

# 7 Ecogeographical Distribution of Orthoptera

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## Introduction

The biology of species is varied in time and space, so their mutual relationships can be understood only through studies of all stages of their populations throughout their total range, usually comprising a set of habitats (Uvarov, 1977; Sergeev, 1991).

I discuss herein problems associated with spatial and landscape distribution of Orthoptera. Spatial problems involve distribution of any individual object (specimens, populations, species, genera, etc.) over different geographic regions of the earth. This distribution is the type generally shown on maps. In the broad sense, it overlaps so-called 'landscape distribution'. The latter is distribution of individuals through a system of connected landscapes (e.g. an individual catena *sensu lato*) or other landscape parts (Samways and Sergeev, Chapter 8, this volume).

## Species Range Distribution

The traditional approach to species distribution is in terms of history, but an historical pattern is unavailable for most species, especially those

distributed widely. The Tertiary and Quaternary history of terrestrial insects, including Orthoptera, is the 'enfant terrible' of historical biogeography. What can we say about the history of widely distributed species? We must seek an answer to their distribution within their geographic ranges.

Generally speaking, different biogeographic phenomena result from historical and spatial interactions between biota and their physical environment. Each regional population may be characterized as both geographic and biological (Matveyev, 1969). The former describes patterns common to animals, plants, and their communities (Emeljanov, 1974). The latter emphasizes ecological and historical differences between biotas that may reflect regionalization schemes (Chernov, 1975).

A regional pattern may be described as the regular distribution of species and other taxa (i.e. the tops of phylogenetic and faunogenetic stocks and branches) (Uvarov, 1937; Cracraft, 1982)<sup>1</sup>. These patterns may be characterized as the solution of dialectical contradiction between vicariance (in which boundaries are isolating lines) and dispersal (in which boundaries may be imagined as partly permeable membranes). Observed boundaries often reflect modern differentiation of the geographic envelope of the earth

(Sushkin, 1925; Smith, 1983; Sergeev, 1986, 1991, 1992). I distinguish between boundaries, which are lines marking divisions of ranges, districts, etc., and barriers, which are agents that control dispersal.

Consistent use of a regional approach should help in understanding age-long oppositions between historical and ecological interpretations of biogeographic and ecogeographic phenomena (Endler, 1982; Smith, 1989) and affirm the validity of both Eldredge's idea of 'process-produced pattern' (Ferris, 1980) and that of the backing influence of pattern (Berg, 1926).

### Ecology or History?

In my earlier work, I analysed orthopteran species' ranges, compared the distribution of their boundaries in relation to ecogeographic barriers, and classified different boundaries, barriers, and regions (Sergeev, 1986, 1988a, 1991, 1992, 1993b).

The Palaearctic Region includes the following (Sergeev, 1992, 1993b; Uvarov, 1921; Emeljanov, 1974): (i) the Eurosiberian Subregion, including two provinces; (ii) the Manchurian Subregion, at least four provinces; (iii) the Orthrian Subregion, at least four provinces; (iv) the Scythian Subregion, at least four provinces; (v) the West-Mediterranean Subregion, at least three provinces; (vi) the East-Mediterranean Subregion, at least four provinces; and (vii) the Saharan-Gobian Subregion, at least 22 provinces.

The Nearctic Region probably includes Canadian, Appalachian, Great Plains, Rocky Mountain, Californian, and Sonoran Subregions. The borders between plains and montane provinces are usually readily visible where montane slopes and piedmont plains come together (Sergeev, 1988b). These schemes are related to the modern geographic organization of the earth's surface, mainly the distribution of life zones, continental regions, landscapes, etc.

Only in continental islands and other special cases do past geologic events explain current orthopteran distributions (Rentz and Weissman, 1981, re: the California Channel Islands; Sergeev and Lee, 1982, re: the southern Kurile Islands). Such historical range boundaries also

may be observed in montane regions where high altitudinal belts are divided into separate plots and, as a result, exhibit endemic taxa (Otte, 1979; Sergeev, 1988a,b, 1991, 1992; Stolyarov, 1990).

## The Ecological, Geomorphological, and Tectonic Factors Behind Range Boundaries

Analysis of these factors begins with investigation of the distribution of species and other taxa. Then their relationships with biospheric differentiation can be established. Finally, extrapolation may provide a basis for spatial predictions. The distributional boundaries of taxa, faunas, and communities tend to coincide with geographic barriers or climatic indices (Kusnetzoff, 1936; Emeljanov, 1974; Sergeev, 1986, 1991, 1992). This regular differentiation of the biosphere enables biogeographers to extrapolate on the basis of their data. For example, the range boundaries of *Oedaleus* spp. coincide with the borders of life zones or vegetational types (Ritchie, 1981; Sergeev, 1986) (Fig. 7.1).

Amédégnato and Descamps (1982) discussed the possible role of rivers as barriers to Amazonian grasshopper dispersal.

*Melanophis*, *Aptenopedes*, and some other flightless scrub grasshoppers have numerous morphologically distinct, allopatric or parapatric populations, often with reduced ranges separated by comparatively trivial barriers (Hubbell, 1985). Insular distribution is typical of flightless montane forms such as *Grylloblatta* spp. (Notoptera), whose individual populations occupy areas ranging from 300 m to 1 km in diameter (Kamp, 1979). Geomorphological barriers such as the different faces of slopes, glacial outwash streams, moraines, etc., all about 10–50 m in breadth, may also pose effective barriers to dispersal.

The boundaries between plains and mountains are typically barriers preventing the spread of species. I have described many such patterns (Sergeev, 1988b), supported by evidence from others (Peshev and Andreeva, 1986; Gorochov *et al.*, 1989). In some cases,

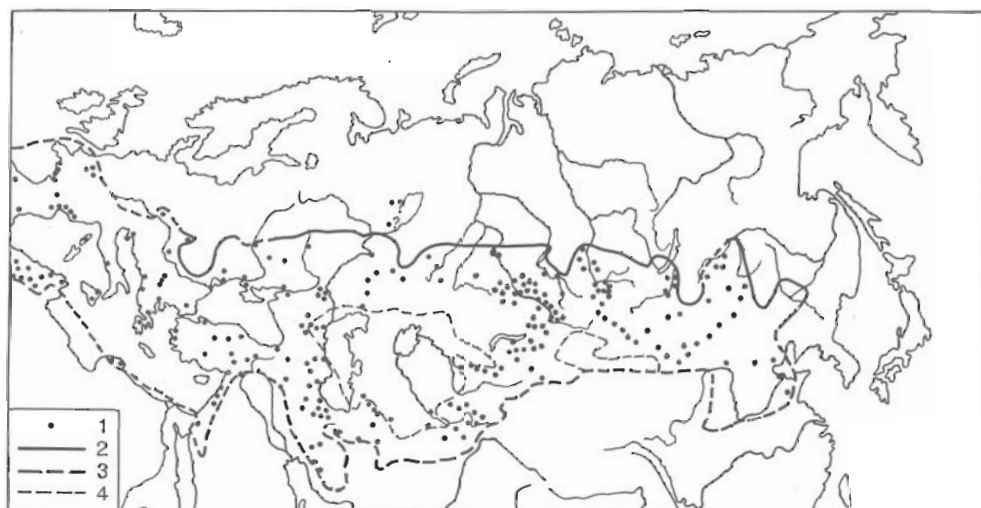


Fig. 7.1. Distribution of *Oedaleus decorus* (Germar). (After Sergeev, 1986.)

1 = locations; 2 = range boundary coincident with the northern forest-steppe limit; 3 = other parts of range boundary; 4 = limits of extreme desert within the species range.

significant coincidence has been described for such borders and for interpopulation boundaries (Schennum and Willey, 1979; Sergeev, 1991; Kazakova and Sergeev, 1992a,b).

Nagy (1987) noted that human settlements, including Budapest, may be a major barrier to the spread of species. There are other boundaries which cannot be attributed to contemporary conditions. They are historical.

Some barriers cannot prevent the spread of species. The oceans and seas are examples usually given of geographic barriers, but even they can be crossed by Orthoptera. The existence of ecological niches is significant with regard to the spread of species into new regions. Such dispersion is mainly associated with human activity. Examples have been provided by Kevan (1990), for Micronesia, and by Vickery (1965) and Nickle and Castner (1984), for North America. In Europe, the northward dispersal of some thermophilic Orthoptera is chiefly by human activity including general landscape change, burning, overgrazing, urbanization, and transportation (Nagy, 1987; Köhler, 1988). Populations of rare species may be eliminated or divided in this way (Samways and Sergeev, Chapter 8, this volume).

## Species Ranges and Centres of Biological Diversity

Analysis of the distribution of centres of diversity and of generic endemism of tribes allows for an understanding of speciation patterns. Historically, such centres reflect locations suitable both for species differentiation and for their coexistence. In northern and central Asia, for example, most centres of tribal diversity and generic endemism are associated with seven locations (Sergeev, 1992, 1993b): (i) the deserts of Turan; (ii) arid parts of Mongolia and China; (iii) nemoral regions near the boundary of northern and eastern Asia; (iv) the mountains of Tien Shan, Pamiro-Alfay, and Hindu-Kush in Afghanistan; (v) the mountains of western Iran; (vi) the mountains of western Himalaya and south-western Tibet; and (vii) the mountains of south-eastern Tibet and the adjoining Himalayan slopes. Centres of generic diversity and species endemism are distributed similarly.

Amédégnato and Descamps (1982) described the centres of biological diversity of Amazonian grasshoppers, which are mainly associated with peculiar climatic patterns and

forests and reflect, in some cases, relatively ancient isolation.

## Metapopulation Distribution

Many problems of biogeography and ecology may be solved by studying population distributions throughout the ranges of species. As a rule, local populations (demes) are distributed over a range in accordance with natural conditions, especially the earth's landscape pattern. These populations may be connected with each other into a single landscape unit or may be divided by different barriers. Such distributions are described as metapopulations (Levins, 1970) or as spatial population structures (Shilov, 1977). Hence, a metapopulation is a system of local species populations throughout their limits of range.

Completely isolated populations are exceptional (Uvarov, 1977). As a rule, they are observed only in the case of non-flying montane or insular forms or under other specific natural conditions. Some examples of insular local populations have been described amongst British Orthoptera (e.g. *Decticus verrucivorus* [L.], *Stethophyma grossum* [L.]) (Brown, 1983). Continuous populations of uniform structure are also rare (den Boer, 1981). Willey (1987) described the North American *Arphia pseudonietana* (Thomas) as irregularly distributed in patches, even within optimal habitat. We described significant differences between valley and watershed settlements of *Chorthippus parallelus* (Zetterstedt) over its range (Kazakova and Sergeev, 1992a).

Distributional analysis of species populations over regions, geographic landscapes, and their units allows for identification of groups with similar ecogeographic relations, including environmental heterogeneity. The investigation of metapopulation distributional patterns also allows for understanding the internal organization of faunas. Certain vicariant genera include species which occupy the same type of habitat but replace each other geographically, but other genera include sympatric species that specialize by occupancy of different habitat types (Phipps, 1968).

It is important to re-estimate the different

ecogeographic barriers limiting the spread of species. For example, Schennum and Willey (1979) emphasized that montane populations show a higher degree of differentiation and discordance than do non-montane ones. Lake Michigan is estimated to be a natural barrier to gene flow (Willey, 1987). Other barriers include those revealed by range boundary analysis and those by correlations between species diversity and environmental variety. The relationship amongst the different parts of species metapopulations may be observed at a regional level. It is also possible to show paths of dispersal and potential contact between parts of spatial population structures.

## Inner Structure of Species Range

The traditional method of two-dimensional geographic analysis of spatial distribution and relationships of local populations within a species range (Tupikova, 1969; Hengeveld and Haeck, 1982) is inadequate with respect to many animal groups, including Orthoptera. Application of the vertical axis is necessary (Zenkewitch and Brotzky, 1939; Gorodkov, 1985). Such a three-dimensional approach is associated with the idea of geographic change of biotopes (Bei-Bienko, 1930; Stebaev and Sergeev, 1982), and it allows for showing vertical distributions of populations on maps. This aspect of orthopteran ecology was discussed by Stebaev (1974), Schennum and Willey (1979), and Sergeev (1986; 1991). The general patterns of metapopulation distribution were described in other papers (e.g. Kazakova and Sergeev, 1992a). Litvinova (1979) tried the three-dimensional approach with respect to the widely distributed *Glyptobothrus biguttulus* L. She emphasized this species' regional and landscape specificities of population dynamics and fecundity. Some earlier two-dimensional maps (especially for the breeding areas of *Schistocerca gregaria* Forskål [Davies, 1952; Fortescue-Foulkes, 1953]) are salient in that they permit division of the species range into plots having different population dynamics.

We can describe three or four species population groups on plains, each linked with a definite

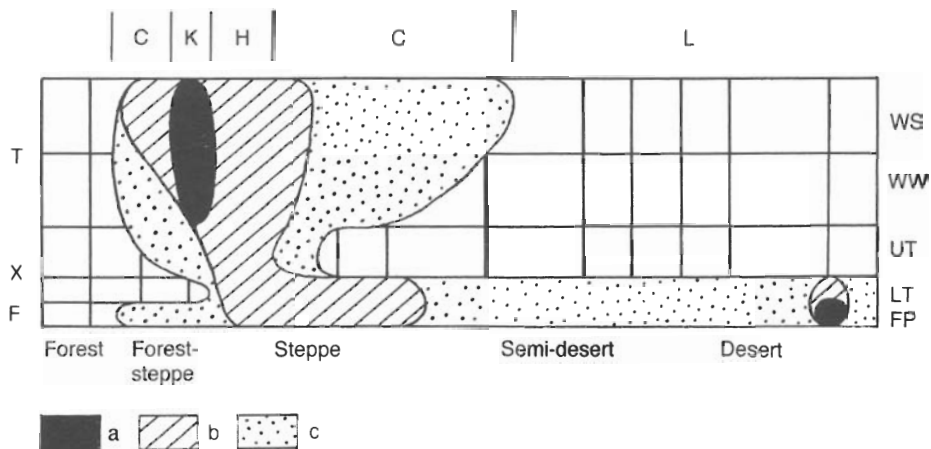


Fig. 7.2. Settlement distribution of *Chorthippus parallelus* (Zetterstedt) (after Kazakova and Sergeev, 1992a).

FP = flood-plains; LT = low terraces; UT = upper terrace; WW and WS = different watershed types.

a-c = levels of abundance (a = + 100 per h; b = 20-100; c = 1-19).

F, X, and T = landscape population groups (see text).

H, K, C, and L = parts of range (see text).

landscape unit: (i) watershed (plakor) populations, which are invariably diffuse settlements (Fig. 7.2, T); (ii) valley population groups associated with flood-plains and low, moist terraces (X), which, as a rule, are insular or linear; (iii) slope (terrace) population groups distributed over the upper and middle terraces of rivers and lakes (F); and (iv) insular high-montane population groups also may be described within the high altitudes of mountainous regions.

These population groups form a limited number of combinations in every region or locality, as with the following described for plains (Stebaev and Sergeev, 1982; Sergeev, 1986; Kazakova and Sergeev, 1992a): (i) the main or optimal part in which species are distributed over all available biotopes at high levels of abundance (Fig. 7.2, H); (ii) the transitional part (K) associated with the beginning of settlement bifurcation into watershed and valley population subsystems; (iii) the basic part (C) in which species populations are found over watersheds and flood-plains and/or low terraces or only over watersheds, sometimes reaching high levels of local abundance; (iv) the marginal part (L) characterized by insular or linear settlements connected to flood-plains and low terraces; and (v) a high montane-valley system may be added in montane areas.

All of the above may not be represented.

Analysis at the regional and basin levels usually shows that the range is a mosaic of transitional, marginal, and sometimes main types of settlement parcels interspersed throughout the dominant background.

Analysis of metapopulation distribution within northern and central Asia (Sergeev and Sergeeva, 1985; Sergeev, 1986, 1991) shows that the juncture between the steppe and semi-desert zones is significant in demarcating parts of the metapopulation and range as a whole. Frontiers between the semi-desert and northern deserts and between the latter and the southern deserts are important. Steppes present optimal conditions for the Orthoptera of northern and central Asia. Taiga (coniferous forest) and tundra are characterized by association between orthopteran settlements and dry or, rarely, bog meadows. Population displacement into river valleys may be observed in arid regions. Likewise, huge demes of steppe and forest-steppe species are found in desert and semi-desert zones.

The described pattern allows for estimation of general situations with respect to every life zone and major region, but the optimal conditions and the corresponding specificity of population distribution may change not only from north to south but also from west to east and vice versa.

## Regional and Local Parts of Species Metapopulations

Regional metapopulations are limited by faunistic or geographic boundaries. Hence, it is important to evaluate differences between regional and general distributional patterns and to analyse the coexistence of species of different origins and life forms.

Local metapopulations are found within the basin limits of small rivers, the landscapes of which are uniform or closely connected by energy and matter transfer. It is possible to show paths of wandering and potential contact between these parts. Knowledge of orthopteran distribution within such small regions allows for an understanding of the pattern of populations, community organization, and dynamics.

Grasshoppers often inhabit particular microhabitats. Such a situation was described by Joern (1982b) for the arid grasslands of Texas.

In the **Manchurian Subregion**, orthopteran distributions are characterized by variably uniform relationships to the landscape units in which they are distributed locally, as islands, within the subregion's limits (Stebaev *et al.*, 1989). Species abundance is low in each habitat. This condition, characteristic of endemics, also may apply to more widely distributed species. The high degree of localization of most of these species is determined by the subregion's landscape peculiarities. In general, differences in species metapopulation organization may be slurred on the background of exceptional species diversity (Stebaev *et al.*, 1989). There is also a wide variety of biotopes into which Orthoptera may spread, e.g. into dry mountain slopes and terraces, and localized Orthoptera may use anthropogenic biotopes such as roads for settlement. As a result, new relationships may arise amongst insular settlements.

In the **Scythian Subregion**, a diversity of favourable conditions allows many Orthoptera to coexist at high levels of abundance. The region is characterized by its widespread species through cultural influences (Sergeev, 1987a). The native populations of Orthoptera are distributed over all the herbaceous biotopes and are connected with the plains of west Siberia and Kazakhstan. The presence of many steppe species in the subregion inhibits speciation and

limits penetration into it of alien species. In the plains section of the Scythian, the local types of grassland are settled chiefly by steppe species. Forms associated with other life zones tend to be found only in insular biotopes. There are many paths of potential spread of species, including anthropogenic ones (Sergeev, 1986, 1987a, 1991).

In the **Saharan-Gobian Subregion**, the populations of native species are separated by barriers, and their abundance is reduced (Kazakova and Sergeev, 1992b). Here, the mountain-plains barrier is important (Sergeev, 1991). Many Orthoptera are associated with river valleys. Even some species usually described as desert or semi-desert forms, e.g. *Doclostaurus tartarus* (Stshelkanovtzev), have a propensity for river terraces (Sergeev, 1986, 1991). Widely distributed species penetrate into the subregion's anthropogenic landscapes, spreading along the disturbed biotopes bordering irrigation canals and roads.

## Problems of Species Coexistence

Generally speaking, the coexistence of species within regions is by differentiation of so-called 'place niches' (Clarke, 1954) supposedly resulting from specific biotope elimination (Elton, 1930) and different species relationships upon succession (Buckley, 1983). Competition at different levels is not the answer; I regard it as insignificant in most cases (see also Evans, 1992). Mulkern (1982), who analysed the multidimensional overlapping in resource utilization by prairie grasshoppers of the United States, found little overlap amongst species.

Comparison of the local metapopulation distributions of Orthoptera in small river basins within the main biogeographic regions suggests the following trends (Sergeev, 1991; Kazakova and Sergeev, 1992b): the valley species component (especially of flood-plains and low terraces) increases from the deciduous (nemoral) forests to deserts; and the plains species component prevails within steppes, although there are similar forms in the mountain basins of Tuva. The latter are associated with Gobian elements that inhabit the local, wide, stone piedmont plains and montane slopes.

The described local metapopulation structure of Orthoptera includes three main components: (i) species that inhabit strongly localized settlements of reduced density, as in the Manchurian and Saharan-Gobian Subregions; (ii) species distributed at high levels of abundance over all available biotopes and spreading through cultural landscapes; these are typical of the forest-steppe zone and of some parts of the mountains of southern Siberia, and, as a rule, their maximal density does not coincide in space and time with one another; and (iii) intermediate, high-density local metapopulations distributed over a number of biotopes and usually associated with each other in the steppes. The latter may be found in local watersheds both in the mountains of southern Siberia and in the northern part of the central Asian mountains, usually localized along the southern slopes.

The above are associated with the original geographic differentiation of each region. They inhabit each region and its landscape units (including anthropogenic ones). The important ecogeographic barriers are essential not only for limiting the spread of species but also for metapopulation differentiation.

## Community Distribution

A community (including a landscape community) is the aggregate of individuals of all species inhabiting an ecosystem (geosystem) of different rank. The terms 'assemblage', 'assembly', and 'multispecies population' are synonymous. A guild is the aggregate of taxonomically related species which share the same resource (Root, 1967) or, more precisely, a functional group of coexisting species which use resources in a similar fashion (Joern and Lawlor, 1981).

Uvarov (1977) criticized the community concept noting that it is not useful in ecological practice. He discussed the possibilities of interaction amongst species within a habitat and suggested use of the term 'ecofauna' (Uvarov, 1938) for the general, common types of community. However, I support Hey-Bienko's different point of view (1949, 1950) holding

that investigations of orthopteran communities are useful not only for synecological purposes but also for autoecological, demecological, and biogeographic ones.

Community analysis is the traditional approach of Russian orthopterology. Now, in light of Uvarov's monograph (1977), some western orthopterists have undertaken this type of research.

A comparison of the investigated communities in different regions makes it possible to determine the main factors in an ecosystem's formation and to estimate the role of its Orthoptera. One can also appreciate probable change in connection with human activity.

The dominance structure of local communities may be determined by microbiotope conditions, especially the different requirements of each species (Pfadt, 1988; Sergeev, 1991).

Communities are composed of the settlements of all species inhabiting all landscapes/ecosystems of all parts.<sup>2</sup> The abundance, biomass, and other features of communities define the role of Orthoptera in every ecosystem from a simple biogeocenosis to the entire biosphere.

All main landscape types may be divided into a number of communities bound together with smaller landscape parcels including biocoenoses (Stebaev, 1976; Joern, 1982a). Communities may be classified by their soil and/or vegetational attributes (Bei-Bienko, 1930; Cantrall, 1943). Clear regional specificity of communities is observed both in natural landscapes and in anthropogenic ones. These reflect the local faunistic peculiarities and pattern of metapopulation distribution.

Some problems of species coexistence within communities were discussed by Joern (1979, 1986). He emphasized that distributional limits may be determined by factors other than those permitting inclusion of a species in a particular community and that habitat structures of ranges may be important for understanding grasshopper community organization. Resource use with respect to diet or microhabitat is apparently not random, so the structure of the community matrix for resource utilization stems from the use of specific resources by grasshoppers (Joern and Lawlor, 1980) or guilds (Joern and Lawlor, 1981).

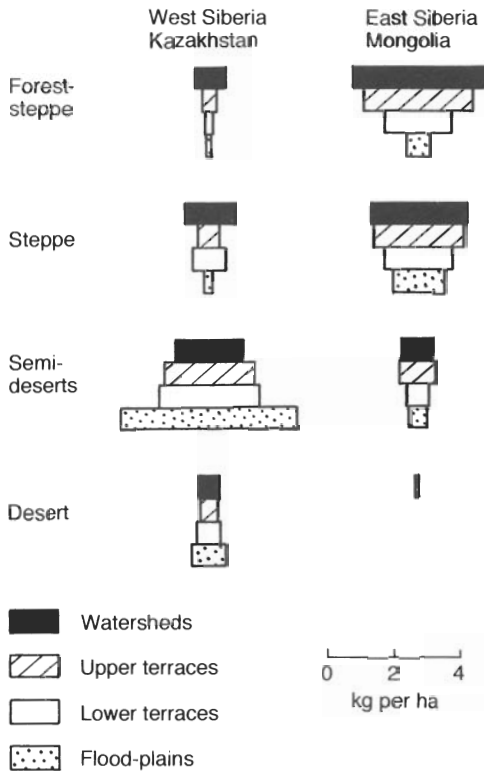


Fig. 7.3. Orthopteran biomass distribution in northern and central Asia (after Sergeev, 1991).

## Zonal Distribution

Patterns of orthopteran biomass distribution within the Palaearctic Region suggest that the insects' main regions of dominance are in east Kazakhstan, south Tuva, and some local mountains (Fig. 7.3) (Sergeev 1989, 1990, 1991). The biomass level is reduced, being less than 1 kg per ha, dried mass, in the western parts of semi-deserts (Sergeev, 1990), in the southern deserts of the Turanian Plain (Sergeev, 1989), and especially in the Gobi (Kaplin, 1989). Maximal orthopteran biomass and abundance is associated with flood-plains, low terraces (up to 6 kg per ha), and the middle parts of montane slopes. The highest levels are observed in the piedmont plains of central Asia (up to 19 kg per ha). Orthopteran biomass is reduced (0.3–0.54 kg per ha) in forest life zones (Suslik, 1984). In European Russia and north-west Kazakhstan, total grasshopper abundance increases from the

memoral (deciduous) forest zone (1900–3700 per ha) to the steppe zone (4800–8600 per ha) (Guseva *et al.*, 1979).

Orthoptera are not typical of **tundra** (Chernov, 1978; Sergeev, 1992), although a few species are described from the southern tundras and forest-tundras. *Melanoplus frigidus* (Bohemian) is common in Eurasia.

Orthopteran settlements in **boreal and sub-boreal forest zones** are chiefly associated with openings, edges, and river valleys. The near-polar steppes of Yakutia are mainly inhabited by typical, widely distributed steppe grasshoppers (Berman and Mordkovich, 1979). The same is true of the dry parts of central Yakutia, in which the common species include *Chorthippus albomarginatus* (De Geer), *Aeropus sibiricus* (L.), and *Omocestus haemorrhoidalis* (Charpentier).

Some communities of the European nemoral zone were described by Ingrisch (1982), Kritzka (1982), and Köhler (1989). Kritzka noted that *Glyptothrus biguttulus* (L.), *Chorthippus dorsatus* (Zetterstedt), *C. albomarginatus* (De Geer), and *O. haemorrhoidalis* (Charpentier) are common near Moscow, and essentially the same pattern was found in Germany (Ingrisch, 1984), Poland (Moczulska, 1979; Liana, 1981, 1982), and Slovakia (Suslik, 1981). Typical boreal forms such as *Chrysochraon dispar* (Germar) and *Roeseliana roeselii* (Hagenbach) settle bog landscapes (Schmidt and Schlimm, 1984). European urban landscapes are settled by other Orthoptera including the widely distributed Palaearctic grasshoppers *G. biguttulus*, *Chorthippus parallelus* (Zetterstedt), and *C. albomarginatus* (De Geer), the European katydid *Leptophyes punctatissima* (Bosc), and the cricket *Nemobius silvestris* (Bosc) (Ingrisch, 1980; Klausnitzer and Klausnitzer, 1982). A similar situation is evident in Far Eastern Eurasia (Sergeev, 1990, 1991; Storozhenko, 1987). The Orthoptera of Kunashir Island (southern Kurils) were analysed by Sergeev and Lee (1982) and Storozhenko (1985). In Kunashir, there are specific species assemblages associated with the local volcanic calderas including the southern thermophilic orthopterans *Diestrammena japonica* Blatchley and *Loxoblemmus arietulus* Saussure. The western and eastern parts of the island vary in temperature according to the prevailing oceanic current.

There are many publications concerning



**forest-steppe** and **steppe zones**. Nagy (1983) analysed the orthopteran communities of Hortobágy National Park, Hungary, within the steppe region of central Europe, where certain widely distributed grasshoppers are common. Included are the transpalaeartic *Chorthippus albomarginatus* (De Geer) and *Omocestus haemorrhoidalis* (Charpentier) and the subtranspalaeartic *O. petraeus* (Brisout), *Oedaleus decorus* (Germar), and *C. parallelus* (Zetterstedt). These grasshoppers spread into fields. However, *Calliptamus italicus* (L.) and *Glyptothorax biguttulus* (L.) actively settle anthropogenic landscapes. A similar situation was described for the Batorliget Nature Reserves (Nagy, 1991), which are western islands of the steppe zone usually settled by Mediterranean and Ponto-Mediterranean Orthoptera such as *Acrotylus longipes* (Charpentier) and *Platycleis affinis* Fieber (Nagy, 1983, 1987, 1991; Racz, 1986). Bei-Bienko (1970) noted a similar distribution with respect to the rangeland forest steppes of European Russia.

Nasyrova (1987) found that slightly grazed plots are settled by diverse communities in the steppes of Kazakhstan and western Siberia.

Some **prairie communities** have been studied. Differences in the taxonomic composition of disturbed and undisturbed plots were described for the sand-hills prairie (Joern, 1982a) despite the long-term stability of prairie community structures (Joern and Pruess, 1986). The typical pattern in the shortgrass prairie of Arizona (Pfadt, 1982) involves decreasing species diversity due to increasing vegetative disturbance. Pfadt hypothesized that a disclimax vegetation of annuals cannot support optimal density, diversity, and richness of grasshoppers. His data relate mostly to common grasshoppers. Mulkern (1980) described the long-term dynamics and composition of the grasshopper community of a tallgrass prairie 'savanna' in which *Aeropedellus clavatus* (Thomas), *Ageneotettix deorum* (Scudder), *Chorthippus curtippennis* (Harris), *Melanoplus dawsoni* (Scudder), *M. sanguinipes* (F.), and *Eritettix simplex* (Scudder) are common. Joern (1979) described the grasshopper communities of the arid prairie and desert grasslands of Texas, which prove to be phenologically varied.

The distribution and composition of the orthopteran communities of the semidesert and

desert zones of middle Asia were described by Pravdin (1978), Pravdin and Fedotova (1983), and Sergeev (1991), who emphasized that these disturbed ecosystems are associated with the local natural communities, both desert and flood-plain.

In Kazakhstan, we observed orthopteran communities with a high level of diversity and abundance, both in natural and in anthropogenic landscapes (Fig. 7.4). Here, the natural landscapes are settled by southern-steppe, semidesert, and desert species such as *Dociostaurus tartarus* (Stshelkanovtzev), *Calliptamus italicus* (L.), *Euchorthippus pulvinatus* (Fischer-Waldheim), *Stenobothrus* spp., and *Mesasippus* spp. Almost all the local species are widely distributed throughout the grassland and desert ecosystems and also spread through anthropogenic landscapes. Their abundance sometimes reaches high levels. I observed mesohygrophilic forms such as *Roeseliana fedtschenkoi* (Saussure) in irrigated fields and along canals.

In Mongolia, local endemics and subendemics (mainly terrioles of the tribe Bryodemini) are characteristic of community composition, both in natural and in anthropogenic landscapes such as annual crop fields, fallow fields, roadsides, and alongside canals. These populations seldom reach high levels of abundance, and their species diversity is usually low.

In Turania, the general diversity of Orthoptera is high overall (Strubinskij, 1979) but may be reduced locally. Different types of desert seem occupied by different species and life forms. For example, *Sphingonotus rubescens* (F. Walker) and *S. maculatus* Uvarov are typical of the stone deserts of southern Tajikistan and *Strumiger desertorum* Zubovsky of local sandy deserts (Sergeev, 1987b). Local anthropogenic landscapes are usually colonized by specific groups of grasshoppers and crickets (Fig. 7.4), all of which are widely distributed Palaeartic species associated with flood-plains, low terraces along roadsides or canalsides, fallow fields, and other early successional stages.

In the arid deserts of central Asia, the orthopteran communities include relatively few species (Kaplin, 1989). Some are common, widely distributed grasshoppers such as the terriolous *Sphingonotus obscuratus* (F. Walker) and the arboricolous *Dericorys annulata* (Fieber). Others are endemic central Asian forms such as the

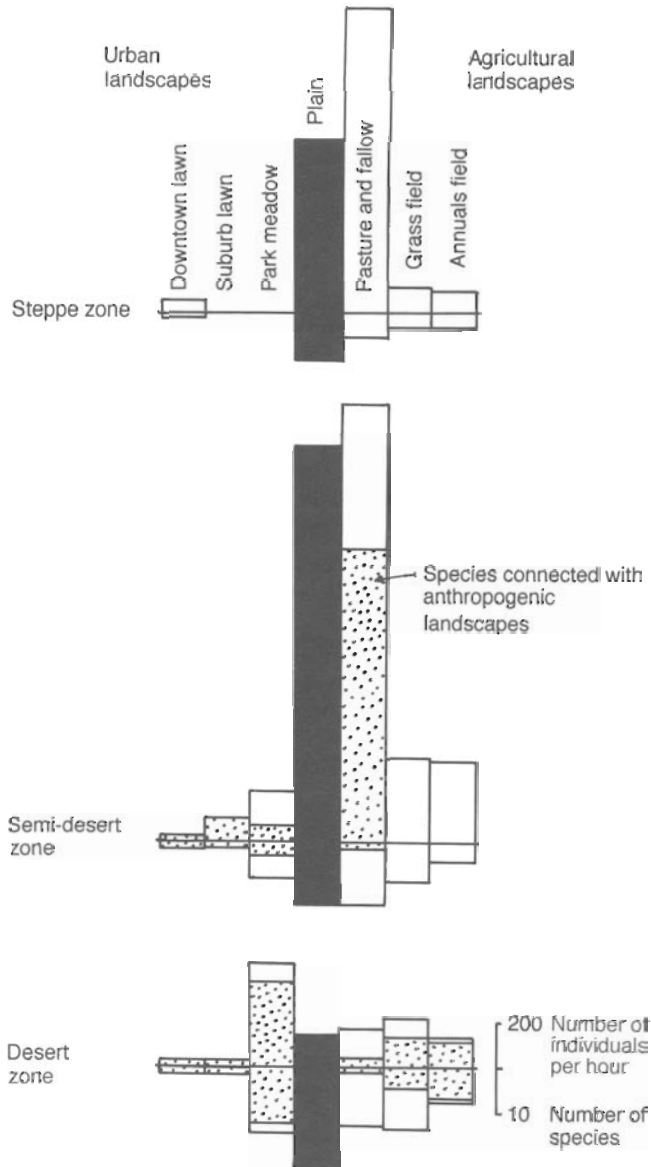


Fig. 7.4. Distribution of species and their abundance over the urban and agricultural landscapes of northern and central Asia.

terricolous *Bryodema* spp. and *Myrmeleotettix palpalis* (Zubovsky).

Community diversity is higher in the central Asian mountains than in the plains of that region. This situation is mainly associated with altitudinal and expositional differentiation (Sergeev, 1991). Montane anthropogenic landscapes are settled by widely distributed species

and resemble, in their composition, both desert and steppe communities.

In general, the Orthoptera of semi-deserts and deserts are varied, the common species of the subregion being determined by local watershed and slope conditions. The incidence of species with reduced ranges and isolated populations increases from north to south and

reflects a decline in general abundance and an increase in community diversity. The valley assemblages of species are relatively uniform (Tchernjachovskij, 1985). The communities of local anthropogenic landscapes are distinguished by species mainly associated with non-plains ecosystems. Irrigated fields are settled mostly by flood-plain Orthoptera. Endemics and subendemics do not penetrate into the agro- and urbocenoses. Thus, the orthopteran communities of anthropogenic landscapes are more closely related to one another than to those of natural landscapes. Increased abundance is not characteristic of moderately disturbed biotopes (Fig. 7.4).

In Mediterranean regions, specific dune communities are distributed along the coastline. In Spain, for example, *Heteracris littoralis* (Rambur), *Calliptamus barbarus* (Costa), and *Aiolopus strepens* (Latreille) are common (Espinosa *et al.*, 1985).

In North America, Rivera (1986) studied the species composition of matorral grasshopper communities. He identified six groups of catenal species. The grasshoppers *Psoloessa texana* Scudder and *Schistocerca nitens* (Thunberg) frequent the upper part of the local catena and *Opeia obscura* (Thomas), *Brachystola magna* (Girard), *Acrolophitus maculipennis* (Scudder), and a few other species the lower part.

Some papers have dealt with grasshopper community composition in the grasslands of the Indostan Peninsula. Hazra *et al.* (1981) described two communities, one characterized by *Aulacobothrus luteipes* F. Walker, *Spathosternum prasiniferum* (F. Walker), and *Oxya fuscovittata* (Marschall) and the other by *Ochrilidia affinis* (Salfi), *Pyrgomorpha bispinosa* (F. Walker), and *Acrotylus humbertianus* (Saussure). The latter are common representatives of Indian grassland communities (Parihar, 1983). Human activity is responsible for significant changes in the structure of these savanna communities (Julka *et al.*, 1982).

Chiffaud-Mestre and Gillon (1985) described the rich cricket communities of Lamto Savanna, Ivory Coast, where the abundance of individuals is high (about 8–10 per m<sup>2</sup>). Interestingly, they found that, after fire, the number of species

decreases from 39 to 35, although the number of individuals increases. Duranton *et al.* (1983) discussed the impoverished grasshopper communities of Cape Verde, of which *Oedaleus senegalensis* (Krauss), *Pyrgomorpha cognata* Krauss, and *Sphingonotus rubescens* (F. Walker) are common species. Total numbers of individuals is high, being more than 5000 per ha.

Gandar (1982) estimated mean grasshopper biomass at 0.34–0.96 kg per ha) in the mixed grass–tree South African savanna at Nylsvley Nature Reserve, where grasshoppers despoil 7–16 per cent of total grass production. Barker (1983) described the grasshopper communities of Kalahari Savanna, noting that each includes relatively few species. *Acrotylus* sp. and *Sphingonotus scabriculus* Stål are common representatives.

The study of the orthopteran communities of **tropical and equatorial forest zones** is complicated because of the highly developed spatial structure of such ecosystems. Amédégnato and Descamps (1980b) analysed the rich, relatively abundant assemblages of arboricolous grasshopper communities in the Upper Amazonian Basin and Guyana. As a rule, each includes more than 50 species belonging to various sub-families. The different species groups of the local forests react to environmental disturbance mainly by variations in population number. Immigrants are either representative of initial succession or those typical of degraded plant formations. In cultivated plots, there are at least three species groups (Amédégnato and Descamps, 1980a): (i) primary pioneers associated with open, non-forest stations whose populations achieve maximal numbers during the 1st year of cultivation and then disappear rapidly; (ii) secondary pioneers whose populations increase during the 2nd, 3rd, and 4th years; (iii) tertiary pioneers which appear only during the 2nd year of cropping. Their most significant decrease – the real potential crisis of non-forest communities – is evident after the 4th year of cultivation, following which species abundance and diversity slowly increase in association with other species and species groups. The true tree communities re-establish themselves about 21 years after clearance.

## Three-Dimensional Patterns of Community Distribution

I have analysed the altitudinal communities of Orthoptera of northern parts of the Carpathians, the Caucasus, and the Altai Mountains (Sergeev, 1993a). Carpathian communities generally include only a few Orthoptera of reduced abundance. The alpine and subalpine meadows are inhabited only by *Miramella alpina* (Kollar). The forest meadow communities are characterized by a number of widely distributed species. The katydids *Phaneroptera falcata* (Poda) and *Polysarcus denticauda* (Charpentier) are common representatives (Cejchan, 1986), being typical of open boreal and subboreal forests.

The communities of the Caucasus are distinguished from those of the Carpathians by species composition and level of abundance. The alpine, subalpine, and forest meadows are inhabited by the transpalaeartic, xerophilous grasshopper *Chorthippus apricarius* (L.), as well as a few montane subendemics and an abundant boreomontane species, *Aeropus sibiricus* (L.). In some regions, local endemics become important (Stolyarov, 1977). The coniferous forest meadow communities are similar in composition. Orthopteran diversity increases in the deciduous forest altitudinal belt where European species such as *Leptophyes albivittata* Kollar and *Pholidoptera griseocaptera* De Geer appear, along with Caucasian endemics such as *Parapholidoptera naxos* (Rammel). A similar pattern was described in Gause's classic paper (1930).

The Altai communities of Orthoptera are distinguished by their great species diversity, which is perhaps merely an artefact of intensive study. They include mainly xerophilous species whose levels of abundance are similar to those of the species of the Caucasus. The alpine and subalpine communities are interesting (Baranov and Bej-Bienko, 1926) in that the typical steppe form *Stenobothrus eurasius* Zubovsky, the southern Siberian montane endemic *Podismopsis altaica* Zubovsky, and the typical meadow form *Aeropus sibiricus* (L.) are found here. Greatest abundance and diversity are in the steppe altitudinal belt, where *Chorthippus apricarius* (L.) is important, along with the eastern Palaearctic

mesoxerophilous grasshoppers *C. hammarstroemi* (Miram) and *Celes skalozubovi* Adelung.

Investigations into the Mediterranean and Balkan Mountain Orthoptera (Dreux, 1962; Peshev, 1974; Claridge and Singhrao, 1978) show a similar pattern of grazing intensity affecting species diversity. High levels of diversity are described for relatively small grazed pastures and vice versa (Ingrisch and Pavicevic, 1992). Claridge and Singhrao (1978) tried to distinguish amongst community types. They hypothesized two possible species associations, namely a Mediterranean and a montane, but their results reflect species' continuous altitudinal distribution. This suggests that, for understanding Mediterranean distribution, an analysis of the interactions between grasshoppers' complex community structure and behavioural patterns is essential. Patterns of density increase and of diversity decrease as a result of overgrazing are described for the sub-Mediterranean mountains (Voisin, 1986).

Pyrenean Orthoptera are associated with vegetation type (Defaut, 1978a,b), hence, the relatively typical boreal communities characterized by *Stethophyma grossum* (L.) and *Roeseliana roeselii* (Hagenbach) in humid places, *Ephippiger ephippiger* (Fieber) in Mediterranean steppes, and *Chorthippus apricarius* (L.) in xerothermic places. Herrera and Larumbe (1990) used vegetational types for dividing the orthopteran communities of Cantabria, Spain, as follows: (i) anthropogenic and disturbed; (ii) grassland; (iii) maquis or scrub; and (iv) forest. Isern-Vallverdu (1990) described relatively uniform assemblages in the grazed grasslands above the Pyrenees timberline, of which *Stenobothrus stigmaticus* (Rambur), *S. nigromaculatus* (Herrich-Schaeffer), and *Onocestus haemorrhoidalis* (Charpentier) are common species. Pascual (1978a,b) analysed the altitudinal distribution of Orthoptera in the Sierra Nevada, Spain, in which typical Mediterranean communities are observed. He observed true high altitude communities above 2000 m. An attempt at classification of the orthopteran communities of the Sierra de Guadarrama, Spain, was undertaken by Presa *et al.* (1983).

Altitudinal communities of Orthoptera on the Kungiz Range of the middle Asian Mountains were characterized by Myrzaliev (1989) and montane and submontane landscape commu-

nities of the Hissar Valley by Fedotova-Seredina (1985). The latter discussed both natural and anthropogenic stations and evaluated their changing species composition in comparison with Mistshenko's data (1949). She noted that (i) species diversity decreases as a result of human activity; (ii) the grasshoppers and locusts of local anthropogenic landscapes are associated with insular plots supporting both natural and semi-natural (e.g. ruderal) vegetation; (iii) species' abundance may be high; and (iv) the insects readily spread through fields and irrigated systems. The Orthoptera of some mountains of Pamiro-Allay (Ajrapetjantz and Tchernjachovskij, 1979) and of Paropamiz (Tchernjachovskij, 1983) were described, along with the oligodominant communities of the Pamirs (Tchernjachovski, 1976). *Oedipoda fedtschenkoi* Saussure, *Sphingonotus nebulosus* (Fischer-Waldheim), and *Glyptothrus biguttulus* (L.) (*sensu lato*) are common in the western part of the region and *Sphingonotus pamiricus* Ramme in the eastern part.

## Conclusions

The spatial (including regional) approach allows for the visualization of whole faunas, both geographically and ecologically. From the geographic point of view, a fauna occupies a given territory having internal and external boundaries, whose distribution is associated with differentiation of the earth's surface. From the ecological point of view, a fauna is an aggregate of species' settlements, united at least in territory. Thus, a fauna may be described as not only an historical combination of endemic and widely distributed forms but also as a specifically arranged aggregate of populations, regularly distributed over local landscapes. These popula-

tions form corresponding communities on every landscape or biotope, including ones in succession.

The spatial approach leads one to appreciate that it is not sufficient to study a local part of a population or a community and, subsequently, to use the data for predicting composition of the whole area. Even neighbouring settlements may be divided by non-evident obstacles (barriers) and can be different in origin, genotype, karyotype, phenotype, biomass, dynamics, behaviour, etc.

An essential biogeographic problem is to estimate the penetrability of different barriers of various scale so as to determine optimal ways for the dispersal of species, settling new landscapes and regions, and creating new populations.

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## Notes

<sup>1</sup> The migration system of grasshopper populations is generally unique to a region (Drake and Farrow, 1988).

<sup>2</sup> The methodology stems from migratory locusts.

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