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Regularities of Distribution of Orthoptera Populations i Natural and Anthropogenic Areas of Mountain Depressions in Southern Siberia*

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Abstract. Four groups of species with similar patterns of topographic distribution are distinguished for 69 species of Orthoptera in depressions of mountains of S Siberia. Regularities of changes of locality preferences of the species from one depression to another are shown. Peculiarities of settling of agrococenoses by species of each group are revealed. Correlation of orthopteran distribution in natural and anthropogenic areas with specific geographical, e.g., climate, features of the hollows is demonstrated.

Keywords. Orthoptera, distribution.

Spatial population structures describe ecoevolutionary characteristics of species and are ne: for the substantiation of forecasts of their activity in biocoenoses, including anthropogenic one: is especially important in such an economically important group as Orthoptera. According to (1977) such groups are expressed in regular distribution of individuals and their groups in are modern concepts of spatial population structures are usually based on the distribution of individ two-dimensional space. In spite of this, an approach is being actively developed (Tupikova, Flint, 1972; Korenberg, 1979; Danilenko, 1980; etc.) which is obviously not sufficient when app small animals, including insects. In this situation it is necessary to introduce the third dim altitude, or the vertical distribution, including drainage differentiation of areas and their (Gorodkov, 1985). One possible way of understanding regularities of the three-dimensional di tion of population groups may be developed on the basis of concepts of inner topographic pop structure of the range (Stebaev and Sergeev, 1982), developed from the classic studies of Bey-I (1930, 1959, 1966) on zonal succession of habitats and worked out mainly for large geog categories of rank of zone, subzone, or sector.

However, in each actual region, beginning with physiographic province and extending including drainage series of areas such as river basins, it is also important to know more patterns of distribution of population groups of species among areas and their subdivisions (Se 1989). Investigations at these levels permit approaching the solution of the problem of the forma local faunas and multispecific communities, including also those of anthropogenic areas. Prev such models were worked out for regions at the rank of physiographic provinces with the exan Orthoptera and some other insects by Stebaev (1971, 1974) and by Stebaev with other rese: (1988). However, such reports are lacking at the basin level and the aim of this paper is to fill thi

The choice of S Siberia with its well-isolated lowlands as our study area was determi

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the fact that its Orthoptera fauna is well studied, the topographic structure is complex, and most natural habitats are little disturbed and combined with diverse anthropogenic areas.

Four lowlands in which investigations were conducted in 1978, 1985, and 1988 form a peculiar series ranging from the warmest and most humid Edigan Mountain depression to the most arid and coolest Khandagay Mountain depression.

The largest, Edigan depression is in C Altai and is associated with the wider part of the Katun River valley and the rift, in which the Edigan River valley is located (Zyatkova, 1977). Here, in the foothill plain, typical steppes have developed. The three remaining depressions are located in Tuva. Among them Balgazyn Mountain depression is the warmest one, adjacent to the NE slope of the E Tannu-Ola Mountain range and is characterized by diverse herbaceous-graminaceous steppes. The Ubsunur Mountain depression is the largest and generally at a higher altitude and therefore its climate is cooler; because it is shadowed by the Tannu-Ola Mountain range its climate is also more arid. Vast foothill plains of this mountain depression in Tuva are occupied predominantly by turf and desert type of steppes. The lesser Khandagay Mountain depression is next to the Ubsunur Mountain depression; it has a similar type of vegetation, but it is at still greater altitude and its climate is harsher.

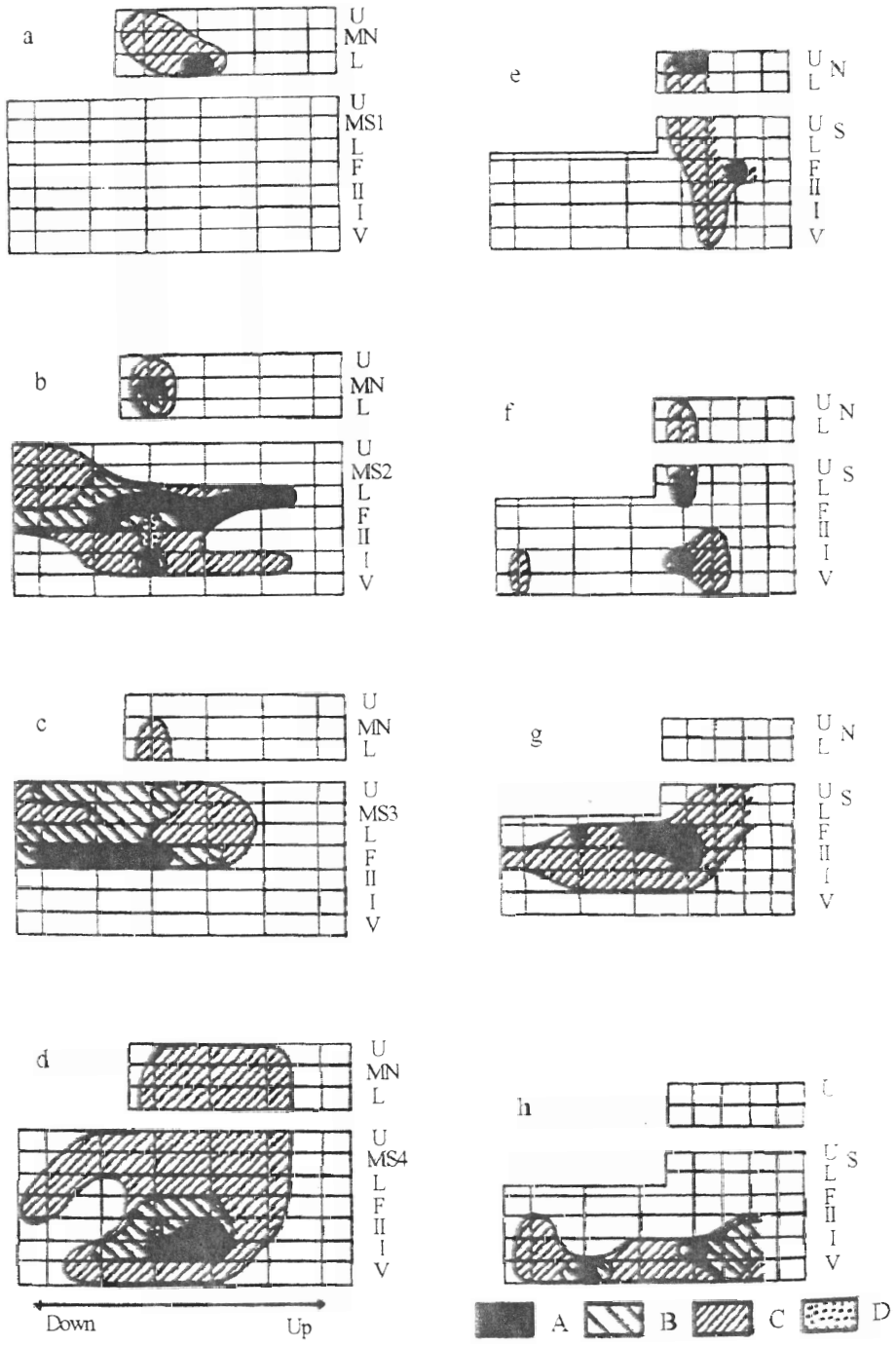
The studied lowlands are characterized by similar species diversity of Orthoptera. In the transects studied in the Balgazyn depression 33 species, in the Kandagay depression 38 species, in the Edigan depression 43 species, and in the Ubsunur depression 44 species were found. The species composition of the Edigan depression is the most characteristic. In this area 17 species were found which until then have never been recorded in S Tuva. Together with W Palearctic Orthoptera, *Poecilimon intermedius* (Fieb.) and *Chortippus parallelus* (Zett.), there are some forms limited largely to the E Palearctic and distributed around Tuva in the N, *C. aethalinus* (Zub.) (Sergeev, 1986). The lowlands of Tuva, especially the Ubsunur and Khandagay lowlands, are similar to each other. However, the Ubsunur depression contains desert Orthoptera, *Compsorhipis davidiana* (Sauss.) and *Sphingonotus beybienkoi* L. Mistsh. At the same time a certain peculiarity of the fauna of Orthoptera of the Khandagay depression is caused by the subendemic species of Altai, *Stenobothrus newskii* Zub., which we found in its high mountain part. The fauna of the Balgazyn depression differs in the presence of mesophilic, multizonal, and forest-steppe species, which are in common with the fauna of Edigan depression, *Decticus verrucivorus* (L.), and *Euthystira brachyptera* (Ocsk).

In each mountain depression we set up a system of ecologic transects, each of which included the entire topographic diversity, from mountain watershed to river and lake valleys. The location of the transects was determined by the character of altitude-related zonality and direction of river valleys. All major topographic plots were investigated by time survey (Gause, 1930; Kashkarov, 1933; etc.). The total number of 423 surveys was made in 28 transects and, as a result, about 40,000 specimens belonging to 69 species of Orthoptera were collected.

We sincerely thank I. V. Stebaev and T. T. Myagkaya for granting permission to examine some of their collections from the Ubsunur Mountain depression.

We made models of local areal-populational structures of species as suggested by Stebaev (1974) and Stebaev and Sergeev (1982). As a basis we had matrices in which transects were shown horizontally from the lowest to highest localities and parts of the area were shown vertically (Fig. 1). Comparison of species matrices of each lowland permits distinction of basic groups of species (naturally, one species in different depressions may belong to different groups).

1. *Group of species associated with N slopes of mountain ranges.* This group is represented by a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few species in all lowlands (Table). In the Edigan and Ubsunur lowlands, these are represented by species widely distributed in the Palearctic, including its forest zone: *Metricoptera brachyptera* (L.), *Tettigonia viridissima* L., and *Melanoplus frigidus* (Boh.). In the Khandagay depression this group includes chiefly species associated with deserts and semideserts of C Asia: *Deracantha deracanthoides* (B.-Bien.) and *Zichya baranovi* (B.-Bien.). Under these conditions they are distinctly associated with N slopes, but only in their lowest parts, with thickets of *Caragana* sp., where these grasshoppers often live (Sergeev and Bugrov, 1988).

Typical habitats of most other Orthoptera of this group are humid, with diverse herbaceous vegetation and rarely with grass-*Carex* meadows. Such species may also occur along forest edges and under mixed forest canopy. A few of them, *Zubovskya koeppeni* (Zub.) were found only on N slopes (Fig. 1a). Most species occur in the S, mainly in quite humid habitats. Some of these species of Orthoptera also inhabit floodplains (*P. intermedium*). The density of such species is not high and only some representatives the abundance exceeds 100 spms. per hour, for example, *Chortippus dorsatus* (Zett.). In general the distribution of population groups of such Orthoptera is of local character, caused particularly by the mosaic distribution of habitats. Species with high population density are distributed relatively continuously, especially in river terraces and lower parts of mountain slopes. It is interesting that Orthoptera associated with N slopes are hardly ever found in field agrocoenoses.

2. *Group of species associated with S slopes.* This group is well represented in all lowlands, except the Ubsunur; in this lowland the group is formed almost exclusively of C Asiatic desert-steppe species of Orthoptera, which in general are associated with mountain foothill plains and upper river valley terraces. In the Edigan and Khandagay lowlands, among species associated with S slopes some forms are widely distributed in the forest-steppe and steppe zones of the Palearctic: *Paracyptera microptera* (F. d. W.), *Chorthippus apricarius* (L.), and *Bryodema tuberculatum* (F.). In the Balgazyn lowlands the S slopes are inhabited predominantly by E Palearctic mesophilic Orthoptera (*Gampsocleis sedakovi* F. d. W., *Calliptamus abbreviatus* Ikonn., and *Chorthippus hammarstroemi* (Mr.)), and to a lesser extent by their W Palearctic ecologically similar counterparts, *Stenobothrus fisheri* (Ev.) and *S. eurasius* Zyb.

Most species of this group are associated with steppe and even desert habitats. In different lowlands their relations to N slopes is different. Thus, in C Altai they all extend their ranges to N slopes, but concentrate in their arid parts; this is also seen in the Ubsunur lowland. In the Khandagay lowland similar species were not found on N slopes. Species of this group hardly penetrate into river floodplains and there occur locally. Some orthopterans reach very high population density, *C. hammarstroemi* having a recorded density above 2000 spms. per hr., *C. apricarius* up to 500 spms. per hr., *Celes skalozubovi* Adil. and *Myrmeleotettix pallasi* (Zub.) over 200 spms per hr. Therefore on S slopes such species are distributed almost continuously, from the most arid to the most humid habitats. In addition, they actively migrate to fields and pastures to form considerable aggregations (*C.*

Fig. 1. Major types of areal-populational structures of Orthoptera of the Edigan (a-d) and Ubsunur lowlands (e-h). *1-4*) Groups of species associated with various areas: *1*) N slopes, *2*) S slopes, *3*) foothill plains, *4*) river valleys; a) *Zubovskya koeppeni* (Zub.), b) *Chorthippus hammarstroemi* (Mir.), c) *Stenobothrus eurasicus* Zub., d) *Chorthippus parallelus* (Zett.), e) *Montana montana* (Koll.), f) *Bryodema holdereri* Kr., g) *B. gebleri* (F. d. W.), h) *Chorthippus fallax* Zub.); N) N slopes, S) S slopes, U) upper parts, M) middle parts, L) lower parts, F) foothill plains and alluvial cones, II) upper terraces, I) lower terraces, V) valleys; A-D) levels of abundance: A) highest abundance of species, B) moderate abundance, C) low abundance, D) intensive invasion into the anthropogenic agrocoenosis.

Distribution of species of Orthoptera associated with areal-populational groups

Group	Lowland			
	Edigan	Balgazyn	Ubsunur	Khandagay
Species associated with				
a) N slopes	6	-	6	4
b) S slopes	12	15	4	10
c) foothill plains	7	10	12	14
d) valleys	18	8	22	10
Total	43	33	44	38

Note. In the Balgazyn lowland, N slopes and anthropogenic areas were not investigated.

hammarstroemi was recorded at a density of 300 spms. per hr.) (Fig. 1b). However, this situation is typical only in the Altai, where species associated with S slopes reach the highest density.

3. *Plain species.* These species are most typical of lowlands of Tuva, where large areas of foothill plains are better developed. In the Edigan lowland, among plain species, the mesophilic W Palearctic species, *Montana eversmanni* (Kitt.) and *S. eurasius* are widely represented. In the Balgazyn lowland, where meadow steppes with diverse herbaceous vegetation are often developed, the transpalearctic forest-steppe species *D. verrucivorus* and *E. brachyptera* are common. In the Ubsunur and Khandagay lowlands most plain species are restricted in their distribution to arid regions of C Asia. These are primarily Orthoptera of the tribe Bryodemini.

Plains Orthoptera are most numerous in mountain foothill plains and alluvial cones with zonal vegetation. In river floodplains they are not found. On N slopes they are distributed locally and on S slopes some species, such as *G. sedakovi* and *S. eurasius*, occur more often (Fig. 1c). In the Altai the most abundant species are *S. eurasius* (over 170 spms. per hr) and *Chortippus fallax* (Zub.) (over 120 spms. per hr.). They rarely spread into agrocoenoses, sometimes forming aggregations, in *C. fallax* up to 210 spms per hr. In the Ubsunur lowland the density of species of this group was higher (in *Oedaleus decorus* (Germ.) up to 600 spms. per hr., and in *M. palpalis* over 500 spms. per hr.). In the remaining lowlands of Tuva their density is considerably lower. Most plains Orthoptera of Tuva form diffuse populations and, unlike those of Altai, actively intrude into agrocoenoses. In irrigated fields, abandoned fields, and roadsides geophilic Orthoptera of the tribe Bryodemini (*Bryodema orientale* B.-Bien., *B. gebleri* (F. d. W.) (Fig. 1g), *Angaracris barabensis* (Pall.) and also *C. abbreviatus*) are common.

4. *A group of valley species.* The specific diversity of this group in the studied lowlands fluctuates greatly. However, ecogeographic characteristics of such Orthoptera in general are uniform: These are Palearctic species widely distributed in the forest, forest-steppe, and steppe zones: *Bicolorana bicolor* (Phil.), *Tetrix subulata* (L.), and *Omocestus viridulus* (L.), etc.

Only in the Ubsunur lowland are the E Palearctic Orthoptera associated with most humid areas of river valleys found (*Eirenephilus longipennis* (Shir.) and *C. fallax*). The C Asiatic species *C. davidiana* and W Siberian species associated with arid upper terraces are distinctly associated with river valleys.

Orthoptera of this group are most abundant in meadows, rarely in swampy and salty parts of

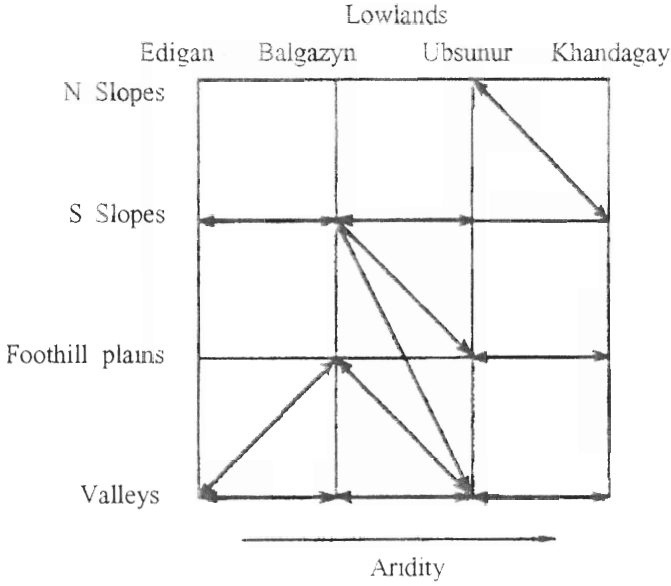

Fig. 2. Major directions of changes of areal associations in the transitions from one lowland to another.

/er floodplain and low terraces (Fig. 1d and 1h). In the Altai about half of them almost do not extend onto mountain slopes and remain in meadow habitats on not only N but also S slopes. Such species as *Omacestus haemorrhoidales* (Charp.) and *C. biguttatus* are associated with river terraces and almost never occur in floodplains. The population density of river valley Orthoptera may be very high (*C. parallelus* and *Stauroderus scalaris* (F. d. W.) reached above 2000 spms. per hr and *Chrotippus intermedius* (B.-Bien) above 1000 spms. per hr.). These 3 species and also *Podisoma pedestris* (L.) actively penetrate into pastures and fields located in lower terraces (Fig. 1d) and in insignificant quantities into other agrocoenoses, mostly those with ruderal vegetation. In Tuva the most valley Orthoptera do not go beyond the limits of the floodplain and floodplain terraces. They are characterized by local centers of high density. This, for example, is typical of *Chorthippus albomarginatus* (Deg.), *C. intermedius*, and *C. dichorous* (above 1000 spms. per hr.). As well as in Altai, some valley species occur in fields. Among them *B. tuberculatum, Tetrix tenuicornis* (Sahlb.), and *C. fallax* are most common.

Comparison of spatial distribution of species found in several investigated lowlands enables one to cite for several the following peculiarities of their topographic associations. A considerable group, about 1/3 of the total number of species, are mesophilic and mesohygrophilic Orthoptera: *M. brachyptera, T. bulata, Chorthippus montanus* (Charp.), *C. albomarginatus*, and *Stethophyma grossum* (L.). At the same time similar habitat association is displayed by some species of the S slopes (*Podismopsis altaica* Zub., *Stenobothrus lineatus* [Panz.]), and species of plains (*G. sedakovi* and *B. gebleri*). Among remaining Orthoptera several groups which changes in their topographic associations in different depressions may be distinguished. It is interesting that the sharpest differences in habitat associations of Orthoptera are observed between the Edigan and Balgazyn lowlands, on one hand, and between the Ubsunur and Khandagay lowlands, on the other hand.

In most Orthoptera the major factor determining distribution of population groups is the degree

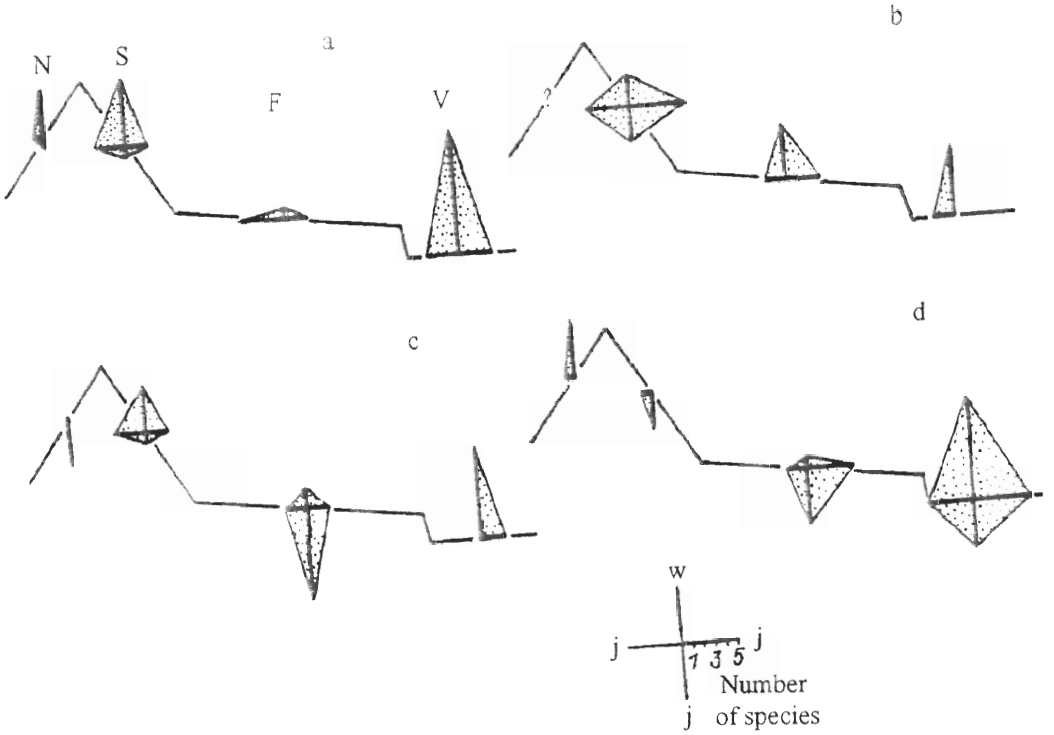

Fig. 3. Composition of topographic-population groups. a-d) Lowlands: a) Edigan, b) Balgazyn, c) Khandagay, d) Ubsunur; N) northern slopes, S) southern slopes, F) foothill plains, V) river valleys, w) widely distributed Palearctic species (multizonal, forest-steppe and N steppe Transpalearctic species); h) W Palearctic species; i) C Palearctic species and endemics of Altai and Sayan mountains, j) E Palearctic species.

of humidity. With increase of aridity, according to successions of habitats (Bey-Bienko, 1930) the shift into more humid and less heated habitats.

At the same time in some species there are different models of topographic associations in whic temperature is a determining factor. Thus, for example, *S. eurasius* in the Edigan lowland is concer trated in foothill plains and alluvial cones, whereas in Tuva, according to our data, it is associate predominantly with well-heated mountain slopes. A similar pattern is observed in *M. frigidus*. These fac are interesting because in many investigations it has been stated that Orthoptera are capable of mair taining constant body temperature within a broad range of environmental temperature which in th presence of direct sunlight secured for them considerable thermoregulatory independence (Chappe 1983; Hunter, 1983; Kemp, 1986). It is possible that *S. eurasius* and *M. frigidus* belong to species which this capability is low.

Finally, there are several species of Orthoptera in which the material studied a distinct rule succession of habitats is not observed. These are species associated mainly with a certain topograph type, but in one lowland are distributed beyond its limits. Thus, *Montana montana* (Koll.), *Arcyptei fusca* (Pall.), *O. haemorrhoidalis*, and *C. intermedius* in general are associated with mesophilic habita of river valleys and mountain slopes, but in the Balgazyn lowland they are distinctly associated wi

foothill valleys, which here are often filled with graminaceous-diverse herbaceous vegetation of steppe-type meadows. The distributional pattern of such species as *C. laxoreviatus, C. hammarstroemi*, and *B. tuberculatum* is associated predominately with S slopes, but in the Ubsunur lowland is associated less clearly with foothill plains and even valleys. Causes of these deviations are probably of different character in each individual case and require further investigation.

All lowlands compared here differ in their local faunas, particularly in the representation of groups of Orthoptera that we distinguished in their zoogeographic characteristics and their distribution in the anthropogenic habitats.

Thus, the Edigan lowland is characterized by predominance of species associated with valleys and S mountain slopes (Table). Here Orthoptera widely distributed in the forest, forest-steppe, and steppe zones of the Palearctic (Fig. 3) are predominant. Mostly W Palearctic steppe species are associated with plains. The pattern observed reflects connections of this small lowland with Altai plain regions along the Katun River valley and in the case with the boreal species such a connection was maintained along mountain ridges.

The Balgazyn lowland connected with the Yenisey River basin in this respect resembles the Edigan valley. Here too the role of multizonal and forest-steppe Transpalearctic species is considerable, but in communities on S mountain slopes with their shrub-steppe mesoxerophilic E Palearctic Orthoptera are especially distinct.

The characteristics of local faunas of the Ubsunur and Khandagay lowlands, which have no drainage, are determined by S steppe, semidesert, and partly by desert C Asiatic species (Fig. 3). Only in high and medium mountains and also in valleys Orthoptera are widely distributed in the Palearctic distinct. Here forms with different types of ranges such as E and W Palearctic species are also associated with valleys.

Therefore, analysis of topographic distribution of population groups of Orthoptera confirms the fact that the lowlands belong to different zoogeographic regions. Thus, the Edigan and Balgazyn lowlands belong to the steppe-type of subprovince of Palearctic, while the Ubsunur and Khandagay lowlands belong to the Ancient Mediterranean subprovince (Sergeev, 1986). The first two lowlands also belong to different regions within the subprovince.

High mountains and river valleys as well are inhabited by relatively uniform ecogeographical complexes of Transpalearctic Orthoptera associated mainly with various meadow habitats. These landscapes are used by similar Orthoptera, but such areas are used by species of Orthoptera as channels for dispersion into arid regions (Stebaev et al., 1988). At the same time topographic habitats in mountains are closest to zonal habitats (foothill plains and to a certain extent S slopes), and are inhabited by C ptera determining the specific characteristics of each fauna.

Analysis of our material indicates that the possibility of the penetration of various groups of Orthoptera into agrocoenoses is determined by two major factors: first, by peculiarities of topographic distribution of agrocoenoses and, second, by the availability of species it is possible to include not only Orthoptera living in habitats naturally similar to agrocoenoses, but also other species reaching high density in adjacent natural habitats.

Thus in the Edigan lowland the major areas of fields and pastures are located not only in foothill pl and upper terraces, but also in lower terraces. Therefore, they are inhabited mostly by valley species and to a lesser extent by plain species associated with S slopes. At the same time, in Tuva

agrocoenoses located almost exclusively in foothill plains (including overgrazed pastures near human communities) are inhabited mainly by Orthoptera of the second group, here reaching high density. Such species actively penetrate not only pastures, abandoned lands, and sparse irrigated crops, but also irrigated fields with dense vegetation. Besides plains-living Orthoptera, valley-preferring Orthoptera also penetrate, but less often

Therefore, by the character of the distribution of Orthoptera in natural regions of mountain depressions in S Siberia 4 large groups of species may be distinguished: species associated with N mountain slopes, with S mountains slopes, with plains, and with river valleys. Species associated with steppe habitats on S slopes and plains are characterized by rather integrated population systems (diffused populations) of considerably density. Valley species also may reach high density, but they are distributed in stripes or narrowly insular type of population ranges (Yablokov, 1987). Finally, population systems of species associated with N slopes are close to the insular type of range structure. Population density of these species is not high.

The importance of each here distinguished group of species in investigated mountain depressions is determined by the climate of each given region and its topographic structure, particularly by the ratio of areas of specific topographic habitats. Most observed changes among depressions in topographic associations of species of Orthoptera are also determined by the climatic gradient. As a rule, they shift from more arid and hot habitats in C Altai to more humid and cool habitats in S Tuva, the decisive factor is mainly the degree of aridity and only in some cases warmth of the climate. However, about 1/3 of the total number of species, mostly valley species, retain their preference for the same habitat.

The population density and species diversity of Orthoptera in different seminatural ecosystems and anthropogenic ecological complexes are determined chiefly by topographic population structure of species living in adjacent natural habitats. Agrocoenoses are usually populated by Orthoptera with the highest population density in adjacent habitats of the same topographic position. Therefore, the pattern of populations of agrocoenoses in mountain depressions of the S Siberia is considerably different from those in many other regions of Asiatic Russia and adjacent countries (Vasil'ev, 1965; Naumovich et al., 1982; Popova and Sergeev, 1983; Sergeev, 1984, 1985, 1987a, b; Kopaneva and Nasyrova, 1988) because in most of them agrocoenoses are inhabited predominantly by species living in similar areas and, as a result, sources of formation of populations of agrocoenoses may be considerably remote. Therefore, in mountain-steppe mountain depressions of S Siberia, population of fields, pastures, and hay fields by Orthoptera precedes more intensively and investigation of the pattern of their topographic distribution and particularly centers of high density becomes critically important.

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