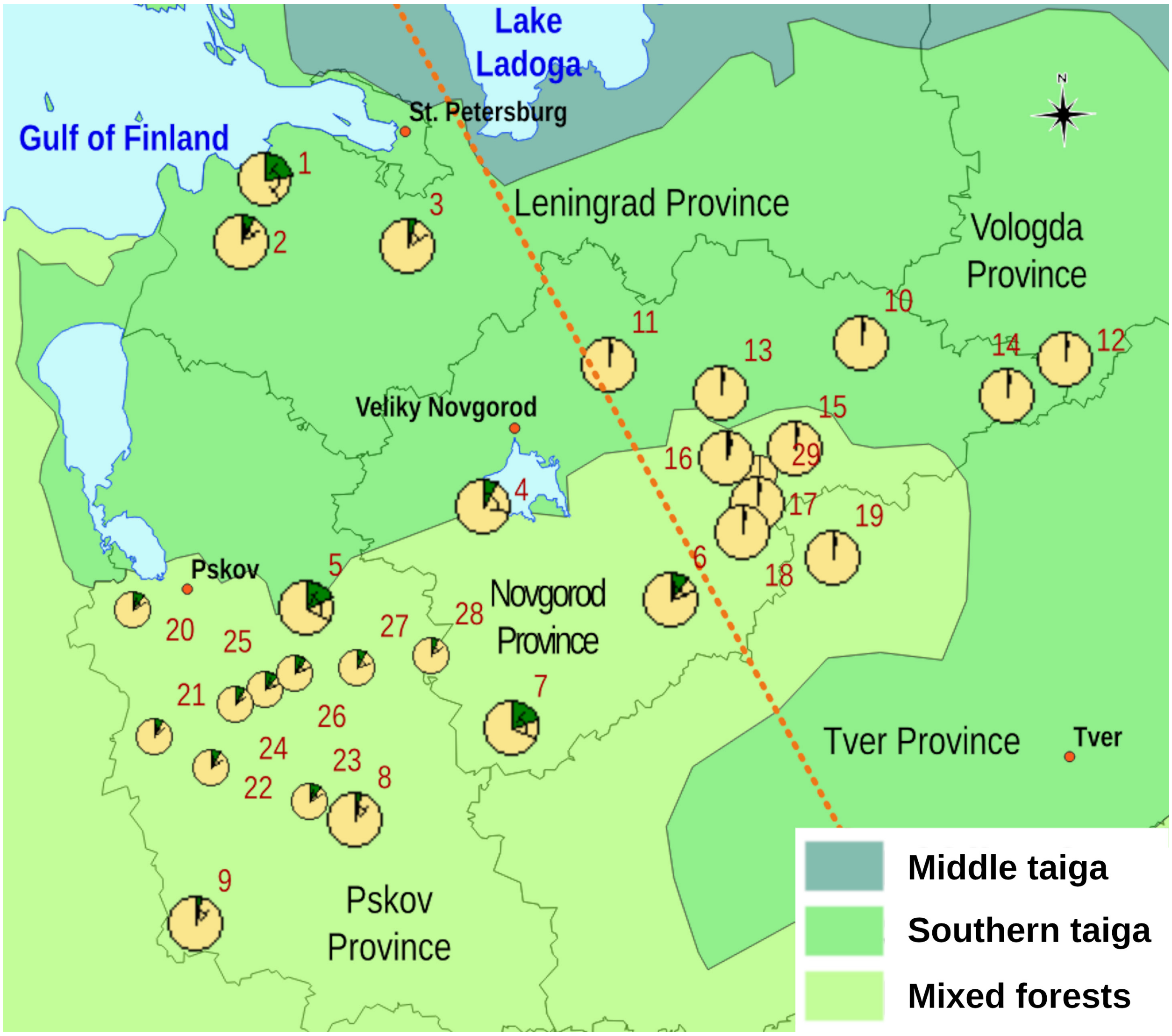

Fig. 1. Distribution of the form viridis in the *O. viridulus* populations in northwestern Russia. Large symbols indicate the data for 2018–2021, small ones – the data published earlier (Ozerski 2018) for 2015–2017. The green sectors indicate the cumulative proportions of individuals of the viridis form; their 95% confidence intervals are given. The dashed line delimits the western and eastern zones, differing in the rate of the viridis form. The boundaries of natural areas and subareas on the territory of Russia are given according to Aleksandrova and Yurkovskaya (1989), outside it – according to Sochava et al. (1960). Localities are marked with numbers. Original data: 1–19 (as in Table 1); previously published data (Ozerski 2018): 20–29 (20 – Izborsk; 21 – Zakharkino; 22 – Velye; 23 – Zubkovo; 24 – Astratovo; 25 – Spiry; 26 – Pozhni; 27 – Khmelevitsy; 28 – Aleksino; 29 – Yablonovka).

RESULTS AND DISCUSSION

Summary data on colour forms are given in Table 2 and in Fig. 2. In addition, generalized data for both sexes on the representation of the viridis form in northwestern Russia, both obtained during this study and those published by us earlier (Ozerski 2018), are shown in Fig. 1.

As can be seen from Table 2, in general, the colouration of *O. viridulus* shows similar patterns in all the studied localities of northwestern Russia. The diversity of colour forms of *O. viridulus* within the indicated territory is low (Fig. 3). The typical grey or olive grey colour form [rubiginosa according to Rubtsov (1935)] was very common among males. Among females, individuals predominate, which,

Table 1. List of record localities of *O. viridulus* in 2018–2021.

No	Locality (neighbourhood of a settlement or a lake)	Biome	Habitat	Geographical coordinates	Record date (d.m.y.)	Number of recorded specimens	
						Males	Females
1	Koporye railway station, Lomonosov district of Leningrad Province	T	m+h	59°44′N, 29°01′E	26.06.21	11	16
2	Kommunar settlement, Kingisepp district of Leningrad Province	T	m	59°26′N, 28°47′E	26.06.21	32	38
3	Vyritsa settlement, Gatchina district of Leningrad Province	T	m+h	59°25′N, 30°19′E	10.08.19, 16.08.19 and 20.08.19	11	16
4	Mston' village, Shimsk district of Novgorod Province	T/M (border)	m	58°12′N, 30°57′E	07.09.19	0	13
5	Turitsy village, Porkhov district of Pskov Province	T/M (border)	m	57°44′N, 29°23′E	16.07.19	15	21
6	Borki village, Demyansk district of Novgorod Province	M	m	57°44′N, 32°35′E	18.07.21	31	31
7	Kholm town of Novgorod Province	M	h	57°09′N, 31°09′E	02.08.20	18	35
8	Lake Loknovo, Loknya district of Pskov Province	M	h	56°44′N, 29°49′E	26.07.20	9	24
9	Ugorinka village, Sebezh district of Pskov Province	M	m	56°15′N, 28°28′E	27.07.18 and 31.07.18	13	19
10	Myakishevo village, Khvoynaya district of Novgorod Province	T	m	58°52′N, 34°24′E	06.07.21	23	27
11	Nekrasovo village, Malaya Vishera district of Novgorod Province	T	h	58°50′N, 32°07′E	28.07.21	38	30
12	Bol'shoe Vosnoe village, Ustyuzhna district of Vologda Province	T	m	58°43′N, 36°13′E	12.07.21	36	24
13	Pamozovo village, Okulovka district of Novgorod Province	T	m	58°41′N, 33°07′E	28.07.21	36	60
14	Ermakovo village, Pestovo district of Novgorod Province	T	m	58°34′N, 35°40′E	12.07.21	54	67
15	Bobovik village, Borovichi district of Novgorod Province	M	m	58°24′N, 33°45′E	06.07.20 and 14.07.20	31	40
16	Peretno village, Okulovka district of Novgorod Province	M	m	58°23′N, 33°08′E	10.07.21	59	31
17	Malaya Krestovaya village, Okulovka district of Novgorod Province	M	m	58°09′N, 33°23′E	20.07.20	25	25
18	Yashcherovo village, Valday district of Novgorod Province	M	m	58°02′N, 33°14′E	18.07.21	31	39
19	Bologoe town of Tver Province	M	m	57°53′N, 34°01′E	24.07.21	32	49

Abbreviations: T – taiga area (southern boreal forests subarea); M – mixed coniferous forests area; h – hygrophytic meadows; m – mesophytic meadows.

according to Rubtsov's classification, belong to the form hyalosuperficies. Occasionally, among females, individuals are found that correspond in colour to the rubiginosa form, and only at one locality – in the vicinity of vil. Bobovik near the town of Borovichi – we noted males of the hyalosuperficies form as rare exceptions. In contrast to these two forms, the occurrence of the viridis form does not depend on sex, while the proportion of such individuals in populations differs in different parts of the surveyed region.

Our statistical comparison (using the Fisher's exact test) of data for the period from 1947 to 1951, given in the monograph by Richards and Waloff (1954), showed that in the British *O. viridulus* micropopulation studied by them the difference between two adjacent years in the proportion of the green form was not statistically significant in any of the cases (the p values: 0.47; 0.65; 0.25; 0.19). A similar result ($p = 1.00$) was obtained when comparing (using the same test) the data which we published earlier (Ozerski 2018)

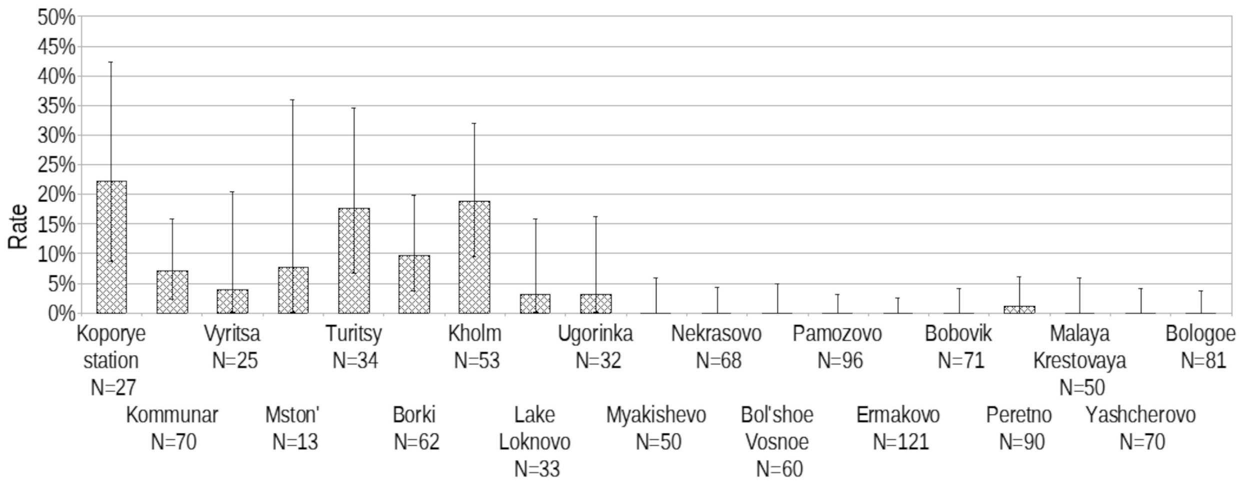

Fig. 2. Rate of the form viridis in the populations of *O. viridulus* in northwestern Russia. 95% confidence limits are given.

for the records of 2015 and 2017 made near the village of Astratovo, Pskov region. On the basis of these results, it was possible to use in a comparative analysis of colour variability in different micropopulations of *O. viridulus* the materials of observations carried out in different years. It was found that the data we obtained in 2018–2021 are in good agreement with the previously published (Ozerski 2018) data for 2015–2017 for ten other localities of the North-West region of Russia (Fig. 2). At the same time, a comparison of data relating to the zone of mixed forests (including also 10 localities studied in 2015–2017) and to the southern taiga subzone did not reveal statistically significant differences in the representation of the viridis form in the two biomes, regardless of which of these biomes included the boundary localities “Mston” and “Turitsy” (the Mann – Whitney test values: see Table 3).

At the same time, summarizing the data for 2015–2021, it is possible to conditionally subdivide the surveyed territory into two zones, western and eastern, along a line passing through the Chudovo town and the Kresttsy settlement in Novgorod Province (Fig. 1). The viridis form occurs quite regularly in the western zone, although it is not numerous. In the eastern part of the region (to the right of the indicated line), this form is extremely rare. The Mann – Whitney test (when comparing rates in different geographical locations) showed that the representation of the viridis form in the western and eastern zones differed statistically significantly ($U=0$; $p=6.18E\text{-}06$).

The rubiginosa form, which is common for males of *O. viridulus*, is rare or absent in females throughout the studied territory. Nevertheless, the western and eastern zones also differ in the representation of such females in them (the Mann–Whitney test value: $U=45$; $p=0.0007$): in the western zone they are somewhat less common than in the eastern zone (the median proportions are respectively 0.00 and 0.01).

Males of the hyalosuperficies form are very rare and so far have been identified only in one of the surveyed localities. The lack of available material does not yet allow us to compare the prevalence of such males in the western and eastern zones.

A comparison of the data obtained for the Northwestern region of Russia with the literature data for other parts of the *O. viridulus* distribution area (Clark 1943; Petersen and Treherne 1949) shows the following. Clark (1943), describing the variety of colour forms of *O. viridulus* in Great Britain, indicates two forms as abundant: with a green top and sides (corresponding to viridis) and with a green top and brown sides (corresponding to hyalosuperficies). In addition, two more forms, with a brown top and sides (corresponding to rubiginosa) and with a green top and purple sides (this colour variant was named by Petersen and Treherne (1949) as “f. purpurata”), are given by them as uncommon (“occasional” and “rare”, respectively). Some doubtfulness of Clark’s data should be emphasized: in particular, the absence in his work of any mention of the connection between the body colour of the common green grasshopper and sexual dimorphism raises questions. In a later

Table 2. Representation (%) of different colour forms of *O. viridulus* in different localities in 2018–2021.

Locality	Form viridis			Form hyalosuperficies		Form rubiginosa	
	Males	Females	General rate	Males	Females	Males	Females
Koporye railway station	27 (6–61)	19 (4–46)	22 (9–42)	0 (0–24)	81 (54–96)	73 (39–94)	0 (0–17)
Kommunar	6 (2–25)	8 (2–21)	7 (2–16)	0 (0–9)	92 (79–98)	94 (79–99)	0 (0–8)
Vyritsa	0 (0–24)	6 (0–30)	4 (0–20)	0 (0–24)	81 (54–96)	100 (76–100)	13 (2–38)
Mston'	–	8 (0–36)	8 (0–36)	–	92 (64–100)	–	0 (0–21)
Turitsy	7 (0–32)	24 (1–47)	18 (7–35)	0 (0–18)	67 (43–85)	93 (68–100)	10 (1–30)
Borki	3 (0–17)	16 (5–34)	10 (4–20)	0 (0–9)	84 (66–95)	97 (83–100)	0 (0–9)
Kholm	0 (0–15)	29 (15–46)	19 (9–32)	0 (0–15)	71 (54–85)	100 (85–100)	0 (0–8)
Lake Loknovo	0 (0–28)	4 (0–21)	3 (0–16)	0 (0–28)	96 (79–100)	100 (72–100)	0 (0–12)
Ugorinka	0 (0–21)	5 (0–26)	3 (0–16)	0 (0–21)	95 (74–100)	100 (79–100)	0 (0–15)
Myakishevo	0 (0–12)	0 (0–11)	0 (0–6)	0 (0–12)	100 (89–100)	100 (88–100)	0 (0–11)
Nekrasovo	0 (0–8)	0 (0–10)	0 (0–4)	0 (0–8)	97 (83–100)	100 (92–100)	3 (0–17)
Bol'shoe Vosnoe	0 (0–8)	0 (0–12)	0 (0–5)	0 (0–8)	100 (88–100)	100 (92–100)	0 (0–12)
Pamozovo	0 (0–8)	0 (0–5)	0 (0–3)	0 (0–8)	95 (86–99)	100 (92–100)	5 (1–14)
Ermakovo	0 (0–5)	0 (0–4)	0 (0–2)	0 (0–5)	99 (92–100)	100 (95–100)	2 (0–8)
Bobovik	0 (0–9)	0 (0–7)	0 (0–4)	7 (1–21)	100 (93–100)	94 (79–99)	0 (0–7)
Peretno	2 (0–9)	0 (0–9)	1 (0-6)	0 (0–5)	97 (83–100)	98 (91–100)	3 (0–17)
Malaya Krestovaya	0 (0–11)	0 (0–11)	0 (0–6)	0 (0–11)	100 (89–100)	100 (89–100)	0 (0–11)
Yashcherovo	0 (0–9)	0 (0–7)	0 (0–4)	0 (0–9)	100 (93–100)	100 (91–100)	0 (0–7)
Bologoe	0 (0–9)	0 (0–6)	0 (0–4)	0 (0–9)	98 (89–100)	100 (91–100)	2 (0–11)

Note: 95% confidence limits are given in parentheses.

work by Richards and Waloff (1954), also devoted to British grasshoppers, the following forms were noted in the population from the vicinity of London studied by them: var. 'Green' (corresponding to the form viridis), var. 'Brown' (corresponding to the form rubiginosa), var. 'Green brown sides' (corresponding to the form hyalosuperficies) and var. 'Purple' [corresponding to the form 'purpurata' in the terminology of Petersen and Treherne (1949)]. At the same time, they indicated the 'Grey' form for *O. viridulus* as characteristic only of males, the 'Grey brown sides' and 'Purple' forms as noted only in females, and 'Green' as occurring in both sexes. Subsequently, this character of colour variability in *O. viridulus* was confirmed by Blackith and Roberts (1958), who also studied this species in the vicinity of London, and Voisin (1979), who studied French material. A similar variety of colour forms of *O. viridulus* at a qualitative level is also found in Scandinavia: according to the above work of Petersen and Treherne (1949), males are represented by the forms viridis and rubiginosa, and females are represented by the forms viridis and hyalosuperficies

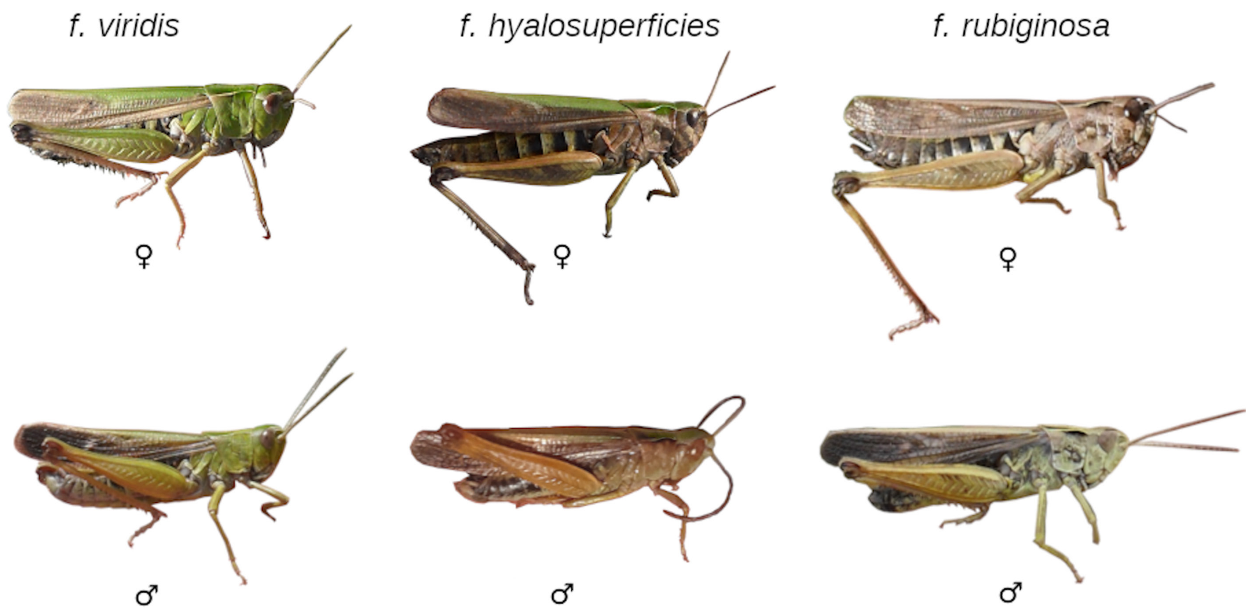

Fig. 3. Colour forms of *O. viridulus* represented in northwestern Russia.

(females of forms ‘purpurata’ and hyalolateralis are mentioned as exceptions; the latter is described in the specified work as difficult to distinguish from the form viridis; however, in the original description by Rubtzov (1935), it is characterized as having a brown top and green sides of the body). In addition, the representation of grey individuals exclusively in males of *O. viridulus* is mentioned in the generalizing work by Ramme (1950).

Thus, at a qualitative level, in Scandinavia, France and the UK, common green grasshopper is represented mainly by the same colour forms as in the localities we studied in the north-west of Russia: rubiginosa, hyalosuperficies and viridis – and at the same time, there is a pattern similar to that described by us for populations of northwestern Russia, a relationship of colour variability with sexual dimorphism. As for the quantitative relationships between colour forms, the use of new material fully confirmed the conclusion of our previous article (Ozerski 2018) that the populations of *O. viridulus* from the northwestern Russia sharply differ from the Scandinavian ones (Petersen and Treherne 1949), which showed a much higher prevalence of the viridis form (ranging from 64.8 to 75.2% of individuals in the populations). When comparing the data related to different localities of the northwestern Russia (both published earlier (Ozerski 2018) and presented for the first time in this work), with the data provided by Petersen and Treherne (1949) for the vicinity of London, a statistically significant difference was demonstrated in the proportion of the viridis form in different geographical locations (the Mann – Whitney test value: $U=0$; $p=0.0001$). When comparing the total proportion of the viridis form in the populations of northwestern Russia studied by us with the literature data (Petersen and Treherne 1949; Richards and Waloff 1954), it was found that Russian, Scandinavian, and British common green grasshoppers differ significantly from each other in this regard (the Fisher’s exact test $p<0.000001$), while the largest proportion of viridis form was found in Scandinavian populations, and the smallest one was found in Russian populations.

From our point of view, the results obtained can be explained as follows. Apparently, belonging to one or another colour form in *O. viridulus* is determined by genetic mechanisms, while the same allele determines the colouration in males corresponding to the rubiginosa form, and in females, to the hyalosuperficies form. It is noteworthy that among the studied individuals of this species in Russian and British populations, individuals belonging to these forms clearly predominate, while the viridis form is relatively rare. Some differences in the representation of the viridis

Table 3. Comparison of the proportion of individuals of *O. viridulus* form viridis in biomes of the southern taiga and mixed forests, taking into account the influence of boundary points.

Boundary localities		U	p
Mston'	Turitsy		
T	T	77.5	0.43
T	M	69.5	0.34
M	T	60.5	0.16
M	M	51.5	0.11

Abbreviations: U – Mann–Whitney test statistic value; p – significance level; T – taiga area (southern boreal forests subarea); M – mixed coniferous forests area.

form in different localities of the territory of northwestern Russia studied by us, as well as differences in this respect between Russian, British, and Scandinavian populations, in our opinion, are unlikely to be of an adaptive nature and, most likely, are the consequences of genetic drift. At the same time, the interpretation of differences in the proportion of the viridis form, which are revealed when comparing Scandinavian, British and Russian data, is difficult due to significant temporal differences when the counts are separated by tens of years.

It should be noted that over most of its distribution area, this species, which is widespread in the temperate zone of the Palearctic, including Western Europe and Siberia, still remains unexplored or insufficiently studied in terms of colour variability. Moreover, even within the northwestern part of Russia, one cannot speak about the complete clarity of the picture of the distribution of different colour forms of *O. viridulus* and even about the exact passage of the conditional dividing line between the zones described above. Taking into account the above-mentioned Scandinavian data, the most interesting and promising so far is the study of populations of this species in Fennoscandia, including Karelian Isthmus and the territory of Republic of Karelia.

CONCLUSIONS

The *O. viridulus* populations living in the northwestern part of Russia are characterized by the predominance of colour forms rubiginosa (among males) and hyalosuperficies (among females). In addition, in the western part of the region, a relatively rare form viridis is present in both sexes with approximately the same frequency, this form is almost absent in its eastern part. The females of the form rubiginosa are rare and recorded only at some localities, and the males of the form hyalosuperfices are exceptionally rare (and recorded at only one locality). The quantitative relationships between colour forms in the northwestern Russian populations differ significantly from those identified in the 40s of the 20th century in Scandinavia and Great Britain, which is apparently due to differences in the genetic structure of the populations.

REFERENCES

Aleksandrova V.D. and Yurkovskaya T.K. 1989. Geobotanical subdivision of non-black soil zone of European part of RSFSR. Nauka, Leningrad, 64 p. [In Russian].

Bey-Bienko G.Ya. and Mistshenko L.L. 1951. Locusts and grasshoppers of the USSR and adjacent countries. Vol. 1. Publishing house of Academy of Sciences of the Soviet Union, Moscow, Leningrad, 378 p. [In Russian].

Blackith R.E. and Roberts M.I. 1958. Farbenpolymorphismus bei einigen Feldheuschrecken. *Zeitschrift für Vererbungslehere*, **89**: 328–337. https://doi.org/10.1007/bf00888639

Clark E.J. 1943. Colour variation in British Acrididae (Orthopt.). *Entomological Monthly Magazine*, **79**: 91–104.

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

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

Ozerski P.V. 2012. About perspectives of use of colour variability in classification of life forms of Orthopteran insects. In: M.A. Gvozdev and P.V. Ozerski (Eds). Functional morphology, ecology and life-cycles of animals. Vypusk 12. Tessa, Saint Petersburg: 11–17. [In Russian].

Ozerski P.V. 2014a. On the colouration variability of Orthopteran insects of different life-forms. *Functional morphology, ecology and life-cycles of animals*, **14**(2): 42–52.

Ozerski P.V. 2014b. Epharmony as a general biological concept. *Functional morphology, ecology and life-cycles of animals*, **14**(1): 32–56. [In Russian].

Ozerski P.V. 2018. To the color variation in the common green grasshopper (*Omocestus viridulus*, Orthoptera: Acrididae). *Principles of the Ecology*, **7**(1): 73–84. [In Russian]. https://doi.org/10.15393/j1.art.2018.7262

Petersen B. and 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

Pravdin F.N. 1978. Ecological geography of insects of Middle Asia. Orthopteroids. Nauka, Moscow, 272 p. [In Russian].

Ragge D.R. 1965. Grasshoppers, crickets and cockroaches of the British Isles. Frederick Warne & Co. LTD, London, New York, 300 p.

Ramme W. 1950. Die parallele Farbungsvariation (Parallelochromie) der Acrididae; ihre genetische und phylogenetische Bedeutung (Orthopt.). *Eos: Revista Española de Entomología*, Tomo extraordinario: 249–260.

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

Rubtzov I.A. 1935. Phase variation in non-swarming grasshoppers. *Bulletin of Entomological Research*, **26**(4): 499–520. https://doi.org/10.1017/s0007485300036841

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

Schielzeth H. and 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://doi.org/10.1186/s12862-020-01630-7

Sochava V.B., Isachenko T.I. and Karpenko A.S. 1960. Zonal subdivision of Soviet Baltic based on medium-scale geobotanical map. *Botanical journal*, **45**(6): 795–803. [In Russian].

Vasil'ev A.G. 2021. Conception of morphoniche and evolutionary ecology. KMK Scientific Press, Moscow, 315 p. [In Russian].

Voisin J.-F. 1979. La détermination des *Omocestus* de la faune de France. *Bulletin de la Société Entomologique de France*, **84**(3–4): 49–52. https://doi.org/10.3406/bsef.1979.21682

Vorontsovskiy P.A. 1928. On the issue of the homologous series of colour variability in grasshoppers. *Bulletin of Orenburg plant protection station*, **1**(27–39). [In Russian].

Winter G., Varma M. and 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