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<https://www.doi.org/10.33910/2686-9519-2026-18-3-1068-1087>
<https://www.zoobank.org/References/16636274-F7A7-41ED-B538-0A0DC769C176>

UDC 595.727

Habitat preferences of three grasshopper species of the *Chorthippus biguttulus* group (Orthoptera: Acrididae) in Kaluga Oblast, Central European Russia

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Abstract. In Kaluga Oblast, *Chorthippus biguttulus* species group is represented by three morphologically similar species. During 2023–2025 grasshoppers were identified using calling songs, while specimens collected earlier or obtained from trap samples were identified by morphology. Each sampling plot was characterized by four parameters: habitat type based on vegetation, landform, landscape type based on Quaternary sediments, and a type of surrounding. Species presence–absence and abundance were analyzed using generalized linear models. *Chorthippus biguttulus* (Linnaeus, 1758) was the most widespread and eurytopic species. *Chorthippus mollis* (Charpentier, 1825) was associated with valleys of large and medium rivers but avoided tall-grass meadows. *Chorthippus brunneus* (Thunberg, 1815) was associated with dry pine forests. Spatial autocovariation influenced the occurrence of *Ch. mollis* and *Ch. brunneus*. *Chorthippus mollis* was abundant in short-grass meadows within river valleys, whereas *Ch. biguttulus* was common in grasslands on watersheds. Pitfall traps showed that *Ch. mollis* reached very high activity density in suitable habitats. *Chorthippus biguttulus* and *Ch. brunneus* did not reach high abundances.

Keywords: Acrididae, habitat, grassland, pine forest, river valley, calling song, activity density, East European Plain

Биотопическая приуроченность трех видов саранчовых из группы *Chorthippus biguttulus* (Orthoptera: Acrididae) в Калужской области (центр Европейской России)

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Аннотация. В Калужской области саранчовые группы *Chorthippus biguttulus* представлены тремя морфологически сходными видами. В 2023–2025 гг. саранчовые определялись по акустическим сигналам, а в другие годы и в материале из ловушек — по морфологическим признакам. Каждая пробная площадь характеризовалась четырьмя параметрами: тип местообитания по растительности, форма рельефа, тип ландшафта по четвертичным отложениям и тип окружения. Присутствие–отсутствие и обилие видов анализировались с помощью обобщенных линейных моделей. *Chorthippus biguttulus* (Linnaeus, 1758) оказался самым широко распространенным и эвритопным видом. *Chorthippus mollis* (Charpentier, 1825) приурочен к долинам больших и средних рек, избегает крупнозлаковые луга. *Chorthippus brunneus* (Thunberg, 1815) приурочен к сухим сосновым лесам. Для встречаемости *Ch. mollis* и *Ch. brunneus* значимой оказалась автоковариация. *Chorthippus mollis* является фоновым видом на мелкозлаковых лугах в долинах, *Ch. biguttulus* — обычным видом на плакоре. При помощи почвенных ловушек выявлено, что *Ch. mollis* в благоприятных местообитаниях достигает очень высокой динамической плотности, а *Ch. biguttulus* и *Ch. brunneus* не бывают очень многочисленны.

Ключевые слова: саранчовые, местообитание, сосновый лес, долина реки, призывной сигнал, динамическая плотность, Восточноевропейская равнина

Introduction

The study of niche partitioning in morphologically similar sympatric species remains an important objective in biodiversity research. Coexisting species must share resources (Hardin 1960). However, in some cases, morphologically similar species may also be ecologically similar, although several studies have shown that cryptic species are less likely to co-occur than congeneric non-cryptic species (Violle et al. 2011; Vodá et al. 2015). Therefore, studying the mechanisms that facilitate species coexistence is important for ecology, evolutionary biology, and conservation biology (Scriven et al. 2016; Hending 2025).

Grasshoppers of the *Chorthippus* (*Glyptobothrus*) *biguttulus* group (Orthoptera: Acrididae: Gomphocerinae) are a suitable model group for studying ecological niche differentiation among closely related species. These species are morphologically similar but can be clearly distinguished by male acoustic signals (Bukhvalova 1993; Ingrisch 1995; Benediktov 1999; 2005; Tarasova et al. 2021). In northern Eurasia, the most widely distributed taxa of this group are the nominotypical subspecies of three species: *Chorthippus biguttulus* (Linnaeus, 1758), *Chorthippus brunneus* (Thunberg, 1815), and *Chorthippus mollis* (Charpentier, 1825). Reliable identification of these species has been possible for more than a century (Ramme 1921). Numerous studies have analysed the morphological variability of these species (Oliger 1971; 1974; Sychev 1988; Bukhvalova 1993; Ingrisch 1995; Nolen et al. 2020; Neumeister 2025). The geographic ranges of these taxa have also been investigated, and sympatry among several species of this group has been documented (Benediktov 2005; 2017; Savitsky 2010; Tarasova et al. 2021). However, information on habitat preferences and spatial differentiation among sympatric taxa of this group remains insufficient.

Most ecological data on the *Chorthippus biguttulus* group have been obtained from Central Europe (Harz 1957; Oschmann

1969; Thorens 1993; Dvořák et al. 2022; Krištín 2026; Orthoptera fauna...2026; Orthoptera.ch...2026). Several studies have also described the distribution of these species in Western Europe (Chopard 1951; Kleukers et al. 1997; Willott, Hassall 1998; Telfer, Hassall 1999). A comprehensive survey of the ecology of *Ch. brunneus* was performed in England (Richards, Waloff 1954). Some data on the ecology of two species are presented for Northern Europe (Elven et al. 2022). In general, all three species are considered relatively xerophilic. *Ch. biguttulus* is regarded as the most eurytopic species, *Ch. brunneus* as the more xerophilic species, and *Ch. mollis* as having the narrowest habitat range and being xerophilic or thermophilic. However, the cited studies do not provide a clear understanding of how the ecological niches of the latter two species differ. Moreover, in Norway, *Ch. biguttulus* was found to be more thermophilic than *Ch. brunneus* (Elven et al. 2022), whereas in Lithuania no differences in habitat distribution between these species were detected (Budrys, Pakalniškis 2007).

In Russia, the first information on habitat preferences of the *Chorthippus biguttulus* group was published by Boris Uvarov (Uvarov 1925). He noted that *Ch. biguttulus* and *Ch. brunneus* inhabit a wide range of habitats, whereas *Ch. mollis* occurs in dry open habitats with sparse vegetation. However, his observations of the latter species were restricted to the Yekaterinoslav Governorate, which corresponds approximately to the present-day Dnipropetrovsk Oblast and adjacent parts of several neighbouring regions. Later, Bey-Bienko (Bey-Bienko 1930) classified *Ch. biguttulus* as a mesophilic species in the forest zone of Western Siberia and showed *Ch. brunneus* to be more xerophilic. In contrast, in the European part of Russia, *Ch. brunneus* was characterized as mesophilic (Tarasova et al. 2021). Several recent studies have described habitat distribution of the *Chorthippus biguttulus* group species in Western Siberia (Sergeev 2019; Sergeev, Efremova 2020).

For European Russia and adjacent regions of Eastern Europe, information on habitats of

these species remains scarce despite a long history of research in these insects. Some habitat data have been reported for Moscow Oblast (Guseva et al. 1979; Chernyakhovsky 2008; 2019), Smolensk Oblast (Sychev 1975), Belgorod Oblast (Prisny 2007), Kursk Oblast (Bey-Bienko 1970), Gomel Oblast of Belarus (Ostrovsky 2023), Tatarstan (Karmazina, Shulaev 2015), and Udmurtia (Adachovskiy 2006). However, these studies do not clearly characterize habitat preferences of *Chorthippus* species. Furthermore, species identification was usually based on morphological characters. Only a few studies are based on identification of these species using acoustic signals (Savitsky 2010; Ozerski 2012; Benediktov 2017). In the Xeno-canto database (Xeno-canto 2026), acoustic records of *Ch. mollis* and *Ch. brunneus* from European Russia are available only for the Middle Volga Region.

Thus, there is still no comprehensive understanding of habitat preferences and habitat distribution patterns of the *Chorthippus biguttulus* group species in Eastern Europe. Since geographic variation in habitat preferences of grasshoppers is well known (Bey-Bienko 1930; Stebaev 1974), data from Central Europe alone are insufficient for understanding distribution patterns in our region. Since species of the *Chorthippus biguttulus* group are common and abundant in grasslands, studying them is important for biodiversity assessment, conservation, and pest management.

Kaluga Oblast is located in the centre of the East European Plain. Despite its relatively small area and predominantly flat relief, the territory is differentiated into uplands and lowlands and is deeply dissected by river valleys. Vegetation includes broadleaved, spruce, pine, and secondary deciduous forests, as well as various types of meadows, agricultural fields, urban habitats, and other anthropogenic environments. Thus, Kaluga Oblast represents a typical East European plain landscape. The co-occurrence of *Ch. biguttulus* and *Ch. brunneus* has previously been documented in one locality

within this region (Benediktov 2013). More recently, habitat distribution of all three species within a river valley (Aleksanov 2025a) and distribution of *Ch. biguttulus* and *Ch. mollis* within Kaluga City (Aleksanov 2025b) were reported. However, habitat preferences and distribution of these species across the entire region have been not discussed.

The aim of our study was to analyse habitat preferences of the three species of the *Chorthippus biguttulus* group across Kaluga Oblast.

Material and methods

Data sampling

Grasshoppers were recorded in Kaluga Oblast between 2003 and 2025. Acoustic observations, sweep nets, pitfall traps, and window traps were used. Calling songs (spontaneous male acoustic signals) were recorded during 2023–2025 in 278 sampling plots. Records were obtained on warm sunny days from July to early September. Species were usually identified in the field by ear. Songs of some specimens were recorded in the field using a Xiaomi Redmi 8 smartphone. Some specimens collected during unfavourable weather conditions were kept in plastic containers and recorded in the laboratory. Species identification was based on audio recordings, oscillograms, and textual descriptions provided by previous authors (Bukhvalova 1993; Ingrisch 1995; Benediktov 2005; Willemse et al. 2009; Orthoptera.ch... 2026; Xeno-canto 2026). Examples of oscillograms of the species from Kaluga Oblast are shown in Figures 1–3. Based on calling songs, three ranks of relative abundance were assigned to each species for each sampling plot: 1 — rare, 2 — common, 3 — abundant (dominant).

Specimens collected before 2023 or captured using traps were identified based on morphological characteristics. Morphological analysis of individuals identified using calling songs showed that the three species occurring in Kaluga Oblast can be distinguished by the shape of the forewings in males, in accordance with recent studies (Bukhvalova

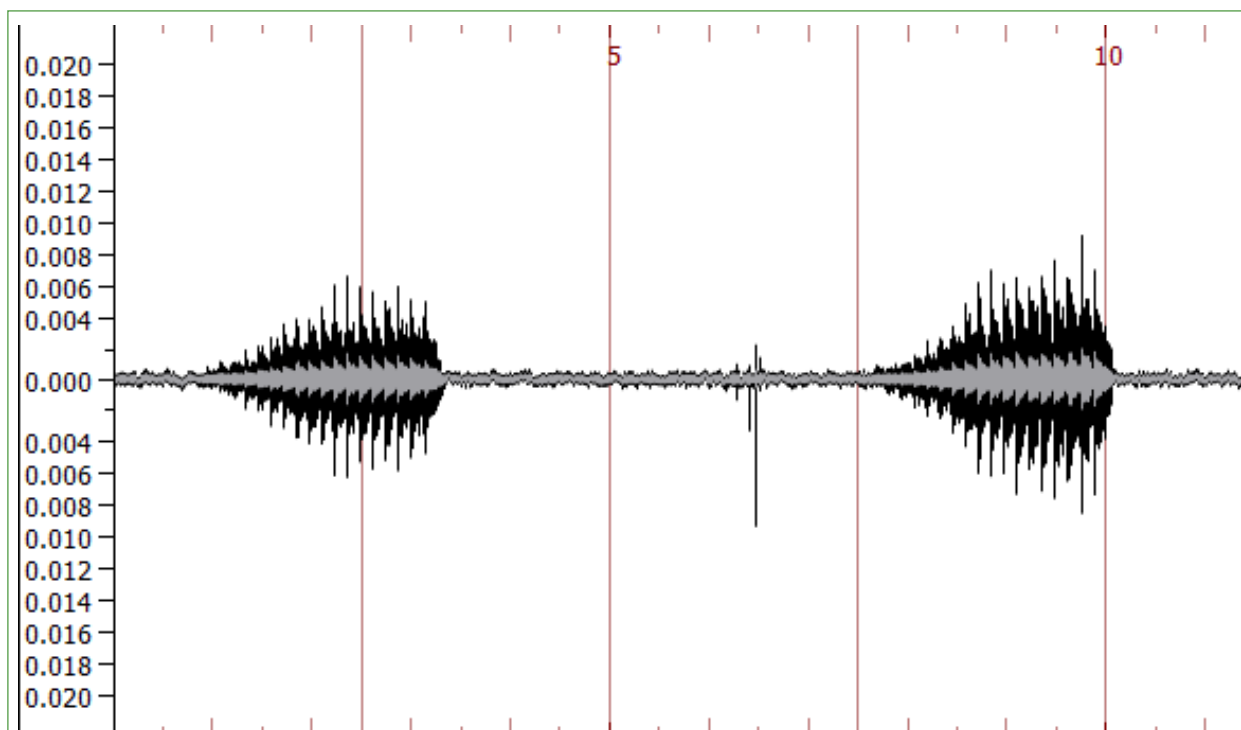


Fig. 1. Oscillogram of a calling song in *Chorthippus biguttulus* from Kaluga Oblast. Ferzikovskij District, Kovrovo, short-grass meadow, 25 July 2023, 15:00, 24°C

Рис. 1. Осцилограмма призывного сигнала *Chorthippus biguttulus* из Калужской области. Ферзиковский округ, Коврово, мелкозлаковый луг, 25.07.2023, 15:00, 24°C

1993; Ingrisch 1995; Neumeister et al. 2025; Orthoptera. ch...2026). Specifically, *Ch. brunneus* is characterized by a long distance between the stigma and the wing tip, and *Ch. biguttulus* has the broadest forewings and the most expanded costal area. In contrast, the density of stridulatory pegs in the stridulatory file varied considerably.

Therefore, specimens collected before 2023 or using traps were identified primarily based on forewing shape. Females were assigned to species based on the males identified in a given sampling plot on a given date.

Pitfall traps were used to compare the abundances of the studied species across different habitat types. Soil pitfall traps

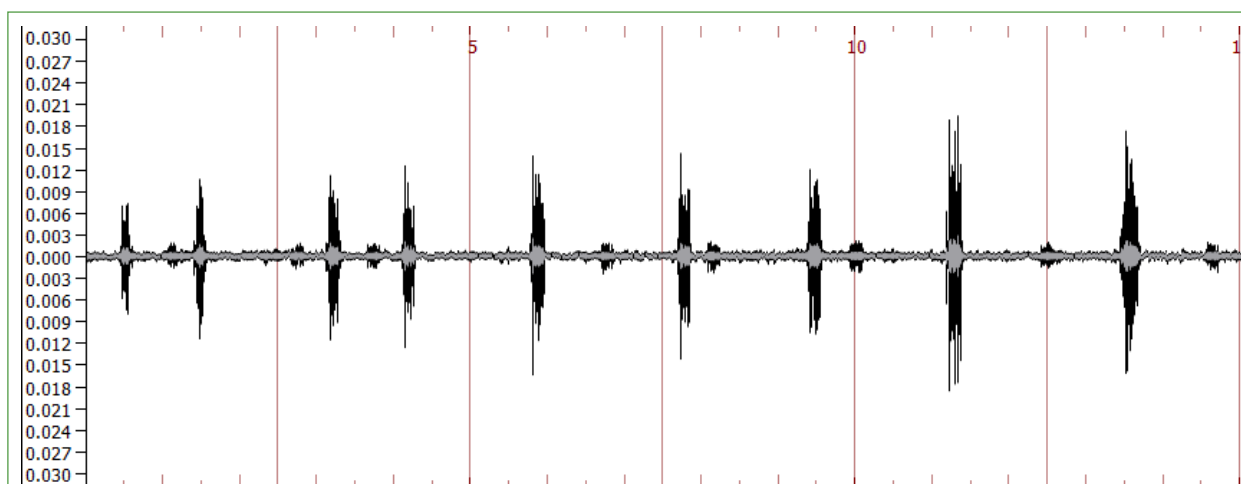


Fig. 2. Oscillogram of a calling song in *Chorthippus brunneus* from Kaluga Oblast. Peremyshlskij District, Golodskoje, edge of pine forest, 06 September 2025, 11:00, 20°C

Рис. 2. Осцилограмма призывного сигнала *Chorthippus brunneus* из Калужской области. Перемышльский округ, Голодское, опушка сосняка, 06.09.2025, 11:00, 20°C

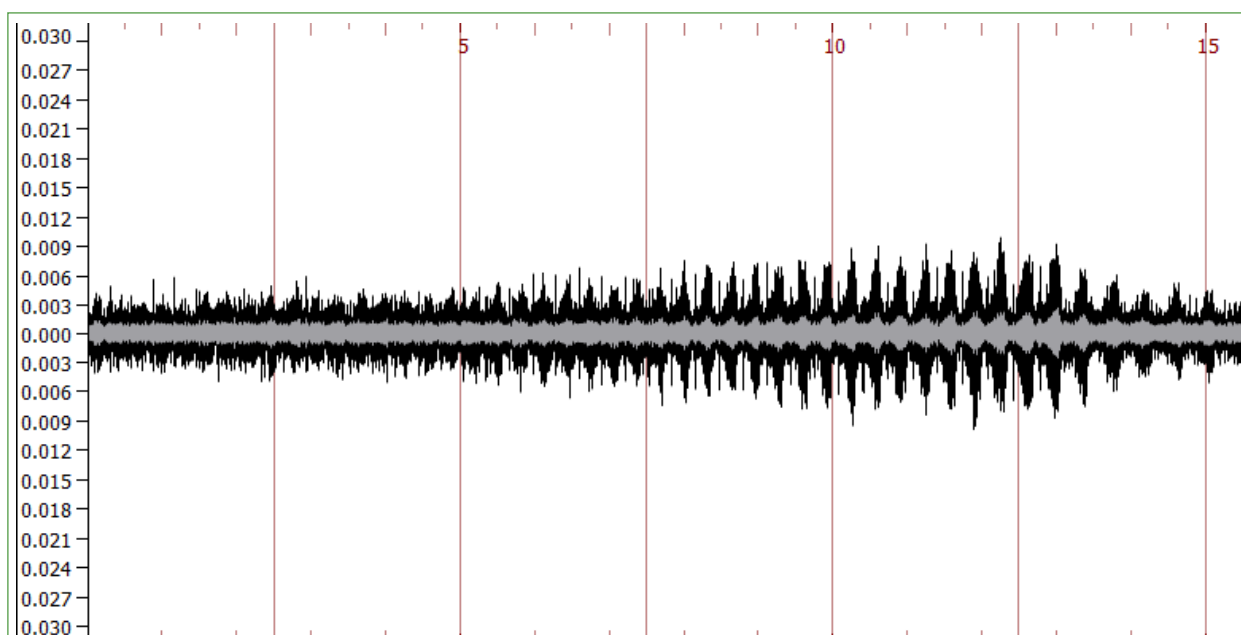


Fig. 3. Oscillogram of a calling song in *Chorthippus mollis* from Kaluga Oblast. Kaluga City, Gorodskoj Bor, short-grass meadow, 10 August 2023, 8:40, 19°C

Рис. 3. Осциллограмма призывного сигнала *Chorthippus mollis* из Калужской области. Город Калуга, Городской бор, мелкозлаковый луг, 10.08.2023, 8:40, 19°C

consisted of transparent 0.5 L plastic cups with an opening diameter of 85 mm, filled to approximately one-third of their volume (150 mL) with a 4% formaldehyde solution and covered with transparent polyethylene film. The number of traps per study plot ranged from 10 to 30, depending on the size and complexity of the biotope, as well as the objectives of sampling other insects. Pitfall traps operated from May to September. However, only the three-month period from July to September was used to calculate grasshopper activity density, measured as individuals per 100 trap-days, because during this period all three species were adults. In total, 96 sampling plots with pitfall traps were used to assess grasshopper activity density.

Window traps were installed in forests and at forest edges at heights of up to 1.5 m above the ground. Therefore, material collected using window traps was considered occasional and was not included in the presence–absence analysis; however, it was used to provide additional information on grasshopper distribution.

Overall, 401 sampling plots where grasshoppers of the *Chorthippus biguttulus* group had been recorded by any method were

mapped. For statistical analyses, plots where species presence was confirmed by acoustic records and plots where grasshopper activity density was assessed were analysed separately.

Sampling plots

Each sampling plot represented a habitat patch with a unique combination of geographical coordinates (decimal latitude and longitude). Adjacent patches of different habitat types were considered separate types, as were patches of the same habitat type separated by patches of other habitat types. Geographical coordinates were determined using the WGS 84 datum based on GPS measurements or Yandex satellite imagery. Each sampling plot was characterized by four parameters: habitat type, landform, landscape type, and a type of surrounding.

1. **Habitat type.** For the *Chorthippus biguttulus* group, eight habitat types were distinguished based on published data on the habitats of these insects, Shennikov's grassland classification (Shennikov 1941), and the system of ecological-coenotic plant groups (Khanina et al. 2004).

(1) *Short-grass meadows* — dominated by short (small) grasses of the dry meadow

ecological subgroup: *Festuca rubra* L., *Festuca ovina* L., *Agrostis capillaris* L., *Agrostis vinealis* Schreb.

(2) *Tall-grass meadows* — dominated by tall mesic grasses of the fresh-meadow ecological subgroup: *Bromus inermis* Leiss., *Elymus repens* (L.) Gould, *Dactylis glomerata* L., and more rarely *Phleum pratense* L. and *Festuca pratensis* Huds.

(3) *Tall-and-short-grass meadows* — dominated equally by tall and short grasses.

(4) *Calamagrostis epigeios grasslands* (in what follows also *C. epigeios*) — grasslands dominated by *Calamagrostis epigeios* (L.) Roth, which is a tall grass belonging to the pine-forest ecological group and therefore often indicates nutrient-poor and dry soils.

(5) *Mown grasslands* — habitats dominated by grasses that are regularly mown and trampled, including urban lawns and grassy patches in gardens. The herb layer contains a high proportion of forbs such as *Taraxacum officinale* F.H. Wigg. Vegetation cover is dense, although small patches of bare ground may occur.

(6) *Pine forests* — habitats dominated by Scots pine *Pinus sylvestris* L.

(7) *Dry sand grasslands* — sandy habitats dominated by lichens, mosses, and psammophilous vascular plants associated with Scots pine, including *Artemisia campestris* L., *Koeleria glauca* (Spreng.) DC., and *Pilosella officinarum* F.W.Schultz & Sch.Bip., occasionally with Scots pine regeneration but lacking a closed tree canopy.

(8) *Forbs* — habitats dominated by annual or perennial forbs, excluding plants of the pine-forest ecological group. Typical dominant species include *Daucus carota* L., *Hieracium umbellatum* L., *Tripleurospermum inodorum* (L.) Sch.Bip., *Leucanthemum vulgare* Lam., *Solidago canadensis* L., *Erigeron annuus* (L.) Desf., and *Echium vulgare* L. This category includes arable fields, fallows, and disturbed sites with ruderal or segetal vegetation.

Other habitat types, such as deciduous or spruce forests, swamps, and bogs, were excluded from the database because they were considered unsuitable for the *Chorthippus*

biguttulus group in Kaluga Oblast, despite occasional observations of single individuals.

2. **Landforms.** Three landform categories were distinguished: (1) *large river valleys* (the Oka River, its major first-order tributaries, and second-order tributaries with broad pre-Quaternary valleys); (2) *medium river valleys* (second-order tributaries with narrow valleys of Quaternary origin); (3) watersheds and valleys of small rivers or streams.

3. **Landscape type.** According to the classification developed by Vitaly Esipov (Esipov 2005) and based on the digital map provided by Alexey Streltsov (the Bioindication Laboratory at Kaluga State University), the following landscape types were distinguished: (1) moraine plains of the latter stage of the Moscow glaciation; (2) plains of the early stage (marginal zone) of the Moscow glaciation; (3) erosional plains outside the boundaries of the Moscow glaciation; (4) fluvioglacial plains of both Moscow and Don glaciations; and (5) landscapes of river valleys.

4. **Type of surrounding.** Based on the surrounding environment, (1) *urban* or (2) *rural* surroundings were distinguished.

Sampling plots were located in most administrative districts of the region, although their highest density occurred in the eastern and southeastern parts, where the terrain is dissected by relatively deep and broad river valleys, resulting in the greatest area and variability of grassland habitats.

Data analysis

Data analysis was performed using R version 4.5.2. Generalized linear models (GLM) were fitted using the *glm* function from the base *stats* package. Model quality was assessed using AIC and McFadden's pseudo- R^2 from the *pscl* package (Jackman 2024). For each predictor, coefficient significance (p -values) and partial R^2 values were calculated using the *Anova* function from the *car* package (Fox, Weisberg 2019).

To identify factors influencing the presence/absence of each of the three species, logistic regression models (family = 'binomial' in the *glm* function) were used. As predictors, we tested the four sampling-plot parameters

described above together with a distance-weighted autocovariate. The autocovariate was calculated using the *autocov_dist* function (type = 'inverse') from the *spdep* package (Bivand, Wong 2018), with a neighbourhood radius of 1 km, which provided the best results. In addition, because a significant correlation between the occurrence of *Ch. biguttatus* and *Ch. mollis* was detected, the presence of the 'twin' species was included as a sixth predictor for these species.

To analyse differences in relative abundance between habitat types assessed by acoustic observation, linear regression models (family= 'gaussian') with subsequent pairwise

t-test with the Holm–Bonferroni adjustment were used.

Differences in grasshopper activity density in pitfall traps were analysed using the Kruskal–Wallis test and subsequent Dunn's multiple-comparison test implemented in the *dunn_test* function from the *rstatix* package.

Results

Factors influencing the presence of the species of the Chorthippus biguttatus group across Kaluga Oblast

Primary data on species records are available in three datasets (Aleksanov et al 2024; Aleksanov 2026a; 2026b). In total,

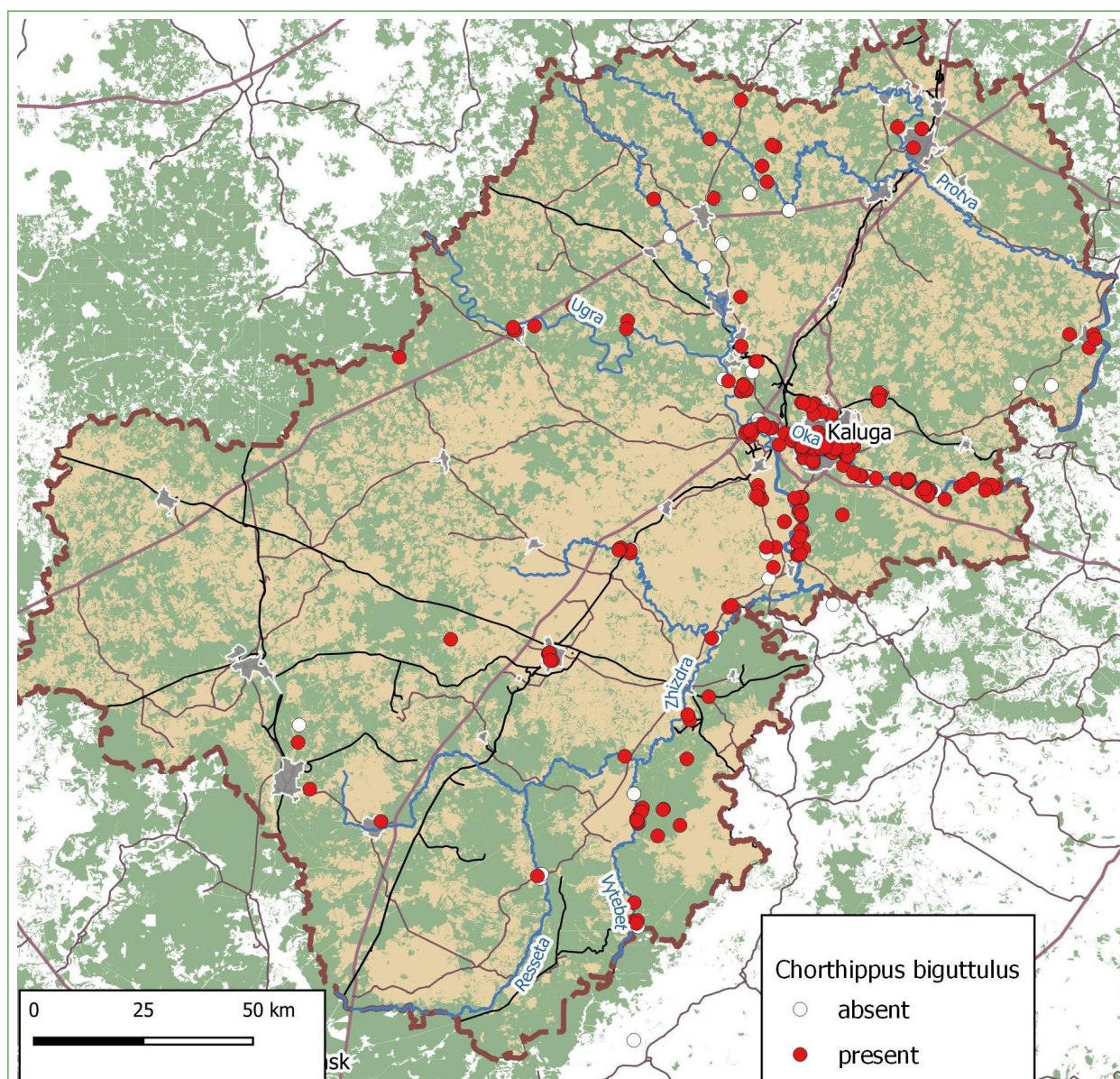


Fig. 4. Map of findings of *Chorthippus biguttatus* in Kaluga Oblast

Рис. 4. Карта мест находок *Chorthippus biguttatus* в Калужской области

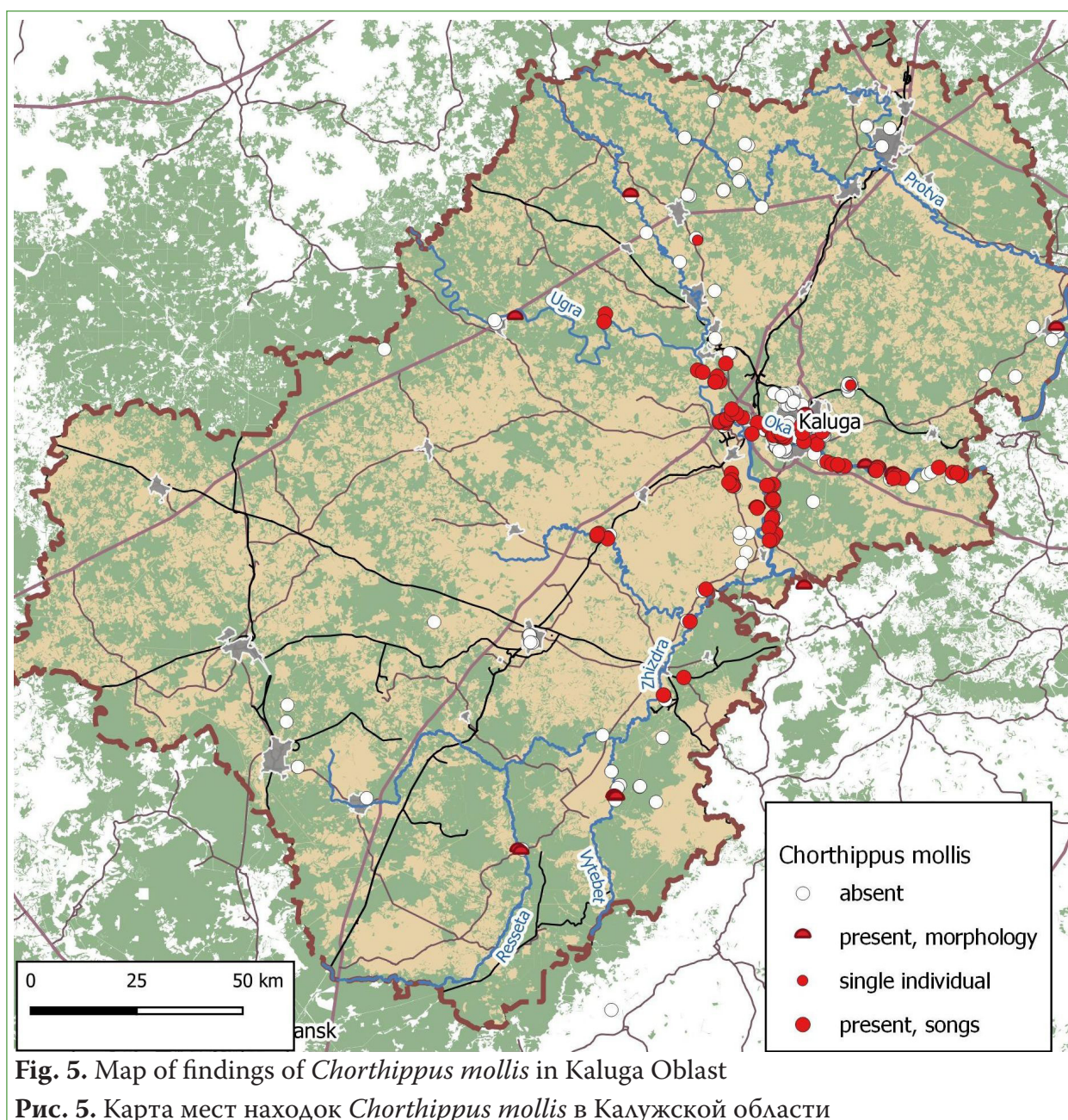
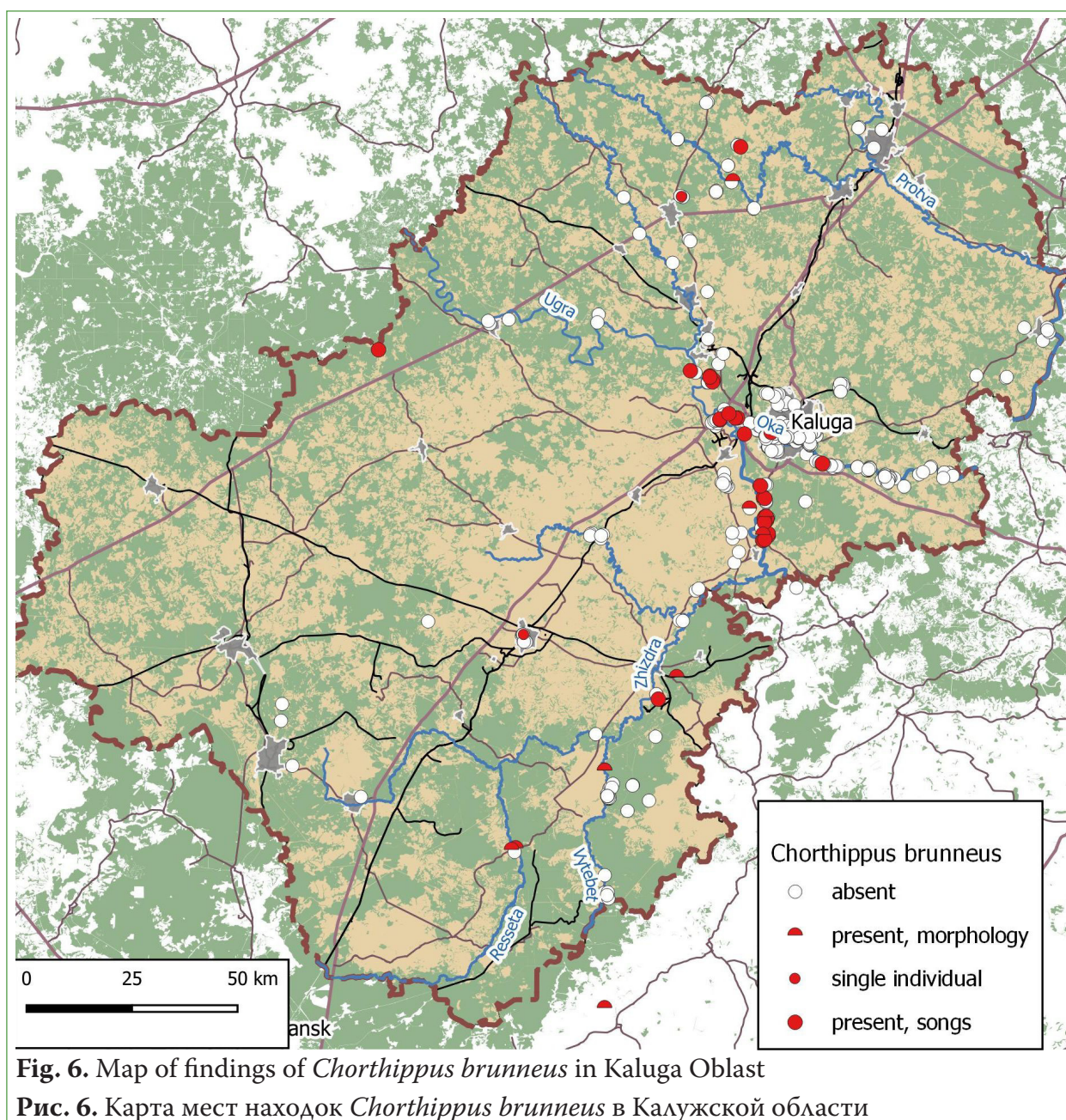


Fig. 5. Map of findings of *Chorthippus mollis* in Kaluga Oblast

Рис. 5. Карта мест находок *Chorthippus mollis* в Калужской области

Chorthippus biguttulus was recorded in 279 of 401 sampling plots, *Chorthippus mollis* in 134 plots, and *Chorthippus brunneus* in 45 plots (Figs. 4–6). Considering only material identified by calling songs, at least one species of the *Chorthippus biguttulus* group was recorded in 217 of 278 sampling plots. The largest group of sampling plots consisted of those where only *Ch. biguttulus* was recorded (93 plots), whereas the second largest group included plots where *Ch. biguttulus* and *Ch. mollis* co-occurred (65 plots). A weak but significant positive correlation between the occurrences of *Ch. biguttulus* and *Ch. mollis* was detected (Spearman's $r = 0.136$, $p = 0.025$).

***Chorthippus biguttulus*.** The regression model showed that the presence of *Ch. biguttulus* was only weakly explained by the six analysed variables (Table 1). Among these variables, only habitat type and landform were significant predictors. *Ch. biguttulus* showed significant avoidance of dry sand grasslands and was positively associated with large river valleys and watersheds, while avoiding medium-sized river valleys. The presence of *Ch. mollis* was also identified as a significant predictor of the occurrence of *Ch. biguttulus*. Therefore, some environmental factors influencing the distribution of these species are likely not fully represented by



the four analysed habitat properties. Across Kaluga Oblast, *Ch. biguttulus* is widely distributed. It was not found only in a few localities characterized by a low proportion of grasslands and the predominance of unmown tall-grass meadows. This species is frequently collected in window traps in gardens and at forest edges.

***Chorthippus mollis*.** The occurrence of *Ch. mollis* was explained by the analysed predictors considerably better than that of *Ch. biguttulus* (Table 2). Habitat type and landform were the main factors determining its occurrence. This species avoided watersheds, pine forests, and tall-

grass meadows. Unlike *Ch. biguttulus*, spatial autocovariation was a weak but significant predictor of the presence of *Ch. mollis*. Thus, some unmeasured environmental factors influencing the occurrence of *Ch. biguttulus* also weakly affected the occurrence of *Ch. mollis*.

The distribution map (Fig. 5) demonstrates a strong association of *Ch. mollis* with large rivers, including the Oka, Ugra, and Zhizdra rivers and some of their tributaries. Outside large and medium-sized river valleys, *Ch. mollis* was represented only by isolated calling males. At two watershed localities where this species was recorded, it was

Table 1
Factors affecting the presence of *Chorthippus biguttulus* in sampling plots of Kaluga Oblast based on calling-song records: results of a generalized linear model

Таблица 1
Факторы, определяющие присутствие *Chorthippus biguttulus* на пробных площадях в Калужской области (на основании призывных сигналов): результаты обобщенной линейной модели

Factors	Levels	Estimate	SE	z	p	LR_χ ²	Partial r ²
	(Intercept)	12.39	882.74	0.01	0.9888	22.389	0.073
Landscape	fluvioglacial plains	-13.67	882.74	-0.02	0.9876		
	early Moscow glaciation	-14.92	882.74	-0.02	0.9865		
	latter Moscow glaciation	-15.39	882.74	-0.02	0.9861		
	river valleys	-13.70	882.74	-0.02	0.9876		
	erosional plains	-15.90	882.74	-0.02	0.9856		
Habitat type	forbs	0.06	0.73	0.09	0.9300	16.619	0.068
	dry sand grassland	-1.64	0.76	-2.15	0.0318		
	mown grassland	-0.20	0.67	-0.30	0.7626		
	pine	-1.16	0.78	-1.49	0.1364		
	short-grass	-1.07	0.72	-1.49	0.1351		
	tall-grass	-0.15	0.64	-0.23	0.8176		
	tall-and-short-grass	1.29	0.97	1.34	0.1813		
Landform	large river valley	2.40	0.80	3.00	0.0027	14.748	0.049
	watershed	3.02	0.88	3.43	0.0006		
Surrounding = urban		-0.05	0.49	-0.10	0.9239	0.009	<0.001
Autocovariation within 1 km		28.20	16.92	1.67	0.0956	3.590	0.012
Presence of <i>Chorthippus mollis</i>		0.94	0.42	2.24	0.0253	5.217	0.018

Note. McFadden's $R^2 = 0.169$; AIC = 322. LR_χ² is Likelihood Ratio Chi-Square. Significant p -values are shown in bold.

Примечание. Коэффициент детерминации Макфаддена $R^2 = 0.169$, информационный критерий Акаике AIC = 322. LR_χ² – χ²-теста отношения правдоподобий. Значимые p выделены полужирным.

not observed during subsequent surveys. Only one habitat with a stable population of *Ch. mollis*, recorded over several years, was found outside river valleys. This habitat is located in an urban area along a railway, and a network of old railway tracks connects it to the river valley. This species was collected in window traps only at a forest edge adjacent to the grassland with an extremely high abundance of grasshoppers.

***Chorthippus brunneus*.** The occurrence of *Ch. brunneus* was explained by the analysed factors better than that of the other two species (Table 3). This species showed a strong association with pine forests and dry sand grasslands. Spatial autocovariation made only a minor contribution to the model, although its effect was greater than in *Ch. biguttulus*, with a significance level slightly above 0.05.

Within pine forests, *Ch. brunneus* was most frequently observed in patches of bare ground and, less commonly, in sun-exposed patches of green mosses. The species was not recorded in patches dominated by nemoral herbs or in moss-covered areas beneath a dense tree canopy. However, it was found at the edge of a nemoral forest, within a narrow (to ten meters) belt adjacent to dry meadow, under young pine trees without herb layer (Kaluga City, Gorodskoj Bor, the bank of the Yachenskoje Reservoir).

Across Kaluga Oblast, *Ch. brunneus* was most frequent in the broad section of the Oka River valley south of Kaluga and downstream of the Ugra River (Figure 6). These areas are characterized by extensive dry pine forests. In the eastern part of Kaluga Oblast, where pine forests occupy relatively small areas and

Table 2
Factors affecting the presence of *Chorthippus mollis* in sampling plots of Kaluga Oblast based on calling-song records: results of a generalized linear model

Таблица 2
Факторы, определяющие присутствие *Chorthippus mollis* на пробных площадях в Калужской области (на основании призывных сигналов): результаты обобщенной линейной модели

Factors	Levels	Estimate	SE	z	p	LR_χ ²	Partial r ²
	(Intercept)	15.67	882.74	0.02	0.9858		
Landscape	fluvioglacial plains	−15.59	882.74	−0.02	0.9859	5.520	0.025
	early Moscow glaciation	−16.05	882.74	−0.02	0.9855		
	latter Moscow glaciation	−16.25	882.74	−0.02	0.9853		
	river valleys	−15.92	882.74	−0.02	0.9856		
	erosional plains	−15.04	882.74	−0.02	0.9864		
Habitat type	forbs	0.26	0.70	0.37	0.7089	42.546	0.165
	dry sand grassland	0.52	0.79	0.66	0.5106		
	mown grassland	−0.75	0.72	−1.04	0.2971		
	pine	−2.47	0.84	−2.96	0.0031		
	short-grass	0.71	0.75	0.95	0.3411		
	tall-grass	−1.76	0.62	−2.83	0.0047		
	tall-and-short-grass	0.26	0.83	0.32	0.7507		
Landform	large river valley	0.26	0.78	0.34	0.7338	24.285	0.101
	watershed	−2.20	0.94	−2.33	0.0199		
Surrounding = urban		−0.79	0.59	−1.33	0.1847	1.777	0.008
Autocovariation within 1 km		46.45	17.60	2.64	0.0083	10.932	0.078
Presence of <i>Chorthippus biguttulus</i>		1.10	0.44	2.49	0.0129	6.585	0.030

Note. McFadden's $R^2 = 0.393$; AIC = 251. LR_χ² is Likelihood Ratio Chi-Square. Significant p -values are shown in bold.

Примечание. Коэффициент детерминации Макфаддена $R^2 = 0.393$, информационный критерий Акаике AIC = 251. Значимые p выделены полужирным.

are mainly represented by pine forests with nemoral cover, *Ch. brunneus* was extremely rare. Nevertheless, the species also occurred in watershed pine forests.

Outside pine forests, *Ch. brunneus* was recorded on bare ground in arable landscapes in the Borovskij and Medynskij districts. The species was also regularly collected in window traps placed in dry clearings within spruce forests. In addition, one specimen was recorded on a lawn in the town of Sukhinichi.

Relative abundance of species of the *Chorthippus biguttulus* group

Relative abundance based on acoustic observations. Using acoustic observations, I found that, in large river valleys, *Ch. mollis* reached its highest abundance in short-grass meadows (Table 4). Its abundance in this habitat type was significantly higher than

in mown grasslands and forbs-dominated habitats. This species was also significantly more abundant in dry sand grasslands than in mown grasslands. Furthermore, *Ch. mollis* was more abundant than *Ch. biguttulus* in all dry habitat types, including short-grass meadows, dry sand grasslands, and pine forests.

At a smaller scale, acoustic observations showed that *Ch. mollis* was most abundant in patches of short grasses lacking dense tussocks and associated with *Fragaria viridis* Weston, particularly in habitats dominated by *Festuca rubra* or *F. ovina* rather than *Koeleria glauca*. The species was observed only rarely in areas with bare ground or in tall-grass patches.

On watersheds, *Ch. biguttulus* was the most abundant grasshopper species in mown grasslands and forbs-dominated habitats. In contrast, only a few individuals of this

Table 3

Factors affecting the presence of *Chorthippus brunneus* in sampling plots of Kaluga Oblast based on calling-song records: results of a generalized linear model

Таблица 3

Факторы, определяющие присутствие *Chorthippus brunneus* на пробных площадях в Калужской области (на основании призывных сигналов): результаты обобщенной линейной модели

Factors	Levels	Estimate	SE	z	p	LR_χ ²	Partial r ²
	(Intercept)	0.13	29977.10	0.00	1.0000	7.726	0.095
Landscape	fluvioglacial plains	-21.17	29232.44	0.00	0.9994		
	early Moscow glaciation	-38.84	29359.98	0.00	0.9989		
	latter Moscow glaciation	-19.63	29232.44	0.00	0.9995		
	river valleys	-20.80	29232.44	0.00	0.9994		
	erosional plains	-20.34	29232.44	0.00	0.9994		
Habitat type	forbs	0.51	1.32	0.39	0.6977	64.311	0.466
	dry sand grassland	3.44	1.20	2.87	0.0041		
	mown grassland	0.17	1.62	0.11	0.9152		
	pine	3.81	1.21	3.14	0.0017		
	short-grass	-0.56	1.51	-0.37	0.7088		
	tall-grass	-19.34	3056.33	-0.01	0.9950		
	tall-and-short-grass	-18.83	6231.35	0.00	0.9976		
Landform	large river valley	17.63	6640.08	0.00	0.9979	3.013	0.039
	watershed	18.95	6640.08	0.00	0.9977		
Surrounding = urban		-18.36	2919.72	-0.01	0.9950	4.357	0.056
Autocovariation within 1 km		129.43	67.34	1.92	0.0546	4.685	0.060

Note. McFadden's $R^2 = 0.659$; AIC = 108. LR_χ² is Likelihood Ratio Chi-Square. Significant p-values are shown in bold.

Примечание. Коэффициент детерминации Макфаддена $R^2 = 0.659$, информационный критерий Акаике AIC = 108. Значимые p выделены полужирным.

species were recorded in grasslands within river valleys. Usually, it was less common than *Ch. mollis* in short-grass meadows and less common than *Chorthippus dorsatus* (Zetterstedt, 1821) in tall-grass meadows. More frequently, *Ch. biguttulus* was observed along roads and railways.

Activity density based on pitfall-trap data. Using pitfall traps, we collected 4,070 individuals of *Ch. biguttulus*, 20,644 individuals of *Ch. mollis*, and 1,265 individuals of *Ch. brunneus*. *Chorthippus brunneus* was collected only in certain pine forests and dry sand grasslands, and its median activity density in occupied plots was 0.44 individuals per 100 trap-days. Therefore, the distribution of its abundance was not analysed further.

The median activity density of *Ch. biguttulus* in plots where it was recorded was

2.31 individuals per 100 trap-days (Fig. 7). No statistically significant differences in the activity density of this species were found among habitat types.

In contrast, *Ch. mollis* reached extremely high abundance in suitable habitats. Its median activity density in occupied plots was 38.33 individuals per 100 trap-days (Fig. 8). The highest abundance of this species was recorded in short-grass meadows, while the second highest abundance was observed in mixed tall-and-short-grass meadows. Differences between these habitat types and all other habitat types were statistically significant (Table 5). The sampling plot with the highest abundance was a short-grass meadow on the first fluvial terrace of the left bank or the Oka River in the vicinity of Novoloki, Ferzikovsky District.

Table 4
Relative abundance of *Chorthippus mollis* and *Ch. biguttulus* in different habitat types in Kaluga Oblast assessed using acoustic observations, average ranks.

Таблица 4
Относительное обилие *Chorthippus mollis* и *Ch. biguttulus* в различных типах местообитаний на основании акустических наблюдений, средние баллы

Habitat type	Large river valley			Watershed		
	<i>Ch. mollis</i>	<i>Ch. biguttulus</i>	n	<i>Ch. mollis</i>	<i>Ch. biguttulus</i>	n
short-grass	2.6	1.8	12	—	2.0	3
tall-and-short-grass	2.1	1.9	10	—	-	-
tall-grass	1.5	2.0	8	—	2.0	13
<i>C. epigeios</i>	1.7	1.5	11	1.5	2.0	3
mown grassland	1.0	1.8	4	1.5	1.3	19
forbs	1.5	2.0	7	1.0	1.9	7
dry sand grassland	2.4	1.7	18	—	—	—
pine forest	2.3	1.3	13	—	—	—

Note. 1 — rare species, 2 — common species, 3 — abundant species. Ranks were calculated only in sampling plots where the species was presented.

Примечание. 1 — редкий вид, 2 — обычный вид, 3 — массовый вид. Баллы вычислены только для пробных площадей, где вид присутствовал.

Discussion

***Chorthippus biguttulus*.** The results show that the three species of the *Chorthippus biguttulus* group differ markedly in their

habitat distribution. *Chorthippus biguttulus* is the most eurytopic and relatively mesophilic species. This is supported by its wide distribution across the region, the absence of a significant autocorrelation effect, and its

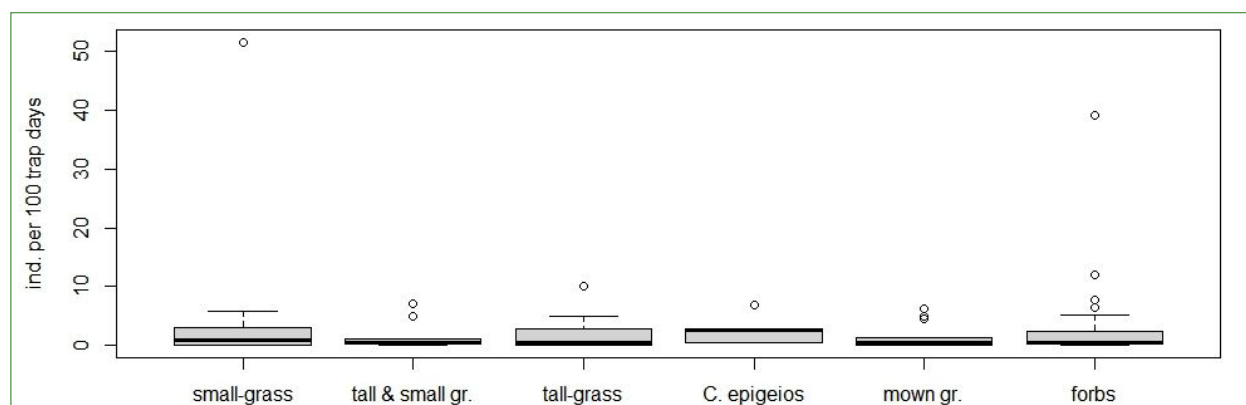


Fig. 7. Activity density of *Chorthippus biguttulus* in different habitats of Kaluga Oblast estimated using pitfall traps. Kruskal–Wallis chi-squared = 2.331; df = 5; p -value = 0.802. Abbreviations: short-grass — short-grass meadows, tall & short — tall-and-short-grass meadows, tall-grass — tall-grass meadows, *C. epigeios* — *Calamagrostis epigeios* grasslands, mown — mown grasslands. Points are outliers (observations lying more than 1.5 interquartile ranges from the quartiles)

Рис. 7. Динамическая плотность *Chorthippus biguttulus* в различных местообитаниях в Калужской области, оцененная с помощью почвенных ловушек. Тест Краскала — Уоллиса: $\chi^2 = 2.331$, df = 5, $p = 0.802$. Сокращения: short-grass — мелкозлаковые луга; tall & short — луга с кодоминированием крупных и мелких злаков; tall-grass — крупнозлаковые луга; *C. epigeios* — луга с доминированием *Calamagrostis epigeios*; mown — часто скашиваемые местообитания; forbs — местообитания с доминированием разнотравья. Точками показаны выбросы (наблюдения, лежащие за пределами 1.5 межквартильного размаха)

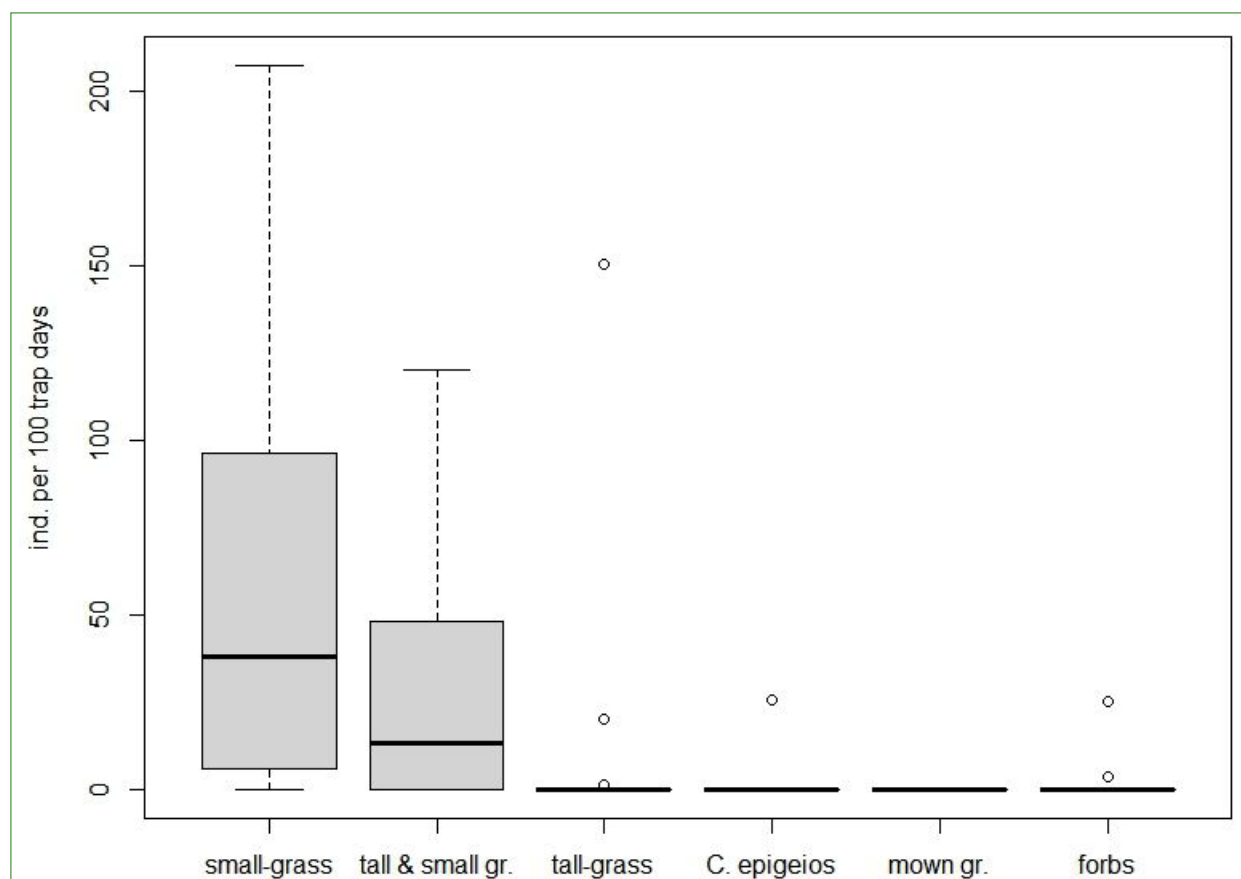


Fig. 8. Activity density of *Chorthippus mollis* in different habitats of Kaluga Oblast estimated using pitfall traps. Kruskal–Wallis chi-squared = 44.702; df = 5; p -value < 0.0001. Abbreviations: see Fig. 7

Рис. 8. Динамическая плотность *Chorthippus mollis* в различных местообитаниях в Калужской области, оцененная с помощью почвенных ловушек. Тест Краскала — Уоллиса: $\chi^2 = 44.702$; df = 5; $p < 0.0001$. Сокращения: см. рис. 7

avoidance only of dry sand grasslands, which represent the driest habitats. Its frequent occurrence in urban areas and in habitats with regularly mown vegetation both in Kaluga Oblast (Aleksanov 2025b) and some other regions (Sergeev 1987; 2016; Rech et al. 2022) also supports this conclusion. This species prefers patches with sparse and low vegetation (Hochkirch, Papen 2001), avoiding, however, areas completely lacking grasses (Harz 1957). In other parts of its range, this species inhabits a wide spectrum of open, non-wet habitats (Bey-Bienko 1930; Sychev 1975; Kleukers et al. 1997; Karmazina, Shulaev 2015; Orthoptera.ch... 2026).

Chorthippus brunneus. *Chorthippus brunneus* inhabits dry pine forests and dry sand grasslands regardless of landform type. Its preference for pine forests may partly be explained by trophic associations with certain

grasses, such as species of *Holcus* (Richards, Waloff 1954). However, this grasshopper is known to utilize a wide range of grasses (Harz 1957). Therefore, the association of *Ch. brunneus* with pine forests is more likely related to its preference for dry sandy substrates and patches of bare ground suitable for oviposition (Choudhuri 1958).

Thus, in Kaluga Oblast *Ch. brunneus* appears to be primarily a xerophilic rather than a thermophilic species. This interpretation agrees with the broad polyzonal distribution of *Ch. brunneus* (Sergeev 1986; Cigliano et al. 2026). Preference for dry habitats with sparse vegetation has also been reported for this species in Western (Richards, Waloff 1954; Waterschoot et al. 2023), Northern (Budrys, Pakalniškis 2007; Elven et al. 2022), and Central Europe (Harz 1957; Kuřavová 2014; Dobos 2026; Orthoptera.ch... 2026).

Table 5
Results of pairwise multiple comparisons (Dunn’s test) of activity density of *Chorthippus mollis* in different types of habitats in Kaluga Oblast. Significant *p*-values are shown in bold

Таблица 5
Результаты попарных множественных сравнений (тест Данна) динамической плотности *Chorthippus mollis* в различных типах местообитаний Калужской области. Значимые *p* выделены полужирным

Groups		Sample count		<i>z</i> -value	<i>p</i> .adj
group1	group2	n1	n2		
short-grass	tall-and-short grass	15	9	−1.624	0.8351
short-grass	tall-grass	15	16	−4.373	0.0002
short-grass	<i>C. epigeios</i>	15	5	−3.012	0.0285
short-grass	mown grassland	15	16	−5.458	<0.0001
short-grass	forbs	15	28	−5.716	<0.0001
tall-and-short grass	tall-grass	9	16	−2.128	0.2997
tall-and-short grass	<i>C. epigeios</i>	9	5	−1.561	0.8351
tall-and-short grass	mown grassland	9	16	−3.065	0.0261
tall-and-short grass	forbs	9	28	−2.986	0.0285
tall-grass	<i>C. epigeios</i>	16	5	0.031	1
tall-grass	mown grassland	16	16	−1.103	1
tall-grass	forbs	16	28	−0.821	1
<i>C. epigeios</i>	mown grassland	5	16	−0.793	1
<i>C. epigeios</i>	forbs	5	28	−0.563	1
mown grassland	forbs	16	28	0.423	1

The species is also known as a forest inhabitant in the western part of its range (Kleukers et al. 1997), as well as in Russia along the Volga River (Karmazina, Shulaev 2015). Pine forests and their edges represent the only naturally dry habitat type in Kaluga Oblast because they develop on sandy alluvial and fluvio-glacial sediments (Soloviyova, Khomutova 1970).

The broader habitat spectrum of *Ch. brunneus* in eastern regions of European Russia (Adachovskiy 2006) and its greater abundance in these regions (Aleksanov et al. 2024) may reflect the principle of habitat change (Bey-Bienko 1930; Stebaev 1974), although this hypothesis requires more comprehensive analysis.

***Chorthippus mollis*.** *Chorthippus mollis* is closely associated with large and medium-sized river valleys, within which it prefers short-grass meadows, especially those located on first fluvial terraces. This distribution pattern may partly be explained by trophic preferences, since *Festuca* species are known

to be preferred food plants (Köhler, Held 2000). However, *Dactylis*, which dominates tall-grass meadows, is also considered a preferred food plant, and *Ch. mollis* is capable of feeding not only on grasses but also on forbs such as *Artemisia* (Köhler, Held 2000). In some regions, this species may even prefer tall-grass meadows (Thorens 1993). In different parts of its range, *Ch. mollis* has likewise been described as a thermophilic species (Harz 1957; Adachovskiy 2006; Dobos 2026; Orthoptera.ch... 2026). The geographical distribution of *Ch. mollis* also characterizes it as a ‘southern’ species (Sergeev 1986; Ozerski 2012). The later emergence of adults compared with the other two species (Harz 1957; Orthoptera.ch... 2026) further supports its more thermophilic character. Therefore, thermophily is likely the principal factor determining the habitat distribution of *Ch. mollis* in Kaluga Oblast. Certain parts of river valleys represent the warmest habitats in flat landscapes because of their slope exposure, air circulation within valleys,

and frequently sandy substrates (Romanova et al. 2003).

However, its strong association with river valleys may represent a specific feature of its distribution in northern lowland regions. A similar preference for first fluvial terraces was documented in part of Moscow Oblast (Chernyakhovsky 2019). In Poland, the species inhabits warm, dry, nutrient-poor grasslands and sandy grasslands (Kuřavová 2014). In the Netherlands, it occurs in dry sand grasslands, sandy dunes, and roadside habitats (Kleukers et al. 1997). In the Republic of Tatarstan, it is found along the edges of pine forests (Karmazina, Shulaev 2015). In contrast, in the southern part of Western Siberia, *Ch. mollis* is a dominant species in steppe habitats on watersheds (Sergeev 2019).

Surrounding by urban areas was not identified as significant predictor for any of the three studied species. This result confirms the good dispersal ability of all species within the group. *Chorthippus mollis* is generally considered to be less mobile than *Ch. biguttulus* and *Ch. brunneus* (Harz 1957; Bruckhaus, Detzel 1997). However, all three species of the group are regarded as highly mobile among European grasshoppers (Reinhardt et al. 2005). The occurrence of isolated individuals of *Ch. mollis* at considerable distances from suitable habitats further supports the high dispersal ability of this species. Therefore, the absence of *Ch. brunneus* and the rarity of *Ch. mollis* in the urban area of Kaluga City (Aleksanov 2025b) are more likely explained by the absence or scarcity of suitable habitats than by limited dispersal ability.

Conclusions

In Kaluga Oblast, habitat preferences of the three species of the *Chorthippus biguttulus* group are clearly differentiated. *Chorthippus*

biguttulus is the most eurytopic species, although it does not reach very high abundance in occupied habitats. In contrast, *Ch. mollis* is a stenotopic thermophilic grassland species, but it can become extremely abundant in suitable habitats. These contrasting ecological strategies probably contribute to the successful coexistence of these two sympatric species. *Chorthippus brunneus* is a stenotopic xerophilic species, and it is not abundant. The ecological advantages of this species remain unclear; however, they may be related to its ability to persist in small habitat patches combined with its high mobility.

Благодарности

Автор признателен С. К. Алексееву и другим сотрудникам Дирекции парков Калужской области за предоставление сборов и организационное содействие исследованию.

Acknowledgements

The author is grateful to Sergey Alekseev and other scientists of Parks Directorate of Kaluga Region for providing collections of grasshoppers and helping with organisation of the survey.

Финансирование

Сбор материала на особо охраняемых природных территориях в 2020–2025 гг. выполнен в рамках государственного задания Дирекции парков Калужской области.

Funding

In specially protected natural areas, millipedes were sampled during 2020–2025 as part of the state-commissioned assignment to Parks Directorate of Kaluga Region.

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For citation: Aleksanov, V. V. (2026) Habitat preferences of three grasshopper species of the *Chorthippus biguttulus* group (Orthoptera: Acrididae) in Kaluga Oblast, Central European Russia. *Amurian Zoological Journal*, vol. XVIII, no. 3, pp. 1068–1087. <https://www.doi.org/10.33910/2686-9519-2026-18-3-1068-1087>

Received 1 June 2026; reviewed 5 July 2026; accepted 16 July 2026.

Для цитирования: Алексанов, В. В. (2026) Биотопическая приуроченность трех видов саранчовых из группы *Chorthippus biguttulus* (Orthoptera: Acrididae) в Калужской области (центр Европейской России). *Амурский зоологический журнал*, т. XVIII, № 3, с. 1068–1087. <https://www.doi.org/10.33910/2686-9519-2026-18-3-1068-1087>

Получена 1 июня 2026; прошла рецензирование 5 июля 2026; принята 16 июля 2026.